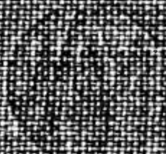

BIO-ECOLOGY

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PREFACE

From the beginnings of life, organisms have lived together in some kind of grouping. Since the differentiation of plants and animals, communities in which both occurred and interacted have undoubtedly characterized the arrangement of living things on the face of the earth. We know now that there are no habitats in which both plant and animal organisms are able to live, in which both do not occur and influence each other. In contrast, the development of the science of ecology has been hindered in its organization and distorted in its growth by the separate development of plant ecology on the one hand and animal ecology on the other.

The authors were brought together in this task of attempting to correlate the fields of plant and animal ecology by the common belief that it would tend to advance the science of ecology in general. It was this common interest rather than agreement in all matters which led to the initiation of this book as a joint project several years ago. In part, it grew out of the fact that the junior author's experience in dealing with the marine communities of the Puget Sound region had led to the discovery of community phenomena paralleling those found on land and fitting the system of classification in use by the senior author.

The phenomena under discussion naturally bring up the question of the community processes, concepts, and nomenclature. A zoologist may be unfamiliar with various ecological terms in use among plant ecologists, and the reverse is also usually true. Here the writers have not introduced all the terms which they are inclined to use in their individual papers, designed for a more limited group of readers, but have attempted to substitute less technical terms. Those terms applicable to communities are given to aggregations of organisms sufficiently well known to enable the reader to build up a fairly clear conception of the whole, so that the terms may be applied to the proper grouping. For example, the term biome has been applied only to those communities in which studies have established something of the processes of development and the character of the final stage or climax. Adjective nomenclatures so extensively developed in fields of limnology and oceanography are deplored by the writers as admitting of an almost unlimited degree of vagueness without commitment to status for either the community or its habitat. On the other hand, the letter nomenclatures used by European students of the sea prove to be very difficult because many of the generic names which have been abbreviated are not known to the reader.

The general plan of the book is in the main that of the senior author. It was already on hand when collaboration began and has been modified only through rearrangement of chapters and the omission of treatments of several large biotic communities such as deciduous forest, coniferous forest, and desert. Their omission results from lack of detailed knowledge of the animal relations, and hence it has become desirable to restrict such discussion to the grassland biotic community. In preparing the book, the authors have not separated their work by making a sharp division into the fields of botany and zoology. The plant ecologist has had experience in the field of animal ecology, and vice versa, so that separation along these lines was not easy. For example, the organization of most of the material in Chapters 1 and 2 was made by the senior author, who also undertook to prepare the tables dealing with the food of birds and the material on bird migration, on all matters relative to sunspots, and the general index. The junior author is almost entirely responsible for the chapters on communities of water; he played a large part in the organization of the grassland chapter and the chapters on climax and sere, and in the preparation of the illustrations. He did the greater part of the work on the bibliography and prepared the author index in connection with it. After the book was considered practically complete, the authors had the good fortune to have the manuscript read and criticized by their sympathetic colleague, Professor John Phillips of South Africa, who made many valuable suggestions and caused them to delay publication in order to give the manuscript an additional period of study.

In the scientific nomenclature for American plants and for both European plants and animals, the authors' names are omitted. Authors' names for all American animals are included at least once, usually at the point of most important discussion of the species, except in a few cases where all the names come from a single source cited in the paragraph or section where they occur.

SANTA BARBARA, CALIFORNIA
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CHAPTER 1

NATURE AND RELATIONS OF BIO-ECOLOGY

Significance of the Name. The term bio-ecology has been proposed primarily for the sake of emphasis, but partly also for greater clarity and definiteness (Clements, 1922). Although the field is here regarded as coextensive with ecology, the meaning and content of that term still vary too widely in use to permit employing the two as exact synonyms at present. This conclusion gains force from the fact that the term ecology is itself not infrequently replaced by biology, sociology, geography, or geobotany, and that its synthetic nature is too often obscured by such subdivisions as autecology, synecology, insect ecology, and human ecology.

To those who regard the cause-and-effect relation as the very essence of ecology, the study of man and of human society is obviously a division of the latter, but it is clear that man's importance to himself will for some time tend to maintain and even emphasize the existing specialization into sociology, economics, behaviorism, psychology, and other fields. This is indicated in particular by the rise of behaviorism, which had its origin essentially in animal ecology, but has taken its own course with diminishing interest in ecological concepts and methods. The consequent loss of focus and of synthesis has been reflected in a generally hostile or indifferent attitude to an approach vital to the ecological study of man.

As matters stand, it appears that the word ecology will come to be applied to the fields that touch man immediately only as the feeling for synthesis grows. The natural procedure will be for its outlook and methods to be adopted gradually by the human sciences and for the use of the term to lag far behind, as is the fate of terms in general (cf. Smuts, 1926; Wells, 1931). Moreover, students of ecology will continue to be trained primarily as botanists, zoologists, sociologists, or economists for some time to come—probably indeed as long as university departments are organized on the present basis. Hence, to emphasize the proper synthetic approach and to maintain the ideal constantly before specialized workers, the term bio-ecology appears to be well warranted. It possesses the further great merit of being immediately understood, a quality certainly not exhibited at present by ecology with its various uses. This advantage will be correspondingly enhanced, as the field becomes on the one hand more analytic, on the other more synthetic. However, it must be admitted that, in respect to terminology especially, habit and point of view will continue to rule for many workers, in spite of the benefits to be procured from uniformity and consistency.

SCOPE AND SIGNIFICANCE

As indicated previously, bio-ecology is considered to be ecology in the widest sense, but with the recognition that the inclusion of human ecology will be delayed until the feeling for synthesis and experiment becomes more general. In consequence, the application of the term will for the present be largely restricted to the study of biotic communities or microcosms, in which man regularly assumes roles of varying importance. Moreover, it is inevitable that the term ecology will continue to be applied to the study of plant or animal communities separately, as a matter of habit or training, or of predilection. Nevertheless, the fragmentation of animal communities on the basis of taxonomic groups is greatly to be deplored, since it destroys the last semblance of unity. Unfortunately, this is such a common practice as to be a matter of much concern to the future of both animal ecology and bio-ecology. This condition can hardly be remedied except by replacing the present highly specialized training with synthetic instruction to a considerable degree.

In view of the great diversity of interests and hence of approaches to this vast field, the word ecology will continue to have a number of rivals, in spite of its unique fitness. In accordance with the emphasis, these range from biology, biogeography, and geobotany to sociology, biocenology, and biocenotics, and the more specialized limnology, hydrobiology and oceanography. This condition will exist as long as investigators are specialists; it is perhaps less to be deplored since each brings a different point of view to the larger field, and this is probably true likewise of the various efforts at a subdivision of the field. However, the very essence of ecology is the synthesis derived from the exhaustive analysis of the community and its habitat, and bio-ecology must rest upon this principle as its secure foundation. The advent of bio-ecology having been delayed by the separation of biology into botany and zoology, its rapid development should not now be hindered by renewed division and philosophical analysis.

Nature. Ecology is in large measure the science of community populations. It is concerned with natural communities primarily, and has developed a considerable fund of organized knowledge of plant communities and their dynamics, and a lesser body of similar knowledge on the animal side. Because of the synthesis inherent in it, ecology is also to be regarded as a point of view and a method of attack for various great biological problems. Not only does it concern itself more or less with the whole of biology, but also it must borrow largely from chemistry and physics, from climatology, geology, and soil science, and at the same time make basic contributions to the practical sciences of agronomy, horticulture, forestry, grazing, entomology, conservation, etc., to say nothing of education, economics, sociology, and politics. It cannot, and does not, venture to draw a line between the past and the present, and it has as significant a role to play in geological as in modern times.

More than a quarter of a century ago, the statement was made that ecology was to be considered the central and vital part of botany, and this is equally true for biology. It was further stated that plant ecology is physiology carried into the actual habitat, and in consequence its paramount theme is stimulus and response. It confines itself primarily and exhaustively with the cause-and-effect relation between the habitat on the one hand, and the organism and the community on the other. All further relations arise out of this, and all other approaches are incomplete unless they lead back to it. With the inclusion of animals in the biotic formation (biome), this relation naturally becomes more complex, but it is none the less valid. Since physiology often finds visible expression in behavior, coaction between the organisms assumes a role often more important than direct response to the habitat.

From this springs the view that development is the basic process of ecology, as applicable to the habitat and community as to the individual and species (Clements, 1904, 1905). It recognizes that life constitutes a dynamic system and that static studies are valuable only as they throw light on development or serve some practical purpose in this connection. Furthermore, it was postulated that development is a cyclic process and that the apparent points of rest in it are relative to cycles of different rank. At the very outset it was clearly perceived that a dynamic system renders measurement indispensable, and hence the past three decades have seen a consistent advance in this respect, especially in plant ecology and to some extent in hydrobiology.

Equally imperative is the thorough-going utilization of experiment, essential not only to finer analysis and more exact measurement, but also to increasingly objective viewpoints.

In connection with the preceding, it should be realized that progress in zoo-ecology has been much slower. The natural unity has been obscured by the separate treatment of taxonomic groups and by such faunistic concepts as that of life zone, which, in view of the widespread destruction of many species, has rendered synthetic interpretation very difficult. Moreover, although animals are obviously physiological in their response to climate, food, etc., much progress can be made in the field of interactions (coactions and reactions) without the use of physiological experiments. Furthermore, the correlations involved are usually to be suggested by studies in the biotic community and then lead properly to physiological experiments that permit more definite control and exact analysis. In sharp contrast to plant physiology, animal physiology as taught and applied has little concern with physical factors, while general physiology deals with particular internal processes and physiological ecology with one or more species withdrawn from the community for some particular study. The consequence is the ignoring or splitting of the physiology of interactions, since this field finds its inspiration in the study of the biotic community itself.

A signal extension of ecological ideas is involved in the application of climax and succession, that is of development, to lake and ocean. This demands the definition and recognition of climaxes in large bodies of water, and hence of corresponding climates. As indicated later in the discussion, this is deemed a logical extension of these terms from land to land and water, and thence into lake and ocean. This further involves questions of dominance, of competition, reaction and coaction, of development and structure, all of which exhibit more or less characteristic differences in deep water.

Relations of Paleo-ecology. Development is a continuous process, and hence its division on the basis of time past and present can be justified only on the score of convenience. No radical division exists in geology, where the flow of time is registered chiefly by major and minor events. With biology and its human subdivisions, however, the technique and usually the evidence also differ so much in nature or form that the distinction appears much greater than it is. This fact has naturally not passed unnoticed by paleontologists, but it is the peculiar province of paleo-ecology to insist upon the basic essence of continuing development and to emphasize the fact that the present is but a passing stage of this.

From the standpoint of development, uniformity is inevitable and universal, but it is a uniformity of process and cycle more than of end results. This becomes all the more evident when it is realized that cycles of varying intensity and duration are so telescoped that lesser ones constantly recur within the next larger, producing a complex system in which the respective cycles are difficult to discover. Moreover, while cycles in deformation, climate, physiography, soil, climax, migration, and abundance bear an organic relation to one another, response takes place at varying rate and degree, and the mosaic of processes becomes correspondingly intricate.

The principles and methods of paleo-ecology have been outlined in more or less detail for vegetation (Clements, 1914, 1916, 1918; Clements and Chaney, 1925–35, 1936), and these have been applied to the revaluation of fossil floras with such success as to indicate their fundamental nature (Chaney, 1925, 1933). As with modern ecology, these must necessarily undergo certain extensions and modifications with the adoption of the biome as the community. Furthermore, while relatively slight changes are needed to fit the case of land climates and climaxes, those of deep water exhibit conditions at once so different and so uniform as to require much greater modification.

As has been emphasized elsewhere (Clements, 1916), it is an axiom that the key to the past is fashioned by the present, to use these terms in their everyday significance. On the other hand, the present is the sole heir to the past, and no adequate understanding of it is possible without tracing the continuity of developmental processes from the one to the other. In short, there is no more warrant, other than that of convenience and emphasis, for separating paleo-ecology than for dividing bio-ecology, and the best development of ecology demands the synthetic organization of the entire field, even though detailed analyses will continue to be made by specialists.

HISTORICAL DEVELOPMENT OF THE CONCEPT

The idea of the plant community in general extends backward for nearly two centuries, but the recognition of the biotic community is a recent matter. Post (1867) recognized that the organic world should be dealt with in its entirety, but seems to have had no definite idea of the community as a unit (cf. P. Palmgren, 1928:27). How clearly Möbius perceived the existence of a biotic community can probably never be settled, in spite of his introduction of the term biocenose. He certainly saw something of a community relation in the oyster assemblage (1877), but carried the concept no further, and his suggestion was practically lost to view for a generation or more. A somewhat similar doubt arises in respect to Dahl's adoption of the word biocenose from Möbius, for it appears that Dahl employed the term mostly as a synonym of zoocenose (1903, 1904). As indicated later in some detail, Clements, Shelford, Francé, and Vestal realized the significance of the biotic community more fully and more or less independently, but the distinction of the biome as the basic concept in climax and succession was first made in 1916.

Since this time, there has been a slow but gradual recognition of the importance of the concept, exemplified in particular on the animal side by Shelford and his students, on the plant side by Phillips. For the reasons already touched upon, it is not to be expected that this will become the universal approach, and this is probably not desirable, since some problems require intensive analysis, such as is best secured by working with plants or animals alone. If it becomes generally recognized that the investigation of climax and succession must reckon with the biotic formation as the natural community unit, this will insure the proper perspective and methods. Although of a secondary character, the historical development of the ideas set forth in this volume is important in an understanding of the terms and concepts presented.

Möbius (1877). Under the title, "An oyster bank is a biocenose or a social community," Möbius gave a detailed account of the animal life of an oyster bed as brought up by the dredge. He stated that very few plants grew upon the banks, namely, a single Zostera and some of the Florideae, while the desmids and diatoms of the plankton served as food for the oysters. Each oyster bed was regarded to a certain degree as a community of living beings, a collection of species and a massing of individuals, and since science possessed no term for such a grouping, he proposed the word *biocenose.* Space and food were held to be necessary as the first requisites of every social community, even in the sea, and he clearly perceived that changes of physical factors, and disturbances by man as through overfishing, often greatly modified the social group.

There is little evidence that Möbius regarded the biocenose as constituted by both animals and plants, though such an assumption has long persisted in connection with the use of the term. The single mention of plants, the emphasis upon their role as food, and the comprehensive discussion of the species of animals all tend to confirm this conclusion. This is supported by Petersen's statement that "Möbius has called the animals living on an oyster bank a *biocenosis,*" and he also employed the term as synonymous with animal community (1913:32). As is shown in the next paragraph, Dahl likewise thought to employ the word in the sense of Möbius, but without rendering his own usage either very definite or consistent.

Dahl (1903–1908). In three successive editions of his guide for collecting and preserving animals (1903, 1904, 1908), Dahl adopted Möbius's term, but clearly not in the sense of a biotic community, at least in most instances. This is further shown by the fact that he speaks only of zootopes or animal habitats, and in addition states that the biocenose is for the zoologist what the plant community is for the botanist. Three types of biocenose were recognized, namely, phytobiocenose, zoobiocenose, and allobiocenose, composed respectively of the animals to be found on a particular plant or its parts, on an animal, or on inorganic or decaying organic bodies. The subdivisions of the first two and especially the phytobiocenose correspond to all the organs and parts of the host and obviously represent only the most minute animal assemblages. Among the allobiocenoses were included autonomous communities, but usually without indication of their biotic nature.

Clements (1905–1918). In "Research Methods in Ecology" (1905:16), it was stated that plant and animal communities frequently coincide. Since animals were regarded as typically motile, their dependence upon the habitat was considered to be less evident. Vegetation as the source of protection and food plays a more obvious if not a more important part. It was stated that the animal ecology of a terrestrial region could be properly investigated only after the habitats and the plant communities have been organized as the basis for studying development and structure.

In a study of the life history of the lodgepole pine burn forest (1910), animals were found to play a controlling part in succession. The frequent regeneration in burns, by contrast with the absence of seedlings elsewhere, led to the conclusion that a major effect of fire was to destroy or drive out the seed-eating animals, and permit the establishment of the pure stand of pine (consocies) as a characteristic subclimax.

In a monographic discussion of succession (1916), the biotic formation was regarded as an organic unit comprising all the species of plants and animals at home in a particular habitat. Plants were considered to exert the dominant influence, although it was recognized that this role might sometimes be taken by the animals. The biotic community is fundamentally controlled by the habitat and exhibits both development and structure. In its development the biome reacts upon the habitat and thus produces a succession. In discussing the scope and significance of paleo-ecology (1918), it was stated that recognition of animals as a part of the community promised to open a new outlook in synthetic ecology.

Adams (1906–1915), Ruthven (1911). In sketching the plan for a survey of Porcupine Mountains and Isle Royale, Michigan (1906), Adams based this upon the relations of the biota to environment, adopting Stejneger's definition of the biota as "the total of animal or plant life of a region." While there was no definite recognition of the biotic community, the emphasis upon the habitat and upon processes in terms of succession, and the use of plant communities as a groundwork, mark the treatment as distinctly synthetic. The actual survey was carried out by Ruthven upon this broad basis and led to the conclusion that the hardwood forest represents the climax of the region, its habitat increasing at the expense of other societies so that the associated biota tend to become general for the area. Later, a more extensive investigation of Isle Royale was made by Adams and his co-workers, utilizing the same methods (1909). Even greater attention was paid to succession, though this was treated separately with respect to the four animal groups, viz., invertebrates, beetles, birds, and mammals. The biological survey of a sand-dune region in Michigan followed the same general plan (Ruthven, 1911).

In a bibliographical treatise Adams presented the conclusion that such projects should deal with the balance within the entire biotic community. It was stated that for any comprehensive study it is necessary to determine the biotic base or optimum toward which conditions tend and at which equilibrium occurs. Some uncertainty exists, however, as to the author's use of the term biotic, since he speaks of all this as providing the best method of studying the animals of a region. Moreover, in the ecological investigation of prairie and forest invertebrates (Adams, 1915), the animals were treated as separate and the plant associations considered as furnishing the environment for them.

Shelford (1907–1913). In a preliminary survey, Shelford (1907) traced the relation of Cicindela to the succession of plant communities. The distribution of eight species of tiger beetles was in close correspondence with the zoned habitats and communities, and the conclusion was reached that a similar harmony existed with respect to the fauna in general.

In a series of five articles on ecological succession, the same author elaborated the developmental relation between plant and animal communities (1911–1912). These were stated to be very generally in agreement. Disagreement was said to be temporary, and to accompany rapid successional changes. Succession was stated to be due to an increment of changes in conditions produced by the plants and animals living at a given point.

In the treatment of the animal communities of eastern North America (1913, *a*), this theme of the interaction of the two groups of organisms was further developed. Several of the communities were designated by means of a prevalent or characteristic animal and one or more plant dominants, though in general plant communities were treated as constituting the habitat for animal ones. Thus were distinguished a white tiger beetle or cottonwood association, an ant lion or black oak, a *Hyaliodes* or black oak-red oak, a green tiger beetle or white oak-red oak-hickory, and a wood frog or beech-maple association. Succession was emphasized as the chief principle underlying the relations of communities. Plants were recognized as the dominant sessile forms of the land, while animals were considered to be the chief members of the successions in streams, and the primary nature of the climax was stressed.

Shelford further endeavored to correlate the behavior of the animal constituents with the life forms of the plants. The terminology was based upon the idea of the uniformity of the physiological responses of the important animals in the community (1914, *a*, *b*, *c*; 1915). However, this physiological basis for community classification was found to be impracticable because of the lack of response data, and the plan was abandoned as not yet susceptible of clear expression.

Enderlein (1908). Enderlein followed Dahl in employing the term biocenose for a wide range of communities, and further adopted the latter's grouping on the basis of habitats. However, he departed from Dahl's usage by distinguishing areas of more or less unrelated biocenoses as *biosynecies* or biosynecie districts, a departure criticized by Dahl in the same year as unwarranted (1908). Enderlein regarded the occurrence of a species in a single biocenose or its extension over two or more as marking a significant distinction, designating the one as *homocene*, the other as *heterocene*. The same concept was extended to the biosynecie, for which corresponding terms, *stenotope* and *eurytope*, were proposed. Upon this basis, four groups of species were recognized in accordance with their occurrence in one or more of both types of community: for example, *stenotope-homocene*, found in but one biocenose and one biosynecie; *stenotope-heterocene*, present in a single biosynecie but in two or more biocenoses. These distinctions seem not to have been applied by the author himself in his studies of the insects of moor and dune in west Prussia, though stenotope and eurytope have been utilized in a small degree, while the distinction between biocenose and biosynecie appears to have dropped from view. In fact, the extensive account of the distribution of insects is based upon taxonomic groups and not upon communities, though the composition of the plant cover is discussed as a background.

Francé (1913). Francé has advanced the concept of the *edaphon*, as the counterpart of the plankton, comprising under this term the community of the permanent animal and plant organisms of the soil (geobionts). This consists of the most varied types, but ones mutually tolerant and thus able to hold their own; they are distinguished by a number of adaptations and an entirely distinct and peculiar mode of life.

The habitat of the edaphon is characterized by a more or less complete absence of light, periodic limitation of moisture by drought or frost, and an excess of nitrogen. The groups of organisms regarded as belonging to the edaphon are as follows: (1) bacteria, (2) fungi, (3) algae, (4) Protozoa, (5) Rotatoria, (6) worms, (7) arachnids. The inclusion of mycorhiza and earthworms was said to require further consideration, while the subterrene mammals, insect larvae, and rooted plants were ruled out of the communal life.

Vestal (1913–1914). In connection with the successional study of a sand prairie in Illinois, Vestal has tested the assumption that plant and animal associations are coextensive and to a large degree interdependent, the animals being entirely dependent upon the plants and the latter partly so upon the animals. In such case, the limits of the animal community are those of the plant association, and both may be spoken of as a single biotic community, composed of plant and animal assemblages. This relation once established, certain problems in animal ecology would be much simplified, for whereas the animal assemblage is at first obscure, that of the plants is evident, its characteristic physiognomy serving as an index to the animals of the community. It was concluded that the evidence drawn from the study of the sand prairie, though very incomplete, was in accord with the theory and justified the treatment of the plant and animal associations together.

This theme was further developed in an analysis of the internal relations of terrestrial associations (1914), as a result of which it was concluded that plants and animals agree in similar response to the common environment and in types of geographic distribution. It begins to appear that plant and animal assemblages are coextensive parts of a biotic association, which as a whole constitutes the real terrestrial community of living organisms. Plant and animal assemblages are mutually interdependent, but the plants are dominant in established associations. Such assemblages are composed of ecologically similar groups correlated with the same physical factors or with each other.

Gams (1918). Gams considers that no logical ground exists for excluding animals from communities of organisms, and hence he incorporates these in the vegetation. To him, "vegetation research" is synonymous with his new term "biocenology" and with "biocenotics" of the zoo-ecologists, both of which he regards as closely related to ecology, though not identical with it. His discussion, however, is confined largely to plants, the most important exception being his outline of the life forms of the combined plant and animal kingdoms. This is based upon the assumption that the criteria available take rank in the following order: (1) motility, (2) substratum, (3) habitat, (4) nutrition. This is thought to be supported by the general acceptance of plankton as a biotic community. The three major divisions of his system are as follows: (1) adnate or attached form, *Ephaptomenon*; (2) radicate or rooted form, *Rhizumenon*; (3) errant or free form, *Planomenon*. The first group is divided into aquatic, amphibious, aerial, and innate, further subdivisions being autotroph and heterotroph, saprobe, parasitic, and phagont.

Gams emphasizes the fact that, while biocenose has been employed by a number of zoo-ecologists, viz., Dahl (1903), Enderlein (1908), Bäbler (1910), Shelford (1911), Hesse (1912), Döflein (1914), and Thienemann (1918), this has been in connection with animal communities of very unequal rank. He further suggests that phytocenose may be utilized for the plant population of a habitat and zoocenose for the animals, but this suggestion is scarcely in harmony with the concept of the biotic community.

BIOTIC RESEARCHES

The Biotic Formation on Land

Vorhies and Taylor (1922); Taylor and Loftfield (1924); Greene and Reynard (1932). Vorhies and Taylor made a study of the kangaroo rat in relation to vegetation which brought out various biotic interactions. Taylor and Loftfield determined the amount of forage taken by the Zuni prairie dog, while Greene and Reynard showed the benefits of some rodent reactions to the soil.

These studies were a part of a project in grazing research which was organized jointly by the Carnegie Institution, the U. S. Biological Survey, the U. S. Forest Service, and the University of Arizona (cf. Year Books 16–30, Carnegie Institution of Washington, 1917–1931).

Palmgren (1928, 1930). In connection with the investigation of the bird life in the forests of southern Finland, Palmgren has discussed the ecological synthesis of plant and animal groups and has recognized that vegetation must form the basis for this. He also subscribes to the principles that animals must be treated as members of the community and that green plants assume the primary role in the latter, with the important corollary that the ecological study of animals must rest in the first instance upon their intimate relations with plants. He has employed the forest types of Cajander and the line surveys of Ilvessalo as the ground plan for his work, which has dealt especially with the numbers and characteristic species of birds. Although he uses the term bird society or association (*Vögelverein*), it appears evident that he does not intend to set these apart from the biotic community.

He finds that the best forest types (Sanicula and Oxalis-Myrtillus) show clearly the influence of the tree species upon the quantitative expression of the bird fauna inasmuch as the numbers are significantly larger in deciduous woods. It appears, however, that the herbaceous layers take the leading role in this and that the nature of the stand of trees comes next. In this connection, his comparisons between deciduous, mixed, and coniferous forests are supported by the relations to be found in North American woods. He gives summaries of bird density for eight different forest types and lists the character species and their abundance for the seven biotopes considered. His methods and results represent the most extensive quantitative attack upon the problem of the role of birds in the biotic community and with the addition of the dynamic outlook will serve as the model for other climaxes.

Weese, 1924; Blake, 1926, 1931; Smith, 1925, Smith-Davidson, 1930, 1931. These authors made a series of studies in a forest in central Illinois composed chiefly of red oak, maple and elm. The work of Weese and the succeeding investigators was essentially quantitative. Weese devoted considerable attention to experiments designed to reveal the factors controlling the position of the prevalents in the layers of the forest; he discussed seasonal communities and described winter movements of invertebrates. Blake (1926) carried on an investigation of the deciduous forest worked by Weese, and for comparison made studies of biotic communities of the pine-hemlock climax in Maine, as well as those of the upper slopes of Mount Ktaadn, taking the mammals and birds also into account. Smith (1928) utilized the same forest, together with its developmental (seral) stages, while the same author (Smith-Davidson, 1930, 1931) endeavored to evaluate the influence of the various animal species, basing this principally upon their abundance and the division into layers and seasonal groups. Some attention was given to differences between the two years of study, as well as to the characteristics of the climax animals. Blake (1931) has instituted a comparison between the results obtained by himself, Weese, and Smith, finding a good general agreement among them, inasmuch as 36 species were important numerically or otherwise in at least two of the lists.

Shackleford (1929); Bird (1930). Shackleford made a study of prairie similar to that of Bird but much farther south; she compared the animal communities of the high and low prairies, treating the seasonal aspects in detail. Bird investigated the biotic community of the aspen parkland of western Manitoba in a comprehensive manner. The animals have been dealt with in quantitative fashion, embracing the determination of the food coactions and the evaluation of many of the constituent species.

Shelford and Olson (1935). The authors showed the close relation of the coniferous forest animals to the plant constituents and evaluated the mammals, birds, and a few invertebrates on the basis of size, abundance, and movements through the climax and seral stages. This study followed the senior author's (1932) suggestion that mammals are usually the outstanding influents in communities of this type.

Phillips (1930–1935). Phillips has made comprehensive applications of the concept of the biome in two regions in Africa, where biotic communities possess an exceptional wealth of animal forms and still retain much of their primeval character. This was first utilized in the study of the Knysna forests of the Cape region, with especial attention to the coactions of plants and animals in the community proper and to their responses under experimental screens. Even more extensive and important investigations were made on the East African plateau in Tanganyika, where the biotic communities remain essentially primitive. The general relations taken into account comprised grazing and browsing, fruit coactions, and soil reactions. The biotic projects were focused upon the ecology of the tsetse fly (Glossina), constituting altogether the most significant program of research in this vast field. His several projects have led him to the conclusion that the most logical working concept is that of the biotic community. To him the view that the community is a complex organism has definite practical value.

Recently, he has given a review of quantitative methods as applied to the animals of the biome, with extensions derived from the researches on the tsetse fly (1930), and he has further considered the concept of the biotic community in a series of three critical papers (1934–35).

Beklemischev (1931). This investigator has discussed the application of the concepts of bio-ecology to the animal members of the community, with emphasis upon the importance of cycles, succession, and climax. He considers abundance, dominance, frequence, homogeneity, and constancy in relation to animals, defining dominance in terms of comparative abundance, by contrast to the concept employed in the present treatise (cf. p. 234). He distinguishes periodic from non-periodic changes, recognizing daily, annual, and pluriennial cycles, corresponding more or less exactly to diurnation, aspection, annuation, etc. The progressive nature of succession is recognized and the significance of stabilization perceived for animals as well as plants. Finally, he accepts the view of developmental ecology, namely, that the climax as a living complex includes all its several developmental stages (seres) as essential to its development. Probably no other Continental ecologist has manifested such a clear perception of the fundamental relations of the biotic community.

In a second paper, Beklemischev, Briukhanova and Shipitzina (1931) have summarized the results of studies on the marshes about Magnitogorsk in the Urals, on the basis of the coactions of the organisms in the development from water to land (hydrosere).

The Biotic Formation in Water

For a number of reasons, it is more difficult to trace the application of the biotic concept in water than on land. The uncertainty attaching to Möbius's use of the term biocenose continues through much of the work of the limnologists, though by some it is definitely limited to the animal community alone (Petersen, 1913; Gajl, 1927). The general dominance of animals in certain types of fresh water and in the sea, coupled with the minuteness of the phytoplankton, furnishes a ready explanation of this. On the other hand, the biotic nature of the plankton and its greater definiteness as a layer often carry the inference of a biotic community when this was not intended. Moreover, the extensive study of food coactions in the sea especially has in some cases given the impression of biotic unity when no communities were recognized or named.

The definite limits of the lake in particular have accorded it an obvious unity, both in terms of habitat and community, rarely to be found in any other area. To a certain extent this has long been recognized, but it was perhaps first clearly expressed by Forbes, in referring to the lake as a microcosm. This view has been emphasized by the limnologists, especially Thienemann, Reswoy and Werestchagin, who consider the lake as a whole to be an organic entity or organism. With them this concept seems to have been a more or less independent development, and it suffers from a lack of acquaintance with the similar concept in vegetation, i.e., the complex organism, which anticipated it by twenty years. In passing, it may be pointed out that to include the habitat in the community obliterates the essential distinctions between the living and non-living, and carries synthesis to the extreme where its very purpose is defeated.

For the reasons given above, it appears desirable to consider here only such contributions as are based intentionally upon the biotic community, supply quantitative materials for it, formulate new principles, or apply those already proposed by the plant ecologist for land. The details of these, moreover, are considered in the chapters to which they pertain, along with the studies set aside for discussion there. However, no sharp line can be drawn between them, and the arrangement subserves the necessary requirements of brevity nearly as much as it does that of historical development.

Forbes (1887). Forbes was apparently the first to express clearly the unity inherent in a lake. He regarded it as a chapter out of the history of primeval time. The conditions in it are primitive and the forms of life relatively low and ancient, while the system of organic interactions by which these influence and control one another has remained substantially unchanged since a remote period. The animals of such a body of water are remarkably isolated—closely related in all their interests but very largely independent of the land. A single body of water exhibits a far more complete and independent equilibrium of organic life than any land area. It is an islet of older and lower life—a little world within itself, a microcosm in which all the elemental forces are at work and the play of life goes on in full, but on a scale so small as to be easily grasped.

Nowhere else is the coherence of such an organic complex so clearly visible; whatever affects one species must sooner or later have some influence on the whole community. One thus perceives that it is impossible for one form to be completely out of relation to the others, and realizes the need for a comprehensive view of the whole as requisite to the understanding of any part. With the black bass, for instance, one learns but little by limiting himself to this species; he must study also the species upon which it depends and the factors that control them. It is likewise necessary to determine the course and outcome of competition, as well as the conditions involved. When this has been done, the investigator will find that he has run through the whole complicated mechanism of aquatic life, both animal and vegetable, of which the bass forms but a single element.

From the title alone, "The Lake as a Microcosm," it may well seem that the author intended to include the habitat in the entity, but this appears not to have been the case, in view of his references to the "organic complex" and to the "equilibrium of organic life."

Cleve (1897). As has been previously stated, for a number of reasons the study of plankton, especially the microplankton, had, more or less necessarily, a biotic character from the beginning. This is chiefly because the organisms concerned represent both the plant and animal kingdoms, but it is also due to the quantitative nature of hauls, as well as to the strikingly seasonal and annual cycles involved. The situation is perhaps best exemplified by the pioneer essay of Cleve to distinguish types or communities of phytoplankton in the Atlantic and its tributaries, based for the most part upon one or more prevalent species of diatoms. The six communities recognized were termed tripos-, styli-, chaeto-, desmo-, tricho-, and sira-plankton, the name being drawn from the characteristic genus. The first of these exhibited several neritic subtypes in the seas about the British Isles and Denmark. In an estimate of Cleve's work, Gran points out certain difficulties (1912:359), but concludes that it yields a biological grouping that is satisfactory in the main.

By means of seven or eight samples throughout the year in the same general area, Cleve was enabled to follow the changes in the abundance of diatoms and cilioflagellates in particular. These swarms or pulses correspond in several particulars to the aspects exhibited by land biomes.

Petersen and Associates (1911–1925). The first organization of the animal communities of the sea bottom was carried out by Petersen (1913, 1914, 1918), as a by-product of the quantitative study of fish food in different areas. Certain species predominated in the bottom samples with such regularity that it proved possible not merely to recognize eight animal communities from the deep water of the Skagerrack to the Baltic, but actually to indicate the distribution of these on a chart of the region. (See Fig. 84, p. 349.) He clearly perceived the great differences between the various groupings and utilized a synoptic method of characterizing these by means of the prevalent animals. The conclusion was drawn that the Macoma community occurred throughout in the shore zone, the Venus community with certain spatangids on sandy bottom in deeper waters, Brissopsis and its associates on soft clay outside these, and other communities in still deeper water.

This classic series of quantitative investigations was centered on the food coactions from producent to consument and upon the composition and distribution of the bottom communities. The first monograph, by Petersen and Jensen (1911), dealt with the animal life of the sea bottom, its food and quantity; the second discussed the corresponding animal communities and their importance for marine zoogeography (Petersen, 1913). A third report (1914) discussed in greater detail the organic matter of the bottom (Boysen Jensen), and also described the food and conditions of nutrition for the invertebrate communities in Danish waters (Blegvad), a theme further elaborated by the latter in 1916. Two years later, Petersen (1918) made a comprehensive account of the so-called valuation studies of the preceding decade, and in 1925 Blegvad gave further data upon the relations of the dominant fishes to the invertebrate communities.

Murray and Hjort (1912). In the "Depths of the Ocean," Murray and Hjort have presented an invaluable summary of oceanography, from what is in some respects essentially a bio-ecological viewpoint. The lack of contact between ecology and oceanography at that time serves to explain in part the absence of a definite and comprehensive account of the biotic communities and their relations, though this is due even more to the enormous number of organisms considered and the necessity of treating various great groups from the standpoint of the specialist. In spite of this, the book constitutes the nearest approach to an actual organization of the pelagic communities in the ocean and supplies a vast amount of data for ecological analysis and coordination. The discussion of the microplankton by Gran takes account of the usual division into neritic and oceanic communities and further suggests the major regions or climaxes of the Atlantic Ocean. Appelöf has described the bottom fauna without defining communities, but with such a treatment of composition and distribution as to indicate their general outlines.

Hjort has recognized and described a number of pelagic communities in both the Atlantic and Pacific Oceans. He has dealt with the vertical ranges of dominants in such detail as to suggest the basis for the distinction of the most important layers. The concept of dominance is more or less clearly in evidence, thus making it possible to outline a number of associations and faciations in a preliminary manner.

Oliver (1915, 1923). In addition to Oliver, Hedley (1915) and Johnston (1917) have studied litoral communities in Australasia from the biotic approach, but the more detailed work of the first will serve to illustrate their general outlook. In his study of the New Zealand shore (1923), Oliver defines the animal-plant formation as a biotic community with its principal ecological groups in definite combination and relation to the habitat. The community is thus based upon growth forms and environment, and formations are distinguished by differences in the dominant ecological forms. The dominants of the littoral formations are attached animals and plants or in some cases sedentary animals. The effect of the substratum is considered to be of major importance. Accordingly, littoral formations are classed as those on rock, with the dominant form varying from algae to shelled animals, and those on sand and mud, ranging from animal to plant by virtue of height above low tide. These two groups are divided into formations, subformations, and associations, but, since this is without reference to climax or successional criteria, it is uncertain how closely these accord with the units employed in the present book.

Limnology. The rapid development of this field has been an outstanding feature of biological progress during the past two decades. In a recent monograph by Naumann (1932), hardly a tenth of the 350 titles given in the bibliography had appeared before 1917. It represents in some measure a movement independent of ecology, apparently deriving its initial impulse largely from practical considerations but going far beyond these in its synthesis of related fields. The number of workers concerned has been large, but the organization of the subject and the formulation of concepts are probably to be credited more to Naumann and Thienemann than to any other two men.

It scarcely needs to be pointed out that limnology is that portion of ecology which deals with fresh-water biomes and habitats. It is characteristically ecological in its emphasis upon the measurement of factors and has perforce devoted more attention to the biotic community than any other portion of ecology. As indicated previously it has been quick to perceive the significance of the concept of the complex organism, and likewise the importance of its reaction upon the habitat. However, it has concerned itself very little with the nature of the community, its composition in terms of dominants and influents, the processes involved in development, and the distinction between climax and seral communities. It uses an adjective nomenclature which allows a wide latitude in the concepts concerned.

Within the scope of the present book, it is impossible to deal adequately with the investigations in this field, a subject, moreover, that is covered in encyclopedic manner by Naumann and Thienemann in the contributions mentioned below. In consequence, the treatment will be limited chiefly to basic concepts and units, and the relations of limnology to the larger theme of bio-ecology, especially as a matter of synthesis (cf. Chapter 7).

Thienemann (1913–1935). In discussing the progress of limnology, Naumann (1932:13) considers the first major step to have been taken by Thienemann (1913–14), in basing lake types upon oxygen content and the consequent composition of the bottom fauna. This has remained a chief interest through a long series of papers, but these have been accompanied by a number of publications dealing with basic concepts and methods of classification in the field of "biocenotics" or bio-ecology. In this connection, the author has emphasized the causal relation between habitat and community, the reaction of the latter upon the former, and the organic unity of the lake as complex organism, all in close accord with the early elaboration of these principles in ecology in 1901 (cf. Clements, 1904, 1905). A general understanding of Thienemann's contributions to the organization of the field is most readily obtained from his papers in Abderhalden's "Handbuch," from "Die Binnengewässer Mitteleuropas" (1925), and "Die Sauerstoff im eutrophen und oligotrophen See" (1928).

Naumann (1918–1932). Naumann's earlier researches dealt mainly with phytoplankton, with more or less special reference to the biology of production, but since 1922 they have been concerned primarily with the broad organization of the field. Regional limnology has occupied the chief place in this program, but physical factors, reactions, and methods have also received much attention, and this has involved also the consideration of concepts and terms. Fortunately for both investigator and student, the author's threescore of papers are epitomized in three recent publications. Methods are discussed in comprehensive fashion in Abderhalden's "Handbuch" (1925), and guiding principles in "Grundzüge der regionalen Limnologie" (1932), while his "Limnologische Terminologie" (1931) is a combined lexicon and encyclopedia of the subject.

Regional limnology, or fresh-water ecology, is considered from the various angles, viz., habitat factors, types of water bodies, plankton, littoral and profundal in regional correlation, types of lakes and their natural succession, modifications in the biology of production, and the relation to applied limnology. The treatment of limnological terminology is a compendium of the present knowledge in the field, detailed but concise, and arranged in alphabetical order to permit ready reference to the host of terms peculiar to the field or borrowed from related subjects.

Shelford and Towler (1925). In their study of communities in the San Juan Channel of Puget Sound, Shelford and Towler found the general principles drawn from plant communities by Clements to be readily applicable. The analysis yielded three benthic formations or climaxes with two associations each and a number of more or less definite seral stages. This investigation was carried forward by several other studies, such as one into the relations of the different barnacle dominants by Towler (1930), the value of these as indicators of salinity (Rice, 1930), and the connection between salinity and the size and form of dominants (Worley, 1930). In 1935, Shelford, Weese, Rice, McLean, and Rasmussen brought together the results of their work covering succession to land, describing a fourth bottom formation and mapping the communities of the area. They found only a little evidence of succession in the partially enclosed waters, though Hewatt (1935) described it for the open coast.

Eddy (1925–1927); Gersbacher (1937). For a number of years, Eddy (1925–1927) carried on investigations of fresh-water plankton from the standpoint of development and traced the origin of a pelagic community in Lake Decatur, formed by impounding water to produce an urban supply. In six years such a community has developed through the addition of species from year to year, but without the disappearance of any of these, thus affording a basis for dealing with the problem of pelagic climaxes. Gersbacher (1937) presented a detailed account of the development of bottom communities in new lakes including fishes (see also Shelford and Eddy, 1929, *a*).

Molander; Gislen (1930). In separate though related investigations of Gullmar Fjord in Sweden, Molander and Gislen have applied the methods of Petersen, employing the bottom sampler to determine numbers and weights. Molander has considered the bottom communities of animals primarily on clay, since the samples from hard-packed sand, coarse gravel, or pebbles are not dependable. He recognizes nine associations, several of them with two or three variants or facies, which are regarded as exhibiting a close analogy with many of those of Petersen.

Gislen proposes three new terms for biotic communities, viz., epibiose, endobiose, and hypobiose, the first two corresponding to Petersen's onfauna and infauna. He employs facies in a different meaning, epibioses showing soft and hard bottom facies, and endobioses oligotropic facies on sand or rock bottoms, eutrophic ones on clay or on substrata with more or less organic material. A system of life forms is outlined, and extensive tables are given of the production in terms of grams per quadrat. Somewhat more than twoscore associations are recognized in accordance with the usage of plant sociologists; many of these are faciations, consociations, or societies in the classification employed by dynamic ecologists.

Bio-ecology and Oceanography. It is evident that oceanography is ecology in so far as it measures the physical factors of marine habitats and the reactions of organisms upon them. In its recent development, the growing feeling for quantities and communities stamps it as marine ecology in every significant respect, though, as with all fields of special interest, it will probably continue to be known as oceanography. The essential identity of the two has been clearly recognized by Russell (1932) with respect to fishery research in particular. He states that the latter in point of view and methods is simply a branch of ecology, and its special problems are those of marine ecology. The soundness of this view is shown by the topics discussed, each of which represents an important phase of ecology on land, namely: (1) census of fish populations, (2) fluctuation and prediction, (3) distribution and migration of fish in relation to environmental factors, (4) food chains and animal communities.

Bigelow (1931) advances a similar point of view in his discussion of the scope and aims of oceanography, even though ecology is not specifically mentioned. This is revealed not only by the emphasis placed upon unity as a basis for research and hence upon the synthesis inherent in ecology, but also by the clear recognition of the paramount role taken by the habitat in the control of life and by the reaction of organisms on it. He is furthermore in complete accord with modern ecology in its insistence upon dynamics as the guide to all relations but especially to the cause-and-effect interaction of habitat and community.

CHAPTER 2

COMMUNITY FUNCTIONS—THE DYNAMICS OF THE BIOTIC FORMATION

THE BIOME AS A SOCIAL ORGANISM

Introduction. The biome or plant-animal formation is the basic community unit; that is, two separate communities, plant and animal, do not exist in the same area. The sum of plants in the biome has long been known as vegetation, but for animals no similar distinctive term has become current. It is obvious, however, that the two do not represent natural divisions of the biotic complex. The plant-animal formation is composed of a plant matrix with the total number of included animals, of which the larger and more influent species may range over the entire area of the biome, including its subdivisions and developmental stages.

The extent and character of the biome are exemplified in the great landscape types of vegetation with their accompanying animals, such as grassland or steppe, tundra, desert, coniferous forest, deciduous forest, and the like. These commonly represent biotic formations or climaxes, which in their general features have been noted by naturalists since the early days of biology. Each of these consists of a great biotic complex of fully developed and developing communities. The mature mass is the final expression of the response of communities to climate.

The term biome, as here employed, is regarded as the exact synonym of formation and climax when these are used in the biotic sense.

Nature of the Biotic Formation. The concept of the biome is a logical outcome of the treatment of the plant community as a complex organism, or superorganism, with characteristic development and structure. As such a social organism, it was considered to possess characteristics, powers, and potentialities not belonging to any of its constituents or parts.

As indicated in the previous chapter, the recognition of the fact that the plant and animal community are generally coextensive naturally led to the assumption that the complex of organisms in a particular habitat constituted an entity. It is further evident that the matrix of this entity is composed of the sessile and sedentary individuals, which on land are almost exclusively plants, and in the sea, invertebrate animals. On land, this view is supported by the much more intimate connection of plants with the habitat as a consequence of the direct action of the latter upon them and of the universal reaction of plants upon the physical factors concerned. Moreover, the food supply of plants is determined by the amounts of energy and raw materials available in the habitat, while all the food of animals is derived directly or ultimately from plants, though in the sea these may grow at a distance. Naturally, these relations had long been known and were to some degree recognized in the general use of the term "biotic factor" by plant ecologists. Nevertheless, the concept involved in this term did not constitute either a logical or natural treatment of plants or animals in a community based also upon the other group of organisms. Such a treatment becomes possible only with the recognition of both organisms as coactors in a complex of effects proceeding from the habitat as the cause.

The tardy recognition of the biotic formation as the essential entity was naturally due, for the chief part, to the specialized training of biologists as either botanists or zoologists. However, a small share in this must be ascribed to the characteristic motility of land animals, which obscured their inherent connection with the smaller communities, and also to such processes as metamorphosis, seasonal migration, etc., as a result of which many species regularly traverse community limits.

The Biome as a Complex Organism. One of the first consequences of regarding succession as the key to vegetation was the realization that the community, as noted above, is more than the sum of its individual parts, that it is indeed an organism of a new order (Clements, 1901, 1905). For this reason, it was considered to be a complex organism, bearing something of the same relation to the individual plant or animal that each of these does to the one-celled protophyte or protozoan. The novelty of this proposal naturally evoked criticism, but in spite of this the concept has slowly grown in favor, with dynamic ecologists in particular, and by an increasing number has come to be regarded as constituting a new basis for almost unlimited development (Jennings, 1918). However, it is essential to bear in mind the significance of the word "complex" in this connection, since this expressly takes the community out of the category of organisms as represented by individual plants and animals. With the object of making this distinction clearer, Tansley has employed the term "quasi-organism" (1920:123) and Wheeler speaks of "real organisms" (1910) and later of "super-organism" (1923) (cf. Clements, Weaver and Hanson, 1929:314).

Moreover, significant support for the concept of the complex organism has been afforded by investigators in other fields. In a vague form, this view now seems to have long been held by foresters, especially by Rossmässler (1863), but it was not definitely formulated in the idea of a "forest organism" until Morozov (1912), and Möller (1922); cf. also Jaczoski (1926), Glinka (1927), and Thatchenko (1930). In a somewhat similar fashion, the life of the soil has been regarded as a distinct entity by Harshberger (1911) and by Francé (1913), but this is obviously true only in the sense of a layer community. More definite is the view of Forbes (1887; cf. Chapter 1) and of Thienemann (1925), the latter agreeing essentially with the former, as the following excerpts indicate: "Each lake constitutes a life-entity, the parts of which stand in intimate connection. It is a microcosm, an organism of higher rank, the organs of which stand in the closest relation." In its general form, this concept has been followed by a number of hydrobiologists. It is readily seen that the definite limits of a lake lend themselves to a concrete application, though with erroneous implications as to the biome, and also afford some apparent warrant for including the habitat itself in the complex organism. Quite apart from the fact that this carries synthesis to the extreme, the mention of "biological" lake types indicates that Thienemann hardly intends to go so far.

As would be expected, the appreciation of the concept of the complex organism has been keenest among students of the social insects, notably Wheeler (1910, 1911, 1923), and of group organization in animals, such as Ferrière (1915), Borradaile (1923), Child (1924), Alverdes (1927), and Allee (1931). Under the title, "The Ant-colony as an Organism," Wheeler (1910) says: "We then have left the following series: first, the protozoon or protophyte, second the simple or non-metameric person, third the metameric person, fourth the colony of the nutritive type, fifth the family, or colony of the reproductive type, sixth the coenobiose, and seventh the true, or human society. Closer inspection shows that these are sufficiently heterogeneous when compared with one another and with the personal organism, which is the prototype of the series, but I believe, nevertheless, that all of these are real organisms and not merely conceptual constructions or analogies."

Equally penetrating is the statement by Child in "Physiological

Foundations of Behavior," as shown by the following excerpt: "In short, whether we are primarily concerned with the organism or with human society, we can not help but see the fundamental similarities in the processes of integration in the two patterns. In fact, the definition of the organism to which the strictly physiological viewpoint of the preceding chapters leads us will serve almost equally well as a definition of society. The organism is a dynamic order, pattern, or integration among living systems or units. A social organization is exactly the same thing. The fundamental difference between the organism and social integrations among human beings is apparently one of degree or order of magnitude" (p. 270).

The philosophical development of the concept of holism by Smuts (1926) has much in common with the view of Child, as the following statements indicate: "The plant or animal body is a social community, but a community which allows a substantial development to its members" (p. 82). "A whole is a synthesis or unity of parts, so close that it affects the activities and interactions of these parts, impresses on them a special character, and makes them different from what they would have been in a combination devoid of such unity or synthesis. It is a complex of parts, but so close and intimate, so unified that the characters and relations and activities of the parts are affected and changed by the synthesis" (p. 122). "The new science of Ecology is simply a recognition of the fact that all organisms feel the force and moulding effect of their environment as a whole" (p. 340).

The most recent, and in some ways the most significant, contribution to the concept has been that of emergent evolution, as embodied in the views of Henderson (1917), Spaulding (1918), Sellars (1922), Broad (1925), Morgan (1926), Jennings (1927), Sumner and Keller (1927), and Wheeler (1928, *b*). While this development has taken place more or less independently of ecology, it is in practically complete accord with the earlier concept of the complex organism. This essential harmony is well illustrated by the following extracts from Wheeler's discussion. "Non-human societies . . . no less than human society, are as super-organisms obviously true emergents, in which whole organisms, i.e., multicellular organisms, function as the interacting determining parts" (p. 25). "Among the heterogeneous associations we can distinguish the innumerable cases of predatism, parasitism, symbiosis and the biocenoses, or animal and plant communities, which constitute a vast series of emergents, varying from those of very low to those of very high integration" (p. 27).

A similar conclusion is reached by Summer and Keller (1927) in the statement: "Human society then, by the diversity of its parts, their specialization, the distribution of functions, the mutual service and support of the parts, and their solidarity, is a true system or organization. It has a life different from that of the individuals. The quality of a combination is not the sum of the qualities of its components. There is a body to study as well as a cell, a society as well as an individual; and the body and the society are things with lives and laws of their own. Hence forces arise in the societal organization which are characteristically societal forces." It is evident that this derives much from Spencer's earlier ideas (1866) and that these may have sprung from the germ contained in Comte's positivist philosophy (1830).

The most recent and illuminating discussion of the theme of the complex or social organism is that of Phillips (1935; cf. Tansley, 1935), which must be read and pondered by everyone who wishes to obtain a comprehensive outlook upon the world of living things. To the forward-looking biologist, it leaves no doubt that this concept is the "open sesame" to a whole new vista of scientific thought, a veritable *magna carta* for future progress, as Jennings has pointed out.

At the most primitive levels, human families and societies are merely integral parts of the biome. It was only with the advent of agriculture and the control of the habitat by culture and especially of urbanization that man achieved such mastery of biome and habitat as to become an outstanding dominant of a new order. Such dominance, however, is chiefly the consequence of the development of steel and machinery. In pastoral areas, man perhaps is still to be reckoned as a constituent of the biome rather than the superdominant in it. Although ecology has advanced beyond the simple distinction of the natural and the artificial, it is evident that this still suggests an important difference in the reactions and coactions exerted by man at the various culture levels, a difference, however, that runs the entire gamut from influence to dominance and superdominance. Consequently, as suggested earlier, bio-ecology may at present concern itself chiefly with modern man in the role of coactor or reactor in the biome, leaving for sociology and related fields the development and structure of human communities per se. However, in basic studies of social processes and origins, bio-ecology must lay the foundation on which the superstructure of the other social sciences can be reared.

Status of the Concept. At first thought it might appear that the recognition of the biome as the basic unit would necessitate much modification in dealing with the development and structure of communities. However, further consideration discloses that this is not the case, because of the fact that land plants in their community relations have given expression to many of the chief features of community dynamics. This is an outcome of the rule that plants are practically the universal dominants on land and in shallow fresh water, and it derives also from the unity of the biome arising out of the coactions of plants and animals. The fact that the role of animals in both reaction and coaction was either ignored or not definitely evaluated merely requires modifying the list of causes involved and the interpretation of community units with reference to one another. As shown in the succeeding chapter, nearly all the reactions on soil, with the occasional exception of those of earthworms and a few rodents, have been ascribed to plants, and the important effects exerted by animals have been mostly overlooked. In general, the field of animal influence in the biotic community from this viewpoint has hardly been touched.

When the ocean is taken into purview, it is seen to exhibit nearly every type of dominance to be found on land and in fresh water, and possibly other types still. For example, Zostera and Phyllospadix are submerged dominants essentially identical with their relatives in fresh water, while *Ruppia maritima* actually occurs in both coastal bays and saline ponds in the interior. The tropical and subtropical corals assume forms often very like those of plants; they may provide resting and hiding places, shelter and food for other animals, much after the manner of grasses and shrubs on land (Brooks, 1893:30). Corals furnish shade, retard circulation, and modify gases and solutes, reactions more or less parallel to those upon light, wind, and air in forest and thicket. In terms of accumulated material, their reaction may surpass that of land or fresh-water plants (Bourne, 1910), since borings reveal coral rock hundreds of feet in thickness in some islands of the Pacific. The coralline algae, though much smaller, play a similar part in warm seas, forming deposits often of great thickness, as Howe has recently shown (1932).

The food coactions in the ocean differ greatly from those on land, and to a large degree from those in fresh water. The overwhelming number of producent organisms belong to the phytoplankton; the consuments run the entire gamut of animal classes from protozoans to mammals. The food relations are further peculiar in that there is a wide transport of plankton organisms, both living and dead, as well as of organic detritus, and a considerable amount of organic material in solution, which may enter into the food cycle.

CYCLE OF CAUSE AND EFFECT

Physical Basis of the Biome. Probably the most important modification of concepts that ensues from the recognition of the biotic community operates upon the current meaning of the term "habitat." The accepted division of factors into physical and biotic has been both logical and useful in the past, but with the rise of the biotic concept this no longer holds. With plants and animals regarded as essential constituents of the community, it becomes undesirable, if not actually misleading, to refer to either as biotic factors. The word factor should, in consequence, be restricted to the various physical forces or conditions that constitute the habitat. Such use promotes clarity of thinking as well as of expression, and accordingly is adopted throughout the present treatment.

The word habitat is deeply rooted in the practice of plant ecologists, but it has been variously applied by systematists and others. It has been employed somewhat less frequently by zoo-ecologists, and chiefly in application to an area with its plants or to the specific "niche" of an organism. It is used here solely in relation to physical and chemical factors. It would be desirable to secure greater uniformity of usage with respect to the complex of physical factors, to which have been applied a variety of terms, such as habitat, environment, station, and biotope.

A new term, not only free from these objections but also with merits of its own, is suggested. Such a word is "ece," derived from the Greek, οἶκος, home, and already familiar in the derivatives economics, ecology, ecesis, ecad, ecotone, etc. In addition to its brevity, euphony, and significance, it combines readily with both Greek and Latin stems, yields attractive compounds, and may be adopted into any language without change. In actual use during the past seven years, its value has become more and more apparent, and it bids fair to be of distinct service in connection with the comprehensive analysis of the habitat (Clements, 1925:321). At the same time, habitat remains as a desirable synonym for a term in such constant use, while environment still has a proper role in application to the total setting of individual or organism.

Nature of the Habitat. In accordance with the preceding, habitat or ece comprises all the physical and chemical factors that operate upon the community. Of these, water, temperature, light, and oxygen are of vast importance to both plants and animals, and carbon dioxide to all holophytes and a few chlorophyll-bearing animals. The raw materials for food making by the plant are obviously ecial factors, but food itself is not, either for animals or hysterophytes. As to the solutes themselves, some can be used by the animal directly, while others are available only, or usually, in combination. Substratum and bottom are of much significance for great numbers of aquatic animals, and soil is indispensable to most plants and of no little importance to many land animals.

It is a significant fact that, though the factor complex differs greatly between land and sea, the same essential factors are present in both. The characteristic distinction is one of degree or quantity rather than of intrinsic constitution. The two extremes are represented by a single medium, air in the case of epiphytes and water for all submerged aquatic organisms. In this respect, rooted plants are more or less intermediate, the roots being essentially aquatic, though imbedded in soil. Between the two extremes lie a series of habitats with diminishing air and increasing water, exemplified by mesophytes, amphibious, floating, and submerged hydrophytes. Amphibious animals exhibit an irregular alternation between the two media; for intertidal plants and animals the alternation is regular, as it is likewise in the life cycle of many insects with aquatic larvae.

Development and Cycles. On land, as in the sea and in some bodies of fresh water, there are two major types of habitats; one of these corresponds to the climax, the other to the sere. Obviously, in the first, climatic factors are paramount; in the second, edaphic, i.e., local, factors are more controlling. Apart from this major distinction, climates are of wide and often vast extent and relatively few in number; conversely, seral communities are for the most part relatively small in size and usually recur in great numbers. Both are essentially dynamic rather than static, but edaphic changes are generally more tangible and progressive than variations of climate. This is due primarily to the reaction of the community, as a consequence of which this and the habitat develop *pari passu* from initial bare area to a climax. In such a dynamic concept, habitat and sere are regarded as correlated processes or stages of a unified development that terminates in the relatively stable climate and biome (Clements, 1916:357).

The sere represents the cycle of development of the community, which resembles in many respects the life cycle of the species-individual. Its duration varies within wide limits, from the few years required for the shortest of subseres to the hundreds or thousands necessary for priseres in lakes or on lava flows. The phase of development is relatively brief, however, by comparison with that of stabilization in the climax, except in those fairly frequent cases where such an agency as repeated fire produces more than one sere on the same area. Moreover, the climate and climax themselves are never entirely static, the relative stability being disturbed in varying degree through cycles of different intensity and duration. The briefest of these are exemplified by seasonal and annual cycles, expressed in aspection and annuation, phenomena that are also exhibited by seral communities, though to a lesser degree. This is likewise true of the less regular effect of the sunspot cycle of 11 years and its double or triple period. The longer solar cycles may comprise thousands of years, as may also such physiographic ones as cycles of erosion, while back of the major climatic and land-form cycles lie the still greater ones of mountain lifting and continent building. To these necessarily correspond the outstanding changes in biomes and the climates that control them. When it is realized that cycles of different kind and length are operating at the same time, with the phases now in conjunction, now in disjunction, it is evident that habitat and climax are in constant fluctuation. Apart from seral areas, however, most of this has to do at any particular moment with the behavior, size, and abundance of the constituent (not from habitat) species, which thus serve as indicators of habitat variations.

It is evident that the subdivisions of the climatic feature of the habitat will correspond to the various divisions of the climax itself, though there is no immediate need for a parallel series of terms. In addition, there are not only the seral habitats or sereces, but likewise one to match each distinct successional stage. There are also the small habitats of individuals, ranging from a huge oak or banyan to sedentary aphids and mites, or sessile algae and fungi. Furthermore, the grouping of organisms in layers supplies a certain warrant for dividing the habitat in the case of those limited to a particular layer (Shelford, 1913, *a*; Yapp, 1922). However, it is obviously illogical to carry such analysis to the extreme of speaking of the root or shoot habitat of a particular individual or species, as has been suggested by some workers.

Finally, a large number of animals are concerned with two or more habitats. This is a characteristic relation for insects with aquatic larvae in the hydrosere, and also for migrating birds and fishes and some mammals. These may occupy two or more climates each year or during their life history, and the birds and mammals in particular may live in both climax and seral habitats. It appears significant that in the forest biomes of North America, at least, the larger mammals are often best represented in subclimax areas, and the birds in forest margins, where herbs and shrubs alternate in a transition belt or an ecotone, or in seral stages.

Although the question of the biotic habitat presents no serious difficulties, the delimitation of habitats in lake and sea is complicated by a lack of visibility. In general, the two major principles of limits of dominants and definite changes in conditions appear to be as applicable in water as on land. The primary divisions of the ocean, for example, should be in close correspondence with the marine communities, and the dominants of the latter should furnish the chief indications of climax limits, with the aid of factor measurements as necessary adjuncts. In the littoral reaches down to 200 meters, or thereabouts, the great density of the medium produces major physical differences in smaller spatial limits, in proportion to the greater density of water as compared with that of air. As a result, the major habitats are correspondingly smaller than on land. The deeper bottom ones are known only in a very fragmentary way, but the impression afforded by the great marine expeditions, as that of gradual change over large areas, may not be correct.

The pelagic communities of the sea have no counterpart on land, and the greater mobility of the ocean, as expressed in currents, upwelling, tides, storms, icebergs and pack ice, appears to render boundaries broad or even vague, a consequence possibly augmented by the mobility and motility of pelagic dominants and influents. The vast depths of the ocean further complicate the problem in a fundamental fashion and probably make it necessary to limit pelagic communities both vertically and horizontally (Murray and Hjort, 1912:617). Such features of the ocean floor as the Wyville Thomson or Iceland-Faroe Ridge (1,500 meters above the Atlantic floor at the south) exert a distinct influence on the deeper pelagic communities, but it is hardly comparable with the striking effects of this ridge upon the benthic communities of the same area or of some ridges of similar height on the land communities near the coast of California.

Whether it is possible or desirable to recognize seral habitats in the pelagic realm of the ocean remains an open question at present. However, it appears probable that the movement of great masses of water by currents, or through upwelling, produces areas relatively free of organisms, into which invaders may press, and it is not impossible that similar effects may be produced by drifting ice. On the other hand, while they often result in great variations in abundance, the seasonal and annual cycles of the microplankton are not to be regarded as successional processes, but are characteristic phenomena of aspection and annuation (p. 315).

In the tidal area, the question of habitats is much simpler and with close parallel on land. The importance of surface for attachment varies inversely with the factors controlling stability. Where wave action is strong, surface for attachment quite overshadows the physical factors of both land and water; where it is reduced to a minimum consistent with the deposition of sand, barnacles attach to small pebbles and sea mussels form mats upon which a community usually characteristic of rock may be essentially complete. However, the building-up of a muddy bottom, as in estuaries and land-locked bays, gradually withdraws the shore from the tidal belt and initiates a halosere from brackish water to land; a somewhat similar transition to land is exhibited by coral atolls and volcanic islands. Small bays may undergo succession to land directly from salt water through the invasion of halophytes, Salicornia, etc. (McLean, 1935). During the past, epirogenic agencies were active in the production of such habitats, especially on the continental shelf, but also in the midst of continents, as illustrated by the withdrawal of the great Mediterranean of North America during the late Cretaceous.

Causal Sequence. Inherent in the very name itself is the basic principle of ecology that the habitat is the complex of factors or causes. Ecology is not merely the science of the habitat, but peculiarly also of the cause-and-effect relation between this and the biotic community, whether on land or in the sea. Some have assumed that its attention was focused so largely or exclusively on the habitat as to preclude any interest in the life found in it, while others have thought that the study of communities was paramount, with little or no consideration of the habitat. The two views are equally incomplete, and the essence of ecology lies in its giving the fullest possible value to the habitat as cause and the community as effect, the two constituting the basic phases of a unit process. The assumption that the habitat is entirely subordinate to the community in value and interest appears to be current in plant sociology, but so far as there is any difference between this and ecology, it resides in the fact that ecology is primarily concerned with causes, but solely by reason of their effects on life. For such researches, the use of quantities is imperative, and hence the cardinal points of ecology, as distinct from its parts, have come to be measurement, experiment, and development, applied to habitat and biome as inseparable cause and effect.

In the plant matrix of the land biotic community, the causal sequence is a fairly simple cycle. The action of the habitat as expressed in stimuli gives rise to responses on the part of the plant or community. These in turn operate on the habitat, producing reactions that modify it, and then again in turn its action on plant life follows. Embraced within this primary cycle is a secondary one of interaction or coaction between species and between individuals, both plant and animal, well exemplified by plant parasites and saprophytes. The end results of these processes are still other reactions, especially on the soil. Animals too are acted upon directly by the habitat and then react upon it in some degree, but their energy relations are primarily a matter of food supply. In consequence, coaction becomes a response of paramount importance, and plants as middlemen between the supply of solar energy and animals may be regarded as constituting a group of secondary or intermediate causes. Plants likewise exert coactions upon animals, and in the case of lethal parasites these lead to soil reactions through the decomposition of organisms. Hence, the complete cycle of causes, and of effects that become causes in their turn, includes the action of the habitat followed by the responses thereto, which in turn become causes of further change.

On land, the plants as dominants and subdominants play the major role in reaction; in the large bodies of fresh water and in the sea the situation is more or less reversed. In the intertidal and subtidal belts of the continental shelf, the animal dominants assume the lead, except occasionally where attached algae become the codominants. In the open ocean, the reactions of the phytoplankton and of the animals are not readily separated or evaluated, as for example in their effect on light. In ponds and shallow lakes, plants are usually the chief reactors. It is obvious that the medium water as the seat of the reaction has much to do with its nature and degree. This subject is discussed in considerable detail in the succeeding chapter.

Adjustment and Adaptation. In the case of plants, the immediate response to the action of the habitat is a quantitative change in one or more functions, which is often followed in time by a more or less evident modification of structure or form. The first phase of this process has been termed adjustment; the second, adaptation (Clements, 1907). Growth is a complex of functions and hence it is to be regarded as adjustment, but when the intensity or duration of a factor is sufficient, it results in a change of behavior or structure. In sessile animals, the processes are similar to those of plants (Wood-Jones, 1910). In motile animals, this relatively simple sequence is modified by virtue of a more or less effective regulatory mechanism, but it is also possible to trace a connection between habitat and behavior.

In spite of the fact that the plant is often more closely dependent upon the land habitat than is the animal, both exhibit much the same or equivalent general adjustments. This is true in broad terms not only of function, growth, and behavior, but also of time of appearance (Clements and Long, 1923), numbers, grouping, and so forth.

Such adjustments are often correlated with more or less striking adaptations, clearly so with most plants, but less evident and frequent with animals. When adjustment has once been stabilized as a special adaptation, a certain degree of plasticity or power of reversion is lost, and new adjustments and adaptations follow a different course. A somewhat similar result occurs when correlation or competition between organs or parts enters to produce effects not directly correlated with the habitat and hence apparently opposed to the rule.

The viewpoint as regards structural adaptations in sessile animals is similar to the older views held regarding land plants (Wood-Jones, 1910). With land plants, the causal sequence that terminates in adaptation may operate upon the individual, the species, or the community. Actually, it affects the individual directly and concretely, and the phyletic and social groups in consequence. In respect to the species-individual or specient, these effects are summed up by the life history in terms of adjustment, and in the life form, etc., in so far as they deal with adaptation. With respect to the community, adjustment is represented by a series of basic processes or functions, and adaptation by the structures expressed in the climax and seral communities of different rank. It is obvious, however, that in a dynamic system life history and life form are constantly interdependent, and that the modification of either organism or community carries inescapable consequences to the other (Clements, 1931).

In motile animals, structural adaptations are preeminently related to activity. From the standpoint of community relation, the significant activities are connected with layers or strata of the community, and hence adaptation is to epiphytic life, especially arboreal in the larger species, to cursorial and to subterranean life. Such modifications are noteworthy, but they may bear no definite relation to the community as a whole: for example, subterranean adaptations in the tundra are hardly distinguishable from those of the tropical grassland. However, the fact of their existence may be an element of much importance in both communities through the activities correlated with them.

Animal organisms come into existence with certain innate behavior characteristics. Some of these are simple reflexes, such as backing off and turning in Paramecium; others are complicated activities. In the larger and more influent animals, these innate or instinctive characters are the basis of the selection of food and habitation and the formation of habits, and thus determine the course of reaction and coaction phenomena. Associative memory and intelligence play an important part in the activities, coactions, and reactions of the vertebrates, arthropods, and Mollusca. Homing intelligence is especially important; thus, "tradition" plays its part in the choice of areas of wintering, as in the Kaibab deer (Rasmussen, in MS). At the same time the habits of animals during the earlier part of their life histories are commonly molded to some degree by their community associates and habitat conditions. The mores are thus, in part, a community product. There is unquestionably some teaching of young among birds and mammals, as in the coyote (Bailey, 1930). Social organization of wolves leads to the formation of pack hunts and to the establishing of regular routes of travel. Ungulates also assemble in herds with some degree of organization. In Africa, where there are many species with great numbers of individuals and where mixed herds occur, the danger signal of any one species may serve to warn the entire herd. In similar fashion, sheep and goats post sentries in outlying positions to give alarm at the approach of danger (cf. Roosevelt, 1910; Holmes, 1911).

In addition to all these activity phenomena, plastic and moldable by community contacts, there are many similar responses which result in "regulating" the organism into a suitable situation. When the organisms find themselves in unsuitable and thereby stimulating or irritating conditions, random movements and activities take place, some one of which relieves the irritation, and the organism comes to rest. In addition, practically all animals possess a capacity for adjustment, e.g., metabolism and temperature regulation characterize warm-blooded animals especially. There is also regulation with reference to respiration, neutrality, water, and osmotic pressure. All these call into play behavior, muscular activity, and special organs not found in plants, and serve to illustrate the greater emphasis which must be laid on activities and physiological processes in animals as compared with plants (Shelford, 1911, *c*, 1913, *a*).

LIFE HISTORY

Definition and Significance. Life history is the life cycle of the individual; it embraces the entire round of activity or behavior from birth to death. It is not only a cycle in its complete expression, but it also often includes minor cycles corresponding to those of the day, season, or year. These serve to mark the phases or stages of what is essentially a continuing process, and hence organize and illuminate the host of details that constitute the round of life. Embryonic stages, though an intrinsic part of a life history, are best treated in the specialized fields of embryology or morphology, with the possible exception of minute or microscopic organisms. Thus, it is most convenient to limit life histories to the round of growth and behavior observable in nature or in culture, but this should involve, as an essential feature, the use of both quantitative and experimental methods. The lack of such methods and measurements has deprived much work in this field of anything more than suggestive value, and it should now be generally recognized that definite and objective results are rarely to be obtained without measuring factors and responses, and also reactions and coactions. To what extent functional response should be included is still to be determined, but the answer is affirmative in respect to plants and sessile animals.

It is evident that the major features of the life-cycle of plants and animals are similar to the extent of passing through the round of birth, growth, multiplication, senescence, and death (cf. Taylor, 1924, 1930, *a*). As has been stated, various forms and characteristics of land plants are displayed by certain aquatic animals. In general terms, this becomes significant in connection with the life histories of the larger organisms playing a role in biotic communities. These large and macroscopic multicellular organisms may for present purposes be divided into sessile and sedentary ones, as opposed to the motile types. The unicellular and microscopic species of both plants and animals require special treatment, which is beyond the scope of the present discussion.

Sessile and Motile Organisms. The former includes land plants generally, the large zoophytes, corals, etc., and a series of smaller hydroids and the like. Most of these attached animals belong to the sea or fresh water and there is also a large group of sedentary forms which have little or no capacity or tendency to move about. Nearly all these sessile and sedentary organisms are producers of disseminules: seeds, spores, etc., are produced by plants; and eggs, free-swimming young or larvae, stages in alternating generations, winter bodies, and specialized parasitic stages, by animals. The disseminules are probably always more widely dispersed than the adults themselves, both as regards space and habitat. Many come to rest more or less accidentally in conditions not compatible with continued existence, though the delicate larval stages of some animals that swim about feebly before seating must not be overlooked in the matter of distributional details.

The life histories of the vast majority of these organisms may be best considered as starting with the successful seating and beginning of growth in the new position. Habitat selection by this means is accompanied by an enormous loss of disseminules before seating, to say nothing of the great mortality among those that find conditions unsuitable for growth before maturity is reached. Only a few are able to grow to maturity under this indirect method of selection.

Among the multicellular motile species, with certain notable exceptions illustrated by a few fishes with pelagic eggs, the eggs or young are very carefully placed in a suitable situation by the parent, and the account of the life history properly speaking begins with the breeding adult. However, land plants and animals differ fundamentally as to nutrition, motion, factor control, and complexity, with the result that in detail their respective life histories have little or nothing in common. It thus becomes necessary to deal separately with the two groups, though obviously this does not preclude taking into account the intimate relations between plant and animal in the course of their respective cycles.

Relation to the Habitat. The relation of the life history to the habitat is direct and intimate in the case of plants, a fact reflected in the close correspondence of the two cycles during the year and embodied in the phenomena of seasonal appearance, or phenology. Such a connection is inherent in the process of aspection, in accordance with which both plants and animals exhibit a seasonal rhythm of appearance, growth, and reproduction. It is likewise concerned, though to a less striking degree as a rule, in the related process of annuation, in which presence and number are modified by the climatic cycle.

As indicated more fully later, hibernation and estivation are to be regarded as peculiar types of aspection, while diurnation is a somewhat similar process operating in a daily cycle. Thus, the flowering of a dandelion shows not only an annual and seasonal maximum, but a marked daily period as well. The metamorphoses and activities of insects and other invertebrates belong in the same general category. In organisms with very short life cycles, such as diatoms, physical factors may bring about two or more maxima of reproduction during the year. One of the most striking examples of direct correlation of habitat and control of life history is that cited by Russell and Yonge for periwinkles (1928:51). The species nearest the low-water mark hatches out in a very early stage as swimmers, the one near the middle of the intertidal belt appears in a later swimming stage, and that near the high-water line produces young like the adult and therefore able to crawl over the exposed rocks at once.

PLANTS

Relation to Life Form and Habitat. The correlation between life form and life cycle is not merely fundamental and comprehensive, but it is likewise reciprocal in a high degree. Not only is the life cycle the dynamic expression of the life form, but, in turn, the round of behavior has a more or less definite and recognizable effect upon the forms assumed by the organism. The first relation is well-nigh universal when the phyletic or taxonomic form and the vegetation or biome form are identical, as is often true of invertebrates and cryptogams. It is little in evidence in flowering plants, except for families with highly specialized shoots, such as the grasses and cacti. Habitat form and growth or competition form bear little or no relation to taxonomic position, with the exception of such rare instances as the water lilies, in which vegetation and habitat form are identical. The influence of form upon the life history is compelling in the phyletic or biome form; it is much diminished in that of the habitat form and disappears more or less completely with the competition form. Conversely, the effect of life history upon morphology is greater with the more recent forms, and it is either absent or little visible in the fixed types.

Outline. The following account is designed to serve a twofold purpose. In the first instance, it is intended to provide a concise guide to the study of particular life histories in such detail as the biotic approach may warrant. In the second, it is to furnish a basis for the investigation of coaction as the essential bond in the biotic community, as revealed by the interplay of the life cycles of the respective plants and animals. This is illustrated by frequent correspondence between active periods in animal life histories and the flowering of seasonal groups of plants which supply food or shelter.

Number of Stages. It is obvious that all plants agree in exhibiting the three cardinal points or stages of a life history, namely, birth, development, and death, or loss of identity at least, as in the case of fission in unicellular algae. Likewise, it is clear that morphological specialization reflects developmental history, with the consequence that stages and activities increase in number from lower to higher forms as a rule. In plants the principle holds without exception, though the alternate generations of mosses and ferns are naturally much more visible than those of flowering plants.

In the great majority of plants, the life history begins with the germination of spore and seed, is continued through growth and propagation, and terminates in reproduction. In the simplest one-celled algae, reproduction does not occur; in others, such as the desmids and diatoms, it has not advanced beyond the fusion of two single cells. Both plant body and reproductive organs undergo some advance in the thallophytes, but this is relatively slight until liverworts and mosses are reached, the mosses exhibiting a threefold differentiation into protonema, leafy gametophyte, and semi-independent sporophyte, The specialization of the shoot in many ferns approximates that of the flowering plants, though the gametophyte is still regularly autonomous and the disseminule is a spore rather than a seed.

With the advent of the flowering plants, the shoot began to undergo a marked differentiation entirely independent of the phyletic form or family, though this process was little felt by the gymnosperms. In consequence, it is only in the angiosperms that the specialization of life forms becomes a characteristic feature and is accompanied by even greater modification of flower and fruit. Since the flowering plants comprise practically all the dominants of terrestrial vegetation today, it will suffice here to consider their life histories alone. These are treated under the following main heads: germination, growth, movement, propagation, and reproduction, together with the expression of these in the community functions, reaction, competition, and coaction.

Germination. Seeds and fruits differ in a number of respects that have a bearing upon that portion of the life history represented by germination. Protection in the form of a hard or bony coat operates against destruction, through digestive fluids, of most fleshy fruits or seeds, though it also may be concerned with rendering them unpalatable. For a few, germination is made possible, or at least is improved, by passage through the digestive tract of some animal, and this is likewise true of some fungus spores. Finally, in a few grasses and geranials, the awns of the fruit serve not merely for dissemination, but also for forcing the seed end into the soil, as is notably the case in Stipa and Erodium.

Growth. The development of a representative flowering plant exhibits three major phases, seedling, juvenile, and adult, though without definite limits between them. Two related processes, propagation and reproduction, are likewise of major significance, but their position in the sequence of development is often less definite. Flowering and fruiting may mark the last phase of the life cycle, as in the annual, or the final phase for the year, but they may also occur at the outset of the season or during its middle course, to be followed by the development of leafy shoot or underground stem. A considerable number of herbs do not flower until the second year, and some require eight or ten years to reach maturity. This is well exemplified by *Erythronium albidum*, which each year produces one-leaved flowerless shoots until the contractile roots have drawn the bulb down to the proper level for reproduction. In nature, it is not usual for trees to produce flowers under ten years, and in some species the period of youth is doubled or trebled.

The life history of the shoot is essentially a matter of the reciprocal development of leaf and bud. Each leafy axis arises from a bud and in its turn gives rise to new buds, typically in the axils of leaves, but also at other places on stems, and even on roots. The further development of a branching plant, especially a woody one, is determined by the relation of terminal to axillary buds and the outcome of their competition for food. At this point, development passes over into the characteristic features of the life form.

Movement. In spite of their stationary nature, flowering plants all possess the power of movement in a restricted sense, for example, growth and the circumnutation of stem and root tips. More pronounced and less general are such tropisms as the turning toward light, water, etc., the opening and closing of flowers, and the changes in position displayed by flowers and fruits. Clamberers owe their habit primarily to growth, supplemented by petioles, prickles, spines, etc.; twiners ascend by means of a spiral movement; and climbers, by virtue of tendrils, rootlets, or specialized petioles. Leaves exhibit a variety of movements, from the active ones of sensitive plants and flytraps to the slow but much more common ones resulting in the day and night positions connected with the so-called sleep of plants. These occur especially in compound leaves and hence are of frequent occurrence in the pea family.

Propagation. This term is here employed in its botanical sense to apply to asexual multiplication by natural rather than artificial means. It involves something more than mere increase, inasmuch as duration and migration are also connected with the process. Among flowering plants, it occurs rarely with annuals, though the characteristic tillering of grains and other annual grasses might be included here. It is not a common feature of trees and shrubs, except when the regenerative process has been set up through some accident, and is then largely confined to angiosperms. While present in other ecological groups, propagation attains its greatest expression in perennial herbs. In fact, these owe their distinctive habit to this process, and their life forms are determined by the manner in which this function is carried out. Process and form are so intimately and obviously related that it is impossible to consider one without the other, but in dealing with life histories the dynamic relations are necessarily emphasized.

Propagation has been the outcome of the progressive modification of the shoot, partly through a changing relation to ecial factors and partly through the differential storage of food for the buds. It has also been deeply influenced by the nature of the shoot and especially the bud. Out of this interplay have sprung a number of well-known propagules widely employed by the gardener for artificial multiplication. These range from leafy shoots, modified only to the extent of developing roots where the tip or the nodes touch the ground, as in the stolon, to types so transformed as to be recognizable as shoots only by the presence of buds, such as corms. Between these lie offsets, runners, scaly and fleshy rhizomes, tubers, caudexes and bulbs (Fig. 1).

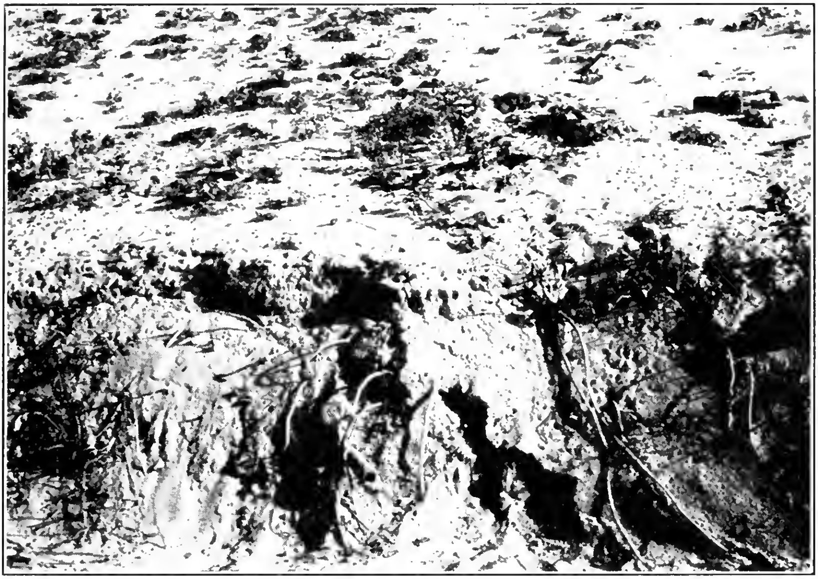


Fig. 1.—Propagation by root stocks and consequent migration of *Convolvulus soldanella* on fore dunes of the strand; southern California. (Photo by Edith Clements.)

The nature of the propagule has a direct bearing upon other features of the life history, such as aggregation, migration, duration, and competition. When the shoot extends in a horizontal direction, as in the scaly root stock of quackgrass or the runner of the strawberry, migration, though slow, is definite and assured. When it is short or erect, aggregation is favored and migration is slight or absent. Duration is partly a matter of life form and partly of the type and amount of growth, as is shown by the varied behavior of the species of Erythronium. The kind and degree of competition are modified by the relation between aggregation and migration, competition between individuals of one species being emphasized in the one instance and between two or more species in the other. For the details of life histories from the morphological standpoint, "Die Lebensgeschichte der Blütenpflanzen Europas" is a mine of information (Kirchner, Loew and Schröter); from the ecological point of view, the life cycle has received attention on an experimental basis (Clements, Weaver, and Hanson, 1929).

Reproduction. By contrast with the preceding processes, sexual multiplication or reproduction is concerned with the flower and its products, fruit and seed. In essence, however, it is but a continuation of the growth of the individual, and the seed is in effect the analogue of the bud. Since the flower is not a food-making organ, it is less intimately related to the habitat than the shoot, though its periodic behavior, both as to season and day, is directly connected with temperature, and to a smaller degree with water and light. A number of flowers exhibit a definite cycle of opening and closing, and related movements not infrequently occur in the flower cluster as well.

The behavior of a flower is determined in large measure by its structure, which is a matter of its phyletic position or taxonomic form. This controls the type of flower cluster and the kind and arrangement of the flowers, and in consequence the major phases of the reproduction cycle, namely, blooming, pollination, fruiting, seed production, and dissemination. In the present instance, the limitations of space permit only the most concise treatment of these, and to obtain a basis for detailed studies in this field it is necessary to turn to the comprehensive accounts of the several processes. As before, the "Lebensgeschichte" is invaluable for this purpose, while for blooming and pollination, Knuth's "Handbook of Flower Pollination" is of particular importance. The experimental approach, especially from the ecological standpoint, is embodied in "Experimental Pollination" (Clements and Long, 1923), and "Anthokinetics" (Goldsmith and Hafenrichter, 1932).

Structure of Flower and Cluster. The life cycle of a flower is dependent upon its structure; the manner of pollination is connected with both structure and arrangement. The daily round of floral behavior is wrought upon the pattern supplied by the number, position, and structure of the four parts, calyx, corolla, stamens, and pistil. It is intimately connected with the task of securing the proper transfer of pollen, preferably by means of cross-pollination. Hence, it is the basis of the many and varied coactions exhibited by the flower-loving insects and birds. When plants are one-flowered, it is obvious that cross-pollination alone is possible, while in such clusters as the head of composites, the automatic transfer of pollen between florets may become a regular occurrence. The relative position and development of the stamens and pistils not only affect the method of transfer, but they also determine the kind of fertilization that results. A detailed treatment of the various types of pollination is to be found in Knuth's "Handbook" (pp. 28–60) and various other works.

Period of Flowering. The time and duration of flowering bear a fairly definite relation to the adult stage of the individual plant. However, in many perennial herbs and woody plants, the relation is inverted, the flowers appearing before or with the leafy shoot, owing apparently to a delayed bud formation overtaken by winter. A few species blossom more or less throughout the growing period and others are somewhat irregular, but the large majority fall within a fairly definite season. As a consequence, it is possible to distinguish these as prevernal, vernal, estival, autumnal, and hiemal plants, each giving character to a particular aspect.

While the flowers of most species open once for all, in a considerable number there is a marked daily rhythm of opening and closing. This cycle depends primarily upon temperature, but in some cases it is connected with light, as radiant energy, or with humidity. The part actively concerned in the movement is the corolla, the calyx assuming an imitative role; in composites, the involucre may be as much affected as the ray-florets. Although opening and closing may occur at almost any time during the twenty-four hours, the tendency is to open in early morning or evening. Species that open during the daytime are termed hemeranthous or day bloomers, in contrast to nyctanthous or night bloomers.

Flower Cycles. Within the seasonal cycle of blooming of each species lies the life cycle of the individual flower, essentially alike for all, except where there are two or more kinds of flowers, such as perfect, staminate and pistillate, or open and cleistogamous. In all flowers or heads with movement, there is also a daily cycle as just indicated, with the exception of ephemerals, in which the life period and the daily cycle coincide (Fig. 2).

It is evident that the seasonal and the daily period of flowers are intimately connected with the coactions of insects, especially pollinating ones. Practically every change of the flower or its parts has some influence upon the procedure in attracting insects and insuring the deposit of pollen, as illustrated later under pollination coactions. In the community sense, the complete floral cycle includes not merely the behavior of flower and cluster, but also the interaction of these with the deportment of the pollinator. While the general subject of pollination has received much attention since the time of Darwin especially, complete and detailed life histories have been a matter of recent concern (Clements and Long, 1923; Clements and Clements, 1913, 1928).

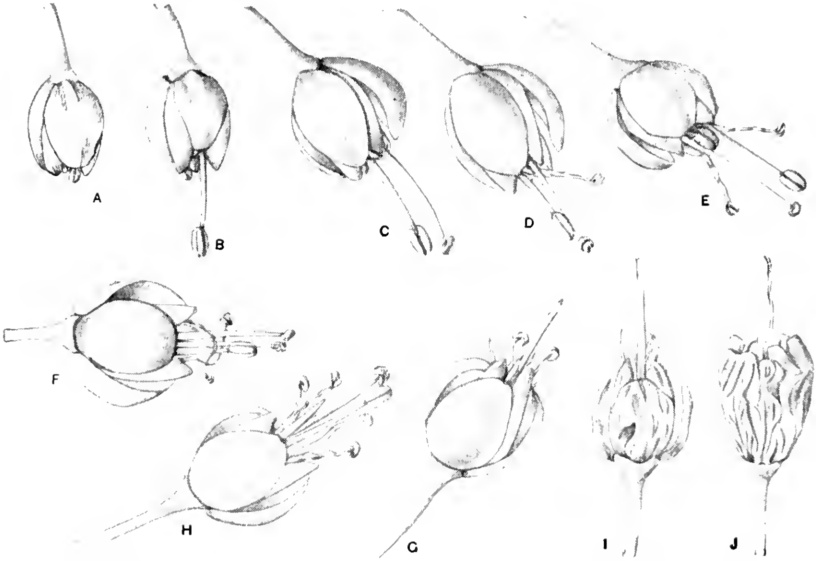


FIG. 2.—Round-of-life in the flower of wild onion (*Allium cernuum*); Alpine Laboratory, Pikes Peak, Colorado. (Drawn by Edith Clements; courtesy of Carnegie Institution of Washington.)

Fruiting and Seed Production. In the great majority of species, the pistil merely enlarges with the developing ovules to constitute the fruit, but in many others another part of the flower shares in its formation. Such changes are not only of interest as a late phase in the life cycle of the flower, but they are likewise of much importance in connection with coactions concerned with food and with dissemination.

Dissemination. Plants fall into two general groups, in accordance with the presence or absence of special devices that aid in the distribution of seed or fruit. Many species possess no such modifications, and their dissemination is chiefly a matter of chance operating upon a high seed production. On the other hand, a vast number exhibit some feature that promotes migration and a considerable group have become highly specialized in this respect. Such specialization has affected the fruit as a rule, by virtue of the available material in the wall; seeds are much less frequently modified, hairs and wings constituting the usual devices. In fruits, the modification may assume the form of a sac, wings, hairs, parachute, chaff, plumes, awns, spines, hooks, or a fleshy pulp. Most of these are adapted to distribution by wind, but awns, spines, and hooks serve for carriage by attachment, and fleshy fruits are distributed in consequence of their use as food.

The principal agents in dissemination are wind, animals, and man. Although many disseminules are carried by water, especially in ocean currents, few of these remain viable after long immersion, except those of water plants. It is obvious that carriage by the wind and by attachment to animals depends upon the development of a suitable modification. This is true, in part, of fruits and seeds used for food, notably the fleshy ones, but a large number of these are scattered incidentally by animals that seek them. From these interrelations springs a vast group of seed and fruit coactions; though these have received much general attention, their comprehensive and detailed study in various communities awaits further recognition of their importance.

Community Relations. It is hardly necessary to emphasize the point that the life history of an isolated individual differs in a number of respects from that of similar individuals in their proper community setting. Hence, complete and detailed life histories can be observed only in the natural habitat, even though garden or other control methods can be profitably employed for the major phases of germination, growth, propagation, and reproduction. In the first place, competition is the outcome of the number and spacing of individuals, whether of the same or different species. It depends primarily upon the reaction of these on the habitat, a process that leads generally to a limited supply of some essential factor. When this effect is marked, growth may be seriously hindered or entirely inhibited at any stage in the life cycle. Thus, competition may lead to the suppression of branches or propagules; it may prevent the formation of tillers or the production of flowers. On the other hand, it may profoundly modify the size, number, or structure of organs or parts, with a more or less corresponding effect upon reaction or coaction.

Because of the primary relations of plants and animals in the community, coaction is always an important and often a controlling process in the life cycle. This is particularly true of food coactions and especially of those concerned in pollination. Grazing animals may keep grasses more or less permanently in the vegetative condition; browsing ones may in addition change the form of trees and shrubs directly, or indirectly by promoting regeneration, while gall-flies may completely transform shoot, leaf, or flower. It is difficult and often impossible to deal adequately with the life history of either plant or animal without taking their coactions into full account. Indeed, this many-sided interaction within the life cycle of associated plants and animals constitutes the essential bond of the biotic community.

ANIMALS

In the life histories of animals, considered from an ecological viewpoint, it is the physiological states through which the animal passes rather than the morphological or form stages that are important. The response systems and instincts where such occur are also of prime importance (cf. Taylor, 1924, 1930, *a*). This has led to the term "physiological life history," which is unnecessary except for emphasis. Again, the usual morphological procedure of starting the account of the life history in the germ-plasm tissues, or with the egg in the case of sexual reproduction and with the somatic tissue changes in the case of asexual reproduction, must be abandoned. A logical discussion of life history in motile animals usually begins with the mature adult and with the primary emphasis on its response system. The new motile disseminules of sessile organisms do not constitute an actual beginning until seating occurs.

Sessile and Sedentary Animals of the Waters. As has already been suggested, disseminules in the form of free-swimming larvae are regarded as the beginning of the life histories. These disseminules are carried far and wide by currents, waves, and their own feeble powers of locomotion. Responses to tactile, mechanical, chemical, and physical stimuli largely govern attachment, but this by no means insures survival to maturity. Many barnacle larvae attach to tidal rock only to be killed after assuming the adult form, by the accident of hot weather falling at the period of extreme low tides and consequent maximum exposure to air (Rice, 1935). The existence of a medusa stage which is both free swimming and a disseminule bearer in some coelenterates does not materially alter these facts. In the northern seas, there is a sequence of disseminules of associated sedentary species (Johnstone, 1908), leading to a season of maximum density and some seasonal groupings (Fig. 3).

The reactions of these disseminules upon the substratum for attachment consist in covering the surface or changing its character.

The ability of many sessile marine animals to attach to each other, however, tends to reduce the effects of the first arrivals on any surface, especially if they are shell bearers.

The duration of life cycles is of vast importance in determining apparent degree of dominance and the arrangement of species found at any time (Rice, 1935). This is especially true of barnacles and bivalves, which are abundant in the tidal communities and in such subtidal ones as occur in the Danish waters. These short life histories (two to ten years) lead to a rapid replacement of individuals and make the arrangement of subordinate groups and the margins of communities shift back and forth rapidly, to a degree unknown on land.

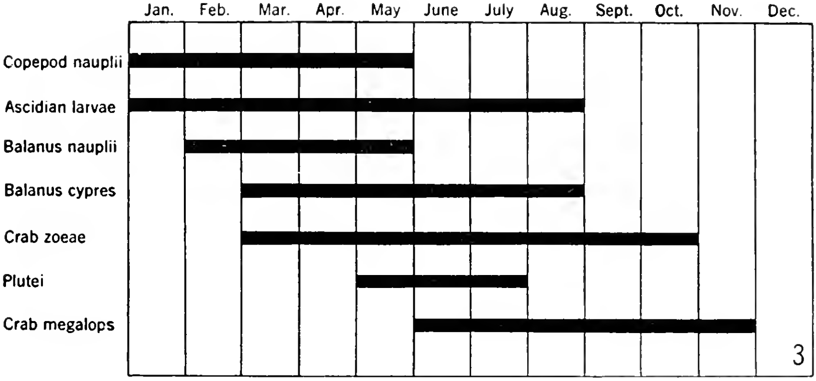


FIG. 3.—The seasonal sequence of larval forms in the plankton of the northeast Atlantic. (After Johnstone.)

Parasites. Parasites are of importance in communities only as they decrease the vigor, fecundity, abundance, etc., of dominant or influent organisms. In every case in which they do have essential relations, the determination of the life-cycle characters is of great significance. Generally speaking, four types of parasites may be recognized: (*a*) bacterial parasites that have the simplest of life histories characterized by very rapid development and decline within the organism and are occasionally responsible for malignant infectious diseases of influent animals; (*b*) internal animal parasites that frequently infect more than one organism and do not ordinarily kill the host appear quite generally to have little or no detrimental effect; (*c*) external parasites, usually chiefly arthropods, with very simple life histories which become important occasionally when they are especially numerous or carry some form of internal parasite; (*d*) internal insect parasites that infect only other insects and their eggs and cause the death of the host.

The life histories of the external parasites of the mammals and the insect parasites of other insects are very simple and not essentially different from those of animals feeding in some other way, but they are of much importance in any attempt to evaluate their coactive effect. The internal parasites are chiefly worms of the several phyla, protozoans and a few arthropods. The life history of the metazoan parasites is often complicated, as it very commonly involves two hosts. Transfers from host to host are divisible into three chief classes: (*a*) through contact with feces; (*b*) through the devouring of herbivores by carnivores and omnivores; (*c*) through contact with water in drinking, bathing, or swimming.

Motile Animals. The breeding activities are the center of the environmental relations of such animals (Merriam, 1890; Shelford, 1911, *a-c*). This does not mean, however, that factors operating at other periods and with reference to other activities may not be more important in some cases (Kendeigh, 1934).

Two types of life history resulting from method of reproduction may be recognized, i.e., some animals are oviparous and others are viviparous. From the standpoint of ecology, the life history of an egg-laying animal may well begin with the adult, usually with the laying female. She selects a place for the eggs that is suited not only to them but also to the young at the time of hatching. The adult appears to be in a physiological state similar in many cases to that of the young at hatching. This is a noteworthy characteristic of the tiger beetles investigated by Shelford (1915). Many fishes construct nests in which the young pass their early sensitive period. In this case both sexes reach a physiological condition similar to that of the young, recurrently each year. The same is true of birds which return each season to the same climatic and habitat complex to breed. The anadromous salmon, however, breeds only once in waters suited to the young, but the young migrate to the sea and back again to the breeding places. In a lesser way, this is true of many animals, notably insects, fishes, amphibians, and reptiles.

In the egg-laying organisms with a metamorphosis, each species presents several seasonal forms in its life history. In *Ambystoma*, the adults, the eggs, the tadpoles, the gilled larvae, and finally the adult form appear in turn between February and July. Since many animals without metamorphosis show similar phenomena, there is a general sequence throughout the year, often made striking by migration to different situations for dormant or unfavorable periods. Many of the smaller forms, notably insects, produce a number of generations in one season (Glenn, 1915). The different generations are often divergent as to response system and other physiological characters. Other animals, though present as adults each year, require several years to reach maturity, and at a given time the various stages are telescoped together in a somewhat confusing fashion. In fishes, measurements of length, scales, and scale rings have served to separate the age classes and illuminate the life history (Walford, 1932). In a few species, such as some cicadas and a few wood beetles, unusually long life histories occur, extending over as much as seven, thirteen, or seventeen years. Again, the production of eggs is occasionally associated with definite astronomical cycles, the palolo worms laying eggs at a definite period of the moon. A correlation with conditions is shown by various other marine worms (Mayer, 1908).

In any community, a considerable series of important stages in the life histories of different species occur together. This is due to a certain similarity of response or of life histories. Some insects, not conspicuous at other periods, occur in middle latitudes at the time migratory birds are pausing on their way to their northern breeding grounds. At the same time, certain plants are in bloom, giving a seasonal aspect to the biotic community, as the result of life history demands.

A few motile aquatic animals deposit eggs that float at the surface and act essentially like disseminules of the sessile animals. The fishes that produce this type of egg belong to diversified taxonomic groups. For example, the cod moves into shallow water near shore to breed, just as do many other fishes. After the pelagic eggs are hatched, the fishes migrate into the protecting tangles of Zostera, where they live during infancy (Blegvad, 1916).

Viviparous species are distributed throughout the more highly organized animal groups. In some cases viviparity does not differ materially from egg laying; e.g., the blowflies and tsetse flies deposit very young larvae instead of eggs. All degrees of adaptation may occur, the condition in the marsupials and placental mammals being more specialized than in the other forms. In these, there is a rutting period often of much importance in that the strongest males frequently become the fathers of the next generation, owing to an intense competition among them for mates, as among the seals and certain ungulates. Again the female sheep does not enter into estrus with any certainty, except when stimulated by sharp changes of temperature from day to night (Johnson, 1924). Rutting time bears definite relations to the weather ordinate; the period before lambing is important to the females, and that of birth and the few days or weeks following are critical for the lambs.

One feature of life histories in general is the occurrence of dormant or quiescent states remarkably well represented in the several groups found in fresh water and on land. The spores and cysts of protozoa, the gemmules of sponges, the eggs of arthropods, the pupae of insects, and the hibernating ground squirrel afford well-known examples, and suspended development in the embryos of a few mammals may be analogous. Such quiescent states have much seasonal significance, and their relations need to be ascertained especially in connection with community aspects.

LIFE FORMS

Concept and Significance. The concept of the life form came into existence originally as a consequence of the interest of plant geographers in the physiognomy of vegetation. It led logically enough to various systems of classification, usually with much in common, but with the emphasis on different criteria. Some of these were constructed in great detail, others were more inclusive; in one case, vegetation was the major objective, in another, floristics. Practically all were static rather than dynamic, and the inductive approach through experiment was entirely neglected, in spite of the fact that life forms afford striking opportunities for the study of adaptation. As a consequence, classification became stereotyped with little direct application to dynamic ecology, though the system of Raunkiaer, with the related biologic spectrum, has been much employed in floristic accounts. Nevertheless, life forms do epitomize the adaptation of the plant body under the compulsion of the environment, and hence are of primary importance in connection with climax and succession. For this purpose, however, it is essential to distinguish various categories, based chiefly on the degree of modification and fixity (Clements, 1920:57; 1928:263).

Kinds of Life Forms. Probably the most logical and serviceable definition of the life form is that which includes under it all the forms exhibited by plants and animals, such as taxonomic, vegetation or biome, habitat, ecad, growth and competition forms (Clements, *loc cit.*). Among plants, the taxonomic and vegetation form are, for the most part, identical in cryptogams; with flowering plants, this is only exceptionally true. For the vast majority of animals, the taxonomic and biome forms are the same; this is especially apparent in invertebrates but holds throughout with few exceptions.

Life forms that bear the distinct impress of a particular habitat or some division of it are known as habitat forms, and those of plants have been termed ecads if they can be produced experimentally. Among animals, a group with a characteristic behavior response has been called a *mores* (Shelford, 1913, *a*); to avoid certain difficulties, especially as to the plural, it is now proposed to employ the word "mune" (*munus*, function, role). Of more recent impress and hence of less import are the growth forms and competition forms. However, plants often exhibit striking forms of the latter type, both in nature and in culture, and this is true only to a less extent for animals.

Bases. The major principles underlying life forms were enunciated by Drude as: (1) the role played by the species in vegetation, and (2) its life history in relation to the habitat, in terms of duration, protection, propagation, and overwintering (1890, 1896). These were later increased to the following five: (1) the basic form, tree, shrub, etc.; (2) form and duration of leaf; (3) protective devices during the resting period; (4) position and structure of the organs of absorption; and (5) reproduction as a single or recurrent process (1913). The system of Warming (1909) took into account three major features, viz.: (1) duration, (2) length and direction of internodes, and (3) position and relations of buds to overwintering; it also took into account five minor ones, namely: (1) structure of buds, (2) size of plant, (3) duration of leaves, (4) adaptation of the green shoot, and (5) capacity for social life (1909). Clements gave more or less equal value to the life period, method of overwintering, conservation of shoots, and success in competition (1920, 1928).

Systems of Life Forms. The essential similarity of the systems more or less current is readily perceived from the fact that Drude makes trees, shrubs, perennial, and annual herbs the basic life forms; Warming's major division of land plants is into monocarpic and polycarpic, essentially annual and perennial, while Raunkiaer's largest groups correspond practically to woody plants and perennial and annual herbs. In accordance with this general agreement, Clements has proposed the following as a simple practicable system, embodying the major features of the others:

1. Annuals
2. Biennials

Herbaceous perennials

3. Sod grasses
4. Bunch grasses
5. Bush herbs
6. Cushion herbs
7. Mat herbs
8. Rosette herbs
9. Carpet herbs
10. Succulents

Woody perennials

11. Halfshrubs
12. Bushes
13. Succulents
14. Shrubs
15. Trees

Each of these types is subdivided as is item 3, as illustrated in Figs. 4 and 5.

The biologist who wishes to pursue this subject further is referred to Tansley and Chipp (1926) and to the comprehensive monograph on life forms of flowering plants by Du Rietz (1931).

Biotic System of Life Forms. Gams has proposed a classification that includes both plants and animals, as an outcome of recognizing the importance of the biotic community (1918). The major bases employed are substratum, motility, nutrition, and duration, and the primary divisions are: (1) the adnate form, *Ephaptomenon*; (2) the radicant form, *Rhizumenon*; and (3) the errant form, *Planomenon*. The difficulties of a combined system are seen in the fact that the radicant form consists exclusively of plants, whereas the other two groups are composed chiefly of animals. Nevertheless, this first essay contains much that is suggestive and may well serve as a basis for future development.

Marine Life Forms. In his study of the communities of Gullmar Fjord, Gislen (1930, *a*, *b*), has proposed a system of marine benthonic plants and animals, the main features of which are as follows:

1. Crustida: (1) eucrustida, incrusting forms; (2) torida, cushion form; (3) mammida, wart form; (4) digitida, finger form.
2. Corallida: (1) dendrida, shrub form; (2) phyllida, leaf form; (3) umbraculida, umbrella form; (4) umbellula form; (5) plume form; (6) rod form; (7) fan form.
3. Silvida: (1) graminida, grass form; (2) foliida, leaf form; (3) sac form; (4) palm form; (5) buoy form; (6) whip form; (7) shrub form; (8) sargassus form; (9) radial form.
4. Radiida, radiate form.
5. Valvida, bivalve form.
6. Conchida, snail form.
7. Limacida, slug form.
8. Vermida, worm form.
9. Crustaceida, crustacean form.
10. Piscida, fish form.

The advantages in the use of such terms are not very evident.

Sessile Multiple-individual Animals. Among plants, life forms have proved very useful in designating and characterizing communities. This is due to the fact that they have segregated themselves into climatic groups that give the essential character to grassland, tundra, desert, deciduous forest, coniferous forest, etc. It is important to emphasize the fact that plant ecologists are led to expect similar conditions in animal communities in general, and usually

FIG. 4.—Tall-grass relict (*Tripsacum dactyloides*) in mid grasses of the true prairie; eastern Kansas. (Photo by Edith Clements.)

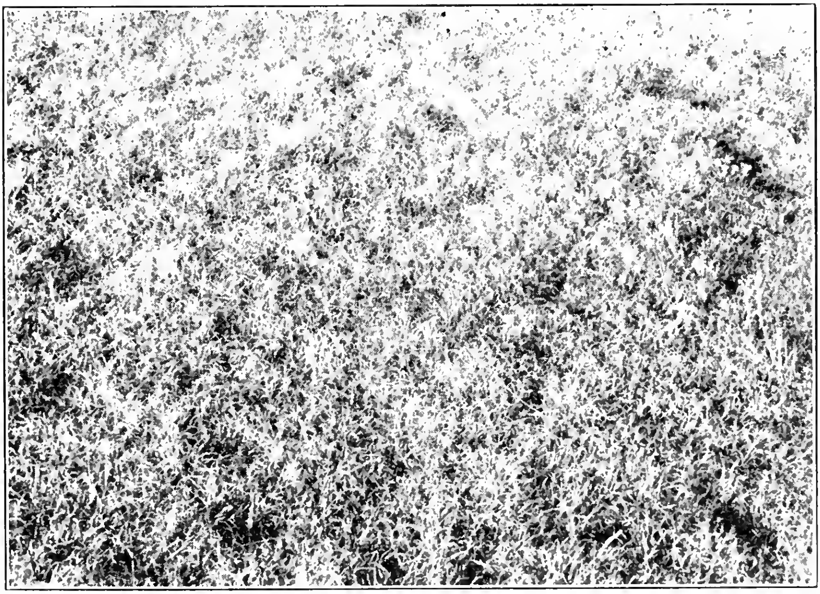


FIG. 5.—Buffalo grass (*Buchloe dactyloides*), a sod-forming short grass, migrating by means of stolons; western South Dakota. (Photo by Edith Clements.)

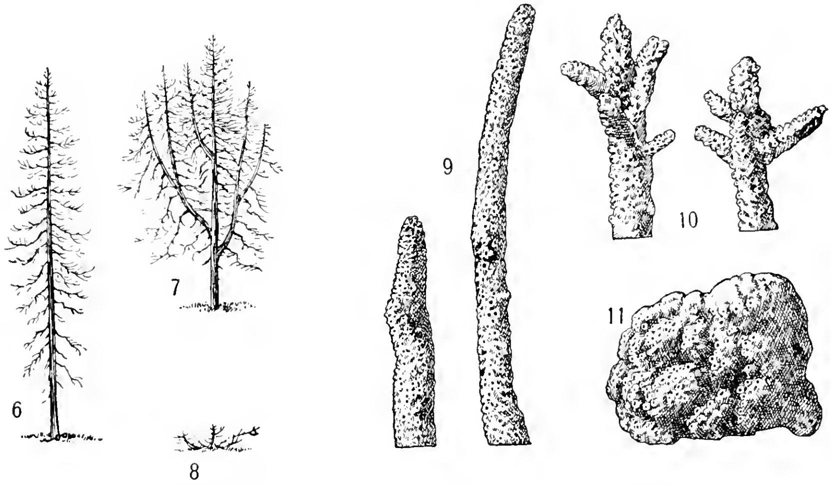
where they are not to be found. The limited character of the similarity has already been pointed out (p. 34) in connection with a comparison of "zoophytes" and land plants. In a bio-ecological treatment, it becomes important to know that the animals of these climatic communities display comparable behavior and physiological characters but lack unity of life-form characters. On the other hand, marine animals may show segregation of characteristic life forms in some communities.

Zoophytes have included chiefly the larger upright, treelike delicate corals, but they may well comprise also the more massive corals with similar branching. The life forms of the notably large species include tree forms with radial symmetry, or more rarely fan forms, produced by branching in one plane, like plants of the genus Areca. On these the zooids are arranged much like leaves, but have a greater tendency to cover the trunk and main branches. A few whip forms have the zooids radially arranged about the trunk like the flowers of the mullein (*Verbascum thapsus*). These rigid plantlike animals are typical in warm seas where corals play an important role in the biotic communities. Their life forms probably have value in characterizing these communities, but no studies from this viewpoint are at present known.

In addition to the large rigid forms, there are many small delicate hydroids and bryozoans that exhibit the same types of branching and zooid arrangement. The life-form peculiarities of these are usually the taxonomic characters of orders, families, genera, or species. They are apparently of little significance in marine communities, playing a role somewhat similar to that of cup fungi and lichens in a forest. There are also sessile multiple-individual animals that assume an essentially spherical form about a foreign body as an axis (Pectinatella). Some others approach spherical form, though the body rests upon a substratum; of these the sponges, especially the commercial types (Moore, 1908), are examples. A few compound tunicates assume a nearly spherical form, *Macroclinum pomum* of the North Atlantic being an example. Some of the massive corals are essentially similar, and on the whole a number of community dominants are included in this type.

Some of the decumbent animals form fans on the substratum; others make simple plates. Still others are amorphous lumps and irregular aggregations owing in some cases to natural and presumably hereditary tendencies, which would classify them as life forms (Shelford, 1914, *d*). This brief statement concerning the life forms and growth forms of aquatic sessile and sedentary animals by no means exhausts the field either as to detail or types, but it does show that the range of life forms in plantlike animals has some resemblance in such land plants as fungi, lichens, liverworts, and even higher plants. However, their segregation into communities so as to give a physiognomic aspect, comparable to those of major plant communities, is doubtful except in the case of coral banks. The phenomenon is also essentially limited to warm seas. The significance and usability of these forms in community study are, in any event, much less than among land plants.

Several genera of corals (Wood-Jones, 1910) develop a tall straight form in deep still water, a much-branched one in moving water, and amorphous lumps in rough water (Figs. 9–11). These are somewhat parallel to the forms of certain conifers in still valleys, windy mountainsides, and timber line (Schröter, 1908). The former is a response to waves and currents, the latter to wind and snow, but both are the result of the injury to a single dominant bud or zooid. The rather striking parallel is shown in Figs. 6–11.



Figs. 6-11.—Showing the parallelism in growth form of a sessile plant and a sessile animal. 6-8, Forms of *Pinus montana* (after Schröter, 1908): 6, from protected valleys; 7, from mountain sides; 8, from mountain moors. 9-11, Forms of Madrepora: 9, from deep water; 10, from barrier pools; 11, from rough water. The differences are due to injury to the leader or dominant growing point. (After Wood-Jones, 1910.)

The commercial bath sponge shows several forms: a sphere when suspended on a wire, a spheroid when growing on an elevation above the bottom, and a palmate irregular form when surrounded by plants or other objects (Moore, 1908). Among the small organisms such as hydroids, some species grow toward the source of light just as plants do. With the small fresh-water types, like Spongilla and Plumatella, one finds frequent reference to growth forms, but rarely any details as to their cause and character. Many of the growth forms noted may be ranked as habitat forms, since they are produced by variation in habitat conditions.

Sessile Single-individual Animals. The forms of these are largely taxonomic, as in the sessile barnacle, gooseneck barnacle, serpulid, oyster, sea mussel, and simple tunicate. The growth forms have been little considered. Pilsbry (1916) has noted long pencil types of several species of barnacles when crowded (cf. Shelford and Towler, 1925). Loeb (1906) has shown that serpulid worms turn toward the light much as do plants, while brachiopods show differences with depth and injury (DuBois, 1916).

Sedentary Forms. Sedentary animals are those which rarely move, or which give the impression of being stationary because of very slow or only occasional movements. These are usually the passive members of active groups, and hence the form is essentially taxonomic, with the exception of the coelenterates. The forms are grouped into types with difficulty, but each of the following represents some degree of geometric likeness: (*a*) hydra, solitary corals, sea anemones; (*b*) some chitons and limpets; (*c*) many worms and a few echinoderms, such as Leptosynapta.

Behavior Forms and Taxonomic Forms. In contrast to the zoophytes and common plants, the vast majority of animals are in no sense multiple-individual, sessile or sedentary. Their outstanding feature is activity and the forms concerned bear a corresponding impress. In terrestrial communities motile animals are well-nigh universal; by contrast to sessile organisms, in which response is through growth, their primary adjustment to physical factors is by means of movement.

The forms of motile animals are usually of direct taxonomic value and at the same time may constitute adaptations determining details of activity. Again, certainly not all the specificities of behavior directly related to structure are of ecological significance. A leaping kangaroo rat may have the same coactions, reactions, and responses to environmental conditions in a grassland community as a ground squirrel which progresses in the more usual way. Accordingly, form in animals is naturally forced into the background. It will therefore not be profitable to go into detail as to form in motile animals. The well-known echinoid, asteroid, snail, bivalve, and vermiform life forms in water often give aspect to marine communities because of a preponderance of one type over another (cf. page 323). Such less active groups also show greater growth-form differences than the more active ones. For example, Baker (1928) finds a river form and a lake form of fresh-water mussels, and Humphrey and Macy (1930) report differences of form and size in tide-pool snails.

The more active animals present walking and running, flying and gliding, hopping and looping, burrowing and swimming, and creeping and crawling life forms. These are rather uniformly distributed throughout the phyla, as well as in water and on land. The presence of segregated groups of these types often gives some character to certain communities, though the use of life habits appears more useful, owing chiefly to the heterogeneity of adaptation characters. This difficulty is well brought out in a series of papers devoted to the adaptations of mammals to arboreal, cursorial, fossorial, and aquatic life (Osburn, Dublin, Shimer, and Lull, 1903). These discussions indicate that the layer adaptation may be effected in a variety of ways, thus placing the emphasis upon activity rather than structure. Again, since the primary adaptation is to layer or level, this also tends to assign a subordinate role to form. Furthermore, some species lack definite adaptations altogether, while more telling is the fact that certain striking modifications have little ecological meaning, and the activities rather than the structural adaptations are of significance. In the study of coactions, it is evident that activity must be taken into account with structure, and may often outweigh it.

Forbes (1914) indicated another relation of structure to activity in the food-getting apparatus and digestive tract of fishes. He found that the fresh-water fishes of Illinois begin life by feeding upon Entomostraca; during development from a very early stage to the adult form some become mud-eaters and others insectivorous or piscivorous, while only a few continue to feed upon plankton. In each type, the digestive tract and gill rakes become adapted to the special food habits, the mud-eaters developing very long intestines.

COMMUNITY FUNCTIONS

Nature and Significance. The development and structure of the biome are due to activities that may be properly regarded as functions of the community. This is likewise true of its subdivisions, both climax and seral, in which the nature of the processes is even more clearly discernible. The group of organisms which constitute the community is acted upon by the habitat, producing social response that leads on the one hand to further reactions upon the habitat and on the other to new coactions between the associated organisms. In succession these processes proceed in a chain or series which finds its summation in the climax. The chain of seral communities has been likened to the series of stages in the life history of an animal undergoing metamorphoses with its final and most perfect stage represented by the adult which is comparable to the climax. The process of succession has also been likened to the growth of plants, but lack of detailed knowledge of both processes renders the comparison quite ineffective.

The functions of the biome may be viewed from the standpoint of the dynamic processes, such as succession, annuation, aspection, etc., or from that of the causal sequence of processes, beginning with aggregation and terminating in stabilization. Both approaches are desirable for a proper understanding of development and its relation to the consequent structures, but the scrutiny of the single functions and their correlations is much the more essential. In spite of the fact that they are more or less simultaneous in operation, it is possible to separate them experimentally and to a certain extent by observation also.

Up to the present, the functions of the community have been studied chiefly with respect to the plant matrix, but it is evident that they also carry over into the biome. Special studies of coactions and competitions made from the standpoint of particular species of animals confirm this conclusion. Their significance with respect to animal groups is most clearly exhibited where animals are the dominants, as in the marine climaxes. However, it is also well exemplified in the various minor communities, such as families, colonies, and societies, both plant and animal, which are essential features of the biotic community. The smaller and simpler the community, the more readily can its functions be followed, and, in consequence, initial stages in succession furnish the best opportunity for this in nature, just as similar artificial groups constitute the best cultures for such purposes.

The following seven functions are considered to be the basic processes in the plant matrix, and hence in the biome, even when this consists primarily or wholly of animal dominants. These are aggregation, ecesis (establishment), migration, reaction, coaction, competition, and cooperation. Out of these arise certain complex processes, such as invasion and succession, while such phenomena as diurnation, aspection, and annuation are more or less closely connected with them. For the present purpose, at least, the most significant of these are reaction, competition, coaction, and aggregation and ecesis (succession), and they are in consequence discussed in considerable detail in the following chapters. For the others the general account given here is supplemented by discussion or specific mention of their role in the biome later in the text.

AGGREGATION

As a technical term, aggregation was first employed in ecology in the dynamic sense, for the coming together of individuals as a result of multiplication (Clements, 1905, 1928). With respect to animals, it has occasionally been given a similar meaning, but more recently Allee (1931, *a*) has used it as the inclusive term for the groups that result from the process. In this sense, it is largely synonymous with community, though more exactly with the family or colony of plant ecologists. However, no serious ambiguity is involved in the double use of the word, which will probably continue until the study of minor communities becomes much more general on a developmental basis.

Aggregation among Plants. In its simplest form, aggregation is the direct consequence of multiplication, though as a rule it is also dependent upon migration in some degree. The first type is exemplified by such algae as Glœocapsa and Nostoc, in which the dividing cells are held together by a matrix of mucilage. Such a group of individuals is a family, the relation being essentially that of parent and offspring, even though the parent disappears as a result of fission. Practically the same type of grouping occurs in terrestrial forms, especially flowering plants, when the germules mature and fall to the ground about the parent. A family is also produced when propagation by offshoots leads to a similar disposition. All these are instances of simple or primary aggregation, in which migration is absent or slight. This is often the case in annuals with high seed production, and, in consequence, these supply by far the largest number of pure families. Moreover, the conditions for simple aggregation are especially favorable in bare areas and secondary ones in particular, so that the initial stages of subseres are regularly characterized by annuals (Fig. 12).

Mixed or secondary aggregation ensues when seedlings (germules) of two or more species become intermingled to form a colony, in the case of a bare area, or when migration carries propagule or seed into an established family. Every community is an example of this type of grouping to some degree, in view of the fact that association is merely the outcome of the interplay of aggregation and migration.

With aggregation paramount, families are the rule; when the processes are more or less balanced, colonies prevail; with migration emphasized, the mosaic of vegetation results. In closed communities, it is practically impossible for annuals to persist or to enter, and the pattern often reflects the tendency of perennials with offshoots to form families, as illustrated by Antennaria or Erythronium.

Aggregation among Animals. In attempting to bring together the knowledge of two fields which have developed as independently as botany and zoology, or more specifically, plant ecology and animal ecology, difficulties as to the different uses of the same term arise frequently, aside from the fact that aggregation long has been used by plant ecologists to apply solely to the process of assembling in a group. Allee's use of the word introduces an additional general term for the communities of small size. Aggregation is accordingly used here only in the sense of the process.

FIG. 12.—Aggregation of a native goosefoot (*Chenopodium leptophyllum*) in a short-grass pasture covered with wind-borne silt; eastern Colorado. (Photo by Edith Clements.)

As compared with plants, aggregation through reproduction is comparatively rare or temporary. Temporary aggregation occurs in the case of vertebrates which care for their young. Nest-building fishes, aquatic and gallinaceous birds, and some mammals afford readily observable examples. Permanent aggregation by reproduction occurs in ants and a few other social insects. Doubtless, sessile animals afford examples of aggregation by asexual reproduction, but aside from the corals, noteworthy permanent examples are not outstanding, either in their conspicuousness or ecological significance. As Allee and others have pointed out, the process of aggregation in motile animals is dependent upon sexual forces, upon social forces, and upon common environmental responses. Aggregation by reproduction as cited above is essentially social. In animals with minimal social tendencies the offspring disperse early or may be loosely held together by common environmental responses (cf. Chapter 5).

MIGRATION

In spite of general agreement in the sense of movement, this term has come to have somewhat different applications in botany and in zoology. This has probably come about as a consequence of the basic contrast in motility, so that it became desirable to distinguish the distant or recurrent movement of animals in mass from local activities. In sessile plants, any movement was of some significance, but the most noticeable ones were those of the individual for a short distance. Moreover, in terrestrial animals the adults are much more motile than the young, while with plants the embryo or seed is often very mobile and the adult immobile, except for the slow and restricted spread of offshoots.

The general dependence of the flowering plant upon the seed is indicated by the word dissemination, which might well replace migration were it not for two facts. The first is that plants bring about effective change of position by means of propagules (Fig. 13), and the second that vegetation often exhibits great mass movements, in which the associated animals are also involved. In consequence, it seems most logical and convenient to employ migration to denote any and all changes of position, whether of individual or community, single or recurrent, over a restricted or local area, or for great distances. The term would still retain its special application to seasonal, annual, or cyclic movements in mass, characteristic of certain insects, most birds, and some mammals and fishes. Dissemination would continue to apply to the local transport of seeds and fruits in particular, whereas migration would be especially applicable to mass movement in response to climatic change, in which seeds, propagules, and motile animals would all be involved (Clements, 1922:351).

Migration in Plants. Although migration devices have long been a subject of interest to botanists, the actual process itself has received little attention, especially in terms of experimental study. Such study is peculiarly difficult in nature, and this fact explains in large part the persistence of the idea that the movement of migrules is as effective as it is universal. This view has received much support from the general abundance of weeds and the readiness with which they take possession of disturbed places. However, it finds little warrant in natural communities, in which not only is movement itself much more restricted than commonly supposed, but also the establishment of invaders is rendered almost wholly impossible by the competition of the dominants. Transport to a great distance has long possessed dramatic interest, but is rare in fact and even much rarer in effect. When the embryo is not destroyed by the agent of distribution, as regularly happens with water and birds, its establishment becomes possible only in disturbed or bare areas. In consequence, dissemination in nature is of little import to the community, unless a change of climate intervenes. Its chief significance is in the colonization of primary bare areas or secondary disturbed ones and in supplying the newcomers for the stages in the ensuing succession. The mainte-

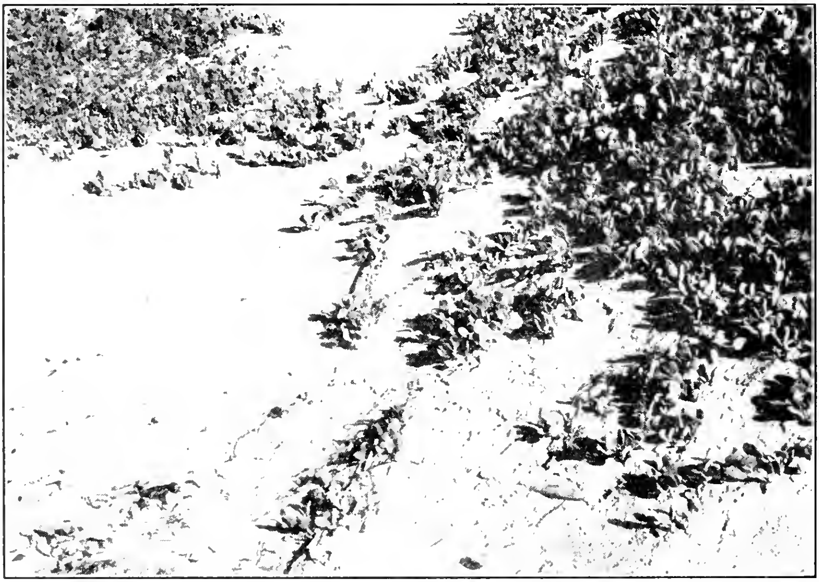


FIG. 13.—Migration of a dune pioneer (*Abronia maritima*) by means of creeping stems; seashore, Santa Barbara, California. (Photo by Edith Clements.)

nance of the climax itself is almost exclusively a matter of propagation, supplemented, in a small degree, by regeneration.

Leaving aside the consideration of movement in water, which is chiefly due to current and wave, mass migration, as contrasted with the transport of individual migrules, regularly takes place in two fashions. Locally, it operates upon minor communities, utilizing propagules in the case of the climax and disseminules in the colonization of bare areas. Regionally, it becomes significant only under the impulse of climatic changes, but the actual advance is due to the slow and repeated movement of dominants and subdominants through both these methods. The migration of ruderals and cultivated species has likewise a mass effect in a large degree, in spite of the fact that transport of weeds by man is unintentional. In all these cases, however, the final value of migration as a process is determined by the success attained by ecesis.

The Migration of Animals. Migration proper in animals does not differ from that of plants. Sessile and sedentary species, as well as animals of limited activity in water, commonly possess a life-history form that may be carried some distance by currents. On land, small animals, especially insects, spiders, and some mollusks, may be moved into new territory almost as readily as the seeds of plants. The number of these carried out of their homes by wind is evidenced by the line of living drift found about Lake Michigan after a storm of short duration. However, the habits of the species are regularly so little suited to life on the beach as to bespeak the rarity of establishment. Nevertheless, the effect of such events in populating denuded areas where animals precede plants cannot be neglected (Smith, 1928), nor can the process be overlooked where climatic changes have favored invaders into established communities. For example, species characteristic of dry oak-hickory woods appeared in moist oak-maple forests following the dry season of 1930, only to disappear soon after.

The random wanderings of the larger motile animals out of their usual range is of no more significance than the movement of the wind-blown insects, since they regularly return and no actual shift of home occurs. Other local or recurrent wanderings occur, but even the more important and definite ones are subordinate to the mass movements involved in biotic migration.

Types of Migration. These may be grouped as: (1) recurrent migrations, divisible into (*a*) annual, (*b*) seasonal, (*c*) metamorphic, (*d*) diurnal; or (2) non-recurrent migrations, divisible into (*a*) extension of range, (*b*) local movements within the home area.

The annual and seasonal migrations are characteristic of many birds, mammals, and fishes, and of a few reptiles, amphibians, and insects and other invertebrates. Practically always, the movement is into a new habitat for reproduction and out again. Some degree of change of place frequently accompanies reproductive activities. In some instances the distance concerned is small, but if it is into a different habitat or set of conditions, it is significant and quite completely homologous to that of the salmon or of birds which travel long distances to breeding places.

Birds are the most noteworthy migrants, and the distances traveled by many well-known species are remarkable. With the approach of spring in the northern hemisphere, they leave their winter homes in the grassland of Patagonia, the tropical forest of Venezuela, the swamps of Louisiana, or elsewhere, as the case may be, and pass northward. The Kaibab deer journeys from the pinyon and sagebrush to the montane forest for the birth of the young. The salmon, shad, and other fish go many miles to places suitable for spawning. Moreover, the behavior of the black bass which moves from its feeding grounds in aquatic vegetation, to a sandy beach is essentially similar. The rose beetle (Microdactylus) leaves its food plant to deposit eggs among grasses. The force that initiates and directs such movements is probably similar in all cases, and the local migrations are sufficiently simple to permit experimental study.

There are many local recurrent annual migrations of insects from hibernation quarters to breeding and feeding grounds, and the reverse, especially between forest edge and grassland, or water and adjacent land. In proportion to size, these flights of small insects are considerable, a few hundred yards for a chinch bug being comparable to miles for a deer. Metamorphic migration, such as the return of the adult to air from water, is typically annual and recurrent, but may be seasonal when two generations occur in one season. Furthermore, recurrently migratory species shift their breeding grounds and their winter rookeries with the mass of associated species, but this does not introduce new features into biotic migration. Diurnal recurrent migration characterizes many insects that move from forest edge to open country, and vice versa, with day and night (Carpenter, 1935). It is also typical of plankton, which moves down and up in both sea and fresh water in accordance with the alternation of day and night.

Non-recurrent migrations are perhaps best illustrated by range extension. The Virginia deer has advanced northward several hundred miles since the settlement of eastern North America. It has taken the place of the woodland caribou in the forests about the Great Lakes and for some distance northward. The opossum has also moved northward two hundred miles or more from Indiana into Michigan. Both of these extensions are due probably to the release of territory, change of vegetation, reduction of enemies, or other activities of man. Extension of range in insects is likewise frequent. The boxelder bug moves northeastward from Oklahoma to southern Michigan every decade or so, and frequently becomes domiciled, until a winter with prolonged low minima destroys the invaders.

ESTABLISHMENT OR ECESIS

By this term is understood the process of making a new home, involving the adjustment and often the adaptation of organism or community to a new place or habitat. It is both more comprehensive and more concrete than acclimatization or naturalization, but differs little in essence. It embraces the widest range of adjustment, from the slight movement of a rhizome in practically uniform conditions to the establishment of invaders in a bare area or the advance of forest or prairie along an ecotone. It is a much simpler and surer process when a single medium is concerned, as water or soil, in which migration and ecesis are nearly synonymous. Ecesis in land habitats, with the necessity of adjustment to two media of great variety, becomes correspondingly complex and difficult. However, this statement applies much more fully to plants than to animals, owing chiefly to their direct dependence upon the ece but also in some part to their sessile nature. It is applicable in varying degree to animals, being fairly simple and direct in wide-ranging species, and more complex in sedentary ones or those with narrow limits as to physical factors or choice of food. By contrast with plants, ecesis in animals involves adjustment not only to the new place or habitat but also to a new group of coactions.

Ecesis in Plants. Differences in the manner and success of ecesis are determined by several elements, namely, the plant or part concerned, the medium, and the habitat. In free aquatic forms the individual itself often migrates and ecesis consists merely in its continuing to grow and reproduce, a result more or less assured by the greater uniformity of aquatic habitats. For the offshoots of land plants, especially underground ones, conditions are rather similar, and continued growth and multiplication are certain within the limits set by excessive competition. However, in the vast migration of seeds and fruits, ecesis requires successful germination, growth, and reproduction, during which seedling and plant must often withstand unfavorable ecial factors, intense competition, or injurious coactions. As a consequence, a migrule may meet one of four fates: (1) it may never germinate;

(2) the seedling, or later the adult itself, may die or be destroyed; (3) the individual may persist without reproducing, a frequent event under keen competition; or (4) normal reproduction may occur, associated in most perennial herbs with propagation. Ecesis, properly speaking, occurs only in the last instance. It regularly involves an expression of the complete life history, though under the influence of marked adjustment this may be modified in details (Fig. 14).

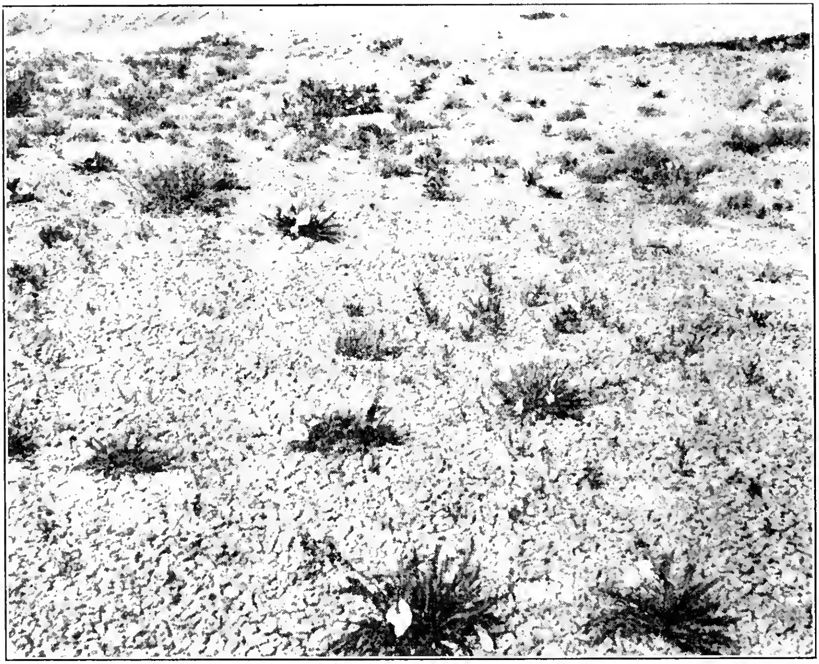


FIG. 14.—*Oenothera caespitosa* establishing itself in the sun-baked clay of the Bad Lands; The Great Wall, South Dakota. (Photo by Edith Clements.)

As already emphasized, migration becomes effective only when followed by ecesis. The latter has usually been regarded as a natural if not regular sequel to movement, but experimental studies have shown it to be altogether exceptional (Clements and Weaver, 1924). This conclusion is reinforced by the slow changes in composition shown by the plant matrix, in spite of the enormous seed production of many species. Not only must the seeds meet the vicissitudes of transport and of germination, but the highly susceptible seedlings must run the gauntlet of untoward conditions, of destructive coactions, and of unfavorable competition. The final survival represents but the merest fraction of the initial seed production and would be practically negligible were it not for the recurrence of bare or denuded areas in which the barrier of competition is absent. So complete is the control of dominants, in climax communities especially, that the ecesis of invaders is all but completely inhibited, becoming possible only in consequence of some marked disturbance or climatic change. From this standpoint, the earlier views of more or less constant and widespread migration or of gradual advance, such as that of woodland along valleys, become entirely untenable, and the great movements of climaxes and subclimaxes are to be explained only on the basis of climatic compulsion, with ecesis as the decisive function of the community (Clements, 1922).

Ecesis in Animals. The motility of essentially all land and many aquatic animals leads to an invasion of new territory in their daily rounds for food, in consequence of fright due to enemies or other incidents. In addition, many of the smaller forms are borne out of their natural area by currents of wind or water. Thus, there are thousands of temporary invasions of new territory by many species to one invasion of significance as biotic migration. The sessile and sedentary animals show a series of phenomena so nearly parallel to those of plants that the essential principles may be found in the preceding section.

Motile animals with power of flight, and one or more generations per year, may invade new territory under agricultural conditions and establish themselves until a cold winter or a dry season kills them off. The boxelder bug (see p. 63), harlequin, and cabbage bug are examples. The birds of forest edge and meadow have doubtless increased greatly over eastern North America with the increase of such habitats about farms and villages. The introduction of the English sparrow and starling is largely a transfer of a European species of the deciduous forest to similar conditions in America. However, Wetmore (1926:211) states that it took ten years for the starling to establish itself firmly in Central Park, though the responses and coactions involved are not known. His account indicates that the starling ranges considerably beyond its breeding area, which is a frequent phenomenon. The instances of the ecesis of animals outside their original ranges in North America have been very numerous under the influence of the rapid modification of the original biomes, but there is scarcely a case in which the detailed causes or processes have been studied. In fact, at present little more can be said of ecesis among animals than that it involves maintaining a population over an adverse year or series of years.

Related Processes. A number of functions consist of two or more processes of which ecesis is ruling or decisive. This is particularly true of invasion, which consists of migration and ecesis, but with its final success and effect depending primarily on ecesis. This is the process characteristic of succession, for which it supplies the materials to be organized into the various stages as a result of reaction and competition.

The other complex functions are concerned largely with the climax community, though not unknown in the later seral stages especially. The most striking of these is aspection, which is characterized by seasonal maxima of number or developmental behavior, in water as well as on land, and with both plants and animals. Related to this in terms of behavior are hibernation and estivation, ordinarily regarded as confined to animals but found in plants also, though under other names. When the behavior response operates upon a daily rather than a seasonal cycle, the process may be termed diurnation, illustrated by the vertical movement of plankton and by the "sleep" movements of flowers and leaves. Finally, the change in abundance or prominence may be annual, as an expression of a larger cycle, such as the eleven-year sunspot period. This is known as annuation, in which the response to climatic variation may produce striking changes in abundance, resulting in widespread migration or in marked differences in composition. Because of the importance of their roles in the climax, the discussion of these functions is reserved also for Chapter 6.

Interrelations of Community Functions. Like those of the individual, the functions of the community are not only most intimately connected with one another, but they are also involved in a complex of activities in which their simple causal relation is obscured or completely lost to sight. The normal sequence exists only in the simplest minor communities; in others the interplay of functions is so kaleidoscopic that the operation of each is difficult to discern. This is peculiarly true of succession, which exhibits the dynamics of function at a maximum. In the climax, aggregation and migration are at a low ebb, and the directive processes of reaction and competition are diminished and are concerned chiefly with fluctuations in abundance in season and year. The normal sequence comprises aggregation, migration, ecesis in terms of reaction, competition and coaction, succession, diurnation, aspection, and annuation. It is obvious that the relation of almost any two of these is more or less cyclic, inasmuch as migration makes aggregation again effective, from which further migration proceeds. In the case of reaction, the ensuing competition in turn influences this, and is itself again modified to correspond. In succession, functional activity rises to an optimum until temporary stabilization is attained in each stage, when it falls off until a new wave of invasion culminates in the succeeding stage. A detailed and comprehensive account of the various community functions is impossible within the scope of the present book, but the salient features of the major processes, their interrelations, and the significance of each for climax and sere are discussed in Chapters 3 to 6, inclusive.

CHAPTER 3

REACTION: THE INFLUENCE OF COMMUNITY ON HABITAT

Definition and Nature. As has been earlier emphasized, the cause-and-effect cycle in the biotic community comprises the action of the habitat upon the associated organisms, their response to this, and the consequent effect upon the physical factors of the habitat. The last process was termed reaction by Clements (1904:124, 1916:79, 1928; Weaver and Clements, 1929:145), and was defined as the influence exerted by an organism or a community upon its habitat. It is entirely distinct from the response of species or group in the course of adjustment or adaptation. For example, the physical factors cause a plant to function and grow, and it then reacts upon the habitat or ece, changing one or more of its factors in an appreciable or decisive manner. The two processes are mutually complementary and often interact in the most complex fashion. Generally, there is a primary reaction with one or more secondary ones, direct or indirect, but not infrequently two or more factors are affected directly and critically.

The word interaction has long been used by zoologists to cover all kinds of interrelations between organisms and habitat, but it is obviously too inclusive for adequate analysis, especially in the broader field of bio-ecology. Although it is desirable to retain it in a comprehensive sense, the need for exactness of reference is best met by recognizing two distinct types of interaction. The first of these is reaction, the effect of organisms upon the habitat; the second, coaction, or the influence of organisms upon each other. Such a distinction becomes of paramount importance when the biotic community is made the basis of treatment.

The reaction of a community is always more than the sum of the reactions of the component individuals and species. In the case of the plant matrix, though it is the individual that produces the reaction in the final analysis, the effect regularly becomes recognizable only through the combined action of the group. In practically all cases, the community accumulates or emphasizes influences that would otherwise be insignificant or transient. This is strikingly illustrated by the reaction of trees upon light. The shadow of a single tree shifts with the sun, and, in consequence, the reduced light intensity is permanent only over a small area about the base. Thus, while a community of trees casts less shade than the same number of isolated individuals, the effect is constant and continuous, and hence becomes controlling. The significance of the community is likewise clearly demonstrated in the production of duff and leaf mold. The litter is again only the sum of all the fallen leaves and twigs of the individuals, but its accumulation is dependent upon the practical cessation of wind action. The reaction of plants upon wind-borne sand and silt-laden waters further exemplifies the unique importance of the community.

The animal members of the terrestrial community are less effective than plants in producing reactions, as a general rule. In spite of this, waste products and hard parts often accumulate in great amounts, while burrowing animals in particular frequently exert a pronounced effect in disturbing soil or bottom, and sessile and sedentary ones in protecting or perforating the substratum. Moreover, animal reactions may be more or less direct consequences of food coactions, as in the tunnels and mounds of pocket gophers, moles, etc.

Relation to Life Forms. Some reactions are the direct consequence of a normal functioning of the organism. With respect to plants this is illustrated by the decrease of water content through absorption, the increase of humidity as a result of transpiration, and the weathering of rock by the excretion of carbon dioxide. The amount of oxygen, carbon dioxide, or solutes in the medium is directly affected by both plants and animals, and animals produce many deleterious excreta. Furthermore, such a functional complex as growth may lead to the direct modification of physical factors, but as a rule this is much more strikingly related to life form.

Reactions in both plants and animals may be directly connected with form. Growth form in plants, however, is primarily an outcome of reaction as brought about by competition. The plant matrix of the community owes its predominant ability to modify land habitats to the vegetation forms represented by the dominants especially. This is best revealed by the contrast between forest and prairie; the former exerts a controlling action upon aerial factors, the latter a much slighter effect. On the other hand, the reaction of forest on soil is primarily surficial, while that of grassland is usually profound, owing to the fibrous root systems, which ramify much more completely through the soil. The successful reaction of pioneers in dunes of sand or topsoil, in gravel slides and badlands, is chiefly a matter of the form assumed by the shoot and root, in consequence of which the movement of material due to wind, gravity, or water is diminished or eliminated. Relations of this kind are less frequent and less evident with animal forms, though burrowing rodents, earthworms, and ants in particular constitute an important group. In areas of salt marsh exposed to alternating land and sea conditions, it is probable that the special study of reactions will disclose many animals of much importance.

Role of Reaction. As has been previously stated, the primary role of reaction is seen in the process of competition. In connection with this, it regularly assumes the directive function in terrestrial succession and in the concomitant development of the habitat, but it may also lead to the production of bare areas as a requisite to succession. In the development of a primary sere, plant reaction begins with the establishment of the first invaders and is narrowly localized about them and the resulting families and colonies. It is largely mechanical at first and results in binding sand or gravel, producing finely weathered material or building soil in water bodies, etc. In secondary seres, extensive colonization may occur during the first year, and reaction may at once be set up throughout the entire area. Reaction then progresses with an increasing advantage to each succeeding stage until the climax is attained, when the reaction of the dominants is so decisive as to exclude other invaders. Thus, in one sense, succession is but a series of progressive reactions by which communities are sifted out in such fashion that only the one in closest harmony with the climate ultimately survives. As an inevitable accompaniment, one seral habitat follows another until the climax habitat becomes permanent during the persistence of the climate concerned. In the aspection and annuation exhibited by the climax itself, reaction continues to have an influence, but this is usually secondary to the control exerted by season or climatic cycle.

In general, animal reactions on land have not been separated from the larger effect produced by plants. However, they are usually present to some degree, owing to the presence of soil-moving and soil-modifying animals in the climax and all seral stages, even initial ones in which the plants have not yet appeared. In water, reactions are evident but observation is more difficult. Reactions of the animal dominants regularly play a large part, sometimes as in shallow fresh waters through their influence on turbidity and sometimes through disturbing the substratum (see p. 301). The microplankton, however, reacts upon light and dissolved gases and salts in such a manner as to produce distinct conditions, comparable in degree to reaction effects on land.

Kinds of Reaction. From their very nature, land reactions are most satisfactorily classified in accordance with the effect upon the habitat (cf. Clements, 1928). However, in extending the scope of the process, the most convenient division is into land and water, with subdivisions into soil and air, fresh water and salt water, bottom, etc. Furthermore, though it is also convenient to refer to them as plant or animal, this distinction often has no corresponding difference in process or effect. As to the processes concerned, though these differ greatly in detail, all are characterized by the addition or subtraction of material or energy, or by some feature of disturbance. Finally, the life form of the reactor may sometimes be taken into account to some advantage, though this may carry analysis and classification further than present needs warrant.

Until recently, the treatment of terrestrial reactions has been mostly qualitative in nature, but the increased emphasis upon soil conservation as a national measure has already placed the reaction of the plant cover upon soil in the forefront of investigation. In addition to such general studies as those of Darwin (1881) and Passarge (1904), a promising start in the direct attack upon the measurement of reaction in relation to competition and to succession has already been made (Sampson and Weyl, 1918; Lowdermilk, 1926, 1930, 1931, 1934; Formosov, 1928; Forsling, 1931; Greene and Reynard, 1932; Weaver and Harmon, 1935; Weaver and Noll, 1935; Kramer and Weaver, 1936; Kraebel, 1936). The most comprehensive attack upon this problem is that which is now being made at the several erosion stations of the Soil Conservation Service. Meanwhile, the increasing attention given to physical factors in the ocean is providing the necessary background for evaluating the reactions of the plankton in particular.

REACTIONS ON LAND

The reactions exhibited by terrestrial communities are logically divisible into the effects exerted upon the soil complex and those that modify aerial factors. In a comprehensive classification, these are further divided on the basis of organism or agent, life-form or life-habit process, effect, and degree. For the present purpose, however, it will suffice to pass reactions in review on the basis of the process chiefly concerned and to discuss the respective parts taken by plants and animals.

SOIL REACTIONS

Reactions upon the substratum may be arranged in three major categories, namely: (1) those that give rise to soil or a new layer of it, or contribute materials that will become soil ultimately; (2) those that protect the soil against erosion, trampling, etc.; and (3) those that change the texture, structure, or character of the soil in an appreciable degree. A new substratum may be produced by four different types of reaction: (1) by the accumulation of organic bodies themselves, regularly under conditions that retard or prevent decay, and usually also of excreta to some degree; (2) by the concretion of mineral matter into shell, marl, or rock as a consequence of physiologic activity; (3) by the weathering of rock into fine soil, chiefly through the excretion of acids; (4) by the resistance that organisms, especially plants, offer to wind and current, resulting in the deposition of particles in transport.

SOIL FORMATION

Reaction by Accumulation. As has been indicated, reaction by the accumulation of organic materials becomes possible only in the absence of processes that remove or rapidly decompose them. It is consequently at a minimum in open communities where wind and sun are constantly at work, but increases steadily with the height and density of organisms. Accumulation is naturally most pronounced in small water bodies without currents and, by comparison with the atmosphere, provided with a low content of oxygen for producing decomposition. The maximum effect is attained in peat mosses, which possess unique powers of thriving in pools with little oxygen and low *p*H, optimum conditions for accumulation. Somewhat similar conditions as to oxygen deficit occur in reed swamps, and these are likewise sites of rapid accumulation. Marshes are also built up by the accumulation of marl or of diatom shells, but these in addition are products of certain chemical activities of the organisms concerned.

Usually, plants and animals share in the formation of biogenous soils, plants commonly assuming the leading role on land. The chief exception is that of deposits of guano, which are not only relatively rare but are likewise to be regarded only as potential soils. In the initial stages of the hydrosere, the bodies of minute animals and excrement may play a large or even predominant part, as in the case of coprogenous deposits. Such sediments are more characteristic of large ponds and lakes; they have been extensively studied and classified by Swedish investigators in particular (cf. v. Post, 1862; Lomas, 1905; Naumann, 1922; Lundquist, 1927).

A number of general studies have been made of the excreta of animals in terms of accumulation and their gross relation to the soil, such as the guano deposits of Laysan Island where approximately a million birds nest in two square miles of territory (Dill and Bryant, 1911). Errington (1930) has made a considerable study of the pellet contents of raptors, which accumulate in some degree about nests and in rookeries, while Kellogg (cf. Stoddard, 1931:209) has analyzed more than a thousand regurgitated pellets of the marsh hawk from a "roost" in Florida. Dearborn (1932) has described the diversified nature of mammal droppings, through which materials of slow decomposition, such as hair, feathers, and bones, are also added to the soil mass.

This contribution of animal matter, a large part of which is available more or less readily, has for the most part been ignored by students of soil fertility, probably because their attention has been focused on field soils where animal life is much reduced. Recently, Greene and Reynard (1932) have made a quantitative examination of this question on a grazing range, with especial reference to the kangaroo rat and the wood rat (Fig. 15). Both these rodents defecate more or less throughout their tunnels, thus leading to an increase in soluble salts, particularly the bicarbonates and nitrates of calcium and magnesium, as well as chlorides from urine. The carbon dioxide of respiration was thought to be the probable cause of the increase of calcium bicarbonate, as a result of the conversion of carbonate, and it was also suggested that this gas increases the availability of phosphorus in the soil. The most outstanding effect was that upon soluble nitrates, which rose from a probable maximum of 15 parts per million for desert soils to 221 and 570 parts per million in two different burrows, making a total of 3.65 and 10.26 pounds, respectively.

The contribution to the soil by animal chitinous bodies and calcareous and bony skeletons, though small by comparison with that of plants, is still a matter of significance. This is a field in which quantitative determinations are practically unknown, and the annual turnover as a whole or for any particular group must be left to conjecture at present. The question is also complicated by the coactions of scavengers and sapronts of all sorts, as a consequence of which the return is indirect or delayed. The effect of any particular species is chiefly a resultant of size and number, and hence it is possible that invertebrates may often play a larger part than birds or mammals. The approximate number of invertebrates per square meter at the time of the midsummer maximum has been estimated at 3,300 by McAtee

(1907), or about 1 to each 3 square centimeters. Since many species produce several generations in a year and others do not appear in the summer aspect at all, the total number annually must be much larger, probably reaching 1 or 2 per square centimeter.

It seems probable that the contribution made by excreta is more evenly distributed in general than the bodies of animals, though just as little is known of its amount, apart from guano and similar deposits. A large ungulate will distribute a considerable amount of excrement in the course of a lifetime, as the "buffalo chips" of the Great Plains demonstrate, but the absence of accumulation renders this much less conspicuous than in the rookeries of birds, bats, etc. Concentration also occurs in respect to many rodents, especially in relation to sanitation, and the intensity of the reaction can be estimated from pellet

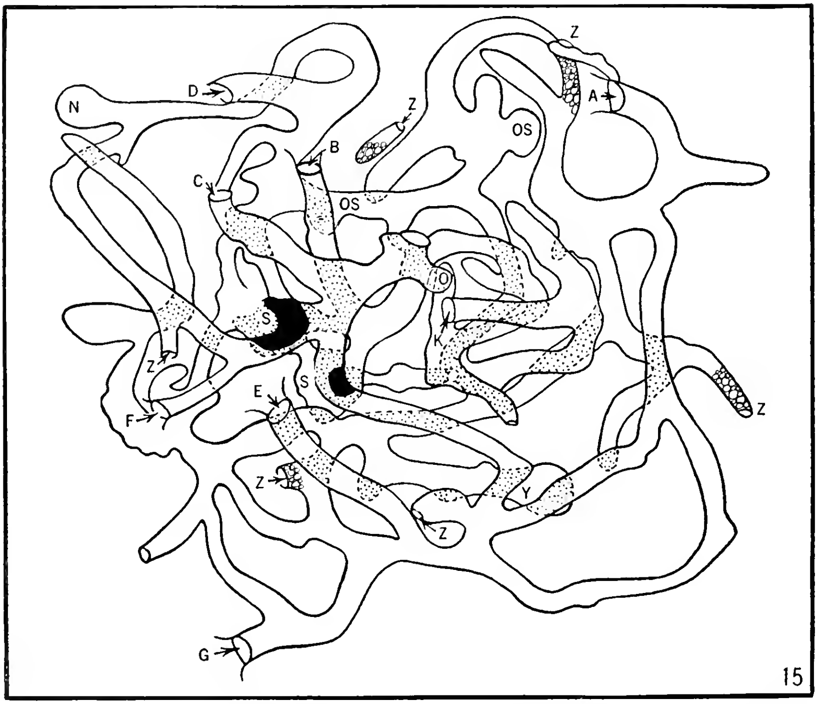


FIG. 15.—Diagram of a typical den of the banner-tailed kangaroo rat (*Dipodomys spectabilis* Mer.). Double shading indicates where one portion of tunnel lies above another and solid black a three-story arrangement; *A*, *B*, *C*, etc., active openings to surface; *N*, nest chamber; *S*, storage; *OS*, old storage; *Y*, probably an old nest chamber; *Z*, old, unused, or partially plugged openings. (After Vorhies and Taylor, 1922.)

counts made to determine relative numbers of individuals (Taylor, 1930, *b*). Even small forms such as insects are not without importance in this connection, since caterpillars are known to add several times their own weight of pellets consisting of partially digested plant material (Jacot, 1936, *a*, *b*).

Reaction by Accumulating Shells and Concretions. The shells of animals, whether chitinous or calcareous, regularly play a minor part in this process on land, though quantitative studies may assign them a greater importance than recognizable at present. The sole group of plants with a similar reaction is the diatoms, though their effect is relatively insignificant today in comparison with the geological past. The production of diatomaceous soil on a small scale may be observed along the margin of many pools and small streams, but marshes of this type are rare. The most extensive and best known are found in Yellowstone Park, where the hot waters have apparently promoted the growth of diatoms, and the consequent accumulation has produced a hydrosere, ending in characteristic meadows.

Apart from shells, the concretions due to direct physiological activity are limited to aquatic plants found in shallow waters. The resulting substrata may be calcareous, represented by marl, tufa, and travertine, or siliceous, as in sinter and geyserite. By far the most widespread of these deposits is marl; it is produced chiefly by Chara and occurs more or less regularly as a layer of variable thickness in fresh-water marshes. It is frequently mixed with terrigenous material and contains small amounts of organic matter from the decaying shoots of the stonewort. Somewhat similar incrustations are produced by a few mosses, while the massive forms known as travertine are the work of microscopic algae, as oölite may be likewise. Sinter and geyserite are also secreted by blue-green and yellow-green algae, but are restricted to the cones and basins of hot springs and geysers, and are consequently of slight importance.

Reaction through Weathering. The conversion of rock into soil, in the usual sense, is the combined effect of mechanical forces and plant and animal activities. The former take the more conspicuous if not the more important part, but the production of fine particles is chiefly the work of the organisms. In the case of woody plants, the growth of roots in thickness is an important factor in mechanical weathering, but the paramount reaction is exerted by root secretions, primarily carbon dioxide in solution. Animals apparently have only a small and indirect part in weathering, and then only after cracks have appeared which they can occupy.

The corrosion of rock by plant roots is the most significant process in the production of fine soil, especially when this accumulates in one particular place. This is a property of all plants from unicellular algae to the largest trees, but its importance depends largely upon the size and extent of the root system. The initial conversion of rock into soil is carried on by the pioneer lichens and their successors, the mosses, in which the hairlike rhizoids assume the role of roots in breaking down the surface into a fine dust. This process is exceedingly slow in granites and lavas, but proceeds more rapidly with sandstones and limestones. It is promoted by the action of frost, as well as wind and water, in forming tiny cracks into which the corroded dust is washed and ants and other animals find space and small herbs may invade. By virtue of their root systems, these carry on the process of weathering more effectually, each successive stage in the xerosere taking a larger part in the process. At the same time, the decay and excrement of each generation add organic matter until a more or less uniform soil is constituted.

Reaction upon Wind-borne Material. The major reaction of the plant body upon wind is to lessen its velocity and thus bring about the dropping of its burden of sand or dust. A minor effect results from its constituting a definite obstacle to the movement of particles, a fact often recorded in the abrasion of stems or the etching of trunks. In addition, the plant serves as windbreak for the accumulation at its base and thus renders it difficult for the wind to pick up the grains again. The life form is of the first importance in this reaction, tall plants and especially those with single stems having little or no effect, while mat, bunch, and bush forms attain the greatest success. Roots and rhizomes exert a complementary reaction by binding the accumulating material, fibrous ones being naturally the most effective. Of even greater significance than form is the faculty of developing new shoots as the crown is buried, thus permitting plant and community to keep pace with the accretion of dune or ridge. The ability of grasses to produce tillers is peculiarly advantageous in this process and hence the grass form is probably the best adapted to dune formation and stabilization.

The action of shoots upon wind-borne snow is essentially identical, but the accumulation is transient, and the reaction is primarily upon the water content of the soil.

Reaction upon Water-borne Detritus. The mechanical action of plants upon currents of water is essentially similar to that already noted for air currents. Movement is impeded, and the load is deposited in whole or in part. Stems and leaves also make difficult the removal of material once dropped, and root stocks and roots take their share in this process. This reaction is often associated with the deposition of sand and silt by the retardation of currents as they enter pond or lake, but the effect of plants is regularly predominant in such deltalike areas. The resultant filling has much of the consequence already indicated for the accumulation of the plant remains, and the two processes usually cooperate to build up the level. However, the movement of water is progressively hindered as the level rises, until the area is overflowed only at times of flood. This sets a limit to the deposition of sediments, and the further reaction is chiefly one of decreasing water content due to the fall of plant parts, to transpiration, etc.

The role of plants in impeding runoff and preventing erosion is even more striking and important, though the action itself resembles in some respects that of a shallow stream. In fact, it is the formation of rills and gullies that renders erosion so effective. A good cover of vegetation operates, in the first place, to prevent the direct impact of raindrops on the soil, but much more important is its action in holding back the fallen rain until it can be absorbed. It further restrains both rills and sheet floods, reducing the momentum as well as the surface affected and consequently minimizing both load and erosive power. In the case of wind, the decrease in velocity through the action of cover is the major factor in reducing erosion. Frequently, especially in arid regions, water and wind act together, producing a landscape of hummocks, which are the result of alternating erosion and accretion.

The organization of the Soil Conservation Service and the nationwide installation of projects in soil conservation and flood prevention have served to draw attention to the plant cover as the paramount factor in protection and control. As a consequence, the reactions of cover, both natural and cultural, have come to be regarded as of the utmost significance to economic and social progress, not merely in terms of agriculture, grazing and forestry, but also to urban populations. No field of conservation research equals this in importance or has been more neglected until recently, and the next decade is bound to see an enormous expansion of knowledge in it, together with almost unlimited application to human affairs.

Reaction upon Slipping and Sliding. The reaction of a plant cover on the soil of slopes may be exerted upon the mass as well as upon the surface. This is particularly true of loosely aggregated materials, as in talus, steep slopes of gravel, sand, snow, and so forth, and it applies likewise to the faces of cuts and fills in the grades of highways and roadways. In the case of sand, volcanic ash, or gravel, the effect is produced by the underground parts, primarily the roots, while that upon snow is due to stem and branches, and to leaves also in the case of conifers. The process known as "slumping" involves, in addition, the saturation of the soil mass so that it flows, producing lava-like streams of mud under extreme conditions. Slumps occur with increasing frequency as highway cuts become deeper with more abrupt sides, and their prevention by means of plant reactions has become a matter of much practical importance from the standpoint of both safety and economy of maintenance.

The species best adapted to retaining the soil on slopes are mats or rosettes with tap roots, or long branching ones which anchor the plant firmly, their greatest extension often being uphill, and the cluster of stems or horizontally appressed leaves prevents the slipping of the surface materials. Each plant or colony exerts a stabilizing effect for some distance below its own area, partly by intercepting small slides above it. The primary reaction is a mechanical one, leading to increasing aggregation and finally to invasion. Where rain or snow is a factor, as in slumping, the grass or bush forms possess additional advantages, particularly in utilizing artificial succession to hold the slopes.

Soil Structure

The reactions that build soils regularly continue to act to bring about modification in them to a larger or smaller degree. The structure of a soil may be changed mechanically by superficial accumulation or by the inclusion of plant and animal remains, by the penetration of roots, and by the disturbances wrought by animals. With these go a number of chemical changes, often of fundamental importance. In addition, plants react upon the soil profile in such a manner as to protect it against the action of modifying forces, such as weathering and erosion by water and wind. The soil is thus a complex of reactions, in which the role and significance of each process can be definitely ascertained only by thorough-going analysis and measurement. This applies particularly to the respective parts taken by plants and animals, though it is obvious that the major effect of animals will be exerted through various kinds of disturbance.

Reaction by Adding Organic Matter. The most important changes in the structure and texture of the soil are caused by the addition of organic matter or humus. This is derived chiefly from the decay of plant parts, though animal remains usually play some part in it, and its working-over and incorporation are due primarily to animals, everywhere the smaller soil organisms and in dry region the rodents also. All plants contribute to the humus in some measure by the death of the entire organism, annually or from time to time, by the annual falling of leaves and the shoots of perennial herbs, and by the exfoliation and decay of roots and underground stems. The amount produced depends upon the density and size of the population and upon the rate and completeness of decomposition. It is small in the pioneer stages of a sere, especially in xeric situations, and increases steadily to reach a maximum in or before the climax. Whatever the contribution made by animals, this is probably greatest in the subclimax or a late seral stage.

The admixture of organic matter not only permits the renewed utilization of the nutrients absorbed by previous generations, but it also produces highly important physical effects, especially upon the water content or holard. At first thought it appears a contradiction that humus should have opposite effects upon sand and clay and yet improve the water relations of both. This is explained by its cementing action, as a consequence of which it makes one more retentive of water and the other more porous. In general, this tends to increase the water content of dry areas and to decrease that of moist soils, though the decrease is to be ascribed in large measure to raising the level. On the other hand, the non-available water or echard of sand is diminished relatively, while that of loam and clay is augmented. Furthermore, penetration by roots, especially fibrous ones, and the activity of burrowing animals, loosen hard soils and increase absorption, and conversely tend to compact sand and raise the water content correspondingly (cf. Romell, 1921–1935).

Reaction by Disturbing the Soil. Practically all the reactions of this group are caused by the activities of animals, negligible exceptions being furnished chiefly by the growth of underground plant parts. The number of genera and species concerned is very large, representing every major terrestrial group. Man naturally stands preeminent in the variety and magnitude of his effects, mammals generally being much more important than all other groups combined, with the possible exception of ants and earthworms. As to the activities or processes involved, digging of all sorts, with the attendant transfer of material, is paramount, trampling, pawing, wallowing, etc., being of quite secondary importance. In a large number of cases, the reaction itself is not a direct object of the activity, but an outcome of a purposeful coaction, as in the rooting of swine. Moreover, the reaction may be superficial or deep seated, temporary, recurrent, or permanent, and in its effect significant or immaterial. As in the case of plants these consequences depend largely upon the degree of aggregation, a community of ants often producing a much greater effect than a single large mammal.

In the brief outline that follows, the divisions are based upon activity and effect, the subdivisions being made in general correspondence with similarity in life form, size, or behavior. The multiform effects exerted by man are reserved for treatment at the end of the section on land reactions.

Digging and Burrowing. Digging may produce hollows, holes, or galleries, or a more or less complicated system of tunnels and chambers to form a burrow or den. These may serve for nests, shelter and housing, for storage, sanitation, or for various other purposes. The dirt freed may be merely thrown out for a short distance, it may be utilized for diking, or may be carried to some distance to be deposited; some of it may be compacted into plugs for sealing abandoned burrows and entrances as is done by some pocket gophers. Its transport may lead to the formation of paths with the compacting of particles, and its piling, systematic or otherwise, amounts in effect to primitive cultivation, while both processes produce coaction effects in destroying plant cover and the latter by stimulating it also. In general, the consequence brought about by a single individual or family is slight (see Fig. 15, page 74), with the exception of such large mounds as those of kangaroo rats, and hence digging coactions are most significant where aggregation becomes pronounced, as in the so-called towns.

By far the most important burrowers are the rodents belonging to the fossorial life habit or mune. While some members of the carnivores, such as badgers, skunks, and even some wild dogs, do dig holes, they are usually scattered and the importance correspondingly less. In the absence of quantitative studies of burrowing reactions, it is impossible to do more than compare different genera on the basis of size and activity, degree of aggregation, and general effect. Perhaps the most widely important in North America are the pocket gophers, followed more or less closely by marmots and prairie dogs (Fig. 16), ground squirrels, kangaroo rats (Vorhies and Taylor, 1922), rats and mice generally being of much less consequence. Some of these may burrow to a depth of fifteen to twenty feet, translocating a prodigious amount of earth for a relatively small animal, while others, penetrating but a foot or two into the soil, may construct mounds several yards across and two or more feet high, or may group small mounds so closely as to cover more than half the surface. In constructing a system of tunnels, the kangaroo rat is probably the most skillful; the viscacha of South America develops a unique set of surface trenches a foot or more in depth for conveying loose dirt (Hudson, 1892:294).

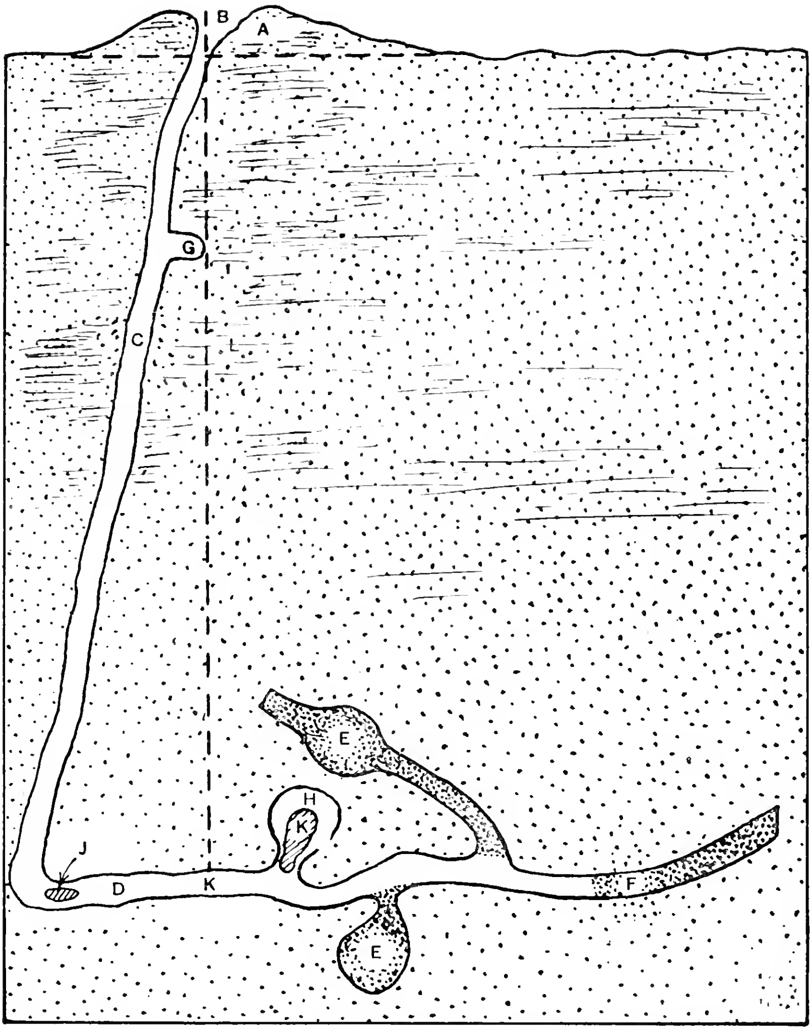


FIG. 16.—A vertical section of a prairie-dog burrow (*Cynomys ludovicianus* Ord.) showing the bringing of soil from a depth of nearly 5 meters. *A*, mound; *B*, funnel-shaped entrance to burrow; *C*, main passage 4½ inches (11.4 centimeters) in diameter, about 15 feet (4.6 meters) in length; *D*, horizontal passage 9½ feet (2.9 meters) in length; *E*, unused nests filled with earth and refuse; *F*, unused part of horizontal passage filled with earth, etc. 4 feet (1.2 meters) long; *G*, niche large enough for one prairie dog; *H*, nest of grass 11 inches (28 centimeters) in diameter by 9 inches (22.8 centimeters) high; *J*, absorbent matter carrying bisulphide of carbon; *K*, position of prairie dogs as found after use of bisulphide of carbon; *L*, depth of horizontal passage 14 feet 7 inches. (After Merriam, 1901.)

The number of general studies of burrowing coactions is of course legion, and one of the major tasks of bio-ecology is to convert these into quantitative terms, as is suggested by some of the more recent researches in this field (Vorhies and Taylor, 1922; Grinnell, 1923, 1933; Formosov, 1928; Greene and Reynard, 1932; Greene and Murphy, 1932).

Among the birds, reptiles, and amphibians there are few true burrowers, the so-called burrowing owl being often a tenant rather than a builder, and the list comprises chiefly kingfishers, certain swallows, the gopher tortoises, and a few true toads. The burrowing reaction is much more common among insects and spiders, often for shelter or hunting, but, among the former, especially for the deposition of eggs. Notable examples are the gryllids, particularly the mole crickets, locustids or acridids among the Orthoptera, tiger beetles, carabids, and dung beetles in Coleoptera, many termites, and digger wasps and ants among Hymenoptera. The burrowing spiders are chiefly lycosids, mygalids, and agelenids, containing the true and false tarantulas, and the trapdoor forms, while of the Crustacea the only considerable burrower on land seems to be crayfish. In nearly all the above examples, while burrowing plays an important part in life history and coaction, significance as a reaction upon the habitat is as yet unmeasured, some termites constituting perhaps the most conspicuous exception.

Probably the disturbance reaction of greatest total significance is that of ants and of earthworms in view of their great number, dense aggregation, and widespread occurrence. The large earth-moving worms are restricted to moist areas, but ants are important throughout the globe. Perhaps no other small animal exerts such a variety of influence as these small insects, though unfortunately there have been few or no quantitative studies of the effect of this group. Only the reactions of the mound builders are strikingly evident. Soil is usually brought from a depth of six to eight feet (Fig. 17). Their hills and cleared circles are a conspicuous feature of grassland and desert, where they are sometimes an aftermath of disturbance by cattle or rodents.

Part of the earthworm reactions are direct; others accompany or follow food coactions. As to the earthworm burrows, Darwin states that these are built in two ways, either by using the pharynx as a wedge to push the dirt away on all sides, or by actually swallowing the soil and ejecting it as castings. The one is accomplished in a short time in loose soils; the other may require a day or more in compact ones. At first the castings are deposited directly on the surface, but as the pit deepens the excreted soil is transported and frequently built into towers often several inches high by the larger forms; castings are also piled in subterranean chambers or cracks. Two minor reactions of interest have to do with the piling of tiny pebbles about the mouth of the burrow and with their use as gizzard stones. Finally, important results spring from the two chief food coactions, namely, the consumption of plant parts and animal material and the utilization of organic matter in rich soils (cf. Jacot, 1936, *a* and *b*).

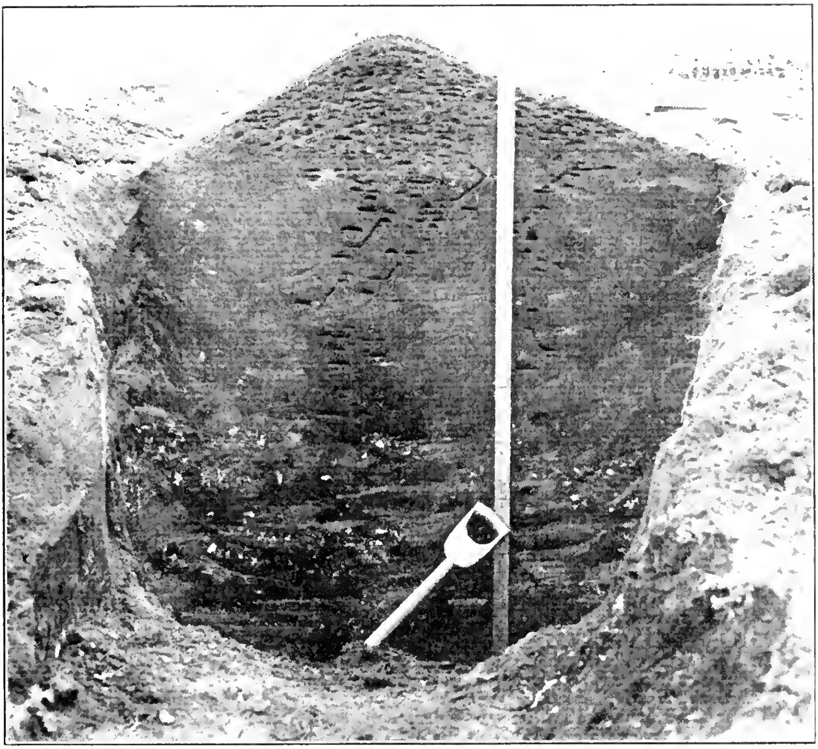


FIG. 17.—A vertical section of a harvester-ant nest (*Pogonomyrmex occidentalis* Cres.) in western Kansas. It is nearly 6 feet (2 meters) from the top of the mound to the bottom of the excavation. (Photo by Prof. G. A. Dean.)

It is manifest that earthworms are in essence cultivators of the soil of moist regions, increasing its fertility, rendering it more uniform in texture, and improving its water relations. They also deepen the fertile dark horizon, especially when the penetration is several feet, and frequently tend to counteract acidity by bringing up considerable amounts of lime from the zone of concentration. This process may be one of compensation for the acidity of decaying plant material as well as for the acid casts, especially in view of the presence of calciferous glands in these organisms. The large amount of carbon dioxide given off in respiration must increase the acid reaction, both with respect to the solution of minerals necessary for plants and the necessity for neutralization. Salisbury, who has studied these relations (1924), finds that earthworms are most numerous in soils approximately neutral, decreasing in the direction of both acidity and alkalinity; they bring materials up from considerable depths, and the general effect is to modify the horizon and diminish its organic content by mixing coarser material with it. As with ants, coaction is often combined with reaction, and this is especially true of harvester ants (Fig. 17, see page 83).

In distribution, earthworms embrace practically all rainy portions of the globe, from Iceland on the north through temperate and tropical zones to Kerguelen in the south, and upward to the alpine climax of lofty mountains. In size, earthworms range from less than a foot in temperate regions to a maximum of six feet in tropical and austral ones, with a girth to correspond. As to number and density, Darwin (1881:158) quotes Hensen to the effect that counts in a measured space indicate a total of more than 50,000 worms to the acre in garden soil and about half this number in fields. Their numbers are, however, greatest in rich cultivated soil, artificial meadows, and rich floodplain silt. Their numbers in original communities are relatively small. In moist tropical areas these characteristics of earthworms may also be reinforced by that of size, some species attaining lengths of three to six feet, with corresponding relations to soil profile and the amount of earth moved.

Surface Disturbances. A host of animal reactions are exerted only on the surface of the soil, or at most in the upper few inches. Obviously, no exact line can be drawn between these and holes or burrows, since digging in some form is regularly involved. However, reactions of this group may be characterized as those in which the surface alone is affected, or in which breadth is increased at the expense of depth, the depth usually being insignificant by comparison with the size of the animal concerned. Such effects, though often of much interest in connection with behavior, are rarely of significance in the habitat, apart from the coaction upon vegetation. This is likewise true of trampling, which, as a disturbance, belongs under compacting, in the next section (Fig. 18).

The more important reactions upon the surface are caused by rooting, pawing, and trampling, chiefly by mammals. Rooting is characteristic of swine and their relatives, and produces the maximum local disturbance of this type. Pawing resembles it closely in effect when roots and bulbs are dug out of the soil by this method, but as a rule the effect of pawing is merged in the greater reaction due to trampling. Trampling acts primarily by destroying the plant cover and working the remains into the loosened soil, improving the penetration of rainfall, and perhaps hastening the incorporation of organic material. On the other hand, the damage done to the plant matrix directly and as a consequence of increased erosion by water and wind far overbalances any beneficial action. The formation of blowouts in sandhills is a frequent outcome of the trampling reaction, particularly about watering places.

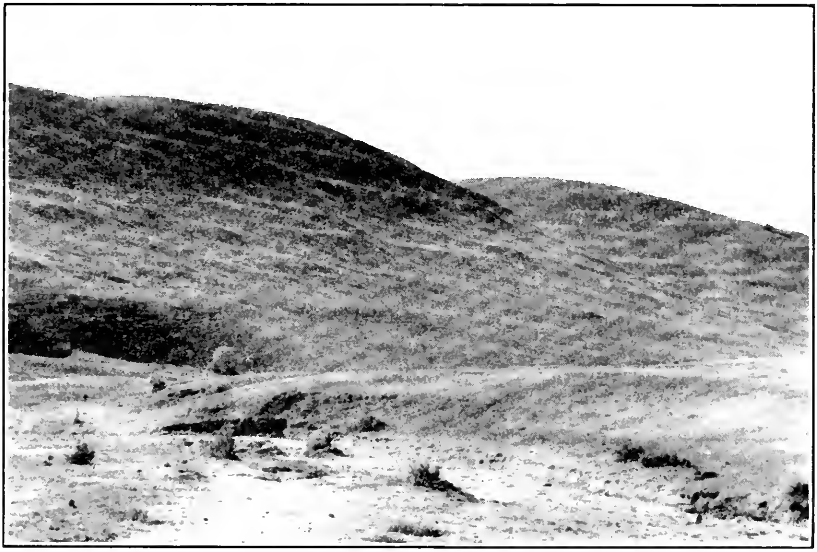


Fig. 18.—Terraces produced by ground squirrels, upper San Joaquin Valley. (Photo by Edith Clements.)

Somewhat akin to pawing and rooting are the scratching and pecking of most ground birds and some perchers, utilized for the finding of food or gravel, for "dusting," making hollows for nests or "forms," and so forth. Aside from gallinaceous birds, those that nest on the ground away from water are relatively few, the lark bunting being an example. Surface disturbance is also a reaction in the case of reptiles. The effects of all such habits are of much the same nature as those of burrowing, the uppermost layer of the soil being modified in structure, water and air content, and organic matter in many cases, but to a much smaller or often imperceptible degree.

Related to the surface as a source of material are the nest-building activities of some birds, e.g., swallows and phoebes, and of a large number of "mud daubers" and masons among Hymenoptera especially. Here the amount of mud or pebbles removed and the consequent reaction are inconsiderable, but when turrets are built, as by Anthophora and others, the effect is often striking.

Reaction by Compacting or Cementing Particles. While roots exert a binding action upon coarse soils and hence compact them in some degree, this consequence is much more characteristic of the activities of animals. It is especially typical of the cursorial life habit, but is also exhibited by fossorial species that make more or less definite runways. The activity regularly concerned is trampling to such an extent that the plant cover is largely or entirely destroyed and the impact is then received directly by the soil surface, the resulting trail often being converted into a gully by erosion. However, it is obvious that compacting results in fine soils only in correspondence with the amount of colloidal material present. In sand, the effect is the same as that produced by trampling, owing to the lack of cohesion between the grains. Other animal activities quite different in nature produce much the same reaction as trampling, for example, rolling, bedding, and wallowing, best illustrated by the "buffalo wallows" of the Great Plains. However, all compacting reactions are narrowly circumscribed, and they are much more striking than important.

The property that humus possesses of acting as a weak cement and thus binding together particles of soil has already been noted (Hall, 1908:47). It operates in practically all soils, but its consequences are most pronounced at the two extremes, sand and clay. Humus is also thought to be concerned in the formation of "ortstein" in heath sand, its soluble fraction combining with mineral salts to produce an impervious stratum. A somewhat similar result is to be found in grassland climaxes, especially in semi-arid or arid regions, where the penetration of water is restricted to the depth attained by the roots. The immediate consequence is that the dry soil beneath becomes compacted into a "hardpan," but this is usually secondary to the striking effect produced by the accumulation of minerals at this level, leading to the cementing of the particles into an impure limestone. In its turn, the hardpan limits the downward growth of roots under normal rainfall, but in times of excess it may be sufficiently softened and dissolved to permit the passage of roots and the reformation of the hard layer at a deeper level.

Soil Water, Solutes, and Gases

These three sets of factors are most intimately associated in the soil, and the modification of one leads to the change of others. This is truest of water content, since the amount of this determines in large measure the concentration of the soil solution, as well as the pore space available for air or other gases. Since water is the chief factor in plant as well as community response, it is more or less affected by nearly all reactions. In addition, the increase or decrease of the total water or holard may be a direct outcome of the activity of plants themselves, and this effect may operate upon the available water or chresard, as well as upon the total amount present.

Reaction by Increasing the Water Content. No flowering plants are known that increase water content as a direct reaction, though they may bring this about by the formation of dew and the condensation of fog. The sole plants to exert a direct effect are a few mosses, notably Sphagnum, and perhaps such algae as the ground forms of Nostoc. The power of the peat mosses to absorb and retain relatively enormous amounts of rain and dew is unique. Because of this property, Sphagnum is able to waterlog or flood small areas, with profound effects upon the course of succession and the accumulation of organic material.

All reactions that enhance absorption or hamper percolation or evaporation increase water content indirectly. Root systems are everywhere of paramount importance in promoting penetration of water into soils, this reaction being most significant in finer or "harder" types. The fibrous roots of grasses are the most effective in augmenting water content, but the deeper-seated ones of perennial forbs and woody plants operate especially in connection with percolation. Humus is likewise a major agent in fostering absorption, and its action is practically universal; even in the initial stages of the xerosere, its small but cumulative effect is decisive.

Much more obvious, but greatly restricted in extent, are the consequences arising from the disturbance of the soil by rodents in particular. Not only do the mounds of loose dirt affect the amount of water that enters and leaves the soil, but the openings and tunnels exert a further action, especially on slopes. It seems to be a common assumption that the reactions of burrowing rodents increase erosion by supplying loose material and in particular by the wearing of tunnels into gullies. However, constant search for evidence of the latter effect has disclosed but a few doubtful instances, while on the other hand there is considerable proof that tunnels and mounds have a beneficial action in promoting absorption (cf. Grinnell, 1923, 1933).

Reaction by Decreasing the Water Content. As a direct reaction, plants diminish the water content by absorption and transpiration. The transpiration of a deciduous forest during the summer may be greater than that from a free water surface, and it may be greater still from streamside trees, such as alder, poplar, and willow. Water loss also attains great proportions in the case of most herbaceous crops and amounts to a large total in true and mixed prairie, in spite of the more or less xeric nature of the grass dominants. Probably the highest transpiration in relation to surface is found in emersed water plants and especially those of reed swamps, all of which have permanently open stomata. The reaction is particularly significant in such seral areas, as it materially hastens the drying-out and successful movement set on foot by the shallowing action of plant remains.

Animals obviously reduce the water level and remove suspended matter in ponds and playas by drinking, but this is of slight importance except in arid regions, where it is usually secondary to drying by evaporation. They may likewise exert an indirect effect by packing the soil and increasing runoff, and this reaction is turned to advantage in the range country for the puddling of earthen reservoirs or "tanks" to insure the retention of impounded waters.

Reaction by Returning Plant Nutrients. This reaction is a recurring one incident upon the annual fall of leaves and the death and decomposition of plants or their parts. A portion of the nutrients may be returned by more or less immediate leaching, but the major part must be unlocked by the coactions that produce decay. The share which animals have in this is unknown. However, the significant fact is that in nature the material returned to the soil corresponds more or less closely to the amount withdrawn, and a fairly definite balance of nutrients is maintained. In crop communities, this balance is disturbed to the extent that the individuals are removed, a headed crop of grain contrasted strikingly, in this respect, with one of sugar beets.

A severe fire and particularly a complete burn permits the much more rapid incorporation of mineral salts in the soil. Under favoring rainfall, the bulk of these may be returned the first season, as is indicated by the exceptional growth made by annuals after a fire. An increase in nutrient content is likewise well known to result from the activity of legumes and other nitrifying organisms, but this is properly considered among coactions.

Reaction by Decreasing Plant Nutrients. A progressive or permanent reduction in soil nutrients, as a consequence of their utilization by plants, probably does not occur in nature. A temporary decrease may follow a season of luxuriant growth, such as is noted above after a burn or in consequence of exceptionally favorable climatic conditions. Even in the case of crops, the amount absorbed each year may be a very small part of the total present, so that cultivation for long periods may produce no appreciable deficiency (Hall, 1905).

The formation of heath sand probably furnishes an example of reduction in nutrient content as a consequence of the formation of acids by humus. These render the mineral nutrients soluble, and they are then removed by the percolating water, beginning at the top. A somewhat similar process takes place in sandy soils in regions of high rainfall, the leaching action of the rain apparently being promoted by the acids derived from partial decomposition.

Reaction upon Air Content. The amount of air in the soil is known to bear an inverse relation to the water content, decreasing as the latter rises, and the reverse. It increases markedly as a result of all animal activities that disturb and loosen the soil, and particularly so by reason of the fact that these are so often accompanied by tunneling. The loosening effect of plant roots and rhizomes also promotes the entrance of air in some measure.

The chief response of plants and of soil animals is to modify the composition of soil air. This involves the absorption of oxygen and the release of carbon dioxide. Since the density of the medium prevents ready exchange with the atmosphere above the soil, the air content is regularly lower in oxygen and higher in carbon dioxide than ordinary air. In soils neither wet nor packed, the reduction of oxygen as a consequence of the respiration of roots is rarely serious, though this is not at all true of waterlogged soils. On the other hand, carbon dioxide diffuses less readily through the pores of the soil and may accumulate to a harmful extent in the deeper layers of many compact soils, though the greatest quantity is to be found in wet soils.

Reaction by increasing the amount of soil oxygen is a property of a number of blue-green and yellow-green algae that grow in the upper layer of moist or wet ground, or even on the latter, but the effect is probably too limited to influence any but the minute organisms of the soil.

Reaction in Terms of Acids and Toxins. A voluminous literature has grown up around the moot questions of bog xerophytes, toxic exudates, and soil toxins, though the questions themselves have by this time been answered mostly in the negative. It has been shown that the effect of bog water can be largely explained on the basis of deficient aeration, and that the evidence for the secretion of toxic exudates by roots is slender, if not altogether wanting. Moreover, the presence of deleterious substances in soils is to be explained chiefly by deficient aeration and resulting anaerobic conditions, as has been emphasized elsewhere (Clements, 1921, *b*). Even animal excreta accumulate only exceptionally to the extent of becoming deleterious.

Reaction and the Soil Profile. The profile of a soil is characterized by the evident differences shown by a cross-section from the surface to country rock or other undifferentiated matrix. Normally, a soil profile consists of three horizons or layers, more or less clearly distinguished by texture, color, structure, and so forth. The uppermost or A horizon is marked by darker color and lighter texture, the middle or B horizon by relatively brighter color and heavier texture. The C horizon is usually set off by a color difference also, owing to the fact that it is the parent rock or sediment, little affected by weathering. In a large number of soils, both A and B exhibit a further but slighter differentiation into subhorizons, known as A_1 and A_2, B_1 and B_2.

In terms of reaction, these three layers show both quantitative and qualitative differences. As the uppermost, A is the level of major reaction, B of minor reaction, and C of little or no effect from the biotic community. The A horizon, as a result of direct contact with the plant cover, is influenced, in some degree, by nearly every one of the reactions described. However, the addition and incorporation of organic material are the characteristic features of it, evoking the chief distinctions between it and the B horizon. In the latter, the outstanding process is the concentration of fine particles and of mineral salts, often leading to the formation of hardpan. Because of its depth, horizon C is beyond the reach of practically all reactions, and hence it is not really a component of the soil in the strict sense. Thus, from the standpoint of reaction, A may well be termed the level of accumulation, B of concentration, and C of inaction. However, it is necessary to recognize that all three horizons regularly shade into one another, with respect both to processes and to visible criteria.

The soil profile further possesses certain important relations to air reactions and consequently to climate, indirectly as well as directly. In fact, from the ecological viewpoint, a soil may well be regarded as a mass of parent rock, more or less consolidated, in which the external portion has been differentiated by climate, biome, and topography. Of these, the influence of the plant matrix is most direct and immediate; that of climate is indirect through its control of climax and direct by virtue of rainfall and temperature in particular. Topography may exert the most striking effects in connection with erosion and deposition, but these are more local and to a large extent conditioned by vegetation. In view of these facts and especially the developmental correlation between climax and habitat (Clements, 1905:292; 1916:357), soils may properly be distinguished on the basis of climaxes, as has already been done to some extent in the recognition of forest and prairie, humid and arid categories. In addition, they may be subdivided with respect to climax and sere, the role of topography being especially important in connection with the latter.

AIR REACTIONS

From the very nature of the medium, the reactions of plants upon the air are usually less definite and controlling than upon the soil. Naturally, the chief reason for this lies in the fact that effects are not readily accumulated in a gaseous medium. However, a notable exception exists in respect to light, in which the time element produces results not unlike those of accumulation. The absence of air reactions by animals is noteworthy, since the functions that produce their striking reactions in water are almost without effect on land.

Reaction upon Light. The leaves of plants react upon light by virtue of reflection and absorption, while the chief role of branches and trunks is interception. The obvious consequence is to reduce the intensity, especially of sunlight, and to produce varying degrees of shade. Since the absorption of leaves is selective, it has frequently been assumed that the quality of light is changed under forest canopies especially. It is now known that this takes place in a considerable degree only in dense forests and thickets, owing to the fact that in the great majority of cases the light beneath the crowns is derived from rays reflected by the leaves or passing between and not through them. The same principle holds true for the successive forest layers, the quantity being affected to the extreme point where the ground layer can consist only of mosses and fungi.

In the initial stage of the hydrosere, the reduction of light intensity by the water itself may be greatly augmented by the reaction of the plant community. This is most notable for floating leaves, such as those of pond lily and pondweed, but it may sometimes be as great for submerged species, for duckweeds, and, under optimal conditions, for microscopic algae of the plankton. The reaction of the dominants of reed swamps is often much more decisive than it appears, and this is true likewise of grassland, in spite of the more or less complete absence of a canopy. In ponds, the minute animals of the plankton exercise an effect when abundant, and this may likewise be true of larger forms under occasional circumstances. In the air itself, animal reaction upon light usually occurs as a secondary effect in the case of phytophagous insects, which destroy foliage, and of other organisms residing upon leaves.

Reaction upon Humidity, Temperature, and Wind. These three factors are intimately associated in a complex that determines the water relations of the community in the highest degree. The energy required to bring about transpiration and evaporation is supplied by incoming radiation, the capacity for taking up the moisture concerned is determined by humidity, and both are modified by the moving and cooling action of wind. The reaction upon all three is practically confined to the plant matrix, since that of animals is essentially negligible in spite of the fact that mammals in particular intercept radiation and wind, and give off moisture in the form of perspiration.

As with light, the reaction upon temperature is due to absorption and interception, together with more or less reflection, and this likewise increases in intensity from the upper to the lower layers of a community. Conversely, the plant cover, living or dead, may also serve as a blanket to retain the heat that has entered. The effect upon wind is even more obvious as a consequence of interception and correspondingly influences both temperature and humidity. Finally, humidity fluctuates directly with the transpiration, and to a less extent with evaporation from plant surfaces of the water condensed or intercepted by them. As the ultimate result, water loss is reduced and the holard relatively increased under a canopy, with characteristic effects upon the function and structure of shade plants.

Reaction upon Carbon Dioxide and Oxygen. Since plants absorb and emit both these gases and animals give off the one and take in the other, it is to be expected that the biotic community will exert some reaction upon the composition of the air. This is an important effect in both soil and water in which diffusion and air movement are much reduced. The mobility of the atmosphere, coupled with the rapidity of diffusion, prevents the accumulation of gases given off and at the same time readjusts the conditions arising from consumption. Hence, it is only where air movement and diffusion are hindered or the emission of carbon dioxide excessive that accumulation can occur. In nature, such requisites are found only in dense forests and thickets, where a tendency exists to increase the carbon dioxide just above the soil layer especially. This is not true of the oxygen content, since photosynthetic activity is weak in the lower layers, owing to deep shade, and also because this gas is replaced by the augmented carbon dioxide in some degree.

Reaction upon Climate. From the preceding account of air reactions, it is evident that plant communities exert definite effects upon climate, especially in terms of water relations. These find expression in the processes of precipitation, condensation, and interception, which are consequences of transpiration, cooling, and mechanical action, and hence most marked in the forest. The long debate over the effect of forestation on rainfall has led to a decision in favor of the affirmative, though the amount of increase is still a moot question to be decided only by organized experiments on a much larger scale. One of the basic problems to be settled is the relative transpiration of forest, scrub, grassland, and crops of various sorts. Thus, a possible exception to the rule that forest increases precipitation may be found in the replacement of xerophytic forest and scrub by grass and crops in Australia, which was followed by a rainfall increase of 3 per cent (Quayle, 1922). While the water loss of a deciduous forest is so great as to support the assumption of Brückner that 78 per cent of the precipitation over the continents is derived from this source, the evidence is still too general to warrant its acceptance as more than a plausible working hypothesis (cf. Brückner, 1905; Zon, 1913; cf. Brooks, 1928).

Reaction by condensation is partly mechanical and in part due to the lowering of temperature in some degree. It produces striking results in regions much subject to fog and fine mistlike rains, the increased precipitation often amounting to twofold or greater. Again the effect is most pronounced in forest and decreases with reduced height and spread in scrub and herbaceous vegetation. Dew belongs in the same general category, but it is much less significant (Marloth, 1903, 1905; Phillips, 1926).

Reaction by interception is wholly mechanical in nature and may be exerted by animals as well as plants, though to a much smaller degree. It is produced by all plants, but is of little import in open communities of forbs. It increases with size and density, reaching a maximum in forests, where it may amount to as much as 25 to 50 per cent of a particular rain, bearing an inverse relation to the intensity of the latter (de Forest, 1923; Phillips, 1926; Zon, 1929:24; Brooks, 1928).

Reactions Produced by Man. As a superdominant, man may exert all the reactions caused by animals and nearly all those due to plants, working more or less directly through his own activities. When his innumerable coactions enter the scene, he becomes also a superinfluent, with the reactions of plant and animal as well as of the entire community at his command. Hence, he is unsurpassed in the variety and intensity of his reactions, though many of these are local and intermittent by contrast with those of the climax. Moreover, his control is conscious and usually intentional, and thus may be extended in space, time, or degree at the behest of need or interest. This is as true of air as of soil reactions, and man has modified or evaded local climates by virtue of shelter, heating and cooling, as well as by a number of minor devices. His effect upon climate in the large has mostly been unintentional or unintelligent, or has dealt with compensation, as by the long-distance transport of water for irrigation or urban needs, or the drainage of large areas. However, he is on the threshold of a new era in which the mastery of fallen rain will become more or less complete and even lead to the increasing control of actual rainfall by virtue of great coactions within the plant matrix of the various biomes. This will be brought about by the expanding knowledge of climaxes and succession, by which the latter may be widely employed as a unique tool for regulating runoff and erosion.

The theme of man as a superdominant and superinfluent is far too vast even to be outlined in its major features as a part of the present treatment, but some of the chief reactions involved are briefly touched upon in the following chapter. (Cf. Sears, 1937.)

REACTION IN WATER

Obviously, the change from air and soil on land to water and soil leads to divergence in the manner of reaction, even though the general processes of adding, subtracting, or modifying are essentially similar. For the most part, the soil becomes merely a substratum for attachment and for the accumulation of detritus, with the loss of its properties as a storehouse of nutrients and gases. At the same time, the air is replaced by a denser and less elastic medium, which must combine in large measure the functions of both media on land. This necessitates a great reduction in the amount of all raw materials in solution, both gaseous and mineral, as compared with soil, for which the slower movement of water provides but slight compensation. Consequently, whereas reaction on land centers about water content, in water it is primarily concerned with the amount and distribution of solutes, and suspended matter, and with circulation.

Reactions in Fresh Water

The transition from land to water reactions is particularly gradual in ponds and lakes, though a similar gradation occurs in estuaries and false bays. The first three stages of the hydrosere are characterized by three types of vegetation, viz., (*a*) submerged, (*b*) floating, and (*c*) emergent. These stages of the hydrosere may be assigned with almost equal propriety to land or water, though developmentally they are an intrinsic part of land climaxes. Since this is largely an outcome of the shallowing effect of plant and animal matter, such accumulation has already been considered under land reactions. Reaction upon the medium belongs properly to the consideration of the water. The same is true of influences on the bottom in sluggish rivers and the larger lakes with silt (terrigenous) bottom. The small floating plants and animals are properly considered in relation to both bottom and the medium itself.

SMALL LAKES AND PONDS

Accumulation and Decomposition. In its general features, accumulation in shallow still water resembles that on land, marsh and swamp forming the connection between the two. However, there are several important differences, as is well known. One of these is that detritus is sometimes transported and deposited far beyond its place of origin, another that excrement plays a larger part in consolidation, and a third is the retarding of decomposition and the emphasis upon anaerobic processes. Furthermore, calcareous and chitinous skeletons may accumulate to the point of constituting a definite layer.

FIG. 19.—View in Little Barren (Mile 474, 760 kilometers from The Pas, Hudson Bay Railway), showing tundra vegetation over several feet of frozen sphagnum. (Photo by V. E. Shelford.)

The nature of the filling process is related to temperature and length of season and is different in different climates. Tundra may overlie deep sphagnum deposits resulting in part from failure of the dead plant bodies to decompose. An area of wet tundra is traversed by the Hudson Bay Railway, and the railway itself rests on frozen sphagnum extending to a depth of as much as 20 feet (6.4 meters) near the southern tundra edge and to 7 or 8 feet (2.3–2.6 meters) near Churchill. The difference in depth is related to topography; Fig. 19

shows the late stages in the filling of a depression, the Little Barren at mile 474 (Hudson Bay Railway). The filling of small lakes farther south, for example in the latitude of the Great Lakes of North America, is often accompanied by floating bogs, the deposition of marl, etc. (Transeau, 1905, p. 364, Fig. 4).

Still farther south where decomposition is more rapid, the plant contribution to bottom deposits is most important in the zones of floating and submerged angiosperms. Some of this material is carried out into deeper waters as coarse fragments and detritus. Where the bottom is suitable, much of this material is consumed by crayfish, mussels, worms, insect larvae, fishes, etc., and further modified for incorporation in the deposit. Dead animal bodies, and excrement especially, often accumulate at a relatively rapid rate. A considerable amount of material arises from the plankton. The phytoplankton and plant fragments quite regularly form a thin brown layer over depositing bottoms in summer, which afford residence for certain types of small organisms.

Such deposits have long been studied by Swedish investigators, who have distinguished them especially on the basis of the amount of coprogenous matter in them (von Post, 1862; Naumann, 1929; cf. Gams, 1921). Finally, the bottom is the chief site of decomposition, which is due to the coactions of micro-organisms, but in its turn exerts reactions upon the medium.

Reactions upon the Medium. These may operate upon light and heat, the color and transparency of the water, or much more significantly upon the materials dissolved in it. The penetration of solar energy may be modified by floating or submerged plants, such as Nymphaea, Lemna, and Potamogeton, by the plankton, or usually to a much less degree by the nekton. The first is a frequent result in shallow waters of temperate climates especially, but its importance relative to the aggregate surface of lakes is slight. The influence of plankton depends upon its abundance, being considerable at times of its maximum and of little effect at other periods. Both the quantity and quality of light are affected, the latter especially by the phytoplankton.

The paramount reactions upon the medium are the consequences of metabolism, in the course of which gases are exchanged and nutrients absorbed and returned, and of decomposition. The three processes concerned are photosynthesis, respiration, and decomposition, the last involving also the respiration of bacteria. The role of plants in absorbing carbon dioxide and releasing oxygen, and of all living organisms in taking up oxygen and emitting carbon dioxide, is too well understood to require comment. However, the ability of green plants to utilize the half-bound carbon dioxide of the bicarbonates is not so generally known, nor is the important consequence in modifying the ion concentration of the water. The detailed reactions are closely related to the times and layers in which the processes occur and especially to the annual cycle of the lake itself in terms of spring and autumn overturn, the relations of epilimnion and hypolimnion, etc. In general, the increase of oxygen and decrease of carbon dioxide pertain to the upper layer in which the phytoplankton is concentrated; the zone of oxygen deficit is usually near the bottom where decomposition is often limited by the access of this gas. When this occurs, anaerobic processes result, in some measure at least, and a variety of gases may be produced, such as methane and hydrogen sulphide (cf. Birge, 1903; Birge and Juday, 1911).

In general, reactions upon the mineral constituents have to do with their abstraction by plants and their return through decomposition. Related to this is the reciprocal conversion of carbonates and bicarbonates, especially of calcium and magnesium, the first change effected by the carbon dioxide released and the second by the demands of the phytoplankton when the free gas is low or absent. Plants alone react upon the medium by reducing the quantity of those minerals that provide essential constituents of the protoplasm, but the demands of different families and genera are not the same. Thus, among plants, only diatoms reduce the amount of silica materially; they also make heavy demands upon nitrates, according to Pearsall (1922:248), while the reaction of desmids upon the nitrates is much less. Animal reactions by removal are due chiefly to shelled forms which exert their major influence upon calcium carbonate. For the most part, these minerals are carried to the bottom in the bodies of certain dead organisms and are there again rendered available by the decomposition reactions of bacteria in particular. In this process, soluble organic compounds are also produced.

Streams

Reactions upon medium and bottom are much reduced in streams, by comparison with lakes, owing to the fact that the current renders accumulation difficult and at the same time brings in new materials. At the same time the producent phytoplankton is less developed as a rule, and the total quantity of reactors is correspondingly less. As a consequence, the significance of reactions in streams depends largely upon the current and its swiftness, sluggish and swift streams being quite dissimilar, though exhibiting various intergrades through mature rivers and "cutoff" lakes.

Apart from man, the beaver is the one animal that produces reactions in streams on a large scale, though the damming and flooding are an outcome of a coaction. At one time this was a widespread effect of much importance, favorable streams often being converted into a succession of ponds with adjacent swamps, but today the reaction is practically confined to remote regions.

Reactions in Swift Water. It is rare that either plants or animals produce reactions of any significance in rapid streams, though algae, aquatic mosses, and amphibious flowering plants may slacken or deflect the current locally. A number of fish bury their eggs in the loose gravel of moderately swift water, but with little or no significant effect. A characteristic minor reaction but likewise without important effect is the habit of larvae of caddis flies in binding together tiny pebbles and attaching the cases to the bottom. This may result in increasing the stable area to which other organisms may attach themselves, but it is quite transitory in nature.

Reactions in Sluggish Water. As reactors, both plants and animals are of more importance in sluggish streams, the former sometimes affecting the slow current materially and both having some slight effect at least upon the gases and solutes of the medium. Their reaction upon the bottom becomes significant only where the current slackens to the point of permitting accumulation, but even in such places, except in baselevel streams, floods continually recur to sweep away the effects. The movements of mussels and snails tend to mix organic matter with the earthy bottom, and the nest-building fishes bury similar materials in the outer rim of the concave nests. Bottom-feeding fishes tend to stir the bottom materials and increase turbidity (see Chapter 9). These are often numerous along the margins of mature rivers, sluggish creeks, and ponds. Crayfish also burrow in such bottoms, bringing up terrigenous material and burying organic matter and other detritus.

The reaction of animals which remove plants from the land and increase erosion is evidenced in streams and sometimes in lakes as increased turbidity. The clearing of the land and attendant increase in stream-borne silt has doubtless shifted the fish constituents of stream communities from the trout-bass type toward the buffalo-sucker type with attendant changes in the invertebrates.

REACTIONS IN THE SEA

Reactions in marine habitats closely resemble those of fresh water for the most part, but they are on a much larger scale, owing to the extent and age of the oceans. They also exhibit certain qualitative differences, due to the presence of halides in particular, and are much influenced by currents, tides, and upwelling. Accumulation of effects is regulated by the presence or absence of these to such a degree as to give further warrant to the grouping of marine reactions on the basis of tidal, benthic, and pelagic climaxes. Manifestly, these differ from one another more in degree than in kind of reaction, though each possesses one or more typical effects, such as deposit in the case of benthos. As dominants, the animals are the chief reactors of the ocean, plants assuming this role relatively rarely.

TIDAL AREAS

Belt between Mean High and Mean Low Tide. Rocky intertidal areas, and areas covered with coarse gravel or strewn with boulders, are occupied by definite communities, in which barnacles are the chief dominants, associated with sea mussels, sea anemones, and often brown and red seaweeds. These react by virtue of attachment and density, holding water on the rocky surfaces and thus reducing the danger of drying during periods of exposure to the sun.

Owing to the water-holding capacity of the bottom materials of sandy and muddy shores, the water withdrawal at low tide has a lesser effect than on rock. This is primarily influenced by the degree of water movement. Strands beaten by waves do not permit the accumulation of the typically small reactions, but in quiet backwaters, where mud and organic matter accumulate, fiddler crabs and various other invertebrates burrow in the substratum, or work it over in ways that differ little from reactions on soil; these communities represent succession to land. However, any area alternately exposed and submerged is of the nature of an ecotone between marine and terrestrial communities.

Littoral Benthic Belt. In protected mud-bottomed bays the processes are similar to those in lakes. However, on tide-swept rocky bottoms in the littoral belt (0–200 meters deep), great numbers of dominants occur in the form of large showy echinoderms, mollusks, coelenterates, and crustaceans. Relatively few of these are permanently attached to the rock bottom, and dredging and sampling show comparatively little skeletal material not belonging to living animals.

The general effect of such organisms is to roughen the surface of rocks and thus favor the attachment of Bryozoa, serpudids, barnacles, etc.

In the pockets that frequently occur in such areas, the tidal currents are retarded and the skeletons of animals may accumulate in considerable quantities. Shells of barnacles, sea urchins, snails, brachiopods, and bivalves frequently cover much of the surface and exist at considerable depth, in some places overlying layers of mud deposited earlier. Hence, the reaction of shelled animals is to produce a hard bottom suitable for the attachment of sessile forms on top of what was formerly mud or sand. In deeper pockets where the current is retarded still more, there occurs a deposition of organic matter derived from these animals, as well as from seaweeds. These are merely early stages of a process leading eventually to a hard bottom such as just indicated above.

The attached plants that characterize faciations within these communities are probably less important while in position than botanists have been inclined to assume. They do produce comparatively dense shade, but their effect upon the carbon dioxide and oxygen content of the water is minimized by the rapid motion of the medium. Shade is a much less important reaction in water than on land, and hence such plants modify the habitat little with respect to animals, and the communities are little influenced by them. Their chief effect is probably exerted when they break loose and settle in pockets where they decompose and add to the matter accumulated there. Furthermore, when tissues of these plants are broken into fine material, they contribute to the total of suspended organic matter, which is of great importance in connection with the marine climate in different areas.

PELAGIC AND DEEP BENTHIC AREAS

Reactions on the Medium. The plankton and nekton exercise a far-reaching control over the physical and chemical factors of the marine climates. One of the most striking effects of the swimming and floating organisms, reinforced by organic detritus and silt, is the obstruction of light rays in the lower layers of the ocean and in bays and inlets.

The reactions upon the gases dissolved in salt water are, in part, essentially the same as for fresh water. The resemblance extends to the decomposition of material on the bottom, excess of carbon dioxide, and deficiency of oxygen, etc. The occurrence of hydrogen sulphide under conditions of poor circulation and deficient oxygen is more characteristic of salt water. The results of the presence of quantities of this substance are several. Colloidal sulphur, which is the most toxic form, often occurs under certain hydroclimatic conditions and kills many of the existing aerobic bottom organisms. Hydrogen sulphide is also acted upon by a remarkable group of sulphur bacteria (Johnstone, 1928:147), and a portion of it, after reaching water containing dissolved oxygen, is transformed into sulphur dioxide. This finally becomes sulphurous acid, which often occurs in minute quantities below depths of about 50 meters.

Reaction also operates necessarily upon the mineral solutes, reducing them as a consequence of food making by chlorophyll-bearing organisms, and restoring them through the oxidation exercised by bacteria, especially the nitrifying ones. Calcium is utilized in large amounts by shelled animals, but the quantity present is constantly renewed by inflow from the land, so that its use is chiefly significant in connection with the reaction of deposit. The situation is quite different with respect to nitrates, phosphates, and silica, owing to the relatively small amounts present, and the reduction due to utilization is frequently the limiting factor, both as to species and abundance. Finally, the organic matter in solution in sea water is an outcome of the presence of living organisms, and a somewhat similar reaction may be the basis for the appearance of growth-stimulating substances in the sea (Johnstone, 1928:165).

Reaction on the Bottom in Deep Water. The most characteristic reaction upon the bottom of oceans is that of deposit, dead material being contributed by all the pelagic communities above and accumulating wherever currents are slight or lacking. Such deposits consist of organic detritus derived from most of the organisms of the sea and their excreta, with which may be mingled more or less terrigenous material, especially in the vicinity of coasts. The continental shelf and adjacent shallower waters are covered with terrigenous deposits of gravel, sand, and mud, but the greater part of the ocean floor is characterized by deposits chiefly of animal origin. From 2,000 to 5,000 meters, approximately, globigerina ooze is the most widely distributed; it consists of the calcareous shells of Foraminifera living in the pelagic climax, and accumulates at the rate of about 2 millimeters per year. Coral mud and sand occur in the neighborhood of coral reefs and islands, and pteropod ooze is often associated with them, though it develops also on oceanic ridges in warm seas. Radiolarian ooze is restricted to certain tropical waters; diatom ooze is confined to colder seas, both in the southern and northern hemisphere. The last two types, by contrast with the others, consist of siliceous rather than calcareous material (cf. Murray and Renard, 1891; Murray and Hjort, 1912).

In Danish waters, Petersen and Jensen (1911) have found that the surface layer of bottom deposits is 1–2 millimeters in thickness and exhibits a distinct brown color. Petersen made a study of the brown layer and stated that it was composed of fine particles loosely aggregated so that the surface was fluffy in texture. In addition to some inorganic particles, it contained the following: (1) shells of diatoms; (2) fragments of tissue of higher plants; (3) chitinous needles and bristles; (4) a few living organisms, comprising bacteria, diatoms, and animals.

The part played by excreta in bottom deposits is not definitely known, but it is probably very considerable and may warrant the frequent statement that such layers have repeatedly been passed through the alimentary canal of animals living at the bottom. Moore (1931, *a*, *b*) has studied the muds of the Clyde and found that as much as 40 per cent of the fine material was consolidated into fecal masses or pellets, though in extreme instances the mud was formed entirely of these. He estimated that these deposits were accumulating at about the rate of a half centimeter a year and that the pellets themselves might persist for a hundred years. The upper 5 centimeters of mud represented the deposit of ten years and was very loose, with a high water content and a complete deficit of oxygen at the surface, while nitrogen and phosphorus decreased with depth. As to their origin, the pellets were derived largely from worms, lamellibranchs, and other bottom forms, though those of the plankton also played an important part, especially of Calanus and several species of euphausids.

CHAPTER 4

COACTION: THE INTERRELATIONS OF ORGANISMS

Nature and Significance. As has been indicated in Chapter 2, all the activities of the biotic community may be summed up in the action of the habitat upon the organisms, the reaction of these upon the physical factors, and the coaction of the organisms upon each other. In a general sense, the word interaction has been applied to some of these (Forbes, 1880, *a*), but the need for exact analysis renders the use of reaction and coaction all but indispensable (cf. Clements, 1916, 1926). The latter is made peculiarly necessary by the concept of the biome and the consequent dropping of the term biotic factor. The word coaction is especially fitted to designate the enormous range of interactions among plants, plants and animals, and animals alone, since it involves not only the idea of acting together, but also that of urging or compelling.

Although the three processes of response, reaction, and coaction are usually sharply delimited, the last two in particular are often closely associated and hence may seem confused. Such a food coaction as that of the mole brings about reaction through disturbance, and this may modify the plant matrix, which is usually not directly concerned in the coaction. Similarly, the reactions of a prairie dog in digging its burrow may destroy, stimulate, or change the plant cover, quite apart from its consumption as food. The material-shelter coaction of the beaver involves a minor reaction in the use of mud, a major one when canals are dug to transport logs, and a combination of coaction and reaction in the destruction of vegetation and modification of the habitat as the consequences of flooding.

It has previously been pointed out that the control exerted by land plants is primarily a matter of reaction and related competition, leading to various degrees of dominance and subordination, and that animals enact a somewhat similar role in river, lake, and ocean. By contrast, terrestrial animals usually exert their major effects through coaction, with the resulting gradations in influence. In consequence, it is coaction that constitutes the chief bond in the biotic community, both on land and in water, but on land especially, while reaction is the characteristic process in the plant matrix. Thus, in the study of the biotic community as distinguished from that of separate plant or animal communities, coaction is commonly a paramount theme, though it is regularly to be considered in proper relation to other community functions.

BASES OF COACTION

Organisms. In its simplest form, each coaction comprises the reciprocal behavior of two individuals of the same or different species; the more complex coactions involve the interaction of one group or community with another. These may consist of plants or animals alone, or more rarely of both acting together. In the main, the general nature of each particular coaction is determined by the life form and life habit of the species concerned. The specific quality of this relation is usually derived from behaviors common to families, or genera of animals; this is frequently true of plants also, but only when life form and taxonomic form are in accord.

It is the exception that the organisms concerned in a coaction play equal or similar roles, though this may frequently be true of social interrelations. As between animals and plants especially, the former are largely active, the latter passive. The difference is usually one of motility, though not necessarily so, unless to this is assigned the movement of food-gathering cilia, tentacles, etc. The distinction is primarily one of initiative, the herbivore, for example, being the agent that acts upon the plant matrix or some portion of it. This essential relation is maintained even by plant parasites upon animals, in spite of striking disparity in size and motility.

With further use of the term coaction, it may prove desirable to distinguish between the two roles and to designate the initiating or directing organism as the *coactor* and the receiving one as the *coactee.* In the large majority of coactions, especially on land, animals take the one part and plants the other, but the behavior is sometimes reversed.

In many social and symbiotic relations, the coactive organisms may exhibit more or less parity in behavior, or at least in values received. Such is the situation in a flock or herd where the members are of the same species, and it obtains likewise in certain mixed herds of mammals. Much more striking instances are to be found in the symbiosis of microscopic algae with such animals as Stentor or Hydra, or such plants as Cycas, of bacteria with legumes, and fungi with the roots of orchids, as well as many trees. These are all mutually beneficial, but the transition to pure parasitism is so gradual that no definite line can be drawn between the two types of coaction, the lichen being a case in point. In groupings of two or more species, such as certain ant colonies, the line between symbiosis proper and parasitism is even more vague.

Objective or Purpose. It is sufficiently obvious that the most universal of coactions are concerned with shelter and food, directly or indirectly. It is impracticable to evaluate the various coactions as to relative importance, especially in general terms. The food relations of the bottom fauna such as occur in the Danish waters are not all significant coactions in the community, for many species feed largely on detritus of remote origin. However, when these same species are studied in other localities, their food relations take on more of the character of community food coactions because they secure more food from the living and dying plankton organisms.

In the propagation of game birds, four essential conditions have usually been noted, depending upon the circumstances, namely: (*a*) cover or covert defined as shelter, (*b*) food, (*c*) suitable nesting conditions, and (*d*) suitable climate. The last, though referring principally to the absence of extremes unfavorable to the species in question, operates with reference to food and shelter and should rarely be considered independently of these relations. The enumeration of needs of game, especially of deer and quail (Leopold, 1933), makes clear that certain relations are direct responses to habitat factors, and not coactions or reactions in the strict sense. The deer requires open spaces to play, and the quail selects sparse cover on a well-drained spot with bare ground near by, where the young may dry out after a rain.

It is difficult to evaluate food, shelter, nesting and breeding site, social relations, etc., in comparative terms, because they operate in accord with the general principle of Liebig's law of the minimum, which is equally applicable to maxima, as extended and restated by Shelford (1913, *a*) as the law of toleration. In addition to operating in this manner, the amount and kind of food and shelter, especially with reference to specific requirements, vary with weather, climate, and the presence of other organisms. In all studies of relations of species to community and environment, it is necessary to seek a proper balance among these factors and resist the general tendency to overemphasize one or two. Food coactions have been more often studied than other relations, and there is a large volume of records as regards organisms of economic importance from which stomach contents can readily be obtained and preserved in fluid. This has naturally limited the studies to medium and small animals, such as birds smaller than the prairie chicken, mammals smaller than the fox, fishes smaller than the full-grown carp, etc. In addition to this, scatology, pellet study, and the observation of browsed plants have contributed important results for a few of the larger forms.

Among higher forms occur the various reproductive coactions, including those of the family as such, which necessarily lead to certain types of social interaction. Naturally, they are likewise part of a composite coaction that includes home making or the securing of food, and they are often combined with disturbance reactions. Out of these basic coactions arise a variety of secondary or correlated ones, more or less distinctive in character but constituting only one feature of a behavior sequence. Such are hunting, storing, combat for the purpose of securing food, materials, territory, slaves or mates, defense and protection, courting, communication, play, etc. In their expression, these are largely an outcome of life form, life history, or life habit, and their development has led to a further specialization of behavior in particular genera and families.

Consequences of Coaction. In a broad sense, all interactions between organisms may be characterized as helpful, harmful, or destructive to certain species, to the community as a whole, or to man's selfish interests, though there are many degrees of each, and consequent gradations between them. Quite apart from the inequality of coactor and coactee, moreover, is the fact that the same process frequently produces both helpful and harmful effects. This is notably true of aggregation, in which the consequences may be beneficial or injurious to the species concerned, or the two may be combined in varying degree. When the first outweighs the second, the result is cooperation in some measure; if the scales are reversed, the outcome may well be termed disoperation. This comprises several types, of which competition is the most important, ranging from mere subordination or displacement at one extreme of effect to complete destruction at the other.

In respect to individuals, destruction is the typical outcome of food coactions, though this may often affect only parts of the coactee. It is but infrequently the result of coactions involving materials, such as those of leaf-cutting ants and the beaver, but with the noteworthy exception of man as a superinfluent. However, even with respect to food, it is evident that symbiosis and slavery exemplify cooperation, often in a high degree, while the destruction wrought by saprophytism is secondary and of a very different type. Parasitism runs the whole gamut from relations that involve at least a modicum of cooperation through an ascending series of disoperations that terminate in the destruction of the host. In the last case especially, it is worthy of note that the effect is often exerted upon an individual by a simple community of countless members.

Direct and immediate, though often partial, destruction is the general basis of food coactions, best illustrated by the consumption of a smaller coactee by a larger coactor. This interaction embraces such widely different types as the eating of a diatom by an amoeba, the engulfing of quantities of plankton by baleen whales, the capture of a rabbit by a fox, or the eating of water lilies by a moose. Though disparity in size is the rule for eaters, there are striking exceptions in which inequality in size is compensated by number, as with a pack of wolves, or by specialization, as in crotalid snakes and mustelids, for example.

Role in the Biotic Formation or Biome. The universal role of coaction is to be seen in the integration of plant and animal relations to constitute an organic complex, which is characterized by a certain degree of dynamic balance in numbers and effects. Obviously, such a balance undergoes a variety of rhythmic changes at different intervals, and is never exactly the same after a period of stress (Chapter 5). Nevertheless, it represents a general process of compensation and adjustment, in which extreme or permanent departures stand out more or less vividly. Hence, it appears entirely desirable to speak of disturbances of dynamic balance in the biome, which arise from an emphasis of one or more of the normal coactions. While it is true that at present little is known of the causes and detailed course of such phenomena, this condition is certain to be remedied as the methods of quantitative ecology are focused upon them (cf. Forbes, 1880, *a*; 1883, *a*).

The nature of the coactions involved in aggregation and competition is reserved for discussion in the next chapter, and it will suffice to point out here certain examples of abnormal intensity which, though not the rule, are far from infrequent. Naturally, the most numerous and important of these have to do with man or his agents, as a consequence of which fire, lumbering, or clearing removes the climax or subclimax in whole or in part and initiates succession. As an indirect human coaction, grazing is usually less thorough in its effects, bringing about modification in various degrees but rarely to the extent of complete destruction. Direct coactions between man and animals also cause changes in abundance and composition by reason of such activities as hunting, fishing, and poisoning, sometimes resulting in practical extermination over larger or smaller areas and the setting up of a new sequence of effects (Fig. 20). Opposite to these in character, but similar in producing a new chain of coactions, is the introduction, intentional or otherwise, of exotic plants or animals. In the case of cultivated plants and weeds, this coaction has played the paramount role in every agricultural region, as a sequel to the coactions concerned in clearing of land of all kinds. It is likewise seen in the introduction of domestic animals, or of such semi-feral ones as the rat, English sparrow, and numerous insect pests, as well as in that of disease-producing organisms, both plant and animal, of which wheat rust and the bacillus of cholera are examples.

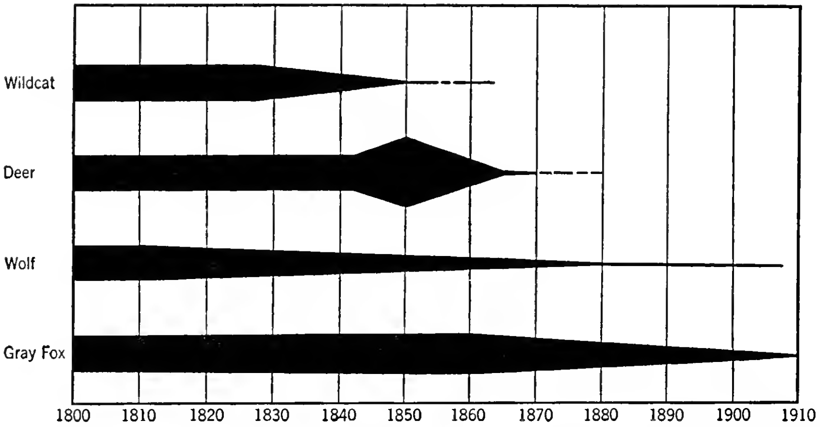


Fig. 20.—Showing the effect of settlement on the mammals of central Illinois. The decline of the Wildcat, *Lynx rufus* (Schreb), and wolf, *Canis nubilus* Say, early reduced by trappers and first settlers, was accompanied by an increase in deer, *Odocoileus virginianus* (Bod.). The gray fox continued in full numbers until about 1850-1860. The decline of this species and of the deer was probably due as much to destruction of the forest habitat as to hunting. (After Wood, 1910.)

Modifications of the community by native animals are less widespread and on a smaller scale as a rule, but are essentially identical in nature. The grazing coaction of antelope and bison probably differed only in degree and perhaps in slightly different preferences from that of cattle on the open range today. The aggregation of certain rodents in "towns" produces more serious effects, though these are too local and restricted in area to modify the climax materially. Most striking of all such coactions are those caused by grasshoppers in migration, which sometimes leave hardly a vestige of field crops. Successive defoliations by caterpillars have been known to cause the death of an aspen subclimax over many square miles of mountainside

(Fig. 21), and similar consequences may follow infestations by other epidemic or endemic insects, notably twig borers and bark beetles.

Fig. 21.—Aspens killed after three successive years of defoliation by the larvae of a noctuid moth; Pikes Peak, Colorado. (Photo by Edith Clements.)

SYSTEM OF COACTIONS

Since processes take the leading part in a dynamic system, the primary division is made upon this basis, as follows: (1) shelter and housing, (2) food, (3) materials, (4) reproduction, (5) social grouping, and (6) attachment. The logical subdivision of these is first with respect to the active agent (coactor) and second with reference to the passive organism (coactee), but the difference between land and water is such as to warrant a preliminary grouping into land and water communities, those of the latter being treated incidentally in the chapters on aquatic climaxes. Among coactors, animals are first considered because of their vastly larger number and importance in this role, followed by plants and then by those partnerships in which each plays the part of coactor in some measure. Coactors differ chiefly in habit and form, which are usually related to the various types of coaction. This is true to a large degree of the inactive agents (coactees) likewise. Plant coactees may conveniently be subdivided on the basis of the organ or part used for food, material, shelter, etc.

a *b*

FIGS. 22*a* and *b*.—A nest of the hooded warbler (*Wilsonia citrina*, Bod.) showing the use of forest floor leaves in construction. Both are of the same nest, built in a small sprout of tupelo, 32 inches from the ground. The long slim crotch is filled with a loose wad of dead beech leaves upon which the real nest is built. The neatly compacted rim of dead beech leaves is bound in place with strips of the inner bark of chestnut, of which a plentiful supply is available owing to the activities of the "chestnut blight." The lining is of finely shredded strips of grapevine bark—quite hairlike in character. This nest was so well done from the standpoint of camouflage that one could look directly at it without perceiving its nature. (Photo by Arthur B. Williams, Cleveland Museum of Natural History.)

In number, coactions are practically countless, and all that can be attempted in a preliminary organization of this vast field is to pass in review the frequent, typical, or outstanding examples and to relate these to the community life of the biome, so far as this is feasible at present. In this connection, composite interactions involving more than two species as individuals and especially as groups are peculiarly significant, but these are naturally more complex and at present less understood.

SHELTER AND HOUSING MATERIAL COACTIONS

The importance of plant shelter has been emphasized chiefly in connection with game management, especially that of game birds.

FIG. 23

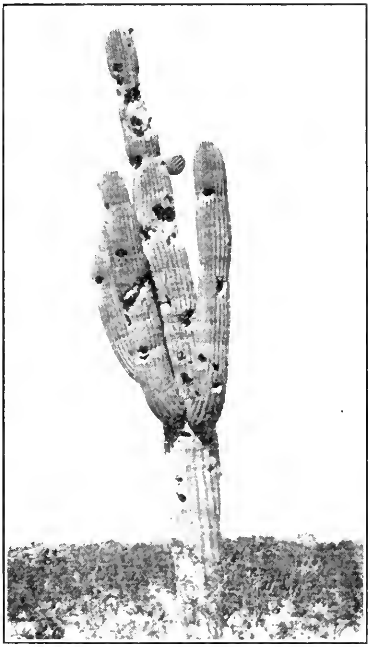


FIG. 24

FIG. 23.—Meadow mouse (*Microtus drummondi*, A. & B.) runway at Churchill, Manitoba. The run stands out most clearly where it passes through the water in the center of the upper section. It also shows as a dark area at the right center of the lower section where it passes through dense sedges at the margin of the depression. (Photos by V. E. Shelford.)

FIG. 24.—Woodpecker, *Colaptes chrysoides* (Malh.), holes in *Cereus giganteus*, Tucson, Arizona. (Photo by Edith Clements.)

Plant cover for shelter during sleep and rest, and during summer heat and winter cold, is a major requirement for game production, and especially for the nesting period. Leopold (1933) describes these in detail for the quail, and brings out the importance of the right density of cover to permit taking flight, of bushes of the forest-edge habitat of the quail to afford refuge when snow is deep, and of open grasslike vegetation for nesting. In game management, diversity of cover suited to the various needs favors large populations.

The small non-burrowing mammals select various types of cover. The snowshoe rabbit prefers a small woody growth so thick that foxes and wolves cannot travel through it with ease. The desert plains blacktailed jack rabbit finds shelter in the mesquite and buck brush and may seek food at some distance. Larger animals also seek shelter in vegetation; the moose frequents dense coniferous forest in winter and hides the young in alder thickets. The great cats, such as the jaguar (Bailey, 1931), commonly take refuge in brush thickets. Small rodents, notably Microtus, hide in the grass cover, making runways from place to place. Many small ground birds, particularly those nesting in swamps and low ground, take full advantage of the vegetative cover in selecting nesting sites. Even the burrowing mammals such as some species of kangaroo rats and ground squirrels prefer to burrow under shrubs, while the nine-banded armadillo selects the center of a thicket or a group of trees for its burrow.

FIG. 25

FIG. 26

FIG. 25.—Ravens (*Corvus corax sinuatus* Wag.) build a nest of old barbed wire in the "Dust Bowl" where other materials are scarce; Dalhart, Texas; 1935. (Photo by Edith Clements.)

FIG. 26.—Nest of a lark sparrow (*Chondestes grammacus strigatus,* Swains.) made of grasses in mixed prairie near Scotts Bluff, Nebraska. (Photo by Edith Clements.)

The importance of shelter has further been brought out experimentally by Gause (1934), who found that paramecia are able to maintain themselves against protozoan predators when cover was provided. The importance of eelgrass in connection with young fishes in the sea is discussed in Chapter 10 (page 336).

Home building, with a few exceptions among burrowers, involves the selection of materials which are nearly always parts or products of plants or animals. Burrowers and ground-nesting species commonly line their nests or breeding chambers with grass or grasslike fibers, sometimes supplemented with hair or feathers from the builder's own body. Ground birds commonly choose sites arched over by grasses or forbs. Animals that build nests in trees and shrubs employ a great variety of materials, and the use of the tree or shrub is in itself a coaction. Usually fiber from bark or the stems of forbs, grasses, or sedges, often mixed with leaves from the trees concerned, are employed by the smaller species. The gray and fox squirrels make summer nests or platforms of green twigs with leaves, and certain apes and lemurs have similar habits. Many of the larger birds use sticks to make a nest platform on the limbs of trees or other high points (Figs. 22 and 25). A number of insects fasten leaves together to make tem-

FIG. 27.—Banner-tailed kangaroo rat (*Dipodomys spectabilis* Mer.) burrows under mesquite (*Prosopis juliflora*). (Photo by Edith Clements.)

porary nests. Examples of this among lepidopterous larvae and spiders are common. (See Figs. 25, 26, and 27.)

The trunks of trees when hollow afford home sites for small mammals, reptiles, and insects. Comb-making bees often utilize such cavities. A goodly number of Coleoptera and a few Lepidoptera and Hymenoptera burrow into dead wood, which serves as shelter and for most of the insects it also supplies food. The larvae of click beetles and the larvae and adults of rove beetles, ground beetles, etc., which also are predatory, find shelter in dead wood. A few Hymenoptera make tunnels into wood in which to lay their eggs, but they are not important as regards influence.

REPRODUCTIVE AND SOCIAL COACTIONS

The reproductive coaction involves mating or the fertilization of the eggs, which calls forth aggregations of individuals. The swarming of marine worms is one of the outstanding types of assemblage for the lower invertebrates; this brings individuals into close contact and permits fertilization of eggs cast into the water. In terrestrial communities the choosing of mates, sometimes accompanied by fierce contests between males, is a well-known coaction.

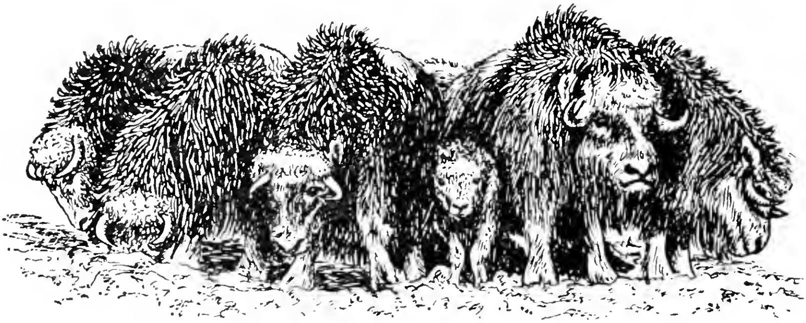


FIG. 28.—Defense circle of the musk ox (*Ovibos moschatus* Zim.). It is an excellent defense against wolves and also affords protection to the young. (Sketched from a photograph by D. B. MacMillan in a report by American Committee for International Wild Life Protection, 1934.)

The care of young is often of much greater importance in the community than nest building in itself, as it involves a greater drain on the food supply. This is especially true among birds, which collect enormous amounts of animal food to nourish their rapidly developing young. The hiding of the young by many mammals is important and varies as to method. Certain rabbits secrete the young individually, the litter being scattered about; this is usually a shelter coaction. The teaching of the young to fly and hunt food is among the important coactions of birds.

The gregarious habit so common among the larger mammals in tundra, grassland, and savannah affords protection from enemies, especially for the young, and constitutes a simple form of cooperation, as in the case of the musk ox (Fig. 28). Social coactions in food getting are exemplified by the wolves, which aggregate in packs for community hunting in the winter and follow more or less regular routes that bear a close relation to dens or homes (Fig. 29). These gregarious habits tend to make both reaction and coaction intensive in some areas and consequently irregular in pattern. The detailed descriptions of aggregation and herding in both small and large animals are easily available in the well-known treatise by Allee and hence do not require further discussion.

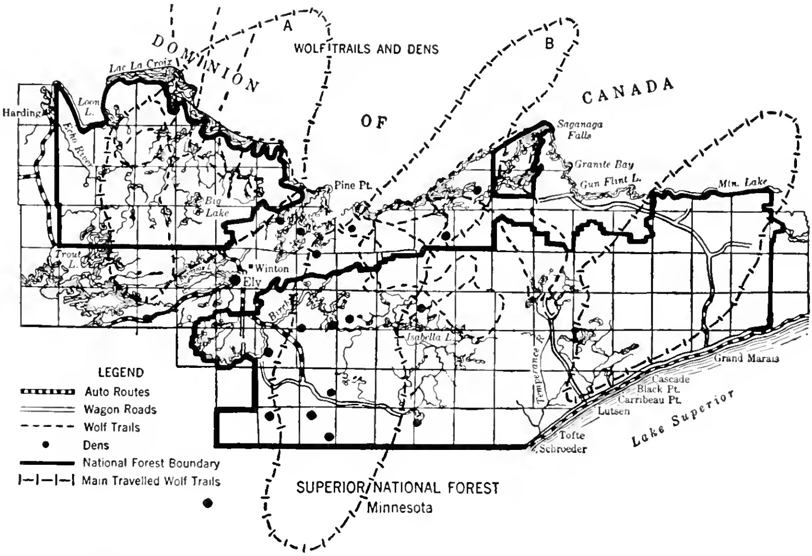


FIG. 29.—Wolf pack routes in the Superior-Quetico area. The long axis of ellipse *A* is approximately 55 miles (89 kilometers), *B* is 95 miles (153 kilometers), and *C* is 60 miles (97 kilometers). (After Olson, 1938, *a*, *b*.)

FOOD COACTIONS

Elton (1927:56) employs the term "food chain" for a sequence of such coactions and refers to all the food chains in a community as the "food cycle." In view of the specialized use of the term cycle, food nexe (*nexus*, tie, bond) appears preferable for the interwoven pattern of food chains, especially because of its basic significance in the biotic community. It further seems desirable at present to employ the term for any particular grouping of food chains rather than all those of a community, owing to the vast number at present in an extensive community.

In the treatment that follows, an endeavor is made to keep the dynamic viewpoint constantly to the fore. The chief purpose is to present a flexible arrangement that can be utilized to reveal the significance of each process in the working of the community as a whole. The length to which food coactions are discussed is not to be construed as indicating an importance greater than shelter or other coactions, but rather that the extensive available facts have been brought together and classified to form a pattern for the study of other coactions.

The plant population changes more or less completely with each stage in succession on land. For a number of stages, the species increase steadily and there is a corresponding increase in the variety and amount of shelter and food produced. In grassland, this may continue into the climax, but as a general rule, and particularly in coniferous forest, there is a marked reduction in both quantity and variety as the climax is approached. The usual consequence is a similar decrease in the kind and number of animal consuments, so that climax forests are often peculiarly monotonous in terms of bird and mammal or even insect influents. Conversely, the subclimax areas are relatively rich in major influents because of the great variety of shelter and materials, as well as food. Hence, it is sometimes both desirable and convenient to refer to food nexes as climax or seral when significant differences exist between them.

ANIMALS AS ACTIVE AGENTS (COACTORS)

The major distinctions between animal coactors are founded upon taxonomic life forms primarily, often with important subdivisions on the basis of life-history stages, as in metamorphic insects, and of behavior types such as are found in many groups. With respect to community significance, the general classification into herbivores (phytophaga or plantivores), carnivores, and omnivores assumes new meaning, but at the same time must be carried further in order to provide more definite pathways through the labyrinth of coactions.

Choice of Food. With respect to the selection of food, it is helpful to begin with the organism as it comes into free existence, whether through hatching, birth, or transformation from other stages. Such organisms usually soon begin to take food, picking up all sorts of material and rejecting those that are distasteful or painful (Holmes, 1911). After a few trials, rejection takes place at sight without testing, the animal selecting only those objects that serve as nourishment, and thus quickly learning to distinguish food from all other things. However, many adult insects in particular render such learning unnecessary by laying their eggs on the very material that is to supply food for the young. Some adults, that in the larval stage were forced to feed upon strange food, have been found to lay eggs upon this same substance. Frequently, larvae that have started to feed upon a plant selected by the female moth will not change to another host plant (Picket, 1911; Brues, 1920, 1924). The general principle is that organisms show a preference for a certain kind or kinds of food, which may be selected from a considerable range of materials. Such a choice may be exercised between groups of various kinds, e.g., between species, or organs of food plants.

PLANTS AS PASSIVE MEMBERS (COACTEES)

The animal coactors of this group may well bear the collective term of plantivores, since the more familiar word herbivore is neither definite nor inclusive. However, it is evident that such a designation is often to be employed in a relative sense for animals whose food is largely but not wholly vegetable, and hence differ only in degree from omnivores. Plantivores sometimes select their principal food from the dominants of a biotic community. Thus, insects on a floodplain feed in general on a variety of trees, though each kind usually prefers but one or two species of the floodplain dominants (Felt, 1906). By contrast, the salt-marsh caterpillar (*Estigmene acraea* Drury) feeds on 140 different species of herbs (Folsom, 1922). Metcalf (1924) has shown that certain leaf hoppers feed on the plants present where the physical conditions are suitable. A number of Phytophaga are confined to plants belonging to a single family, a preference for willow and cottonwood being not uncommon (Folsom, *loc cit.*; Brues, 1924). A striking instance of a similar predilection is furnished by the potato beetle, Leptinotarsa, which passed from the wild *Solanum rostratum* to the cultivated *S. tuberosum* to become one of the generally distributed North American pests.

The general relations of a pure phytophagous group to its food plants is well illustrated in a recent monograph of the aphids or plant lice of Illinois (Hottes and Frison, 1931), which includes a discussion of 251 species and varieties. Since the food plants and much of the life histories were known, a compilation of food habits was made from this monograph. Eleven species were thrown out because of restricted catches of new species, or because the host plant was unknown, etc. The percentages of the 240 species considered are shown below:

	Per Cent
A. On food plants belonging to more than 10 genera	2
B. On food plants belonging to 2 to 10 genera	31
C. Only genus named—several species implied	30
D. Genus and one or more species cited	10
E. On a single species	27
	100

The food plants of some of these in the last category are known only in Illinois, and thus the percentage in the last item may be very materially reduced with further study throughout their range. In general, there is a considerable number of coactors that are confined to a single genus or even species of host plant, though the general flexibility of food relations suggests that all supposed instances of such restriction demand especially careful and thorough investigation.

Seeds and fruits are particularly subject to attack by many species of birds and some small mammals and numerous insects, by reason of the relatively large amounts of food stored in them, but roots, subterrene shoots, stems, leaves, and flowers are each the object of a host of coactions, especially on the part of insects and a few birds. Further distinctions may arise from the nature of the tissue concerned, as in woody or herbaceous stems, the pith of a sunflower, or a stone, seed, or pulp of a fleshy fruit. Finally, either living or dead parts of tissues may be utilized, and sometimes this difference in condition is immaterial to the coactor.

In addition to the central coaction of eating, there are a number of related processes such as collecting, harvesting, storing, and planting. These may be simple and general in character, as with most of the animals concerned, or they may be highly specialized, as with the harvester ants and the fungus cultivators. So far as these are pertinent to the present treatment, they will be considered under the respective groups.

RELATIONS OF FOOD COACTIONS TO THE COMMUNITY

A proper ecological approach to the study of food coactions is one that brings out the community interactions. The investigator first learns what foods are present and the quantity of each in the community or communities which the coactor frequents, and then proceeds to determine the items selected from the available food and the quantity in which each is taken. The work of Petersen, Blegvad, and others at the Danish Biological Station is the most thorough of this type, and is discussed in connection with coactions in the sea. Baker (1916) did some similar work in fresh water, but with reference to Mollusca. Bird (1930) made community observations relative to the food of a few birds, but the terrestrial studies in general, even some of the more recent ones, lack the full force of the bio-ecological viewpoint. For example, proportions of the different types of plant or animal food may be given, but the relative amounts of each on the range are not indicated.

The presentation of coactions from the viewpoint of taxonomic groups, illuminating as it may be to the general biologist trained in this manner, also fails to stress the bio-ecological viewpoint. In addition, it may fail to take account of variations in habits among related species. The American bison (*Bison bison* L.) is a grassland animal grazing by preference; the closely related European species (*Bos bonasus*) is a forest dweller, living by browsing. Again, some Carnivora, for example, the small meerkats in South Africa, have the food habits of prairie dogs, and the small tree hyraces (ungulates) those of raccoons. (cf. Lydekker; he calls the American Bison *Bos americanus*).

GRAZING AND BROWSING

As previously suggested, there is no definite line between the grazing and browsing habits. Not only do nearly all grazing animals browse in varying degrees, but there is also no clear-cut distinction either in the original meaning or the current usage of the two words. Moreover, forest undershrubs may be grazed practically like grasses and forbs, while tall herbs are often browsed as though they were shrubs. Even more significant is the fact that some ungulates may graze in the summer and browse in the winter, that they may change their food plants as a range becomes overgrazed, or their food habits as they pass from one seral stage into another. In spite of all this, however, nearly all ungulates manifest a distinct preference for one type of behavior or the other (cf. Farrow, 1925).

Grazing Life Habit

Grazing animals fall into three classes, arranged in the order of their importance: (*a*) large cursorial grazers; (*b*) small grazers resident underground; and (*c*) small grazers resident among the grasses.

Large Tramping Grazers. The most representative grazing animals of North America are the bison, pronghorn antelope, musk ox, and tundra caribou. The first three prefer grasses and sedges; the tundra caribou seem to favor lichens, grass, and forbs. Elk, deer, sheep, and goats may shift according to the conditions from the grazing habit through various combinations to a browsing coaction, or the reverse.

Quantitative studies of the food coactions of feral grazing animals have been rare, and the scattered observations are for the most part incomplete and undependable. Even the few examinations of stomach contents leave much to be desired, owing to inherent difficulties and the scattered nature of the observations. There is an increasing body of knowledge as to the food habits of domestic cattle, sheep, and goats, all of which are unfortunately of European or Asiatic origin, and some of the observations are both quantitative and specific as to plants used. This knowledge will be steadily augmented by the experimental installations now in existence at the several range reserves and grazing experiment stations. However, these need to be supplemented in detailed manner by extensive observations on the actual process of grazing in terms of life forms and species, closeness of cropping, seasonal preference, etc., with reference to the most important wild ungulates.

The observed effect of grazing coactions upon the plant matrix is primarily an outcome of the selection and utilization of the constituent plant species by domestic animals. Every association of the grassland climax in North America has been thus modified, some of them in most striking and puzzling fashion as an outcome of the choices of domestic stock, but the results of grazing by native animals cannot be expected to be the same. Similar modifications have occurred in grassland the world over.

Probably the best-known example of such a modified community, viz., the "short-grass plains," was long supposed to be climax in character (Pound and Clements, 1898; Clements, 1920, 1922). Similarly, the bunch-grass prairie of California has been converted almost entirely into an associes of annual grasses, chiefly Avena and Bromus, while the true prairie of the Middle West has been largely transformed into a tall-grass postclimax of Andropogons. Under more intense grazing pressure, the grasses have yielded to dominants of adjacent scrub climaxes, such as Artemisia or Larrea, to consocies of such undershrubs as Gutierrezia and Haplopappus, or have been replaced by introduced annuals like Salsola. Thus, each kind and degree of overgrazing produces its proper indicators, and in consequence it is possible to reconstruct the history of a range by the indicators that characterize it.

Small Grazers Resident Underground. This group includes notably the prairie dogs, marmots, and conies in North America. Grasses and forbs are also taken by certain species of kangaroo rats, ground squirrels, etc. There is no universal connection between subterranean habit and grazing, but the animals of this group exhibit such a correlation as an important feature of their community relations. Prairie dogs crop herbs and also dig them out, their choice being somewhat the same as that of the native ungulates and domestic animals. Marmots (Marmota) usually choose forbs rather than grasses, owing to their general relation to forest regions, while conies graze and store herbs of all kinds. Another important characteristic of this group of grazers is the occurrence of quiescence in many species during unfavorable seasons. This takes them out of competition with the large grazers

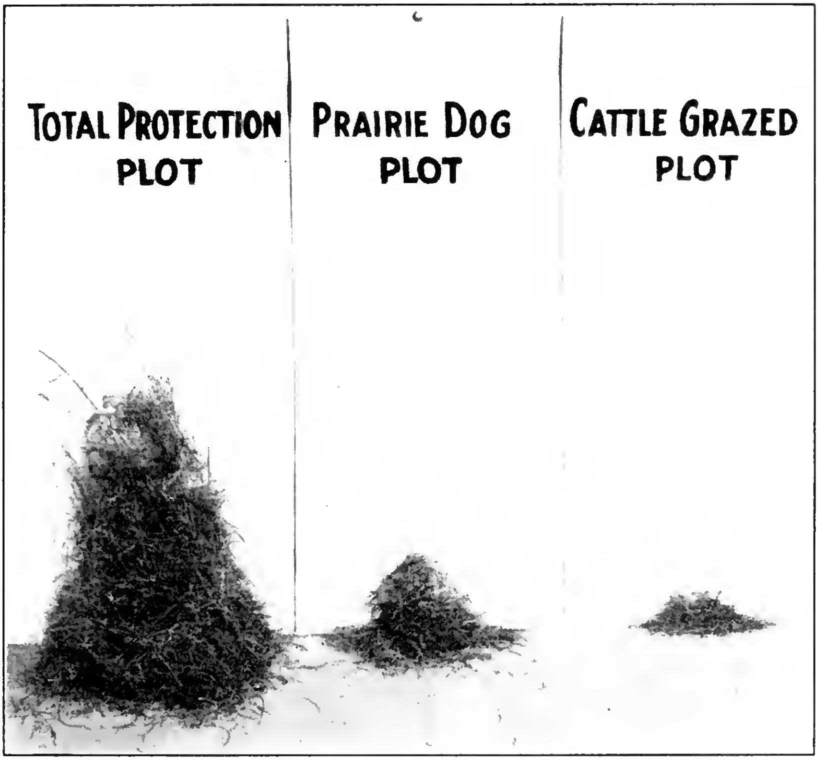


FIG. 30.—Fall clippings of blue grama (*Bouteloua gracilis*) in grazing exclosures at Williams, Arizona. The pile labeled "cattle-grazed plot" is from the open areas where both cattle and prairie dogs grazed. (After Taylor and Loftfield, 1922.)

which must eat dead grass and forbs, frequently digging away snow to secure them.

Taylor and Loftfield (1922) have measured the coaction of the prairie dog, *Cynomys gunnisoni*, in northern Arizona in connection with the grazing exclosures and found that this species may destroy as much as 80 per cent of the total potential annual production of forage where the vegetation still persists. Under extreme conditions of crowding, prairie dogs may consume the entire cover and be forced to move elsewhere. Many social burrowers, especially those that form "towns," often bare the surface more or less completely; this is also true in a large degree of the solitary kangaroo rats (Vorhies and Taylor, 1922) and in some measure of the ground squirrels when closely aggregated.

Pound and Clements (1898:414) pointed out the characteristic dominants of the extensive "dog towns" in western Nebraska, and the changes involved have been traced in greater detail in and about the grazing exclosures mentioned above (Clements, 1919). Similar studies have been made of the areas denuded by kangaroo rats in the grassland and desert scrub climaxes of southwestern Arizona, where the destruction of the cover is sometimes complete (Clements, 1920:90; 1928:297).

Small Surface Resident Grazers. In this group are included rabbits, mice, etc., which feed on green grass and forbs in summer and their dead tops in winter. The principal animals of this type in North America are voles and jack rabbits. In localities where shrubs or cacti occur, jack rabbits may feed on these in winter or during drought periods. However, it must often be necessary for them to eat dry grasses, though the food records are few as yet (Vorhies and Taylor, 1933). Certain gallinaceous birds may belong here also, but nearly all those that graze do so only for a portion of the year and then not exclusively.

In addition to those whose activities have been described, various omnivores such as squirrels, most ground squirrels, many mice, porcupines, some foxes, and birds compete with the large grazers in a minor way. However, phytophagous chewing insects are often more important in the destruction of herbaceous plants in competition with grazing mammals. This is most strikingly true of grasshoppers, which in general are most abundant in grassland areas, where grazing is the prevalent coaction.

BROWSING LIFE HABIT

This coaction type characterizes chiefly the large mammals (ungulates) and some of the larger birds and rodents that inhabit the forest. In North America and probably elsewhere, browsing is the primary coaction during the season unfavorable for plant growth. It alternates with grazing of aquatic plants, forbs, fungi, etc. (mainly mammals), and with scratching for small ground animals or seeds (some birds). In the coniferous forest of North America, the moose browses chiefly on deciduous trees and shrubs, especially in winter, but eats aquatic plants and some herbs in summer, while the Shiras or mountain moose apparently browses the year around. The woodland caribou uses lichens in winter and browse similar to that of the moose during the remainder of the year. Likewise, various rabbits and the Hudsonian spruce partridge browse on the growing tops of spruce seedlings or trees, and the ruffed grouse eats buds of deciduous shrubs and trees. The effect of this on the plants is not unlike light browsing by large mammals. The tassel-eared squirrels feed on the bark of terminal twigs (Figs. 31, 32).

Deer browse regularly, but in favorable seasons they may also consume large quantities of mushrooms and sometimes forbs. The elk possesses the ability to live both in open forests with grassy parks and in savanna areas, and at one period it ranged across the northern part of the Great Plains. It divided its time, seasonally and daily, between the timber along the streams and the open prairie (Bailey, 1926). Elk browse at all seasons, but especially in winter; they also eat all kinds of herbs, including much grass, thereby differing from the deer. Rabbits browse in the unfavorable season and also take bark from woody plants; the porcupine is similar in this respect but more arboreal, eating the bark at some distance above the ground. Squirrels, especially the red squirrel, nip off the end buds of conifers in a similar manner (Hatt, 1929). All these rodents resemble the deer in taking herbaceous plants in the growing season, and consequently compete with ungulates in grassy parks as well as in wooded areas.

Defoliation and Bud and Twig Injury. This is chiefly the work of insects and arachnids; the lepidopterous and hymenopterous larvae play an important role. In the coniferous forest, the hemlock looper, spruce budworm, and larch and jack pine sawflies are of some small importance in competition with the browsers. The subclimax deciduous trees are at times defoliated by sawflies and moth larvae. In the deciduous forest, the cicadas, twig girdlers, and twig-boring beetles have somewhat the same effect as the browsers, but native defoliators

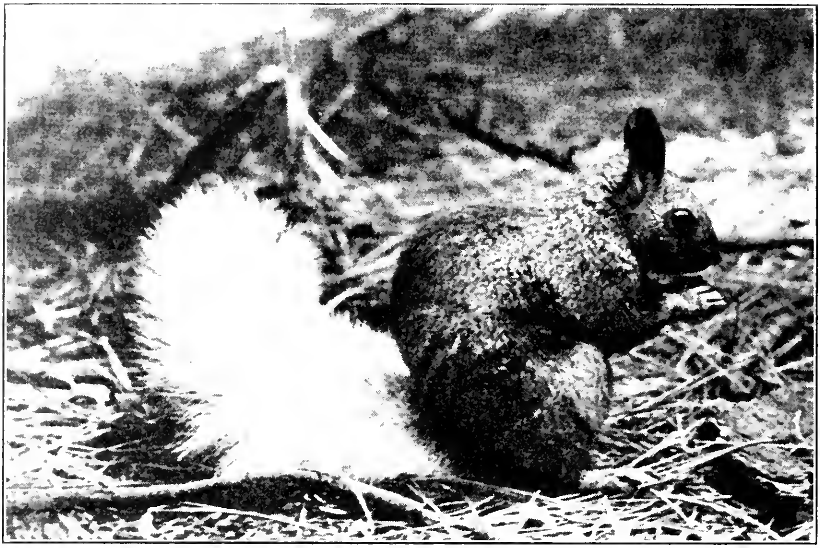


FIG. 31.—The Kaibab squirrel (*Sciurus kaibabensis* Mer.) feeding. One of its favorite foods is the new bark at the tips of twigs. (Photo by Frasher Photos, Pomona, California.)

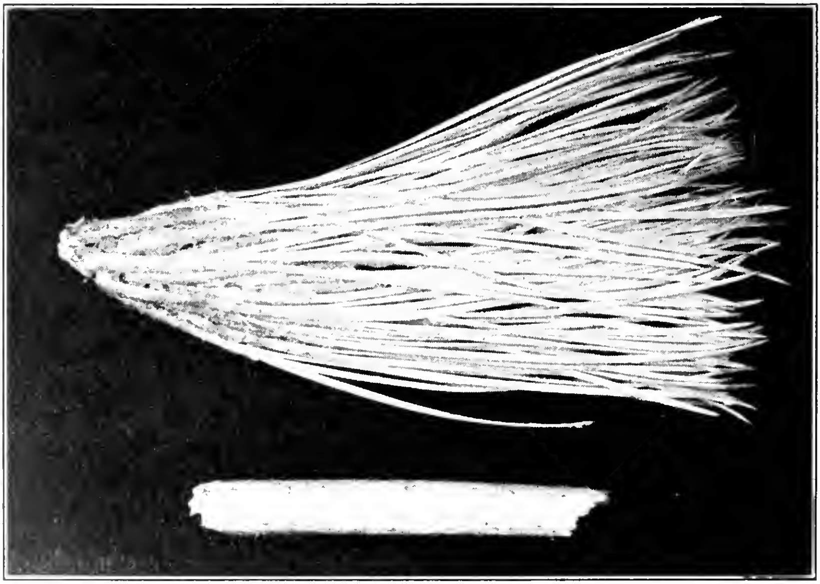


FIG. 32.—Shows needles cut off and piece of peeled twig of the usual length. (Photo by R. R. Hamm.)

are not abundant. Grasshoppers, the army worm, and a few other insects when epidemic remove foliage of all kinds as completely as the large grazers and browsers with which they may compete.

Importance of the Browsing-grazing Coaction. Browsing by domestic animals (and also by wild ones) has exerted considerable influence upon grassland where this contains certain shrubs or is in contact with them. Species with edible fruits but protected seeds, such as the mesquite (Prosopis) and juniper, are widely scattered by cattle and goats in particular, and frequently increase to a point where the grass dominants are more or less completely replaced by them, especially where fire is a regular process. In addition to such changes of composition, there is usually a striking effect upon the form and branching of species that are regularly browsed, by which they assume more or less globular shapes, though these effects are not frequently due to native species.

Recently Vorhies and Taylor (1933) have given a comprehensive account of the food coactions of *Lepus alleni* and *L. californicus*, as an outcome of the researches on the Santa Rita Range Reserve in Arizona. This deals not only with the quantity of forage consumed, but also with stomach contents, and the utilization of browse, cacti, grass, and forbs. Most of the plants present are eaten to some extent. The percentages for the respective species were as follows, grass, 45 and 24; mesquite, 36 and 56; cacti, 7.8 and 3.3; forbs, 12 and 17. Nevertheless, the authors state that jack rabbits are more abundant where forbs are prevalent than they are in stretches of climax grasses (pages 541, 563), a fact that is more in accord with the food habits of the larger rodents generally.

In the Old World, the common rabbit under agricultural conditions has spread from its original home in the Mediterranean region and is often the most serious of rodent pests (Tansley, 1922; Farrow, 1925). In Australia and New Zealand it is paramount, tens of millions being destroyed in a single year in New South Wales alone (Vorhies and Taylor, 1933:571, 567).

SEED AND FRUIT COACTIONS

To this group belong the squirrels of the western mountains of North America (except the tassel-eared group), some chipmunks, antelope squirrels, some kangaroo rats, and many wood rats. Outside the tropics this type of coaction is not common among the larger animals; usually some animal food is taken also. The animals belonging strictly to this coaction type are chiefly insects. For example, Korstian (1927) found that insects may destroy about 10 per cent of the acorns in white oak and up to a maximum of approximately 50 per cent in black and overcup oak. The nut and fruit destroyers include various weevils, some larvae of other beetles, flies, e.g., apple maggot, various nut weevils, some larvae of other beetles, and moths, e.g., cranberry worm (cf. Weese, 1924; Zazhurilo, 1931).

Storage by Mammals. The absence of actual hibernation in the squirrels renders some sort of storage desirable if not imperative in regions with much snow. The Abert squirrel and the flying squirrels are thought not to store food at all, though the former appropriates the stores of the Mexican woodpecker, according to Mearns (1907), as does the California gray squirrel those of other woodpeckers. The red and Frémont's squirrels employ stores almost exclusively, hiding them away in hollow trees, in fallen logs, or in the ground.

The bulk of the cones gathered by the Douglas squirrel are placed in sizable hoards. The simplest type of storage is exemplified by the gray and fox squirrels, and to a minor extent by the Douglas squirrel, which merely bury each nut or acorn singly in the soil. It seems clear that the method by which many of these hidden nuts are found should suffice to disclose most of them, as is indicated by the statements of Seton, Morris and Merriam (cf. Seton, 1929:33, 92). It is accordingly probable that the debt of hickories, oaks, and cone bearers to the squirrels has been much overestimated, in spite of Seton, who states that there can be little doubt that three out of five nut trees were planted by squirrels, chiefly the gray (cf. Korstian, 1927:35). The nuts that are not stored away are usually eaten by deer, bears, and other animals.

In special studies of the reproduction of conifers in the Rocky Mountains, no instance has been seen of buried cones producing sturdy seedlings, owing to the intense competition of the germinules. The seed crop in an even stand of trees, especially a climax, is not of special value as only occasional replacements are needed. It is the cones and nuts in mixed stands at the border lines between the two stages of succession that may be of vital significance. It follows, of course, that they may become effective under various modified conditions in forests.

The food coactions of squirrels sometimes produce an effect just the opposite to that which is generally inferred. This has been demonstrated by tracing the succession after fire in the montane and subalpine forest of Colorado (Clements, 1910). The maintenance of a burn subclimax of lodgepole pine is due primarily to the fact that the population of squirrels, chipmunks, and nutcrackers is driven out by the fire just before an enormous amount of seed is released by the opening of the cones. After trees again begin bearing and the animals return, the cones are so completely harvested that seedlings rarely appear, even where space and germination conditions are favorable.

Seasonal Coactions in Birds. This group includes the vast majority of gallinaceous and passerine birds, the species and individuals concerned being very numerous. In the large forms such as wild turkeys, pheasants, and quail, a scratching reaction on litter and leaf mold is similar to the rooting of peccaries and swine, turning up fruits, seeds, nuts, and invertebrates. The diet of the bobwhite has been studied much more thoroughly than that of other members of the group, especially by Handley (Stoddard, 1931) and by Judd (1905). The food of chicks was found to consist of 84 per cent of animal matter, by contrast with 22 per cent for adults; the two largest items were beetles 38 per cent and grasshoppers 27 per cent. For adults, the plant and animal material, and the major items in each, fluctuated greatly during the year. The maximum for the plant material occurred in January and February with 98 per cent, contrasting with 2 per cent for animals, but the animal material rose to 38 per cent in October, leaving 62 per cent for plants. In nature even these larger birds rarely if ever bring about denudation other than in minute areas, but they may affect composition and invasion directly through eating or disseminating seeds and fruits.

Perching Birds. The food coactions of this vast group may be exemplified by the following tables. These have been compiled from several sources, chiefly Forbes, McAtee, Henshaw, Beal, and Gabrielson; although the values are more or less typical, they cannot take account of all regional, annual, and individual variations.

The fruit- and seed-eating birds do much under agricultural conditions to plant certain shrubs and trees. The prevalence of sumac, trumpet vine, mulberry, etc., along fences is evidence of their work. One of the best demonstrations of the effect of this group of birds on the composition of communities resulted from the controversy as to whether trees would grow on prairie soil. In 1875 and at various subsequent dates, some 18 acres of prairie soil on the campus of the University of Illinois were set with trees of about 30 species. Many of these died, and frequent cutting of the undergrowth largely prevented the development of the forest which would have succeeded. However, under a grove of green ash the recurrence of seedlings was striking, especially of cherry, hackberry, sassafras, grape, Virginia creeper, currant, and other shrubs with fruits having indigestible pits, indicating that the succeeding forest would have been planted by birds.

TABLE 1

Relative Composition of the Food of Common Birds

Species	Seed Fruit	In-sects	Species	Seed Fruit	In-sects
	%	%		%	%
White-winged crossbill	93	7	Arkansas goldfinch	67	33
Purple finch	90	10	Brewer's blackbird	67	33
California towhee	85	15	Lazuli bunting	67	33
House finch	85	15	Slate-colored junco	67	33
Phainopepla	85	15	Yellow-headed blackbird	60	40
Horned lark	80	20	Towhee	60	40
Blue jay	75	25	Chipping sparrow	58	42
Mocking bird	75	25	Catbird	52	48
Song sparrow	75	25	Bushtit	50	50
White-crowned sparrow	74	26	Crow blackbird	50	50
Varied thrush	74	26	White-breasted nuthatch	50	50
Redwing blackbird	73	27	Brown thrasher	43	57
Bobolink	70	30	Robin	42	58
Cardinal	70	30	Black-headed grosbeak	40	60
Indigo bunting	70	30	Lark sparrow	40	60
White-throated sparrow	70	30	Rose-breasted grosbeak	40	60
American goldfinch	67	33			

TABLE 2

Seasonal Differences in the Food of Granivores

(Gabrielson, 1924)

Species	Winter		Summer	
	Seeds	Insects	Seeds	Insects
Evening grosbeak	100	0	79	21
Pine grosbeak	99	1	84	16
Red crossbill	99	1	82	18
Common redpoll	99.6	.4	75	25
Pine siskin	87	13	72	28
Snow bunting	97	3	71	29
Lapland longspur	96	4	53	47
Vesper sparrow	100	0	0	100

Scansorial Life Habit. This group comprises those woodpeckers that feed chiefly upon plant materials. However, in spite of the marked structural adaptations of this family, its food habits are fairly generalized, and most of the species are to be regarded as bivores. The most sharply differentiated are the three species of Sphyrapicus, the sapsuckers, which have adapted themselves to a diet of sap and cambium, supplemented in considerable degree by fruits and ants. In Colaptes, the gilded flicker seems to be largely vegetarian, favoring the fruits of cacti; the red-shafted lives on a diet about half ants and half fruits and nuts, while the northern flicker prefers ants to fruits. The red-headed woodpecker mixes plant and animal materials in a ratio of about two to one, but offsets this by a fondness for eggs and nestlings. The California and Lewis woodpeckers prefer acorns, and the former in particular stores these in single caches in the trunks of oaks and pines (cf. Weiss, 1909; Griscom, 1923; Burrt, 1929; Chrysler, 1930).

The enormous number of acorns taken by certain species suggests that woodpeckers have some effect upon the reproduction of oaks, but of this there is no definite evidence. However, the sapsuckers not only affect the health of trees and deface them by the production of burls and adventitious buds, but likewise injure some of them, especially young individuals, to the extent that they die. McAtee (1911) has listed 267 species of trees and shrubs attacked by the yellow-bellied sapsucker.

Dissemination by Animals. In addition to the distribution of fruits and seeds by animals in the course of food coactions, a number of modifications are concerned with wholly unintentional dissemination. There are four types of these, namely, hooks, spines, awns, and viscid excretions. The first are by far the most numerous and important, hooks and barbs of various form occurring in families as far apart as the peas, parsleys, asters, borages, and mints, as illustrated by the familiar sticktights, beggar's ticks, cockleburs, etc. Spines on fruits are fairly common, but only a few are sufficiently stout to bring about attachment, the best known being the sandbur and the caltrop. The spiny heads of thistles are sometimes caught by the hair of animals, as are the fruits of some cacti, but the most effective distribution of the latter is through the food coaction, the fruits and upper joints of cylindric opuntias especially becoming attached to the jowls of cattle and thus spread about locally. Stipa and Erodium are examples of distribution by means of a sharp callus, and Stipa, Aristida, Bromus, Hordeum, and many other grasses of dispersal by virtue of awns. The use of sticky substances is quite exceptional, and is found only in a few glutinous fruits and in the so-called catchflies in which the stems may be caught by animals. Finally, there is some dispersion of small seeds and fruits in mud on the feet of mammals and birds, but this is far less important than has been supposed (Clements, 1907).

Dissemination by animals is often of much significance in connection with bare areas or those in early stages of the subsere, where there is good opportunity for establishment or ecesis. It is regularly ineffective when seeds are carried into unfavorable habitats or into communities in full occupation of the soil. When this condition obtains in the community to which the species concerned belong, the consequence is much the same, since new individuals can rarely be established until mature ones die out or the turn of annuation brings temporarily an enlarged opportunity.

Sucking Coaction. There is a large group of food coactions in which the plant is injured or killed by having the sap sucked out by aphids, leaf hoppers, many other Hemiptera, certain larval Diptera, and so forth. The chinchbug affords a notable example of the destruction of cultivated species by this means, but it is not especially detrimental to native grasses in adjacent areas. Some forms of this group alternate to some extent between plant juices and the blood of animals, as well as that of man.

While anthophilous insects secure nectar by sucking, this coaction differs in practically all other respects and hence is considered under symbiotic relations (page 141).

Cambium Feeders. This coaction is characteristic of certain insects, especially the so-called bark beetles (Scolytidae), which are particularly numerous on conifers. When they occur in epidemic form, they may kill trees over a considerable area, as does the Black Hills beetle (*Dendroctonus ponderosae* Hopk.). Other borers, usually Coleoptera, also girdle trees occasionally, but a much larger number drill into dead wood or heartwood with little or no effect except to hasten decay (see also Brues, 1920, 1924, and 1930).

Galls. While these are not restricted to insects and mites as coactors and flowering plants as coactees, the overwhelming number are concerned with these groups. The exact nature of the stimulus is not known, but apparently it is due to the injection of a secretion by the insect, though the use of food by the larvae may sometimes be involved also. The three chief groups of insects are aphids, gallflies (cecidomyids), and cynipids (Hymenoptera), with the spiderlike mites perhaps next in importance. All plant parts may be more or less affected, but the shoot, stem, or leaf figures in the most bewildering variety of modifications. Though much rarer, flower clusters and even individual flowers exhibit some of the more striking transformations.

In exceptional cases where the number of shoots, leaves, or flowers is increased, a certain degree of mutualism appears to enter, but this is more apparent than real, since such parts are rarely quite normal in functioning. Nearly always, the relation is one of pure parasitism, the gall providing both food and shelter for the young of the coactor, regularly with some slight or even considerable disadvantage to the host plant. This rarely has decisive significance, though there may be a minor effect upon the competition between individuals or species, especially when flower and seed production are diminished.

Invertebrate Omnivores. As has been pointed out elsewhere, the tendency is for animals to select a wide variety of food from the great diversity present in most habitats. Even in the predaceous beetles, a number prove to be plant eaters in part. Forbes (1883, *b*) made an exceptionally thorough analysis of the contents of the alimentary tract of common genera of carabids and coccinellids and found them to be more vegetarian than ordinarily supposed (Webster, 1880). Of the 20 genera of ground beetles studied, 8 preferred a diet more than half vegetable, while in Harpalus the percentage rose to 88 and in Amphasia to 97. For the ladybugs, 2 genera fed exclusively on plant material under certain conditions, while the general range was from a half to three-fourths. An unexpected result was the increase in plant food taken in the midst of an infestation of chinchbugs, but this was chiefly due to the concomitant abundance of fungus spores.

ANIMALS AS PASSIVE MEMBERS (COACTEES)

In the general sense of the term, carnivorous animals appear in all classes and embrace a large majority of the orders among mammals. They comprise more than half the families of terrestrial birds, most of the snakes, lizards, and amphibians, and a vast number of insect families, especially if larval coactions are taken into account. The animal-eaters fall into two major divisions, carnivores proper and insectivores, while many omnivores are carnivorous by preference when the food supply permits.

The carnivorous habit has led to certain related coactions which may be regarded as offensive or defensive. These may pertain to the individual or the group; in the one case they usually arise out of the structure of the species concerned, in the other from some social habit, especially cooperation. Read (1920) has advanced the idea that hunting in packs was the first social organization of primitive man. He assumes that the human type separated from the rest of the anthropoid stock through (*a*) the adoption of life on the ground, (*b*) the addition of flesh to a diet of fruit and green plants or the assumption of a more or less complete flesh diet, and (*c*) hunting in packs. Such hunting would be a necessity only when food from plant sources failed in the dry or cold season.

Recourse to the social hunting of large game in a climate with severe winters is exemplified by the wolves. During the summer their food consists of small mammals, birds, bird's eggs, and even insects, but in winter this kind of food is inadequate or wanting and cooperation becomes requisite to the securing of large mammals. Olson (1938, *a*) has mapped wolf dens and hunting-pack routes in the Superior National Forest and Quetico Park. One main traveled trail to the northeast forms a narrow ellipse about 60 miles long and 15 wide, while the southwesterly course constitutes a similar ellipse approximately 90 miles in length. Each of these appears to be hunted over at fairly regular intervals. Family dens are scattered about near the hunting trail, and the size of the pack naturally varies with the number of families participating. Social organization also accompanies hunting habits in other genera (Houssay, 1893), as well as in other groups, such as certain steppe birds in Asia (Brehm, 1896), and South American weasels and birds (Hudson, 1892). It has been noted in a high degree of perfection in fishing squadrons of the white pelican on lakes of Southern California (cf. Bailey, 1917:43).

The Prey of Carnivores. The distinction between carnivorous species and insectivorous or omnivorous species is far from absolute. Most of the carnivores eat insects regularly or on occasion, even the cougar being said to take grasshoppers, while mole and shrew feed upon flesh to some degree. More than half of the common carnivores of North America eat fruits to some extent, with the consequence that this group passes more or less gradually into the omnivores. Notwithstanding these exceptions, the general habits of the group are well marked and are reflected in dentition, claws, and other structural features.

Life habits characteristic of the herbivorous mammals are found in somewhat less degree among the carnivores. The marten is arboreal, and its relative, the fisher, rather less so. The foxes and wolves are cursorial; the weasels and skunks exhibit the ferreting life habit; the hog-nosed skunk is more or less of a rooter, and the badger fossorial. The natatorial habit is represented by the otter; the mink is essentially amphibious, and the fisher rather less of a swimmer. Nearly all the group exhibit a strong tendency to be nocturnal, and some of them are strictly so. Practically all of them live in burrows or dens, more rarely in hollow trees, but only a few, such as the badger and the common skunk, hibernate to any considerable extent.

As would be expected, the prey of a carnivore is determined largely by relative size and activity, and by the habitat, the choice of which often has some connection with food preference or amount. Thus, the cougar kills deer, elk, mountain sheep, and antelope for the most part, while the foxes and coyotes are largely confined in nature to animals not larger than a jack rabbit or grouse, with emphasis on rodents. The wolverine as the largest of the mustelids regularly catches animals of the size of woodchucks and beaver, and is said to be able to pull down caribou and moose on occasion, but its smaller relatives find the rabbit and muskrat the upper limit in size. As a rule, the lesser mammals and ground birds furnish the bulk of the food of carnivores, but this is supplemented by snakes, lizards, frogs, insects, carrion, and fruit, as well as by fish, crustaceans, etc., in some species. The most completely carnivorous are the weasel and mink among the smaller forms, and the gray wolf, lynx, and cougar of the larger ones.

The snakes of North America are typically carnivorous, taking chiefly small animals, none of them being known to eat fruit, which is the nearest to flesh in texture. Two genera, the green and worm snakes, are mainly insectivorous, with the addition of earthworms in some instances. However, the great majority restrict their food to larger forms and differ chiefly in the degree of preference for warm- or cold-blooded animals.

It is evident that the carnivores may exert a telling effect upon the number of herbivores and through this upon the composition of the biotic community. The relation is necessarily reciprocal and involves the whole question of dynamic balance in nature, which is discussed in the following chapter. Connected with this is that of the indirect effect upon the plant matrix as a consequence of the destruction of herbivorous rodents on a large scale. Campaigns of eradication of flesh-eaters fail to reckon with these complex relations and have sometimes brought about an actual increase in rodents, usually detrimental to the human interest that prompted the destruction of the carnivores.

Carnivorous birds are not separable from mammals on the basis of any coactional effect, but stand out by themselves on account of their flight and special methods of securing prey. The vultures may be considered exclusively carrion-feeders, a habit in which they are joined by the caracara and the bald eagle. The hawks and owls exhibit less difference than would be expected in view of the nocturnal habits of the owls, though these must be reflected to a considerable degree in the small animals captured. Both live chiefly upon small mammals, birds, and reptiles; about two-thirds of each include insects in the diet. The osprey or fish hawk lives entirely upon fish, and the bald eagle largely so, while fish are a regular feature in the food of several other hawks, but only one owl, the screech owl. The Cooper and sharp-shinned hawks prey chiefly on larger wild birds, as do the American and western goshawks. A few species such as the pigmy owl and the sparrow hawk are mainly insectivorous, 314 out of 410 stomachs of the latter containing insects; 129, small mammals; and 70, small birds (cf. Henshaw, 1921).

Among the few carnivorous birds in other North American families, the kingfisher prefers fish, but his tastes cover lizards, frogs, insects and crustaceans. The shrike is said to feed principally upon grasshoppers, but it captures many small mammals and some birds; its lack of talons causes it to impale its large prey, and it is also supposed to use this device for *al fresco* storage. The road runner alone of the bird carnivores employs a mixed diet, adding cactus fruits to a long list of animals ranging from mice and small birds to snails and caterpillars.

The examination of more than a thousand pellets of the marsh hawk in Florida disclosed that this bird lives largely upon cotton rats in the particular region. The number for this rat was 925 to 21 for the cottontail and 7 for the common mole. Of more than 40 species of birds taken, only 3 were found in more than 10 instances, namely, song sparrow, 64; meadow lark, 26; savanna sparrow, 23 (Stoddard, 1931). By contrast, Cooper's hawk yielded 38 stomachs with poultry and game birds, 60 with other birds, and 12 with mammals, out of a total of 123 (Henshaw, 1921).

First and last, the raptores take a prodigious toll of the smaller mammals, birds, reptiles, and insects, both in number and species. This is strikingly shown at the time of lemming migrations, as well as in other cyclic concentrations, but definite knowledge of the direct effect upon the composition of the biotic community is exceedingly difficult to secure. This is even truer of the indirect influence upon the plant matrix, but, in terms of seed- and fruit-eating coactees, this may well be considerable and in some instances locally decisive.

The Prey of Insectivorous Animals. Two groups occur, namely, cursorial and aerial. Those possessing powers of flight include many species of small birds, bats, and some insects. Of the birds, probably the swifts and creepers are the only common families that are exclusively insectivorous, though the flycatchers, kinglets, goatsuckers, swallows, vireos, wood warblers, and wrens are predominantly of this habit. Among the well-known species, the brown creeper, bush tit, barn and cliff swallows, chimney swift, house wren, nighthawk, phoebe, wood pewee, purple martin, yellow-billed cuckoo, and yellow-throated vireo rarely if ever consume vegetable matter, as is true in a high degree of the white-headed and arctic three-toed woodpeckers. Fruits and seeds constitute about 15 per cent of the food of kingbirds, kinglets, and pipits, though under compulsion this may rise greatly, the last eating as much as 51 per cent in December. Approximately a fourth of the diet of the meadow lark, bluebird, chickadee, and myrtle warbler consists of plant materials, and much the same ratio obtains with the downy and hairy woodpecker and certain ant-eating flickers. Beyond doubt, the more truly insectivorous birds and the omnivorous forms that confine themselves to insects in the summer make vast inroads on the insects of all climax communities and their seral stages, but definite values cannot even be approximated until quantitative studies are much more the rule (cf. McAtee, 1911).

In the United States practically all species of bats live upon flying insects, though frugivorous and sanguivorous types occur to the southward. Dragonflies, some Hymenoptera (solitary wasps), and Diptera (robber flies) seize prey on the wing. In any one locality, an opening made through a natural forest by a stream would be frequented by certain birds and dragonflies during sunlight and by other birds and bats soon after sundown and possibly by other bats as darkness comes on or in the night. The different groups are thus out of direct competition with one another as they encounter different prey.

The cursorial type of insectivorous animals includes mammals, reptiles, amphibians, and invertebrates; it is possible that some few birds should be included. They are probably most important in the communities of arid areas, though some are found in all regions. The mammals that restrict their diet largely to termites are confined to warm communities in the tropics and subtropics. The lizards are chiefly insectivorous, though a few such as the desert iguana and the chuckwalla are entirely herbivorous, and some, like the collared and leopard lizards, feed upon plants as well as insects and other cold-blooded animals. The larger number confine their attentions to insects, though earthworms are sometimes added; some include slugs, frogs, and other small lizards, and others like the "glass snake" and the skunks vary the diet with bird eggs, nestlings, and young mice.

Insects carnivorous in the broad sense are termed predaceous when they capture other insects, spiders, etc. (Webster, 1880; Forbes, 1883, *b*); however, many tend to be omnivorous. Those that suck the blood of vertebrates, especially birds and mammals, may be regarded as truly carnivorous. The free-living bloodsuckers are chiefly Diptera, especially in the tundra and swampy areas of the coniferous forest. Ectoparasites are numerous among insects and arachnids, and an insignificant number of bats are also bloodsuckers.

PLANTS AS ACTIVE AGENTS (COACTORS)

Plants as Passive Members (Coactees)

Like animals, this group is best divided with respect to the type of coactee, whether plant or animal. Apart from the host of parasites represented by the fungi and bacteria, the number of genera is small, the mosses and ferns having practically none and the flowering plants a few among scattered families of the dicotyledons. To this group are also to be assigned the many saprophytes on dead or decaying matter, a few of which occur among flowering plants.

Flowering Plants. In this group belong those species that manufacture no food or but a part of what they require. Like other dependent plants, they belong to the great physiological category of hysterophytes, and may be more or less definitely divided into partial parasites, parasites proper, and saprophytes. They exhibit practically all possible stages in the evolution of this special habit, from rooted green plants such as Castilleia to chlorophyll-free genera reduced to flower and haustorium, as in the tropical Rafflesia. Many of them are more singular than important in the community, but some, like dodder and mistletoe, may exhibit a destructive coaction of significant effect.

Hysterophytes occur in a small number of families, i.e., twelve, some of which contain no holophytic or autonomous genera, though this may be a consequence of basing the family on the food habit. Several of these are tropical, containing such unique forms as Rafflesia, which is reduced to a single flower sometimes three feet across. In temperate regions, the most important families are Loranthaceae, Monotropaceae, and Orobanchaceae, together with scattered genera such as Corallorhiza among orchids and Cuscuta among bindweeds. A large majority of these are root parasites and do not often cause serious injury to the host, but certain of the mistletoes and many of the dodders may exert fatal effects. Cuscuta is especially destructive in California, often producing bare areas of considerable extent, on which succession is initiated.

Fungi and Bacteria. The destructive coactions of many of the flowerless hysterophytes are too well known to require comment apart from the role they take in modifying community processes such as competition and ecesis, and hence in changing the composition. On the other hand, the saprophytic forms, especially of bacteria, are invaluable in breaking down organic matter and converting it into nutrient substances for green plants. Among the most important fungous parasites of plants are the rusts, smuts, and mildews; the other great groups, namely, black, cup, pore, and gill fungi, and the molds, contain many parasitic species along with a much larger number saprophytic on dead leaves, wood, or humus material in the soil. It is exceptional that even rusts and smuts kill their host plants, but they sometimes handicap them sufficiently to lead to their partial elimination through competition or unfavorable climatic conditions. Many smuts, such as those of wheat and corn, destroy the seed and thus have a significant effect upon numbers and through them upon competition. Bacteria play a similar role, but one of relatively little importance by comparison with that in animals and man.

Animals as Passive Members (Coactees)

Insectivorous Plants. These resemble partial parasites inasmuch as they obtain a portion of their food from other organisms, but they exemplify an entirely different physiological habit. The latter is likewise more unique than socially significant, though it does denote a minor coaction bond in the community, and some of the species are more or less important seral dominants. Practically all the species grow in wet or boggy situations where inorganic nitrogen is deficient, but they differ much in the device for catching and digesting insects and other invertebrates. The modifications concern the leaf and range from ascidia or pitchers in *Sarraceniaceae*, *Nepenthaceae*, and Cephalotus in Saxifragaceae to sensitive glandular hairs or leaves in Drosera, Pinguicula, and Dionaea, and bladderlike traps in Utricularia. The so-called catchflies, belonging to the genera Silene and Viscaria of the Dianthaceae, entrap insects by means of a viscid secretion on the stem, but it is doubtful that they digest them. Because of its submerged habit, Utricularia is the most important coactor of the entire group; Forbes found 93 animals of 28 species in ten bladders (cf. p. 165), a fact that justifies his contention that the bladderwort is a formidable competitor of small fishes.

Fungi and Bacteria. Fungi that parasitize animals and man are found scattered through the algal fungi, sac fungi, yeasts, molds, and dermaphytes, the last mostly confined to man. Two groups, Empusaceae and Laboulbeniales, are restricted to insects, and another, the water molds or Saprolegniaceae, occur chiefly upon small aquatic animals. The genera Empusa and Saprolegnia are known to cause epidemic diseases, the first in flies, aphids, chinchbugs, grasshoppers, etc., and the second among fishfry, especially in hatcheries. A few molds, such as *Sporotrichum globuliferum* and *Botrytis cinerea*, are peculiarly fatal to true bugs and many larvae, and often become epidemic on a large scale during wet periods or seasons. A sac fungus, Cordyceps, is not uncommon on large grubs and caterpillars, the fruits forming long hornlike projections.

The number of bacterial diseases found among insects, birds, and mammals is large; some of these become epidemic and bring about the destruction of flocks and herds on a vast scale. To them has been ascribed the "crash," but the probability of such a happening is discussed in Chapter 5.

SYMBIOSIS

As stated earlier, the concept of symbiosis has sometimes been so broadened as to become meaningless, while on the other hand it has suffered from superficial observation and vivid imagination. Moreover, precise definition is impossible and exact application equally so in the general absence of critical study. At bottom, symbiosis is parasitism in some form or degree, and most so-called examples of symbiosis are little or nothing else, even in such classical illustrations as that of the lichen (Pound, 1892; Clements, 1897; cf. Oltmanns, 1923:501). The coactions involved have chiefly to do with food and, since at least two organisms are concerned, have potential value for the formation of colonies. When one or both are represented by a single individual, no colony results, but in many cases, such as in ants, the production of colonies is the rule. Among water animals, a number of supposed instances of symbiosis have to do with shelter or attachment, and these are found among plants as well (cf. Step, 1913).

The following account is confined largely to an enumeration of cases in which there is some evidence of mutual benefit, though often slight on one side at least, and to a brief consideration of the community significance of the various types. These may be conveniently grouped as relations between plant and plant, plant and animal, and between animals. Likewise, for convenience sake, those that deal with food coactions are passed in review here, regardless of whether they occur in land or water biomes.

Plant and Plant. In practically all examples of this type, the parasitic nature of one of the symbionts is more or less evident, and the vast majority of these are fungi or bacteria. Even in the pigmented algae, epiphytic species grade into endophytic ones, some of which are partial parasites, while others have become more or less completely dependent upon the host without as yet losing their chlorophyll, with the exception of Geosiphon which contains Nostoc as producent. This is almost certainly the relation that exists between blue-green algae and higher plants, as in the coaction of Anabaena with the water fern, Azolla, and Nostoc or its relatives in Sphagnum, certain liverworts, the Cycadaceae, and an occasional angiosperm, as Gunnera.

The outstanding symbiont among the bacteria is *Pseudomonoas (Rhizobium) radicicola*, which produces the characteristic root-tubercles of nearly all Fabaceae and is probably directly concerned with fixation of atmospheric nitrogen. Similar nodules are to be found in Alnus, Elaeagnus, Myrica, and Ceanothus (Neger, 1913), and in Casuarina and Podocarpus (McLuckie, 1923), and in most cases they are also to be ascribed to the same bacterium, though rarely a fungus may be concerned. Since Pseudomonas seems to be an obligatory endoparasite and the legume gains the boon of an added supply of nitrogen, this symbiosis constitutes one of the relatively few convincing examples of mutualism among plants, though even here the host grows normally in the absence of its symbiont. A somewhat similar physiological relation is thought to obtain between certain soil algae, Nostoc, Cylindrospermum, etc., and nitrogen-fixing bacteria, especially Azotobacter. Bacteria and yeasts may also exhibit certain characteristic types of symbiotic relation in the fermentation of kephir and ginger beer.

The lichen has long been cited as the chief example of mutualism between alga and fungus, but when allowance is once made for the microscopic size and nature of the host, the essential relation is one of parasitism in varying degree. This is clearest in the higher forms especially, in which the fungus sends a haustorium into the algal host, finally destroying it, but destruction of the host is the general result in practically all cases, it seems. Probably all the host algae can, and many of them do, live independently, and this is true also of a considerable number of the fungus parasites among the less integrated forms. As would be expected, a score or more of different fungi occur on the same species of algal host, and several of them may have two hosts enwrapped in the thallus. Furthermore, over a hundred species of lichens contain in addition to the proper host a second or rarely a third alga near the surface, always blue-green and producing a peculiar structure, the cephalodium, but of unknown function. Finally, there may be a secondary fungus, apparently parasitic on the lichen, but actually deriving its food also from the host algae.

From their life form, lichens also exhibit attachment coactions, as a result of which they may injure bark or leaves by shading, and in the higher forms, the thallus may also live parasitically on the bark, as Phillips has shown for Usnea (1931, *d*).

The association of fungal hyphae, regularly of Hymenomycetes, with roots has long been known as mycorhiza and explained as a rule in terms of mutualism. Its exact nature is still much debated, however, and recent investigators are in disagreement as to the proper interpretation of the majority of cases. This is readily intelligible in the light of Melin's statement that a double parasitism is involved (1925). In the case of conifers, he states that the fungus supplies organic nitrogen to the holophyte, perhaps also potassium and phosphorus, and in extreme cases serves to absorb all the water and nutrients needed by the host. On the other hand, McDougall regards all ectotrophic or external mycorhizas of forest trees as pure parasites (1914, 1922), and Masui (1927) states that it is going too far to say that mycorhiza is in general a symbiotic phenomenon, but that on the contrary it is purely parasitic, or at most only hemi-symbiotic. To the latter he assigns the mycorhizas formed by Boletus, to the former those produced by Armillaria, Polyporus, Hydnum, etc.

Mycorhizas are widely distributed through the orders of seed plants, and are also found in some ferns and liverworts. However, they are more characteristic of the roots of conifers, of diclinic trees such as alder, beech, birch, oak, etc., of Ericaceae, Rutaceae, and Orchidaceae. The fungus symbionts belong chiefly to the gill fungi, with some members of the pore fungi and puffballs, and rarely of other groups. Practically all the genera concerned also grow saprophytically in the soil and thus exemplify another type of coaction bond in the community.

Plant and Animal. The major categories of this type are coactions (1) between invertebrates and algae, rarely bacteria or fungi; (2) between insects and fungi; and (3) between flowers and pollinators. The animal symbionts with green algae, such as Zoochlorella, Chlamydomonas, Pleurococcus, and Scenedesmus, are represented by infusoria (Amoeba, Frontonia, Paramecium, Stentor, Vorticella, etc.), a few sponges, hydroids, ophiurids, and the flatworm Convoluta. These coactions have been much studied, and in the Infusoria in particular prove to be comparable with that in the lichens, the alga as a species deriving some benefit but the individual succumbing to parasitism. An identical coaction is exhibited by a yellow algal symbiont, Zooxanthella, with Foraminifera, Radiolaria, ciliates, sponges, and Bryozoa, and Convoluta as well. From their very structure, sponges are also susceptible of symbiotic relations with filamentous or massive algae of the Chlorophyceae and Florideae, though many of these are quite elementary in nature (Oltmanns, 1923). Pigmented bacteria appear to enter into partnership with the simpler Infusoria, as probably colorless ones also.

Probably the simplest combinations of insects with bacteria or fungi are those investigated by Schwartz (1924, 1932) for a scale insect, Lecanium, with which a variety of yeasts and molds may live as endosymbionts. Much better known are the coactions between the cultivator ants and termites on the one hand and various species of fungi on the other. These have been discussed briefly in another section (p. 152), and for the details the reader is referred to Wheeler's treatment (1923). As to the protection of flowering plants by ants, and the relation of the ants to such epiphytes as Myrmecodia and to the distribution of seeds with fleshy appendages, none of these appear to involve any real degree of mutualism. With respect to the symbiosis between ants and epiphytes described by Ule (cf. Forel, 1930: 518), Wheeler has justly expressed much skepticism (*loc. cit.*, 204).

Pollination Symbionts. The universal coaction that involves mutual benefits between plants and animals is found in the process of pollination. In flowers with highly specialized corolla, fertilization and consequent seed production are often impossible without insect aid, while in the vast majority of all flowers, cross-pollination through the agency of animal or wind appears to bring several decisive advantages. Even inconspicuous flowers may attract visitors by virtue of nectar, as in willows, or by means of an abundance of pollen. As is well known, the mutualism is all but purely a beneficial one, the insect obtaining food for itself or its young and the plant insuring the production of seed. The pollen consumed is a minor detail, being much less than the wastage incident to wind pollination, while the removal of the nectar is an advantage, directly as well as indirectly.

In detail, the plant profits by the production of more and better seed, and probably better offspring as well, when the flowers are cross-pollinated. In his classic study of the effects of cross- and self-fertilization (1876), Darwin found that the height of crossed morning glories was regularly greater than that of the selfed, the average ratio being 100:75, and the number of seeds was greater in much the same degree, as was the weight also. As between the two treatments, the seeds exhibited much variation in number and weight, but in general there was an advantage of 10–15 per cent in favor of cross-pollination. The greater vigor of the crossed plants was also demonstrated by exposing them to cold or to sudden changes of temperature and likewise by subjecting them to competition, and was further seen in earlier flowering.

The gains to the pollinator have to do entirely with the question of food supply, apart from shelter and protection in the case of lodgers. The food may be nectar for the immediate use of the adult or for storage, or pollen for producing bee bread to feed the larvae of bees. Both may be gathered from the same species or each one from a different species, but the general effect in pollination is the same. In one-flowered plants, crossing alone can occur, and this is probably the rule with few-flowered ones. However, when the number of flowers rises to hundreds and thousands, the manner of working by bees, butterflies, and hummingbirds in particular renders it probable that the great majority will be fertilized by the pollen of the plant that bears them. Furthermore, it is possible for certain sturdy

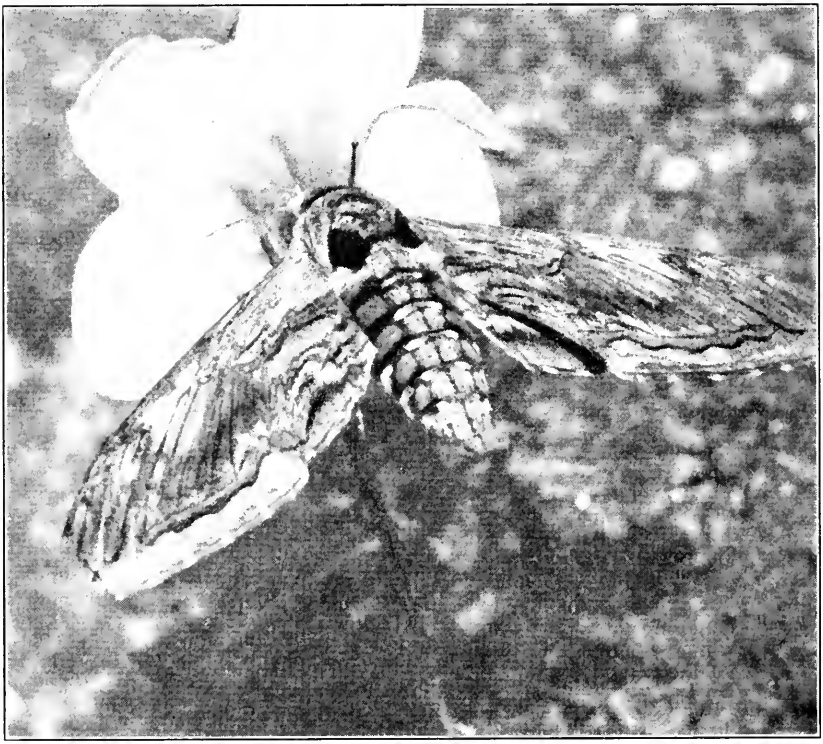


Fig. 33.—Insect pollination: The sphinx moth (*Protoparce quinquemaculatus* Haw.) visiting evening primrose. (Photo by Edith Clements.)

pollinators to pierce the corolla tube and secure the nectar without rendering the proper return, from which a chain of coactions may be set up. In California, the tanager punctures the thick tube of *Bignonia cherere*, and various species of hummingbirds that can neither do this nor obtain the nectar directly profit by his fondness for sweets, as do the ants and other insects that follow. On the other hand, nectar may rarely be poisonous, as in *Aesculus californica*, and the symbiotic relation leads to tragedy.

These direct effects do not comprise the whole relation between flowers and insects, or other pollinators such as the birds. The experimental study of pollination has brought much objective evidence to the support of the views of Darwin, Mueller, and others, who believed that the two partners have mutually affected the evolution of each other. Flower form and color are most intimately linked with the structure of the preferred visitor, while the form and size of the latter have been reciprocally molded by its flower preferences or by its collecting behavior, as exemplified by the so-called pollen baskets of bees (cf. Clements and Long, 1923; Clements and Clements, 1928).

The community consequences of this type of mutualism may be inferred from the usually greater size and vigor of crossed plants and their enhanced seed production. These not only insure a steady and even an augmented supply of nectar and pollen for the animals concerned, but also a tangible increase in the food supply of all graminivores and frugivores, from weevils to birds and rodents. This is reflected in the larger number of seeds that escape destructive food coactions and hence are available for germination and the maintenance of the species.

Animal Symbionts. The question as to the presence of symbiosis in many animal coactions has been complicated by observation of a general nature and the not infrequent injection of prepossession (cf. Step, 1913). It is manifest that a very large number of assumed symbioses, and especially those that merely involve attachment, shelter, or lodging, are not at all mutualistic or only to such a slight degree as to be insignificant. Even in the fresh-water mussels (Anodonta, Unio, etc.) and the bitterling (Rhodeus), the relation appears to be a matter of reciprocal parasitism of a sort rather than symbiosis, at least in the sense indicated by Step (*loc cit.*, page 83). This interpretation is supported by the fact that there is no such mutual relation with other fishes that serve as hosts to the glochidia.

Many examples of symbiosis have been drawn from the social insects, especially ants, but only a relatively small number of these are mutual in any important degree. Most of these are covered by

Wheeler's term, "trophallaxis" (cf. page 154), while the many special trophic relations among ants belong to the general category of parasitism, or "parasitoidism" (Wheeler, 1923:196, 200). Forel (1930:250) would include under symbiosis "the more or less constant and intimate union of one species with another," but his definition and its application take in various types of parasitism. The resulting confusion in thought is exemplified by his statement in connection with the tree Cecropia that "on the side of Azteca, symbiosis is complete and successful, and the plant does not suffer in any way, rather the reverse"! Apart from the symbiotic trophism of adult and young, the most convincing examples of mutualism are to be found in the coactions between ants and aphids, coccids, etc., the so-called ant cattle (Forel, *loc. cit.*, page 492; Wheeler, page 178). For a concise but comprehensive account of the food coactions of ants, the reader should consult Wheeler, and further details are to be found in the two volumes of Forel. In the case of the bird-insect nesting relations described by Moreau (1936; Myers, 1929, 1935), an incomplete symbiosis appears to be involved in certain cases, but little is known of the cause and nature of the coaction in which birds build their nests alongside those of social insects.

CHAPTER 5

AGGREGATION, COMPETITION AND CYCLES

General Relations. The process of aggregation lies at the basis of social life in the biotic community, and hence it exhibits the most intimate relations with the other functions of the complex organism. It is the very essence of the association of organisms in the dynamic sense, and is primarily concerned with the integration of all the groupings, from the simplest family of plants or animals to the most highly differentiated climax. Like all community functions, it is the collective response of organisms to their environment, and in its turn it produces social patterns of all degrees of complexity. For plants, its general features have been elaborated by Clements (1901, 1916); for animals, its operation has been treated in much detail by Allee (1931). As with the other concepts of ecology, it now becomes necessary to examine it from the biotic standpoint and to make such modifications in it as the community life of plants and animals renders desirable.

The purpose of the present chapter is to discuss aggregation as a social process, to treat its significance in cooperation and competition, and to trace its relation to population numbers and movements and the consequences that flow from this. It is evident that reaction is dependent in the first degree upon aggregation, since this alone makes it possible to combine the effects of individual organisms into a cumulative and permanent whole. A somewhat similar relation obtains in respect to coaction. Though the latter may concern but two individuals, as in the case of food or reproduction, this is aggregation in its simplest form, from which all other forms arise directly or indirectly. The kind and degree of aggregation will determine whether cooperation or competition will rule in the resulting community, or whether they will alternate in space or time, as in the stages of succession. The connection with migration is even more intimate, since the two processes exhibit constant reciprocal action. All mixed aggregation, that is, every community unit above the rank of family, depends upon the operation of migration, while in the opposite direction the increasing pressure of numbers due to aggregation is probably the chief inciting cause for movement. In turn, ecesis or establishment rests in a large measure upon the cooperation of invading individuals or species, while the progression of seral stages is the outcome of the interplay between invaders and occupants in terms of cooperation and competition. Finally, the problem of populations and their fluctuation, of cycles, in short, is essentially a matter of aggregation, first of a particular species in a mounting phase of numbers, and then of its coactors, both predator and parasite, ushering in a second phase of sharp decline in the entire complex.

AGGREGATION AS A PROCESS

Causes of Aggregation. The basic explanation of aggregation is to be found in growth with consequent multiplication of individuals and their grouping about the parents for a longer or shorter period. The individuals once produced, the course of aggregation will depend upon several considerations, such as the medium, the type of organism, whether motile, mobile, or fixed, and the terrain, whether bare or occupied. The process is at its simplest in forms that remain together after fission, such as Merismopedia and Nostoc among the algae, Vorticella and Fuligo among protozoans, Volvox, and Hydra. Even among flowering plants, the behavior is very similar when the seeds or bulbils germinate on the parent plant, as in some onions, *Polygonum viviparum*, etc. However, the almost universal rule among rooted plants is for the spores or seeds to fall about the parent and give rise to a family in bare areas or a colony in those already occupied. In annuals, the family consists of one generation; in biennials and perennials, of two or more. Moreover, aggregation in the latter is promoted by offshoots of various sorts and may come to depend upon them almost wholly, especially in cultivation.

In the simple aggregation due to the fall of spores or seeds, gravity takes the primary role, and it has also some part to play when other factors enter. When transport occurs, simple aggregation is hindered and mixed aggregation is favored, in more or less correspondence with the efficiency of the migration device. However, even in the process of migration, simple aggregation recurs frequently when obstacles are interposed to the movement of wind, water, or soil, exemplified especially by windrows of tumbleweeds and wave lines of hydrophytes. On a smaller scale, a similar result ensues when barbed fruits are carried by animals or a rodent hoard is overlooked, though competition between the seedlings usually prevents ecesis in such instances. In the case of free algae, as well as of zoospores, aggregation may result from the combined or separate action of wind, wave, or current, the

Sargasso Sea being the outstanding example; and light may have a distinct effect upon motile forms.

As with plants, aggregation among animals is regularly a direct outcome of reproduction in the absence of dispersive processes. Likewise, it may result from the compulsion of such factors as currents of air or water, or from a more definite tropistic response to light, temperature, solutes, etc. More complex and autonomic in nature is aggregation in consequence of the search for shelter or for food, and still more a matter of internal urge is the grouping arising from the quest for mates. Such aggregation not only contains in itself a rudiment of social grouping, but, even more important, it leads to the reproduction upon which family aggregation at the various levels of integration is based.

It is evident that compulsion, tropism, and self-regulated movement may be combined in endless variety and that they may operate to produce or modify communities of all sorts, from the simplest family to the biome itself. In the latter, the plan is naturally most complicated and the pattern is to be recognized only through the analysis of the coactions that have led to the integration of the innumerable minor communities. This is well exemplified by the pioneer attempt of Forbes to sketch the coaction bonds operating in the black-bass community of fresh water (1887; Allee, 1931, *a*:83).

In two illuminating chapters (1931:38–80), Allee has discussed the physical factors and the animal responses concerned in the formation of families and colonies, as disclosed by the experimental studies of a considerable number of investigators. He has also summarized the results so far obtained in determining the sense directive in various types of integration, for example, touch in harvestmen, odor in moths, sight in catfish, and sound in beetles and ants (pp. 88–97).

Aggregation on Land. Definite studies of the process of aggregation in connection with the origin or modification of terrestrial communities have dealt chiefly with plants and with primary reference to succession (Clements, 1910, 1916). The investigation of grouping in land animals has been largely incidental to other objectives, though Shelford has described pioneer aggregations concerned in succession (1911, *a–c*; 1913, *a*). The first organisms to invade bare areas in sand dunes at the south end of Lake Michigan are the tiger beetle, *Cicindela lepida* Dj., and the spider, *Geolycosa pikei* Marx. The entrance of the adult beetles may occur in autumn, or in spring when the eggs are deposited in the sand at some distance from one another. Upon hatching, each larva remains in position, merely drilling downward to a depth of about 45 centimeters. This constitutes an example of simple aggregation, comparable in a general way with that of plants. The spider probably invades as a consequence of the nocturnal wanderings of adults, the two species then forming an open colony as a result of mixed aggregation. At this point, plants enter to give the sand some small stability, the grass Ammophila in particular being quickly followed by a cutworm and this by Microbembex, a solitary wasp with social tendencies. With a steadily increasing number of invaders, both of plants and animals, complex aggregation assumes control of the development, to continue until the climax is reconstituted.

In the present situation, no definite rule can be laid down as to the type of invaders in bare areas. In certain subseres, the soil community remains in possession more or less intact to constitute the initial stage, which is quickly followed by the visible aggregation of either plants or animals or both. In the case of a severe burn, much of the soil fauna and other animals are destroyed or driven out for a time, and simple or mixed aggregation may follow in a very short time from the wind-blown spores of mosses and liverworts. In primary succession on rock, the process of aggregation concerns lichens alone for many years, the soil algae and fauna and the sparse insects usually appearing with the mosses. On the other hand, the hydrosere exhibits a more complicated type of aggregation inasmuch as plankton and larger aquatic forms are already in occupation, and complex aggregation of a sort operates from the first entrance of the submerged plants characteristic of the initial stage. However, the course and significance of aggregation have received little detailed attention in the past, and this situation will hardly be much improved until the biotic approach to the study of succession becomes more or less the rule.

Kinds of Aggregation. In the present scanty knowledge of details and of quantities in the process, a comprehensive analysis of aggregation seems to be unprofitable. As a working basis, it appears sufficient to distinguish simple aggregation, which results in a family with wide variation in numbers and generations. Contrasted with this is mixed aggregation, in which two or more species are concerned, giving rise to a colony of plants, animals, or the two combined, and also varying greatly as to numbers. Less definite as to concept but of even greater importance is complex aggregation, characteristic of most seral stages and of climax units, in which the simple and mixed types play a continuous or recurring part. The distinction between simple and mixed aggregation was also later recognized by Deegener (1918) in his designation of "associations" and "societies" as homotypic and heterotypic, in which he was followed by Wheeler (1930). Apart from this agreement, however, the viewpoint of the leading students of social behavior in animals differs materially from that of the bio-ecologist, and this is reflected to a large degree in both concepts and terminology.

This divergence is exemplified by Deegener's classification of animal communities, in which he distinguishes "associations" as accidental and serving no useful purpose to the individual members, and "societies" as essential and rendering a useful return to the individuals, or at least some of them (1917, 1918; cf. Allee, 1931, *a*:15). These are divided and subdivided to yield more than a hundred types, but, as the system is primarily a static one and burdened with a sesquipedalian terminology, it possesses little pertinence for the present treatment (cf. Allee, *loc. cit.*, page 14). It appears certain that aggregation will sometime be analyzed in considerable detail, especially with reference to the groupings of plants and animals both on land and in water, but this must follow much more extensive quantitative and experimental studies in the field.

Consequences of Aggregation. It is obvious that the coaction of coming together in a family or other group will set up other coactions as corollaries of this, and each may be of greater or less significance in the life of the community. The community may react upon the habitat, or the individuals may interact with one another, in such manner as to produce either beneficial or harmful effects. Quite frequently the two results may be combined in various degrees, though one or the other usually rules. In general, the intensity of effect depends chiefly upon the space relations of the individuals in the group, that is, upon the degree of crowding, so called, but it is also influenced by the qualities of the organisms concerned. In general, helpful coactions are more characteristic of the family and colony, and harmful ones of the more complex communities, but there are striking exceptions in both instances. The property of motility naturally plays a large part in crowding and its consequences, as does also the type of habitat, whether water, soil, or air.

In accordance with the above, it becomes necessary to distinguish three types of coaction following upon aggregation, on the basis of mutual effect. Two of these, cooperation and competition, are well known by name, but still too little understood as to fact; the third deals with processes indirectly harmful and may consequently be termed *disoperation*. It is clear that all three coactions may operate in any community and that they are in fact exhibited in some degree by practically all, though each grouping derives its distinctive character from the predominant process.

COOPERATION

Origin and Nature. Cooperation is the universal outcome of simple aggregation; in fact, it appears axiomatic that community life is impossible without it in at least some degree (Kropotkin, 1915). Even when the benefits are slight or obscure at the lowest levels, they must outweigh the disadvantages to render the community more than a transient affair. The advantage must be mutual, though often far from equal, and it may exist along with definite, though less critical, handicaps. In essence, then, cooperation is to be considered as a dynamic social process in which mutual benefit of some sort constitutes the chief bond and overrules the unavoidable disadvantages of massing or crowding. In the family, this bond is at its strongest, even when the members are counted by the thousands. It is less controlling in the colony, except when this has an adoptive pattern, and in communities of higher rank it breaks up into a looser complex of relations between families, colonies, and larger groupings.

It is obvious that, while cooperation rests upon mutual tolerance in terms of habits and space, its positive values are derived from the conservation of energy and material, especially food, from division of labor, and from increased care, parental or nutricial. The analysis of any cooperative community must be directed primarily to these processes, as has been so ably exemplified by Wheeler in particular (1923), and the success of community life is to be measured in such terms, with adequate recognition of the attendant disoperation or competition. So vast is this theme, especially in its human connotations, that even the barest outline is beyond the scope of the present treatment and little more can be attempted than to point out its major features in the biotic community. Of the extensive literature in this field, none exhibits so much of the spirit of dynamic ecology as Wheeler's "Social Life among the Insects," and the interested reader is referred to this as the most illuminating introduction to the subject.

Cooperation in Plant Community and Matrix. Though cooperation is generally on a much lower level in plant than in animal communities, it does occur and is not without significance. Its beginnings are to be seen in the cenobic algae, such as Gloeocapsa, in which the gelatinous sheaths of the initial cells serve to protect the whole family, or Microcoleus, whose outer filaments secrete a similar protection. In Nostoc and its relatives, division of labor appears in addition to a protective matrix, and community functions are assumed by spore and heterocyst, while another type of differentiation takes place in the motile Volvox. Similar phenomena are to be found among the Protozoa and are well exemplified by the plantlike slime molds, in which movement, protection, spore production, and dissemination are all more or less specialized functions of the community.

With respect to attached plants in general, cooperation is chiefly concerned with reaction, by means of which the community modifies the habitat in some degree to its advantage. This exists in small measure at least with some lichens and most mosses with respect to water relations, but is much more important in ferns and flowering plants, which may modify practically any one of the factors of the habitat. Such effects have been considered in some detail in the chapter on reactions, and hence it is necessary here merely to emphasize the cooperative nature of the process. Cooperation also plays a role in dominance and hence in the layering of communities, though the original selection is made by competition. It likewise operates in mass migration and invasion, and its effect is to be seen in both climax and seral stages. To a more limited degree, it is involved in local migration wherever the parent plant takes some concern for the fate of its offspring by such devices as catapult fruits or stolons and runners.

In symbiotic relations between plants of two species, cooperation is present in varying degrees, but it is rare that two respective families are concerned. In some instances, a single individual of each is involved, as is probably the case in many mycorhizas of trees and the fungi of orchids; in others, the microscopic organism is present in vast numbers in the tissues of a single symbiont, as with Nostoc and cycad, or clover and the nodule bacterium. This may prove to be the rule with lichens, though the fungus element is often derived from more than one germule. There are a few striking instances of symbiosis between a plant and an animal community, but these can best be treated in connection with similar relations between animals.

Cooperation in Animals below the Social Level. In considering the beneficial effects of aggregation, Allee has discussed in several chapters the results of the past decade that bear upon the stimulation of growth and reproduction by crowding, and the effect of crowding upon survival, as well as upon sex determination and morphology (1931, *a*:147–334). As a consequence, he reaches the conclusion that interdependence or automatic cooperation is so widespread among animals as to rank as a basic property of animal protoplasm, and probably of all organisms, an opinion supported by what has been said above as to plants. Such a type of cooperation has been more or less definitely demonstrated for tropistic aggregation in more than a hundred different groups, from bacteria and Infusoria to fishes and reptiles, the great majority of which are far below the level where distinctly social groupings occur. As in plants, such unsocial aggregation is a consequence of the response of the individual to physical factors, and the resulting cooperation arises out of the reaction of the group upon the habitat. It differs essentially from cooperation on the social level, in which coactions among the members of the group are the motive forces that bring about group organization and differentiation. However, the simpler type passes more or less imperceptibly into the other and no hard-and-fast line can be drawn between tropistic and social communities (cf. Kropotkin, 1915).

Cooperation in the Family. Although aggregation into families often involves something of the tropistic relation to a physical factor or to food, it is primarily determined by sex. The simplest cooperative unit in this category is the potential family, consisting of a single male and female in which the latter is fertilized, as, e.g., in a nuptial flight. A distinct advance in the nature of the social bond occurs when a pair remains mated for a longer period, such as a season or more. Reproduction leads to a second type of family comprising only the young organisms, in which the binding force may be purely tropistic or more or less social in nature. The first step toward parental cooperation is taken when one of the parents, usually the female, takes some concern for the fate of the eggs, and true cooperation results when this is shared by its mate. The first step toward actual cooperation within the family occurs when one or both parents remain to care for the young for a longer or shorter time, as do many of the vertebrates. However, this is realized only when the offspring assumes a certain and often the major share in the family tasks, as is best illustrated below the human family by Hymenoptera and termites (cf. Forel, 1930).

In the families of social insects, cooperation finds its chief expression in division of labor and in conservation of food. The former may occur without the origin of castes, as in Belanogaster, in which the older females lay eggs, the younger gather food and materials, and the youngest feed the larvae and tend the nest. Among the social wasps, a distinct worker caste first appears in the vespids, and then remains more or less typical of the three families of social bees, and especially of the honeybee. In certain ants, the division of labor is fourfold, a soldier caste being added to the three, males or drones, queens, and workers found among the social bees. A similar development of castes has taken place in the termites, but has been carried much further, to the point of producing eight castes, each containing both males and females, and as many as five or six of these may be found in the termite family (Wheeler, 1923:252).

In many desert ants, both division of labor and conservation of food, in the original as well as the derived sense, have been brought about by employing certain workers or soldiers (Wheeler, 1908; 1923: 179,335) as "honey jars." The honey is stored in the crops of such individuals, which become so distended that the ants are unable to walk; when stroked by the workers, they regurgitate droplets to serve as food for them. Such reciprocal feeding, or trophallaxis, as Wheeler terms it, usually concerns larvae and adults in ants, as well as in the social wasps, but is entirely lacking in social bees. In wasps, the larvae are fed with pellets made of caterpillars, flies, etc., and the nurse adults imbibe the sugary saliva that exudes from the mouth of the larva. Ant larvae may be given solid food such as pieces of insects or pellets or liquids regurgitated by the workers that nurse them. In turn, the larvae yield secretions that are eagerly sought by the adult; these may be sweet saliva or fatty substances excreted through the integument. With termites, trophallaxis is primarily an adult coaction, in which they feed each other with saliva, with regurgitated food, and with feces. In addition, they also produce fatty exudates, which are consumed by other individuals, the outcome being a complex food bond beyond that of any other family group of insects.

Outside of the groups of social insects, cooperation occurs but sporadically until the fishes and higher vertebrates are reached. Though there are scattered instances in other groups of care of eggs or young on the part of one parent, it is rare that the two parents cooperate in this respect. In birds, and many groups of mammals, the cooperation of male and female is the rule, as a consequence of which there results much division of labor in terms of behavior. Among the ungulates, the general absence of nest building and the necessity of constant foraging for food affords much less scope for family cooperative behavior. In the large aggregation families, such as flocks of birds and herds of ungulates, there may be a certain degree of division of labor in terms of leaders, scouts, and sentinels, but this apparently does not often assume a definite pattern.

Finally, cooperation in families is promoted by a means of communication among its members. There is no reason to discuss here the moot question of language among bees, ants, and other insects, especially since this hinges largely upon definition. It appears probable that a large number of species possess methods of communicating observations, warnings, and intentions to one another and that these play a large part in the integration of the family group, as well as its protection. One of the most remarkable examples of such cooperation is furnished by squadrons of white pelicans, which perform a number of evolutions with faultless precision in driving fish to shoal waters. An illuminating inquiry into this subject has been made by Stoddard and his associates (1931), who find a dozen distinct calls in the vocabulary of the bobwhite quail (*Colinus virginianus* L.). The best known and most characteristic of these is the "bobwhite" call, which appears to be uttered chiefly by the unmated cocks. The others are the crowing or caterwauling call, the scatter or covey call, the lost call, the decoy ruse call, the distress call, the cackle note, the battle cry, the alarm note, the food call, and the conversational tones, most of them having to do with the guidance of the covey.

Cooperation in insect families has been carried to the incidental guests of the family. Wheeler (*loc. cit.*, page 174) says: "I have endeavored to indicate how trophallaxis, originally developed as a mutual trophic relation between the queen and her brood, has expanded with the growth of the colony, like an ever-widening vortex, till it involves, first, all the adults as well as the brood and therefore the entire colony; second, a great number of alien insects that have managed to get a foothold in the nest as scavengers, predators and parasites (symphiles); third, alien social insects, that is, other species of ants (social parasites); fourth, alien insects that live outside the nest and are 'milked' by the ants (trophobionts)." Wheeler has also named and classified the relations of ants to other organisms (*loc. cit.* page 200), of which social parasitism, myrmecophily, and trophobiosis have to do chiefly with families. The term *family* is here applied to so-called colonies of Hymenoptera and termites as a matter of fact (Read, 1920:35), and its use is in accord with the general implications of the term as applied to plants. However, it is to be understood that various small animals occur on and among the individuals that constitute the plant family just as these alien insects and fungi (usually not noted) occur in the animal family.

Cooperation in the Colony. Colony is here used in the sense of a new group of invaders of new territory composed of two or more species. This is the plant-ecological connotation. Cooperation in colonies is generally a matter of symbiotic relation, in view of the fact that two or more species are involved. Naturally, the best examples are found in animal colonies because of their activity and food demands, but they occur also among colonies of plants and animals and probably among those of plants alone. The debatable question of the nature of the relation between ants and Acacia, Mymecodia, etc. (cf. Lubbock, 1882:57), may be left to one side, since this is not a matter of a plant-animal community

The most familiar examples of cooperation in an animal colony are those in which insects that excrete "honey dew," such as plant lice, mealy bugs, and scale insects, are attended by ants or by beetles such as the silvanids. These gather the sweet excrement as it falls on the leaves of the host plant or take it directly from the bodies as it is made. Some species of ants have developed the habit of stroking individuals of the phytophthora to cause them to excrete more liquid. Moreover, they conserve and increase the supply of this food by protecting the producers from marauding enemies, caring for them in special shelters, gathering and distributing the eggs, and transporting the adults to their proper host plants (Wheeler, 1923:178,31).

Cooperation in Plant-animal Colonies. The simplest cooperation in such colonies is found both in water and in soils that contain algae. The carbon dioxide required by the algae for photosynthesis is supplied in large measure by the animals, and in turn the algae give off oxygen for animal respiration. The waste products of the animals as well as the dead bodies are broken down by bacteria and the simple materials elaborated to the point where they can be utilized by the algae. A specific example of such a relation at or near the surface is furnished by Nostoc and Azotobacter.

A much more striking behavior cooperation exists between several groups of insects and the fungi they cultivate for food when setting up new colonies and entering new areas. Such a symbiotic relation is exhibited by beetles, ants, and termites, the general features being more or less similar for the three groups. The "ambrosia" beetles tunnel in twigs or wood, placing the eggs singly in pits and then filling these with chips and mycelium, which is renewed by the mother from time to time. She also clears the refuse away from the pits, and this is utilized for further development of mycelium. When the female leaves her pit, she carries conidia of the particular species of hyphomycete to her new home. Though there is considerable choice in the selection of a nesting site, each species of beetle makes use of a particular species of mold.

By comparison, the fungous gardens of the ants and termites are huge affairs, in keeping with their large compounds, but the members of these two groups are in accord with the ambrosia beetles in selecting a single species of fungus for culture. The ants are known to use the mycelium of agarics, polypores, and black fungi, while the first and last have been found in the cultures of termites. The higher genera of ants cut segments from leaves and carry them to the nest to be comminuted and made into a medium for growing the mycelium. The hyphal threads are manipulated by specialized workers in such fashion as to produce swellings or bromatia, which serve as food for both adults and larvae. The transfer of a hyphal pellet from the old to a new nest is made by a queen, who also fertilizes the growing mycelium with various materials. The fungous gardens of termites are similar to those of ants, but the sowing of conidia is supposed to be through the feces of workers. However, among the adults neither the workers nor soldiers make use of the fungus.

Cooperation in Larger Communities. Apart from the families and colonies found within the larger units, cooperation in communities is more or less general or obscure by contrast with the processes discussed in the preceding pages. It is said to occur to some degree in mixed herds of African game (Selous, 1908; Roosevelt, 1910), where several species of ungulates herd together and respond to the signal of any one of them, and to exist between cowbirds and bison (Seton, 1929:3:685). The best-known and most definite type of cooperation in the biome in general is that between plants and anthophilous insects, in which the relation is not only intimate and detailed, but is likewise more or less obligatory for both organisms. In spite of these facts, however, the organization of such cooperative communities is both loose and temporary, and follows the kaleidoscopic pattern of most of the smaller biotic units in faciation or association.

Cooperation and Human Communities. Like all other social organisms, man is subject to the operation of aggregation and exemplifies its effects, though he has it much more in his power to modify or escape the results if harmful. As with all social groups, cooperation in rudimentary form first developed in connection with mating and then appeared in the family, to be further emphasized in the super-family or tribe. Division of labor with attendant increase of parental care and conservation of energy and materials must have been present almost from the outset, but necessarily became more marked with each successive stage in culture, from hunting to the pastoral to the agricultural. This was not merely because of greater differentiation in each new culture, but also for the reason that the preceding stages persisted in some degree beside each later one. Urbanization placed an enormous emphasis upon division of labor and consequent specialization, and at the same time insured that the ancient vocations of hunting, war, grazing, and farming should feel a similar impetus, but in lesser degree. As a consequence, while the modern urban community seems to be far withdrawn from kinship with the biome, in fact its dependence upon it has never been greater.

DISOPERATION

Nature and Scope. As suggested previously, the harmful effects arising from aggregation or crowding may well be termed disoperation. This stands in direct contrast to cooperation in consequence, but it is less clearly distinguished from competition. However, the essence of competition is the attempt to secure more than a proportionate share of a limited supply of something, e.g., raw materials, food, space, or material for construction. In comparison, disoperation includes chiefly those harmful effects that have to do with changed conditions or behavior, as in the accumulation of carbon dioxide, toxins, or excreta. Since all coactions may be classed as beneficial or harmful with respect to the needs of a species, it is evident that no absolute line can be drawn between them, since even cooperation may present disadvantages. Nevertheless, the four main types of coaction, namely, cooperation, disoperation, competition, and destruction, correspond to definite differences in process and outcome, and hence serve a useful purpose in the analysis and organization of the myriad of interactions between organisms.

As with other coactions, disoperation may concern plants or animals, or both may be involved in the same process. Moreover, it may be combined with other types of coaction in some measure, or it may be a secondary effect of any one of them.

Disoperation in Plant Communities. Disoperation among plants is largely an outcome of additive reactions, as in the production of carbon dioxide or other toxins in the soil. This occurs, as a rule, only in colloidal or waterlogged soils, where it is a concomitant of competition for an inadequate supply of oxygen, with the consequence that the two effects are difficult to separate. Acids and other more or less deleterious substances are produced by the decay of plant remains in wet climates especially and may serve as a physiological barrier to certain invaders or lead to the actual elimination of some species (cf. Clements, 1921 *b*). The accumulation of leaves in forests may be disoperative to a high degree in dry climates, or wherever a thick layer of duff is produced or a dense interwoven carpet of pine needles is formed. Such conditions not only render germination difficult or fruitless, but they likewise hinder seedlings from rooting in the mineral soil beneath, with its proper supply of water and nutrients.

Disoperation may also act through the canopy of forest or thicket by decreasing the light intensity or the effective rainfall. The light effect is felt in the competition between individuals of the canopy (e.g., Fig. 34) or of the layers below, but it results also in a direct handicap to each successive layer, as well as to the seedlings of the dominants. The last effect in particular is likewise exerted by the progressive interception of falling rain from canopy to the lowermost layer. In regions such as that about Pikes Peak where summer precipitation is mostly in the form of light showers, interception by the coniferous crowns regularly accounts for a large portion of the rainfall, with a corresponding reduction in ground cover and the germination of tree seeds. Furthermore, though reaction and competition are regarded as the driving forces in succession, it is clear that disoperation plays a regular though secondary role.

FIG. 34.—Disoperation between Spanish moss (*Tillandsia usneoides*) and live-oak (*Quercus virginiana*), northern Florida. (Photo by J. R. Watson.)

Disoperation in Animal Communities. With the exception of competition in the proper or strict sense, all coactions that result in discomfort or disadvantage to individual or group may be regarded as disoperative, if the effect falls short of the destruction of the organism. Here again the effect is naturally one of degree, since the same parasite may weaken, cripple, or kill its host in accordance with the intensity of its action. Hence, internal and attached parasites have been considered in the chapter on coactions, leaving for the present treatment the independent parasites, which exemplify the original meaning of the word. Apart from human society, the most striking of these are probably represented by insects and a few birds. In one direction, the beginning of such a relation is to be seen in cases of trophallaxis where there is an actual exploitation of the larvae without an adequate return, as in certain social wasps (Wheeler, 1923:83). An advance upon this relation is made by such ant guests as Lomechusa and its relatives, which beg food from their hosts. The step from beggary to thievery is a short one, as is shown by Antennophorus in particular (*loc. cit.*, page 226), as well as by the thief ants and certain mymecophiles (*loc. cit.*, pages 201, 221). When eggs or larvae are stolen, thievery often leads to slavery in varying degree (*loc. cit.*, page 207).

Crowding brings about disoperation among animals, especially in families or colonies of aquatic organisms, and this may be expressed in terms of growth, reproduction, or survival. Aggregation probably produces these effects chiefly through competition for food or oxygen, but toxic substances in excreta also play a large part, and it is at least possible that volume and space as such may be involved in some instances (Allee, 1931, *a*:118).

There are instances of disoperation of bloodsucking insects which carry fatal diseases and thus destroy their food supply, but all clear cases are associated with human disturbance of natural communities. However, Ricker (1932) has pointed out that, in certain ponds under conditions that might well occur without man's interference, suckers remove submerged vegetation which supports various aquatic invertebrates and produce a mud bottom in which only bloodworms (chironomid larvae) occur. The suckers thereby decrease the favorite food of trout which pick a considerable part of it from the plants, and the number of trout is decreased. This is a clear example of disoperation, and Ricker points out that at the same time trout and suckers are to some extent in direct competition for the same food (cf, Cahn, 1929).

COMPETITION

Nature and Correlation. In contrasting competition with other coactions in preceding sections, it has already been defined in brief, but a comprehensive treatment demands that the lines be drawn with more exactness and in greater detail. The process may be defined inclusively as a more or less active demand in excess of the immediate supply of material or condition on the part of two or more organisms. It may concern a particular object or a set of conditions; it may be exhibited by as few as two individuals, by a vast family horde as with many ungulates, and in communities of every possible size and complexity. Its most striking manifestations are associated with crowding in the usual sense, though keen competition frequently occurs in what is visually open spacing, as with desert shrubs and bird territories. Competition is regularly most marked between organisms with the same or similar needs, as within a particular life form of plant or animal, but it may even take place between plants and animals in soil, aquatic, or parasitic communities.

In general, competition is to be distinguished from all other coactions by the test of a common demand upon a limited supply. This criterion applies even to the combat between two males for the same mate. However, the active or passive contest between an animal and its food organisms, as well as combat between two animal families, belong to a different category. This non-competitive type includes in particular the destruction exerted by carnivores, though an active competition often exists among these. Similarly, for example, the parasitism of the cowbird is not competition in the stict sense, in spite of the fact that passive competition occurs among the nestlings. Moreover, there is an element of competition in certain types of disoperation, instanced by the examples of beggary and thievery cited in the preceding section. Furthermore, though cooperation is the exact antithesis of disoperation, it is also antithetic to competition, since competition is regularly harmful in its effects. On the other hand, when competition leads to dominance and subordination, as it often does, especially among plants, a certain degree of cooperation is established. Consequently, while coaction is regarded as embracing all the interactions between organisms, competition comprises only those directed to a common need.

Types of Competitors and Objectives. It is evident that organisms compete with one another only when they make the same or similar demands and typically at the same time, in the absence of an adequate supply. This may be for one, for several, or for all the essential factors of the habitat. However, there can be no significant competition between an oak and a forb of the forest floor after the latter has become subordinated, though it may exist when the oak is a yearling or when the ground layer is well developed. As a consequence, competition depends in the first instance upon the life forms and life habits involved, and in the second upon the manner and degree of aggregation. Plants and animals will compete least frequently with each other because of certain basic differences in their demands, but when they are similar in size, as in microplankton, or in nutrition, as with leaf parasites, competition does arise. Competition will be keener between mammals than between mammals and birds, as a rule, but there is little between carnivore and herbivore except in so far as some tend to be omnivorous. However, the rivalry among squirrels and nutcrackers for pine seeds may be intense. In other words, similarity in behavior, that is in life habits, may often overrule life form.

Since the term itself denotes common seeking, there is no further competition without a proper degree of density or crowding, and the effects increase more or less geometrically with the crowding. Competition thus becomes peculiarly a community function, and hence is necessarily affected by the manner of aggregation, the structure in terms of layers and minor communities, and the developmental stage attained.

Course and Outcome of Competition. As with other phases of competition, the absence of detailed studies renders it impossible to trace more than its general course in animal communities (cf. Forbes, 1887; Howard, 1920; Allee, 1931, *a*). On the other hand, plants and plant communities have received considerable attention from this approach, and the nature and course of this function are fairly well understood, as is shown later in this section. The general stages of the processes are epitomized in the outcome, which is represented by dominance in varying degree for the successful competitors and by subordination or elimination for the unsuccessful ones. Subordination may result in subdominance to produce the layers of forest and thicket or the aspect societies of grassland, or it may lead to suppression in the guise of secondary species and communities. When suppression reaches the extreme of elongation or dwarfing, it passes into elimination, which constitutes a universal feature of succession.

A similar series of competition phenomena is to be found in animal communities, though in the absence of dominance on land it is less pronounced and visible. It is readily seen in the leadership of old males in polygamous herds, in the culls of broods and the runts of litters, and in such social phenomena as the "peck order" of fowls. It is exemplified in some measure in the drawing of territorial limits by many species, but usually reaches its most characteristic expression among the sessile constituents of marine communities.

Reduction or Evasion of Competition. Competition may be reduced in intensity or more or less completely avoided in a variety of ways. It is obvious that such results may be secured by a reversal of the relations or conditions that promote competition, such as similarity of life form or life habit, close spacing, etc. The greater the variety in life forms or behavior, the larger the number of species that can exist side by side in essential harmony. This is well exemplified by subordination, as a result of which a large number of shrubs and herbs may thrive under a forest canopy, or a wealth of forbs flourish amid prairie grasses. A similar adjustment or evasion is evident in the insects and birds of tree trunks by contrast with those of the crowns, and it characterizes also the subterrene moles and gophers.

Evasion in time is perhaps even more general than that in space. It is best illustrated by aspect societies of plants or animals, or both, as a consequence of which the maximum demand is distributed through three or four major phases of the growing season or the year. Something of the same advantage, only in a smaller way, accrues from the nocturnal habit and in some degree also from estivation and hibernation. Though less regular in operation, annuation may possess similar value. This is particularly true of winter annuals in the Southwest and desert regions generally, and must apply in a large degree to the animals dependent upon them. It must also play some part in the dynamic balance of animal populations.

Similarities and Differences. With respect to the chief prerequisite for competition, namely, a common demand in excess of the supply, all communities, whether plant, animal, or mixed, are in complete accord. But beyond this, striking differences arise in the process as a result of the divergent demands made by autonomous plants and animals. The plant, and hence the plant matrix, as the producer of food from raw materials, makes demands, that are peculiar to it, upon water, carbon dioxide, nutrient salts, and light. The need for oxygen is felt by both plants and animals, and they are likewise in accord as to the essentials of respiration. As to appropriate working conditions, both groups of organisms are dependent upon temperature and radiation in varying measure, but there is no actual competition for these, apart from that for light. They may also exhibit competition for certain solutes, as diatoms, chara, Infusoria, and mollusks for lime and silica, though the movement of water or organism may obviate this to a certain extent.

Competition for food is characteristic of animals alone, with the exception of plant parasites and saprophytes. Animals are unique in competing for mates, though the rudiments of such competition may be seen in the motile gametes of a few algae. However, a process with a certain similarity is that of insect pollination, in which flowers compete with one another for pollinators.

PLANT COMPETITION

Nature and Kinds. By contrast with animals, the general lack of motility among plants renders their competition passive and hence inconspicuous, if not invisible. It is based upon reaction rather than coaction and is consequently more or less indirect in operation. Except for the early stages in succession, crowding is a regular feature of the plant matrix, and both individual and species regularly bear the impress of competition in some measure. The process begins with increasing aggregation so that shoots or roots occupy the same space to a certain degree and thus make joint demands in excess of the available or immediate supply. However, this effect is really exerted through reaction, each leafy shoot reducing the light intensity and thus affecting its neighbor, while each root system reacts similarly upon the water content and solutes of the soil. No direct coaction is involved except for those rare instances where growth leads to the compression or heaving of tuberous roots, chiefly under cultivation. A similar passivity characterizes the competition among flowers for insect visitors, relative success or failure depending upon the form, size, and color of the competing flowers.

The experimental study of plant competition as a process was discussed by Clements (1905) and later was developed on a comprehensive scale in the prairie climax with Weaver (1924) and with Weaver and Hansen (1928). This concerned itself with transplant cultures, sod transplants, and denuded quadrats in subclimax and true prairie, and utilized a number of dominants, subdominants, and ruderals as paired competitors. These represented a variety of life forms and a large number of species, namely, tall, mid, and short grasses, annual and perennial forbs, shrubs, and trees. Similar studies were carried out in the ecotone between woodland and prairie in order to disclose the essential relations between forest, scrub, and prairie, and the nature of competition between individuals of the same species was analyzed in several field crops. The course and outcome of competition were traced in terms of measured reactions, of functions, and of changes in form and structure to afford a detailed and coherent picture of the entire process.

The Factors in Competition. While such indirect factors as humidity, pressure, and wind may have some effect upon the process, plants can actually compete only for energy or materials, namely, for light, water, nutrients, oxygen, or carbon dioxide. However, competition for the last two is more or less exceptional, oxygen being at a deficit chiefly in saturated soil and carbon dioxide in pond and lake, the small amount in the air being kept fairly uniform through air currents. Of the three major factors, water is regularly first in importance in natural communities, light second, and nutrients last, though nutrients may stand first for intensive field crops. However, in temperate humid regions especially, water content may become of relatively little importance, while soil air or nutrients may become paramount, in accordance with the general rule that the factor present in the smallest amount relative to the demand will be the critical one.

With respect to layered communities, water is the decisive factor in the competition of the dominants of forest, scrub, or grassland. The grouping into the lower layers is largely an outcome of the competition for light, but within each layer it is probable that water is more important. However, in all but the most open stands, both water and light are concerned, and their relative significance is to be determined only by a specific study.

The Equipment of Plant Competitors. The most significant feature of competing plants is the life form, since this determines the behavior and relations of shoot and root. It bears the ecological impress of climate and soil, and hence largely determines the response to the direct physical factors, as well as to the reaction due to competition. The most telling characteristic of the life form is the duration or length of the life period, as a result of its effect upon occupation and to a large degree upon stature as well. Next in importance comes the rate of growth, which finds its most effective expression in the expanse and density of shoot and root systems, and the depth of the latter. Rate and amount of germination often yield an initial advantage difficult to overcome later, and these are related to the number and kind of seeds produced, which in turn are influenced by the competition among flowers for pollinators. Vigor and hardiness of root or shoot may also play a decisive role, since they frequently determine survival under unfavorable conditions, and especially under the stress of winter. Such qualities may be inherent in the protoplasm itself, but as a rule they are related to growth and structure, and particularly to ripening and dormancy.

In the final outcome, the species with the best equipment will furnish the dominants for the plant matrix, while those with somewhat less advantageous features will become subdominants. It is doubtless a matter of primary significance that the dominants of climaxes are drawn almost wholly from the three types of life form, namely, trees, shrubs, and grasses.

Competition among Flowers. In contrast to the competition among plants which rests chiefly upon the life form, that between flowers is based in some measure upon the taxonomic form. The actual success in attracting pollinators in large number depends mostly upon the size, color and odor of the flower, but with respect to effective visitors the form of the corolla and the arrangement of stamen, stigma, and nectary are of decisive influence. Floral competition is at work in many communities throughout the season, but it is probably most in evidence in meadow and prairie in early summer, when it may have a critical effect upon fertilization and seed production. Some species avoid competition to a certain extent by blooming earlier or later, but the number of pollinators is likely to be less at such times also. More effective evasion is secured by species that flower at unusual times or for brief periods, as with nocturnal and many ephemeral blossoms. A decisive advantage may also be obtained by such specialization as will favor a particularly skillful pollinator, such as red flowers which have long tubes especially adapted to hummingbirds.

Competition between Plants and Animals. From what has been said previously, it is manifest that plants and animals will compete with one another only when they need the same thing. As a result, such a coaction is hardly to be expected of green terrestrial plants, but may occur with parasites and saprophytes, aquatic forms, and in small degree with soil organisms. Such competition is primarily for food, but it may concern materials, like lime and silica, or working conditions, as oxygen. Dependent plants must secure their food supply from green plants directly or indirectly, much after the fashion of animals, and hence the two will come into competition with one another when they are living on the same host, even though not side by side. This is likewise true of saprobes, for example, bacteria and Infusoria, whether in water or soil, and it obtains in some measure in respect to geophilous fungi and the soil fauna. In both soil and water, there is inevitable competition for oxygen whenever the air content runs low, and a similar result ensues when great numbers of diatoms and radiolarians make excessive demands on the supply of silica, or coralline algae and anthozoans upon calcium carbonate.

There are occasional instances of direct competition between plant and animal, such as is exemplified by the flower-spider, *Misumena vatia* Clerck, which deprives the flower of pollinators. Equally striking, though less evident, is the competition between bladderworts (Utricularia) and young fishes, a relation that Forbes (1883, *a*, *c*) has emphasized as tending to decrease the number of fish. Ten bladders from a plant bearing several hundred contained 93 animals representing 28 species; of the total, 76 belonged to the Entomostraca and 8 were insect larvae. In ponds or lakes with well-defined communities of this plant, it is evident that its competition might prove decisive, at least in local areas.

ANIMAL COMPETITION

Nature and Kinds. It is desirable to stress again the fact that competition comprises a relatively small number of the countless coactions among animals, and involves only those in which two or more individuals seek to secure the same object, class of objects, or space. Such competition is an evident coaction when it is direct, but it leads to a wholly different type of interaction in the destruction of one of the competitors. Competition between carnivores may often result in a third coaction, namely, that of combat, also not infrequent among herbivores when competing for mates.

It is a well-known principle, emphasized by Darwin, that the struggle for existence is keener the more nearly identical the demands, and hence that competition is usually greatest between individuals of the same species. However, the investigation of competition by definite methods will doubtless reveal many exceptions. From its nature, competition is determined in the main by life form and in detail by behavior or life habit, though size or peculiarities of activity may also play a large part. All the animals of a particular district are in potential and often direct competition, though the smaller carnivores may take what is left of the kill of the larger ones. In nearly all cases the food preferences are overlapping near their margins, rather than identical at the center or first choice.

All examples of supposed competition outside of controlled conditions are open to some question. The black rat reached North America about 1775 and became well established before the brown or Norway rat arrived nearly a century later. Upon the arrival of the Norway rat, the black rat began to decrease in numbers and gradually disappeared until it has become rare. In the United States and Canada it appears to have survived in some large buildings in large cities because of its smaller size and has also survived in some one or two remote sections of the country districts. Whether the brown rat attacked and destroyed the black rat, or merely appropriated all the nesting places and food, there is no doubt that competition was a factor. The large wolf was early reduced in numbers and extirpated from many areas, and this was followed by a great increase in coyotes. Apparently the wolf does not prey upon the coyote, but competition probably involved suitable home sites and hunting territory.

Chapman (1931) is probably correct in referring to the limits of population imposed in cultures of Drosophila and of Tribolium in small spaces as due to competition, but has not presented the data on the mechanism of competition and biotic control, as they have not yet been worked out. He called attention to the work of Pemberton and Willard (1918, *a* and 1918, *b*), relative to a number of insect parasites of the fruitfly introduced into the Hawaiian Islands. A species of Opius was most effective, as it parasitized a large percentage of the host; a species of Dichasma was less so, but when both placed eggs in a host larva the less effective Dichasma overcame the Opius and survived. The conclusion was reached that the end result of the operation of both parasites cannot exceed that of the more successful one in any event.

The equipment of competitors and the course of the process is generally more evident in animals than in plants, but even in the simpler examples too little is known about these as yet. However, the effect or the outcome is frequently visible in subordination, suppression, changes in habit, numbers, and so forth, and hence is felt in varying degree in the composition of the community concerned. Finally, competition, like coaction in general, is sometimes important in connection with food, at other times in connection with shelter, space, or territory. Birds and mammals regularly exhibit a more or less definite competition for mates, and in some form this occurs in the large majority of animals; different herds or flocks in gregarious species not infrequently compete for what may well be termed economic position.

Because of the difficulties attendant upon them, experimental studies of competition among larger land animals are practically unknown, and until extensive exclusion and inclusion areas are available such study will be difficult. Except for the recent inquiries into competition among insects and minute or microscopic aquatic invertebrates (Allee, 1931, *a*), little experimental work has been done.

TERRITORY

Territory among Birds. Although but recently reinvestigated, the concept of territory may be traced back for more than a century, but with only occasional mention or consideration until the work of Howard in England (1907, 1914, 1920; cf. Miller, 1931; Nice, 1933; Michener and Michener, 1935). It has now become the favorite theme of many ornithologists and has been taken up in other fields, such as those of mammals and insects. In the most typical instances among birds, it involves both direct and indirect coaction—combat, song, and the choice of a mate all exemplifying the former.

In spite of the late emergence of the idea, territory has been much defined and redefined, and will doubtless experience much more refinement with increasing objectivity. Howard (1920:73) states that each male establishes a territory at the beginning of the breeding season, and there isolates itself from the members of its own sex. But the change is carried further, so that the bird becomes openly hostile toward other males with whom it had previously lived on amicable terms. The seasonal organic condition is responsible for the functioning of the disposition that results in this intolerance, just as for that concerning the selection of a territory. This intolerance applies also to the selection of a mate. This may be summed up in the later brief statement that the male "isolates himself, makes himself conspicuous, becomes intolerant of other males and confines his movements to a definite area" (1920:64). Nice (1933:91) would limit the term still further: "territory can not mean just the nest spot when the adults feed in common; this may be the 'nest territory,' but is a very different matter from a territory in its strict sense, to which the parents confine themselves during the breeding season. Again the very essence of territory lies in its exclusiveness; if a bird's range is not defended, it is not a territory."

The extent of territory is supposed to be determined by the space available, as well as the amount of food in it; when food is scarce, the area required is larger. The boundaries are apparently arrived at by both direct and indirect competition, in connection with such features of the terrain as watercourses, openings, trees, bushes, etc. Once in possession, the male endeavors to keep all other males of the same species out of the area, and when their requirements are much the same, those of other species as well. Nice states that the complete procedure for acquiring a territory consists of four steps, namely, staking out the claim, the chase, the combat, and the final proclamation of ownership on the part of each bird (*loc. cit.*, page 94) (Fig. 35). Conspicuousness of the male is regarded as an essential feature of the process, which in passerines is chiefly secured through song, though the author states that the assertions made concerning the latter are pure theory. She further says that the bird students of the world "are in danger of going territory-mad," and it is patent that the present superstructure is out of proportion to its foundation, even Howard admitting in the preface of his book that much is mere speculation (cf. Errington and Hamerstrom, 1936:315, 398; Allen, 1934).

In a recent study of sex rhythm in ruffed grouse, Allen (1934) concludes that this has a direct bearing upon the problem of territory, as the following excerpt indicates:

"Bird behavior, including the earlier arrival of males than of females on the nesting ground, and of adults than first-year birds; selection of territory, song, fighting and display of plumage are explainable on the basis of the necessity of synchronizing the mating

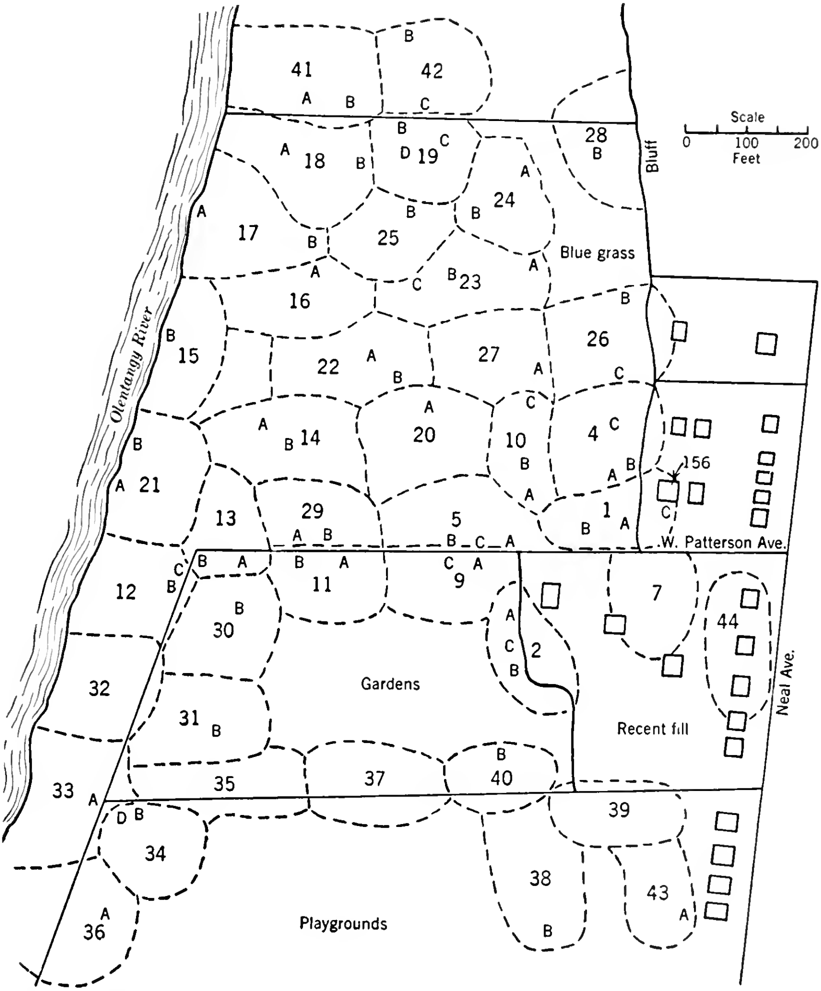


FIG. 35.—Map of song-sparrow territories. The letters *A*, *B*, *C*, represent the first, second and third nestings. (After Nice, 1931.)

cycles of male and female. In order to insure the propagation of the strongest birds, the virile male must keep all other males out of his territory and must drive out all females that are not in the same reproductive cycle as himself, lest another male mate with his female or lest he waste his energy on a female that does not synchronize with him."

Territory among Mammals. Red squirrels are thought by Hatt (1929) to possess territories with a range of about 250 yards, within which they seem to know every tree and hole. They have been seen to drive off intruders, but the limits are evidently not fixed, since they go beyond them for food. Mice of the genus Peromyscus may have a home range about 100 yards in diameter, but *P. maniculatus artemisiae* (Rho.), has been known to return over distances as great as 5 miles. No dispersal of the young is definitely known, and many individuals find suitable homes roundabout the original one. The porcupine has also been assumed to establish territories with reference to food supply and den sites (Gabrielson, 1928), breeding, shelter, and food all apparently being involved in the territorial coaction (cf. Klugh, 1927; Murie and Murie, 1930).

Among the mammals that feed in the sea and breed ashore, as well as in certain sea birds, the selection and establishment of territories are often accompanied by intense competition and fierce combats. In such instances food usually has little or no influence; thus, the males of the fur seal do not feed during the period of control of the harem territory, while the females may journey 50 to 100 miles to gorge themselves with fish (Preble, 1923). Howard also notes that in the guillemots the competition is necessarily for space in terms of nesting sites and not of food (1920:215).

Heape (1931:28) brought together a fund of information bearing upon the territorial habits of mammals in particular, but much of this is of the nature of general and often isolated observation, and in consequence it possesses little significance. The treatment is far from critical as attested by the statement that wolves respect the territory of caribou when small game is abundant, but do not when the supply of rabbits fails (page 46). In addition, the fable of the happy family of rattlesnake, prairie dog, and burrow owl appears in a new form, in which the voracious Sphenodon and petrel live together amicably in the same burrow (page 47). The inescapable tendency to broaden the concept of territory in order to fit all the facts is shown by Heape's distinction of a breeding or "home territory" ("almost invariably recognized as a sanctuary, though not always respected"!), a much wider "hunting territory," and a "neutral territory." Exclusiveness is not regarded as essential, and the term territory loses its justification in all such cases (cf. Nice, 1933:91).

Territory among Ants. Elton (1932) has outlined the territories of wood ants (*Formica rufa*) in a bird sanctuary in southern England.

The ants were chiefly engaged in "farming" the aphids on the trees and shrubs, especially the birches. Trackways extended from each nest to such trees as seemed to determine the size and form of each territory. Some of the trackways persisted in relation to the same trees for the period of three years, but others changed as a result of invading parties or the appearance of new trees. Each nest possessed its own distinct system, but there was normally no hostility among the families, and hence no defense of territorial rights was needed. However, the respect for such rights was not sufficient to prevent raids and the destruction of a nest (Fig. 36).

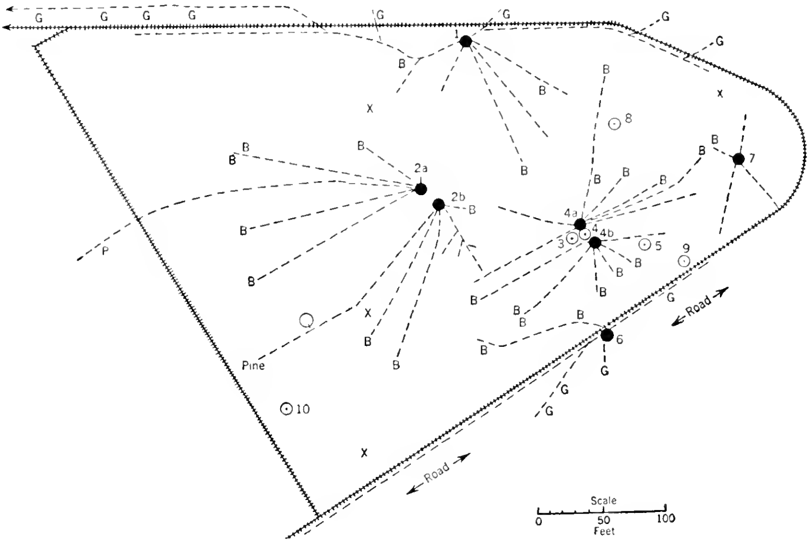


FIG. 36.—Sketch-map, July 20, 1929, of wood-ant trackways and nests in bird sanctuary at Picket Hill. Black dots are nests; circles with dots are places of former nests; broken lines are trackways; barred lines are fences or hedges; some, but not all, birch trees are put in (*B*), including majority visited by ants. Track from nest 1 outside the hedge continued 100 feet further west among gorse bushes (*G*). Approximate positions of willow wren nests in 1929 are shown by four crosses. (After Elton, 1932.)

Elton's account indicates that the territories observed were primarily a consequence of convenience and efficiency. Observations by the senior author of a vast aggregation of harvester ants (*Messor* species) in a community of Aristida, in the Colorado Desert, indicated that there were no definite trails and no territorial limits (see Fig. 17, page 83). In a neighboring region where four species were busily engaged in collecting grass fruits, the trackways intersected in all directions, so that independent ranges were out of the question in these species. However, in general, territories and runways are usually distinct and nests spaced well apart.

BIOTIC BALANCE

The older naturalists expressed the untenable view that a stable, static equilibrium existed among the organisms of any community, and in nature in general. It was further thought that fluctuations in populations of insects pests and other small forms were due to biotic modification by agricultural practices. This appears to have been assumed (Forbes, 1880, *a*, and others) in the face of locust outbreaks in the undisturbed western grassland to the contrary. Forbes says: "There is a general consent that primeval nature, as in the uninhabited forest or the untilled plain, presents a settled harmony of interaction among organic groups which is in strong contrast with the many serious maladjustments of plants and animals found in countries occupied by man."

In regard to the larger animals whose life histories and life spans are long and whose rate of replacement is slow as compared with the rapidly reproducing rodents and invertebrates, there is some evidence for distortion of equilibrium as regards numbers. Disturbance of balance in the deciduous forest is suggested in a diagram by Wood (1910), which is reproduced in Fig. 20, showing an increase of deer accompanying the decline of predators. The fact that prairie dogs increased with the reduction of wolves and coyotes (Merriam, 1901) is further evidence of some kind of a balance among the larger forms. Increase of deer to a point endangering their food supply has occurred repeatedly in recent years under protection and the reduction in numbers of predators. Such facts, so far as experience had brought them to attention a half century ago, were perhaps responsible for the idea of a stable equilibrium in regions not affected by man.

A natural result of this view has been so much tampering with communities in the name of agriculture, game conservation, and the preservation of rare species that it has been difficult to ascertain what the normal fluctuations are. Custodians of parks, forests and game preserves have usually viewed all declines of popular animals and all increases in unpopular ones with alarm, and immediately proposed and often executed useless or detrimental remedial measures.

The difficulty has arisen from the fact that normal fluctuations in abundance in areas not influenced by man had been but little studied. However, in the past decade, investigations have brought out the fact that such fluctuations occur in the sea relative to animals little influenced by man's activities (Blegvad, 1925) and in the arctic regions where such influences have affected only some of the larger species. This knowledge has been responsible for a new view of biotic equilibrium which assumes, as normal, a rather wide fluctuation in the number of individuals for many species. Frequently, several species rise to a maximum or sink to a minimum at about the same time. The abundant species react upon the habitat and destroy or provide food for other organisms, but the onslaught on the excess population due to flexibility of food habits, or the pressure of climate and the limitations of shelter and food supply, are the important factors in checking the increase of various species. In addition, disease may become a factor.

Elton (1930:17) is a strong advocate of a continuing state of lack of balance in nature, as the following excerpts indicate:

" 'The balance of nature' does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are themselves independently varying in numbers, the resultant confusion is remarkable.

"I shall take from this region one example, which illustrates very clearly the vast degree of *unbalance* that nature presents to the unaided eye. . . . Any animal community that is watched for a number of years presents a restless picture of unending changes in numbers, which are more often than not accompanied by striking changes in their habits of life.

"This instability is partly due to the external influences, and partly to the inherent manner in which every animal community is constructed. The environment (and in particular the climatic factors of the environment) does not remain the same from day to day and year to year. These changes react on the animals either through their direct effect or indirectly by affecting the plant-life of the region. On the other hand, internal factors dependent upon the manner in which animal communities are organized, also play a part in upsetting the balance of numbers. Epidemics caused by parasites are a very important example of this, while the change of habits consequent on the scarcity of food forms another. Irregular migration is one of the most important of all."

Criddle (1930) has pointed out a series of interactions connected with maxima of the sharptailed grouse in southern Manitoba. He states that the maxima for this grouse are preceded and accompanied by grasshopper outbreaks or maxima, the enhanced food supply being the primary cause of the rise. Furthermore, the beginning of a grasshopper maximum is nearly always preceded or followed by abnormally dry seasons, and the increase may be stopped by excessive rains. The decline in the grouse cycle is attributed mainly to heavy rains and cold, which reduce the amount of food taken to the nest by a third, owing to the inactivity of insects, and thus results in starving the young birds. Disease is regarded as the probable major factor in the reduction of the adults, but they are also decimated by the goshawk, a single predator destroying as many as 50 grouse in a winter. Criddle's explanation ignores possible direct physiological effects of the climatic factors in limiting populations, but nevertheless gives a broad explanation of the observed facts.

The view of Uvarov (1931) likewise takes food and predators into account along with climate: "The theory of stable equilibrium is based on the assumption that the numbers of an organism depend mainly on the numbers of their enemies and on the quantity of food, i.e., on factors which in their turn are dependent on other organisms. No one will deny the controlling value of these factors, but the evidence collected in this section, as well as in the whole of this paper, should go far towards proving that the key to the problem of balance in nature is to be looked for in the influence of climatic factors on living organisms. These factors cause a regular elimination of an enormous percentage of individuals under so-called normal conditions, which in fact are such that insects survive them, not because they are perfectly adapted to them, but only owing to their often fantastically high reproductive abilities. Any temporary deviations in the climatic factors, however slight they may be, affect the percentage of survival, either directly, or indirectly (through natural enemies and food-plants), and thus influence abundance."

Nicholson (1933) has recognized the importance of climate and enemies, but also points out the limitations of climate in rather strong terms, as follows: "We will suppose that the animals in a certain population would increase one hundredfold in each generation if unchecked, and also that, on the average, climate destroys 98 per cent of the animals. It is clear that the number of animals would be doubled in each successive generation if no other factors operated. Climate could never check this progressive increase, for it would continue to destroy only 98 per cent, its action being uninfluenced by the density of the animals. If, however, there is some other factor, such as a natural enemy, the action of which is governed by the density of animals, the destruction of the remaining 1 per cent, necessary to check an increase, would soon be accomplished. If this example were observed in nature, one would be tempted to conclude that, because climate destroys 98 per cent of the animals while the natural enemy destroys only 1 per cent, the limitation of the population is mainly due to the influence of climate. However, it is clear that the natural enemy is wholly responsible for control, because climate, by itself, would permit the density of the population to become indefinitely great."

He further concludes that there is a particular or "steady" density at which balance exists for each species, and that competition always *tends* to cause animals to reach and maintain this density. Climate and animal behavior "cannot themselves determine population densities, but they may have an important effect upon the values at which competition maintains these densities." It appears that these views fail to take into account the climatic cycle and its signal effects, and there is also grave doubt that the statistical approach is applicable to such an intricate complex of causes and effects. Powerful as competition is in the community, its action may be largely or almost entirely suspended, in the plant matrix at least, by optimum climatic or edaphic conditions.

In his studies of the wintering of quail in Iowa in relation to population, Errington (1934) reaches the following conclusions: "Food is the first essential constituent of a winter quail territory; cover is the second. The quality, distribution and convenience of food and cover, together with the bobwhite's intolerance of crowding, probably determine in largest measure the carrying capacity of environment for the species.

"Cover is of value to the bobwhite chiefly as protection or concealment in case of attack by enemies. Lack of cover means vulnerability to predation, whether enemies are few or many. Cover also has a certain value as shelter during periods of wet or cold weather, or during storms, but the necessity of shelter for the bob-white is usually over-rated about as much as escape cover is under-rated." For the southeastern United States, the earlier account by Stoddard (1931) is a mine of information as to causes of dynamic balance in quail populations.

CYCLES AND NUMBERS

Several important cycles of different character and rank find more or less definite expression in the structure and development of the biome. Chief among these are climatic mass migration and succession, while annuation, aspection (including hibernation and estivation), and diurnation represent a descending scale of effects. All these processes are concerned with numbers in varying form or degree, though this is particularly true of annuation, which comprises the fluctuations from year to year. With respect to the plant matrix, the primary influence is one of structure, and hence these topics are mostly considered in a later chapter (Beveridge, 1921; cf. Taylor, 1934; McAtee, 1936). By contrast, cycles of animal reproduction and migration are characterized by outstanding changes in population, often directed by competition, and are properly treated as more or less correlated results of the same or similar causes. Closely associated with them is the problem of dynamic balance or equilibrium in the biome, a condition that has usually been regarded as a more or less static norm.

Since land plants are stationary, fluctuations in their numbers are less dramatic than with animals, but they are of the same order and, as food and shelter, often assume a prior role in the causal sequence. Such phenomena are most evident in annuals, as these are more susceptible to the climatic features of a single year. The most striking instances are afforded by winter annuals in the Southwest; these may be present by billions in arid grassland or in the Colorado and Mohave deserts one year, and all but totally absent the next when the rainfall is seriously deficient. Similar "flushes" are exhibited by phytoplankton in small or shallow lakes, particularly by the blue-green algae; fleshy fungi often display great variation also and many parasitic species as well.

With perennial forbs and grasses, the departures are naturally much less striking, the annual effect being expressed largely in number and height of shoots and in seed production, since the competition of parents precludes the ecesis of most of the offspring. The production of dry material, as well as of seed, may vary severalfold, and this is directly reflected in the coactions of grazing animals in particular. With woody plants, the increment of each year is diffused over all or most of the plant in the form of an annual ring and as short twigs, and hence is hardly to be noted. However, more noticeable fluctuations are recorded in the seed crop, especially of conifers, oaks, hickories, etc., and reflected in the ecesis, as well as in the coactions of seed-eating animals. All these growth responses bear a more or less definite relation to the sunspot cycle, and it is an interesting fact that this relation was first seen in the annual rings of trees (Douglass, 1909) and was later extended to vegetation in general (Clements, 1916).

ANIMAL CYCLES

The question of animal cycles has been a subject of interest for more than a half-century, though the locust plague, as the most serious expression, has been a matter of concern for hundreds of years. Scientific activity in this field has been much stimulated by the work of Collett with the lemming (1895) and the observations of Seton in Arctic America (1911), and today it constitutes one of the most significant, as well as most difficult, lines of research in bio-ecology. However, as a field in which quantitative methods are paramount, the study of animal populations in nature still lingers on the threshold. It is manifest that many species have already dwindled beyond the point at which their fluctuations can be profitably investigated, a consequence that rules out practically all settled districts. So far as mammals are concerned, only regions in high latitudes hold much promise, but these are the very ones, as a rule, in which the difficulty of resident study over a long period all but eliminates adequate quantitative determinations. In the succinct account that follows, it should be constantly borne in mind that numbers and cycles are still based, for the most part, upon general and incidental observations and that discrepancies and contradictions are frequently to be encountered. Moreover, the only records that approximate accuracy are those of the fur returns of the Hudson Bay Company, and it is obvious that even such data as to populations fail in complete accuracy.

Nature of Animal Cycles. Cycles are characterized by alternating phases of plus and minus departures that pass more or less gradually into each other, the sunspot cycle being the best-known example. Cycles in populations are rather more variable, the rise to a maximum or the fall to a minimum occasionally occurring in a single year, while a high or low level may be maintained for two or more years. Low levels are the rule with desert annuals, a "flush" appearing only at intervals of several years. Low levels are likewise frequent in animal cycles, but maxima nearly always take the form of sharp peaks, as illustrated by the rabbit curve (Fig. 37). Fig. 38 shows seasonal variation in insect larvae and suggests an unusual abundance for *Chironomus bathophilus* for 1935.

In mammal cycles, the fall to the minimum has been regarded as a catastrophe that signalizes but one or, at most, two seasons, and hence has been commonly known as the "crash." However, an inspection of the curves of furs taken makes it clear that the rise is rapid quite as often as the fall and that the idea of a crash is in part due to the necessarily local, brief or discontinuous and superficial observa-

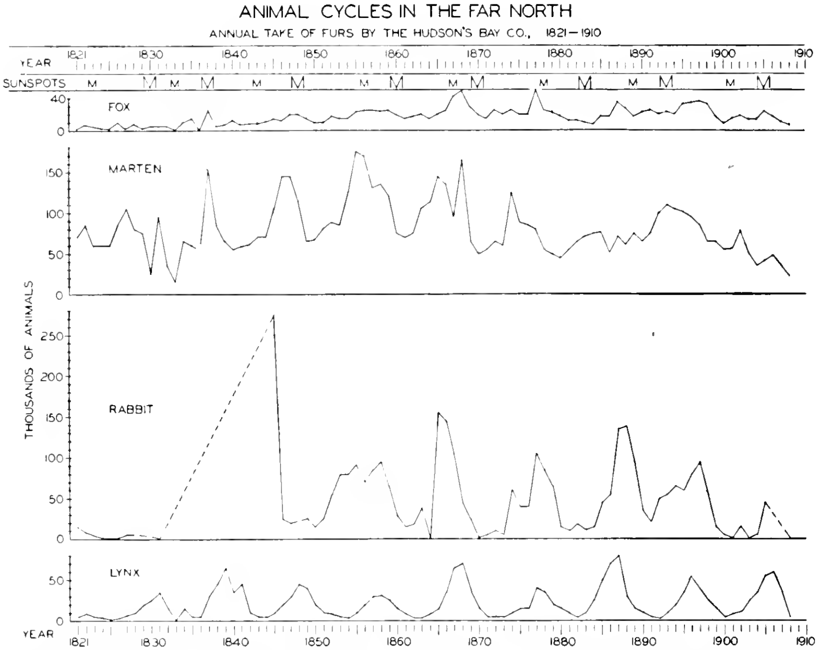


FIG. 37.—Sunspot cycles are shown in connection with Hudson Bay fur receipts. Small capital M indicates minimum and large capital M indicates maximum.

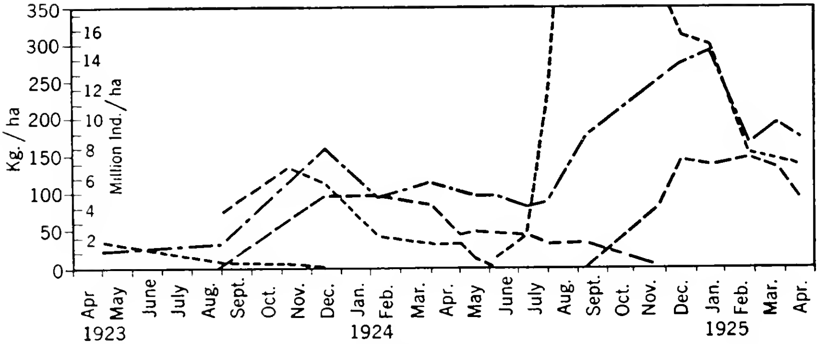


FIG. 38.—Showing variation in the number and weight of the larvae of Chironomus from month to month, April, 1923, through April, 1925, in Platten Lake (Plöner Becken). The short dashes are for the numbers of *C. bathophilus* larvae; the long dashes for the numbers of *C. plumosus* larvae; and the dot-dash line is for the total weight of larvae of both species. This is the average for the whole lake for the second year and all but the zone 0 to 4 meters for the first. (After Lundbeck, 1926.)

tions upon the fluctuations of numbers. Such defects in the method appear inescapable, and hence the data derived from the fur trade will probably for some time remain the best quantitative basis for studying cycles among animals.

An examination of the rabbit curve (Fig. 37), shows that the greatest change in a year was a drop from about 285,000 to about 20,000 skins during 1845–46, while over against this are two rises of a year each. The following table for the rabbit and lynx permits a

TABLE 3

PHASES OF RABBIT AND LYNX CYCLES

Rabbit				Lynx			
Phase	Period, Years	Dates	Rate M.	Phase	Period, Years	Dates	Rate M.
				Low...	5	1821–25	5–10
				Rise...	5	1826–30	5:35
				Fall....	2	1831–32	85:5
				Low...	3	1833–35	5–15
				Rise...	3	1836–38	5:65
				Fall....	4	1839–42	65:5
				Low...	1	1843	5
Fall.....	1	1845–46	285:20	Rise...	4	1844–47	5:45
Low....	3	1847–49	15–25	Fall....	3	1848–50	45:10
Rise....	4	1850–54	20:90	Low...	3	1851–53	10:5
High....	3	1855–57	70–95	Rise...	3	1854–56	5:30
Fall.....	3	1858–60	95:15	High...	2	1857–58	30
Low....	3	1861–63	5–40	Fall....	4	1859–62	30:5
Rise....	1	1864	5:155	Low...	2	1863–64	5
Fall.....	5	1865–69	155:5	Rise...	3	1865–67	5:80
Low....	3	1870–72	5–10	Fall....	4	1868–71	80:10
Rise....	4	1873–76	5:105	Low...	2	1872–73	5–10
Fall.....	3	1877–79	105:15	Rise...	4	1874–77	10:40
Low....	4	1880–83	10–20	Fall....	5	1878–82	40:5
Rise....	4	1884–87	15:140	Rise...	5	1883–87	5:80
Fall.....	3	1888–90	140:20	Fall....	4	1888–91	80:5
Rise....	6	1891–96	20:90	Low...	1	1892	5
Fall.....	4	1897–1900	90:5	Rise...	4	1893–96	5:55
Low....	3	1901–03	5–15	Fall....	4	1897–00	55:5
Rise....	1	1904	5:45	Low...	2	1901–02	5
Fall.....	4	1905–08	45:5	Rise...	4	1903–06	5:60
				Fall....	3	1907–09	60:5
				Low...	1	1910	5–
				Rise...	3+	1911–13+	3+

clearer view of the intervals than the curves do, and also makes it possible to determine the average length of rise and fall as approximately 3.3 years. These figures would seem to dispose of the "crash" as anything more than a rare catastrophe. They constitute a direct contradiction of the statements that "in a few weeks usually, the rabbits are wiped out," and that "to explain the variations we must seek *not* the reason for the increase—that is normal—but for the destructive agency that *ended the increase*" (Seton, 1911; cf. Leopold, 1931, 1934).

CAUSES OF ANIMAL CYCLES

In some cases the rise in abundance is important; in others, the decline. There are cases in which the decline affords the key to the explanation, while in others some special factor brings about an increase and the reverse causes a decline.

It is customary to view cycles as produced by conditions favoring reproduction and survival; however, all plants and animals produce more spores, seeds, eggs, or young than can normally develop to maturity. Under ideal conditions the tendency for any species is in the direction of an almost unlimited population. Such large numbers are unattainable because of various forces which tend to reduce the number of individuals. Small reproductive populations, though frequently a contributing factor, are responsible for minima, if at all, only in special types of life histories, such as that of the salmon. The maximum may appear important in one case, the minimum may be equally so in another. For convenience, the problem of fluctuations in abundance, whether these be cyclic or irregular, may be approached more often from the standpoint of the causes of failure to produce large populations of mature individuals or, in other words, causes of small populations.

There are eight causes of failure to produce a large number of late juvenile or adult offspring, which means the decrease in numbers of any abundant species. They are (1) decrease in the number of eggs produced or fertilized, owing to various causes, or destruction of eggs and very young stages; (2) death of adults and late juvenile stages from adverse physical conditions; (3) destruction by enemies and disease; (4) quantitative or qualitative insufficiency of food; (5) unsuccessful competition for space, shelter, or food; (6) physiological changes in reproductive vigor; (7) initial shortage in reproducing population; (8) cannibalism. To these may be added certain assumptions such as loss of immunity, etc., but of these little is definitely known.

Loss of Eggs and Early Stages. The codfish affords a noteworthy example of loss of eggs after fertilization as well as before. Though each female deposits from 3 to 9 million eggs annually, the North Sea is said to contain less than 45 million cod, of which about 23 million are probably females (Johnstone, 1908). The eggs must be fertilized while floating in the water, and hence bad weather at the time of spawning may cause a large number to fail of fertilization. The eggs of various insects are destroyed by unfavorable weather. Heavy rains prevent hatching of chinchbug eggs; loss of grasshopper

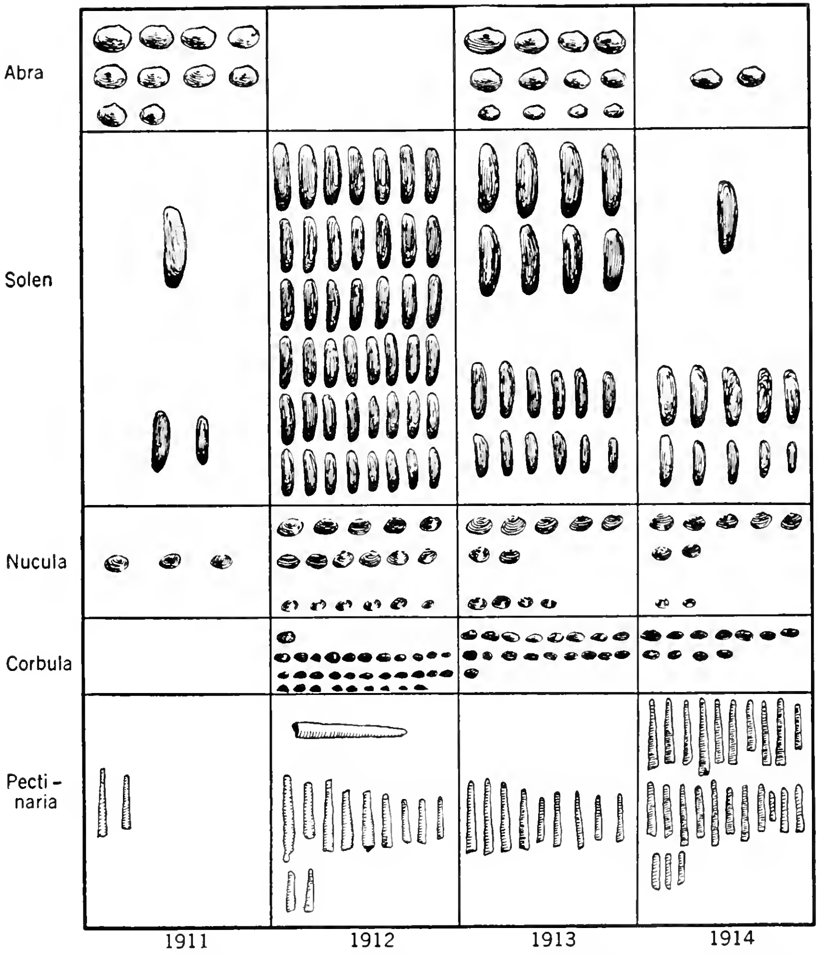


Fig. 39.—Some constituents of a marine bottom community in the Thisted Broad belonging to species eaten by plaice. The numbers shown are those occurring in the random samples of 1911-1914, on one-fifth square meter. It shows marked fluctuations of some of the predominants. (After Jensen, 1919.)

eggs is also great under adverse weather conditions. The eggs of many fishes are commonly destroyed by storms, floods, etc.

Losses during young stages are of even greater importance than loss of eggs. During periods of great abundance, the chinchbug may be practically wiped out, owing to drowning of young by early spring rains. Blegvad (1925) (Figs. 39 and 40) finds that the abundance of bottom invertebrates in Danish waters is in part controlled by physical conditions during the transition period from the pelagic to the bottom stage (cf. Johansen, 1927, 1929).

A decline in the reproductive rate may be brought about by failure to mate. Unsuccessful lamb raising may result from failure of sheep to mate, on account of lack of sharp temperature changes from day to night, which tend to stimulate the reproductive processes (Johnson, 1924). Foetal atrophy is common in the pig and rabbit, according to Hammond (1921). A decline in the production of eggs is associated with reduced numbers of grasshoppers (Parker, 1930). There are other cases of reduced reproductive rates for which no apparent cause has been assigned.

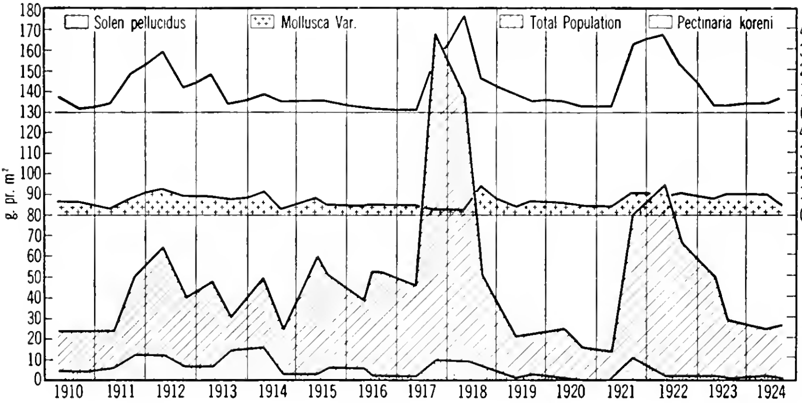


FIG. 40.—Showing the rough agreement between the three species of fish-food invertebrates, in relation to the total invertebrate population of the same community. Such relations appear to be the usual rule. (Modified from Blegvad, 1925.)

Death of Well-developed or Mature Stages from Adverse Physical Conditions. The later instars of insect larvae, weaned mammals, birds out of the nest, etc., and adults of all types of animals often succumb to unfavorable factors. Porpoises, fishes of various kinds, including well-known species such as cod and plaice, crustaceans such as crabs, lobsters, shrimp, and amphipods, are destroyed by extremely cold winters (Johansen, 1929). Blegvad (1929) cites death in cold winters as one of the principal causes of the decline of fish food in Danish waters, and he also frequently found quantities of partially grown and adult invertebrates dead following cold winters. He has shown that this is not due to enemies and is much more important than the destruction wrought by them.

Many adult insects are killed by unfavorable winter weather. The survival of the codling moth is poor in cold dry winters. Most insects unfavorably located in their hibernation quarters succumb to extreme cold lasting over long periods. The box elder bug, Harlequin cabbage bug, brown-tail moth, and many other insects that make their way northward during favorable years are frequently "frozen back" several hundred miles southward by extremely low temperatures.

Birds are often, though at irregular intervals, killed by storms while in migratory flight; some are driven to sea or into large lakes. The beaches of some of the Great Lakes have at times been strewn with birds caught in storms (Roberts, 1907; Saunders, 1907; Kendeigh, 1934). Even the English sparrow succumbs to severe storm (Bumpus, 1896). The destruction of adult mammals by severe weather is reported for the bison. A large number of bison skeletons are to be found in localities where severe blizzards have occurred, and the last herd of wild bison was practically exterminated by blizzards in 1886 (Seton, 1929, 2:677).

Enemies and Disease. Destruction by enemies is commonly cited as a cause of the decline of game. Examples of decline in the abundance of game related to attacks by their predatory enemies, resting upon definite scientific evidence, are still rare. Brooks (1926) has inferred that the general absence of deer in western Canada was due to the work of the puma, which was present in numbers about two years before, when deer had been unusually abundant. The decline of the European lemming is probably correctly ascribed to predators, since hawks and owls are known to congregate at points where lemmings are abundant. Moreover, the investigations of Blegvad and Petersen have shown that the food taken by the fishes is a real factor in changing the abundance of various species in the Danish seas.

Disease is commonly cited as the cause of the decline of the number of animals. It may be defined as any abnormality of the form or function of the body or any of its parts, or as any state in which the organism is not in the best condition. It is accordingly necessary to restrict the use of "disease" as a cause of population decline to malignant infectious diseases, which commonly occur in epidemic form. The disease question was long ago worked through to its conclusion on insects. In 1890, Snow (1891) distributed a chinchbug fungus to the farmers and the first reports were thought to indicate that it was effective. It was found later that these so-called disease fungi were present not only on chinchbugs but also on other insects and objects and always in the cultivated field, becoming conspicuous only under favorable moisture conditions. Headlee (1913) found that this fungus played the role of a pathogenic organism only under a mean temperature of 75° F. and a humidity near saturation, but that in ordinary conditions it is of no importance whatsoever.

A bacterium (*Coccobacillus acridiorum*) has proved to be pathogenic in locusts in Yucatan. It was introduced into North Africa by d'Herelle, but the bacterium gave none of the expected results, and further investigation showed that it was a normal symbiont in all locusts. The bacterial action liquefied the internal organs of the locusts, but only when the temperature was low and the humidity very high, a condition harmful to locust but favorable to bacterium (Pospelov, 1926). This and other experiences have caused economic entomologists to turn to other fields for explanations of the decline of insect pests.

Workers on birds and mammals have paid no attention to these findings and have partially duplicated all the experiences of the entomologists. Piper (1908), in his report on mouse plagues, refers to Loeffler's experiment with the supposed positive results in destroying field mice in Thessaly in 1892–93 by means of *Bacillus typhimurium.* Piper failed to find any definite bacterial disease in the rodents of the declining phase of the Nevada mouse plague, and referred to the apparent success attained with *Bacillus typhimurium* as probably merely the synchronizing of the experiment with the natural abatement of the plague. In 1926, Elton was inclined to refer to the decline in abundant vertebrates as a result of epidemic diseases, but his long and careful studies of dying mice reported in 1931 gave no actual evidence of pathological conditions, and the mice may have died of old age. They might readily represent a group of vigorous individuals resulting from a favorable period of a few years before.

Recently, MacLulich (1937) has given a succinct account of the bacteriology of the varying hare and its external parasites (71–86), and of the correlation of numbers with disease (91–99), reaching the conclusion that decrease was due to wholesale dying-off (125). However, even though Horn discovered bacterial causes for typical lesions in the Norway lemming, the significance of this in reducing the numbers of lemming has not been shown. The reduction of rabbits and grouse by tularemia in Minnesota (Green, 1932) appears probable, but still lacks absolute proof, and this is perhaps a fair statement also of the relation between Microtus and Toxoplasma in Britain (Findlay and Middleton, 1934; Elton, Davis, and Findlay, 1935). Some of these cases may prove to be similar to that of the chinchbug fungus and grasshopper bacillus. However, the presence of such diseases must be made manifest by all the critical tests of modern bacteriology and pathology before the death of any wild animals can be properly ascribed to them. Rush (1931) says of animal parasites: "Under ordinary conditions parasitic infestations of wild animals are not serious; it is only when the animals are concentrated under unfavorable conditions that the parasites, figuratively speaking, gain the upper hand."

The Qualitative or Quantitative Failure of Food Supply. There is perhaps no better example of the destruction of large numbers of animals due to both qualitative and quantitative depletion of the food supply than that of the Kaibab deer (Rasmussen, MS. '32). This was due, however, to an unprecedented destruction of predatory enemies, the cessation of hunting by natives, and very restricted hunting by whites, coupled with the isolated nature of the area which prevented migration. When the cyclic maximum arrived, the already large population led to an enormous increase in numbers. The winter food was depleted, and the herd was reduced from 30,000 to 20,000 in two years (1929–31). Figs. 41–44 show the condition of winter browse and of the evidences of death of deer in 1936. There were probably various causes of the decline in deer numbers, but the lack of winter fodder was the principal one. This was accompanied by some disease in the herd. Some fawns were infected with calf diphtheria from which losses in nature were light, and some exhibited the pathological condition popularly known as pink eye (Rasmussen, MS. '32), but these disturbances were believed to be the result of the malnutrition that caused the decline. This is very different from an epidemic of malignant infectious disease.

Competition for Space and Crowding. Crowding sometimes appears to limit the population, even though food is not involved as a factor. The mere absence of suitable places to go for existence appears to reduce the population. This is shown in experiments by Pearl (1925) and seems evident in quail (Leopold, 1933). Piper brings out the importance of this fact in connection with cycles.

There remain certain obscure possible causes of decline in numbers and reproductive rate. Allee quoted Kucynski (1928) as follows: "In studying the balance of births and deaths among the human population of western Europe, he described the differential effect of changing conditions upon fertility and upon the death rate and con-

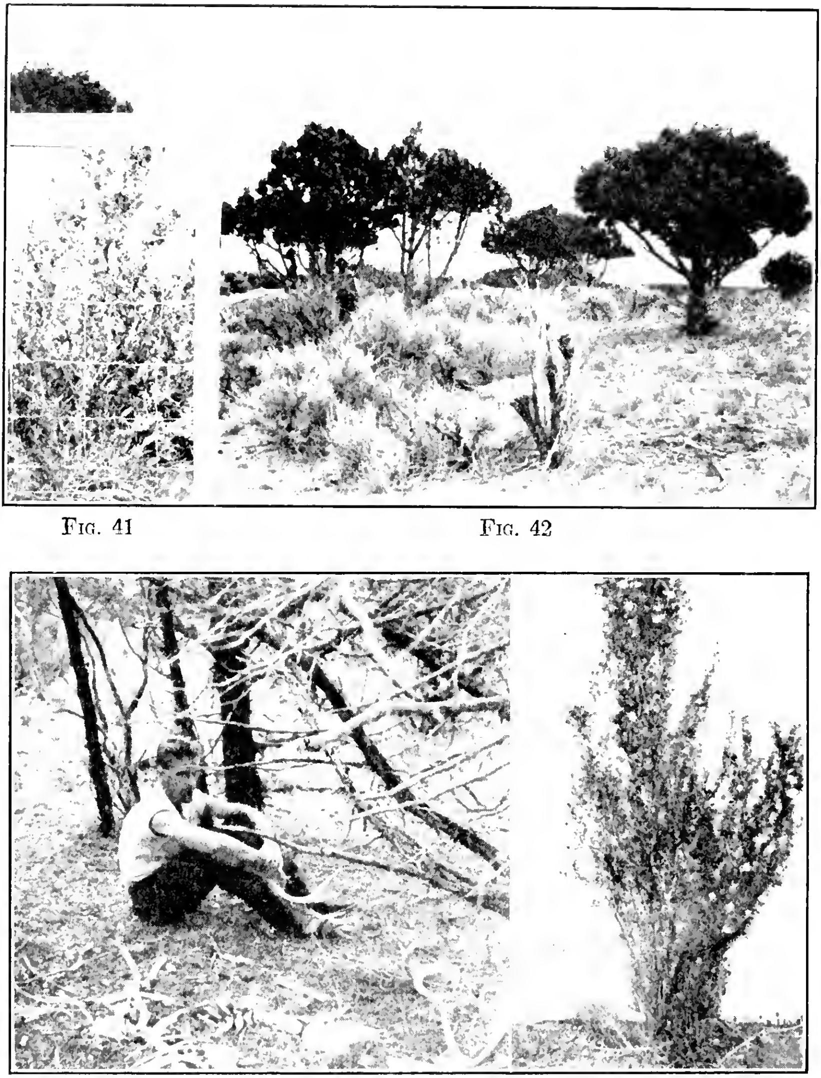


FIG. 41 FIG. 42

FIG. 43 FIG. 44

FIGS. 41-44.—Showing the overbrowsed area in the northwest slope of the Kaibab plateau. 41, Cowania, the cliff rose, one of the principal winter foods of the deer in an exclosure fenced about the time of maximum deer abundance. 42, General view showing branches of pinyon and cedar denuded to the level of the deers' heads, sage brush damaged, some dead at the right, and the favorite deer winter browse, the cliff rose, disfigured and nearly dead in the center of the foreground. The specimen in center of the foreground bears three dense tufts of branches with leaves. 43, Denuded lower branches of the cedar, and deer skeleton. 44, Normal cliff rose on the north slope of the plateau. (Photos 41 and 44 by Rasmussen and Kay; 42 and 43 by H. L. Andrews.)

cluded that human fertility has become a problem in itself largely divorced from the problem of mortality." This indicates that there is a certain amount of regulation enforced upon the human population, giving it some of the properties of a climax species. The assumption that it will be necessary to use every square foot of land to grow food for coming millions overlooks the possibility of a fundamental change in human fertility from crowding. The well-known cyclic changes in death rate are probably related to weather, nutrition, and disease, but the increase in the world's population has been connected with the discovery of new lands, the industrial and mechanical revolutions. The last two developments mentioned have made crowding possible, but at the same time, have brought a measure of control of housing, nutrition, and disease.

Physiological Changes in Vigor. Changes in reproductive vigor, especially, were experimentally demonstrated in the chinchbug (Shelford, 1931, *a*). Individuals collected out-of-doors each spring and bred in cages during ten consecutive summers showed maximal reproductive vigor in 1919 and again in 1926, 1921 being a year of extreme weakness. No explanation for the phenomenon was evident. Green (1932) further suggests a change of tularemia from a virulent to an immunizing stage in the rabbit population as the chief cause of variation in game populations in Minnesota. Changes already noted in the number of eggs shed by mammals perhaps belong here. Graham (1929, *b*) correlates mouse abundance with the condition of the larch sawfly.

Cycles in salmon have long been noted. Initial shortage of reproducing population may be suggested to explain the small "runs" of sockeye salmon in the three years between the "big runs." The "big run" population dies of old age, but leaves either a more numerous or physiologically superior progeny which matures another equally large population at the end of three years (see Babcock, 1908–1914). Because of enormous fecundity of fishes, this is an hypothesis requiring more investigation, but the case of the mammals is different. Let us assume that mice die of old age when about three years old. A favorable year may lead to a saturation of available space. Survival of young will then be limited to the space left by accidental death of "favorable-year" individuals and migration out of the area. In the third year, at a time when reproductive capacity is reduced by senility, more than half the mouse population dies of old age, causing a sharp decline. Recovery could start only the following year. This hypothesis cannot be tested until some method of ascertaining the age of mammals is determined. The most promising field here is studies of teeth (Schour, 1936; Schour and Poncher, 1937; and Steadman, 1935) (cf. Napier, 1914; Clemens and Clemens, 1926; Cobb, 1922; F. A. Davidson, 1934; Gilbert, 1914, *a*, *b*; Gilbert and Rich, 1927).

Cannibalism. The black crappie population of the bottomland lakes along the Illinois River varies in density through a five-year cycle. During this time the average weight of all black crappies taken with 1-inch tackle ranged from a minimum of 0.056 pound each, at the beginning of the cycle, up to a maximum of 0.458 pound each, at the end of the cycle. During the increase in size of the fish, the population density decreased from 852 black crappies per acre down to 118 per acre. The black crappie is the largest and most numerous piscivorous fish in these waters. The adults apparently devour nearly all newly hatched young crappies before they are one year of age, until the number of these adults is so reduced that they are unable to devour their progency, when the cycle again repeats (Illinois Natural History Survey, unpublished results, personal communication from Dr. D. H. Thompson).

Irregular Fluctuations. Irregular fluctuations must be separated from the larger cyclic phenomena. Fluctuations in an abundance of organisms are continuously going on. One may best conceive of the great mass of life in any area as comparable to a lake in which there are fluctuations in the general level or quantity of water and, in addition, a considerable rising and falling of the surface in the form of waves, ripples, etc. The truly cyclic phenomena are comparable to changes in the volume of water in the lake, while the waves and ripples represent more or less erratic changes of abundance in a particular species which must be prevented from obscuring the investigator's view of the truly cyclic phenomena. This calls for comparisons over a considerable range of territory so that differences due to local phenomena may be eliminated. These erratic changes in abundance are usually determined in some brief but very sensitive period in the life cycle of species with short developmental periods and life spans.

An example of this erratic change and difference in abundance is found in the bottom fauna of Danish waters, where a particular species is lacking in certain spots, although it is present throughout the general region. This was described by Blegvad as being due to local unfavorable physical conditions in connection with the transition from free swimming to the bottom stage; the change at any one point in such a set of faciations is entirely comparable to the larger cycles. Several maps (Fig. 45) show erratic shifting of the areas of great abundance of chinchbugs over the state of Illinois in the years 1922 to 1925. In the study of cycles, such local phenomena make neces-

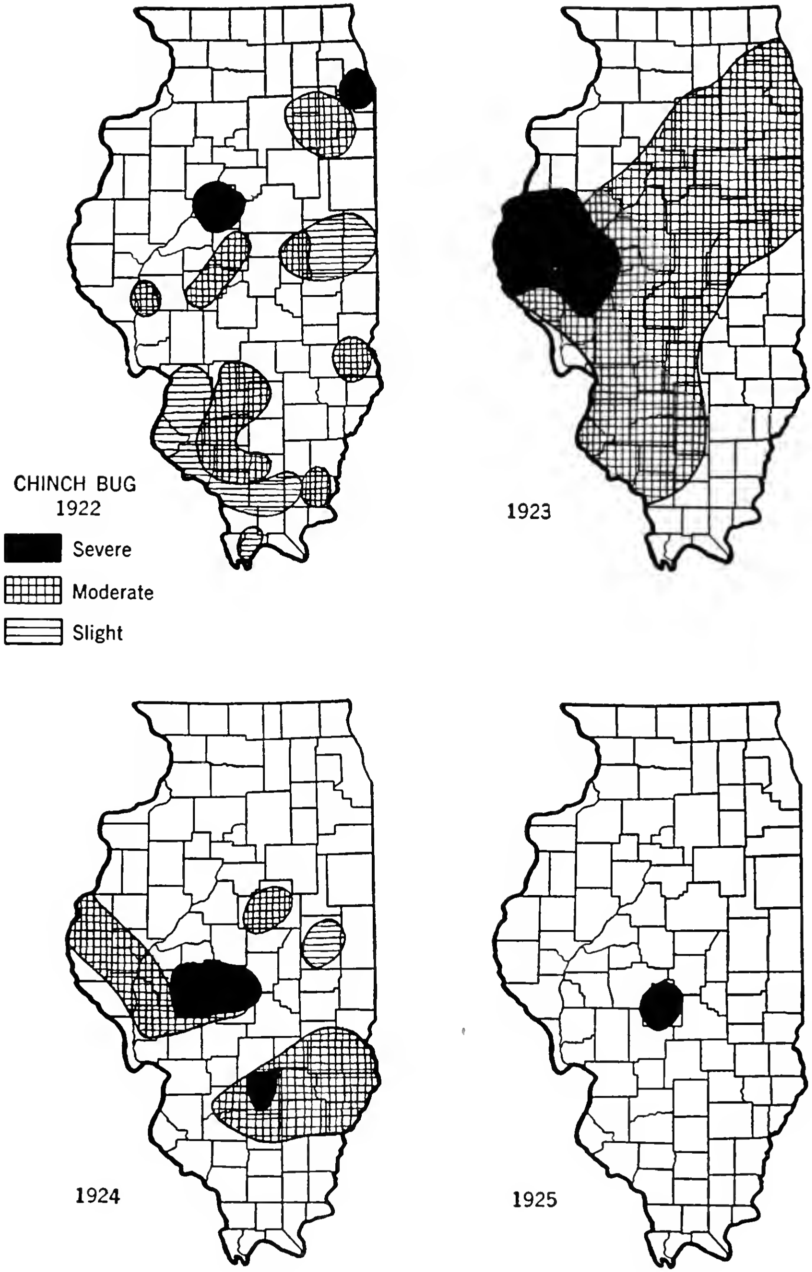


FIG. 45.—The shifting of chinchbug abundance in Illinois as indicated by crop damage during four years. (After Shelford, 1932 *a*.)

sary a comparative study of stations distributed over a sufficiently large area to eliminate the possibility of erroneous conclusions being drawn from quantitative observations made at unfortunate locations. An example of short-period effects is presented by Seamans (1926), who found that the number of rainy days in a very brief period practically controlled the abundance of the pale western cutworm (Saskatchewan and Alberta). Thus, if there are less than 10 wet days in May and June, the number of cutworms will probably increase the following year; if there are between 10 and 15 wet days, there will be a decrease.

The Rise to Maximum Abundance. The unusual reproductive capacity of the chinchbug at certain times has already been noted (page 189). It is evident that successful reproduction is sometimes greatly accelerated above the maximal expectancy, as Collett has indicated for the lemming (1895). Before the exceptional emigration in the autumn of 1891, the number of litters increased to 4 during the summer, the first appearing very early in the spring. The greatest number per litter was found in the second, with a frequent maximum of 11; the third litter averaged 5 or 6 with 10 as the extreme, while the rule was 5–7 for the fourth. In the case of pregnant young females the number of the first litter was reduced, ranging from 3 to 6 (cf. Heape, 1931:81). Manniche (1910) holds the opinion that skuas and snowy owls breed chiefly or solely during the lemming maximum, while an even more striking illustration of the cycle sequence is afforded by the short-eared owl and peregrine falcon in south Norway. The former gathers in large numbers and feeds upon the hordes of lemmings, while it is then preyed upon by the falcon, which migrates for that purpose (cf. Elton, 1924).

Apart from Heape's view as to the role of vitamins (1931:95), there has been little consideration of the part specifically taken by metabolism and by hormones. The significance of these in the migration of birds creates a strong presumption that they are likewise of importance in the reproductive and migration cycles of other animals, primarily in connection with the maximum.

Migration is not an uncommon feature at the time of the maximum or near it, and it is not improbable that it bears something of a causal relation to the minimum in such cases. In striking instances such as those of the European lemming, this is true emigration (Heape's sense), perhaps due to overcrowding and the need for food, but with some, if not all, of the birds, whether herbivores or carnivores, the process is remigration at more or less cyclic intervals. As to the emigrants themselves, they belong almost wholly to the new generation of the lemming (see p. 192).

The Sunspot Cycle. The evidence for a solar cycle in the weather of the globe and in related biological phenomena is now so strong that this must be regarded as by far the most probable primary cause involved. It furnishes much the best explanation of the fluctuations in numbers of plants and animals, and practically all recent studies of these are concerned with it. As indicated earlier, the data as to animal numbers in particular are mostly based upon the opinions of untrained observers and are narrowly limited in both space and time, so that they often show wide discrepancies as well as contradictions. The solar cycle alone seems capable of bringing order out of the confusion and of assigning proper values to the primary and secondary causes concerned. The most definite expression of this cycle is found in the fluctuation of sunspots, and hence the sunspot cycle is first considered as the necessary foundation for organizing biological cycles in a consistent fashion.

It is generally understood that the sunspot cycle comprises two extremes, a minimum and a maximum, separated by respective phases of increase and decrease with variable and unequal intervals. The average length is generally taken as 11.2 years, but within the period of definite record beginning with 1749, this has ranged from 7 years (1830–37) to 17 years (1787–1804). Since the last date given, the variation has been much less, namely, from 10 to 13 years. In addition to the more or less regular progression between extremes that characterizes it, the intensity varies greatly at both maxima and minima. The highest maximum recorded was an average of 154.4 spot numbers for the year 1778, the lowest 45.8 for 1816; for the minimum the respective values were 11.4 for 1766 and 0.0 for 1810. The five maxima from 1750 to 1787 varied from 83.4 to 154.4, and the three from 1804 to 1830 from 45.8 to 71; the highest successive maxima were 138.3 for 1837, 124.3 for 1848, 95.7 for 1860, and 139.1 for 1870. From this date, relatively low and high maxima have alternated, viz., 63.7 in 1883, 84.9 in 1893, 63.5 in 1905, 103.9 in 1917, and 77.8 in 1928, indicating a double cycle. Furthermore, the sunspot cycle differs in the length of the two phases, the interval from minimum to maximum being usually several years shorter than for the reverse phase (cf. Clements, 1916, 1929).

For more than a century the relation between sunspots and terrestrial processes has been a subject of speculation and assumption, but investigations of it were few and scattered until about 25 years ago. New momentum came from Douglass's study of tree rings in relation to rainfall and sunspots (1909), and the last two decades have witnessed a steadily increasing attention to the problems in this field. The use of tree rings in Sequoia has extended the available record from that of less than 200 years for the longest tables of rainfall, to 3000 years (Douglass, 1919, 1928, 1936; Huntington, 1914, 1925; Antevs, 1925), and the varve layers promise to increase this more than threefold (Antevs, 1922, 1928). Clements has dealt with the sunspot cycle in connection with rainfall and drought and the effect upon ecological processes (1916, 1920, 1921a, 1929), while Elton has devoted much attention to the relation between sunspots and animal numbers (1924). Meteorological contributions, notably such as those of Walker, Clayton, Clough, and Brooks, have been numerous (cf. Clements and Chaney, 1936). In the general field of cycles, the classical endeavor is that of Brückner (1891); though this was not primarily concerned with the sunspot cycle, the view is now widely accepted that the Brückner cycle of about 35 years is its triple.

It is now generally recognized by students of the subject that the sunspot cycle is reflected in cycles of magnetic phenomena, of pressure, temperature, and rainfall, but that these may differ for major regions of the globe at any particular time. In central and western United States, the average temperature is slightly higher at the sunspot minimum than at the maximum, while the present evidence favors the view that rainfall tends to be deficient at both minimum and maximum and to be above the normal in the median years between the extremes. An apparent outcome of this is the division of the sunspot cycle into two half-cycles of 5-6 years each. In addition to the double cycle already mentioned and the triple or Brückner cycle, there are others of greater length; these are mostly multiples of the simple cycle of 10-12 years, but have little relevance to the present purpose.

Cycles in Mammal Populations. The best-known cycles among mammals are those of the European lemming and of the varying hare or snowshoe rabbit of North America and its major predators. These also serve to illustrate the two major types, namely, a short cycle of 4-5 years and a longer one of about 10 years, which appear to correspond more or less closely with the half-cycle and simple cycle of sunspots, respectively. As the case of the lemming shows, the length of the short cycle may be highly variable. Though the maximum in Norway has usually occurred at intervals of 3 or 4 years, migration was absent in 1898 altogether, and it has occasionally recurred in 2 or 5 years. In southern Sweden, the time has varied from 3 to 6 years, while the maximum itself has twice persisted for a period of 3 years.

The last fact may serve to explain in part the differences in duration, as well as a variation of a year in either direction, in the Swedish cycle. As this indicates, cycles are not necessarily synchronous, even in adjacent regions, but this is likewise true of the climatic effects related to sunspot numbers.

As the only material in which the actual numbers are known, as opposed to guesses or estimates, the fur returns of the Hudson's Bay Company furnish the best, though imperfect, scientific basis so far available for the study of cycles in mammal populations. These records were first made known by MacFarlane (1905), who had been chief factor of the Company, and they have since been utilized by Seton (1911, 1929), Hewitt (1921), and Elton (1924). MacFarlane recognized that the lynx passed through a cycle of increase and decrease about every decade, and that the numbers of this and the marten in particular fluctuated with abundance and scarcity in the rabbit. His statement that the Company did not trade rabbit skins in the interior, but only at the posts situated on the shores of Hudson Bay, helps to explain some of the discrepancies between the curves for these skins and for their predators, which were bought throughout the vast extent of the North. Seton (1911) has given graphic expression to the numbers for the various species and finds a close agreement between the basic curve of the rabbit and those of lynx, marten, skunk, fox, and mink; the basic curve for the wolf is discordant, while the bear, badger, and wolverine fluctuate but little. Hewitt's conclusions are essentially in accord, the cyclic animals yielding a period close to 9.5 years, with the exception of 4 years for the arctic fox. The basic cycle of the rabbit is given as 8.5, but it is actually 10 years if the subcycle of 1854-57 is not included.

Elton (1924:136) points out that the take of skins for any year includes some from the year before and hence it is not possible to determine the actual date of the maximum. Moreover, there may be a variation of a few years between different regions. He also emphasizes the fact that there is nothing in physiology to support the view of a mysterious and obscure rhythm of reproduction. He finds "that there is a rabbit maximum just before or on, or just after each sunspot minimum, except in 1905, when there was a small maximum near the sunspot maximum." However, when the years of maxima for the rabbit and lynx are compared with the year of each minimum, as in Table 5, the agreement is seen to be less satisfactory. Thus, 4 of the 8 rabbit maxima are 2 or 4 years away from the year of sunspot minimum, while 5 of the 9 lynx maxima depart as much as 3-5 years. Nevertheless, the table of intervals brings out a clear cycle of numbers, which is in interesting agreement with the sunspot interval, especially when the various discrepancies in the data and the lack of synchrony in different regions are taken into account. If, as seems most probable, maxima are caused by a favorable conjunction of temperature, rainfall, and food supply, a correlation must first be sought with these, since they are rarely uniform over a continent and frequently not through a major region at any particular time in the sunspot cycle.

TABLE 4

Years of Maximum Animal Numbers in Relation to Dates of Sunspot Minima (m) and Maxima (M)

Figures in the table are the last two figures of the year with apostrophe omitted. Irregular columns emphasize lack of agreement.

	m–'23	m–'33 M–'37	m–'43	m–'56	m–'67	m–'78	m–'89	m–'01	M–'05
Rabbit.			45	57	65	77	88	97	05
Lynx.	31	39	48	59	68	78	88	97	06
Red fox. . . .				59	68	78	88	98	07
Cross fox. . .				59	68	78	88	97	07
Black fox. . .				59	69	78	88	97	07
Marten. . . .	27	37	46	56	66	75	86	95	03
Fisher.		40	50	60	70	79	90	98	08
Mink.		40	46	58	69	78	85	97	03

TABLE 5

Number of Years between Successive Sunspot Minima and Animal Maxima

	m–'33	m–'43	m–'56	m–'67	m–'78	m–'89	m–'01
Sunspot	10	10	13	11	11	11	12
Rabbit.			12	8	12	11	9
Lynx.	8	9	11	9	10	10	9
Red fox.				9	10	10	10
Marten.	10	9	10	10	9	11	9
Fisher.		10	10	10	9	11	8
Mink.			12	11	9	7	12

Beginning with 1933, Elton has each year brought together the results of the Canadian snowshoe rabbit inquiry. This is the most extensive study of animal cycles to date and is to be continued through a 10-year interval. The results are summarized for the fourth year, as well as for the 4-year period: "Altogether 673 reports were received for 1934–35 and most of these have been mapped. They cover most of Canada (including Anticosti) and sample areas of Alaska and the United States. In the Northwest, rabbits were still increasing and abundant. Over much of the rest of Canada a steep decline had set in, partly associated with epidemics. Rabbits in Northeast United States had also declined in numbers. Those in the Rocky Mountain areas were stable or showed no consistent regional trend, except for an increase in Montana. The figures for previous years, summarized with trends in furbearer catches in Canada, show a well-marked cycle of about ten years.

"The cycle of about ten years in lynx and red fox is clearly shown, also the lack of any cycle in the marten, which has gone steadily down to about a third of the catch for 1919–20. The marten used to be one of the furbearers showing the most conspicuous ten-year cycle. After about 1900 the cycle gradually broke down and this is probably connected with overtrapping. There is a marked parallelism between lynx, red fox, and snowshoe rabbit, and it is apparent that the snowshoe rabbit inquiry should provide a firm basis for forecasting the general trends of some of the furbearing animals. The peak in lynx and red fox ought to occur in the winter of 1935–36 or 1936–37. Of course, it is realized that we are not comparing exactly homogeneous data, since the richest areas for furbearing animals are not necessarily, at the present day, the most important snowshoe rabbit districts, and there are important regional lags in rise and decline."

Elton (1933) has recently given an informative account of the unique conference on animal cycles sponsored in 1931 at Matamek, Canadian Labrador, by Mr. Copley Amory, as has Huntington likewise (1932). The minutes of the conference have been collated and unfortunately not published in full. (See Huntington, 1932.)

In Britain, Middleton (1930) has indicated a cycle of 4 years, with a range from 3 to 5 years, in two species of vole, which resembles the cycle in the related lemming of northern Europe. He also finds marked fluctuations in the number of rabbits and hares as compiled from old game records on estates (1934), but these seem to bear little if any relation to the sunspot cycle or its extremes.

MacLulich has recently published the results of a comprehensive and detailed investigation of numbers in the varying hare (1937), which support some of the conclusions reached in the above account. He states that the year of fur production is the second year before the year of sale, a fact that results in a corresponding displacement of agreements previously noted between sunspot minima and peaks of abundance. For the whole period of lynx returns from 1751 to 1925, he finds the average cycle to be 9.7 years, while the sunspot cycle is 11.1, indicating that the two are independent. This is confirmed by the lag of rabbit peaks after sunspot minima and maxima, as well as by the low correlation between rabbit figures and sunspot numbers. The abundance of the lynx was found to be correlated with that of its chief prey, the hare, as shown by the earlier students of the subject. It is interesting to find that the last year of great rabbit numbers for the three recent cycles fell one year after the corresponding minimum, namely, in 1914, 1924, and 1934, that the fluctuation from district to district revolved about the year of minimum, 1933, and that peaks appeared latest in the higher life-zones.

MacLulich's work reaches higher quantitative values than any previous study, as a result of the cross checking rendered possible by his use of four methods, viz: trapping, censuses, hare transects, and quadrats of droppings. This permitted assigning average numbers for the rise and decline of the last maximum, as, for example, at Frank's Bay, where the respective figures for hares were: 1932, 600; 1933, 1200; 1934, 100, and 1935, 70 per square mile. The estimates at Buckshot Lake show how rapid the drop may be in a single season, but at the same time prove that the fall to the minimum requires 3–4 years and that a fair breeding population must be left in or near an area to produce the next rise. The correlation of numbers with the possible factors concerned placed the emphasis upon disease and food, though it appears probable that both of these bear a complex relation to weather and to each other.

Cycles in Bird Numbers. As would be expected, studies of population in birds are practically confined to those regarded as game, and even for these the data are rarely quantitative in any strict sense. The most notable exception is afforded by the Siberian nutcracker, for which Simroth thought he had found a correlation between its European invasions and sunspot maxima, but these were 2 and 3 years out of exact accord with the latter for the two occasions noted (1908). According to Witherby (1920; cf. Elton, 1924:149), the sunspot cycle or its double is reflected in the massed migration of the sandgrouse from the saline deserts of central Asia. Recently, Formosov (1933) has pointed out a relation between nutcracker invasions and decreased numbers in the squirrel skins taken in certain regions of northern Russia, and he ascribes this to poor harvests of the seeds of *Pinus cembra*.

Cycles in game birds have been studied chiefly by Criddle (1930), Leopold (1931), Leopold and Ball (1931), Middleton (1934), and Wing (1935). The conclusions of Criddle as to the sharptailed grouse have already been given in connection with the discussion of biotic balance (page 172). Leopold has brought together the data with respect to the fluctuations in ruffed grouse and prairie chicken, which appear to be in general agreement with the maxima and minima of the sunspot cycle. In summing up the situation as to grouse, Leopold and Ball conclude that American and British grouse fluctuate rhythmically, but the period is different. In America it averages 10 years with a range of 9–14; in Britain the average is 6.5 and the range 4–8 years. The differences between the two countries are thought to refute the assumption that cycles are due to variations in solar radiation or in sunspots, but this does not reckon with the evidence that sunspot and climatic cycles are regularly or frequently opposite in different parts of the world, as well as with the little-understood half-cycle, which appears or disappears from time to time in the same region.

Middleton (1934) has examined the records of shooting on several English estates with respect to cycles and finds an approximate cycle of 8 years in the partridge (Perdix) and of 6 years in the grouse (Lagopus). Woodcock (Scolopax) and blackgame (Tetrao) were also found to exhibit distinct fluctuations of a cyclic character.

Wing (1935) has made use of the records of brant shooting compiled by Phillips (1932), averaging the annual "bags" for four periods to obtain the following figures: 1867–76, 405 birds; 1877–88, 169; 1889–98, 276; 1899–1909, 231. He concludes that the largest number of brant were killed during the highs of the Brückner cycle and that this coincides with the maximum population. However, as Phillips points out, other factors than relative abundance enter into the size of the annual bag, and there is considerable question as to whether the data are sufficiently accurate to yield dependable results. This is further indicated by the statement that the number of brant observed was never greater than in 1887, though the bag was but 380 by contrast with 9 other years when it ranged from 410 to 715. Wing has further compared the curve of numbers for prairie chicken, ruffed and sharptail grouse, and house wren with that of the sunspot cycle and states that the highs occur at or near the year of sunspot maxima and minima.

Cycles in Insect Populations. The locust plague so far transcends all other fluctuations in insect numbers as to warrant almost exclusive consideration of it, especially when the drama of migration is taken fully into account. Though at present determination of numbers is a regular practice, in the past the phenomenon of migration and its effects constitute the best and often the sole mark of the maximum of population. In spite of the distinct progress made during the past decade or so, especially in the matter of phases (Uvarov, 1928, 1931), the paramount problem of numbers and migration in terms of causes and processes still demands much more experimental and quantitative investigation. For this reason, as well as that of brevity, the following discussion is limited to a consideration of cycles in locust or grasshopper populations and their relation to solar phenomena.

The observation that locust outbreaks often coincided with or immediately followed drought, occurs here and there in the older chronicles, and was perhaps most definitely expressed by Purchas (1657; Thomas, 1880), who said that "great droughts produce them, at least cause a prodigious increase of them; in 1553, after five years' drought, there were great armies of them." This relation was emphasized by Koeppen (1870), and the view has received the support among others of Riley, Packard and Thomas (1880), Filipjev (1928), Parker (1930), and Uvarov (1931). Koeppen also appears to have been the first to consider the question of a connection between the frequency of outbreaks and the sunspot cycle. He decided that "the greatest number of locust years falls in the first five years after the minimum of sunspots, particularly in the third and fourth year (16 times); in the fifth and sixth year (i.e. during the probable maximum of sunspots), there were 12 and 13 years of the appearance of locusts." For years 7, 8, 9, and 10, the respective numbers are 10, 12, 5, and 7. Since the correlation between the minimum and increased temperature characterizes the year of the minimum, it is difficult to explain the occurrence of the greatest number of outbreaks the third and fourth year afterward. However, the major criticism of Koeppen's table is that it is impossible to know the exact course of the sunspot cycle before definite records began in 1749, and the dates from 592 to this year are without adequate foundation.

Swinton (1883) returned to the task of correlation a decade later, but the careful scrutiny of his figures affords little warrant for his conclusion that "Properly generalized observations show almost invariably an exact concordance between the *sun changes* and these *effects*." A few years earlier, as a result of the comprehensive studies of the U. S. Entomological Commission during the "grasshopper years" of the seventies, Thomas expressed the opinion that "locust migrations" are not governed by any law of regular periodicity, in spite of the fact that the average interval between 173 invasions in China and 30 in Germany was a little over 11 years. However, he thought it but fair to state that for the "noted locust years in our own western country, to wit, 1820, 1855, 1866, and 1874–'76, the interim in each case is very nearly a multiple of 11 years." It is worth noting that all these preceded the corresponding sunspot minimum by 1 to 4 years, contrary to Koeppen's assumption.

Uvarov (1928) reports the attempt of Krasilshchik (1893) to evolve a law of locust periodicity in accordance with which *Locusta migratoria* should appear at the mouth of the Danube every 12 years and in the Caucasus every 5–6 years, but dismisses this on the basis of the unreliability of many old records. He also discusses briefly (1931:158) the views of Simroth (1908, 1909), his supporters and critics, and concludes that it is hardly to be disputed that the fluctuations of certain insects coincide to some extent with the 11-year cycle. As an example, he cites the widespread appearance of the desert locust from Morocco to India in 1915–16 and again in 1927. However, these were respectively 2–4 years after the minimum and 1–2 years before the maximum, so that their cyclic relations are confused.

The most striking and definite instance of a relation between the sunspot maximum, drought, and grasshopper outbreaks has been furnished by the studies of Parker (1930). The sunspot maxima of 1870 and 1917 were associated with 4 years of drought in the Montana region studied (cf. Clements, 1921, *a*), and were immediately followed by 3-year outbreaks of grasshoppers. However, it is difficult to understand why the equally severe drought of 1893–95 produced no like effect, unless the local region was exempt from its action. The investigations of Criddle (1932) deal with fluctuations in Manitoba, and lead to the conclusion that there is a correlation between sunspot minima and high numbers of grasshoppers, though this is often obscured by other factors. This qualification is reinforced by the fact that, out of 11 single or initial years of grasshopper abundance, 6 fall nearer the maximum than the minimum, 2 being the maximum year itself.

Cycles among Fish. Phelps and Belding (1931, 1933) have investigated the salmon catch in the Restigouche and Grand Cascapedia rivers in Canada over a period of 50 years and recognize a conspicuous cycle of about 10 years. The dates of the maximum period of catch were about 1885, 1895, 1905, 1915, and 1925. It is interesting to note that the first two are 2 years after the respective maxima, the third is a maximum year, and the last two are 2 years after the minimum (cf. also Wing, 1935). The cod and other species are also known to exhibit remarkable fluctuations from year to year, but it is doubtful whether these show intervals that may be related to the sunspot cycle (Kyle, 1933).

CHAPTER 6

MIGRATION

Probably a clearer understanding of migration may be attained if shorter movements are discussed first. Some movements of animals tend to lead them into new territory, as already indicated in Chapter 2. Diurnal-nocturnal migrations are often important; insects and some vertebrates migrate from forest to grassland at night, returning to the forest for the day (Carpenter, 1935), There are also foraging cruises, as in those of the wolf group already mentioned (Olson, 1938, *a*). Migration proper is concerned most often with a change of position having to do with adverse seasons, reproduction, or some obscure cause as migratory birds. When the organism does not revisit the starting point, its movements may be termed emigration. When a return journey is made by different individuals or at irregular times the migration may be called return migration or remigration.

Emigration is usually said to be a consequence of population pressure in relation to the food supply, but evidence for this conclusion is very often wanting and in some instances evidently incorrect as in the emigration of certain grasshoppers. Heape distinguishes emigration proper from diffusion, dispersal, and nomadism, though the distinctions do not always hold, especially with what he calls "drift emigration." It is again most frequent in ungulates, but occurs also in rodents and carnivores. A conspicuous example is afforded by the lemming of Europe. This is the most discussed if not the most dramatic of known mammalian emigrations, particularly in relation to cycles, as indicated in the preceding chapter (Collett, 1895; Elton, 1924; Heape, 1931).

With respect to adverse seasons, regular migrations are most commonly made with reference to altitude or latitude. The best-known examples are among animals with powers of flight, such as birds, bats, and insects, and among the ungulates, but are by no means confined to these groups. Latitudinal migrations are so well known for birds as to require no comment; even the flight routes are fairly well known (Lincoln, 1935). Mammalian migrations are well illustrated by the barren-ground caribou (Preble, 1908) and the bison (Seton, 1909, 1929).

Altitudinal migrations occur in all the migratory groups, but the community relations of such movements are best known among the ungulates, especially deer. Russell (1932) has discussed the seasonal migration of the mule deer from high to low altitudes in Yosemite and Yellowstone National Parks; this is governed by snowstorms which operate through covering and rendering food inaccessible. The spring return also is dependent upon forage conditions, which in turn depend upon temperatures. The Kaibab deer leave the coniferous forest of the higher altitudes in the autumn and move, generally in a westerly direction, to the pinyon-cedar belt lower down. The favorite winter browse is cliff rose, with juniper and sage less favored; they less frequently resort to a long list of other woody plants (Rassmussen, MS 1932). In was recently estimated that 80 per cent of the favorite winter food plants were destroyed by overbrowsing during one of the last cyclic maxima, when many deer died of starvation and resulting disorders. When faced by a food shortage (cf. Figs. 41–44, page 186), this species did not migrate east to accessible districts with much better food supplies, but stayed in the favorite ancestral area to their own detriment, and contrary to the usual assumption as to what always happens when food is scarce.

Fishes. Recurrent migration appears to be more characteristic of fishes than of any other aquatic group, but emigration is more or less exceptional so far as is known. The former is regularly associated with spawning and hence involves a marked change from the usual habitat of each species, such as a change from salt to fresh water, or the reverse. Typical of the marine species that move from deep to coastal waters for breeding is the herring, the behavior of which has been described by Meek (1916), and summarized by Heape (1931). The European herring passes the spring breeding period, and the subsequent feeding one, in shallow waters and then retires northward into deep water for the quiescent season of winter. The young are said to follow the adults for part of the spring journey for several years, until they too are mature and ready to spawn, thus indicating that instinct is not the guide. Other fish with a more or less similar habit are the mackerel, tarpon, tunny, pilchard, hake, garfish, bluefish, the sharks, and perhaps the cod. The number of species known to move from coastal to deep waters is much smaller, but among them are the conger eel and swordfish.

The behavior of anadromous fishes has attracted much attention. If it is assumed that the bony fishes probably originated in fresh water and that the salmon, shad, etc., belong to a fresh-water group, the usual procedure in describing the life history should be reversed, and the migration of the young fishes to the sea regarded as an excursion to an area of rich food supply, much prolonged over the initial visits when the habit began (cf. Rich, 1920). The return may be to the stream in which they hatched from the egg, a fact that has not quite been demonstrated (O'Malley and Rich, 1920; F. A. Davidson, 1934).

Such anadromous fishes as the salmon and shad are characterized by a return migration from the rivers to the sea. It is the return up the rivers at maturity that has attracted attention. The individuals of many species die after spawning. During the long journey upstream, the salmon do not feed and have few important relations with other animals. However, in the lakes in which they breed, the dead bodies of the adults foul the shores and waters, though the effects of this have not yet been investigated. By virtue of a longer life span, the shad and alewife return to the sea after spawning, and hence may repeat the visit to the parent stream several times.

Catadromous fishes are marked by the reverse habit, but they are relatively few in number. The most remarkable example is the eel, the breeding grounds of which lie between the Bermudas and the West Indies. The young migrate from these breeding grounds in the spring, entering the estuaries and rivers of western Europe and eastern America, where they remain for five to twenty years or more. When mature, they set out upon the return journey of three thousand miles and upon arriving they spawn and die, as it seems (Schmidt, 1922–1924). Heape concludes that the entire procedure is incomprehensible, but while the medium renders a solution much more difficult, it appears highly probable that it will be compounded of metabolic conditions and external factors (cf. Ward, 1921). The behavior of fresh-water fish is like that of marine species to the extent that many of them seek the shallower water of rivers or their tributaries, while a few travel in the opposite direction.

Insects. In the insect group there are examples of emigration and return migration, but the tracing of individuals, as has been done in birds by banding and in ungulates by deformed antlers and other recognition marks, is all but impossible. Return migration is less common among insects than in other groups and when it occurs in grasshoppers, the returning individuals are the offspring of the emigrants. The migrations of insects have been summarized in considerable detail by Felt (1928) and by Heape (1931); those of butterflies in particular have been treated in a comprehensive fashion by Williams

(1925). The only known instance of the return migration of the same individuals is afforded by the monarch butterfly (*Anosia plexippus* L.), though it is not improbable that *Pyrameis atalanta* L. may exhibit a similar behavior. The monarch probably owes this unique ability to its remarkably strong flight, as well as to the fact that it is one of the longest-lived species of its order, hibernating in winter in the South as enormous masses in the treetops. Some butterflies, such as *Pyrameis cardui* L., display a special type of migration in which the adults fly north to lay eggs and the young travel to the south in the fall. Mass flights of dragonflies occur at infrequent intervals and are probably to be ascribed to migration in search of breeding places, especially when drought has dried ponds and marshes. Local diurnal migrations are common (Beklemischev, 1934; Carpenter, 1935).

Grasshopper migrations which have resulted in their invasion of cultivated areas with devastating effects are known to have occurred since the beginning of historical records (Exodus 10: v. 13–15; Figuier, 1868) in all temperate and tropical areas of the world (Thomas, 1880; Uvarov, 1928). The early accounts are much exaggerated except for local areas, as the grasshoppers rarely devour all the herbage or foliage, and the presence or absence of food is usually not the cause of the departure of the insects, either in their initial movements or after a stop.

The chief migratory locust of North America is *Melanoplus mexicanus* Sauss., the solitary phase of which was formerly *M. atlanis* Riley, and the migratory, *M. spretus* Walsh. This species has been in outbreak and has migrated from the Rocky Mountain area into the states immediately west of the Mississippi at various times, notably 1874–79. Parker (1930), working over a period of years in Montana and Minnesota on temperature relations of this species, found that the activity is controlled by temperature, the average low temperature for the beginning of movement of nymphs being 16.3° C. and of adults 16.6° C. Normal activity of nymphs takes place from about 18° C. to about 33° C., and they migrate in bands or clusters from about 22° C. to 34° C. Feeding begins with normal activity, but ceases at about 27° C., the insects climbing into vegetation to escape the heat. Under falling temperature, at 20° C. to 21° C., the grasshoppers start clustering in warm sunny places and arrange their bodies so as to secure the maximum heat from the sun's rays.

Referring to the adults, Thomas (1880:155) states that flight begins on warm days, but that there is none on days with a maximum of 21° C. and a minimum of 16° C. Swarms arrive on a warm day, alight in the late afternoon, and remain for several days. He further states that swarms starting in a given direction are not readily turned back. For many years previous to 1932, it was believed that there would be no more outbreaks accompanied by migration. Migration reappeared, however (1932, etc.), but *not* in the *spretus* phase, and again the states immediately west of the Mississippi were visited.

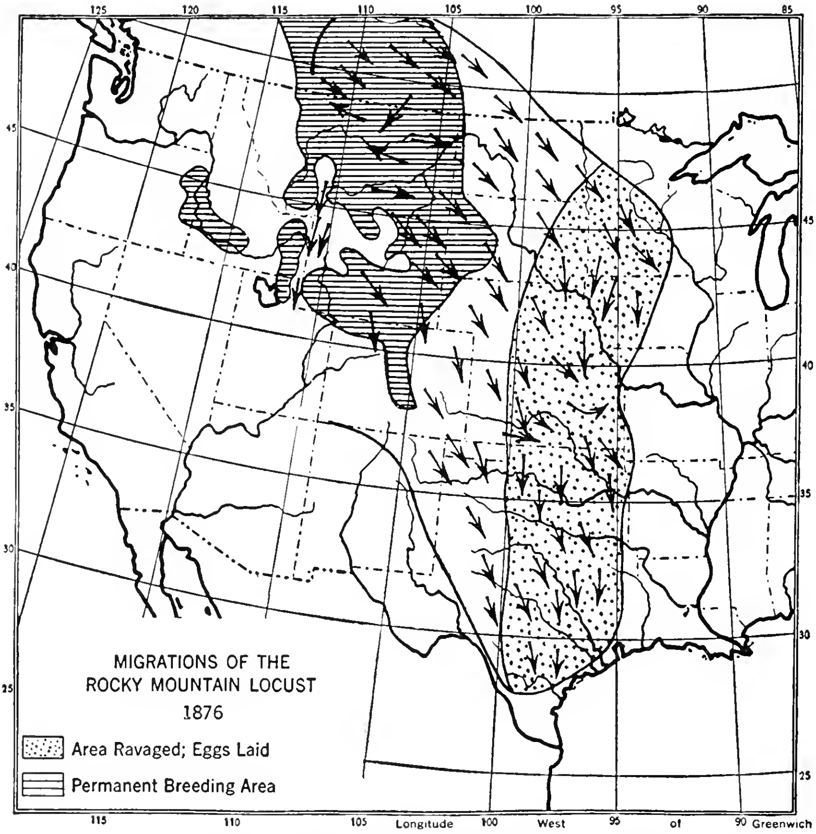


Fig. 46.—Showing the permanent breeding area and the outward migration of the grasshopper (*Melanoplus mexicanus spretus*) in 1876. (After Packard and Thomas, 1878.)

Return migration or remigration is well illustrated for *mexicanus*, the outward flight in Fig. 46 (1876) (Packard and Thomas, 1878), and the extensive return flight in Fig. 47 (1877). The location of the egg-depositing area is also shown. The phenomena of migration in grasshoppers, while perhaps more fully explained than those of birds, are hardly less remarkable (cf. Packard, 1880).

Several African and Eurasian species are migratory, and return movements occur rather frequently. *Schistocerca gregaria* Forsk. has been studied; it exists in two phases, the so-called migratory form and the solitary form. The coloration and the structure of the pronotum distinguish the two phases, while comparable features also characterize the nymphs. The normal distribution of this species covers the arid grassland and semidesert areas of Africa and southern and western Asia. Uvarov (1928) states that Kunckel's list of food plants contains more species avoided than eaten, but asserts that the caper plant (*Capparis aphylla*), the ornamental casuarina tree, and all standing crops suffer. Dr. Richard LePelly writes in a personal communication that the insects when swarming in Africa alight and feed

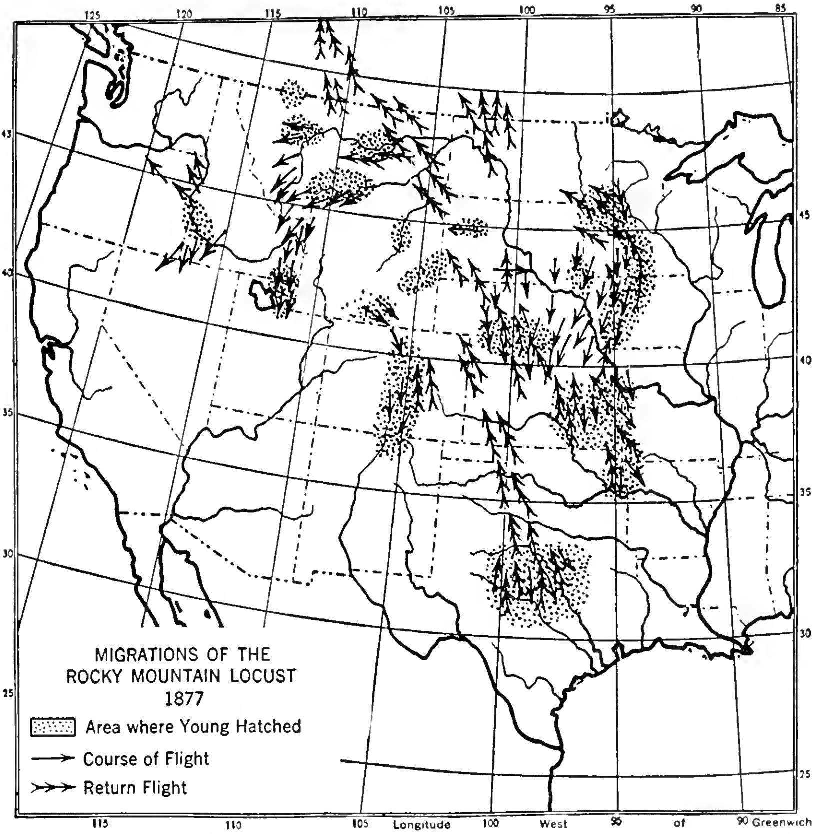


FIG. 47.—Showing the breeding areas of the grasshopper, migrants of 1876 and the 1877 return flight. (After Packard, 1880.)

during the afternoon and evening, but do not devour all the food before leaving an area, their departure being a response to stimuli other than hunger (cf. Lean, 1931; Uvarov, 1931; Faure, 1932, 1935).

Bodenheimer (1929) has made a careful study of the nymphs of *Schistocerca gregaria* Forsk. with results similar to those of Parker. He found that most of the nymphs emerge between 7 and 10 A.M. and do not wander much during the first day, but remain near the egg site, sunning themselves on stones, and some aggregating into bands. The wandering nymphs of stages 1 to 5 differ little in life habits. Early in the morning with temperatures below 20° C., nearly all rest on plants. Later on, at 20° C. to 26° C., the nymphs assemble in aggregations in warm places in the sun, turning their broad sides to the sun and ceasing their wandering. At 27° C. and above up to 39° C., migration takes place, the direction being determined largely by the wind. With the rise of the soil temperature to 40° C., usually from noon to 2 P.M., the insects arrange themselves with the long axis of the body parallel to the sun's rays, which gives a minimum body exposure. Some climb plants later in the afternoon, but as the temperature falls, the insects assemble in dense swarms and arrange their bodies to give maximum exposure to the sun; after sunset the majority gather on plants, while a few remain on the ground, and during exceptionally warm nights they may migrate (cf. Filipjev, 1928, 1929, *a*, *b*).

H. B. Johnson (1926) was the first who succeeded in actually proving the transition between the migratory type, *Schistocerca gregaria* phasis *gregaria* Forsk., and the solitary type, *S. gregaria* phasis *flaviventris* Burm., in the Sudan. He discovered that the solitary phase is the most numerous among the non-migratory locusts and that the gregarious phase is typical of locust swarms. Bodenheimer (1929) found that in Transjordania the hoppers, with a few exceptions, belonged to the migratory phase. He further states that the physiological conditions that cause the accretion of migrant swarms and compel the insects to remain in them are not clear. He quotes Fraenkel's summary, however, as follows: "The social life of the locust may be based on two fundamental instincts: (1) the aggregation instinct and (2) the imitation instinct. The insects live, migrate, sun themselves, and eat—always in groups. Apart from this, one animal imitates the actions of its neighbor. It is due to the fact that the insects are always together and each insect directs its body in accordance with that of its neighbor, that mass migration takes place. If different swarms meet, they immediately unite and migrate henceforth together, for the imitative instinct impels the first to follow the direction of movement of the second. It has not yet been determined as to how far the direction of migration is dependent on external factors. Light and topographical conditions have apparently no influence at all on the direction taken by the migrant swarms. As against this, it appears possible that the wind plays a certain role; in the majority of cases investigated the hoppers were driven by the wind."

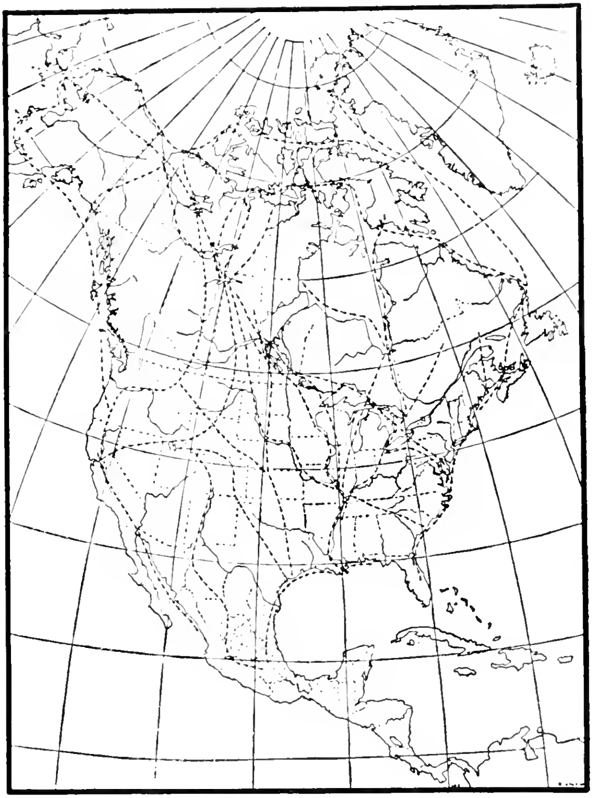


FIG. 48.—Migration routes of North American birds. Though this map was prepared chiefly to show the flyways used by waterfowl, most of these routes also are utilized by innumerable land birds. For example, the important Mackenzie Valley-Great Lakes-Mississippi Valley route is shown (with its tributaries) from the Arctic coast to the delta of the Mississippi River. (After Lincoln, 1935.)

MIGRATION OF BIRDS

The migration of birds is presented rather fully because it is a universal phenomenon of great interest and significance. Much attention has been given to it, and the diversity of opinion engendered has led to endless and often fruitless discussion (cf. Walter, 1908).

No other biological field numbers so many and such ardent amateurs as ornithology, and it was perhaps inevitable that the mystery of migration should loom far too large in the consideration of the theme. Even professional students have too often appeared sympathetic with views such as those of Lucanus (1922), who resorts to an incomprehensible migratory impulse that requires no particular external stimulus and an instinct that determines direction automatically. Diametrically opposed is the attitude of Nicholson (1929), Grinnell (1931),

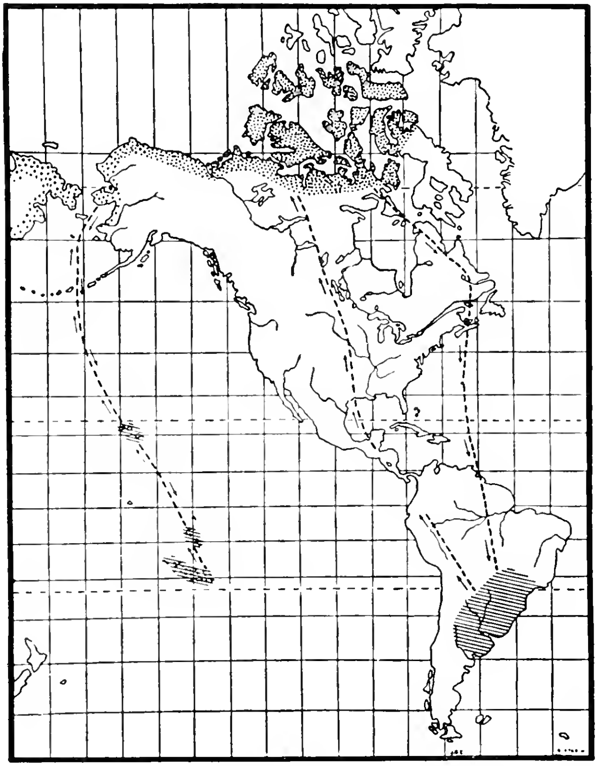


Fig. 49.—Distribution and migration of the golden plover, *Pluvialis dominica* (Müll). Adults of the eastern form (*P. d. dominica*) migrate across northeastern Canada and then by a non-stop flight reach South America. In spring they return by way of the Mississippi Valley. Their entire route is therefore in the form of a great ellipse with a major axis of 8,000 miles and a minor axis of about 2,000 miles. The Pacific golden plovers (*P. d. fulva*), which breed in Alaska, apparently make a non-stop flight across the ocean to Hawaii, the Marquesas Islands, and the Low Archipelago, returning in spring over the same route. (After Lincoln, 1935.)

and others to the effect that all aspects of the problem are susceptible of solution by research, in which experiment must take the leading role.

The range of migration in birds varies from the shifting of much of the population of those species called permanent residents over most of their range, southward in autumn and northward in spring, to the migration of all the population of certain species such as the golden plover from the Arctic region to Patagonia and back each year. The bluejay, regarded as a permanent resident from Newfoundland to Florida, is an example of shifting. Birds banded in Illinois and Iowa during the summer have been caught 200–300 miles south of the banding station during the cooler months. Groups of individuals are also often seen working south through the trees in the cool days of autumn (Lincoln, 1933, 1935). See Figs. 49–51.

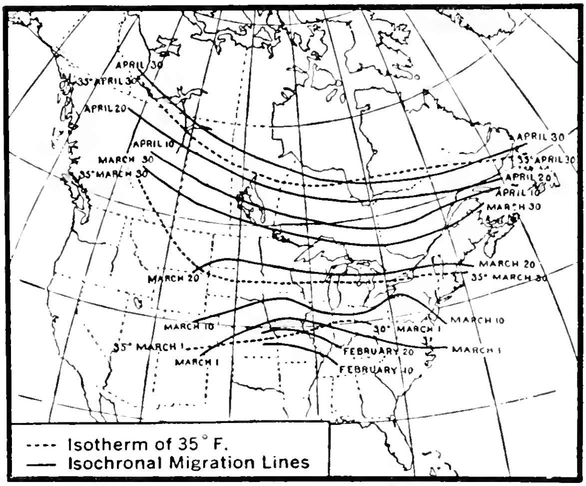


Fig. 50.—Migration of the Canada goose. The northward movement keeps pace with the advance of spring, in this case the advance of the isotherm of 35° F. agreeing with that of the birds. (After Lincoln, 1935.)

The study of migration is at present passing from the first period, that of observation and speculation, into one of experimentation. Such a preliminary phase was as indispensable as it was inevitable, and the student of migration, when beset by the many conflicting views, should not overlook the great services rendered by the observers of this epoch. They have not merely builded a broad foundation of incontestible facts, but they have in addition brought forward all possible explanations and insured their consideration. Moreover, ornithologists are primarily naturalists, and experiments awaited the growing interest of physiologists and ecologists in the problem, which in turn was an outcome of the extraordinary advances in the field of vitamins and hormones. Nevertheless, though observation will always have its peculiar values, it should henceforth be more fully informed through experiment and be content to recognize that conclusive and objective results are the province of the latter (Baldwin and Kendeigh, 1932).

The literature of migration is too extensive to be read by anyone other than the specialist, but a knowledge of its general content is essential to securing an adequate historical background and the proper perspective for the future of experimentation. For this, the sources are time-consuming, and it is preferable to turn to compendia and summaries for the most part. These are well exemplified by the following: Cooke, 1885, 1910, 1913; Gätke, 1895; Dixon, 1895; Whitlock, 1897; Taverner, 1904; Walter, 1908; Henshaw, 1910, 1921; Clarke, 1912; Coward, 1912; Cathelin, 1920; Lucanus, 1922; Thomson, 1926, 1936; Wetmore, 1926; Grinnell, 1931; Heape, 1931; Rowan, 1931, 1932; Chapman, 1932; Lincoln, 1935.

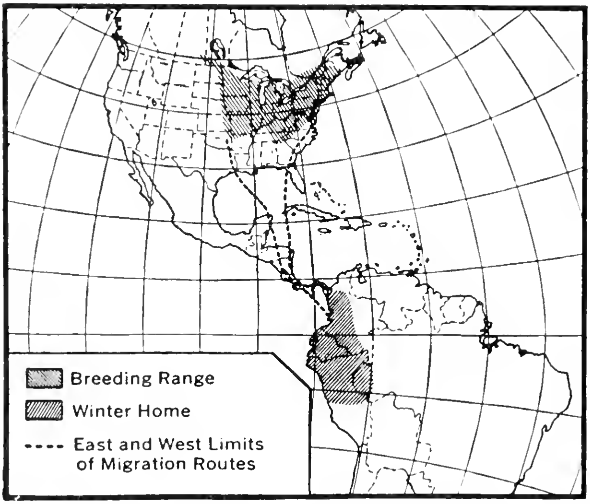


Fig. 51.—Distribution and migration of the scarlet tanager. During the breeding season individual scarlet tanagers may be 1,900 miles apart in an east-and-west line across the breeding range. In migration, however, the lines converge until in southern Central America they are not more than 100 miles apart. (After Lincoln, 1935.)

The divergent views concerning migration have centered about three major questions, namely, the origin of the behavior, the factors and stimuli concerned, and orientation or sense of direction. The first of these is naturally beyond the reach of experiment; in it the influence of the glacial period has probably been much overemphasized, and migration may well have begun earlier. Certainly, the assumption that the climate during middle and late Tertiary was notably warmer and more equable and hence attended with little or no zonation far into the arctic regions is no longer tenable, as the revaluation of the classic fossil floras of North America has shown in particular (Clements, 1916:362; Chaney, 1925; Berry, 1922, 1930). The other two problems are appropriate subjects for both direct and indirect experiment, and the positive advances recently made have been obtained from such procedure. In this must be included bird-banding, which has become increasingly definite and experimental since its first use in 1899 (Mortensen, 1906), and bids fair to develop into the primary method (cf. Baldwin, 1919; Lincoln, 1924, 1927; Thomson, 1926:143, 1936).

FACTORS AND STIMULI

Historical. Before considering the experimental studies that bear upon the causes of migration, a helpful background may be afforded by a brief account of views as to the role of light, length of day, and gonad hormones. The opinion that light, as such, furnishes the signal for migration has long been held and often expressed in poetic form (Eifrig, 1924). It was trenchantly criticized by Newton (1874), who pointed out that the theory refuted itself in view of the fact that the southern movement, in particular, was initiated and in large part accomplished at a time when the birds were journeying to increasingly shorter days. Nevertheless, it was restated by Seebohm (1888), who expressly eliminated temperature and food to emphasize the search for light as the sole cause. Schäfer (1907) seems to have been the first to recognize that light was properly to be interpreted in terms of length of day, and stated that this was important not in itself but only for the purpose of gathering food. Eifrig (1924) has enthusiastically championed the cause of light and day length, and Thomson (1926) regards it as possibly important. Allard appears to give restrained support to the hypothesis (1928), and Bissonette (1937) indirectly conveys the same impression. Rowan (1926, 1932) at first ascribed much influence to length of day, but later regarded this as largely if not wholly a matter of time for activity and food gathering (cf. Cole, 1933). Heape (1931) concluded that light does not exert a direct effect on migration, but acts in a mediate fashion through vitamins upon gonads.

The general assumption that migration is caused by the reawakening of the reproductive instinct has come down from much earlier times, and in more definite form has received the support of the consensus of ornithologists during the past quarter of a century or more. It was advocated by Brehm, who later turned to the scarcity of food as the explanation (1896:234), and was combated by Gätke (1895), as indicated in the following discussion. Chapman (1894) enunciated similar views in America, and Marshall (1910) rendered them more definite by turning to internal secretions for the exciting cause, while Schäfer (1907) pointed out certain critical difficulties with the hypothesis. Cahn (1925) and Bergtold (1926) regard sex hormones as the primary if not sole cause; Wetmore (1926:27) also considers them the prime influence, and Thomson (1926:295) assigns them the chief though not exclusive role. This is essentially the attitude of Heape (1931:240), as it was of Rowan in his earlier experiments (1926, 1929) (cf. Garner and Allard, 1920; Marcovitch, 1924).

Rowan's Researches (1926–1932). The chief credit for initiating the experimental attack upon the causes of migration is to be ascribed to Rowan, who has combined both direct and indirect methods in his procedure. In the main series of experiments, this comprised the artificial increase of length of day, a device to insure increased activity, and the liberation of experimental and control birds. On the basis of the results obtained he concluded that the changes observed could probably not be assigned to ultra-violet radiation. The rhythm of the gonads could be readily modified by control of lighting, but compulsory exercise produced practically the same effect, and hence it was suggested that the greater length of day operated through the opportunity for increased exercise and that the latter was the primary factor in the development of the gonads. His extensive results were summed up in 1931 in the two statements: "Variations in day-length are assumed to be the primary external stimulus. The internal stimulus is assumed to be a hormone produced by the interstitial tissue of the reproductive organs."

The most remarkable direct experiment was organized in 1930 with crows (*Corvus brachyrhynchos* Brehm), through the efforts of a wide group of cooperators (Rowan, 1932). The birds liberated for the purpose of determining the presence and direction of migration comprised four major groups as follows: (1) experimentals receiving increasing illumination from October 15 to November 17; (2) experimental capons (castrated males), with exactly the same treatment; (3) controls; and (4) control capons, both of which were given no illumination. "Of the controls there is little to say. The high percentage of traveling birds was somewhat unexpected, but it proved less surprising than the results obtained from the remaining groups. The behavior of the capons was wholly unforeseen. The control capons instead of proving sedentary, all traveled southeast. The experimental capons, although not quite so uniform, were also southward-bound. These two groups seem to have settled one point. Whatever may be the case with the northward migration, the southward is evidently not associated with the state of the reproductive organs. The movement must depend on some other, at present undetermined factor. . . . That a revision of the original hypothesis is necessary is evident. . . . Castration does not inhibit the southward passage, which appears to be independent of the influence of the gonads."

Kendeigh (1934). Kendeigh has recently carried out a comprehensive and thoroughgoing investigation of the response of the house wren (*Troglodytes aedon* Vieillot) and English sparrow (*Passer domesticus* L.) to physical factors, which gains much through the previous studies of the temperatures of birds by Baldwin and Kendeigh (1932). The factors specially considered are temperature, solar radiation, humidity, precipitation, and wind, each of which is treated with respect to distribution, migration, and abundance. Of these, temperature is the most significant, though it bears a necessary relation to the quantity and duration of radiation. For adult passerines, a body temperature below 38.9° C. (102° F.) is suboptimal, though one as low as 23.9° C. (75° F.) may be withstood for a short time. The interval between the highest normal body temperature, 44.6° C. (112.3° F.), and the lethal, 46.1° C. (116° F.), is much narrower, with the consequence that air values of 35° C. (95° F.) or higher seem to have a more immediate and fatal effect than low air temperatures. During spring and autumn, night time is the critical period since the body temperature reaches a minimum then, as does the air temperature also, and the birds are inactive and without food for several hours. For the day, especially in midsummer, the critical time in the tolerance of high temperature falls at the afternoon maximum for air and bird.

As for the role of food in survival and migration, it was found that starvation lowers the body temperature materially, individuals of three species dying when the latter fell to 32.8° C. (91.1° F.), as a result of lessened resistance. Emphasis is also placed upon the high food intake needed to maintain normal metabolism, granivores consuming daily about 13 per cent of body weight in air-dry food, 90 per cent of which is digested, while for insectivorous species the amount ranges from 8 to 14 per cent in dry weight of insects. The results of Stevenson (1933) and of Rensch (1931) are cited to indicate the need for more food with lower temperatures, both daily and regional, and those of Rörig (1905) and of Groebbels (1931) with respect to greater consumption under enhanced activity. Similarly, the work of Price (1929) and of Heape (1931) is assumed to show the need of vitamins in the bird's diet, with a possible correlation with migration.

To quote from Kendeigh: "The southward migration of the eastern house-wren in the autumn is necessary for the continued existence of the species, while the northward migration in the spring avoids unfavorable breeding and existing conditions in the south. By migrating south in the autumn and north in the spring, the bird maintains itself in a more nearly uniform and favorable environment throughout the year. The regulation of migration as to time is controlled in the spring by rising daily maximum and night temperatures and changing relative proportions daily of light and darkness. In the autumn, decreasing temperatures particularly at night, longer nights and shorter days, and, for some species, decreasing food supply are most important. The conditioning factor that may act directly or indirectly as a stimulus for initiating migration is an excessive change in the metabolic or physiological state of the body. Changes in physiological state are induced by and correlated with changes in environmental conditions, both directly and through the intervention of the endocrine system" (page 408).

Riddle, Smith, and Benedict (1932). A number of the studies of Riddle and various associates on the hormones and metabolism of columbids are of indirect importance, but the one of most direct significance is that which deals with the basal metabolism of migratory and non-migratory species. "Individuals of a feral, cold-avoiding, migratory species of dove, when reared in captivity, have been found to have a higher basal metabolism than that found in related non-migratory domesticated doves and pigeons. At 20° C., and measured at all seasons, the mean values found for the two sexes in these several species are: 904 (mourning dove), 792 (ring dove), and 680 (tippler pigeon) calories per square meter per 24 hours.

"Seasonal changes in the metabolism of these species are especially difficult to interpret because possible responses to hot and cold weather and an extraordinary autumnal involution of the gonads, apparently the equivalent of functional castration, are involved. The highest metabolism is found in September; lower and quite interchangeable values are found during the breeding season, November and winter. However, due to the conditions under which the birds used were kept, the results may not be applicable to unsheltered wild birds.

"It is possible that the thyroids of this species do not respond to cold weather in the same manner as do those of the non-migratory forms and that this is significantly or causally related to the migratory instinct. This migratory, cold-avoiding species must do more work—must produce more heat—to maintain itself at lower temperatures than is required in either of two related non-migratory species of dove already studied."

Present Status. A synthesis of the results of the preceding researches serves as a touchstone to test the various hypotheses brought forward in the past, especially those based upon gonad hormones or the length of the day. As early as 1890, Gätke maintained that it could not be the reproductive instinct that prompts the spring migration, since many species do not breed in the first, second, or even third year, but migrate to their homes like their fully mature congeners. Marshall (1910), though favoring the gonad hypothesis, admitted the grave objection presented by the behavior of juveniles, and Kendeigh has recently emphasized the decisive nature of this. The evidence supplied by Bergtold (1926) to the effect that migratory males have heavier gonads than those of non-migratory species is too inconsistent to be significant, since 6 of the 11 non-migratory forms exhibit a 200-fold or greater increase, while 5 of the 13 migrants are below this level and 2 others but little above. However, the notable experiment of Rowan with normal and castrated crows appears to remove gonad excitation from the list of possible causes, and all the more definitely because of the conclusions drawn from his earlier studies. When these are taken in conjunction with the absence of such stimulus in migrating juveniles, gonad control seems eliminated and to be at most only a concomitant.

As to length of day, Schäfer, Groebbels, Rowan, Kendeigh, and others are evidently justified in interpreting this primarily as a matter of time for greater activity and food gathering. With respect to the question of radiation, Rowan feels that exercise and not ultraviolet is concerned, while Bissonette (1930, *a*, *b*, 1933, 1937) believes that it is light alone and that the male gonads are conditioned by the daily period, intensity, and wave length of the light. Rowan has disproved the influence of the gonads on fall migration, but has not dealt experimentally with their effect in the spring movement. Allard (1928) from the vantage ground of a pioneer in the field of photoperiodism, inclines to reserve judgment as to the duration factor. Finally, no one seems to have pointed out in this connection the significance of the altitudinal migration in the Rocky Mountains and the Sierra Nevada. Here there can be no possibility of the influence of day length.

From the synthetic and objective approach to the problem of migration it appears manifest that metabolic condition is the crux of the matter, especially as influenced by hormones, vitamins, blood physiology, temperature, and food consumption in terms of length of daylight and darkness. This might well be considered to be axiomatic were it not for the diversity of hypotheses and the fact that experiment has as yet been too little focused upon it with respect to migration. The chief contribution is that of Kendeigh, on the basis of which he is justified in stating that the critical prerequisite to southward migration is the average night temperature combined with the number of hours of darkness for which the bird is without food. It is obvious, however, that only the first can apply to movement from higher to lower altitudes.

As to the northward migration, the chief factor appears to be high air temperature in the form of the daily maximum. The food supply plays an indirect part inasmuch as wider areas and longer days will be requisite for the acquisition of territories and the feeding of the young. By reason of the high body temperatures of birds, the margin of safety in the upward direction is much narrower, and this is likewise true of the range within which the food-getting activity is comfortable or possible. It is a matter of common knowledge that activity is greatly reduced during afternoon maxima or hot periods in summer, and Kendeigh has brought together some of the outstanding examples of this response (1934:344). Perhaps the most striking illustration is afforded by such ground birds as the horned lark and meadowlark, which follow the moving shadow of the fenceposts on the Great Plains where other shade is lacking. The evidence drawn from repeated observations of this response is supported by Riddle et al, (*loc. cit.*) who find that the metabolism of doves is so reduced at an air temperature of 86° as to lead to abnormal functioning, as well as by Kendeigh (1934), who determined a temperature of 93° F. to be critical, curtailing activity and interfering with normal behavior and reproduction.

The relatively enormous amount of food needed to maintain a bird in normal activity lies at the bottom of the metabolic condition for migration, as it is also for tolerance of winter conditions by permanent residents and throughout the reproductive cycle for all species. One function assigned to the establishment of territories during the breeding season is the insuring of an adequate food supply for rearing the young in the nest. When the young leave the nests, the demand for food within the community is not necessarily enhanced, as the juveniles scatter, abandon the territories, and may leave the region (Williams, 1936). Such an early departure may occur when the production of plant and insect foodstuffs is at or near its height. In general, summer or autumn migration begins in a period of waning days and usually falling temperatures. There is a gradual tendency in the direction of a necessity for more activity to secure the same amount of food with the accompanying tendency toward a changed metabolic state. It is not improbable that a diminishing fund of vitamins may have some share in the general outcome.

Some of the major features of the biochemistry of the metabolism that leads up to the migration emerge from the studies of Riddle and his associates, and still others may be inferred from them. Of basic importance in this connection is the seasonal cycle of blood sugar, its relation to food and activity, and its fluctuations with temperature, falling with cold and rising with heat. It tends to drop in autumn with lower temperatures and increased thyroid function, and it rises in the spring in response to warmer weather and especially to the greater activity of the suprarenal glands. These glands would appear to play a leading part in metabolism at the time of the spring migration through their varied effects. Adrenalin not only calls forth glycogen from the liver, with an ensuing rise in metabolism and heat production, but it may also constrict the capillaries and prevent the release of heat, while at the same time acting directly upon the nervous system. Riddle's studies have shown that the suprarenals enlarge and that blood sugar and calcium increase at the time of ovulation in pigeons, which may well represent the causal sequence together with pituitary control. If it be shown that this hypertrophy is associated with the storage of vitamin E in the glands (Szent-Györgyi, 1933), then the way is opened for relating the entire process directly to the green food supply of spring (cf. Heape, 1931). In this biochemical pattern, the antagonism between the thyroid and the suprarenals, and possibly the gonads as well, would seem to bear some part, as well as that between adrenalin and the oxidation promoters, such as insulin.

Regularity of Return. Much emphasis has been laid upon the regularity of appearance of migratory species, especially in spring and particularly by proponents of the hypothesis based upon day length and gonad hormones (cf. Wetmore, 1930:73; Schäfer, 1907). With the evidence against the latter, the supposed regularity no longer seems important, but it is worth while to examine it for itself, as well as in relation to length of day and to temperature.

J. C. Phillips (1913) expresses his view of regularity as follows: "This brings us back to our inquiry into the mechanism by which birds are enabled to arrive each year at a given locality at almost exactly the same time. From a physico-chemical standpoint, the accuracy of time sense in certain species is little short of marvelous." Wetmore (1926, 1930) considers that "the regularity of travel when birds are on migration constitutes one of the most interesting facts in connection with this phenomenon and is one familiar to all ornithologists. Through years of observation average dates of spring arrival and autumn departure have been established for many localities, and birds come and go with surprising regularity on their appointed dates. Arrival in spring is particularly punctual with the majority, and unusual is the season when the first of the travellers fail to put in their appearance within a few days of the average dates. At Washington, D. C., the barn swallow, on the average, arrives April 12, the least flycatcher May 2, the chipping sparrow March 22, and the house wren April 18. On or near these dates one is always sure to find them. Individuals which breed about our homes come with particular promptness on their appointed days. Severe indeed is the weather that delays them for any length of time. Departure for the south in autumn is prompt, but has greater range of variation, particularly in middle latitudes, as prolonged mild weather may induce birds to remain beyond their custom." It is manifest that "regularity," "punctual," and "prompt" are here to be interpreted in terms of averages, and hence it is interesting to examine the records to secure an objective evaluation.

The belief in regularity has been fostered by averages over a short period, which convey fictitious values, but it springs chiefly from prepossession. The most striking example of this has been cited by Phillips (*loc cit.*, page 195) in the following statement: "Cooke's method of averaging migration arrivals consists in throwing out dates which are more than six days out of the way, his experience teaching him that 'birds seldom vary on account of the season more than six days either way from the average date of their arrival.' The method may seem to some, as to the writer, rather arbitrary." Just how arbitrary is revealed in the following paragraphs, where it may be noted that few species possess the degree of regularity demanded by the method.

A brief record is misleading. Of the six utilized by Phillips, five range from 6 to 11 years; the other is 23 years in length, during which time the chimney swift varied 13 days. However, the irregularity of this species amounted to 23 days in the 25-year record of Woods and Tinker at Ann Arbor and 22 days in the 41-year record of Jones at Oberlin. It rose to 34 for the combined record of a half-century at Ann Arbor, and was still greater for the autumn departure, namely, 45 days. Cooke (1913) based his conclusion as to variation being small from year to year upon a single record of 6 years.

Over the period from 1896 to 1930 at Oberlin, Ohio, Jones (1931) has noted 52 common species that vary 20 days or more in the date of arrival in spring, i.e., between the earliest and latest dates for all the years of record, and 24 with a range of 4 weeks or longer, such as cowbird and fox sparrow, 40 days, rusty blackbird and hermit thrush, 39 days, etc. Data compiled by Roberts for southern Minnesota (1932) as to the spring return of 50 species gave a variation of 17–19 days for six, 3–4 weeks for another six, and 1–3 months for the remainder. The irregularity of return is still more striking in the longer 50-year record of Wood and Tinker for the vicinity of Ann Arbor, Michigan (1934).

However, it should be pointed out that the above data refer to first records and not actual arrivals and make no allowance for variations in observation. Most migration observation is fragmentary at best, especially over a long period of years, since most observers, both amateur and professional, are not able to be in the field every day. The amount of observation varies from time to time and especially from year to year. Consequently, there is often considerable difference between the "first record" and the actual (unknown) arrival of a species. Also, the migration data are not quantitative. Too much emphasis is placed on the occasional extreme early or late dates involving only a few individuals; rather the appearance of the bulk of the individuals of the species should be considered. As a consequence, accurate determination of the variation in mass arrivals cannot be made from even the best long-term data now existing.

Nevertheless, it would appear that the amount of variation is greater than commonly supposed, especially during early spring and other periods when the weather is less stable. The use of average date of return has given an impression of regularity where proof is wanting and has led to the attitudes justly criticized by Phillips. Lesser regularity is indicated by average deviation and standard deviation, which do give a serviceable statistical expression of irregularity. They must be interpreted in the light of the total range in return, since the standard deviation, for example, means that only two-thirds of the cases fall within the period of twice its length, while one-third fall between this and the extreme dates. This significant relation is brought out clearly in the following table, which comprises migrants representative of different periods of variation in re-

TABLE 6

Species	Record, Years	Extreme Dates	Average Date	Variation in Days	Standard Deviation	Average Deviation	Average Variation
Birds							
Marsh hawk	34	1/1–5/10	3/8	130	32.3	22.6	
Yellow-bellied sapsucker	39	1/27–5/22	4/5	116	16.6	10.4	
Canada goose	40	1/4–3/31	3/3	86	17.3	12.1	11
Chipping sparrow	45	3/13–3/1	4/3	50	10.7	8.5	2.1
Ovenbird	43	4/3–5/15	5/4	43	7.1	4.8	1.4
Black-throated blue warbler	41	4/25–5/20	5/7	26	4.6	3.3	
Black-poll warbler	26	5/8–5/27	5/18	20	5.1	4.2	4.9
Plants							
Blue violet	28	4/8–5/8	4/28	31	6.9	5.1	
Columbine	28	5/5–6/2	5/16	29	7.5	5.6	
Yellow adder's-tongue	26	4/14–5/5	4/23	22	6.1	5.1	

TABLE 7

IRREGULARITY OF SPRING RETURN IN PALM WARBLER AND COWBIRD
(From tables of Wood and Tinker: 1906–1930)

Palm Warbler

	+ +	+ +	+ +	+		+ +	+	+ +	+ + +	+ + +
Apr.	21	22	23	24	25	26	27	28	29	30
	+		+	+	+		+	+		
May	1	2	3	4	5	6	7	8		

1913–14: April 26

Cowbird

+	+ +			+	+ +			+ +	+ + +	+	+ +	+
Feb. 15–Mar.	9	10	11	12	13	14	15	16	17	18	19	20
	+	+	+	+				+	+ +	+		
Mar.	21	22	23	24	25	26	27	28	29	30	31	
				+		+						
Apr.	1	2	3	4	5	6						

1918–19: March 17

turn. Several of them occur likewise in Cooke's table of average variation, from which his figures are taken (1913). On the basis of the standard deviation, the warblers alone exhibit a variation as small as 10 days or less, and this applies to but two-thirds of the returns. As an argument for an "accuracy of time sense little short of marvelous," it is unconvincing, and particularly so when viewed in the light of the performance of spring flowers, which possess no "time sense." Incidentally, it is difficult to understand why this sense in warblers should be twice as poor in fall as in spring (cf. page 220).

Irrespective of other considerations, it is manifest that wide ranges in time may furnish much cogent evidence for control by temperature and food than by length of day as such. The latter is perfectly regular year after year, and it appears quite difficult to correlate such a highly variable phenomenon as date of return with it. This factor has seemed particularly attractive in the case of species that start south in July, but this explanation has not reckoned with the slow decrease in day length at this time. During the first 2 weeks after the June solstice, this amounts to but 8 minutes for the day, and for the first month only to 17 minutes less of morning and 7 of afternoon. These correspond to decreases of less than 1 and 3 per cent respectively, even the latter appearing quite too small to be tangible in terms of food gathering. By the September equinox, the day is 3 hours shorter, but by that time frost is beginning through the United States and surface ice is frequent to the northward. In short, by the time length of day has decreased to the point where it is effective, reduced temperatures are in operation much more decisively, and these then act in combination with food shortage in terms of ability to maintain body warmth. During the spring months of migration, the rate of increase in day length is decidedly more rapid, but even at that it lags behind the mounting temperatures of April and May, which are directly related to the bird's metabolism and bodily comfort.

In this connection, it is interesting and probably significant that the leaf behavior and the blooming of plants, which are known to be directly connected with temperature, exhibit much the same degree of fluctuation. It is a happy coincidence that the most remarkable record of phenology in America at least was made by Mikesell from 1873 to 1912 at Wauseon, Ohio (Smith, 1915), which is not much more than 100 miles from Oberlin. During this period, the time of blooming of 32 out of 39 forbs varied from 20 to 50 days, while that of 46 woody plants ranged from 22 to 57 days. The change of foliage in the autumn was of the same general magnitude, though the average was much higher. As suggested earlier, these results support the view that aspection and annuation are due to much the same factors in both plants and animals.

Time of Arrival in Relation to Sunspots. The hypothesis that migrants return earlier at the time of sunspot minima was first advanced by De Lury (1923), in consequence of a study of the records kept by the Chandon family at Montdidier, France, from 1794 to 1869. He found a periodicity in the arrival of birds and in rainfall corresponding to the sunspot cycle of about 11.5 years (Fig. 52).

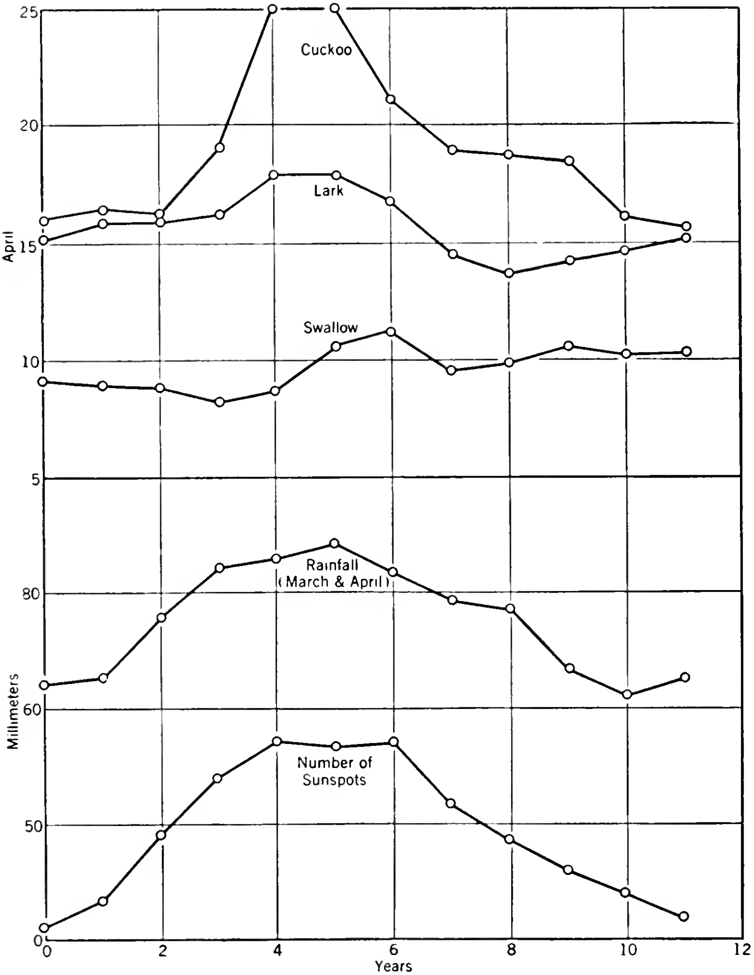


Fig. 52.—Number of sunspots and the time of arrival of migratory birds. (After DeLury, 1923.)

The arrivals of the cuckoo, lark, and swallow were respectively 9, 3, and 1 day later at sunspot maxima than at minima. The cuckoo exhibited the relation quite clearly, the lark much less, and the swallow but little, the conclusion being that some birds manifest in their migratory movements a relationship to the 11.5 cycle of solar and climatic variations. This theme was further developed and some interesting predictions made in a later paper (1925). However, in a recent article (1936) MacLulich concludes that correlation coefficients between sunspots and dates are too small to be significant.

Wing has carried this study forward in a series of papers dealing with several species of migrants in the United States (1934, *a*, *b*; 1935). These comprise the loon, pied-billed grebe, sandhill crane, brant, chimney swift, kingbird, and purple martin. His results are described as follows: "In the two cases just pointed out, we appear to have a case of differential response to the sun. The loons and grebes were stimulated to early movements by both the highs (maxima) and lows (minima) of the sun, while the crane moved early only at the highs. The kingbird (and purple martin) reaches a high directly with the sun, its cycle being the same as the cycle of the crane. The chimney swift, however, parallels the half-cycle as in the loon and the grebe, the peaks of its cycle coming at both the maxima and minima of the sun. . . . The opposing character of the two cycles, the brant going up when the Wolf [sunspot] numbers go down, best described as a 180° difference in phase, contrasts strongly with the kingbird-crane cycle (in phase with the 11-year sunspot cycle) and the chimney-swift-loon-grebe cycle, half the 11-year."

Since the total number of species concerned in both investigations was but 10, it was deemed desirable to take a much larger number into account in order to afford a more adequate test of the assumption, as well as to throw light on the three different types of behavior. For this purpose, three of the longest records available in this country were selected, namely, Wood and Tinker at Ann Arbor (50 years), Jones at Oberlin (36 years), and Brimley at Raleigh (32 years). With respect to the earliest date of arrival for each species, it was found that this had occurred on the year of maximum (M) or minimum (m) for 64 out of 217 species at Ann Arbor between 1880 and 1906, and for 25 out of 171 species from 1906 to 1930. In the Oberlin record, there were 16 earliest arrivals at m and 15 at M, or a total of 31 species at these extremes by contrast with 128 on other years. For Raleigh, 9 earliest arrivals fell at m and 16 at M, giving a total of 25, to 115 at other times. The respective ratios for the four records are 64:153, 25:146, 31:128, and 25:115, while the corresponding percentages are 42, 17, 24, and 22 per cent. For the combined lists, the number of earliest arrivals on the year of sunspot maximum or minimum is 145 by comparison with 542 at other years of the cycle, or a percentage of 27.

When a period of 3 years centering on M or m is employed, thus giving a relation comparable with the smoothed curves of De Lury and of Wing, the number of earliest arrivals at these times is greatly increased, in accordance with the expectation. For Oberlin they are nearly trebled, amounting to 88 out of 159 and yielding a ratio of 88:71 and a percentage of 55, while for Raleigh they are 87 of 140, with a ratio of 87:53 and 62 per cent. If the two successive Ann Arbor records are combined and the earliest rate of arrival taken for each species, the respective values are 104 species out of 169, 64 making their earliest appearance about the maximum, and 40 about the minimum.

In the case of 25 species with the most complete records at Ann Arbor, the 3 earliest and 3 latest arrivals were taken for each, some dates being duplicated in the first, and the number that fell at or within 1 year of the maximum or minimum determined. For earliest arrival, the ratio was 93:163 or 57 per cent; for the latest, 75:149 or 50 per cent. For arrivals on the precise year of an extreme, the number was the same for both, namely 31. The number of M and m years in which there was no early arrival ranged from 4 in the kingbird, with 2 such years lacking in the record, to 6–9 in a possible total of 9 for 19 of the 25 species. By combining the records of Atkins at Locke (1883) and Wood at Ann Arbor, made less than 50 miles apart, a record of 76 years is obtained for the redstart, the spring return ranging from April 5 to June 5, or 62 days. This yielded but 1 very early return, namely, April 5, 1903, 2 years after the minimum, the next 3 in order being 20–23 days later, 1 on the minimum of 1889. Of the 13 April dates, all of which might be considered early, 3 occurred at the minimum and none at the maximum.

The above summary affords little support to the hypothesis that spring arrivals are earlier at sunspot maxima and minima, only a few species exhibiting a limited amount of agreement. However, the degree of general accord may prove somewhat greater than now appears, when the sunspot extremes are correlated with temperature and rainfall and resultant food, and these with the time of migration. Such a procedure might serve to explain the wide divergence in date of arrival for the same year between two localities. Thus, the day of return of the piedbill grebe at Ann Arbor and Oberlin may differ as much as 4–6 weeks for a particular year and hence partly reflect regional variations in the advance of spring. This regional discrepancy is exhibited likewise in the ratios between returns at extremes and at other years; these are respectively 2:3 at Ann Arbor and 1:7 at Oberlin for the grebe, 1:4 and 0:6 for the loon, and 1:6 and 0:7 for the chimney swift. However this may turn out, it seems evident that there is no direct correlation between sunspot numbers and time of return. This is indicated furthermore by the occurrence of returns at both maxima and minima, in spite of differences of 50-100 spots. It is also indicated by the fact that the number of early returns within 1 year of the various extremes, beginning with 1883, bears no consistent relation to the number of spots, as seen in the following:

TABLE 8

			Maximum		
Year	1883	1893	1905	1917	1928
Spots	64	85	63	104	78
Returns	3	9	20	17	14
			Minimum		
Year	1889	1901	1913	1923	
Spots	6	3	1	6	
Returns	14	4	10	12	

Migration and Aspection. As in the case of the plant matrix, birds and insects also tend to appear in more or less definite seasonal aspects. In the deciduous forest area at about 40° north latitude, the prevernal group of birds begins to pass through in February or March and continues until late April; May is marked by the second or vernal group, and this is followed by a few species that are estival and serotinal. In these northward movements the birds appear in so-called waves (Wood, 1906; Smith, 1930), approximately a dozen of these being regularly noted in the region of Oberlin (Jones, 1931). The assumption is that species move forward until low temperatures halt them, a considerable accumulation forming, and that the mass resumes the northerly movement as soon as this barrier is lifted. Stone (1891) has pointed out that the greatest migration takes place on warm nights with falling or low barometer and the least on cool nights of rising pressure, and the conclusions of Cooke (1913) and Smith (1930) are in essential accord. Smith, who carried on observations from 1903 to 1922 at Urbana, Illinois, states that "the greatest migratory activity in spring occurred at times when the weather maps showed an area of low barometric pressure approaching from the west.

with the south winds and rising temperatures which normally accompany them."

Each of the aspects is characterized by a special group of insects and other invertebrates from which the migrants take enormous toll. In addition, the summer residents, which breed in the community, require untold numbers of insects and other organisms to feed their young as well as themselves, and a heavy demand continues as the juveniles are added to the local population. The return of birds from the north is in part late estival, but is chiefly serotinal or autumnal. The population is again greatly augumented during this period, with a corresponding increase in the number of insects, seeds, and fruits devoured. By contrast, the hiemal or winter aspect exhibits relatively few species, and the pressure from coaction is consequently greatly lessened.

Orientation and Sense of Direction. Like the causes of migration, opinions as to the choice of direction and route have run the entire gamut of possibilities from the attitude of insoluble mystery to the view that birds use the same faculties as other animals. The extreme form of the first assumption is exemplified by Cathelin (1920), who regards migrants as automatons driven by equinoctial electromagnetic currents. The popular view is probably represented by Lucanus (1922), who concludes that the bird requires no particular guidance, but follows an instinct that determines direction automatically. In spite of an open-minded and comprehensive treatment of this question (1926), Thomson feels constrained to the conclusion that there is some inherited memory of path and goal. On the other hand, Nicholson (1929) is of the opinion that "a great part of migration is performed simply by the travelers keeping to one appointed direction instead of traveling round and round one little area." Grinnell (1931) is even more definite in expressing the view that migration employs the faculties of everyday in the statement, "No so-called sixth sense, or sense of direction *has* to be invoked to account for birds finding their way during long seasonal migratory flights any more than in their courses of daily movement."

To these two views the ecologist can make no dissent. Testimony as to this can be drawn from the training of "homing" pigeons (Lincoln, 1927), from the experiments of Watson and Lashley, and in particular from those of the Peckhams (1887) on the homing faculties of wasps. Fabre's studies had led him to the conclusion that wasps were guided in their return by a special sense not to be explained (1879), a view that gained much support, but was decisively disproved by experiments of the Peckhams, who demonstrated conclusively that memory alone was involved. A comparison of the ganglion brain of the wasp with that of the bird can leave little doubt that the latter is capable of far greater powers of perception and memory, as it is of vision and flight (cf. Grinnell, loc. cit., page 24). As to the homing of the noddies and sooties tested at the Tortugas, the results were regarded by the authors as being negative in character (Watson and Lashley, 1915), though they opposed the assumption of some new mysterious sense. However, an examination of their tables shows that there were 40 returns and 7 failures when the point of release ranged from 19 to 66 statute miles, and 17 returns to 59 failures when it was from 418 to 855 miles. This accords with the expectation on the basis of memory for location, while a special "sense of direction" should have permitted all the birds to return at all distances, barring accident.

The existence of a special sense or an automatic instinct is rendered still more improbable by the behavior of homing pigeons, in connection with which Thomson (1926:313) states that "the remarkable performances recorded are not explicable by assuming a hereditary factor." In their training, not only do few manage to achieve the longer returns, but it is also known that the birds make definite observations to ascertain the direction of flight, much after the manner of wasps. Moreover, they are unable to find their way from distances of a few miles in fog and they are confused by thunderstorms. According to Rodenbach (1895; cf. Watson and Lashley, *loc. cit.*), they experience difficulty in returning home at night or in cloudy weather if the sun is obscured, while Hachet-Souplet (1903) states that blind birds are quite incapable of finding their way home, even when released but a few miles away.

In his valuable summary of recent progress (1936: 515), Thomson cites the work of Rivière (1929) with untrained birds and those of Casamajor (1927) with birds partially handicapped, neither of which supports the assumption of a homing instinct or a special sense of direction, apart from observation or tropistic response.

Results of the same general tenor have been secured by Rüppell (1934, 1935) with the starling (*Sturnus vulgaris* L.). Seven out of 11 birds returned to the breeding place from a distance of 71 miles, the shortest time being 28½ hours, while but 2 out of 6 came back from a distance of 127 miles, requiring 4 and 9 days, respectively. In other tests, nearly two-thirds of the birds failed to return, namely, 233 out of 353. Hilprecht (1935) released a thousand birds at distances of 130 to 290 miles, but obtained only 33 returns and at intervals of a month or more (cf. Thomson, 1936:516-7).

The question of the guidance of young storks has recently been revived (Rüppell, 1931), but again without definite evidence that they can find their way alone. In one series of studies, the young from 46 nests left before the old, mostly 4–5 days earlier, while in 28 cases they departed together or the parents first. It is not only quite possible that the mature birds overtake the juveniles, but Rodenbach also cites observations in which the latter joined flocks passing overhead, which might well contain older birds. The best evidence at present of the lack of a sense of the direction of their ultimate goal in young storks is advanced by Skovgaard (1929), who reports that of five young banded from the same nest, two were found in Holland and France, and another two in Hungary and Roumania.

Though there can be no serious question as to the manner in which adults find their way, there is still to be explained the migration behavior of juveniles. Since these too cannot possess a special sense, they must likewise make use of perception and memory. The difficulty naturally exists only when the young birds leave the breeding grounds after the parents have departed. Departure takes place more or less by groups and at successive intervals and in a definite direction. Thus, it is probable that many flocks of young contain one or more adults as actual if not intentional guides. Those that start southward without such guidance must do so in consequence of a memory of the direction taken by their parents or by virtue of physiologic orientation in response to the incidence of the sun's rays.

Here, again, it is assumed that an understanding of southerliness in terms of warmth is as certain in connection with direction and path of migration as it is in relation to local behavior. In evidence of the latter, reference may again be made to the movement of ground birds during hot days on the Great Plains, when they shift for hours to keep fenceposts between them and the sun, leaving the shadow with reluctance and returning to it almost at once. Similarly, on the northward journey, it seems that the need for cooler conditions favorable to normal metabolism is realized by means of an orientation apparently thermotropic but in reality directed by perception. Since the three sets of evidence are all drawn from experiment, the probability is strong that the conclusions will stand the test of more extensive experimentation with some of the common migrants, but final judgment must await such researches.

CHAPTER 7

CLIMAX AND SERE

NATURE AND SIGNIFICANCE

General Relations. Climax and sere have been the chief topics of study in plant ecology but at the same time have received sufficient attention in animal ecology to make their meaning clear. The present treatment may well be limited to the expansion of the concepts as demanded by bio-ecology. This involves the extension of the term to the climatic plant-animal community and renders it synonymous with the biotic formation (biome), as already indicated in Chapter 2. A corollary of this is the inclusion of the biomes in the ocean, sluggish rivers and larger lakes. As a consequence, it becomes necessary to recognize hydroclimates in bodies of water (Huntsman, 1920; Wasmund, 1934) and to establish comparisons between them and those on land.

Climax and Climate. Although the usual meaning of the word climax is in harmony with its application to the adult or final stage of community development or succession, its primary sense is more significant of the concept involved here. It is derived from the same root as climate, and hence this cognate relation is well adapted to express the cause-and-effect bond between the two. As a consequence, climax is peculiarly appropriate when it is desired to emphasize its causal connection or ultimate nature, and biome when the idea of the biotic community is uppermost. The basic principle that climaxes constitute the most exact expression and hence the best indicators of land climates appears susceptible of extension to the waters. The nature of the aquatic climate is discussed in some detail in Chapter 9, where the greater density of the essential medium, its circulation, greater carrying power as compared with air, the floating organisms and non-living suspended matter with their effect on light penetration, etc., are considered. Wasmund (1934) has also discussed hydroclimate and hydrometeorology in comparison with the corresponding phenomena of the air.

Life Forms. Though a biome may be composed of several different life forms, its characteristic physiognomy is due mainly to a single life form in the case of land climaxes, but usually to several in the case of aquatic ones. In fact, a change of life form or life-form combinations is the most essential difference between biomes. This is illustrated on the plant side by grassland, scrub, and forest as to grand divisions, and by coniferous, deciduous, and broad-leaved evergreens as subdivisions of the tree type. Among animals, the life forms are more varied, owing to the presence of sessile, sedentary, and motile forms of large size. The several types of motility (and associated forms), manifested in the vertebrates as flying, running, swimming, and burrowing, are repeated in some of the other major divisions of the animal kingdom and serve to show how complicated the field becomes.

Life form has been but little used in designating animal communities. Coral communities have been discussed (Brooks, 1893) in comparison with plants, but it has not been found possible to treat them here. Shelford (1935) recognized bivalve-annelid, barnacle-mussel, and gastropod-echinoderm communities. The last two may be combined under barnacle-gastropod and the first subdivided to give the classification found in Chapter 9, all of which indicates the relation of life-form types to the invertebrate phyla and the diversity of form that enters a community.

TABLE 9

LIFE-HABIT STATISTICS OF 15 INFLUENT ANIMALS EACH OF GRASSLAND AND CONIFEROUS FOREST, ALL OCCURRING IN SOUTHERN MANITOBA (SHELFORD, 1915)

Activity Layer		Forest Species	Grassland Species
Breeding	Arboreal	34%	0%
	Ground	40%	30%
	Subterranean	26%	70%
General habit	Arboreal	33%	0%
	Ground	64%	53%
	Subterranean	3%	47%

The fact that each major marine community may be distinguished by life-form combinations is readily brought out by an inspection of the quadrat-content illustrations published by the Danish Biological Station (Figs. 75, 76, 78, 79, 81, 82, page 335, etc.; Petersen, 1918), which show several life forms: bivalve, worm, starfish, etc. By contrast, the dominants of land climaxes typically belong to a single life form, such as grass, shrub, or tree, but two or more secondary forms may occur in prairie, such as mid and short grass, sod and bunch grass.

As is suggested by these examples, life form may sometimes be used to separate subdivisions of the biome, both in the sea and on land.

In general, among the more motile animals, life habit is the practical equivalent of life form in sessile animals and plants. The form characters of motile animals of the same life habit differ so greatly as to render form of doubtful significance. The life habit characteristics usually must be brought out by statistics, as shown in Table 9. Such statistics bring out specific differences, but do not take into account quantity or potency.

Convergence in North-Central Indiana

Sand Ridge	Clay Bank
Cottonwood 1. *Cicindela lepida*	Bare ground 1. *Cicindela limbalis*
Jack pine 2. *C. formosa generosa*	Shadbush 2. *Polygyra monodon*
Black oak 3. *Cryptoleon nebulosum*	Cottonwood 3. *Polygyra monodon*
White oak—Black oak—Red oak 4. *Hyaliodes vitripennis*	Hop-hornbean 4. *Fontaria corrugatus*
Red oak—White oak 5. *Cicindela sexguttata*	Red oak—Hickory 5. *Cicindela sexguttata*

Beech—Maple
Red-backed salamander
Plethodon cinereus

Hickory—Red oak 5. *Cicindela sexguttata*	Soft maple—Tulip 5. *Plethodon cinereus*	Birch—Soft maple 5. *Plethodon cinereus*
Elm 4. *Panorpa venosa*	White elm and white oak 4. *Pyramidula striatella*	Tamarack 4. *Hyla pickeringii*
River maple 3. *Helodrilus caliginosus*	Buttonbush 3. *Asellus communis*	Poison sumac 3. *Hyla versicolor*
Willow 2. *Succinea ovalis*	Cattail—Bulrush 2. *Chauliodes rastricornis*	Cattail—Bulrush 2. *Sistrurus catenatus*
Ragweed 1. *Tetragnatha laboriosa*	Water lily 1. *Musculium partumeium*	Water lilies 1. *Musculium partumeium*
Floodplain	Shallow Pond	Deep pond

Tests of a Climax. The essence of a climax is found in its relation as effect to the climate as cause, typically expressed on land in a single life form for dominants. The nature and unity of a biome are also indicated by the course of succession, owing to the fact that the various seres all converge toward the climax. Since numerous examples of these are to be found in each stage of development, their comparative study furnishes evidence of the first importance. This is particularly true of subseres, in which the regeneration of the climax may take place within a lifetime, or even less. Fire, grazing, clearing, draining, and cultivation all provide universal opportunity for such seres, the later stages of which are practically conclusive as to the composition of the climax.

The convergence diagram above is concerned with primary seres. It is compiled from "Animal Communities in Temperate America" (Shelford, 1913). The seral stages and substages are given in terms of one or more plants and one animal; five stages are recognized in each case though they are not of equal rank. Beginning in the upper right-hand corner with the sand sere, the cottonwood comes in on sand areas very early and is accompanied by the white tiger beetle which disappears at about the time the cottonwood does. The jack or banksian pine appears as seedlings in the shade of the old cottonwoods and is accompanied by the tiger beetle *Cicindela formosa generosa*. Later black oak seedlings come up among the declining pines. The ant lion *Cryptoleon nebulosum* becomes a characteristic animal with its funnels near the black oak. Later white oaks appear among the black oaks, and together with them the oak plant bug, *Hyaliodes vitripennis*. Later come red oaks, and still later beech and maple.

The clay bank occurs where erosion causes slumping of clay. There is usually seepage, and progress is very rapid owing to abundant seeds of trees and plants which occur above on the upland. Sweet clover crowds out the tiger beetle of the bare ground, and the shadbush, cottonwood, and sweet clover with associated animals really constitute one associes; they are separated in the diagram in the order of establishment.

The hydroseral stages are shown below the climax and are to be read upward. Here again the stages do not constitute associes but represent associated plants and animals. The shallow pond series represents five associes. The white oak referred to is the swamp oak. The sere of the deep tamarack lake or pond as diagrammed is composed of associes. All these stages are quite readily found southeast of Lake Michigan. The beech maple climax is to be found on at least a dozen different types of soil including dune sand.

Convergence is usually traceable without great difficulty even when not all the organisms are known. The investigator is most likely to be misled by postclimaxes toward which all communities in the area appear to converge, the climax being one stage before the postclimax. Watson (1925) has indicated the convergence of a postclimax in northern Florida.

Stability is one measure of a climax, except where, for example, a rock substratum controls a seral community, such as rapid-water communities or lichen communities on granite. The length of time for a climax to develop on the non-rock substrata noted above renders it necessary to appeal to indirect evidence of biotic stability. Such evidence is supplied by the seral position in climatic seres by the comparison of transition communities (ecotones) with the adjacent formations, and by the presence of relicts, especially in the form of those from drier periods (preclimaxes) and from moister periods (postclimaxes). Where the community covers the general level and is absent from the topographic extremes, it is to be regarded as the climax proper. Some attention must be given to the meaning of general level. For example, in southern Illinois the beech-sugar maple climax covers the valleys, hilltops, and hillsides where the difference in level is 500 to 600 feet and the annual rainfall 40 inches. With less rain the climax would cover a much lesser relief and the meaning of "general level" would be different. The seasonal distribution of precipitation must also be considered. When one community is found in small areas in narrow valleys, another on the large area of hillside, and a third on hilltops 900–1000 ft. above the valleys, they are usually considered as postclimax, climax, and preclimax, respectively. Additional evidence may frequently be drawn from the trend of annuation, in view of the fact that the difference between the wet and dry phase of a cycle may exceed that of a full climate. Further testimony can be secured from micro-climates (ecoclines) since the divergence between northerly and southerly slope exposures often amounts to half a climate or sometimes an entire climate. Observation in water is much more difficult; convergence is less evident, and the criteria indicated above can hardly be applied.

Types of Climaxes and Climates. As has been previously indicated, the inclusion of animals in the climax to constitute the biome renders it necessary to broaden the definition of climate and to designate the corresponding communities as climaxes. In consequence, three major types are to be recognized and considered, viz. (1) terrestrial, (2) fresh-water, and (3) marine. In respect to North America, the knowledge of land climaxes has undergone progressive organization for nearly two decades, and the plant matrix and its relations are fairly well understood, though relatively less animal material has been published. On the other hand, though much preliminary work has been done on succession in fresh-water communities, the existence of true climaxes is barely demonstrated in rivers and large lakes. In the ocean, in spite of the paucity of successional studies on marine communities, the age and stability of these justify considering them as climax, provisionally at least.

THE STRUCTURE OF CLIMAXES

Evaluation of Constituent Species. It is sufficiently obvious that the first requisite to the evaluation of a biotic community is a list of component species, showing relative abundance and size. In the case of a climax such as a prairie or a lake, this can be obtained only by means of quantitative studies in which all available methods of collection and enumeration are employed. Through the several seasons and for two or more years at the very least, sample catches over a wide extent of territory are indispensable. The range within which important species retain their dominant or influent character must be determined. The important species of a community will vary within extreme limits in practically all their characteristics, ranging from size to number and role, and the next essential task is to take account of these in accordance with their significance.

Composition of the Biome. Constituent species differ with respect to life form and life history, size, abundance, frequence, constancy, and space and time relations, such as aspection, annuation, and succession. Practically all these have some significance in the role of each organism, but life form and life habit, size, and abundance are regularly the most decisive. On the one hand, they determine the response to the habitat and the reaction upon it, and on the other the interrelations of the species in terms of competition and coaction, such as food and shelter. Moreover, these processes exhibit essential differences in plants and animals, or with respect to their location on land or in the sea, and in climax or sere. However, in spite of the distinctions between terrestrial climates and hydroclimates and climaxes, the bases for the ecological classification of the organisms involved are identical for the most part. These have long been applied, in part, to the role of plant species in land climaxes and their seres, and the present task is to employ them for the evaluation of land animals, and of both plants and animals in water communities.

In the three succeeding chapters, the biome constituents have been classified as dominants, major influents, subdominants, influents, subinfluents, and secondary species. When the categories are extended to include animals and cover the phenomena of the waters, often no sharp line of demarcation between the categories remains.

Dominance and Influence. Dominance is the condition of control of community character and composition that results from the successful outcome of reaction, coaction, and competition, the opposite effect being seen in subordinance (Clements, 1916, 1920). Naturally, no sharp line can be drawn between them, since species run the entire gamut from one to the other and even the same organism may sometimes vary widely in this respect. Cahn (1929) has pointed out that fishes dominate by a combined coaction and reaction, and Petersen (1918) has described dominance due to coaction alone.

Dominance on land is commonly so much a matter of advantage in terms of life form, size or height, and abundance among plants, as to be readily determined when quantitative results are available. Dominants are most potent, and major influents usually second in importance. On land, dominance has been understood to mean the control of habitat through reaction, though dominance through coaction is possible. It is locally evident through the exclusion of forest from the Kaibab parks by deer. The exclosure shown in Fig. 53*b* and viewed in comparison with the unprotected area (Fig. 53*a*) after a period of nine years is significant. The three clumps of aspen stems (*a*, *b*, *c*) are the effect of deer browsing on the unprotected area. Some exclosures at the margin of the larger parks are more convincing because aspens have occupied areas exclosed from the grass-covered spaces at the forest edge.

In water, by contrast, the habitat is of secondary interest, and the community, which is directly and indirectly controlled, is the primary consideration. In marine and fresh-water climaxes animals evidently often dominate largely through coactions by which the character of the community may be almost completely changed (cf. Petersen, 1918; Cahn, 1929; Shelford, 1935; Gersbacher, 1937).

The significance of animals on land has often been questioned by plant ecologists, but this cannot be taken too seriously, as the work has usually been done in areas where the more significant animals have been extirpated. The early efforts in animal ecology suffered from the same causes, and in both fields lack of training necessary to cope with animal problems was evident. This was naturally most striking among plant ecologists, and until more studies such as those of Vorhies and Taylor (1922) are made, the basis for the interpretation of animal relations and importance must be considered inadequate for anything more than provisional evaluation. Cahn (1929), Ricker (1932), and others have credited certain fishes, such as carp, suckers, and their relatives, with eating vegetation, disturbing the bottom, and increasing turbidity. This reduces or eliminates the vegetation, and such fishes dominate through both coaction and reaction. The marine cases cited by Petersen (see page 350) are probably pure coactions.

The concept of dominance has heretofore been limited to plants on land, and reaction, competition, and response manifested in the plant matrix itself have formed the threefold basis. In the sea, a parallel series of phenomena may readily be recognized among corals.

FIG. 53*a*.—Deer-browsed area marked off at the time the exclosure fence was built in 1927 (Fig. 53*b*). *A*, *B*, and *C*, mark clumps of overbrowsed aspen stems. (Courtesy U. S. Forest Service, W. G. Mann, Supervisor. Photo by H. L. Andrews, 1936.)

Since the equipment of sessile organisms differs more or less in all three respects noted above, there are corresponding differences in the degree of dominance. These are reflected primarily by the life forms and secondarily by size, abundance, or both. On land, at least, the first is peculiarly decisive as to the period of dominance, and hence regularly marks the distinction between the dominants of climax and sere, and the successive stages of sere.

By contrast with plants, land animals exhibit very little direct structural response to the habitat, but exert more or less reaction upon it, chiefly through disturbing the soil. Their competition is mainly connected with shelter and food coactions, and not with reaction. On the contrary, aquatic sessile and sedentary animals resemble plants more or less closely in all these respects.

Influence. In the case of land animals, the chief effect is exerted through coaction upon plants, and their role is commonly one of influence rather than of dominance. Although burrowing animals regularly exercise a definite reaction upon soil, this rarely leads to the destruction of the plant matrix. Modification of it is a more frequent consequence, as exemplified by the hills of mound-making ants and those in prairie-dog towns. Moreover, though influence may sometimes produce striking changes in the appearance of a community, as in the short-grass condition of the mixed prairie, it does not often lead to permanent transformation. Even in the short-grass community or disclimax, the mid grasses are regularly present in suppressed form, and attain expression during wet phases at least.

Fig. 53*b*.—An exclosure plot showing the large growth of aspens at the edge of a parklike opening, Kaibab forest, 1936, when protected from deer. (Courtesy of the U. S. Forest Service, W. G. Mann, Supervisor.) The exclosure was similar to the area shown in Fig. 53*a* at the time of fencing. (Photo by H. L. Andrews.)

Influence is the outstanding characteristic of the animals of the terrestrial biomes, and constitutes the basis for placing them in the proper ecological relation to plants, as well as to each other. This applies likewise to man under primitive conditions, especially before dominance resulted from cultural accomplishments such as the production of steel (Shelford, 1935). But civilized man has also become a reactor through extensive development of human culture. Lumbering, as a direct coaction, and grazing, as an indirect one, produce reaction only incidentally, but fire, clearing, cultivation, draining, flooding, and construction regularly react on soil conditions and often extend over wide stretches.

It is evident that influence, like dominance, depends upon the life form, and in a large degree upon size and abundance as well. This is particularly true of the basic coactions that concern shelter and food material. In all such relations, the animal typically assumes the active role and the plant a passive one, and hence it is not desirable to treat the plant as an influent, unless it is parasitic or poisonous. Coactions of introduced parasitic plants have at times produced striking results, e.g., the chestnut blight which has practically destroyed the typical dominant of the oak-chestnut association. In water, some animals play the part of dominants, as distinct from that of influents taken by others. However, influence is more commonly exerted upon other animals than on plants, though plankton-eaters devour both the plant and animal members of the microplankton.

Kinds of Dominants. Apart from the obvious distinction of dominants as plant or animal, land or sea, climax or seral, they have been distinguished on the basis of their role in the community (Clements, 1916, 1920, 1928; Shelford, 1935). The major division in land communities is into dominants and subdominants, and it is probable that this applies to some aquatic ones also, especially in the benthic climaxes. The term codominant has been variously employed, usually for one of several dominants. In this sense it appears to be superfluous, and it is here proposed to utilize it for dominant species belonging to the other kingdom, such as seaweeds in the ocean and carp in ponds.

From the standpoint of the food nexe of lake and ocean, the minute forms of the plankton possess an importance quite out of proportion to their size. In recognition of this fact, they have been termed *vedominants* (*ve-*, small), a treatment further justified by their direct response to the hydroclimate and their reciprocal reaction upon it. Similar small or microscopic organisms take the leading part in the short succession, or *serule* (*-ulus*, diminutive), typical of dead plants and animals, logs, food masses, etc. To these, the term *dominule* is applied, in taking account at the same time of their role and size.

The Dominant. According to the prevailing interpretation, a dominant is an organism with such definite relations to climate and such significant reactions upon the habitat, or in water upon the other community constituents, as to control the community and assign to the other species subordinate positions of varying rank. The resulting interrelations have been analyzed in considerable detail for land-plant communities (Clements, Weaver, and Hanson, 1929), but it is quite probable that the zoophytes of coral areas exhibit them in a degree not unlike that of grasses and shrubs. The graded series from these to the motile dominants of marine pelagic and fresh-water biomes presents such relations in constantly diminishing measure, but when more is known of the response, reaction, and coaction of the animals concerned, it is probable that pronounced dominants will be found throughout.

The major characteristics of dominants may be indicated as follows:

1. Dominants receive the full impact of the climate or of the aerial factors in the case of terrestrial seres.
2. They are the species best adjusted to climate or habitat as the case may be, and hence are regularly most abundant in terms of density or weight, as well as most stable in reproduction.
3. They react directly upon the climate, modifying water and light relations especially on land, and the gas and salt content in the sea.
4. Climax dominants take possession of territory and hold it against all comers as long as the climate oscillates only within its proper range, while the occupation of seral dominants is limited by the succeeding stages.
5. Climax dominants are able to continue to grow and reproduce in the conditions due to their reactions, while seral ones react upon the habitat in such a way as gradually to favor the invasion of their successors.
6. Dominants on land, by virtue of life form and abundance in particular, are the major sources of food, material for building, and shelter, and usually constitute the basis for the ruling coactions, which serve as a primary bond in the biotic community.
7. Codominants are essentially dominants in terms of reaction or coaction and control, but differ from the typical dominants of the community in the nature of these processes, since they are constituted by plants in communities chiefly dominated by animals, or the reverse.

Subdominants. A subdominant has been defined as a species that exhibits a secondary dominance within the area controlled by a dominant. It gives character to pure or mixed societies, either spatial or seasonal, in the climax, and to similar socies in the sere. Subdominants are the successful competitors among the species that accept the conditions imposed by the dominants. In grassland, they are the outcome of a double competition, namely, among themselves as well as with the dominants; in forest the struggle is chiefly between the species of the layers. They regularly differ from the dominants in life form, consisting of forbs in grassland and desert, and of forbs and shrubs in forest. Their alternation over an area or through the season is largely determined by competition, which is decreased or evaded in some degree by such a disposition.

From the nature of their relation to both habitat and dominant, subdominants on land are very generally restricted to plants, the corresponding groups among animals being termed influents. In water, where the chief dominants are animals, societies, and to a smaller extent socies, are undoubtedly to be found (Eddy, 1934), but the necessary analysis has barely begun in lake and river, and in the ocean. It is already evident, however, that subdominants occur in the pelagic communities, both fresh-water and marine, and often characterize striking seasonal societies.

Dominants in Aquatic Communities. In fresh water, no true climaxes appear to be established outside of sluggish rivers and large lakes, and the dominants are hence usually seral in character. The rooted marginal vegetation, which produces such notable reactions as the filling of lakes, marshes, and bayous, all belongs to the hydrosere of the climax of the region in which the body of water occurs. The tidal climaxes exhibit successions (Hewatt, 1935), and both seral and climax dominants occur in them, though the latter are much more numerous and important. Since this includes a belt of the marine algae, it also exhibits codominants, which form faciations or lociations in respective climaxes.

Seral dominants probably play a small part in the deeper parts of the ocean, owing to the constancy of conditions and the lack of processes that produce bare areas. However, the great physical differences at various depths appear to demark horizontal climates with corresponding climaxes and dominants (Fig. 73, p. 317). The latter differ greatly in life form as a rule and exhibit even greater differences in size. For these reasons in particular, it seems possible to set the phytoplankton or produceents and the small zooplankton consumnents apart as miniature dominants. The chief organisms of the pelagic and benthic climaxes are best characterized as dominants in the usual sense, while those less important but still significant in abundance or importance are miniature dominants. As suggested earlier, it is not unlikely that quantitative studies on a larger and more extensive scale may also render it desirable to distinguish societies of subdominants, especially in the benthos.

Kinds of Influents. As indicated previously, the term influent is practically to be restricted to animals because of their role as coactors. In water climaxes, the effects of animal dominants have not been evaluated as to the relative importance of reaction and coaction. Influents fall less definitely into the primary categories of dominants, namely, land and water on the one hand, and climax and seral on the other. They may in time be grouped in accordance with importance of coaction into various categories, such as major influent, minor influent, subinfluent, and veinfluent. Lack of knowledge and opportunity for the study of the more important influences due to extirpation and reduction in numbers, and fluctuation in abundance, renders such classification difficult in some communities at present. Major influents include the larger mammals and birds or intermediate forms of marked coactive significance, the fishes, and other aquatic organisms of considerable size or vast number. Minor influents comprise the smaller rodents, insectivores, bats, most of the birds, amphibia and reptiles, and a host of marine forms. Subinfluents embrace the larger insects, arachnids, snails, isopods, etc.; and veinfluents, the disease organisms, micro-insects, the fauna of the soil, and the macro- and microplankton. Though no hard-and-fast line can be drawn between these groups, especially in the present state of our knowledge, they may serve to bring out the comparative roles of coactors in a particular community.

On the basis of abundance and time of appearance, smaller influents may be classified as prevalent or predominant when they are present in numbers throughout the several significant seasons, as seasonals when they occur during one or two aspects, such as spring, summer, etc., and as cyclics, when they exhibit marked fluctuations or appear only at intervals, like certain cicadas. The larger influents may fall into a similar grouping, though quite possibly their fluctuations were less under primeval conditions. In many cases, migratory species are influents in more than one climax and hence must be listed as seasonals in two or more communities. Animals probably do not range outside the biome in which they are influent farther than plants, except when migratory; for example, a few grasses dominant in the prairies may range east into New England in dry sandy spots, but they bear no significant relation to the deciduous forest climax. The difficulty on the animal side arises from lack of evaluation as to abundance and lack of appreciation of the intricate interlacing of biomes at their borders. No special terms to apply to the range of animals seem necessary, since the significance of the few exceptions to the usual rule can readily be discussed without them.

The most illuminating facts in regard to the animals of a biome are found in the relation to climax and sere and to permanent bodies of water, such as rivers and large lakes that are not necessarily seral. The relations of plants to early seral stages and to watercourses were long ago recognized in Schimper's (1898) distinction between climatic and edaphic communities. This stands in sharp contrast to the attempt of Merriam (1890) and his followers to mix the two and use edaphic or local climaxes species as indicators of life zones supposedly based on temperature. Schimper's suggestions laid the foundation for further development of succession and other dynamic ideas, while the life-zone view has served to confuse values.

Choice of habitat by each species of animal constitutes an important response, expressed chiefly by the term niche. While Elton (1927) employs this word to sum up the relations to food and enemies, so that it is largely synonymous with coaction, Grinnell (1928) and Park (1931) used it in the sense of place. For purposes of locating the animal in the biotic community and defining its life habit, the space relations, plant matrix, specific plants frequented, and soil and water requirements are of first importance. Many animals occupy several minor habitats during their life history, a fact well illustrated by the bobwhite, which according to Leopold (1933) requires somewhat distinct places for rest, sleep, nesting, drying young, and hiding with and without snow cover, whereas the deer of the Lake States requires five types of places for its different activities. Other animals resemble the deer and bobwhite more or less in this respect, and hence niche is often a compound space concept, to which role of food and enemies must be added, and the term then becomes synonymous with life requirements.

The life requirements of many large influent species during the yearly cycle include a series of different places, thus bringing them into contact with most of the seral stages of the region and with the climax. Such influents have been termed permeant. On the basis of size, they may be divided into major and minor permeants. The boundary line between major and minor is based on the inability of the major influents to hide in vegetation, hollow logs, etc., while minor influents can do so readily. Influents that are confined largely to the seral stages may be termed seral, those confined to the climax, climax influents. Further, because of the great difficulty of estimating degrees of influence, the term arthropod influent may well be applied to the numerous insects, arachnids, etc. (Shelford and Olson, 1935).

Structure of the Climax. Each climax is the product of climatic differentiation operating upon an original community of vast extent and fairly uniform composition. Such a climax under the compulsion of climatic shifts became a panclimax comprising two or more climaxes. The best illustrations of this process today are to be seen in the circumpolar tundra, coniferous forest, and prairie-steppe panclimax or panformation, each of which is divided into an old and a new world climax. Such a process of community evolution has operated alike upon the plant dominants and the animal influents. The old and new world biomes are as closely related in one as in the other respect, while the community bonds in terms of coaction especially are very similar, when not identical.

Major Units of the Biome. The climatic factors that produced climaxes or formations have continued to act, with the consequence that each biome has been further differentiated into divisions known as associations. The common origin of the associations of a formation is still attested by the fact that the dominant genera are largely the same throughout and that several species serve as "binders" (or perdominants) between the various divisions and especially the contiguous ones. This principle is well exemplified by the grassland formation in which the dominants are certain species of Stipa, Bouteloua, Sporobolus, Agropyrum, Koeleria, and Andropogon that occur over most of the climax area, while such dominants as *Stipa comata, Koeleria cristata, Bouteloua gracilis,* and *Sporobolus cryptandrus* recur in nearly all six associations. The distribution of influents is comparable to a large degree, as is indicated by such animals as *Bison bison, Antilocapra americana, Canis nubilus, Taxidea taxus,* and species of Citellus, Dipodomys, and Geomys.

In their turn, associations are divided into faciations, on the basis of subclimates as reflected in the entrance or disappearance of one or more dominants. Although faciations have now been recognized in most of the major associations of the continent, such analysis has been carried out most completely in the mixed prairie, which is thought to represent the original matrix of the grassland climax. The presence of *Buchloe dactyloides* as a major dominant marks a central faciation, *Hilaria jamesi* and *Stipa pennata* a southwestern one, and *Festuca ovina*, one at high altitudes. To what extent animal influents are to be correlated with such units is at present uncertain, but there are at least some examples of agreement. The faciation itself may be characterized by subordinate groupings of dominants. These minor units are termed lociations, and as the name indicates are relatively local in extent, occupying a few thousand square miles. They have been studied chiefly in the grassland, and their biotic composition is almost untouched as yet.

In the sea, all the essential relations described above for the mixed prairie are evident in communities of the sea bottom about Denmark (see Chapter 7) and in Puget Sound. Weese (in Shelford et al., 1935) described a series of faciations in the bivalve-annelid community of a narrow bay. Faciations also occur in the large gastropod-echinoderm communities in the same region. Marine lociations are best illustrated in the Balanus-Littorina biome of the Pacific Coast of North America, where Rice (1930) and Towler (1930) have described many peculiar local variations in the arrangement of barnacle dominants. These are explained by Rice (in Shelford et al., 1935) as caused by the combination of low tides and warm sunny weather during the seeding and early stages of the barnacles. She points out that the arrangement of the dominant species is controlled by mortality, etc., during accidental combinations of conditions, a fact that leaves the arrangement of adults and nearly grown individuals without meaning unless the series of past events is fully known.

Among plants, a concrete community, the consociation, stands by itself as a climax unit consisting of a single dominant. In associations with several dominants, such as grassland and deciduous forest, consociations reach expression regularly only in limited areas that are especially favorable to each. However, when the major dominants are but two or three in a particular association, one of these may form an almost pure community over a large area. This is true of *Pinus ponderosa* and of *Picea engelmanni* in the Rocky Mountains, of *Pseudotsuga mucronata* on the Pacific Coast, of *Artemisia tridentata* in the Great Basin, and of *Larrea tridentata* in the deserts of the Southwest. In the bunch-grass prairie of California, a similar role was played by *Stipa pulchra* up to the later historical period, and still more recently by *Agropyrum spicatum* in the Northwest.

Some subspecies of animals, chiefly subinfluents, find their range wholly or largely in such consociations, and the number of these will probably be increased. Finally, in view of the fact that any major dominant may recur more or less pure in repeated local examples, it has proved convenient to refer to it as a consociation, even though it is part of a particular faciation; that is, the association is divided into faciations, in which the consociation appears only as local expressions. The dense communities of the bivalve, *Spisula subtruncata*, in the

North Sea (Davis, 1925), have been referred to as consociations (Shelford, 1935), but when compared with plant consociations certain differences are seen to exist. In view of the apparent dominant function of brittle stars already referred to, and the possible dominance of marine fishes, further investigation may indicate that Spisula is a secondary dominant. Furthermore, while Spisula outnumbers other constituents a thousand to one, the latter are nevertheless present.

The sea exhibits other groupings that resemble consociations, the oyster bed constituting an example. The oysters form a substratum which encourages hard-bottom species and hence serves as the basis for a community that would not otherwise occur in the area, especially where water is quite brackish. The bivalve, *Modiolus modiolus*, forms similar groups and supports hard-bottom communities on the shells, while resting on bottom too soft to support these associates. These are more far-reaching in their effects and relations than the consociation dominant in a plant community. It must further be recognized that, while the oyster and Modiolus communities appear like fragments of other biomes, such as groves of deciduous trees in grassland, they are not so, but are unique certainly so far as the oyster is concerned. However, the Modiolus communities of the North Pacific have been regarded as the subclimax stage of the Strongylocentrotus-Argbuccinum biome because (*a*) they support this on their shells, and (*b*) they are climax dominants of the hydroclimate above, regardless of the unfavorable bottom.

Minor Units. As has been indicated earlier, the subdominant plants constitute secondary groupings within the community of dominants. In the main, the life form of subdominants is that of the forb, but bush and shrub are also to be included, chiefly in layered forests. Communities of this rank have long been known as societies, being called simple or pure when composed of a single species, and mixed when comprising two or more of similar importance. The two most significant categories are those of aspect or seasonal and layer societies, the former marking the change of tone in the plant matrix through the seasons and the latter being best developed in forest. Communities of small animals, chiefly arthropods, restricted to the layers have been called layer societies. The plants most nearly equivalent to the invertebrates of these societies are the mosses, lichens, and fungi.

The vast majority of the arthropod constituents of the layer animal societies of the deciduous forest biotic community (Weese, 1924; Blake, 1926; Smith, 1928) move to the ground surface and under fallen leaves for the winter, greatly increasing the population of that layer and constituting an hiemal layer society. It is not correct to assume that shrub and tree top hiemal layer societies do not exist, as birds and ants still occupy these levels during the winter (Smith-Davidson, 1930). It is true also that many arthropod inhabitants of herbs do not leave these until they have been broken down by frost and snow. A few of them come up early in spring or even in warm weather in winter and feed on the buds and shrubs before herbs have appeared.

The question of the relations of the plants and animals of the subdominant communities to the chief dominants of a terrestrial biome, to each other, and to the group as a whole is a difficult one. At the outset of our discussion of this topic, it was thought that the entire group of subordinate organisms could be treated together under the term presociety, in the sense of a prevalent rather than a dominant or controlling group. With further study of the literature and the communities of waters, it became impracticable to recognize and separate these two divisions of the biome, and the trend of investigation naturally caused the term to be applied to animals only (Smith, 1928; Shackleford, 1929; Bird, 1930), while in general the consideration of plant layers has not concerned itself with the associated animals, or the small and more subordinate lower plants.

The problem of a natural or at least a logical classification of societies is connected with the need of modifying the concepts of family and colony. In plant ecology, these have been employed for the first two stages in succession, the family comprising all the individuals of the pioneer species, and the colony, the group constituted when one or more additional species invade the area. In zoology generally, family and colony possess essentially the same significance, though the term colony is more frequent and is usually restricted to invertebrates. In the endeavor to render these terms both definite and distinctive, it is proposed to employ family for the simplest grouping, in which the individuals belong to the same species, whether plant or animal. In the case of animals, they will have sprung from the same parents or parent as a rule, though with plants this will have more frequent exceptions. The family will retain its character as the simplest initial community, but it may appear in the climax as well as constitute the first stage of a sere. In consequence, the colony will be limited to a relatively small community of two or more species, either of plants, plants and animals, or animals alone; in other respects, its position and role in the biome will be much like those of the family. By contrast, the society has denoted a climax community of higher rank, larger extent, and greater importance in terms of subdominants and influents, but it is now proposed to employ it as a general term for subordinate communities, including seasonal ones (Clements, 1936).

In connection with the above terms, as well as those later discussed under succession, it should be borne in mind that each has a concrete or local application and, in addition, a general one. Thus, the pioneer family of tiger beetles on a particular dune or sandhill may recur in all identical habitats in the local area, or through an extensive region, to constitute the pioneer family of a dune succession. The community formed in the climax true or mixed prairie by *Psoralea tenuiflora* exists today in thousands of separate fragments, as a consequence of topographic diversity and especially of disturbance, but the local examples are best regarded as parts of an extensive community. The same is true of nearly all fresh-water communities. The validity of this conclusion is all the clearer in the true prairie, for example, where an originally continuous association of wide extent has been fragmented by tillage into many thousand pieces, often but a few acres in extent.

General Comparison of Land and Sea Communities. It is obvious from the foregoing that size is an important criterion for the rank or the significance of communities. The next paragraph indicates, in very general terms, the comparative magnitude of climax and seral communities of the land and sea bottom. It is based upon grassland as one of the most extensive of North American biomes (Clements, 1920; Weaver and Clements, 1929; Shantz and Zon, 1924), and upon the marine communities of the North Atlantic and North Pacific (Petersen, 1914; Jensen, 1919; Davis, 1923; Shelford and Towler, 1925; Shelford, 1935).

The following facts are brought out relative to the size of various units. The biotic formation (biome), such as the North American grassland, may cover as much as 1,000,000 square miles and be divided into five or six associations covering 100,000–300,000 square miles. Although the association is accepted as the most uniform unit, there is still variation which the original workers such as Warming had not discovered. A large association like the mixed prairie may show faciations characterized by the dropping out or addition of species which are as large as 9,000 square miles or even larger, and lociations or local variation may be as large as 900 square miles. The climax is more or less continuous but may be much fragmented at its periphery.

Seral communities are generally very much smaller and usually much fragmented. A continuous seral area of 200,000 square miles illustrated by the southeastern pine forest, or still larger areas of black spruce at the northern edge of the transcontinental coniferous forest, do exist. The latter may be two or three times as large as the pine area. Perhaps the total area of black spruce consocies is 1,000,000 square miles, one-half of which is black spruce forming lacework, the meshes of which are composed of water and open muskeg. Again the northern and southern large seral areas are only two out of hundreds of types such as those on sand areas, floodplain, rock outcrops, lakes, ponds, and swamps. These are all small, being fragmented in an almost unlimited manner, so that a continuous area of 25 square miles is out of the ordinary and facies may well be only 2.5 square miles, while local variations (locies) are small and perhaps a quarter section (160 acres).

The marine aquatic communities show various sizes, but near land, 1 100 the size of the North American grassland is to be expected, and other groupings in proportion are likely to be the rule. Fresh-water communities rarely are large; as a rule they are either long narrow strips, or are greatly fragmented, or both. They also possess a minimum of decomposed vegetation. The communities of small lakes, ponds, pools, swamps, marshes, bayous, and oxbows associated with streams, bays, and other marginal fragments of large lakes, together with the smaller ones about arms of the sea, are seral stages to the land climaxes of the region.

The preceding discussion shows size to be important though largely relative, but on the whole communities as described herein are large. They differ strikingly from the communities covering a fraction of a square meter such as are often discussed by plant sociologists and students of animal aggregations. The development of climax communities in small denuded or retarded areas has received attention at the expense of broader features or extensive areas of the biome, which makes it unnecessary to treat the subject in detail in this connection.

The Dynamic Nature of the Climax. While climaxes may persist and have persisted for thousands or even millions of years, each one is the seat of dynamic processes of varying intensity and extent. The outcome of these is a vast mosaic of great complexity, the understanding of which can be obtained only by the study of the processes themselves. The motive forces involved are climate, topography and soil, reactions and coactions of all sorts, of which those of man are paramount. Cycles in climate produce a climatic succession (or clisere) in which climaxes replace each other in their fixed geographic sequence, a process best exemplified during glacial advance and retreat. In the course of geological epochs and periods, each climax will leave relict areas of itself in favored situations in the two adjacent climaxes, and these constitute the preclimaxes and postclimaxes that form the most illuminating pieces of the mosaic.

Next in significance are the topographic processes that initiate succession and bring about ontogenetic (short successional) changes in the climax by contrast with the phylogenetic (climatic) ones just mentioned. Lake, pond and stream, lava flow, rock fields, dunes and sand hills all break the continuity of the biome and serve as foci for the development of hydrosere and xerosere. Though these finally culminate in the climax, the opportunity for their initiation is constantly renewed from time to time and place to place, and this taken with varying rates of progression explains why immature stages of the climax are to be found everywhere through it.

To the variety wrought in the climax picture by these primary successions are added, in most communities available for scientific study, the modifications intensified and initiated by man. These are less deep seated but much more frequent and result from disturbances of all kinds, notably fire, trapping, hunting, animal control, clearing, cultivation, and grazing. Fire, lumbering, clearing, hunting and trapping have destroyed or modified the climax in practically all forest regions. Cultivation, together with hunting, trapping, and mammal control, has left but scattered and incomplete fragments of the humid prairies, and grazing and mammal control have changed the composition of semi-arid ones by favoring certain dominants and influents at the expense of others.

Under natural conditions, the numbers of animals fluctuate greatly, in more or less definite response to climatic cycles, as already indicated in Chapter 5. It is true also that the dominants and subdominants of the plant matrix of grassland, for example, undergo great variations in growth and number of individuals from year to year. This process of annuation often produces striking differences in the composition and appearance of the climax at the wet and dry extremes of the sunspot cycle. The greatest fluctuation in forest is in seed crop and herbaceous growth. Annuations and variations in abundance also operate in fresh-water and marine climaxes (Blegvad, 1925). Quite as pronounced in many instances is the orderly procession of aspects through the biome from spring to fall and winter. In this, the changes in the plant matrix are concerned wtih dominance and pattern rather than with composition, but with the subinfluent and veinfluent animals marked changes in population occur from aspect to aspect.

In preparing this book two courses were open to the authors: either to present a description of examples of the natural phenomena with which the book is concerned as a basis for general discussion to follow, or to reverse the order. The reverse order was chosen, but not without misgiving, and accordingly the last task is to describe enough natural phenomena to illustrate the general principles that have been brought out. This of necessity consists in describing at least three major communities—a terrestrial, a fresh-water, and a marine one. The treatment of all the major communities of northern North America is a major task in itself, though a provisional account is entirely possible. Fresh-water communities have not been sufficiently explored from our viewpoint, and the great variety and meager knowledge of marine communities make more than a cursory treatment impossible. The major communities or biomes (usually termed biotic formations, but we have in various earlier papers substituted "biome" as a much more convenient term of the same connotation) are the desert, the chaparral, several in the coniferous forest group, the tundra, alpine meadow, deciduous forest, and grassland. The last was chosen to illustrate general principles because it is probably most completely known.

CHAPTER 8

THE NORTH AMERICAN GRASSLAND: STIPA-ANTILOCAPRA BIOTIC FORMATION (BIOME)

Introduction. The grassland is well suited to illustrate the characteristic features of the biome and the interdependence of the constituents and their relation to climate. This results not merely from its wide extent and exceptional differentiation structurally, but likewise from the unusual number of striking coactions.

From the ecological viewpoint there is no essential distinction between so-called prairie and plains, just as there is also no consistent diversity in topography. Both are uniformly characterized by a cover of perennial grasses in close harmony with the climate and likewise by a former population of grazing animals. The usual conception of a prairie is that of a rolling landscape by contrast with the level expanse of plains, a view that receives much support from the so-called high plains of the West, but over the entire area of the grassland the exceptions are so numerous as to obscure the rule. The plant life form (grass form) is further to be regarded as the decisive criterion in many districts of sandhills and foothills in which the relief is much bolder than in traditional prairie, though the cover exhibits the usual dominants (Pound and Clements, 1898).

The peculiar physiognomy of grassland is well known to all who have visited it. The vegetation itself offers little or no obstruction to vision. Large areas of the central portion of our North American grasslands, green in summer and brown in autumn and winter, stretch away as far as the eye can reach. Generally, however, the uniformity is relieved by slopes, rolling ground, small hills or ranges, and ravines and valleys often marked by relict or seral communities of trees or shrubs. Consequently, strong contrast and sharp delimitation of valley and plain are among the striking features. Near the grassland margins where the contacts are with tree or shrub communities, there are small groups of shrubs that break the monotony and afford habitations, shelter, or perching places for various animals.

In conformity with the biotic concept, animals have a distinct role in the physiognomy of grassland, but this was naturally much more evident before the period of settlement. At that time, an ecologist standing on a small rise of the plain on an August morning might well have seen a large herd of bison grazing to the right, and a smaller herd of antelope to the left, while nearer at hand a coyote or wolf would be seen slipping away to its den. Even today, as one walks about, a long-eared jack rabbit bounds up from behind rock or forb and gallops away, often starting others as it goes. Birds such as the horned lark, lark bunting, Sprague's pipit, and the lark sparrow fly past, singing on the wing. The bee flies and robber flies are unusually conspicuous in flight, and grasshoppers are everywhere in evidence. Such prospects, except for the bison and pronghorn, came into the experience of the authors 30 or more years ago and stand in sharp contrast to the limited outlook in primeval forest.

Life Forms and Life Habits. The distinctive life form of the prairie is the perennial grass, and to such a degree that an abundance of annuals is an all but infallible index of disturbance. In exclosures, annual grasses have been found to disappear steadily under the competition of perennial ones, at least up to the time when the accumulation of dry shoots becomes a handicap, and this has been confirmed by the outcome of competition cultures. Moreover, the grass form is to be understood in the ecological and not the taxonomic sense. In their community and habitat relations, such sedges as *Carex filiformis* and *stenophylla* are short grasses in effect, and a number of other sedges and of rushes play the role of grasses locally (cf. Weaver and Fitzpatrick, 1934).

As indicated earlier, life habit in animals corresponds in physiognomic value to life form in plants; it is expressed by the terms cursorial, subterranean, arboreal, etc. The life-habit ratios of different

TABLE 10

Number of Common Species Using Different Portions of the Habitat in Breeding, Expressed as Percentages of the Total Number of Species

Breeding Places	Number of Species	Burrows or Pits in Ground	Ground Surface	Rock Ledges and Fallen Trees	Weeds or Shrubs	Trees
Grassland birds	28	4	53	4	34	5
Forest birds	41	0	20	5	7	68
Grassland mammals *	22	82	18	0	0	0
Forest mammals *	22	26	18	18	0	38
Grassland bats	2	0	0	100	0	0
Forest bats	9	0	0	44	0	56

* Exclusive of bats.

taxonomic groups, such as the mammals, birds, or insects, exhibit significant figures for expressing the characteristics of a particular biome and permitting comparison with others.

These data are based on lists by Cary (1917) for Colorado grassland and Howell (1921) for deciduous forest in Alabama. The two sets of data were gathered for the U. S. Biological Survey at the same period. Comparison can be made only within a natural group, for example grassland birds may be compared with forest birds, mammals with mammals, etc.

In the case of grassland birds the majority breed in nests built on or near the ground, 53 per cent contrasting with 20 per cent for the forest. On the other hand, fallen or standing trees are used by 68 per cent of the forest birds. A great preponderance of subterranean species characterizes the grassland mammals, exclusive of bats. There are other life-habit characteristics which cannot be expressed in tables. For example, Craig (1908) points out that forest birds rarely sing on the wing, but eight species of common North Dakota birds do so, namely: horned lark, bobolink, Smith's longspur, chestnut-collared longspur, lark sparrow, lark bunting, purple martin, and Sprague's pipit.

Visibility in grassland is high, and animal habits are adjusted in accordance with it. Eyesight is keen in prairie species, and observation from vantage points takes the place of secretive retreat (Bailey, 1931:307; Seton, 1929:443), which characterizes similar animals in the forest. The prairie dog sitting up on its burrow mound exhibits a habit shared by its ecological equivalents, the Richardson ground squirrel and picket-pin gopher. This outlook habit also characterizes the behavior of one or more burrowing forms of other grasslands, e.g., the viscacha in southern South America; the bobac or tarbagan in central Asia, and the meerkat, a carnivore, in Africa.

Several of these live in "towns" or are aggregated into groups, this particular mode of life evidently fitting well into the grassland community. The large prairie-dog towns, large herds of antelope (400 animals or more reported by early explorers), and the enormous herds of bison (100,000 to 2,000,000; Seton, 1929) bespeak this habit, which is evident also in the grasslands of Eurasia and Africa. In southern South America, where larger game is scarce, the pampas deer is not particularly gregarious, but the weasel or tayra and the ostrichlike rhea assume this habit (Hudson, 1892). As to smaller birds, Hudson also reports the carancho as hunting in bands, and, according to Brehm (1896), flocks of the lesser kestrel and the redfooted falcon seek insects on the Asiatic grasslands. Craig (1908) points out the gregariousness of the prairie chicken in contrast to the solitary habit of its relative, the ruffed grouse.

Modern ecology has appeared so late as to require reconstruction to evaluate properly the various species of the grassland, either plant or animal, as well as those of other communities dominated by man. This is especially true of the animals, as few relicts of this biome have remained entirely unmodified in this respect. The habits and habitat relations of each species must be known to interpret its past and present range. The gradual removal of the generally continuous forest cover of the eastern states and southern Canada for nearly three centuries gave abundant time for birds, insects, and other animals of the forest edge, swamp, and moist meadows to invade the eastern United States. Again, the planting of trees in the prairie from 1860 to 1938 has afforded opportunity for forest-edge species to extend westward. This period undoubtedly represents marked expansion of the populations of those animals favored by man directly or indirectly.

The community and habitat relations of an animal species can usually be ascertained from good field data, but unfortunately, in the early period of scientific exploration previous to 1890, the ecological results of expeditions were commonly lost by the process of segregation of collections to specialists and by the practice of stressing the description of the species only. In the mid period (1890–1910), taxonomic monographs and other papers gave little habitat data in connection with the life-zone work, although any life zone includes many unlike habitats. Moreover, all the drier grasslands were confused with desert, and even in typical grass communities few or no grasses were listed as habitat or zone indicators, attention being focused upon the conspicuous woody and succulent forms. With the rise of the ecological viewpoint, natural history works of definite ecological value began to appear; those of Seton (1929), the excellent state treatments by Bailey (1931), Hebard (1925–1931), and others are noteworthy.

Climate. In harmony with its wide extent, the climatic relations of the prairie exhibit a greater range than those of any other climax on the continent. On the east its boundary lies close to the isohyet of 40 inches from Texas to Indiana, while on the northeast it drops from that of 35 to 25 inches in correspondence with lessened evaporation. The extremes of temperature are even more striking, varying from a frost-free season of but three or four months in Canada to one of practically an entire year in southern Texas. The chief explanation of this seeming anomaly is to be found for both plants and animals in the evasion of temperature extremes by virtue of the habit of perennation on the one hand and that of burrowing on the other (cf.

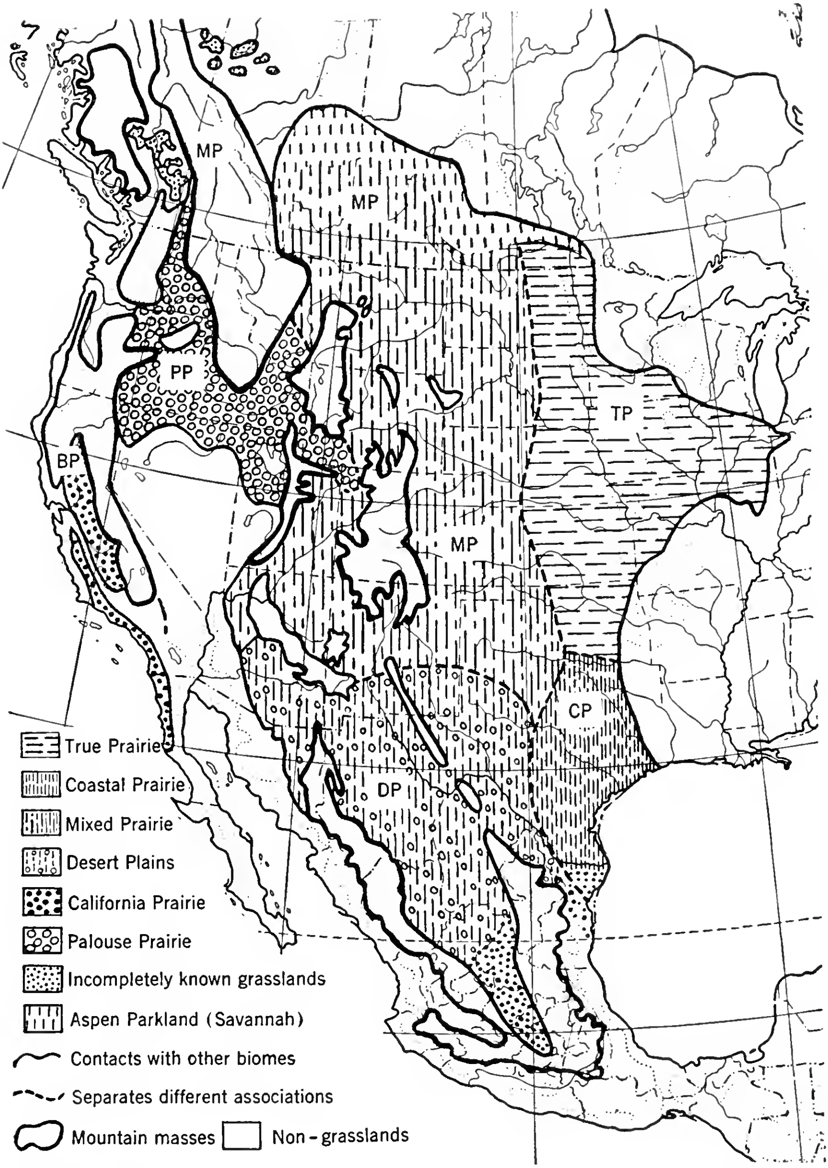


FIG. 54.—Map of the grassland climax and its associations. The areas in which the climaxes occur outside of low mountains are indicated. *TP*—true prairie; *CP*—coastal prairie; *MP*—mixed prairie; *PP*—Palouse prairie; *BP*—California prairie; *DP*—desert plains.

Savage and Jacobson, 1935; Weaver and Albertson, 1937; Weaver, Stoddart and Noll, 1935).

The xeric limit of the grassland confronts the desert in the southwest along the line of 5–6 inches of rainfall, and the sagebrush to the northwestward with an effective rainfall a few inches higher. The assumption that grassland is restricted to regions with a spring-summer precipitation of about three-fourths the total, though still more or less prevalent, is no longer tenable in view of the fact that the Pacific and Palouse prairies obtain most of their moisture during the winter. Where freezing temperatures do not obtain, as in southern California, the native bunch grasses may start growth in any month from September to February and are not infrequently in bloom in December.

STRUCTURE AND UNITY (Fig. 54)

The grassland under consideration is divisible into six types or associations, namely (1) the mixed prairie, occupying a large central area lying east of the Rocky mountains and in the main west of the 100th meridian; (2) the true prairie, which lies east of mixed prairie and in contact with forest; (3) the gulf coastal prairie, lying near the Gulf of Mexico; (4) the desert plains, mainly in southern Arizona, New Mexico, and Mexico; (5) the California or Pacific prairie; and (6) the Palouse prairie in the northwestern states. These associations are distinguished by the prevailing dominant grasses and influent animals, as well as by secondary differences in appearance. They are bound together by certain major features of physiognomy and by plants and animals in common, which may be called binding species.

Binding Dominants of the Prairie.[1] Binding dominants are species of perennial grasses that occur as climax species in three or more associations of the grassland biome and are all found in the ancestral mixed prairie. They are as follows, the sequence indicating a generally decreasing wideness of range.[1]

Sporobolus cryptandrus
Koeleria cristata
Stipa comata
Stipa viridula
Agropyrum smithi
Bouteloua gracilis
Bouteloua curtipendula
Bouteloua hirsuta
Elymus sitanion
Poa scabrella
Festuca ovina
Andropogon scoparius
Buchloe dactyloides

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[1] The names employed are those of long-accepted species of definite ecological significance rather than the more recent minor species, or better, subspecies (Clements and Clements, 1913; Hall and Clements, 1923).

It is manifest that these are the dominants that bespeak the unity of the grassland as a climax formation and constitute the primary pattern in which the differentiation into associations has been carried out. Other grasses have similar extensive areas, such as *Andropogon saccharoides* and *Sporobolus airoides*, but the former is climax in but a single association and the latter is generally a subclimax dominant of the halosere.

Binding Influents. Among the influents which give unity to the biome are the bison (*Bison bison*), the pronghorn antelope (*Antilocapra americana* and variety), and the badger (*Taxidea taxus* and varieties) which covers all the climatic grasslands and is almost restricted to them, merely extending into some savanna areas. It is found in all the grassland associations from Indiana to the San Joaquin valley and from the bunch grass of British Columbia to the desert plains of the Southwest. It invades other biomes only locally in seral stages, as in the saltbush subclimax of the Larrea desert, though maps suggest its presence in the desert generally (Figs. 55–57). The buffalo wolf (*Canis nubilus*), the horned lark (represented by a different variety in several of the associations), and a few insects, of which the orthopteran (*Mermiria neomexicana*) is an example, occur in nearly all the associations. The differences between the associations as to influents are given on pages 264, 273, etc.

The genus Geomys (eastern pocket gopher) is largely confined to the moister grasslands likewise, and the smaller Thomomys (western pocket gopher), is also a grassland influent. Certain species are characteristic of climax grassland; others extend into mountain meadows and into seral communities dominated by a mixture of grasses and trees. The same is true of the several species of Onychomys, the grasshopper mouse, and Citellus, the ground squirrel.

The genus Lepus includes the varying hares and jack rabbits which occupy open and brush-covered areas in grassland and tundra. Jack rabbits comprise two quite distinct groups: (*a*) the northern white-tailed jack rabbit closely related to the varying hare, and (*b*) the southern black-tailed jack rabbit. Certain species or varieties of these two groups range through the climatic grassland and into the park-like types of vegetation and grassy seral stages in low altitudes.

Some genera of birds divide their time or range between tundra and grassland, such as Calcarius (longspurs), Otocoris (horned lark), and Anthus (pipits). Other genera range between prairie and meadow. Among them are Dolichonyx (bobolink), Sturnella (meadowlark), and Ammodramus (grasshopper sparrow) (Pearson 1923). Of the reptiles two species of bullsnake or gopher snake (Pituophis)

Fig. 55

Fig. 56

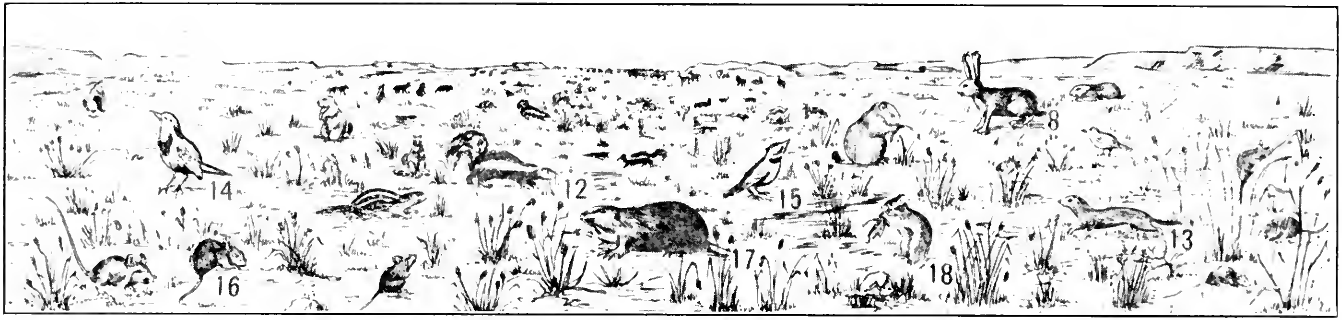

FIG. 57

FIGS. 55-57.—A three-view diagram showing the common grassland influents such as were once present but active at different times of day, near the center of the grassland area, for example, in central Nebraska (Number of individuals not to scale). From top to bottom attention is centered on a series of animals of decreasing size. The numbers indicate—*1*—bison (*Bison bison* [L]); *2*—antelope (*Antilocapra americana* [Ord.]); *3*—buffalo wolf (*Canis nubilus* [Say]); *4*—badger (*Taxidea taxus* [Schr.]); *5*—prairie dog (*Cynomys ludovicianus* [Ord.]); *6*—prairie chicken (*Tympanuchus cupido americanus* [Reich.]); *7*—coyote (*Canis nebrascensis* [Mer.]; *8*—jack rabbit (*Lepus californicus melanotus* [Mearns]; *9*—spotted skunk (*Spilogale interrupta* [Raf.]); *10*—black foot ferret (*Mustela nigripes* (*A* and *B*)); *11*—kit fox (*Vulpes velox* [*Say.*]); *12*—skunk (*Mephitis hudsonica* [Rich.]); *13*—weasel (*Mustela* sp.); *14*—W. meadow lark (*Sturnella neglecta* [Aud]); *15*—horned lark (*Otocoris alpestris leucolaema* [Coues]); *16*—deer mouse (*Peromyscus maniculatus nebrascensis* [Coues]); *17*—pocket gopher (*Geomys lutescens* [Mer.]); *18*—grasshopper mouse (*Onychomys leucogaster articeps* [Rhoads]); *19*—harvest mouse (*Reithrodontomys megalotis dychei* [Allen].

with their several varieties are found throughout the grassland as very important coactors, feeding on rodents. Among the insects (Hayes 1927), the Orthoptera are the outstanding group, especially the various grasshoppers. Kansas exhibits 118 genera and 301 species, of which 59 range eastward (Hebard, 1931). New Jersey shows but 152 species of orthoptera in 60 genera (Smith, 1909), several of them suspected of having extended their range into the deciduous forest area since clearing. There are approximately 240 more species of the grassland orthopterans than of those in New Jersey. This is in spite of the fact that the latter has a greater diversity of habitat. The genus Melanoplus comprises 58 species in Kansas, while only 10 are recorded from New Jersey, 8 of which are common to the two states; Trimerotropus has 23 species in Kansas and only 1 in New Jersey. The Hemiptera are well represented, and among the Homoptera, the genus Flexamia is a characteristic grassland genus.

MIXED PRAIRIE

Nature and Extent. The name of this association is drawn from its two most characteristic features. The first and more obvious is the mixture of mid and short grasses, though this is an outcome of the second, namely, a mingling of dominants from very different sources. The mid grasses are circumpolar in origin, the short grasses southwestern, and the tall grasses of the postclimax southern or subtropical as a rule. Ecologically speaking, several species of Carex are reckoned among the short grasses, though by contrast these are northern in derivation. In addition, the central position of this unit in the formation has led to much interchange of influents with the other associations, of which it is regarded as the parental type (cf. Visher, 1916) (Figs. 58–59).

The mixed prairie covers a much larger area than any other unit of the grassland, extending from central Alberta to Texas and thence westward to the Colorado Valley. It includes the prairie districts of Alberta, Saskatchewan, western Manitoba, the western two-thirds of North and South Dakota, the western half of Nebraska, Kansas and Oklahoma, northwest Texas, northern New Mexico and Arizona, eastern Utah, Wyoming, and Montana. From Canada to northern Texas, it lies in contact with the true prairie to the east through the medium of a broad ecotone. It meets the coastal prairie in north-central Texas and the Palouse grassland in western Montana, eastern Idaho, and northern Utah. The ecotone between it and the desert plains extends from central-west Texas through central New Mexico and Arizona,

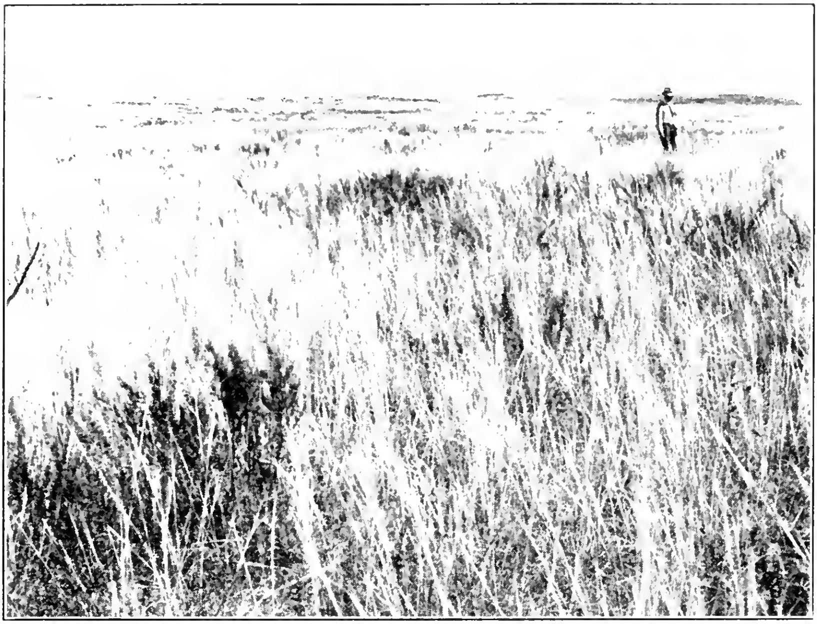

FIG. 58.—Mixed prairie of *Stipa comata*, *Bouteloua gracilis*, and *Carex stenophylla*; Agate, northwestern Nebraska. (Photo by Edith Clements.)

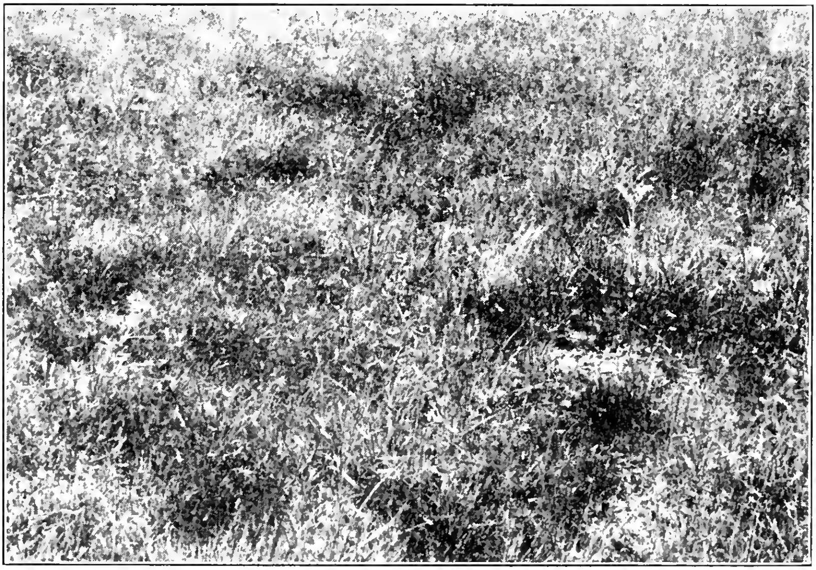

FIG. 59.—Short-grass disclimax of *Bouteloua* and *Carex*, produced from mixed prairie by grazing; Colorado Springs, Colorado. (Photo by Edith Clements.)

though much interrupted by mountain ranges. It no longer touches the California prairie, owing to the intervening desert, but probably did so in the Pleistocene.

Climate. The mixed prairie has the widest range in latitude, altitude, and longitude of all the grassland associations, and a corresponding variation in rainfall and temperature. It is semi-arid to arid in character, its eastern boundary shifting from about the isohyet of 27 inches in the south to 13 in the north, and the western falling near the line of 10 inches in general. As a rule, more than half the precipitation comes between April first and September first. The seasonal evaporation is approximately 60 inches at the south and less than 30 at the north. The mean annual temperature and the length of the frost-free season decrease steadily with increasing latitude and altitude, but here also the temperatures of the summer period depart less widely. Drought periods are a recurrent feature, with marked effects upon the growth of vegetation.

Dominants. The dominants of the mixed prairie are as follows:

- *Stipa comata*
  - *pennata*
  - *viridula*
- *Sporobolus cryptandrus*
- *Agropyrum smithi*
- *Hilaria jamesi*

- *Oryzopsis hymenoides*
- *Bouteloua racemosa*
- *Festuca ovina*
- *Agropyrum pauciflorum*
- *Stipa richardsoni*
- *Elymus macouni*

- *Koeleria cristata*
- *Aristida purpurea*

- *Elymus sitanion*
- *Poa scabrella*
  - *nevadensis*
  - *arida*
- *Muhlenbergia montana*
- *Eragrostis spectabilis*

- *Bouteloua gracilis*
- *Buchloe dactyloides*
- *Carex stenophylla*
  - *filifolia*

- *Carex pennsylvanica*
- *Bouteloua hirsuta*
- *Muhlenbergia torreyi*

The first column contains the mid grasses, the third the short grasses and sedges, while the middle one comprises species of mid-grass habit but of lower stature. The break in each list separates the species of greater from those of lesser importance. Of the entire number, three alone are sod-formers, namely, *Agropyrum smithi* and *Carex stenophylla*, by virtue of root stocks, and *Buchloe dactyloides* by means of stolons. *Bouteloua gracilis* and *hirsuta* and *Muhlenbergia torreyi* often form mats that approach a sod in the north, but these are composed of tufted culms as a rule. The remaining species are all bunch grasses, both habit and spacing corresponding to the xeric climate.

A few species are abundant throughout the association, or were before the opening of the historical period; such are *Stipa comata, Bouteloua gracilis, Sporobolus cryptandrus, Agropyrum smithi,* and *Aristida purpurea.* Some, like *Hilaria jamesi, Stipa pennata,* and

Muhlenbergia montana, are southern in distribution; others are northern or in high altitudes, as with *Carex stenophylla*, *Festuca ovina*, or Koeleria. By contrast with the bunch grasses, the sod-formers have become relatively more abundant since the advent of overgrazing, and it appears probable that Buchloe at least has spread more widely. Differences in distribution within the mixed prairie are reflected in its structure, and hence its subdivisions or faciations form a series irregularly parallel from north to south.

Subdominants. The number of subdominants or perennial forbs that characterize the aspect societies or sociations is large, though considerably less than in the true prairie. The abundance of individuals is likewise reduced, both features being consequences of the competition for a lower water content due to a lessened rainfall. The subdominants of the first importance amount to a score or so, of which three-fourths occur in the region from Canada to Texas and an equal number are found also in true prairie. The chief species of the prevernal aspect is the common pasqueflower, *Anemone patens*, together with *Leucocrinum montanum* and *Townsendia sericea*, and these are followed by *Senecio aureus*, *Oxytropis lamberti*, and early species of Astragalus. The estival period is marked by *Psoralea tenuiflora* and *Malvastrum coccineum* in particular with *Petalostemon candidus*, *P. purpureus*, *Oenothera serrulata*, *Lupinus argenteus*, *Verbena bipinnatifida*, *Castilleia integra*, and species of Astragalus and Pentstemon widespread and important. The serotinal aspect is characterized by composites, of which the most abundant are *Aster multiflorus*, *A. canescens*, *Artemisia dracunculus*, *A. vulgaris*, *Liatris punctata*, *Solidago missouriensis*, *Chrysopsis villosa*, *Kuhnia glutinosa*, and *Grindelia squarrosa*. Most conspicuous of all are *Artemisia frigida*, *Gutierrezia sarothrae*, and *Amphiachyris dracunculoides*, but these are indicators of the disclimax due to overgrazing.

Proclimaxes.[1] The mixed prairie contains two postclimaxes, namely, floodplain woodland and tall grass, and one omnipresent disclimax, the so-called short-grass plains. The first two are to be regarded as relicts of former climaxes, the fringing woodland being a mere fragment of an earlier and much more extensive deciduous forest. The tall-grass community not only forms meadow in the stream valleys, but also covers large areas of sandhills and river dunes and persists likewise on foothills and escarpments. Three species of Andropogon, namely, *furcatus*, *nutans*, and *scoparius*, are more or less

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[1] The term proclimax is used for all communities that suggest something of the permanence or extent of a climax, but are not controlled by climate. Those that originate and are maintained by disturbance are disclimaxes.

regularly typical of it, together with some *Panicum virgatum* and *Elymus canadensis,* but in sandhills the leading roles are usually taken by *Calamovilfa longifolia* and *Andropogon halli.*

The most interesting feature of the mixed prairie today is its conversion over large areas into a disclimax caused by overgrazing. Such disturbance is rarely so thorough as to eliminate the mid grasses completely, but under extreme conditions they persist only in reduced form and number or in sites with more or less protection from grazing. While the original composition of the climax can be readily inferred from these, and especially from fenced railways, it can actually be restored by means of exclosures, such as have been employed in the several faciations. The characteristic dominants of the short-grass community are *Bouteloua gracilis* and *Buchloe dactyloides,* though several other grasses and sedges of this life form play some part. The reduction or suppression of the mid grasses depends primarily upon the intensity and duration of grazing, but it is also related to rainfall and hence increases to the southward as a rule. It is likewise subject to marked annuation, the mixed composition being evident during seasons of high rainfall and being correspondingly obscured during drought periods.

Influents. The bison occurred through practically all the extent of mixed prairie except western New Mexico and Arizona, the number formerly present being estimated at 30 million. Though generally harassed by the buffalo wolf, *Canis nubilus,* herds of a million or more bison were reported by the early explorers. These aggregations were of the greatest magnitude during migration, as the herds moved north a distance of several hundred miles in early summer and south again in late autumn. The pronghorn antelope occurred in great numbers in this association, the population on the mixed prairie being variously estimated at 4 to 8 millions. It preferred the rolling portions and sought shelter in ravines and cottonwood valleys during storms, or shifted to areas without snow during winter; otherwise the bands remained in the same general locality (cf. Watson, 1911).

The prairie dog ranged over the entire area, except the portion north and east of the Missouri River in North Dakota, where its place was taken by the Richardson ground squirrel. The former occurred in large aggregations, often covering 20 to 640 acres, but also scattered about. The northern white-tailed jack rabbit reached southward over about two-thirds of the north-to-south extent, where it overlapped the black-tailed jack rabbit which occupied the area north into Nebraska. Grasshopper mice, as well as a series of species of pocket mice, supplemented each other in covering the plains. The pocket gopher is represented by a characteristic species, while in the higher and drier westerly parts another genus (Thomomys) is added.

The buffalo wolf, *Canis nubilus*, was quite abundant over the mixed prairie area; it is often described as following buffalo herds in the early days, though it fed on ground squirrels and mice to a large extent in summer. Badger holes were commonly enlarged as lairs by both wolf and coyote. The abundant form of the area was the Nebraska coyote (*C. nebrascensis nebrascensis* Merriam) which fed on rodents, a few insects, and fruit. The kit-fox (*Vulpes velox velox* Say) occurred practically throughout, and the entire area was likewise covered by one or another of several species of skunk and the plains weasel.

The birds which are most conspicuous over the plains are the desert horned lark, Smith's longspur, chestnut-collared longspur, western lark sparrow, lark bunting, purple martin, Sprague's pipit, Brewer's sparrow, lazuli bunting, and the western meadowlark. The prairie chicken was abundant at one time but is infrequent today. The marsh hawk, western red-tailed hawk, and prairie falcon are common, but, with the exception of the burrowing owl, the owls are poorly represented. Among the reptiles, the plains gartersnake (*Thamnophis radix* [B. & G.]), the prairie rattlesnake (*Crotalus confluentus* Say), and the bullsnake (*Pituophis sayi* Schleg.), make up the principal influents, which take a heavy toll of ground squirrels, pocket mice, harvest mice, etc. (Guthrie, 1926).

One of the outstanding influents of this area is the grasshopper, of which seven common or very abundant species are characteristic of the Great Plains, feeding on low, dry grasses or other herbage.

Of climax and subclimax Orthoptera, the following occur in South Dakota, Kansas, Colorado, Montana, and Alberta, and the majority in Oklahoma and Texas also:

Acrolophitus hirtipes (Say)
Amphitornus coloradus (Thomas)
Cordillacris occipitalis occipitalis (Thomas)
Ageneotettix deorum (Scudder)
Psoloessa delicatula (Scudder)
Aulocara elliotti (Thomas)
Arphia pseudonietana (Thomas)
Encoptolophus costalis (Scudder)
Spharagemon equale (Say)
Metator pardalinus (Sauss.)
Phlibostroma quadrimaculatum (Thomas)

All the above apparently are more or less abundant and well distributed. *Melanoplus mexicanus* is present at all times, but at long intervals develops in enormous numbers to constitute a plague, sometimes as the migratory form, *M. m. spretus.* In the grasshopper years of the seventies, this form moved eastward in great swarms that destroyed crops over wide areas. Most of these grasshoppers deposit their eggs in the soil, and quantities of them are destroyed by ground squirrels, mice, etc. It has been estimated that grassland insects may devour more forage than the cattle that might be grazed on the same area (cf. Isely, 1904).

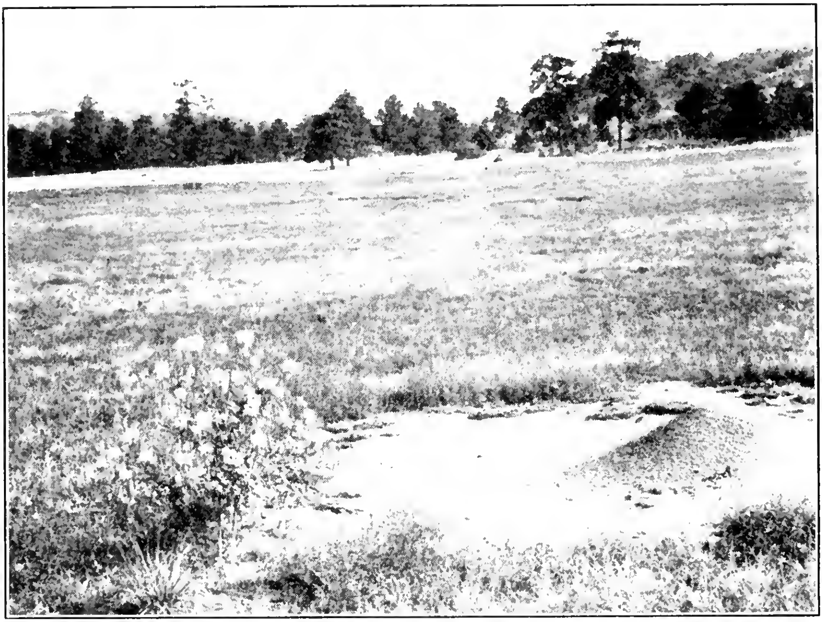

FIG. 60.—Ant garden near Colorado Springs; ten other anthills are visible. The presence of the forb (*Cleome serrulata*) is due to ant coactions. (Photo by Edith Clements.)

Robber flies are usually very numerous, and also the various flies that originally bred in the buffalo droppings. Hemiptera are not well represented, at least as to number of individuals. Harvester ants are often conspicuous (Fig. 60). The ground beetles familiar in the moister lowland prairie are displaced by Tenebrionidae. The ground-inhabiting tiger beetles, such as *Cicindela purpurea graminea* Schp., *audubonii* Lec., *pulchra* Say, and *obsoleta* Say, all of which make vertical burrows in the soil, occur in open spaces among the grasses.

Seral Stages. Over much of the mixed prairie area, the bottom lands of the small rivers and larger creeks are occupied by tall grasses, so there is a whole group of seral stages leading from the newly deposited alluvium through the meadow stage to the climax of the region. The margins of these rivers are usually occupied by *Cicindela repanda* Dej., the somewhat higher ground by *C. tranquebarica* Herbst, while the moist grasses of the floodplain support various species of grasshoppers, as follows:

Acridium acadicum (Scudder)
Orphulella pelidna (Burm.)
Arphia conspersa (Scudder)
Chortophaga viridifasciata (De S.)
Dissosteira carolina (L.)
Conocephalus fasciatus (De G.)

Some of these grasshoppers occur in considerable number and destroy grasses locally. Belonging to this class are also a number of widely distributed species found in the true prairie and in the moist places in the mixed prairie association. They often increase and extend to planted crops and do striking damage. In the overgrazed grasslands of southern Colorado and New Mexico, such species as *Trimeratropis pallidipennis* (Burm.) become very abundant.

River Bottoms. These are sometimes covered with a narrow fringe of cottonwoods, but often no trees occur, as in the valley of the Cimarron in southwestern Kansas. Small dunes and sand fields cover portions of the floodplain, in which sand sage (*Artemisia filifolia*) is common. The small skink (*Eumeces obsoletus* [B. & G.]) and horned toad (*Phrynosoma cornutum* [Harlan]) occur in such areas. The tiger beetles (*Cicindela scutellaris* Say and *C. formosa* Say) are associated with the plants of sandy areas, while *C. repanda* Dej. and *tranquebarica* Herbst dwell on clay soil near streams.

Steep Banks and Ravines. Steep banks of small ravines support a group of characteristic tiger beetles, such as *Cicindela splendida* Henz of the eastern part of the plains and *C. denverensis* Casey of the western. Both are found on the escarpment of the Cimarron. The larvae and adults burrow in the steep banks to the exclusion of level lands. Such ravines also afford convenient places for wolves and coyotes to dig their dens.

Sandhills. There are numerous extensive sand areas throughout the area of the Great Plains. On the bare and partially bare sands occurs a grouping of animals, including a number of species of tiger beetles such as *C. scutellaris* Say, *formosa* Say, *venusta* Lec., grasshoppers, a great many burrowing wasps, etc. The western hognosed snake (*Heterodon nasicus* [B. & G.]) and box tortoise (Fig. 61) are common inhabitants of sand areas.

Among the sandhills are numerous ponds and lakes with rush- and sedge-covered margins, in which the grasses invade with greater rapidity than in the dry sand areas (Pool, 1914). The ponds are often alkaline, and those that dry up leave white barren flats. A tiger beetle, *Cicindela fulgida* (Say), is characteristic of such areas, as are some other insects.

Reactions and Coactions. The effect of the community on the habitat is marked, owing to the very deep root systems of the prairie grasses and to the large number of burrowing mammals and insects, especially ants. The abundance of pallid ground squirrels and the extensive network of burrows made by each pair bespeaks a considerable movement of soil materials by this single species. The prairie dog digs deeper, commonly to a depth of 12 to 15 feet, and brings enormous quantities of soil to the surface. Since it is commonly concentrated in towns, the result is much more conspicuous but less generally distributed than for the ground squirrel. Probably the soil-moving type of reaction originally reached its greatest intensity in these mixed prairie areas. Another type of reaction, formerly of much local significance, was the tramping of enormous herds of bison, which was likewise most marked in this association.

FIG. 61.—Painted box tortoise or sand turtle (*Terrapene ornata* Ag.) in the sand hills of the mixed prairie area. According to Cahn (1937), Ortenburger found this turtle feeding on grasshoppers, caterpillars, and robber flies, while Cahn found only vegetable matter in the stomachs. (Photo by Edith Clements.)

The outstanding coaction was grazing or clipping of grasses by the large ungulates, the prairie dog, the ground squirrel, and other rodents.

The great quantity of droppings of the herds of bison is well indicated by the fact that early settlers found dry buffalo chips their principal source of fuel. These dry portions were what was left after this material had afforded sustenance for numbers of insects, and shelter in the dry state for tenebrionids and various crickets.

TRUE PRAIRIE

Nature and Extent. The designation of the easternmost association of the grassland as true prairie was made originally upon both ecological and historical grounds and appears still to be well warranted by the facts. It was inevitably that portion of the climatic grassland with which trapper and pioneer first came in contact and to which the word prairie was regularly applied, the "plains" then being regarded as essentially different. Ecologically, it differs from the mixed prairie by the absence of the lower layer of short grasses, as it does also in being less xeric. Not infrequently the postclimax of tall grasses has been mistaken for true prairie, but, with the exception of the subclimax border and "openings" of the deciduous forest, it is a disclimax produced by the disturbances accompanying settlement and development (Clements, 1934, 1936; cf. Shimek, 1911; Transeau, 1935) (Fig. 62).

True prairie once occupied the entire region between the mixed prairie and the forest to the east, which belonged, for the most part, to the oak-hickory climax, but today it is represented only by small and scattered relicts in the corn and wheat belts of the Middle West. Its western boundary was that of the ecotone between it and mixed prairie, as indicated on page 260; its eastern limit was formed by the subclimax tall grass along the forest edge. This extended from southern Manitoba diagonally through Minnesota to southwestern Wisconsin and included the northern two-thirds or more of Illinois and part of northwestern Indiana. The true prairie includes northern and western Missouri and the eastern half of Oklahoma for the most part, passing into the coastal prairie in the region of the Red River. Its major contacts are with the mixed prairie along the entire front of the latter and with the narrow and somewhat interrupted band of postclimax tall grasses that confront the forest. In extent, true prairie ranks second among grassland associations, being surpassed only by the mixed prairie. Characteristic grassland animals such as the striped ground squirrel and badger occurred in scattered eastern prairie islands (Fig. 63).

Climate. The true prairie differs from the mixed chiefly in being more humid, the rainfall along its southeastern boundary from Oklahoma to Illinois approaching 40 inches. This drops to about 23 inches in southern Manitoba, while along the western limit the precipitation decreases from 30 inches in Oklahoma to 25 in Nebraska and about 20 in northeastern North Dakota. By virtue of lesser extent from south to north, evaporation also exhibits a smaller range, and this is likewise true to some extent of temperature. Drought periods are correspondingly less frequent and severe, and hence rarely affect the density and survival of the dominant grasses and subdominant forbs (cf. Weaver, Stoddart, and Noll, 1935; Weaver and Albertson, 1936; Savage and Jacobson, 1935).

Fig. 62.—True prairie in eastern Iowa; *Stipa spartea, Sporobolus heterolepis,* and *Bouteloua curtipendula* chief dominants, with *Koeleria, Andropogon scoparius,* and *Sporobolus asper* also present. (Photo by Edith Clements.)

Dominants. The following dominants constitute the true prairie:

Stipa spartea
Sporobolus asper
  heterolepis
Andropogon scoparius
Bouteloua curtipendula

Koeleria cristata
Agropyrum smithi
Muhlenbergia cuspidata
Panicum scribnerianum
Carex pennsylvanica

The first group comprises the eudominants of the association, occurring as climax species in no other unit of the grassland. The members of the next group are more wide-ranging, being found in two or more

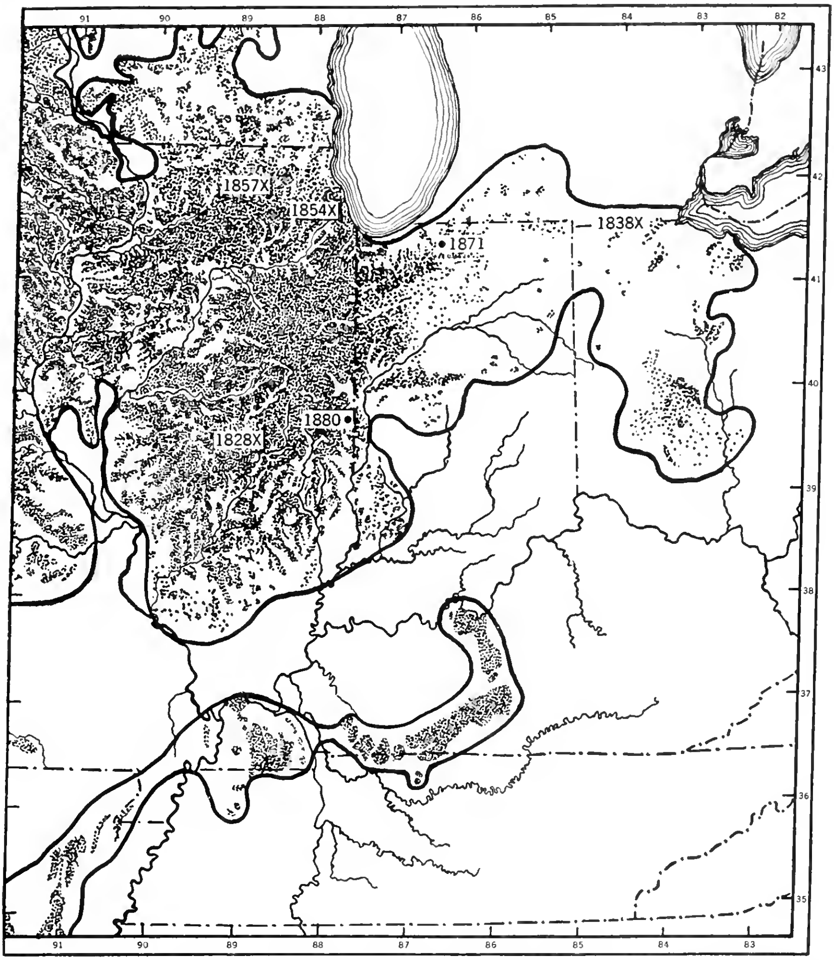

FIG. 63.—The prairie peninsula (after Transeau, 1935); the stippled areas are prairie. The early records of the badger are shown with the dates. 1871 and 1880 are dates of disappearance from the locality.

associations, four of them in mixed prairie. The generally lower stature of the last two renders them less important, though they are frequently of great abundance. As preclimax relicts, *Bouteloua gracilis, B. hursuta,* and *Buchloe dactyloides* are fairly widespread, especially in the western half. With respect to life form, the bunch grasses make a large majority, Agropyrum and Muhlenbergia alone forming a definite sod.

In view of its extent, it is significant that most of the dominants occur throughout the true prairie. All of them range through its entire width and the major number of them over the whole area from north to south. *Stipa spartea* and *Muhlenbergia cuspidata* find their southern limits along the boundary between Kansas and Oklahoma; *Sporobolus asper* extends northward only into Central Minnesota and North Dakota, and *Carex pennsylvanica* but little farther. In consequence, there may be distinguished three faciations, a central major one containing all the dominants, and a northern and a southern one, each lacking a eudominant, respectively *Sporobolus asper* and *Stipa spartea.* Such a subdivision is reflected in the distribution of the large number of subdominants, as indicated below.

Subdominants. The general unity of the true prairie is reflected as strongly, and even more visibly, by the perennial forbs as by the grasses. The rainfall is regularly sufficient to reduce the competition of the dominants to a point where a wealth of subdominants find opportunity for development. More than a hundred species are concerned in characterizing the various aspects, and the abundance of individuals is often such as to obscure the grasses more or less completely. The prevernal aspect is marked by a few rosette forms such as *Anemone patens, A. caroliniana,* and *Antennaria campestris*; the vernal stage comprises a much larger number of species, mostly of modest stature, that are disposed to form pure societies over considerable areas. Chief among these are *Astragalus crassicarpus, Viola pedata, V. pedatifida, Tradescantia virginiana, Phlox pilosa, Senecio aureus,* and *Baptisia leucophaea.*

The estival aspect is the most varied in composition, with about a third of its components drawn from the pea family, nearly as many from composites, and the remainder widely scattered in relationship. Erect forms of moderate height are the rule, in response to the competition of the grasses. Probably the most characteristic species is the shrubby *Amorpha canescens,* with *Psoralea tenuiflora, P. argophylla, Petalostemon candidus, P. purpureus, Erigeron ramosus, Echinacea angustifolia* and *Glycyrhiza lepidota* also of the first rank. The serotinal aspect is distinguished by an all but complete ascendency of composites, represented by Aster, Solidago, and Helianthus with six species each, and Artemisia, Liatris, Silphium, and Vernonia by three each. The characteristic species widely present in great abundance are *Aster multiflorus, A. ericoides, levis* and *novae-angliae, Solidago* *speciosa, rigida* and *nemoralis, Helianthus rigidus, occidentalis, grosseserratus, maximiliani* and *orgyalis, Artemisia vulgaris* and *dracunculus, Liatris scariosa* and *punctata, Vernonia fasciculata,* and *Salvia pitcheri* (cf. Sampson, 1921).

Proclimaxes. The most interesting and important of these is the tall-grass community, which occurs regularly as a postclimax in valley and lowland, as well as in many areas of sandhills or dunes. This has often been termed low prairie, in allusion to its habitat but not its stature. Under the impact of settlement, the tall species of Andropogon in particular have moved up the slopes in the wake of the disappearing mid grasses, giving rise to the adage of pioneer days that bluestems followed the settler. This consequence has been so general, especially in the east and south, that most of the true prairie relicts today are modified and many of them dominated by tall grasses. On the surface they give the appearance of being climax dominants, but in reality they constitute a disclimax caused by the varied and often obscure disturbance incident to settlement. In the western portion of the association another disclimax is to be found in pastures, where confined grazing has led to the production of a short-grass sod similar in most respects except extent to that of the mixed prairie.

Valley woodland constitutes a postclimax to the true as well as to the mixed prairie, though the higher precipitation renders it much richer in tree dominants. Relicts of similar composition also occur in extensive tracts that simulate climax forest, owing to the local compensation afforded by sandy soil or mountain outliers, as in central Oklahoma and along the western edge of the Ozarks.

Influents. The bison was originally plentiful (estimated at 12 million or a bison to 20 acres) throughout the true prairies. Its wallows and paths through the river-skirting woods may still be seen in Illinois. In 1679, at the beginning of winter, LaSalle saw bison stuck in a marsh near South Bend, Indiana; in 1680 he found the prairie near Morris, Illinois, "alive with buffalo." It disappeared east of the Mississippi River about 1800; according to an Indian tradition, most of the herd in Illinois was killed by a blizzard about 1775 (M. B. Shelford, 1913). There was some competition with elk near wooded areas, especially in summer. This was particularly the case in the true prairie areas, where valley forest afforded shelter and winter browse for the elk.

The gray or buffalo wolf (*Canis nubilus* Say) was originally described from the true prairie country of Iowa. The coyote (*Canis latrans* Say) is confined to the true and subclimax areas and is fond of the forest margins of the region; it still occurs in Illinois and Indiana. It extends into Missouri, where its place is taken southward by *C. nebrascensis texensis* Bailey (Henry, 1897; Bailey, 1905, 1913, 1931).

The badger, as a typical grassland animal, ranged eastward to the border of deciduous forest, and it still occurs sparingly in Illinois and Indiana. It digs a hole usually about 6 feet deep; its reaction reaches greater depths than do the reactions of other burrowers in the true prairie and subclimax. It moves much soil in digging out its prey, which consists of ground squirrels, pocket gophers, etc. The thirteen-lined ground squirrel (*Citellus 13-lineatus* [Mitchill]) and the pocket gopher (*Geomys bursarius* [Shaw]) disturb the soil near the surface; the former feeds on a great variety of food, including numerous insects. The prairie meadow mouse (*Microtus ochrogaster* [Wagner]) occurs quite generally, but the prairie deer mouse belongs to seral developmental stages; neither of these influences the soil to any extent, as they rarely burrow (cf. Stephens, 1922).

The greater prairie chicken (*Tympanuchus cupido americanus* [Reich.]) is the characteristic resident bird of the true prairie. The southern two-thirds probably originally contained the bobwhite, which was unknown in forest localities until after the land was cleared. Other strictly prairie birds are the eastern meadow lark, dickcissel, eastern field sparrow, and prairie horned lark. All these nest on or close to the ground, consume vast amounts of seed, and feed their young with quantities of prairie insects. (Cf. A. O. U. Check List, 1931.)

The reptiles of the true prairie climax are limited to snakes through all but the southern portion. The chief rattlesnake of the central portion is the massasauga (*Sistrurus catenatus* Raf.), which dwells most often on wet ground. The blue racer occurs throughout, and the bullsnake (*Pituophis sayi* Schleg.) is common well into Illinois; it feeds on striped and Franklin ground squirrels and meadow mice. The commonest snake of all is the prairie gartersnake (*Thamnophis radix* B. & G.), which feeds principally on earthworms, frogs, and toads (Shelford, 1913; Adams, 1915; Hankinson, 1915; Shackleford, 1929; Hendrickson, 1930).

Insects of all kinds occur on the prairies in abundance; by late August they have usually attained a great variety and quantity, sometimes reaching 10 million individuals per acre. Grasshoppers are especially important, one of the most typical being the lubbery locust (*Melanoplus differentialis* [Thomas]), which places its eggs in the ground. This feeds on lush vegetation and is usually found in wet places. The sword bearer (*Neoconocephalus ensiger* [Harris]) prefers grasses as food and deposits its eggs between the stem and lower leaves of the Andropogons. The meadow grasshopper (*Orchelimum vulgare* [Harris]) lays its eggs in the stems of subdominant forbs, especially composites (Hancock, 1911; cf. Hebard, 1934).

An abundance of Hemiptera characterizes the true prairie; many of these suck the juices of plants and may seriously weaken them. The plant bug (*Adelphocoris rapidus* Say) is common in the various grassland habitats of Illinois and Iowa and with it are about 15 other common species. Some of these are predatory; the ambush bug (*Phymata erosa fasciata* Gray) is common on forbs, often found lurking in goldenrod. The sucking Hemiptera may impair the vigor of grasses, as is illustrated by the ravages of chinchbugs, which are claimed by many to be original inhabitants of the true prairie. Upwards of a dozen species of Orthoptera are found in true prairie in considerable numbers, *Melanoplus dawsoni* Scud. occurring from Alberta south to Missouri.

The Coleoptera of the grassland include such forms as the so-called cucumber beetle (*Diabrotica 12-punctata* Fabr.) and various others that feed on forbs, decaying material or excrement (*Aphodius distinctus* Mull.), or are predatory, as the lady beetle (*Hippodamia convergens* Guer). However, the common and abundant species do not ordinarily feed directly on the grasses. Lepidoptera are more or less abundant, but in general are not grass feeders, though significant in the pollination of many subdominants. The extended studies of Hendrickson (1930) showed that only one species (*Cercyonis alope olympus* Edw.) was found persistently in the Iowa prairies.

Diptera are always abundant, but their relations are little known. Notable among them are the long-legged flies, several species of the genus Dolicopus being common or abundant. Syrphus flies, whose larvae feed on aphids, and robber flies such as Asilus and Promachus, abound; the latter prey on flying insects, picking them up with great dexterity and often taking forms larger than themselves. Hendrickson found them most abundant in an Andropogon community.

The Hymenoptera are represented chiefly by the ants, which constitute important coactors by gathering both plant and animal food, and also produce important reactions in moving soil. In Hendrickson's study the species were found to differ sharply with changes in the grasses present. Halictus, Bombus, and Andrena are usually the abundant bees of grassland. Thysanura and Collembola occur in prairie soil and work on decaying vegetation. Earthworms are usually abundant; the small white forms are nearly always present, as are small zonitid and pupid snails of minute size. Both enter into the food of birds, and the snails sometimes serve as carriers of bird parasites.

Seral Stages. The most important seral habitats due to recent glaciation are ponds and marshes. The temporary ones are usually dominated by Spartina, though in many cases rank forbs are also present. There is nothing especially characteristic about prairie ponds so long as they are permanent. In the later stages, however, they differ from forest ponds in the lack of shrubs and trees in the margin (Shackleford, 1929). Prairie marshes, especially those dry in autumn, were formerly extensive, particularly in Illinois and Indiana, and were the favorite haunts of numerous insects and vertebrates, such as the massasauga or swamp rattlesnake, and the bobolink and other swamp birds.

Sand areas were important but were marked by more xeric conditions and hence supported the plains insects and reptiles adapted to drier regions.

Contacts. The most important contact is with the deciduous forest, which as a proclimax extends westward in the river valleys of the true prairie. In it are found the Virginia deer, black bear, gray squirrel, the timber rattler, and numerous wood-boring and tree-dependent insects, among which the green tiger beetle (*Cicindela sexguttata* Fabr.) is a conspicuous example. The edges of these woodland areas are fringed about with low trees such as hawthorn and wild plum, and outside these are such shrubs as sumac, dogwood, snowberry and coralberry, and accompanying forbs. Most of this prairie has some of this forest and forest edge at intervals of a score or so of miles. These woodlands also supported elk, which commonly grazed on the prairie grasses, but browsed in the woodland, particularly in the winter. Even the Virginia deer was not excluded from the forest edge, although, being a browser, it perhaps did not take food in quantity from the grassland.

Such prairie animals as the coyote (*Canis latrans* Say) sometimes entered the wooded areas, and the gray or Franklin ground squirrel usually held relatively close to them, as did the jumping mouse of the region. A great number of song birds nested especially in the shrubby margins of these forests, and other birds such as the crow lived or nested in the woodland and sought food on the prairie; various hawks and owls belong in the main to this class. There were also numerous insects usually limited to such forest edges.

The contact with the aspen belt which lies between the coniferous forest and the grassland in Canada is particularly significant in bringing out the relations of animals (Bird, 1927, 1930). The badger and other burrowing animals, in constructing dens near the edges of the woodland, broke the sod and made possible the establishment of snowberry on their earthy mounds, which led to the naming of the plant, "badger willow." This was succeeded by aspens, and thus the woodland invaded the prairie.

COASTAL PRAIRIE

Nature and Extent. The name of this association not only suggests its position around the long curve of the Gulf of Mexico, but also indicates the general influence of its particular climate. It stretches northward along the line of the Red River and reaches its western limit in the vicinity of the 101st meridian. Its greatest extension, however, is along the coast, beginning at the western edge of the pine subclimax in eastern Texas and continuing for 200 miles or more into northeastern Mexico.

FIG. 64.—Coastal prairie chiefly of *Stipa leucotricha*, in the vicinity of Austin, Texas. (Photo by B. C. Tharp.)

On the east, the coastal prairie lies in direct contact with the pine subclimax or the oak-hickory forest, some of the dominants penetrating these in the form of grassy openings. Owing to the large number of common dominants and particularly subdominants, it forms a broad ecotone with the true prairie to the north, with the general boundary rather southward of the Texas line. In the direction of the Panhandle, it passes gradually into the mixed prairie, and along the extended western line it comes in touch with the desert plains grassland of western Texas and adjacent Mexico. Along the shores of the Gulf it is bordered by a narrow band of subclimax coastal marsh, more or less interrupted or paralleled by coastal dunes (Tharp, 1926).

Climate. By reason of its proximity to the Gulf, the coastal prairie is signalized by higher rainfall than any other association of the grassland; it is also warmer than any except the desert plains, and evaporation bears a corresponding relation. Perhaps the most significant feature is the relatively warm winter over much of the area, which favors the presence of subtropical dominants. Toward the northwest, however, the climate rapidly becomes continental in type, with an extreme range from zero to 110° F., and with a striking change in faciation as a consequence.

Dominants. The dominants of this prairie are the following:

Stipa leucotricha
Andropogon saccharoides
scoparius
furcatus
contortus
ternarius
nutans
Trachypogon montufari
Elyonurus tripsacoides
Manisuris cylindrica
Paspalum plicatulum
Panicum virgatum

Bouteloua curtipendula
Sporobolus asper
berteroanus
Agropyrum smithi
Koeleria cristata
Aristida purpurea
Buchloe dactyloides
Hilaria cenchroides
Bouteloua texana
trifida
hirsuta
Triodia pilosa

The generally subtropical nature of this association is shown by the presence of 9 species of Andropogoneae, while other southern derivatives number as many as 6, such as *Stipa leucotricha*, *Sporobolus berteroanus*, *Hilaria cenchroides*, and *Bouteloua texana*. Five dominants are possessed in common with the true prairie, 6 with the mixed prairie, and 7 with the desert plains. The eudominants are *Stipa leucotricha*, *Andropogon saccharoides*, Trachypogon, Elyonurus, Manisuris, and *Bouteloua texana*.

Owing to the long growing season and favorable rainfall, the distinction between tall and mid grasses is somewhat less clear than further north, but in general the three groups of the list represent tall, mid, and short grasses. By far the larger number belong to the bunch form, only Agropyrum, Buchloe, and Hilaria making a close turf.

Subdominants. The coastal prairie is even richer in perennial forbs that constitute aspect societies than is the true prairie. This is to be ascribed chiefly to the longer growing season and higher temperatures, though somewhat better water relations doubtless play a part. The general harmony between the two is well demonstrated by the fact that of the 90 major subdominants of the true prairie, 75 take a similar role in the coastal association. In addition, there are a considerable number of species of southern or southeastern range that belong to the same genera, e.g., Baptisia, Petalostemon, Salvia, Liatris, Silphium, etc., as well as a score of genera peculiar to the south, such as Atamasco, Cooperia, Herbertia, Berlandiera, Engelmannia, etc.

Proclimaxes. As would be expected from the presence of several short grasses, the coastal prairie is converted into a disclimax by overgrazing just as in the mixed prairie. The dominants most concerned are Buchloe, Hilaria, and *Bouteloua texana*, together with the alien *Cynodon dactylon*. This change has naturally occurred earlier and most completely in the west and north of the area, but it has moved steadily eastward with increasing grazing pressure. Entirely dissimilar in appearance, but likewise caused by grazing, together with fire, is the disclimax characterized by Prosopis and Opuntia, or by Prosopis and a variety of shrubby associates found in the southwest and in Mexico. Over much of the area of the coastal prairie the two disclimaxes become one, overgrazing producing a short-grass sod in a savanna of mesquite and cactus.

Through the central portion of the association, prairie with more or less mesquite alternates with bands of postclimax woodland of oak-hickory, the one found regularly on hard soil or "black land," the other in sandy areas. The woodland belts or "Cross Timbers" are to be regarded as the shrinkage relicts of a former oak-hickory climax, now persisting in sand under a drier climate as a consequence of the compensation afforded by the water relations of this soil. With the occasional exceptions afforded by small denser stands or "motts," the trees have decreased in size and density to the point of forming savanna. The species chiefly concerned is the postoak, *Quercus stellata*, with which is often associated blackjack, *Q. marilandica*, and sometimes hickory, *Carya buckleyi*.

The coast is bordered by a persistent subclimax of marsh varying from 5 to 10 or more miles wide. This receives slow but constant accretions gulfward and passes at a similar rate into the coastal faciation of the prairie in the landward direction, slight changes in level producing a mosaic of fragments of the two communities. The dominants of this coastal marsh are *Spartina spartinae, S. patens,* and *Sporobolus virginicus.*

Influents. The bison occurred in goodly numbers throughout the prairie area, but the antelope was present only along the northern and western margins. The wolf was represented by the Texas wolf (*Canis rufus,* A. & B.) and the Texas coyote took the place of the northern species. The Gulf spotted skunk lives in the clusters of Opuntia scattered over the prairie. It is probable that the badger was present in this region, but as a fur-bearer it would be extirpated early. A species of pocket gopher (*Geomys breviceps sagittalis* Mer.) is restricted to this region, and also one of white-footed mice (*Baiomys taylori subater* Bailey). The little gray harvest mouse and the Louisiana vole are present. The Attwater prairie chicken, the Texas horned lark, and the boat-tailed grackle are characteristic birds (Bailey, 1905).

Tall-grass Orthoptera such as *Melanoplus differentialis, Ophulella pelidna,* and *Scudderia texensis* are common. *Amblycorypha huasteca* reaches north into the true prairie as far as Kansas. (Cf. Isely, 1937.)

Seral Stages. The seral stages of this prairie are the gulf bayous, mud flats, and sand areas. The Texas mole (*Scalopus aquaticus texanus* Allen) is a sand-area species. In the marshes the rice rat (*Oryzomys palustris texensis* Allen), the swamp wood rat (*Neotoma floridana rubida* Bangs), and the swamp rabbit (*Sylvilagus aquaticus littoralis* Nelson) are the chief mammals.

DESERT PLAINS

Nature and Extent. The term applied to this association refers to the relation between these elevated short-grass plains and the true desert. They lie in contact with the latter on the west and south and partake of the same climatic nature to such an extent as often to have been mistaken for climax desert, an assumption further supported by the large number of succulents and other xeric shrubs (Fig. 65).

This association occupies western Texas south of the Panhandle and stretches through large portions of northern Mexico to western Sonora. It is found throughout southern New Mexico and Arizona below elevations of 4,500–5,000 feet, reaching its western limit near the isohyet of 5 inches and approximately 100 miles east of the Colorado River. It lies in contact with the coastal prairie, or better, forms a wide ecotone with it in west-central Texas and meets the mixed prairie near the southern line of the Panhandle. Its limits and contacts in Mexico are little understood, but it once occupied large areas of the central plateau, and a considerable number of its dominants extend into Central and South America.

The desert plains extend along the southern line of the mixed prairie in the central regions of New Mexico and Arizona, though direct contact is prevented for long distances by mountain ranges in western New Mexico and the Mogollon Rim in Arizona. Where barriers do not intervene, the two grasslands combine in a wide ecotone, and a similar condition obtains where the desert plains swing around the western flank of the mixed prairie at the edge of the Colorado valley. From northern Mexico to northern Arizona it faces the desert climax of Larrea and its associates.

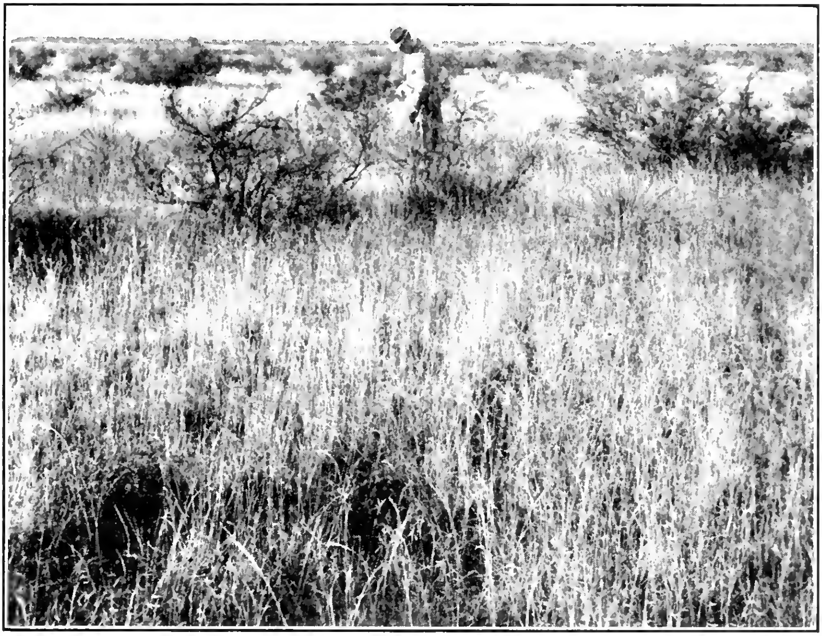

Fig. 65.—Desert plains dominated by *Bouteloua eriopoda;* southwestern Texas. (Photo by Edith Clements.)

Climate. High temperatures during the summer and mild to warm winters in the western portion are responsible for the impression of a desert climate, together with the low humidity and the corresponding high evaporation. But the annual rainfall confirms the evidence drawn from the climax vegetation to the effect that the climate is that of xeric grassland, unmatched in this respect elsewhere in the formation. With an extent of nearly 12 degrees in latitude and 4,000 feet in altitude, the average precipitation ranges from 18 inches or more in the east and at the upper elevations to 6 inches or thereabouts along the margin of the desert.

Like the mixed prairie, the eastern third of the area falls within the rainfall belt characterized by receiving 70 per cent of its precipitation between April first and September thirtieth. The percentage drops to the west rather rapidly, falling to about 45 at the eastern line of the desert. Over much of the region, in consequence, there are two rainy seasons, winter-early spring, and late summer, separated by two almost rainless intervals, and two corresponding growing seasons.

Dominants. The dominants of the desert plains are as follows:

- *Bouteloua eriopoda*
  - *rothrocki*
  - *radicosa*
  - *chondrosioides*
- *Aristida californica*
  - *arizonica*
  - *ternipes*
- *Hilaria mutica*
- *Muhlenbergia arenicola*
  - *monticola*
  - *porteri*
  - *emersleyi*
- *Sporobolus cryptandrus-flexuosus*
  - *c-contractus*
  - *c-giganteus*
- *Scleropogon brevifolius*
- *Panicum halli*
- *Trichachne californica*
- *Leptochloa dubia*

- *Eragrostis lugens*
- *Andropogon cirratus*
  - *hirtiflorus*
- *Bouteloua gracilis*
  - *hirsuta*
  - *curtipendula*
  - *trifida*
- *Aristida divaricata*
  - *purpurea*
- *Hilaria cenchroides*
- *Triodia pilosa*
  - *mutica*
  - *pulchella*
- *Epicampes rigens*
- *Panicum obtusum*
- *Setaria macrostachya*
- *Sporobolus cryptandrus*
  - *airoides*
- *Andropogon scoparius*

The desert plains possess a larger number of dominants than any other unit of the grassland, as well as much the largest group of eu-dominants, amounting to half or more of the total, as shown by the left-hand column. This is in accord with the assumption that deserts and adjacent arid regions are centers of active evolution. This association may well be regarded as the true short-grass community, since half of the species belong to this life form which characterizes three-fourths or more of the area. As would be expected, the bunch form is overwhelmingly the rule, the ratio to the sod-formers, viz., *Bouteloua eriopoda*, *Hilaria cenchroides*, and *Panicum obtusum*, being more than 12 to 1. Of the total number of dominants, 34 are found in Mexico, 9 extend to Central or South America, and only 10 northward of the ecotone with the mixed prairie.

Subdominants. The vast majority of the long list of subdominants are southwestern in origin and distribution; relatively few have been derived from the mixed prairie or from the Gulf region. Owing to the desertlike climate, the western and southern portions are signalized by a large number of dwarf and half shrubs, which are to be reckoned among the subdominants as a rule. Equally characteristic is the presence of two major aspects, summer and winter, the latter, in particular, marked by a host of annuals. A large number of these are to be found in the desert, where they probably originated, and many of them occur also in the prairie of southern California. These may be regarded as the forb dominants of a subsere of bare soil, as they are in the desert, but it is simpler at present to treat them as annual subdominants of the desert plains or California prairie, as the case may be.

Proclimaxes. The most striking feature of the desert plains is the general presence of shrubs, giving it the character of savanna. Chief among these are Larrea, Yucca, Flourensia, and Ephedra on the general levels, with Prosopis or Mimosa at somewhat higher ones, while Prosopis, Acacia, Parkinsonia, and Olneya occur in the washes. These have undoubtedly been present since some distant dry-phase migration of subtropical shrubs and trees to the northward, but they have also multiplied greatly in consequence of overgrazing. This disturbance has likewise favored the replacement of perennial grasses by annual ones, such as *Bouteloua aristidoides, B. parryi,* and *Aristida adscensionis,* especially in the drier areas, giving rise to a widespread disclimax savanna composed of these "six-weeks grasses" with Larrea and other shrubs.

Two other shrubby proclimaxes, which appear to be postclimax in nature, are found in the immature soil of the rocky slopes of foothills and escarpments. The one is composed of Agave, Dasylirion, and Nolina in particular, and is found at its best in the "sotol" region of western Texas; the other is marked chiefly by Carnegiea, Fouquiera, and Parkinsonia and stretches from eastern Arizona to the Colorado Desert.

Influents. The bison was never present in this grass type in any abundance, except in west Texas. The pronghorn antelope originally occurred in goodly numbers; the subspecies differs somewhat from the northern form, but chiefly in spending the summer in the higher country and winter in the lower grass-covered plains. The distinction between this community and the Great Plains is reflected in the addition of two species of kangaroo rats. *Dipodomys spectabilis spectabilis* Mer. (Figs. 66–67) is essentially a grassland species, feeding

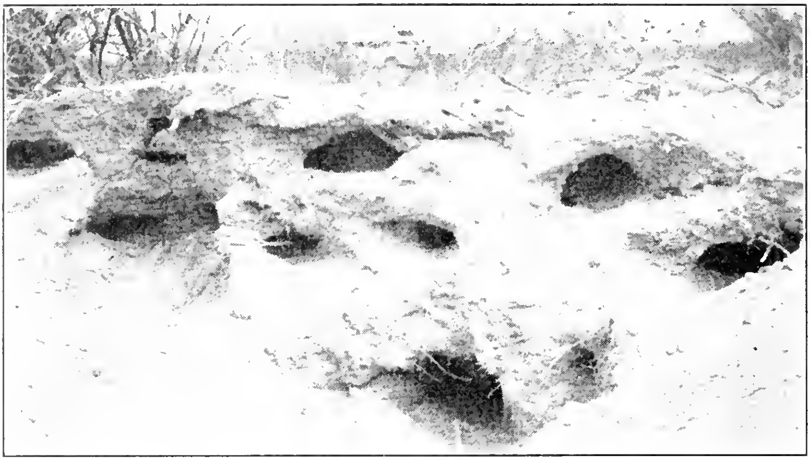

FIG. 66

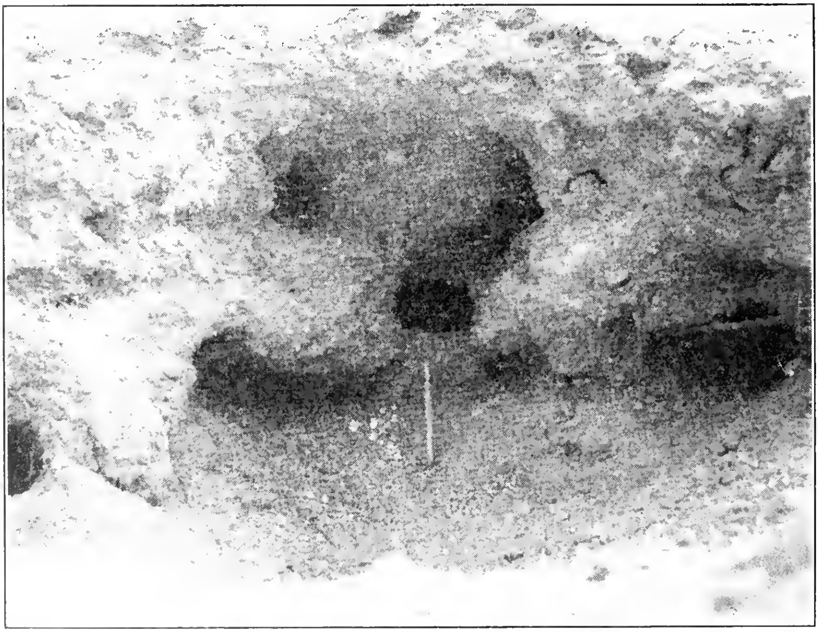

FIG. 67

FIGS. 66–67.—The burrow of the bannertailed kangaroo rat (*Dipodomys spectabilis*) in desert plains of western New Mexico. The upper photograph (Fig. 66) shows the burrow partially excavated. (Photo by E. Rigg.) The lower photograph shows the stores chamber opened, with a lead pencil inserted into about a pint of yellow seeds of a forb. (Photo by C. E. Williams.)

upon and storing grass seeds; it has been the subject of careful study by Vorhies and Taylor (1922). The second, *D. merriami merriami* Mearns, is a desert species much smaller and much less abundant; it does not store food and is accused of pilfering the hoards of *spectabilis*. Grass vegetation is, however, important to it.

Spectabilis ranges outside the grassland proper, decreasing toward the desert and toward pinyon-cedar and yellow pine. The mounds are often associated with shrubs. Geckos, camel crickets, and wingless female cockroaches are common in dens (Vorhies and Taylor, 1933), which also form a retreat for rattlesnakes, grasshopper mice, ground squirrels (*Citellus tereticaudus* [Baird] and *Ammospermophilus harrisii* [A. & B.]), when kangaroo rats have deserted them. These rats are probably the most important influents of the association. They are preyed upon by the badger (*Taxidea taxus berlandieri* [Baird]), the kit fox (*Vulpes macrotis neomexicana* Mer.) and the Mearn's coyote (*Canis mearnsi* Mer.). The wolf, now extirpated, was represented by the small dark Mexican species. The area possesses an outstanding jack rabbit known as the antelope jackrabbit (*Lepus alleni* Mearns) because of its swiftness and its exceptionally large ears. The prairie dog is represented by *Cynomys ludovicianus arizonensis* (Mearns). The habits of the species present in this area are similar to those of other grasslands, and all the important life habit types are present (cf. Vorhies, 1936).

CALIFORNIA PRAIRIE

Nature and Extent. This has been termed Pacific prairie as well as California prairie, but the latter is to be preferred as being more definite, since this unit is restricted entirely to California and Lower California. By reason of the barriers interposed by mountain range and desert, this association is today almost completely isolated from the others of this climax. It passes over quickly into the extension of the Palouse prairie in northern California, and a former contact with the mixed prairie and the desert plains on the east is now represented by a few straggling relicts in and about the Mohave and Colorado Deserts (Clements, 1936). South of Mount Shasta, and from the coast to the foothills of the Sierra Nevada, this prairie and the related disclimax covered more than three-fourths of the land before the period of intensive agricultural development. Much of the most extensive areas were found in the plainlike valleys of the Sacramento and San Joaquin, and southward of the Cross Ranges, but all the lateral valleys and the adjacent slopes and foothills from central California well into Lower California were once grassland, as attested by numerous relicts of the perennial dominants (Fig. 68).

Climate. The climate of this prairie differs from all those previously considered in having a winter rainfall, the maximum occurring in December, January, and February. It is reflected in the two growing seasons of the desert plains, the winter season being the counterpart of the single growing season in California. Except in the neighborhood of the coast, the summers are hot, as in all southern grasslands, and the winters are mild, with little or no snow within the range of this association.

FIG. 68.—California prairie composed of *Stipa pulchra*; San Joaquin Valley. (Photo by Edith Clements.)

The annual rainfall varies from about 6 inches in the upper San Joaquin and in the Antelope Valley at the west end of the Mohave Desert, to 25–30 inches along the coast. In view of the fact that most of the grassland climax receives 70 per cent of the precipitation between April first and October first, it has sometimes been doubted whether the climate of California is favorable to such a climax, especially with the low minimum indicated above. However, the extensive relicts of fine grassland throughout the general area leave no question on this point, and this evidence has been reinforced by field and garden studies of the life history of the dominant grasses.

Dominants. In the following list, the eudominants are given in the first group:

Stipa pulchra
lepida
coronata
speciosa
Melica imperfecta
harfordi
Elymus triticoides
glaucus
condensatus
sitanion
Koeleria cristata

Poa scabrella
Festuca rubra
occidentalis
idahoensis
Danthonia californica
Bromus carinatus
Hordeum nodosum
Agrostis exarata
Epicampes rigens
Aristida divaricata
purpurea

As a consociation, or in mixture with Melica, Poa, or Koeleria, *Stipa pulchra* occupies a larger area than all other dominants combined. *Elymus triticoides* resembles it in forming an extensive consociation, which once covered the central portion of the San Joaquin, Salinas, and other large valleys. *Elymus glaucus* is more or less characteristic of the oak savanna, and *Stipa lepida* and *coronata* of upper slopes leading to chaparral.

With the exception of *Stipa pulchra,* which extends to the upper end of the Sacramento Valley, the eudominants do not occur north of the central portion of the state, while Epicampes and Aristida are southern in range. Festuca and Danthonia, as well as *Melica harfordi,* reach their southern limit in the central region, but the remaining species are of wide distribution, not only throughout the association but extending far to the north and east. The life form is that of the bunch grass, only *Elymus triticoides* being a sod-former, in response to the higher holard of its lowland habitat.

Subdominants. The aspects of the California prairie anticipate the calendar, and this fact must be kept clearly in mind with respect to the designation vernal, estival, and so forth. The prevernal period falls as a rule in midwinter, the vernal in late winter and early spring, and the estival in late spring; the serotinal is all but absent, owing to the dry summer which begins in late May or early June.

The perennial forbs fall into two principal groups, namely, monocotyls with bulbs or corms, and dicotyls with root stocks or crowns. The first are practically all vernal, the most important being the grassland species of Brodiaea, Calochortus, and Allium, supplemented by *Sisyrinchium bellum*, Mullia, Bloomeria, Fritillaria, Zygadenus, and

Chlorogalum. The other perennials belong to the genera typical of mixed and true prairie for the most part, though with uniformly different species and earlier times of blooming. The most characteristic of the perennials is naturally Eschscholtzia, but Ranunculus, Delphinium, Lupinus, Sidalcea, Pentstemon, Viola, Artemisia, Helianthus, and Solidago are of the first rank also. Even more typical are the great masses of annuals, representing more than 50 genera and several hundred species. These fluctuate widely with the amount and distribution of the rains and the proper conjunction with rising temperatures. Under favorable conditions in the upper San Joaquin, where the competition of the grasses has been all but eliminated by overgrazing, the number and size of such annual communities are beyond belief. In the spring of 1935 with supranormal rainfall, the carpet of brilliant blues, oranges, and yellows covered an area approximately 50 miles wide and 100 miles long.

Proclimaxes. The outstanding community of this group is the disclimax composed of weedy annuals, chiefly grasses, introduced from Europe during Spanish days. As a consequence of excessive grazing pressure during the dry season from May to December, this covers nine-tenths or more of the non-cultivated portion of the original bunch-grass climax. The major dominant is wild oats, *Avena fatua*, usually forming a dense tall consocies that simulates natural grassland. It may alternate or mix in varying degree with several species of Bromus, Hordeum, and Festuca, as these do with each other or with one or more of the three common Erodiums (Fig. 69).

The shrinkage of the woodland climax under climatic desiccation has produced an oak savanna along the margins of valleys and over foothill slopes generally, and in this digger pine (*Pinus sabiniana*) is often an important element. A similar process has operated upon the coastal sagebrush of Artemisia, Salvia, Eriogonum, and their associates, as well as upon the lower consociation of chaparral composed chiefly of Adenostoma. The interesting Joshua tree (*Yucca brevifolia*) of the margins of the Mohave Desert likewise forms savanna with *Stipa pulchra*, *S. speciosa*, Elymus, and Poa in the semi-desert arm known as Antelope Valley, a phenomenon entirely in harmony with the behavior of other species of Yucca elsewhere in the grassland climax. As to semi-permanent subclimaxes, there are two of wide extent. One of these is the great complex of "tule" marshes in the deltalike region where the Sacramento and San Joaquin rivers meet in central California, and the other an extensive belt of stable coastal dunes found largely in the general region of Pismo and Monterey Bays.

Influents. The antelope was very abundant in the San Joaquin Valley, occurring in herds of two or three thousand; it was also originally numerous in other valleys. As to California, Stephens (1906) says, "Antelopes are found in open treeless regions, very seldom among trees, and never in dense forests. Their food is mostly grasses, seldom twigs or leaves of bushes or trees." The bison and wolf are not known to have been found within historic times in the central and southern parts of California occupied by the bunch-grass association. The valley coyote (*Canis ochropus* Esch.) usually hunts in groups of three or four and runs down its prey, which probably consists largely of jack rabbits. It also eats grasshoppers, other insects, and fruit.

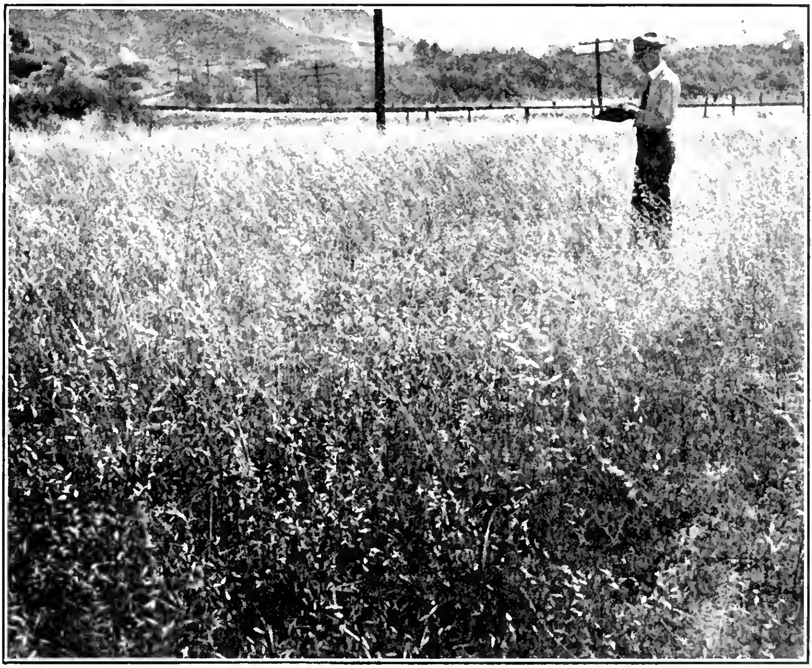

FIG. 69.—Disclimax of annual *Avena* and *Bromus*, produced from California prairie by grazing; San Fernando Valley. (Photo by Edith Clements.)

The badger (*Taxidea taxus neglecta* [Mearns]), according to Stephens, was not abundant in California in 1906, but he referred to its occurrence in open country. Today this subspecies has a distribution in California which conforms to the grassland. The outstanding larger rodents of this association were ground squirrels and jack rabbits. The latter (*Lepus californicus californicus* Gray and *richard-*

sonii [Bach.]) evidently occurred in great numbers, which were further increased by the destruction of carnivores, especially the coyote, for in 1893 a drive at Fresno resulted in the destruction of 20,000 rabbits (Palmer, 1897:51). With a single county as an exception out of a total of ten, all drives were in counties originally containing large areas of climax grassland (see Grinnell, 1933).

The California and Fisher ground squirrels (*Otospermophilus grammurus* Say, subspecies *beecheyi* and *fisheri*) constitute one of the most characteristic species of this grassland, which extends also into other grass-covered areas in the foothills and mountain parks (Grinnell and Dixon, 1918). The seeds of grasses and forbs were probably the chief original foods, and grasses are very largely used in lining nests.[1] The enemies of the abundant animals within this prairie include the rattlesnake (*Crotalus confluentus oreganus* [Holbr.]), the gopher or bullsnake (*Pituophis catenifer* varieties), the red-tailed and red-bellied hawks, the badger, and the coyote. The pocket gopher (*Thomomys bottae* [E. & G.] in several subspecies) extends throughout the great valley, but is most abundant in the San Joaquin. Kangaroo rats (*Dipodomys nitratoides* [Mer.]) are common along the flanks of the upper San Joaquin valley, and the pocket mouse (*Perognathus californicus* [Mer.]) is present in the same region (cf. Van Denburg, 1922).

PALOUSE PRAIRIE

Nature and Extent. This association is characteristic of the great agricultural region of the Palouse, where it occurs in its most typical form. As such, it is found in southeastern Washington, northeastern Oregon, and adjacent Idaho, but its major dominants extend much more widely to reach western Montana and northern Utah. They also form the grassland of northern California and of part of southern Oregon, but yield to chaparral and forest in the region about Mount Shasta, so that there is little or no direct contact between this and the California prairie proper. Owing to the mountain barriers in the east, the transition to mixed prairie is generally rather abrupt, though somewhat obscured by the presence of *Stipa comata* and *Agropyrum smithi* in both (Fig. 70).

Climate. Owing largely to the climatic barrier fashioned by the Cascade Range, the Palouse is a region of hot summers and winter snows. Its most distinctive feature is the fact that the bulk of the

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[1] This animal is notorious because of its taste for introduced agricultural plants and fruits, which it will climb to get, and also because of carrying bubonic plague.

precipitation falls in general during the four months from November through February, while July and August may be practically rainless. Because of the snow cover, the utilization of water is higher than in the other associations and the grass cover is often unusually luxuriant in consequence.

Fig. 70.—Palouse prairie in southeastern Washington; *Agropyrum spicatum*, *Festuca idahoensis*, and *Poa secunda* chief dominants, with *Koeleria* and *Stipa* less abundant. (Photo by A. L. Hafenrichter; courtesy of U. S. Soil Conservation Service.)

Dominants. The eudominants of the Palouse prairie are listed in the first column:

- *Agropyrum spicatum*
  - *s-inerme*
  - *smithi dasystachyum*
- *Stipa occidentalis*
  - *o-elmeri*
  - *o-thurberiana*
- *Poa nevadensis*

- *Poa scabrella secunda*
- *Agropyrum pauciflorum*
  - *smithi*
- *Festuca idahoensis*
  - *occidentalis*
- *Stipa viridula*
  - *comata*
- *Elymus condensatus*
  - *sitanion*

- *Elymus triticoides*
  - *glaucus*
- *Koeleria cristata*
- *Melica harfordi*
- *Danthonia californica*
- *Oryzopsis hymenoides*
- *Hordeum nodosum*
- *Carex filifolia*

The most distinctive dominant of the Palouse prairie is *Agropyrum spicatum*, together with its variety *inerme*. Its usual associate is *Poa scabrella secunda*, a smaller bunch grass of the intervals; it is often mixed with *Stipa comata*, *S. occidentalis*, or Koeleria in large quantity, or the first two of these may form small consociations. *Agropyrum pauciflorum*, *A. smithi*, and *Elymus condensatus*, singly or together, are often associated with *A. spicatum*, though Elymus is most abundant in pure stands in valleys, often of alkaline nature. With the exception of *Festuca idahoensis*, which usually mingles with Agropyrum at higher elevations, the remaining dominants are generally of rather less abundance or are more or less localized. It is significant of this association that the grasses are almost exclusively northern in origin and distribution.

Subdominants. The principal societies and clans of the typical Palouse prairie of Washington and Idaho have been listed by Weaver (cf. Clements, 1920); Lupinus and Astragalus are both well represented, while composites belonging chiefly to the genera Balsamorhiza, Wyethia, Solidago, Carduus, Agoseris, and Aster are the major contributors to the estival and serotinal aspects. Piper (1906:51) has found that the subdominants have been derived from three different sources and listed them as belonging to the flora of California, the Rocky Mountains or the Columbia Basin (cf. Taylor, 1911; Taylor and Shaw, 1929).

Proclimaxes. By far the largest portion of the Palouse prairie today is characterized by sagebrush, *Artemisia tridentata*, frequently with one or more of its major associates, namely, Atriplex, Chrysothamnus, or Purshia. This assumes the form of savanna, which is almost indistinguishable from the true sagebrush climax, over extensive areas in which the grass dominants have been destroyed. However, all sources of evidence combine to establish the fact that this is a disclimax produced by overgrazing, as in the case of Larrea in the desert plains or Prosopis in the coastal prairie. This relation was established two decades ago by the discovery of prairie relicts throughout the region wherever protection against grazing had existed since the period of settlement, and especially in cemeteries. It is confirmed by scientific record of nearly forty years ago (J. C. Merriam, 1899) and by stockmen of the region who had been attracted to the John Day valley by the fine grassland more than sixty years since. Finally, the field observations upon the dominance of the grasses under protection and the success of sagebrush under heavy grazing have been verified by the results obtained by means of exclosures and by the removal of sagebrush.

The disclimax of annual grasses so characteristic of the California prairie has a counterpart in the Bromus cover composed almost wholly of *B. tectorum*. With this are frequently found two other annual dominants, *Sisymbrium altissimum* and *Lepidium perfoliatum*, most abundantly in regions of cultivation. Generally, Bromus and Artemisia occur together to constitute the savanna typical of the area of this association.

Influents. The bison was present in small herds in southern Idaho and northern Utah, but decreased in numbers westward; a few remains have been found in extreme northeastern California. The pronghorn antelope was originally distributed over most of the Palouse prairie, and at one time there were large herds in eastern Oregon. The badger was present throughout and has persisted even after overgrazing caused extensive invasion by sagebrush. The area is well provided with ground squirrels, coyotes, and formerly wolves also. The so-called sage grouse (*Centrocercus urophasianus* [Bonap.]) belongs properly to this region, and it also has remained after the practical removal of the grasses. The area in which this grassland occurs contains large outcrops of rock and is dissected by numerous deep valleys, giving a characteristically different set of local conditions in seral stages (Merriam and Stejneger, 1891; Dice, 1923; Preble, 1925; Wight, 1925; Bailey, 1936).

CHAPTER 9

AQUATIC CLIMAX COMMUNITIES

FRESH WATER COMMUNITIES

Introduction. Only those aquatic communities that are similar in general character to the climaxes on land are considered as water climaxes. These are the stable and relatively permanent communities that show some degree of biotic development; their constituents exercise a large control over the habitat and over community composition.

There are two or three types of climaxes in water, namely, fresh-water climaxes that characterize very large fresh-water lakes and sluggish streams, and marine communities which are probably climax and characterize the ocean. In addition, there are alkaline and very salty lakes in arid areas of internal drainage, which contain life and in which climaxes probably occur. Generally speaking, the communities included in this discussion are on silt (terrigenous), as opposed to humus, bottoms. The rapid accumulation of humus in small fresh-water lakes and ponds assigns all small bodies of still fresh water to the seres of terrestrial climaxes; some shore waters of the sea are similar in character.

HYDROCLIMATES

The major communities on land are dependent on a complex of physical factors called climate. It is not unusual to refer to the combinations of various physical and chemical conditions in the sea and fresh water as hydroclimates (Wasmund, 1934), and such a procedure is not difficult to justify, since it concerns physical conditions and is not without earlier precedent (Huntsman, 1920). Animals live in water at all depths, both on the bottom and suspended in the medium. This distribution stands in contrast to terrestrial climates, in which only the lower atmosphere is in contact with most organisms. Because of physical properties and by virtue of the contained inhabitants, water and water climates exhibit some of the properties of soil and soil conditions. Accordingly, any attempt to analyze marine and fresh-water hydroclimatic complexes discloses a set of conditions more obscure and complicated than those presented by terrestrial climates. In the main, physical principles governing conditions in air on the one hand and fresh and salt water on the other are the same, but a few differences must be noted.

HYDROCLIMATIC FACTORS

Density. The density of water is nearly a thousand times that of air. This increases difference with changes in depth as compared with changes in altitude. The addition of water vapor to air decreases its density, while an increase in salinity increases the density of water. Salts and water vapor are constantly varying in their respective media, and mention of salinity or mineral content is as frequent in literature regarding water as humidity is in that regard to air. The osmotic pressure of sea water is 20 or more atmospheres, while that of fresh water is relatively small. The salt content of the sea is relatively uniform, but that of fresh water may vary to 20 or more times the minimum found in mountain streams in rainy districts. The density of water as compared with air further tends to crowd major differences in conditions into a much smaller space, especially in shallow water.

Circulation. In the ocean and in large lakes, much of the water in the deeper portions of their basins is comparatively, if not entirely, without currents of measurable magnitude, but even here slow drifts of considerable importance occur.

In the lesser depths and the more rapidly moving surface, an outstanding general climatic factor in water is movement of the medium. As such, it is concerned with the modification of temperature and salt content. Circulation attains major importance in part on account of its relation to the transportation and deposition of floating materials of various kinds, together with their decomposition products. Where currents are sluggish, deposition occurs, and if the water is not deep, temperatures are higher. The plankton accordingly multiplies, the dead and decaying organisms settle to the bottom in quantity and, in their decomposition and that of the debris resulting from the breaking down of rooted plants, consume oxygen and increase carbon dioxide and sulphur compounds, producing a climate of distinctive character for both benthic and pelagic communities. In Washington Sound these factors differentiate sharply the climates of two major communities (Shelford et al., 1935).

Suspended Matter and Color. By way of contrast with aerial climates, one of the important general factors that must be considered is the material carried in suspension in water. This includes mineral matter, floating and swimming plants and animals, together with dead bodies and parts and the feces of animals. A portion of the detritus originates from pelagic and part from benthic organisms. The amount of this is great, and it is often carried some distance from its origin. However, the terrigenous material carried in suspension in the sea is small in amount when compared with that of rivers, and on the whole is less than in most lakes. It has been demonstrated that lake waters are stained with brown coloring matter resulting from the decomposition of vegetation (Pietenpol, 1918). A similar condition undoubtedly exists in the sea, especially in coastal water (Knudsen, 1922).

Light and Temperature. Radiant energy is transformed into heat in water; essentially all the seasonal differences due to the sun's relative position are felt in waters as variations in light penetration and heat. The climatic zones are, however, even less recognizable than on land, owing to the high specific heat and general lag of a dense medium. In shallow water, differences in temperature, light, etc., are great in proportion to differences in depth. In deep water, however, the reverse is true, variations in temperature being small, but animals proportionately more sensitive. All the swimming and floating objects obstruct radiant energy and thereby heat. They also affect light intensity in proportion to their abundance, and at the same time the penetration of various wave lengths is a function of their selective absorption. Through the obstruction of radiant energy, the pelagic community, including plankton, produces a reaction similar in some respects to the shade cast by an open leafy canopy (Shelford and Gail, 1922; Shelford, 1929, *b*; Williams, 1929; Oster and Clark, 1934). Detritus and terrigenous matter are comparable in some respects to dust in the air (cf. Humphreys, 1920).

Dissolved Substances. Another striking difference between air and water is the marked variation in solutes from point to point in the latter, especially the products of metabolism and of decomposition of organic matter. Dissolved oxygen is an important feature of hydroclimates, largely because of the variation in amount. Birge and Juday (1911) have considered it in detail for glacial lakes, and the horizontal and vertical distribution in the Atlantic has been outlined by Murray and Hjort (1912:255–256). Its consumption is primarily affected by the respiration of living organisms, and especially the decay of dead bodies. It is added to the water by chlorophyll-bearing organisms only near the surface and during the day. The open waters of Washington Sound always show a deficiency of at least 1–2 cc. per liter as compared with saturation. This indicates a very large consumption by dead and living organisms, which constitutes an important reaction on marine climates. The amount of dissolved oxygen usually varies inversely with the carbon dioxide pressure.

The sulphur compounds of the sea, such as hydrogen sulphide, sulphur dioxide, and colloidal sulphur, are much more important than in fresh water; free sulphurous acid is often found below 75 meters in salt water. The extent to which the various products of metabolism and decomposition accumulate or are carried away from an area of abundance by currents constitutes one of the outstanding features of a marine as well as a fresh-water hydroclimate. The accumulation of all life products in situ is of prime importance on land, while the extent to which they are moved in the sea and large lakes is the foremost limiting factor. There is little doubt that the total effect of organisms on a marine or fresh-water hydroclimate is comparable in magnitude to that of plants on land.

Certain physical factors or complexes have little effect on aquatic organisms. Pressure is of some small significance, but necessarily operates in the same fashion in both fresh and salt water (Regnard, 1891). Tides do not constitute a climatic complex for subtidal animals, but merely produce a special climate for intertidal ones; they have no counterpart in fresh water. The thermocline phenomena of lakes (Birge, 1903) also characterize bays and fjords with threshold outlets (Murray and Hjort, 1912:257), producing somewhat similar results.

FOOD RELATIONS

One other important difference between terrestrial climax communities and aquatic communities with climax characteristics lies in the presence of food in the form of detritus and plankton distributed throughout the water medium. The communities that are not clearly a part of a terrestrial sere, such as most marine communities and those of permanent streams and large lakes, lack the growth of rooted vegetation that forms the primary food supply for practically all herbivorous land animals. Food supplies in water have their basis in (1) microscopic plants, (2) detritus from organisms in the plankton and from the rooted vegetation along the shores, and (3) possibly dissolved organic matter.

Some microscopic animals may possibly absorb dissolved organic matter. The earlier views of Frankland and Armstrong (1874; cf. Birge and Juday, 1926) and of Pütter (1908) have been revived by Krogh (1934) for the sea, and by Birge and Juday (1934) for fresh water. Krogh (1934) has made the suggestion that probably only the very smallest organisms can utilize the dissolved matter. The majority of microscopic animals feed on microscopic plants or minute particles of detritus. The great mass of medium-sized animals live on smaller plants and animals or detritus, while the large motile forms are chiefly carnivorous. Brooks (1893) had earlier called attention to these facts as regards the sea. The importance of copepods as the food of young fishes has been emphasized by Forbes (1880) and Lebour (1919, *a,b*, 1920, 1921, 1923, *b*).

Another peculiar characteristic of the constituent species of aquatic communities is the short developmental period and short span of life. One to 7 years will cover the life span of the majority of aquatic noncolonial animals. The rapid overturn makes annuation and aspection phenomena stand out sharply (Jensen, 1919; Blegvad, 1925). In general terms, many constituents of marine communities have a span of life of 2–3 years in contrast to 25–50 years for climax grasses and 300–500 years or more for forest trees.

CLIMAX FRESH-WATER COMMUNITIES

Introduction. The only fresh-water communities possessing the properties of land climaxes to a noteworthy degree are discussed here. These properties are:

a. The organisms of the community exercise a considerable degree of control over the habitat.

b. The controlling reactions and coactions tend to maintain habitat and community in the climax condition.

c. The climaxes exist under stable physiographic conditions.

d. They undergo development on denuded areas, and during this development a series of changes take place both in the habitat and in the composition of the community.

Climax communities obviously exist in permanent streams under conditions of stable bottoms composed of mud, silt, or very fine sand, accompanied by usually gentle currents, but high water and high turbidity in certain seasons. The last condition is productive of an abundant plankton (Eddy, 1934), which further reacts upon the bottom and provides one of the conditions of the climax and of its maintenance. In streams and possibly large lakes, this plankton must be regarded as a layer, because there are no organisms having the properties of dominants which occur exclusively in the pelagic level.

The communities of large lakes with terrigenous bottom are similar in taxonomic composition to those of streams of corresponding depth. In the largest lakes the pelagic grouping constitutes a unit with a considerable degree of independence and may have some or all the properties of a major community.

River Climaxes

In middle North America these communities are usually composed of plankton organisms, fishes nesting on the bottom and feeding largely on detritus, mussels, sphaerids, mayfly nymphs of the genus Hexagenia, and the larvae of various midges (Chironomidae), etc. Attached vegetation plays only a minor role because of its slight abundance. This type of climax community occurs in the sluggish pools of most small and large rivers, but in general it exists only as local fragments where the current is slowed to a minimum. In most streams, however, a fragment no sooner becomes established than severe floods bury it or sweep it away, leaving only sterile silt. In those that are at baselevel practically throughout their courses, so that the load of silt is not large and the fall of the streambed so small as to make the greater part of its course a pool in character, the entire stream may have this community on its bottom. The Illinois River, a tributary of the Mississippi, originally contained climax communities over various portions of its course, and the same is true of some of the streams affluent to the Great Lakes. The Mississippi is at baselevel only in its lower course, and the development of extensive climax areas is prevented in a measure by the load of silt from the small tributaries and headwater streams. High turbidity is a characteristic feature of its aquatic climate, and there is also an annual rhythm of high and low water.

There is more or less difference between the communities of small and large rivers, but since the former have been studied more, they will be treated first.

Small-river Climaxes. Gersbacher (1937) has investigated the development of these communities as regards the bottom constituents, with some attention to fishes, and Eddy (1934) has made a study of their plankton. Thompson and Hunt (1930) have depicted the conditions of the habitat and noted the dominant and less abundant fishes, as well as their food and associates. This account of the fishes is supported by the extensive work of Forbes (1883, *a*, *c*; 1888), Forbes and Richardson (1913, 1919), Richardson (1921–1929), and others. Finally, the work of Cahn (1929) on the introduced European carp as a dominant forms the background for this discussion, since this has equivalents in the river carp and buffalo fishes, which are similar in exhibiting the sucking habit (cf. Ellis, 1931).

The small-river climax occupies the long deep pools in streams with a drainage area of 100 to 250 square kilometers, a width of 15–25 meters, and a depth of 1–23 meters; the bottom is of mud, and the water is sometimes turbid, with trees and bushes usually lining the bank. The rooted aquatic vegetation is wanting, but floating duckweeds and blue-green and other algae occur in late summer (cf. Leathers, 1923).

Dominants and Subdominants. The dominants are fishes, which are here arranged in accordance with their general importance:

PERMANENT RESIDENTS

Carpiodes difformis Cope	Blunt-nosed river carp
Carpiodes velifer Raf.	Quill back
Ictalurus punctatus Raf.	Channel catfish
Aplodinotus grunniens Raf.	Drum or sheepshead
Dorosoma cepedianum (Le S.)	Gizzard shad
Ameiurus melas (Raf.)	Black bullhead
Megastomatobus cyprinella (Ictiobus) (C. & V.)	Red-mouthed buffalo
Erogala (*Notropis*) *whipplii* (Gir.)	Steel-colored minnow
Hyborhynchus (*Pimephales*) *notatus* (Raf.)	Blunt-nosed minnow

MIGRATORY SPECIES

Moxostoma aureolum (Le S.)	Red horse (breeds in swifter water)
Moxostoma breviceps (Cope)	Short-headed red horse (breeds in swifter water)
Catostomus commersonii (Lac.)	Black sucker (breeds in small tributaries)

SUBDOMINANTS

Hexagenia (*bilineata, etc.*) nymphs	Burrowing mayfly nymphs
Chironomus plumosus (Larvae and other species of Chironomidae)	Bloodworm
Limnodrilus sp.	Worm

SECONDARY SPECIES

Musculium transversum (Say)	Finger-nail shells
Sphaerium striatinum (Lam.)	Finger-nail shells
Pisidium sp.	Finger-nail shells
Anodonta grandis (Say)	Mussel
Proptera alata (Say)	Mussel
Lasmigonia complanata (Bar.)	Mussel
Campeloma	Snail

Influents. These prey on other organisms and do not affect the habitat as the dominants do:

Pomoxis sparoides (Lac.)	Black crappie
Huro floridana (*Micropterus salmoides*) (Le S.)	Large-mouthed black bass
Cambarus propinquus (Gir.)	Crayfish
Chelydra serpentina (L.)	Snapping turtle
Chrysemys marginata (Ag.)	Painted turtle

Plankton. The plankton contains many genera of diatoms and other types of algae, which settle slowly to the bottom and produce a brown layer. There are many Protozoa, rotifers, and crustaceans of which certain typical forms are conspicuous in their proper seasons, namely: two protozoans, *Condonella cratera* and *Ceratium hirundinella;* rotifers of the genera Brachionus, Synchaeta, Polyarthra, and Keratella; various cladocerans, particularly *Moina affinis*, *Daphnia longispina*, and *Bosmina longirostris;* and three copepods, *Diaptomus pallidus*, *D. siciloides*, and *Cyclops bicuspidatus* (Eddy, 1934).

The Nature of Dominance. The species that constitute this community appear to be very closely knit together. The frequency with which all the fishes except the bass and crappie are found to eat duckweed, bloodworms (Chironomidae), Hexagenia and sphaerids, Campeloma, mussels, detritus, and mud is quite remarkable (Forbes, 1878, etc.). The crappie may feed largely upon plankton, but the bass preys on the young of other fishes and on minnows that occur associated with them. A trematode parasite (*Crespidostomum cooperi* Hop.) (Hopkins, 1934:62–73) has Hexagenia and sphaerids as its alternate hosts, and a fish as the final host.

The pool community in favorable conditions, such as are presented in sluggish portions of rivers of the Mississippi drainage, represents fragments of a true climax. The role of the fishes such as the various suckers, several catfishes, buffalo group and other bottom feeders, which often eat vegetation, mud, and detritus, is such as to remove plants or prevent their increase and therefore maintain the terrigenous bottom suitable for themselves. They also increase turbidity and make conditions less favorable for plants by this means (see Coker, 1929, *a,b*).

The European carp possesses the qualities of a climax dominant, but probably not to a greater degree than many of the American silurids, catastomids, cyprinids, etc. There have always been complaints about carp and fishes of like habit increasing turbidity and driving out other fishes. Cahn (1929) described the effect of the carp when introduced into one of the artificial pools formed by a dam in Wisconsin. At the end of a few years, this fish had successfully removed essentially all the rooted vegetation, uncovering the silt bottom to which it is best fitted, whereupon it became the most abundant fish. The basses, sunfish, plant- and insect-eating fishes were reduced to a few scattered individuals. The carp in this case acted as a dominant, actually transforming a habitat into one in which it lives to best advantage and changing the composition of the community almost completely. Unfortunately, this experiment has not been carried out with native species.

The native fishes of the pools are referred to as digging or plowing the bottom. Of the buffaloes, Forbes and Richardson (1909) state that they are reported to "plow steadily along with their heads buried in the mud,—a search for small mollusca and insect larvae living in the mud." The carp suckers (Carpiodes) eat a greater amount of mud than the nearly related buffalo fish. The same authors refer to the use of the sturgeon's hard beak to stir up the mud in its search for food, the intestines being generally more or less filled with mud. The bullheads and catfishes of the climax are obvious inhabitants of the mud bottom in still water. They feed on aquatic insects, mollusks, and detritus. The fishes of this class are abundant in the larger sluggish rivers.

These fishes, as is readily seen from their habits, stir up the loose flocculent bottom detritus and mud and increase turbidity in the same manner as the introduced carp. Turbidity is unfavorable to plant growth, and the fishes do much to maintain silt and organic materials in suspension. It is the activities of the fishes of the Mississippi drainage that justify placing them among the foremost dominants of the river climax.

In permanent communities, terrestrial plants play the important role as dominants through reaction in situ. The plant reaction in the climax consists in producing conditions suitable for their own survival and continuous reproduction. The general effect of the large pool fishes is the same, though it is brought about by an entirely different set of processes; the most important are probably the increase of turbidity and destruction of plants either in adult form or as seedlings or seeds. Mechanical disturbance of the soil is in itself also important, but this process has not been evaluated.

It must be remembered that any portion of a community separated from the river channel, such as an oxbow, takes an immediate start as a land sere, characterized by increases in vegetation and the extinction of the terrigenous bottom community. This separation and the stoppage of current constitute a fundamental change in aquatic climate, and the fishes are consequently unable to retard the process.

Biotic Development. Areas of sterile bottom are presented in small rivers which are dammed to make large artificial pools for the water supplies of towns in central Illinois. Eddy (1934) has traced the development of plankton in an artificial pool at Decatur, Illinois, making collections from 1923 (one year after the reservoir was filled with water) to 1930 inclusive. The results showed an increase in constituent species throughout the period at the rate of three or four per year from 1925 to 1930. There was a suggestion of one species dropping out, but this may have been due to annuation. In general, the process was additive development without succession. At the time the studies ended, the plankton had reached a condition approaching that of the Illinois River, which was regarded as essentially the climax plankton of the stream (Table 11; cf. Kofoid, 1908).

TABLE 11

NUMBER OF PLANKTON ORGANISMS AVERAGED FOR JUNE, JULY AND AUGUST COLLECTIONS IN LAKE DECATUR, SHOWING DEVELOPMENT FROM 1923 (DAM BUILT IN 1922) TO 1928

Key: Al. Alga; Co. Copepod; Pr. Protozoan; Ro. Rotifer; P. Perennial; S. Seasonal (from Eddy, 1934)

		Thousands per Cubic Meter			
		1923	1926	1927	1928
P	*Lysigonium granulatum* Ehr. (Al)	68.3	891.2	10,667.4	90,214.0
S	*Euglena viridis* Ehr. (Pr)	13.9	3.8	49.4	1,982.1
	Cyclops viridis Jurine (Co)	533.7	3.9	.3	11.8
S	*Eudorina elegans* Ehr. (Pr)	11,033.8	6.6	8.6	4.5
P	*Synchaeta pectinata* Ehr. (Ro.)	541.7	21.2	....	3.6
S	*Closterium acerosum* Schrk. (Al)	NEW	.1	....	.1
S	*Tintinnidium fluviatile* Stein (Pr)		.8	53.2	1,107.4
P	*Trachelomonas volvocina* Ehr. (Pr)		1.3	8,702.8	18,786.4
S	*Cyclops bicuspidatus* Claus (Co)		133.7	....	16.3
P	*Microcystis aeruginosa* Kütz. (Al)		10.2		
P	*Synchaeta stylata* Wierz. (Ro)		NEW	9.3	3.7
	Brachionus havanaensis Rous. (Ro)			0.2	0.1
S	*Euglena acus* Ehr. (Al)			1.7	
	Brachionus budapestinensis Daday (Ro)			8.3	
S	*Conochiloides natans* (Sel.) (Ro.)			NEW	0.1
	Anabaena circinalis Kütz. (Al)				400.0

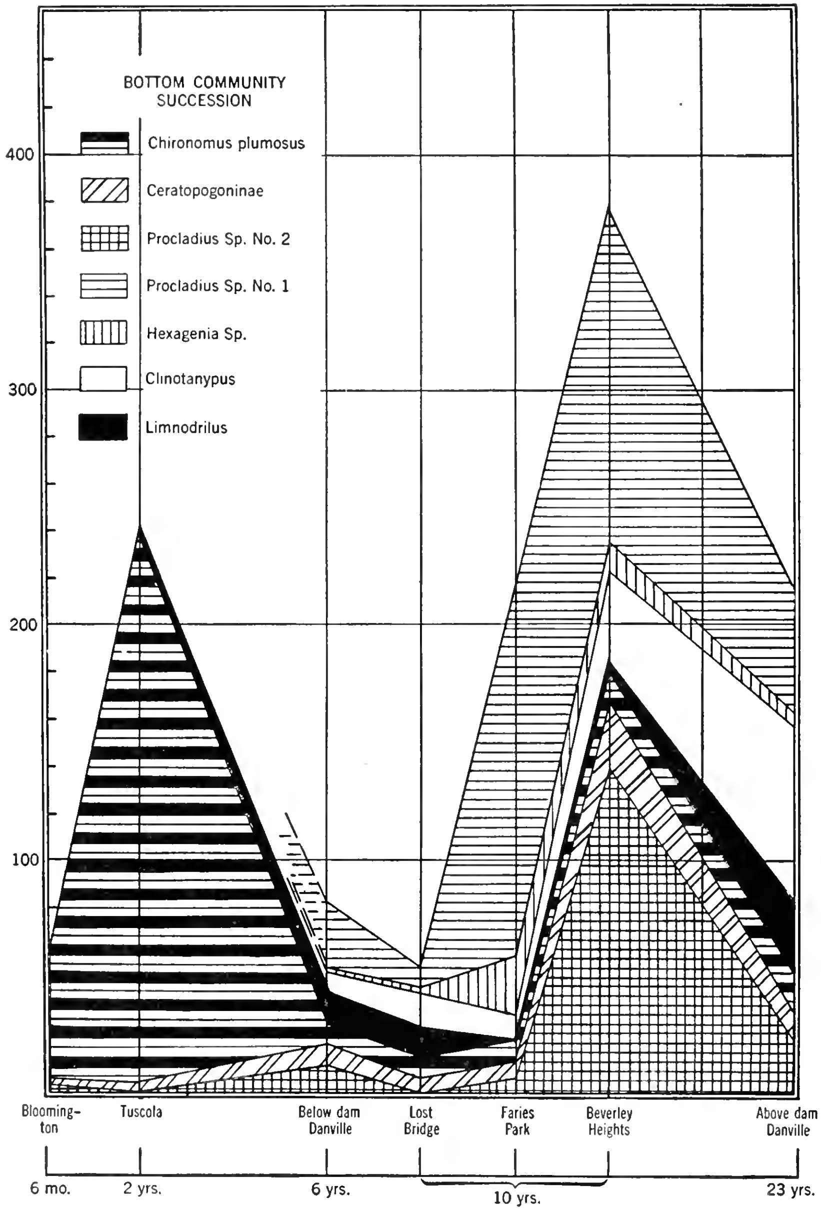

FIG. 71.—Successional development of the bottom community in still water, based on five water-supply reservoirs. The time indications below are not to scale. (After Gersbacher, 1937.)

Gersbacher (1937) has found that artificial pools are populated by species living in the natural pools of a stream that has been dammed, all the usual dominants being present. The gizzard shad is one of the early fishes to occur in increased numbers. Larvae of *Chironomus plumosus* (bloodworms) appear within two or three months; these are followed by the larvae of Corethra and Procladius (midge) and after four or five years by Hexagenia nymphs. The appearance of these is correlated with large amounts of plankton and its detritus. Some may await a certain accumulation of the latter in the mud, and some the presence of other animals. Coincident with the Hexagenia nymphs, sphaerids and mussels usually have appeared and are nearly half-grown by the time the bottom communities have developed this far. (The development is illustrated in Fig. 71.) The work of Behning (1928) indicates similar communities in the Volga, but the taxonomic composition is different.

Faciations of the Climax. The communities of medium and large rivers differ somewhat from those of the small ones, which for convenience are considered as typical. There has been no extended study of this type in rivers of various size, but a gradual change takes place between essentially equivalent species, especially in regard to fish dominants and bottom subdominants.

DOMINANT FISHES

a. Occurring in dominant abundance only in *medium and large* rivers:

Polyodon spathula (Walb.) Food, plankton; reaction, plows bottom	Spoon-bill cat
Scaphirhynchus platorhynchus (Raf.)	Shovel-nosed sturgeon
Ictiobus urus (Ag.)	Mongrel buffalo
Ictiobus bubalus (Raf.)	Small-mouthed buffalo

b. Increasing in abundance as the larger streams are approached:
(For equivalent species see list for small-river climaxes)

Dorosoma cepedianum (Le S.)	Gizzard shad
Ictiobus urus (Ag.)	Mongrel buffalo
Ictiobus bubalus (Raf.)	Small-mouthed buffalo
Opladelus olivaris (Raf.) (60 lb.)	Mud cat
Ictalurus furcatus (C. & V.) (150 lb.)	Blue cat

LAKE CLIMAXES

These climaxes are found in the largest lakes, such as the Great Lakes of North America, including Lake Superior, Michigan, Erie, Ontario, etc. (Rawson 1928, 1930), Lake Baikal, Leman, and others of comparatively large size.[1] These lakes have sufficient circulation to prevent chemical stagnation and to maintain a bottom primarily of silt (terrigenous), as well as sufficient depth and area to support numbers of fishes of the types described as river dominants and for a large pelagic assemblage.

The Great Lakes have been too little studied quantitatively to make possible any adequate description of their bottom communities. Lake Erie, however (Shelford and Boesel, 1939), offers somewhat of an exception, also the pelagic life has not been described from a community standpoint. In the plankton studies of Eddy (1927), the pelagic animals belonging properly with the plankton were not considered along with it.

The smaller lakes of Wisconsin (Muttkowski, 1918), Michigan (Eggleton, 1931, 1935), Germany (Lundbeck, 1926), Ontario (Rawson, 1928, 1930), etc., and most small lakes studied in Europe and America are early stages of land seres.

Dominants. These are all bottom feeders (Forbes and Richardson, 1909; Clemens, Dymond, et al., 1923).

Acipenser fulvescens Raf.	Lake sturgeon
Aplodinotus grunniens Raf.	Sheepshead
Haustor lacustris (Walb.)	Catfish
Carpiodes thompsoni Ag.	Lake carp
Coregonus clupeiformis (Mitch.)	White fish

Bottom Subdominants. Bottoms off sand-deposition shores, which characterize the south end of Lake Michigan, have an extremely limited fauna in 0–8 meters' depth, and communities hardly exist. Bottom conditions are very unstable, as the sand is constantly shifting. In water of 8 to about 35 meters' depth in Lakes Erie, Michigan, and Ontario, a community dominated by snails and sphaerid bivalves occurs on a stable bottom composed of fine sand and mud and some organic detritus. In Lake Michigan, abundant individuals of two to four species of Amnicola, two or more of Valvata, and five to ten of Sphaeridae occur together, some of the latter extending down to about 100 meters or below. Leeches and worms of the genus Limnodrilus are associated with Mollusca but extend more deeply, and crayfishes are of common occurrence (Shelford, 1913, *a*; Adamstone, 1924). Midge larvae occur in much shallower water and also extend to considerable depths. This community gradually thins out toward the

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[1] There is much literature on some of the large lakes, but very little concerned with communities.

shifting sandy shores and toward deeper water. A similar assemblage occurs in Lakes Erie, Ontario, and Nipigon, but with nymphs of Hexagenia added (Adamstone, 1924; Adamstone and Harkness, 1923).

Influents. In the pelagic layer which includes plankton, the following fishes are important because of their destruction of other fishes and invertebrates:

Lota maculosa (Le S.)	Burbot or ling
Cristivomer namaycush (Walb.)	Great Lake trout
Leucichthys artedi (Le S.)	Cisco

The waters of the Great Lakes support a luxuriant plankton. Eddy (1927) has recently studied that of Lake Michigan and found a number of the important species to be the same as in mature rivers. The large lakes contain several species of fishes, such as the whitefish, which are pelagic in their young stages but bottom feeders as adults.

Dominance of Lake Fishes. The phenomena are similar to those of a river. Evidence of the dominant character of the sucker is given by Ricker (1932), who stated that this species (*Catostomus commersoni*) reduced and removed Chara beds from a certain Ontario pond. The number of trout were diminished in the pond by the destruction of the Chara, which supported trout food (see page 301). Chara has some tendency to grow locally in depressions at less than 25 meters in Lake Michigan (Ward, 1897). Its extensive growth would eliminate the sphaerid community, destroy much of the fish-breeding grounds, and thus change the character of the community (see also Baker, 1916, 1918, 1922, and 1928).

Stream Habitats and Their Communities

Rapids usually alternate with pools and may be intermittent, especially in the earlier stages and in climates with dry seasons. Wherever the habitat is stable for a considerable period, definite communities tend to develop. As a stream ages, a series of communities pass a given point, much as a series of terrestrial biomes passed a point near the Ohio River with the retreat of the icesheet. In the case of the stream, invasion and succession take place, but the larger phenomenon is the migration of a series of communities over the same ground. In the process described as physiographic succession, the habitats are frequently denuded by flood before the baselevel is reached (Shelford, 1911, *a–e*). In each one of these denuded stages, a community develops to a point that appears to have some permanency, only to be swept away again (cf. Moffett, 1936).

The different habitats in a small-river system flowing through an area without rock outcrops, such as characterize many of those in the eastern portion of the Mississippi Valley, comprise the following, in the order of importance:

1. Mud-bottomed pools.
2. Shifting sand-bottomed pools.
3. Semi-pools with gravel bottoms.
4. Coarse-gravel and rocky rapids.

Farther west on the Great Plains, sand bottoms predominate (Jewell, 1927), while in hilly and mountainous regions, rapids with larger rock and gravel-bottomed semi-pools are typical. Obviously, the character of the underlying rock determines the quality of the bottom material and the degree of benching. This results in the alternation of deeper and shallower water with corresponding differences in rate of flow.

In dealing with the community history of a stream, its development as discussed by Adams (1901) and by Shelford (1911, *a–e*) is a source of confusion rather than a help toward clarification of biotic succession. There are, however, two community types that are recognizable as distinct, namely, those of mud-bottomed pools and swift water with rock bottom. The well-known distinctive taxonomic composition, as well as its brief development, makes the swift-water community stand apart sharply from the climax on mud bottoms.

Swift-water Community. The rapids community of streams in the Mississippi Valley occurs regularly on rocks, usually covered by *Cladophora glomerata* (Fig. 72). Hydropsyche (caddis fly) larvae are commonly of outstanding abundance; they spin Cladophora threads together, making a mat over the rocks or forming the small stones into cases. Among the stones are darters of the family Etheostomidae (one or more species, such as *Nanostoma zonale* [*Cope*], *Oligocephalus coeruleus* [Storer], and *Catonotus flabellaris* [Raf.], or the like, and sucker-mouthed minnows such as *Phenacobius mirabilis* [Gir.]). Usually crayfishes of the genus Cambarus are present, though the species differ from place to place. Mayfly numphs (Heptageninae) are very common, clinging under stones; less abundant in the same position are damsel-fly nymphs (Argia), stone-fly nymphs (Perla), and also dobson larvae (Corydalis), while a snail (Goniobasis) is often abundant on rocks. The rapids of the major streams contain some of the larger fish, such as the hog-sucker (*Catostomus nigricans* Le S.), and a few insects likewise. The rock and gravel shores of large lakes may have somewhat similar communities

(Krecker and Lancaster, 1933; cf. Needham, 1901; Needham and Christenson, 1927).

Although the development of this community has been observed but little, it is evident that it takes place very rapidly in denuded areas through invasion (*a*) by individuals that have lost attachment farther upstream, (*b*) by the deposition of eggs (aquatic insects) or (*c*) by movement upstream, as in the case of fishes. Invasions by the third method have been especially noticeable following floods in small tributaries ordinarily intermittent. The rapids in these acquire a large part of the prevalents of the swift-water community during two seasons of continuous flow in a rainy period. However, these prevalents do not have the characters of dominants for the following reasons:

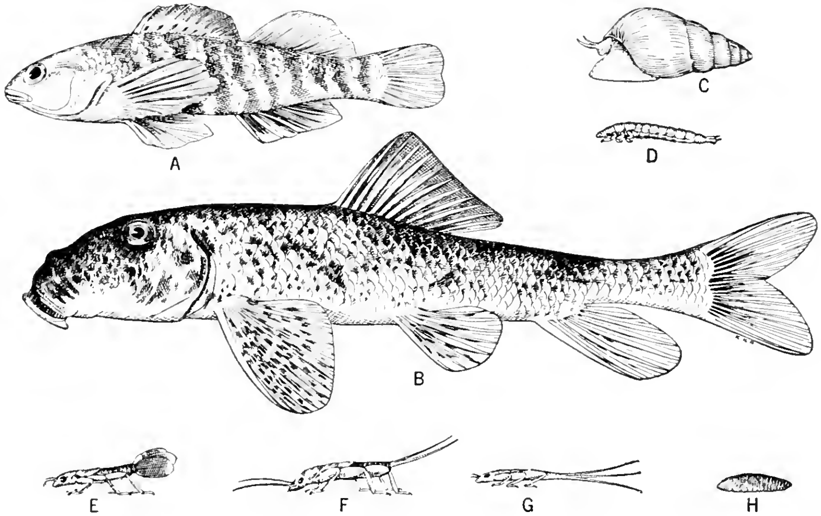

Fig. 72.—The constituents of a rapids community. Figs. A–H, general form of rapids animals. Drawn on the same scale; all about natural size; seen from the side slightly above. A, the rainbow darter (*Oligocephalus coeruleus* Stor.); B, a third-grown hog-sucker (*Catostomus nigricans* Le S.); C, snail (*Goniobasis livescens* Mks.); D, caddis worm (*Hydropsyche*); E, damsel-fly nymph (*Argia* sp.); F, stone-fly nymph (*Perla* sp.); G, may-fly nymph (*Heptageninae*); H, water penny (*Psephenus* sp.).

1. They do not control the habitat, but modify it only slightly.
2. The control is primarily by physiographic forces.
3. The different species are not dependent upon one another since they neither render conditions more suitable for other or-

ganisms nor maintain conditions suitable for themselves. They are neither climax nor subclimax dominants. They are comparable to lichens on granite rock, though far less effective.

Comparison of Aquatic Communities. The habit ratios based upon species of animals outstanding in importance for the rapids and for the muddy pool community in a stream in central Illinois are shown in Table 12.

TABLE 12

		Community	
		Pool Climax	Rapids: Quasi-climax
		Hexagenia-Ictiobus-Elodea	Hydropsyche-Etheostomidae-Cladophora
Life Habit	No. Species	Life-habit Ratio	Life-habit Ratio
Clinging to rock	4	0	67%
Resting between rocks	2	0	33%
Burrowing in mud	4	30%	0
Resting on or disturbing mud	5	39%	0
Resting in vegetation	1	8%	0
Floating—swimming	3	23%	0

It is difficult to experiment with the animals of most communities, but the swift-water community lends itself to such treatment. Shelford (1914, *a*) found that it is characterized by two common reactions: (*a*) marked positive response to a comparatively strong water current, (*b*) positive response to rock as opposed to sand or other bottom materials. This was so striking as to constitute a life-habit characteristic of the community, which was consequently termed rheotactic. This characteristic is easily illustrated by experiment on the common species listed above as belonging to the rapid-water community, such as Etheostomids, Hydropsyche, Heptageninae, Perla, and Corydalis. These forms practically always show an 80 to 100 per cent positive response to a fairly strong water current and a similar one to large stones as opposed to sand. In the study of current, it is necessary to consider only those individuals actually in it, and this may be accomplished by omitting all those resting in contact with objects against which the current strikes at right angles. Many will show the clinging reaction as an expression of their choice of large rough rock surfaces.

OTHER COMMUNITIES

Intermediate between the swift-water communities and the pool climax are various others, chiefly on sand and gravel bottoms. Those on gravel partake of the general life form, life-habit characters, and, to some degree, of the taxonomic composition of those of the rapids. Sand communities resemble the pool climax. A type of community noted by Gersbacher (1937) on sand is characterized by a predominance of various sphaerids and fresh-water mussels. It lacks sharp distinction from the pool community and its developmental stages, and more study is required to determine its rank. Obviously, animals do not dominate the sand habitat in the way they do in the baselevel mud-bottomed pools (cf. Reighard, 1908).

The relation of stream to lake communities is made evident in glaciated areas such as northern Illinois and Wisconsin. Here the very sluggish rivers connect lakes which are in several cases merely broad and sometimes irregular expansions of the river itself. These rivers sometimes contain the climax community, but vegetation grows in them and often covers much of the bottom, which contains much organic matter. Dr. D. H. Thompson (Illinois National History Survey) has observed that during the recent drought period vegetation appeared in the Rock River, which includes areas of climax. He believes this is due to lower turbidity resulting in better light conditions. In the Fox River (at Cary, Illinois), vegetation occurs along the margins and the climax at points between the vegetation and the center of the stream. In other words, there is a tension between land and water climaxes which manifests itself in these wide sluggish waters.

Streams are in constant state of change from season to season or from year to year, except in the physiographically stable old age or baselevel condition or in other conditions approaching this, due to retarded flow.

The small unstable streams likewise show communities in which development may be traced for a time, but which are soon destroyed by flooding and thus rendered difficult to study. The literature dealing with the stable or climax communities is cited in connection with the description of them on pages 305 to 307 (see Cole, A. E., 1932).

Fresh-water climates and climaxes have only very recently been recognized. One of the earliest ecological classifications of communities divided them into edaphic (including water) and climatic. The local character of the edaphic communities and the very extensive character of the climatic ones was stressed very early. In dynamic ecology, the edaphic communities become seral stages of the climatic community or climax.

The communities of small bodies of water, such as ponds, small lakes, oxbow cut-offs of streams, and swamps, are merely seral stages leading to the climax of the region. They illustrate numerous routes by which such bodies of water may pass to the appropriate climax. Since space permits the consideration of only general principles governing the terrestrial, marine, and fresh-water climaxes, it is not practicable to discuss the hydroseral stages of the terrestrial climaxes.

Limnologists have not made use of these distinctions, which are essential to dynamic ecology. The voluminous literature of this field deals largely with lakes and ponds, which are early seral stages of the deciduous and coniferous areas of North America and Europe (Welch, 1935:306). The nomenclature is detailed and characterized by many adjectives. The large dictionary of terms prepared by Naumann (1931:7–776) indicates the extent of the investigations in this field (cf. Ekman, 1911, 1915; Needham and Lloyd, 1916; Shelford, 1918, *c*; Borner, 1922; Lundbeck, 1926; Thienemann, 1926; Carpenter, 1928). The work on streams has been less extensive, but is treated in the general works cited.

CHAPTER 10

MARINE BIOTIC COMMUNITIES

INTRODUCTION

The marine communities possessing the qualities of land climaxes appear to occupy the greater part of the surface of the globe. Obviously, the corals and certain coralline algae produce reactions upon the habitat equal to if not greater than those of forest trees, and doubtless of greater duration in any particular place and set of conditions (cf. Herdman, 1906; Bigelow, 1930).

Several types of communities occur in the sea. Certain communities are commonly considered as dependent upon the character of the bottom, but it has been pointed out (Shelford et al, 1935) that these are frequently more closely related to the physiographic forces than to the bottom materials. The amount of circulation and the force with which it acts are of great importance in determining the entire marine climatic regime and may sometimes overshadow bottom conditions.

The tidal community on hard bottom is distinctly marine and has no counterpart in fresh water. It is dominated by acorn barnacles and mussels in the Northern Hemisphere, and by mussels, barnacles, tunicates, and oysters in the Southern Hemisphere (Oliver, 1923). This type of community occurs between the average of the lower half of the low tides and of the higher half of the high tides; it has no counterpart on muddy and sandy shores (cf. Davenport, 1903; Southern, 1915).

Subtidal communities of muddy and sandy shores or clam communities on gently sloping beaches do not reach as high above low tide as do the tidal barnacle groups. Clams usually extend about two-thirds of the way between the low tides and the high tides. This distinction prevents confusion and serves to emphasize the fact that the subtidal community reaches up into the tidal area. The areas farther landward from clam beaches on low depositing shores commonly represent seral stages to land occupied by halophytes mixed with other land plants, or bare sand beaches. On sandy shores protruding rocks are occupied by tidal communities.

The great oceanic or pelagic community is similar in some respects to that of large lakes like the Great Lakes of North America. However, it is infinitely richer in diversity of size and form of animals and in taxonomic groups represented.

Hydroclimate. The conditions of existence in the sea differ from those of fresh water in certain important respects. The occurrence of tides is most important in producing circulation; otherwise they have little or no effect on the pelagic or on bottom communities outside the intertidal area. The most important difference in climatic conditions lies in the presence of a large amount of salt, principally sodium chloride, and the occurrence of sulphur compounds in the form of hydrogen sulphide, sulphurous acid, and colloidal sulphur, which often have important relations to aquatic life. The salt present increases the density of the water, and hence variations in salt content are credited with playing a very important role in the climate of the sea.

The hydroclimatic factors (Wasmund, 1934) are greatly modified by reactions. Greater density of life in the sea produces far greater reaction on the habitat in the way of light reduction, chemical changes, etc., than in lakes. These bioclimatic factors are so important and generally present as to be essentially a part of the hydroclimate itself. The great depths of the ocean and the lack of rooted or attached plant life except at irregular intervals along the shore also produce differences between fresh and salt water (cf. Harvey, 1927; Knudsen, 1922).

PELAGIC COMMUNITIES

The communities of the sea have been so incompletely studied that it is difficult to outline their arrangement in any adequate manner. On account of their outstanding peculiarities, it seems best to begin with pelagic communities. Only those of the North Pacific are familiar to the writer, while most of the work has been done on the North Atlantic. The discussion of marine pelagic communities from a biotic viewpoint has not often been attained, but Murray and Hjort (1912) and Bigelow (1924) have made progress in this direction (see Gran, 1912, 1931; Allen, 1921–1932).

Pelagic Communities of the Enclosed Waters of the North Pacific

The pelagic communities include the plankton or floating organisms taken together with the swimming animals or nekton. The separation into those two groups as a basis for investigation has led to an unfortunate failure to recognize the pelagic community proper. The general relations of the various elements of the pelagic community may be brought out for the waters inside the south end of Vancouver Island. This description is, however, handicapped by a lack of information on the food habits of the nekton.

Plankton. Studies of the diatoms of this community have been made by Gran and Thompson (1930) and Phifer (1933, 1934); the Protozoa have been treated by Eddy (1925, *a*), and the Crustacea by Campbell (1929, 1930). The last has found all types of smaller plankton organisms most abundant at a depth of about 4 meters, including copepods, peridinia, tintinnids, and diatoms. Phifer (1933, 1934) reported diatoms most abundant at 10 meters in the Strait of Juan de Fuca. The depth of maximum abundance differs greatly in various localities and on different dates, but is probably always in accord with physical conditions. In July, 1928, two series of four simultaneous water-bottle samples, separated by 20 minutes at slack tide, were taken over each of the two major bottom communities (Shelford et al., 1935:250). Over the sea urchin-triton snail community (Strongylocentrotus-Argobuccinum biome) which usually occurs on relatively hard bottoms, counts by Gran of collections distributed from 1 to 225 meters showed that the maximum abundance of diatoms was at 20 meters. They were about 1/10 as numerous at the surface and 1/16 as abundant at 225 meters as at the maximum. The plankton over a clam-worm community (Pandora-Yoldia biome) at 28 meters' depth, usually on soft bottom or fine mud, was sampled in a similar manner within an hour. Diatoms were about 10 times as abundant as over the sea urchin-triton community, and the maximum was at 10 meters instead of 20 meters.

An examination of the animal plankton taken in the net-haul made at the same time from bottom to surface over the clam-worm community yielded a few copepods, rotifers, and tintinnids, very many dinoflagellates, and various larval stages. Over the sea urchin-triton community, it differed chiefly in the lack of dinoflagellates and in the presence of a greater variety of the larval stages. A few Sagitta were taken from the deep water here, but none over the Pandora-Yoldia community. Jellyfishes abundant during the summer months throughout both the inner and outer waters are: *Aequorea forskalea* (P. and S.), *Phialidium gregarium* Haeck., and *Thaumantias cellularia* Haeck. These, together with less abundant species of Sarsia, Stomotoca, Polyorchis, and the common ctenophores (Mnemiopsis and Pleurobrachia), make up a great part of the volume of the plankton of midsummer. There is a large seasonal element including many eggs and larval stages of invertebrates and a few fishes (Bovard and Osterud, 1919; Weese and Townsend, 1921; Strong, 1925).

Nekton. The larger animals with effective swimming powers in this area consist chiefly of fishes and mammals (Shelford and Powers, 1915; Shelford, 1918, *a*; Powers, 1921).

FISHES

Culpea pallasii (Cuv. & Val.)	Herring
Hypomesus pretiosus (Gir.)	Surf smelt
Thaleichthys pacificus (Rich.)	Eulachon
Oncorhynchus nerka (Walb.)	Sockeye salmon, anadromous
Oncorhynchus kisutch (Walb.)	Silver salmon, anadromous
Oncorhynchus gorbuscha (Walb.)	Hump-back salmon, anadromous

MAMMALS

Orcinus rectipinna (Cope)	Killer whale
Rhachianectes glaucus (Cope)	Gray whale
Globicephala scammonii (Cope)	Pacific blackfin
Phocaena phocaena (L.)	Porpoise

The killer whale appears to be most abundant and was frequently seen in the San Juan Channel; the blackfin was noted less often. Originally, gray whales congregated in muddy bays and came to the surface daubed with bottom mud (Scammon, 1874).

Coaction and Reaction. The food coactions among North Pacific plants and animals are little known, though the work of Lebour (1919–1923) on the North Atlantic makes possible inferences as to the food of plankton animals and young fishes in general. The food habits of only a few adult fishes have been studied. The killer whale is known to prey upon other whales and fishes, salmon especially being mentioned by Scammon (1874); the same author states that the blackfin feeds upon squids and fishes. The reaction of pelagic organisms in shutting out much light from the waters below has already been noted (Shelford and Gail, 1922; Shelford, 1929, *b*). In addition to this, plankton organisms, sinking to the bottom at death, absorb oxygen and produce carbon dioxide (Atkins, 1922), as well as sulphur compounds and organic mud, having a profound effect upon bottom conditions, especially in quiet water.

Physiological Characters. The independence of the bottom and shores is striking. Most of the work on physiological characters has been concerned with fishes, which are very sensitive to differences in the character of the water. The herring responds to variations of 0.1° C. in temperature and is sensitive to changes of 0.1 *p*H. The resistance of the pelagic herring and surf smelt to carbon dioxide was rated as 10 and 8 respectively, while the viviparous perch, an inhabitant of shore vegetation, had a value of 25 (Shelford, 1918, *a*). Based on sulphur dioxide, the pelagic herring was rated at 10, the perch at 21, and the bottom flounder at 1100.

Pelagic Communities of the North Atlantic

The only modern consideration of pelagic communities in which the larger organisms and plankton are treated together as a unit is that represented by Murray and Hjort (1912:101–108; 617–704).

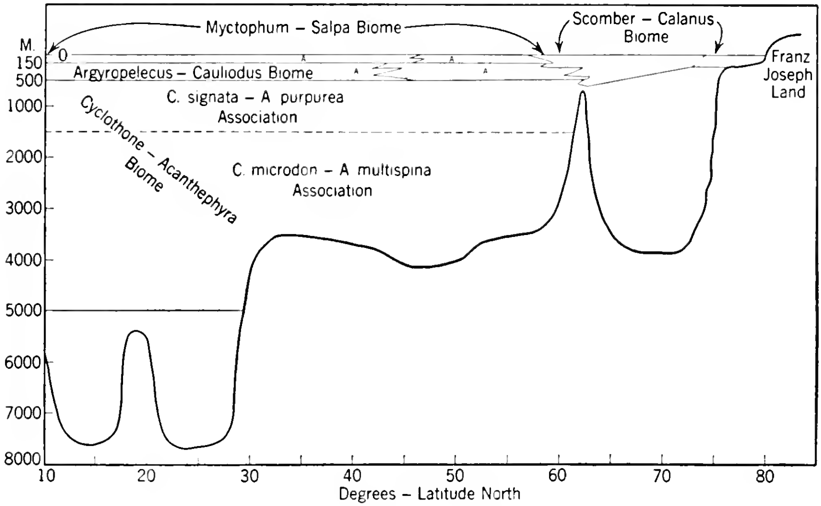

Fig. 73.—Diagrammatical vertical section of the North Atlantic with the several communities described by Murray and Hjort indicated, arranged so as to follow the practice in terrestrial communities. The depths to which the communities occur probably decrease from the equator to 60° N., owing to the difference in the penetration of solar radiation, but this is not indicated.

These writers describe various communities of the pelagic waters of the North Atlantic which may perhaps be interpreted as biomes as suggested below. Furthermore, each appears divisible into two or more associations based upon the abundance of certain fishes and other larger animals that may be regarded as making the nearest approach to dominants. The boundaries are apparently less definite than those between major land communities, but this is by no means certain, as the facts are much more difficult to ascertain. The arrangement of these (following Murray and Hjort) is suggested in Fig. 73. While the small amount of observation renders the classification more or less hypothetical, it serves to illustrate probable comparisons with land communities. To this end, units have been renamed according to the plan followed for the terrestrial and fresh-water communities, and suitable technical names are carried in parentheses.

Slenderfish-red prawn Community (Cyclothone-Acanthephyra Biome)

(See Murray and Hjort, Bathypelagic Communities, also Plates I and III, following page 664.)

This lies south of the Wyville Thompson Ridge at a depth of 5,000 to 500 meters. It is characterized by slender dark-colored fishes of which Cyclothone is predominant, deep-red prawns of which those of the genus Acanthephyra are outstanding, and some species of peteropods, squids, etc. This community appears to be divisible into two lesser communities (associations), each characterized by a different species of Cyclothone and Acanthephyra. The young of various of the fishes, especially Cyclothone, occur near the surface, forms intermediate in size in the next community below, and the adults in the deep water. Beebe (1929) and Beebe and Hollister (1930) noted Cyclothone in great numbers off the Bermudas from the bathysphere but mainly in the community above this one. They also record scarlet crustaceans of the genera Notostorium and Gnathophansis, and an eel of the genus Serrivomer (Beebe, 1932, *a*).

Telescope-eyed Fish Community (Argyropelecus-Chauliodus Biome)

(See Murray and Hjort, Fig. 454, page 603, and 458, page 604.)

This community lies above the one containing the red prawns in 500–150 meters. The telescope-eyed fish (Argyropelecus) occurs in large numbers, a fact recorded by both Murray and Hjort and by Beebe (1929, 1932, *a*, *b*). According to the former (page 631), the characteristics of the predominants are as follows: "The fishes are as a rule laterally compressed, with a mirror-like silvery skin; when colored, the back is generally blackish brown, and the resplendent mirror-like sides of the body are blue or violet. The eyes are very large, very often telescopic, and the body is usually provided with a number of light organs varying in size. . . . All the silvery fishes of the region between 150 and 500 meters are small, and the same remark applies to the other organisms of the community. These consist almost exclusively of small crustaceans (copepods, ostracods, amphipods), sagittids, pteropods, and small medusae. Besides these, we commence to find larvae of squids and fishes, which, however, become more numerous in the layer above 150 meters." Beebe and Hollister record numerous shrimp jellyfishes and fishes in great numbers, as seen from the bathysphere.

Two associations are suggested for this community. One, the southern, characterized by fishes of the genera Valenciennellus and Ichthyococcus; another, more northerly, typified by *Stomias boa* (Murray and Hjort).

Fish-Tunicate Community (Myctophum-Salpa Biome)

This community occurs from 0 to 150 meters and lies south of the Wyville Thompson Ridge. It is characterized by numerous animals such as Foraminifera, Radiolaria, Copepoda, and pteropods, and microscopic plants, chiefly diatoms which are most abundant at 10–20 meters and scarce below 100 meters (Gran, 1912). The larger predominant animals include jellyfishes, the Portuguese man-of-war (Physalia), quantities of compound tunicates (Salpa) (cf. Brooks, 1893) and numerous scopelid fishes, e.g., seven species (Myctophum) which are of outstanding importance. The animal grouping also includes cephalopods belonging to seven genera. Sperm whales and certain right and hump-back whales occur. The color characteristics of the community are illustrated by "the minute young of Scombresox living at the very surface, the sides of which are mirror-like, while the backs are intense blue. One group containing seablue forms is represented by the flying-fish. The pilot-fish are also blue, but with some darker transverse bars. In the surface layers most animals are colorless. The eel larvae (Leptocephali) are indeed so transparent that one can only see their small black eyes; even their blood is transparent and devoid of haemoglobin" (Murray and Hjort, *loc. cit.*, 669–670).

Mackerel-Calanus Community (Scomber-Calanus Biome)

A pelagic community of rather wide distribution in the colder waters of the North Atlantic is suggested in Bigelow's account (1924, *a*, *b*) of the plankton of the Gulf of Maine and the work of Murray and Hjort on the Norwegian Sea. It is characterized by a great abundance of *Calanus finmarchicus* as the most abundant and uniformly distributed copepod associated with other copepods, Sagitta, jellyfishes, etc., mackerel (*Scomber scombrus* L.), herring (Culpea species), and whales of the genera Balaenoptera and Megaptera, which feed upon fishes and pelagic crustaceans. This community appears to exist in the upper 150–200 meters. It illustrates the principle found to characterize terrestrial communities by showing a wide distribution of some of the predominants which bind together two associations, one present in the Norwegian Sea and another well represented in the Gulf of Maine (cf. Hjort and Rund, 1929; Fuller and Clark, 1936).

Herring-Calanus Community (*Clupea-Calanus Association*)

This is also well represented in the Norwegian Sea; the species with outstanding abundance of individuals are Calanus, Thysanoessa, the mackerel, herring, and certain whales, all common to both the Norwegian Sea and the Gulf of Maine. In addition, there are present the sprat (*Clupea sprattus*) and salmon (*Salmo trutta*), numerous copepods and other crustaceans, as well as certain pelagic Mollusca, fishes, and whales that do not occur in the Gulf of Maine (Murray and Hjort, 1912; Bigelow, 1924, *a*).

Menhaden-Calanus Community (*Brevoortia-Calanus Association*)

The association found in the Gulf of Maine contains the mackerel (*Scomber scombrus*), the copepod (*Calanus finmarchicus*, Gun.), and several other abundant species that serve to bind the two associations together in one biome. Some of the other species characteristic of the association are *Sagitta elegans,* certain euphausiid shrimps (species of the genus Thysanoessa), the menhaden (*Brevoortia tyrannus* [Latrobe]), and the North Atlantic right whale, together with many others less prominent. In his exhaustive treatise on the plankton of the Gulf of Maine, Bigelow (1924, *a*) brings out many features that illustrate the character of dominance and the coactions in pelagic communities. Clark (1933) has discussed light relations and distribution of plankton down to 114 meters.

NATURE OF DOMINANCE IN THE PELAGIC CLIMAXES

The oceanic communities present a distinct aspect because of the remarkable adaptations to pelagic life exhibited by the organisms characterizing the different depths. Their permanency is no doubt greater than that of any of the land climaxes. Two or three important questions arise with regard to the role of microscopic plants and animals, and the nature of the control exercised in the habitat by the organisms. The effect of organisms near the surface on the conditions surrounding those deeper in the water is important and has already been discussed.

Bigelow's studies (1924, *a*) and those reported by other investigators and summarized by him bring out some features of dominance in pelagic communities in connection with the whales. The whalebone whales are the largest constituents of the biome in the Gulf of Maine; their food consists of copepods and euphausiids (schizopods), supplemented with fishes. In the long run the crustaceans are apparently of greatest importance in most cases (Brooks, 1893; Clark, 1933 *a*, *b*, 1936). The food is strained from the water by whales and by some fishes also, and Bigelow stresses the fact that the finer strainers are better adapted to the catching of small forms, and less effective in catching fishes, etc.

Bigelow further points out tendencies for particular consuments to seek certain types of plankton or nekton. The menhaden feeds on the unicellular algae (chiefly diatoms) throughout life. Copepods also feed on diatoms, and some other fishes subsist chiefly on Crustacea, chiefly copepods. Sagitta appears more important in reducing copepod numbers than fishes. These crustaceans are present in reduced number where Sagitta is abundant. He also states that certain ctenophores take nearly all living things that come in contact with them. Wherever these creatures abound, most of the small animals tend to be extirpated. On the other hand, ctenophores, themselves, are not eaten by larger animals.

The character of dominance, or in other words the control of the community by organisms, is puzzling. One may, however, venture to suggest that dominance by the copepod, *Calanus finmarchicus,* is indicated in the Gulf of Maine. It is present in outstanding quantity, being able to replace population losses so rapidly as to supply the greater part of the food for fishes and many other forms both large and small. It is thereby assumed to serve as the basis for much of the pelagic life of the bay (cf. Brooks, 1893). Again the menhaden may also be regarded as an important dominant because of its ability to utilize diatoms, as well as by reason of its great abundance.

The wide distribution of the microscopic plants and the small animals that make up the smallest constituents of plankton, and the relatively non-selective manner in which they are taken by important dominant organisms such as Calanus, hardly puts them in the dominant class. They are, however, of fundamental importance as the basis of the food supply of the entire group of pelagic biomes, and constitute a sort of universal mass of food materials for such large crustaceans, mollusks, fishes, etc., as probably may properly be considered as the dominants of pelagic communities.

The bathysphere observations of Beebe (1930, 1932, *a*, *b*) indicate that pelagic animals are far more numerous than was formerly supposed. Such species of fishes as constitute the genera Cyclothone, Stomias, Chauliodus, and Argyropelecus appear to be voracious feeders in the oceanic communities south of the British Isles, while squids and the better-known pelagic fishes operate in a similar manner in the Norwegian Sea. Dominance in pelagic communities appears to depend upon superior fecundity and numbers, as well as greater ability to hunt or strain out and devour other animals, as well as plants. The principal larger dominants appear to be partially non-competitive in their food relation, which suggests a much finer adjustment of the constituents to one another than is found in terrestrial communities.

Ecotone between Pelagic and Bottom Communities

A goodly number of bottom animals swim about, entering the pelagic conditions just as the species independent of the bottom and shore do, in a manner comparable to that of birds, bats, insects, etc., in land communities. Some of these motile forms roam over two or more major communities (biomes), using one for breeding, and another for feeding and other activities of a non-breeding portion of the year. The fishes have a mobility of about the same magnitude with reference to major communities as do birds and a few of the largest mammals, while bottom crustaceans, mollusks, echinoderms, etc., have a power of movement roughly equal to that of the smaller animals (cf. Hutchinson, 1928; Hutchinson, Lucas, and McPhail, 1929; F. S. Russell, 1928–1932).

The ecotone between the benthic communities of the continental shelf and the pelagic ones is also quite evident. It is characterized by fishes and crustaceans dividing their time between the bottom and the water above, though primarily dependent upon the bottom. Furthermore, the pelagic community, as the enclosed waters are approached, presents a series of communities characterized by the loss of oceanic species and the addition of larval stages of benthic animals and adult and post-larval fishes of the continental shelf.

COMMUNITIES OF THE SEA BOTTOM

Sea-bottom communities include both sessile and motile animals, together with plants. Unfortunately, like pelagic communities, these three groups have been considered separately and the community unity and many of the coactions have been passed over or treated in an isolated manner. The sessile, sedentary, and slow-moving invertebrates of bottom communities have commonly been roughly subdivided into three life-habit and life-form groups. The most conspicuous of these types is that attached to, or resting upon, the substratum, as exemplified by barnacles, gastropods, large echinoderms, and mussels on rock or other hard bottom. These may be called barnacle-gastropod communities. The second life-habit type burrows into soft bottom and includes clamlike mollusks, worms, and a few wormlike echinoderms.[1] These may be called bivalve-annelid communities. A third type is represented by corals, especially those associated with coral reefs; the life forms of these resemble plants, as indicated by the term zoophyte commonly applied to them. The predominants of most communities thus combine two or more sedentary life habits and life forms with those of the strictly motile constituents.

From a physiological viewpoint, bottom communities are separable into two principal types: (1) those that do not tolerate exposure to the atmosphere and are practically always submerged in water, and (2) those that tolerate or require exposure to the atmosphere and occupy stable and usually hard substrata exposed to the full force of the air with each important fall of tide. The latter ordinarily became subtidal only locally, when under peculiar conditions of salinity or temperature (Huntsman, 1920). The former are divisible into two subgroups: (*a*) those whose habitat (tidal clam beaches) may be partially exposed to the atmosphere during low tides without exposing the community constituents, and (*b*) those that are always well below low tide.

Aside from the corals, the location and relation of the two remaining life-form types and the two physiological types are essential to an understanding of marine bottom communities in general. The physiological types are readily separated, superficially at least, into two categories, those requiring and those not requiring or tolerating rhythmic exposure to the atmosphere.

As noted above, strictly speaking, the (clamlike) bivalve-worm communities are never rhythmically exposed to the atmosphere with tidal changes. In the so-called clam beaches, both the bivalves and the worms are restricted to sands having a large water-holding capacity (Bruce, 1928). When the tide is out, they retract their fleshy organs and remain in the water held by the sand, and even if this water is partially withdrawn, they are not exposed to the sun and atmosphere. Those bivalve-worm communities that reach above the

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[1] The first two life-form types are respectively the "on fauna" and "in fauna" of Petersen. Unfortunately, in describing communities Petersen did not stress the motile influents. The term benthic is often applied to the species or communities living on or in the bottom, but it is not used here because it seemed confusing.

average low-tide line also extend several meters (8–10) below low tide (Petersen, 1918:18; Wisner and Swanson, 1935). They are essentially subtidal, as are all other described communities of this type.

The use of the term intertidal is misleading, as are most habitat designations for communities, as it implies that all aggregations observed between the tide lines are distinct communities, whereas this is not true. The barnacle-gastropod-mussel community might be called intertidal, but since it is evidently adjusted to, and probably requires, tidal rhythm it seems best to call it a tidal community. The primary division with which we have to deal is, however, the two life-form groups noted on page 323, which for convenience may be referred to as

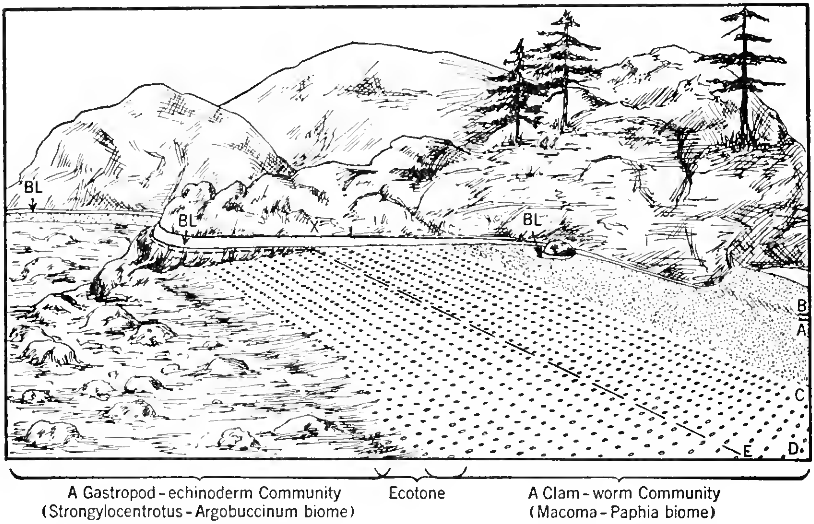

Fig. 74.—A diagram showing the relations of three major marine communities at the north shore of the Straits of Juan de Fuca in the northeast Pacific. Starting at the left the Strongylocentrotus-Argobuccinum biome has its upper limit above the level of the extreme low tides (*E*), and at the level the average of low tides (*D*) this boundary is very sharp. The Balanus-Littorina (*BL*) biome is differentiated between the mean of the lower tides (*D*) and the mean of the higher tides (*A*) but does not reach the mean of high tides (*B*). Toward the right, the Balanus-Littorina biome is bounded at its bottom by sand and its strip becomes narrower. The Macoma-Paphia biome reaches downward through about 8 meters with a wide ecotone between it and the Strongylocentratus-Argobuccinum biome. For convenience in making the diagram, it is shown as ending abruptly at a ledge of hard rock at about 6 meters. *C* indicates the upper limit of this community which is about half way between high and low tides, making it essentially a subtidal community and at average low tide only 1½ meters (*C-D*) of the 8 meter belt is exposed.

the barnacle-gastropod and the bivalve-annelid community types. The latter type, being subtidal, is not subdivisible, while the former is divisible into tidal and subtidal type (cf. Kirsop, 1922).

BARNACLE-GASTROPOD TIDAL COMMUNITIES

Wherever the substratum materials are not moved by wave action, and the area of the seashore alternately exposed and submerged by the rise and fall of the tide, a tidal community exists. Such communities appear to occur on all stable shores, except the icebound ones. They are made up of species tolerating or requiring exposure to the atmosphere at daily intervals. The tidal community proper is a barnacle-gastropod-mussel one, which in the Puget Sound region of the Pacific begins near mean low tide and reaches to a vertical meter or meter and one-half above the upper limit of the large bivalve-worm community. Its presence may be governed almost as much by water movement as by substratum, since mussels may form a bed in still water, or on the upper portions of a sand beach, and constitute a substratum for the attachment of barnacles. These two species may be followed by others and thus build up the entire barnacle-gastropod-mussel community. The general principles governing this community type may be illustrated in the North Pacific. The community has been sufficiently studied to show its climax nature, permanency, etc., and may be termed a biome.

Balanus-Littorina Biome

The most important dominants include three species of barnacles (*Balanus cariosus* [Pall.], *B. glandula* Darw., and *Chthamalus dalli* [Pil.]) and two species of mussels (*Mytilus edulis* L. and *M. californianus* Conrad). The gooseneck barnacle (*Mitella polymerus* [Sow.]) plays an important role in some parts of the community. A few others, such as the green anemone (*Cribrina xanthogrammica* Brandt), are local and less important. There is evidently competition for space among the dominants, for, when one is seated on a rock surface through some favorable condition, the others are excluded or may attach to the shells of the true dominants in sparing numbers.

The most characteristic motile forms are gastropods of the genus Littorina (*L. sitchana* Phil., *L. scutulata* Gould, and other species) and of limpets (*Acmaea digitalis* Esch., *A. cassis* Esch., etc.). The food relations of these are not well known but evidently are based upon microscopic plants and animals. Other mobile influents of irregular occurrence are gastropods of the genera Thais, Purpurea, and Amphissa, the first two of which feed upon barnacles locally and destroy considerable numbers.

Rhythmic migrants and ecotone species play a considerable role. The purple shore crab (*Hemigrapsis nudis* Dana), the place of which is taken by an equivalent species on the California coast, is significant. Several fishes, especially blennies such as *Xiphister mucosus* (Gir.) and *Epigeichthys atro-purpureus* (Kitt), have habits similar to those of the shore crabs. These motile species move into the community and feed when the tide is in and retreat as it falls, stopping under stones near the average low-tide line. They are not present on vertical cliffs, but are numerous on boulder and loose rock-covered slopes and are much more abundant in the more protected waters. A few ecotone species, unable to live long when exposed to air, inhabit the upper portion of the community below and the lower portion of the Balanus-Littorina biome. The starfish, *Pisaster ochraceus* Brandt, is an example; it may be very destructive of barnacles and mussels locally. Other less influent species such as the six-rayed star are more generally distributed.

Extent, Rank, and Boundaries of the Balanus-Littorina Biome. This community occupies an area bounded roughly at the lower limit by the mean of one-half the lowest tides in each month and at its upper limit by the average high tides. It is, therefore, from 2 to 4 meters wide (vertically) in the area studied. The difference in taxonomic composition between this and subtidal communities is sharp. *Balanus cariosus* and *glandula* cease to be present at a distinct boundary, as do all other important species. Subtidal barnacles are almost as definitely distributed and only occasionally overlap the lowest portion for a few centimeters. Rasmussen (in Shelford et al., 1935) found a subtidal barnacle overlapping the intertidal species in southern California, but waves and constant ocean swells furnish the probable explanation. Gislen (1930, *a*, *b*) indicates a similar possibility on the Swedish coast (cf. also Hewatt, 1937).

In a horizontal direction, the Balanus-Littorina biome is apparently widely distributed around the North Pacific. It is narrow because of its dependence upon the rise and fall of the tide, but the sharp difference in 1 meter of height within the belt occupied by the biome may easily be the equivalent of 1,000 meters on a mountain side. For example, in the month of August at 48° 30′ north latitude where the biome occupies 3 meters' vertical height, its lower edge is exposed to the air about 1 per cent and the upper edge about 96 per cent of the time; hence differences in physical conditions are very great within the biome. Its longitudinal extent is enormous, owing to the sinuate nature of coastlines, and is expressible in thousands of kilometers.

Equivalent communities occur along most of the coasts of the northern hemisphere, where not crushed off by shore ice. However, in spite of the general circumpolar occurrence of *Mytilus edulis* as a dominant, it is not possible to consider the North Atlantic and North Pacific communities as associations of the same biome (Appellöf, 1912; Pearse, 1913; Flattely and Walton, 1922; Beauchamp, 1923), although Newcombe (1935, *a, b*) has applied the same name. The other dominants are not the same, and the motile influents are all different. The two biomes, however, are of the same type and life form, and belong to a closely related group similar to that of the coniferous forest biomes of North America and Eurasia (see also Colton, 1916).

Associations. The Balanus-Littorina biome of the North Pacific is probably divisible into several associations, but only two appear to have been fully identified in the North Pacific. These are the *Balanus-M. californianus* association of the outer exposed shores and the *Balanus-M. edulis* association, usually in the more protected places. The former is the more definitely integrated and will be taken up first.

Balanus—M. californianus Association. This is best developed on the open exposed shores and headlands of the Pacific coast of the northern United States and southern Canada. *Mytilus californianus* Conrad and *Mitella polymerus* (Sow.) are the most characteristic species. There is a more vigorous growth of all species and commonly a sharp separation into vertical groupings, termed faciations. This is well shown in the results of a study on the west coast of Vancouver Island (Table 13), where the sessile and motile species are separated as two groups and arranged in the order of abundance.

The belts shown are often less definite, and occasionally all the species are mixed together. The variations are therefore properly called *faciations.*

Balanus-M. edulis Association. On the coast where extended studies have been made, this association occupies the more sheltered shores and waters of low salinity. *Mytilus edulis* and various species of Fucus are most characteristic; *Balanus glandula* plays a more important role. Cribrina, the green sea anemone, Mitella, the gooseneck barnacle, and the ribbed mussel do not occur. There are also marked differences in the less abundant species present. The arrangement of the various dominants in this association has been studied by Rice (in Shelford et al., 1935), who found in the case of barnacles that combinations of tides, cloudiness, temperature, rainfall, etc., over short periods control the arrangement of dominant species and the consequent local variations in community composition. Such local differences have no significance except in the light of knowledge of conditions at the time of setting and later survival. Other locations such as tide pools are controlled by conditions evident at the time and place. The usual rock-bottomed tide pool is an example that contains Balanus of two species, both species of Littorina, Mytilus, and limpets, as well as hermit crabs and snails that frequent the intertidal area

TABLE 13

FACIATIONS OF THE BALANUS-M. CALIFORNIANUS ASSOCIATION (SHELFORD, 1935)

The term faciation is applied to minor subdivisions of communities characterized by the presence or absence of some of the characteristic species. Here they occur in a very short vertical space.

	No. per Square Meter
Balanus-M. californianus Association (190 cm. wide):	
1. *Littorina-B. glandula* Faciation (20 cm. wide)	
Balanus glandula Darw., barnacle	2,400
Littorina scutulata Gould, snail	200
2. *Littorina-B. cariosus* Faciation (45 cm. wide)	
Balanus cariosus (Pall.), barnacle	3,140
Littorina scutulata Gould, snail	338
Acmaea digitalis umbonata (Nutt.) Reeve, limpet	70
Thais emarginata Desh., snail or whelk	38
3. Mitella-Mytilus Faciation (65 cm. wide)	
Mytilus californianus Conrad, California mussel	1,945
Mitella polymerus (Sow.), gooseneck barnacle	1,506
Balanus cariosus (Pall.), barnacle	1,363
Acmaea cassis Esch., limpet	380
Littorina scutulata Gould, snail	225
Thais emarginata Desh., snail or whelk	180
Red sea anemone	120
Acmaea digitalis umbonata (Nutt.) Reeve, limpet	110
Littorina sitchana Phil., snail	50
4. Cribrina Faciation (60 cm. wide)	
Cribrina xanthogrammica Brandt, green sea anemone	3,140
Mytilus californianus Conrad, California mussel	3,000
Chthamalus dalli Pils. 1,* small barnacle	3,000
Chitons	40
Pisaster ochraceus (Brandt), common starfish	6
Balanus cariosus (Pall.)	3

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* Chthamalus does not average this density over the area, but occurs in local clans having about this number per square meter.

and are regularly found out of water at low tide. In addition, there are fishes that stay near the water margin and hence are quasi-residents of the biome. To these are added a few subtidal animals, such as a Cucumaria, serpulids, and occasional snails and chitons.

Relationship of the Associations. Locally, the change from one association to the other may be found in passing from the outside of an open coast island to the inner or protected side. At a point on the south shore of the Strait of Juan de Fuca, all the principal species of both associations of the biome appeared on the same shore and were quite generally mixed together. This is the transition between the communities which may contain Mitella and *Mytilus californianus* as important general dominants, and those in which the former occurs in clans and the latter is not abundant. This arrangement simulates that of the dominants of the deciduous forest which occur together in certain parts of the Appalachians (Braun, 1935), though in other places they are separated into three associations: oak-hickory, beech-maple, and oak-chestnut, each covering a large area.

Community Development or Succession. Pierron and Huang (1926), in a brief study of the *Balanus-M. edulis* association, concluded that all the dominant species were present as juvenile stages on denuded rocks after a few weeks. An examination of pilings of known age in the *Balanus-M. edulis* area showed that the three principal dominants, *Mytilus edulis*, *Balanus cariosus*, and *B. glandula*, were all present on piles six months old. Piles one year old merely showed more and larger specimens of the same species. But Rice secured suggestions of non-survival of barnacles on planted rocks taken from land. These studies, however, were carried on only in the summer.

Hewatt (1935, 1937) has found true succession in the *Mytilus californianus* area, which he describes as follows: "The results of this investigation seem to indicate that ecological succession in the Mytilus habitat progresses in the following manner: (1) a clean area first becomes covered with a film of algae; (2) those forms which feed on this algal growth, such as the limpets, are the first animals to appear in the area; (3) during their respective spawning seasons, the mussels, gooseneck barnacles and rock barnacles attach themselves to the cleaned surface; (4) these sessile forms gradually come to occupy the greater part of the surface and make the habitat unfavorable for the larger specimens of limpets; (5) the limpets thus move to a higher zone in which the mussels and barnacles cannot exist. The upward migration of the limpets becomes quite evident soon after the appearance of the rock barnacles. The concentration of the larger limpets along the upper margin of the Balanus covered area forms a very obvious line." He further states that the climax is reached only after more than two and one-half years. The rapid replacement and overturn in the community constituents, however, stand out in contrast to terrestrial phenomena, and marked changes in the arrangement and abundance of certain constituents take place in short periods of time.

In the Bay of Fundy communities, the predation of the starfishes, sea urchins, and whelks limits the downward extent of the biome, while in the North Pacific physical factors appear to control the lower boundary. In the Bay of Fundy and Gulf of St. Lawrence, the corresponding biome or many of its constituents extend well below mean low tide (Mossop, 1922; Huntsman, 1924; Newcombe, 1935 *a*; see also Brandt, 1896).

Subtidal Barnacle-Gastropod Communities

Marine communities have been so little studied from a quantitative standpoint that only one example of this community has been even partially evaluated. It characterizes the sea floor about the San Juan Islands in Puget Sound and on the west shore of Vancouver Island. However, it is to be expected that it occurs over the continental shelf of the North Pacific in the clearer and more open waters. The prevalence of large echinoderms and snails has led to its designation as a sea urchin-gastropod community (Shelford and Towler, 1925; Shelford et al., 1935; Wisner and Swanson, 1935). Its succession, extent, etc., have been so little studied that it cannot be named with certainty.

Green Sea Urchin-Triton Community

(Strongylocentrotus-Argobuccinum Biome)

The most important sessile dominants are three species of Balanus, of which *B. nubilis* Darw. is the largest and most conspicuous, along with the sessile cucumber (*Psolus chitinoides* H. L. Clark), the rock oyster (*Pododesmus macroschisma* Desh.), and scattered brachiopods. These or similar species are always present; they do not, however, cover large areas of bottom to the exclusion of other species, as the tidal barnacles do. The control of the habitat and community is effected by slow-moving forms such as the sea urchins (*Strongylocentrotus drobachiensis* Müll, and *franciscanus* A. Ag.) which commonly are abundant, snails such as *Argobuccinum oregonensis* Red., *Trichotropis cancellata* Hinds, *Calliostoma costatum* Mart., and numerous crepidulas. Two or three sea cucumbers occur, the most noteworthy being the very large *Stichopus californicus* Ed., and pectens are often abundant.

The motile influents include fishes and crabs of the genera Hyas, Cancer, Oregonia, and shrimps of the genus Pandalus. Of the most regularly occurring fishes are the northern sculpin (*Icelinus borealis* Gibb), the giant sculpin (*Myoxocephalus polyacanthocephalus* [Pall.]), and the grunt fish (*Rhamphocottus richardsoni* [Gunther]). There are also various crabs, shrimps, gastropods, and starfishes, all of relatively large size.

Subdivisions. The major community is divisible into two subordinate communities in accordance with depth. The first ranges from the surface to 35–50 meters and the other from 35–50 to 225 meters, or even deeper.

Green Sea Urchin-Kelpcrab Community (Strongylocentrotus-Pugettia Association). The biome building influents already enumerated occur throughout and make up a considerable part of the population. The large echinoderms, *Stichopus californicus* and *Strongylocentrotus franciscanus,* are abundant and conspicuous in this association and very few in the one in deeper water. Two other cucumbers, several snails, and limpets occur in noteworthy abundance. Various fishes such as rock fishes (Sebastodes), several sculpins, but particularly the blennies, frequent the shallow waters. There are also numerous characteristic Mollusca. This association is characterized by algae, both red and green. They are usually irregularly distributed and do not have a marked effect on the animals present. They are hardly to be classed as dominants, but since they occur over only a portion of the bottom, the areas which they cover are best regarded as faciations. A faciation of Melanophyceae occurs between mean low tide and depths of 15 to 20 meters, and those of Rhodophyceae mainly between depths of 10 and 20 meters, only a very few small animals being characteristic of the latter. Other faciations occur where the bottom soil differs; thus on mud bottom two or more of the numerous Strongylocentrotus-Pugettia prevalents drop out and *Cardium californense* Desh., *Yoldia scissurata* Dall, and other species of similar habits take their places. The community otherwise retains its biome and association prevalents (see Andrews, H. L., 1925; and Andrews, F. B., 1925).

Green Sea Urchin-Cushion Starfish Community (Strongylocentrotus-Pteraster Association). This occurs below 35–50 meters and down to at least 225 meters; the species characteristic of the Pugettia association either become scarce or drop out. Several large showy echinoderms take their places; these are notably the cushion star (*Pteraster* *tesselatus* Ives), the rose star (*Crossaster papposus* [L.]), and the basket star (*Gorgonocephalus eucleмis* M. & T.). There are also characteristic species of brachiopods, hydroids, pecten, and of crabs and shrimps. The rat-tailed fish (*Asterotheca alascona* [Gilbert]) and Gilbert's sculpin (*Gilbertidia sigolutes* [J. & S.]) are perhaps most common among the several species here. The species listed on page 330 as characteristic of the whole major community are usually present in abundance.

Faciations and Relations. This association is characterized by a Modiolus faciation, which covers mud bottoms in the deeper parts of the continental shelf in which the hydroclimate is suitable for the biome (Strongylocentrotus-Argobuccinum). The shells form a hard bottom on which the other dominants may rest. Again some depressions may have been filled with silt and shells which support the dominants. A sere may be traced beginning with burrowers in the mud of such depressions. These are later smothered out by Modiolus, and this in turn eventually gives way to shells of dead animals which are used as a resting place for the biome constituents.

BIVALVE-WORM COMMUNITIES

Two major communities of the Puget Sound area in the North Pacific belong to this type; one is characterized by mollusks of the genera Macoma and Paphia and the other by two other mollusks belonging to the genera Pandora and Yoldia, the former being in shallower water than the latter. Both stand out in contrast to the barnacle-gastropod communities because of the less showy and generally smaller size of most of the constituents, as well as the striking differences in life form and life habit. However, neither has been studied sufficiently to be named with certainty. Communities of the same two types occur in the partially enclosed waters of both the North Pacific and North Atlantic. Petersen's Macoma community (Macoma-Mya biome) and the Macoma-Paphia community are of the same type, and the known facts regarding the two supplement each other (cf. Huntsman, 1918; Ford, 1923; Hunt, 1925; Stephen, 1931, 1933).

SHALLOW-WATER COMMUNITIES
(HABITAT PARTIALLY EXPOSED AT HIGH TIDE)

Macoma-Paphia Biome

In the Puget Sound waters (North Pacific), this biome is usually found well developed between 8 meters below and 1 meter above mean low tide (the tidal amplitude being 3 and 4 meters). There are about 2 meters of true ecotone between 8 and 10 meters' depth and the community thins out to nothing between 1 and 1½ meters above mean low tide. Clams of four species, *Macoma nasuta* Con., *secta* Con., *inquinata* Desh., and *Paphia staminea* Con., usually make up the great bulk of the population. The clam worm, *Nereis virens* Sars., is also a regular constituent. Several other species of bivalve mollusks always occur, but in varying numbers. The most important motile influents are several species of flounder (especially *Psettichthys melanostictus* [Gir.] and the tide-pool sculpin (*Oligocottus maculosus* [Gir.]) (cf. Fraser and Smith, 1928, *a*, b).

Two subdivisions or associations have been recognized, of which the Macoma-Paphia association fits the general description of the biome. The second association (Macoma-Leptosynapta) possesses the same constituents but in different abundance. The butter clam (*Paphia staminea*) is much less, the cockle (*Cardium corbis* Mart.) much more, abundant. The lugworm (*Arenicola claperedii* Lev.) and the wormlike cucumber (*Leptosynapta inhaerens* Ver.) take the place of various smaller worms of the other associations.

Both associations are characterized by eelgrass, usually in restricted areas representing depth belts. The eelgrass is quite important and supports algae, numerous crustaceans such as Caprella, large amphipods, isopods, and snails such as Haminoea and Lacuna, especially in the Macoma-Paphia association. In the Macoma-Leptosyapta association the additional species are more numerous, and in some cases sand dollars are abundant locally (Shelford et al., 1935). The importance of eelgrass has been brought out by Petersen and associates and will be discussed later.

The Pacific oyster evidently represents a fragmented faciation in the southern part of this community, which with overfishing was completely destroyed by the burrowing and earth moving of the large crustacean, Upogebia. The communities of the northeast Atlantic and adjacent Arctic which are similar to Macoma-Paphia community in life forms and position relative to tidal levels have been studied, but their rank in terms of biome and association can only be suggested and may prove incorrect.

Macoma-Astarte Community (Biome)

This is an arctic ocean community with relicts farther south which Spärck (1935), who calls it the *Macoma calcaria* community, describes in the following terms: "This community is characterized by the occurrence of *Macoma calcaria* as the constantly predominating species. Beside this species, forms such as *Astarte borealis, elliptica, montagui,* Portlandia, *Yoldia hyperborea, Nucula tenuis,* Leda, etc., may occur; also *Nephthys ciliata,* species of Pectinaria and Harmothoe, *Onuphis conchylega* and several other Polychaeta have been found. Among echinoderms, *Myriotrochus rinki* and *Ophiocten sericeum* are the most frequent. This community has been described from the coasts of the East Greenland fjords (Thorson, 1933, 1934; Spärck, 1933), where it seems to occur everywhere on clay bottoms and on sand mixed with clay. It occurs in different locally and bathymetrically determined varieties. The lower limit of this community in the East Greenland fjords is about 50 meters. Outside the East Greenland fjords this community has been described from various other arctic waters, namely the Storfjord in Spitzbergen (Brotzky, 1931), where this community is present in the inner part of the fjord, on soft bottoms near the Spitzbergen Bank (Idelson, 1931), in the waters near the Kanin Peninsula (Zenkevitsch, 1931), in parts of the Barents Sea, in the White Sea (Zenkevitsch, 1927), and northern Norway (Soot-Ryen, 1924). In the Barents Sea it occurs at greater depths than in the East Greenland waters, down to 100–150 meters. The *Macoma calcaria* community occurs at Iceland and the Faroes (Spärck, 1929)." The fragments in the Baltic are regarded as relicts (Fig. 76).

Macoma-Mya Community (Biome) (Petersen's Macoma Community) in the North Atlantic (Fig. 75)

It occurs slightly above mean low tide to 20 meters' depth in the Baltic. The outstanding bivalves are *Mya arenaria, Macoma balthica,* and *Cardium edule,* polychaete worms, *Arenicola marina,* Aricia and Nephthys. Blegvad (1916) divides the community into three parts, essentially based upon depths. We have ventured to call these faciations in accordance with the facts brought out on page 247.

The Mya-Cardium-Arenicola faciation occurs in the shoreward side of the Zostera. This is frequented by fishes such as sticklebacks and is the breeding place of gobies, each at the proper season. Blegvad does not record a barnacle-gastropod-mussel community such as is

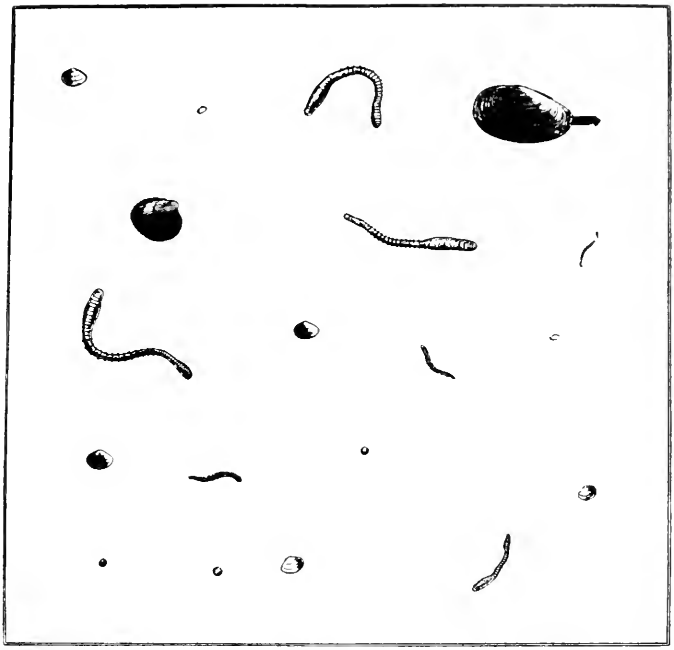

FIG. 75

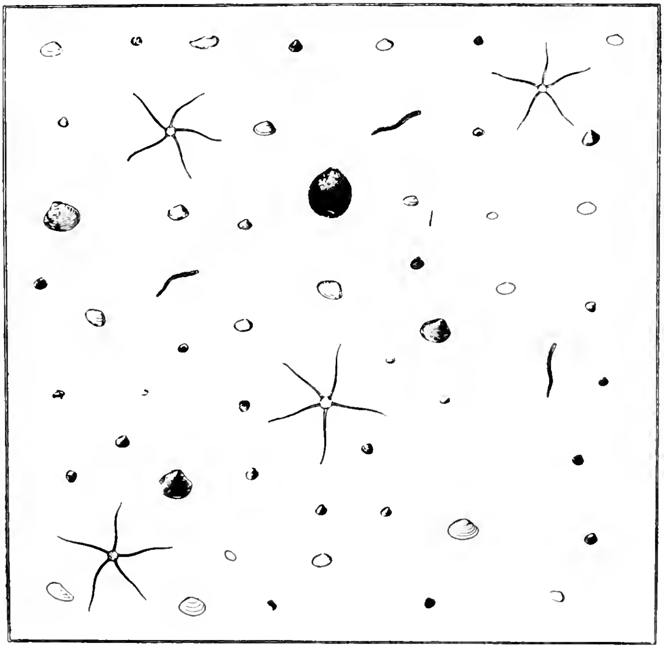

FIG. 76

FIGS. 75–76.—Aspects of the sedentary constituents of the marine communities about Denmark. (After Petersen, 1918.) Fig. 75. The Macoma biome. Fig. 76. The Syndosmya relict or ecotone community.

built up on the shoreward side of this faciation just as on protected beaches of the North Atlantic.

The Zostera-Rissoa-Cardium faciation, in which burrowing species remain the same, is characterized by a large addition of forms that attach to or hide in the Zostera. Small snails belonging to five species, and numerous crustaceans, including small representatives of all the higher groups, crowd the surface and interspaces of the Zostera. The *Crustacea* are especially important to fishes; some five or six kinds of small fishes, including several of gobies, feed upon them and in turn are eaten by cod (*Gadus callarias*). The sea scorpion competes with the young cod, as both live largely on the Crustacea. The viviparous blenny, the young of the eel, and the flounder also feed in the Zostera. The cod leave these habitats when the juvenile stages are passed and feed mainly in other communities, although schools of adult cod from the north come in to the Zostera belt in autumn and feed on the great variety of foods (cf. Ostenfeld, 1908).

In addition to the two faciations discussed, the Macoma-Asterias faciation occurs outside the Zostera belt in deeper water. The same characteristic dominants occur and in addition large crabs, gastropods, and starfishes. Most of the fishes of the Zostera faciation are to be found here. The cod, plaice, and dab are only visitants.

Extent and Variations. Two and perhaps three associations are suggested. A Macoma-Tellina association, which Spärck (1935) considers a different community, occurs in the Kattegat on low open sandy coasts exposed to strong wave action (see Blegvad, 1916:54). It appears to correspond to the Macoma-Paphia biome in the North Pacific. There are communities of this type also on the Atlantic coast of North America (cf. Newcombe 1935, *a*, *b*), for example Allee's (1923) sandy bottom community in the Wood's Hole area (cf. Sumner, Osburn, Cole and Davis, 1911).

The importance of Zostera in this community as a source of detritus has been stressed by Petersen and Lewisohn (1899), Petersen (1913, 1914, 1915 *a*, *b*). Blegvad (1914) has found that the nonpredatory bottom-inhabiting species of this type, and of strictly subtidal communities of the same type, feed upon detritus. He has classified most of the slow-moving dominants as detritus-eaters or predators. The larger and more motile influents commonly feed upon the bottom detritus-eaters. In the enclosed waters east of Denmark, the contact of the Macoma-Mya biome is, with the northern communities, characterized by Syndosmya, Fig. 76 (Peterson's Abra Community) which is probably an ice-age relict.

The oyster communities to which Möbius (1877, 1883) applied the term biocenosis, meaning a social community, have been much studied. Generally speaking, those of the coast of northern Europe and of the Atlantic and Pacific coasts of northern North America occupy areas in the Macoma-Mya community or its ecological equivalent, but are restricted to a portion not ordinarily exposed at low tides.

Communities of *Ostrea edulis* L. have been described in terms most easily interpreted from our point of view. Their arrangement in relation to shore, tides, and currents is shown in Möbius's illustration (1883). They occur on areas swept clean of the very fine materials, which have coarse sands and pebbles to which attachment may be made. According to Blegvad (Petersen, 1908), they are not piled up in close masses, but scattered about in groups. They can reproduce in the conditions resulting from their own presence and are capable of widening their area by lateral extension due to the growth of shells attached at the periphery. The oysters are true dominants, which build up the communities and habitats which they control. They are

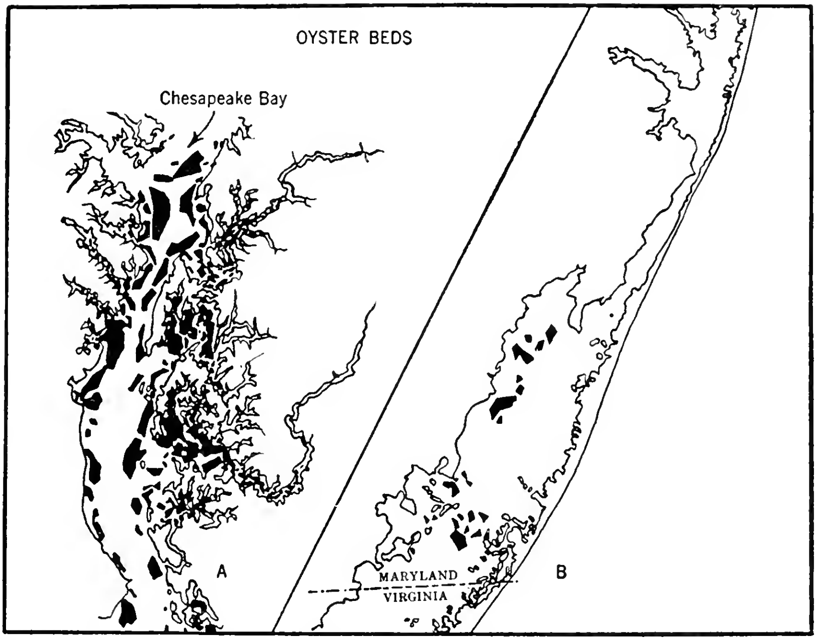

FIG. 77*a* and *b*.—Showing the relative abundance of oysters in the reduced salinity of Chesapeake Bay (77*a*) as compared with the outer Atlantic waters (77*b*). (Drawn from maps by the Maryland Dept. of Conservation; courtesy R. V. Truitt.)

accordingly climax communities, probably best designated as fragmented faciations. With reduction of numbers by fishing, the beds are occupied by cockles and mussels.

The habitats and communities of *Ostrea virginica* Gmel. on the North American coasts are similar to those of the European species. This oyster community, as well as the others referred to, is climax, being capable of building its own substratum and maintaining itself indefinitely. It is, however, always local or fragmented. In waters of high salinity the oyster community is commonly exposed at low tides. The size of the fragments and the area covered are much greater in waters of low salinity. This is probably due to a variety of physical and biological causes. Among these, Professor R. V. Truitt points out in a personal communication the small numbers of oyster enemies, such as starfishes and drills, between the tide lines in waters of high salinity. In these waters, exposures between tides are numerous, which results from their occurrence at a higher level, where their enemies do not flourish. In the brackish waters of Chesapeake Bay, the oyster builds up a community which includes a number of species that are of uncommon occurrence outside the oyster-dominated areas. *Ostrea lurida* Carp. of the North Pacific coast is smaller than the other two and occurs in bottoms with considerable mud. Thompson (1913) pointed out the close dependence of this oyster on the shells of clams and cockles as a base for attachment. Depleted beds are said to have been destroyed by the earth thrown up by the large burrowing crustacean Eupogebia (cf. Stevens 1926).

DEEPER-WATER COMMUNITIES

(HABITAT NOT EXPOSED AT LOW TIDE)

The community characterized by bivalves of the genera Pandora and Yoldia in the north Pacific and asymmetrical sea urchin-bivalve community of the northeast Atlantic are similar in many respects. Both are typical bivalve-annelid communities of the kind always submerged, differing chiefly in the type of large echinoderms, which is added among the abundant constituents of characteristic life form such as bivalves, annelids, and brittle stars. In the northeast Pacific large starfishes (Asteroidea) take the place of the asymmetrical sea urchins of the northeast Atlantic.

North Pacific Communities

Pandora-Yoldia Community (Biome)

This community has been found on mud bottom in 3 to 75 meters of water on shoreward protected spots among the islands south of the Frazer River. The bottom is characterized by fine mud and a deep layer of plankton detritus. The forms generally present are the asymmetrical bivalve (*Pandora filosa* Carp.), the yellow bivalve (*Yoldia limatula* Say), and the thin-shelled clam (*Marcia subdiaphana* Carp.). Certain annelids, such as species of Sternaspis and Amphicteis, are usually present and also one snail (*Phacoides tenuisculptus* Carp.). The fragile starfish (*Luidia foliolata* Grube) is always found in some numbers, and the large 20-rayed star is represented by scattered individuals. The biome is divisible into two associations, one of which has been studied much more than the other; however, it appears that the Alaska shrimp (*Crago alaskensis* [Lock]) and the small bottom-inhabiting fish called red devil (*Lyconectes aleutensis* Gilb.) are common in both. In general, crabs and hermit crabs, especially the latter, are few. The two associations may be recognized through outstanding differences in about half the constituent species.

Cucumaria-Scalibregma Association. This community occurs in areas of somewhat higher salinity and with less silt than the other association described below. The white cucumber (*Cucumaria populifera* (Stimp.) and the expanding worm (*Scalibregma inflatum* Rath) are usually found in great abundance, together with the forms listed as characterizing the biome. Among the brittle stars, *Ophiopholis aculeata* var. *kennerlyi* (Lyman) was present in varying numbers during the several years of study. The short-finned eelpout (*Lycodes brevipes* Beau.) and the Pacific eelpout (*Lycodopsis pacificus* Coll.) were usually infrequent. A number of faciations have been described by Shelford and by Weese (Shelford et al., 1935), and the latter discusses succession from this association to land.

Clymenella-Yoldia Association. This occurs near the mainland where the fine mud of the bottom contains more silt and less organic material than the other association. The bamboo-worm (*Clymenella rubrocincta* John) and the giant nudibranch (*Dedronotus giganteus* O'Don) are very abundant. The brittle stars are represented by *Amphiodia urtica* (Lyman); Scalibregma is sparse, but usually present. All the species characteristic of the larger community are to be found.

North Atlantic Communities

Two communities comparable to the Pandora-Yoldia of the North Pacific are found in the North Atlantic near the European coast. One of them is the Abra community of Petersen, which he indicates is a portion of a larger northern community very evidently sharply differentiated from the others. The second is widely distributed on the continental shelf of western Europe. Both are bivalve-annelid communities with a few brittle starfishes (ophiurids), but neither is rich in annelids. They differ, however, from the Pandora-Yoldia community because of the presence of bilateral sea urchins (Spatangoidea) instead of the large starfishes (Asteroidea).

Petersen (1918) recognized eight communities about Denmark. He furthermore appeared to have them in mind when he prepared a generalized map (1914:App.) of the communities of the North Atlantic. He combined the *Echinocardium cordatum-Amphiura filiformis* (E. Fil.) with the *Haploops* (Ha), and *Brissopsis lyrifera-Amphiura chiajei* (B. Ch.), communities and called the resulting major community the Venus community. He thus brought together the several communities with important species in common (binding species) and tacitly recognized the formation as described by most plant ecologists or the biotic formation (biome) as used in this work. The writer has ventured to add Petersen's *Brissopsis lyrifera* (B.S.) community to the Venus community as suggested by aspect and the occurrence of common or binding species, and to call it the Echinocardium-Thyasira biome.

Lack of contact with the actual materials has been outweighed by the authors' desire to suggest the parallelism with the grassland associations and other terrestrial associations and these well-known marine communities. This addition further suggests a resemblance between fishes and the land birds that drift through two or three land biomes in a north and south migration in connection with wintering and breeding. The eel and salmon are comparable to the more spectacular bird migrants.

Echinocardium-Thyasira Community (Biome)

This is composed of five or more associations representing Petersen's five communities (1915, *a, b*:9; Blegvad, 1930:23–55) of the open waters, and others noted by Spärck, Ford, et al. These are all ranged over by cod plaice, haddock, flounder, dab, long rough dab, roa, pipe fish and a few of the gobies etc. Among the bivalves, *Thyasira* *flexuosa,*[1] *Nucula tenuis, Spisula subtruncata,* etc., are found generally distributed throughout. The brittle stars are represented by one or more species of Ophiura or Amphiura; Spatangoidea are usually present, represented by Echinocardium, Spatangus, or Brissopsis. Annelids vary in number, but Nephthys, Aricia, and Glycera are commonly to be found.

The community is distributed in the area to the south of Iceland about the British Isles, across the North Sea, about the Danish Peninsula, and along the west coast of Norway to North Cape. The associations are those described by Petersen, Davis, Spärck, Ford et al. The description of typical portions and the mapping of the communities follow Petersen, modified only slightly by the data of other writers who give no maps. Petersen's map is provisional, but confirmed in the main by others. He recognized several communities which, to follow the arrangement used or the communities of Puget Sound, would be regarded as the associations that constitute the biome. They may be briefly described in the order presented by Petersen, and his names are given in parentheses. The community characterized by *Syndosmya (Abra) alba,* found locally, is perhaps to be regarded as an ecotone between the Macoma biome and the Echinocardium-Thyasira biome. (As provisionally arranged here this major community combines Spärck's, Amphiura, Haploop's and *Venus gallina* communities [Blegvad, 1922, 1923, 1927; Spärck, 1935].)

Venus-Echinocardium Association (*Venus with Echinocardium Community*) (Fig. 78). The community occurs in open sandy coasts at an average depth of 10–12 meters. The bivalves, *Venus gallina, Tellina fabula,* and *Montacuta ferruginosa,* together with *Echinocardium cordatum,* make up the greater part of the population. Brittle stars are usually present; gastropods are few or wanting. Annelids are represented by *Nephthys hombergi* which is most abundant (Blegvad, 1930:36), and two to six other species occur. The fishes enumerated as characteristic of the biome are all present, as are other motile forms such as amphipods (Fig. 78).

Echinocardium-Amphiura Association (*Echinocardium-filiformis: E. Fil. Community*) (Fig. 79). This occurs at 12–40 meters of water. The bulk of the population is made up of the bivalve, *Abra (Syndosmya) nitida,* the brittle star, *Amphiura filiformis,* and *Echinocardium cordatum.* Gastropods are relatively few here, except for the genus Turritella (spp.), but the quantity of annelids is large. The

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[1] Authors' names are omitted in connection with northeast Atlantic species; all names are listed by Blegvad (1930), and are to be found in many other publications.

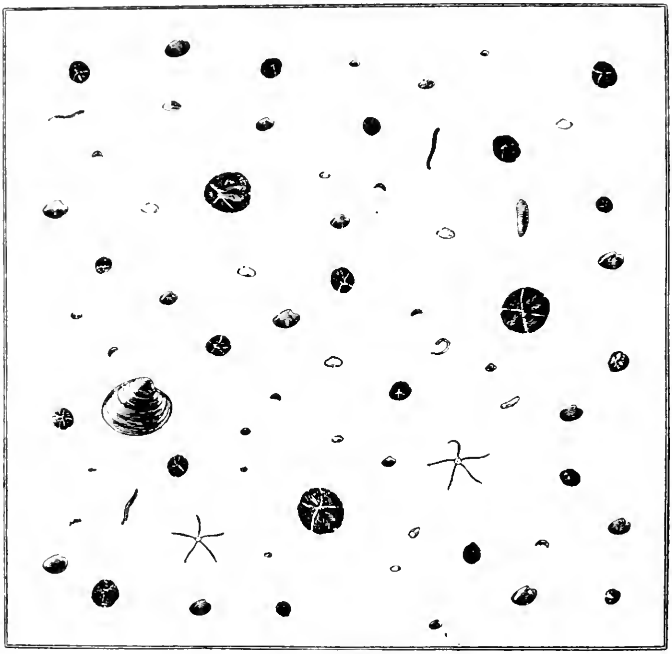

Fig. 78

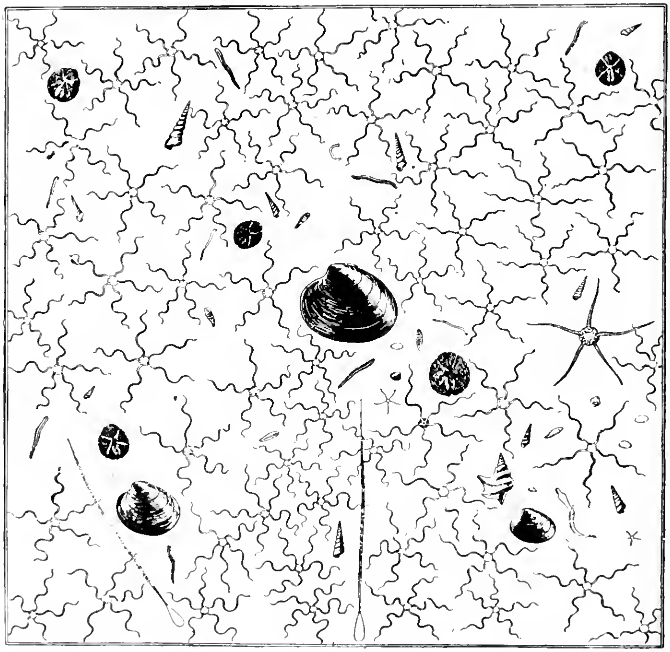

Fig. 79

Figs. 78–79.—Showing aspects of the Echinocardium-Thyasira biome. (After Petersen, 1918.) Fig. 78. Venus-Echinocardium association. Fig. 79. The Echinocardium-Amphiura association.

gastropods and the annelids occur in greater abundance in this than in the Venus-Echinocardium association. In addition to fishes characterizing the biome in general, Blegvad (1916) mentions the whiting and dragnet. The aggregation described by Davis appears to belong in this association (Fig. 80).

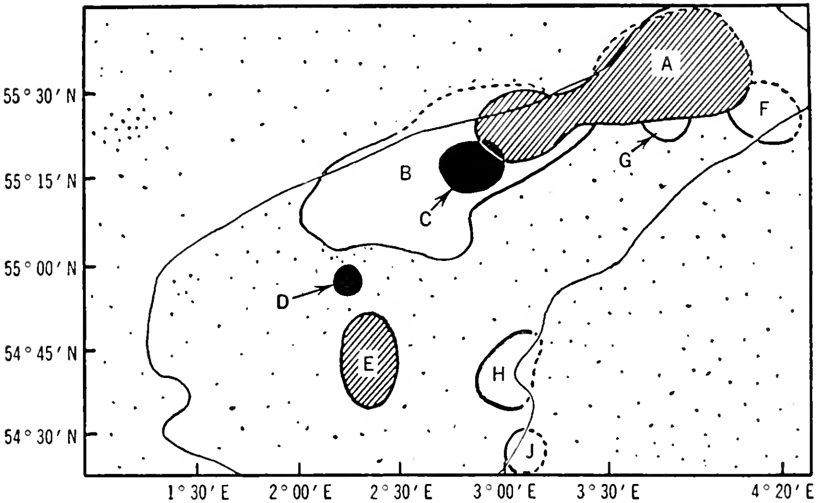

FIG. 80.—*Spisula subtruncata* consociations. The oldest areas are solid black; those of medium age, shaded; and the youngest, unshaded. The stippling of areas outside the patches is purely diagrammatic. Each dot represents a large number of individuals of Spisula outside the aggregations because Davis gives only frequency and not spatial relations. (After Davis, 1923.)

Brissopsis-Amphiura-Ophiura Ecotone. Spärck (1935) states that *Brissopsis-Amphiura chiajei* (*BCh.*) and *Brissopsis-Ophiura* (*Ophioglypha*)* *sarsi* community appear to represent a transition which (in

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* Changes in generic names which involve the naming or other designation of communities or their predominant species in the North Atlantic and adjacent waters are as follows:

Abra becomes *Syndosmya*

This changes the designation of Petersen's Abra community (Abra with Echinocardium; b(abc E) and renames the constituents of others.

Ophioglypha becomes *Ophiura*

This involves changing Petersen's Brissopsis-(Ophioglypha) sarsii designation as noted above.

Axinus becomes *Thyasira*

Thyasira flexuosa is a common or abundant constituent of two communities which may be united as a biome (see Fig. 84, p. 349).

Mactra becomes *Spisula*

The species *subtruncata* is prominent because of the very dense aggregations in the North Sea (Fig. 80).

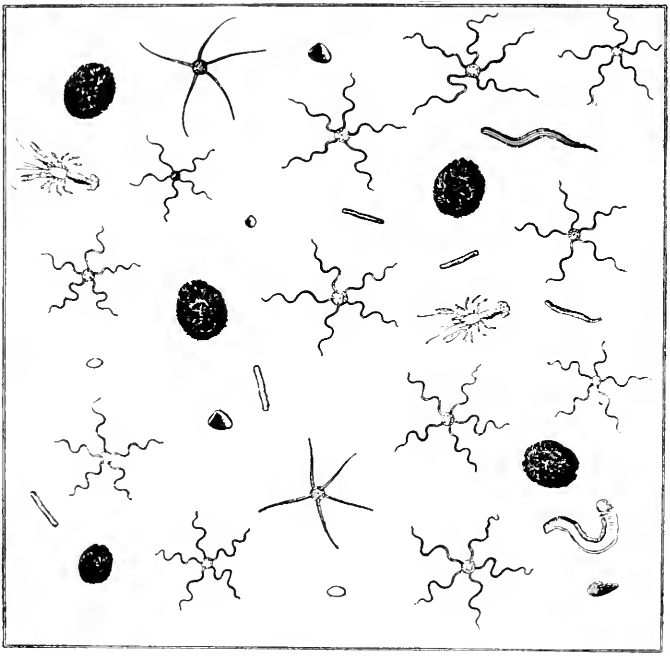

Fig. 81.—The Brissopsis-Amphiura ecotone. (After Petersen, 1918.)

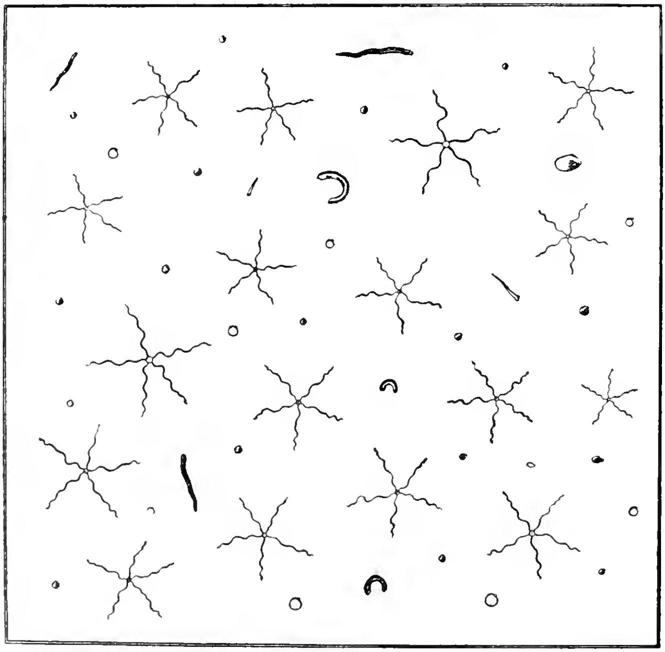

Fig. 82.—The Amphilepis-Pecten biome. (After Petersen, 1918.)

our nomenclature) would lie between the Echinocardium-Thyasira Biome and the Amphilepsis-Pecten Biome. This ecotone appears to occur between about 50 and 380 meters depth in the Danish waters.

Haploop's Community (Association or Faciation). This is a small area northeast of the island of Zealand, omitted from the map. Haploop is included here because of its small size and the presence of several predominants of the major community among the Haploops crustaceans. These appear to be another association of the same major community. The arrangement which we venture to present here is in a considerable measure for the purpose of paralleling the phenomena found on land.

Astarte—Arca Community (Biome)

This community is characterized by *Astarte crenta,* by *Arca glacialis,* and also by several of the lamellibranchs and annelids which were also found in the *Macoma calcaria* community, several species of Portlandia, Cardium, *Pecten groenlandicus,* for instance. "This community is described from east Greenland waters, inside the fjords and also in the pack-ice belt at depths from about 50 meters to about 250 meters (Spärck, 1933; Thorson, 1934). Further, according to the papers by Zenkevitsch, Brotzky, and Idelson it seems to occur in the central parts of the Barents Sea and in the Kara Sea, and it therefore appears to occur in arctic seas—in several varieties below the *Macoma calcaria* community. It seems also to occur in Ramfjord in northern Norway (Soot-Ryen, 1924)" (cf. Spärck, 1935, 1937).

Amphilepsis-Pecten Community (Biome) (Fig. 82)

The Amphilepsis-Pecten community occurs in deeper water, oceanward from the Echinocardium-Axinus biome (see map, page 349). A more northerly type termed by Spärck (1935) the *Astarte crenata* community may perhaps be appropriately called the Astarte-Arca biome.

Foraminifera Community

This occurs in deeper water than the preceding as a rule. Some annelids and mollusks are found with the Foraminifera. The observation of Verrill (1871–72) suggests a series of communities east of Massachusetts resembling those west of Denmark.

Variations in the Bivalve-Annelid Communities. Two types of variation in composition have been described, and called lociations or faciations, depending on the extent. Jensen (1919) describes the former in the various broads of the Limfjord. In the quotation below,

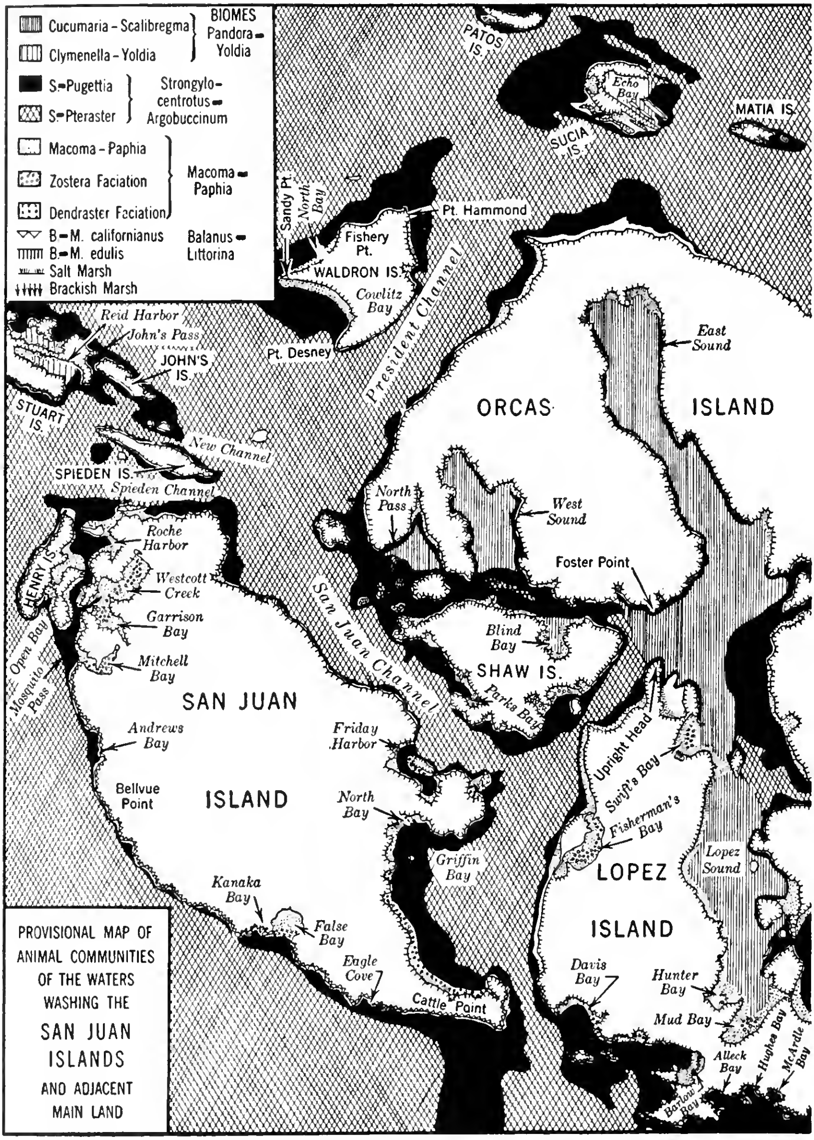

FIG. 83*a*

FIG. 83.—Communities of a large protected bay of the northeast Pacific. (After those represented for land in Fig. 54, page 255, which shows the associations or 12

Fig. 83*b*

Shelford, 1935.) The phenomena indicated on the map are in agreement with of the grassland. (One inch on the map equals approximately 6 nautical miles kilometers.)

the terms applied to communities of different rank in this discussion are inserted after those used by the author quoted. The variation appears rather small to fit our concept of the association; the brackets indicate the nomenclature of our system.

"1. A Nucula-Corbula-association [faciation], characterized too by its nearly total want of Solen. This association [faciation] is found purest in Nussum Bredning, where the Nucula amount for a series of years has been ca. 30–50 g. per square meter; during the last years it has decreased a little, yet only to ca. 10 g. In the other Brednings, an amount of Nucula exceeding 10 g. only appears as an exception. Corbula, which is found in great amounts in Nissum Bredning together with Nucula, is probably in much smaller degree a characteristic animal; it is, for instance, still found in rather important amounts in Skive Fjord. In the Nucula-Corbula association [faciation], Abra is only found in smaller amounts, Solen is rare and *Mya truncata* is not found at all. That Abra and Solen appear in such small amounts in Nissum Bredning is probably caused by the fact that they are specially persecuted by the plaices.

"2. An Abra-Solon association [faciation], where Nucula and generally also Corbula are of subordinate importance. This association [faciation] is most typically found in Livø Bredning. As mentioned above, the two bivalves are found in very fluctuating amounts in the various years.

"In Lavbjerg and Kaas Brednings transitions between the Nucula-Corbula and Abra-Solen associations [faciations] are found.

"3. An Abra-Solen-Mya (*truncata*) association [ecotone], found in the side-Brednings originating from Livø-Løgstrø Bredning, respectively Thisted-Visby Brednings and Risgaards and Lovns Brednings. This association is displaced by the occurrence of *Mya truncata*.

"When entering into shallow water or in the very inmost Brednings, this association is displaced by the *Macoma baltica* formation [biome]. One of the characteristic animals of this formation, *Mya arenaria,* is found together with animals of the Abra-Solen-*Mya truncata* association [faciation] in Lovns Bredning as mentioned above."

Another important type of variation has been discovered in the Echinocardium-Thyasira community by Davis. On the Dogger Bank, he described several areas dominated by *Spisula* (*Mactra*) *subtruncata* (da Costa), from 500 billion to 5 trillion individuals covering several hundred square miles. He believes that these result from failure of the spat to scatter about (Fig. 80, p. 343).

Changes from year to year (annuations) are shown in Fig. 40. The near absence of some of the dominants in certain years is noticeable. The variation of non-mobile species in the same community is also illustrated in Fig. 39, page 181.

The Nature of Dominance in Bivalve-Annelid Communities

All the communities of this type that have been investigated include bottom-feeding, rapid-moving and often migratory fishes, which range over two or three major communities as do the birds and large mammals of the land. A second group of slow-moving and relatively stationary, but usually important, influents, are ophiurids in the North Atlantic and both asteriods and ophiurids in the North Pacific. They are in part predatory and play an important role. Gastropods and large crustaceans such as crabs and shrimps are present, but ordinarily of lesser influence owing to the small numbers and, in the case of

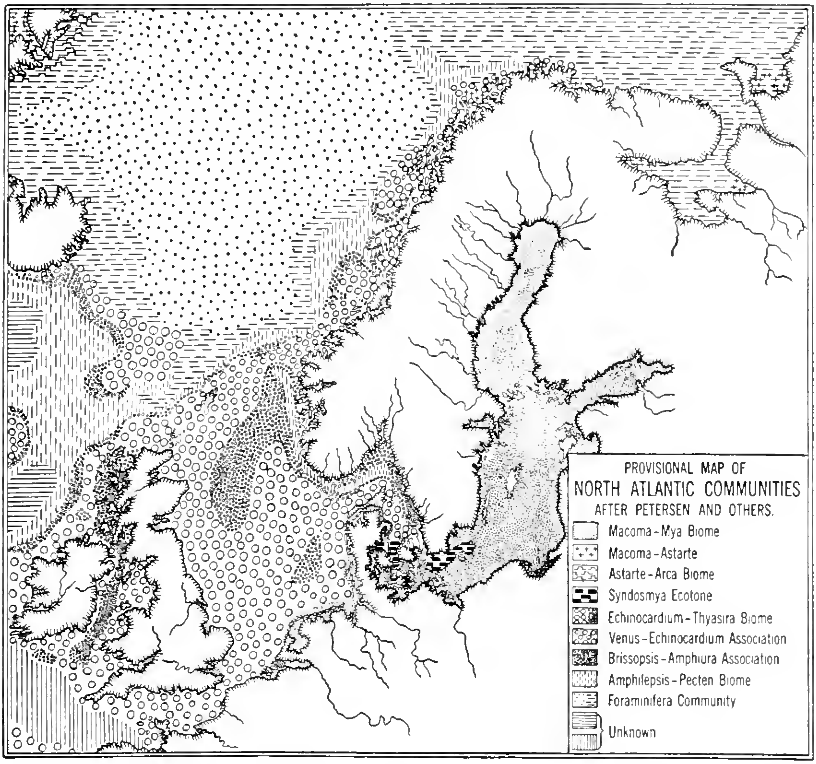

FIG. 84.—Communities of the North Atlantic interpreted in accord with the principles found among the North American land communities Fig. 54, page 255, and the marine communities of the shore waters of the North Pacific. (Fig. 83 and pages 346–347, modified from Petersen, 1914.)

the gastropods, to the relatively small size of the individuals also. The great majority of bivalves and annelids are stationary; they constitute the most important constituents as regards competition for space and reaction on the substratum.

Blegvad (1914) made a study of the nutrition of the bottom invertebrates, classifying the foods as follows:

1. Plant food consists of fresh-growing benthic plants.
2. Detritus is divided into two classes:
   (a) Plant detritus which is floating plant material; some of it is fresh.
   (b) Bottom detritus, which consists of fine particles of plant and animal material settled on the bottom.

He not only examined the stomach contents of the animals, but also made aquarium experiments and observations. The material studied includes the more important representatives from the stationary and slow-moving bottom constituents of the Macoma-Mya, and Echinocardium-Thyasira biomes.

The bivalves were found to live entirely upon detritus. A few invertebrates are herbivorous detritus-eaters; Rissoa, a small snail abundant on Zostera, is an example. Most Polychaeta are detritus-eaters. All the serpent stars of the genera Ophiopholis and Ophiura (Ophioglypha), which play a prominent part in the communities, are carnivorous detritus-eaters. Echinocardium belongs here also; it feeds on detritus and young bivalves.

Petersen (1918:17) has pointed out the scarcity of bivalves where serpent stars are abundant and credits them with the control of communities. In the second paragraph of the quotation, by "grounds near land" he refers to those areas occupied by the Macoma community. He states his conclusions in the following terms: "Most common marine animals living on the bottom commence their existence as minute larvae in the water, and sink to the bottom at a very early stage, as for instance the bivalves. And it is remarkable to note how in those communities where the Amphiura spread their arms abroad, forming a network in the bottom (see Pl. IV and V), extremely few bivalves are found at all. The young bivalves will here doubtless as a rule be devoured, while still quite small, by the Amphiura, and only a very few individuals of certain species manage to survive. Both in shallow water near the coasts, and farther out where it is deeper, where few or no Amphiura are found, there are quantities of small bivalves (see Pl. VI and I, II and III) of many different species, for instance, Mactra, Tellina, as also in summer on grounds near land, where few or no echinoderms at all are found. That the great majority of these young individuals never attain full growth, is doubtless primarily due to the fact that the environment is here unfavorable in the long run; the action of the waves, for instance, will at times be too violent; very low water will kill off numbers of the young, as also severe cold in winter, etc., presumably the same factors which account for the absence of echinoderms in the same localities. It is in such places as these that the species of the Macoma communities can live and thrive continually; they are the only forms that are able to withstand the severe conditions prevalent in a degree sufficient to ensure the maintenance of the species.

"It is remarkable, having in mind the hardiness of these Macoma species, that they should not be found deeper out in the Kattegat, throughout the whole of the Venus area, where we might imagine they would find the most favorable environment of all, and where Mytilus also make their appearance on any buoy set out, but hardly ever live on the bottom itself. It cannot be the depth which keeps the Macoma species away from these areas; we find for instance, *Mya arenaria, Cardium edule, Macoma baltica* and Hydrobia out in at least 20 meters depth in the Baltic where their predominance is undisputed; in the Baltic, however, east of Gedser, there are, as we know, no echinoderms, nor are such found in the low water on the shores of the Kattegat. I must, therefore, suppose that it is just certain echinoderms which prevent the animals of the Macoma community from spreading over larger areas than they occupy in fact."

The fishes have potent effects in the communities, but these are greatest in determining abundance, life span, and replacement among those community constituents that are able to exist with them, but their effect in eliminating certain forms from the communities entirely has been but little investigated (Jensen, 1919). However, the work of Blegvad (1925) shows the coaction of fishes on the bottom-inhabiting species to be sufficiently great to class them among the dominants. All the community constituents influence the bottom, especially where this is little disturbed by waves and currents (Moore, 1931, *a, b*); succession by reaction is to be expected but cannot be followed without great labor over long periods. Here again, as in fresh water, dominance is as much a matter of coaction as of reaction, if not more.

The relatively short life histories and life span of marine plants and animals and their frequent fluctuations in abundance led Petersen to select single species as indicators of communities. For the selection of a species as a community indicator from this point of view, it must be:

1. Abundant.
2. Uniformly distributed.
3. Always present in considerable abundance when other species decline almost to zero.
4. The limits of its range must coincide with those of various less stable constituents.

The life forms that signalize the most important constituents serve as important criteria, just as they do for land plants.

Petersen's use of single species as indicators has led to apparent confusion in the minds of other investigators (Ford, Davis, Stephens, et al.). A closer adherence to the practice of plant ecologists allows a greater latitude. In this, a large series of dominants of a limited number of life forms is recognized, and in some situations nearly all are found mixed together (Clements, 1920; Braun, 1935). They usually segregate into large units or associations, each characterized by a definite group of wide-ranging and restricted species characteristic of the particular association. Toward the outskirts and in local areas some of these drop out and occasionally some species are added. These variations are those called faciations.

Petersen's reluctance to consider fishes and other motile forms a part of the bottom community left something to be desired. His work, however, was superior, from a bio-ecological viewpoint, to that of most plant ecologists, because he and his associates were primarily concerned with the food of fishes and worked out the interchange of effect between the motile and sessile constituents. They merely found difficulty in connecting fishes with the communities in mapping, and the fishes, etc., were treated in a somewhat detached manner. They made many facts available; however, our attempt to organize them in the preceding pages is doubtless quite imperfect. The same is true of the endeavor to synthesize the animal constituents of the land communities considered. A certain amount of reinvestigation will be necessary to establish definite facts in all cases.

COMPARISON OF MARINE AND TERRESTRIAL COMMUNITIES

The preceding pages have indicated that the phenomena of distribution of relatively stationary organisms on the sea bottom and on land are quite similar and lend themselves to a similar type of classification for greater ease in description. The failure to find successional phenomena in the faciations of the Balanus-Littorina biome in the enclosed Puget Sound waters (Shelford et al., 1935) had seemed to offer a difficulty. These studies, however, were carried on only for a short period, and the work of Hewatt (1935) on the *Balanus-Mytilus californianus* association on the open shore over a long period has demonstrated a clear succession. This fact, and the almost certain occurrence of succession where bottom must develop, covers nearly all the distribution phenomena of the bottom fauna to parallel those described for plants and considered together on the surface of the land. Since climax and succession have formed the natural basis for classification on land and promises to do so in the sea, the study of community development in connection with public works, especially those in waters of high salinity, where new channels are opened and piers built or dredging done, should be encouraged. The investigation of successional changes in deeper waters is much more difficult but not impossible. Pelagic communities in themselves, which appeared to afford unusual difficulties as regards dominants, have gradually become susceptible of analysis as knowledge has advanced, and study of succession or invasion of denuded water is coming into the range of the possible.

APPENDIX

METHODS

General methods of ecological investigations are treated in various reference works (Abderhalden's Handbuch, 1925-1931; Adams, 1913; Shelford, 1913, *a*; 1929, *a*), and only a few features of procedure with reference to animals are presented.

Let us assume a sample catch of all the organisms from 10 square kilometers of primeval grassland (or a similar area of sea bottom). The grassland catch would include everything from the bison to the soil bacteria and Protozoa. The community function of these various organisms could not be determined from inspection. Some of them would be relatively large and conspicuous, others numerous and made noticeable by their numbers and extension over large areas. Quantitative methods are absolutely necessary. On the basis of size and abundance, various degrees of influence and dominance may be roughly recognized, but the actual community functions still have to be determined by long study, both field and laboratory; but no matter what the results may be, the abundance of any organism is a matter of first importance, though often very difficult to ascertain.

After all the dominants, subdominants, and influents of various grades have been evaluated as far as is ordinarily practicable in a field investigation, there may remain many small organisms to which no relative value can be assigned. These are small herbs, insects, fungi, bacteria, protozoans, lichens, and various invertebrates. The more abundant of these still have to be called predominant or prevalent among their kind. After evaluation in one locality is completed, organisms have further to be evaluated as to their geographical extent, uniformity of distribution, and stability of numbers. This further evaluation is usually accomplished in connection with the recognition of the largest communities of which the local ones are a part. Abundance is always a prime consideration, though ideally the force exerted by the populations is the fact required and sought.

In terrestrial communities two principal methods are used in dealing with smaller invertebrates. Placing an inverted can over a known area at the time of minimum activity and killing and recovering the organisms (Wolcott, 1918; Shelford, 1929, *a*; Beall, 1935) is one standard method. The use of the sweep net to secure invertebrates from the vegetation is a general one and has been discussed especially by Zubareva (1930), Gray and Treloar (1933) and Beall (1935). Gray and Treloar selected an alfalfa field because of its uniformity, but their results indicate that the insect population is more heterogeneous than that of a climax vegetation, and this is to be expected because of the youth and agricultural disturbance of the habitat. Beall recommends a square net, a 250-cm stroke, and the study and statistical treatment of *each sample* separately. This is justified by the variation in strokes, loss of individual animals, etc. (cf. Graham, 1929, *a*).

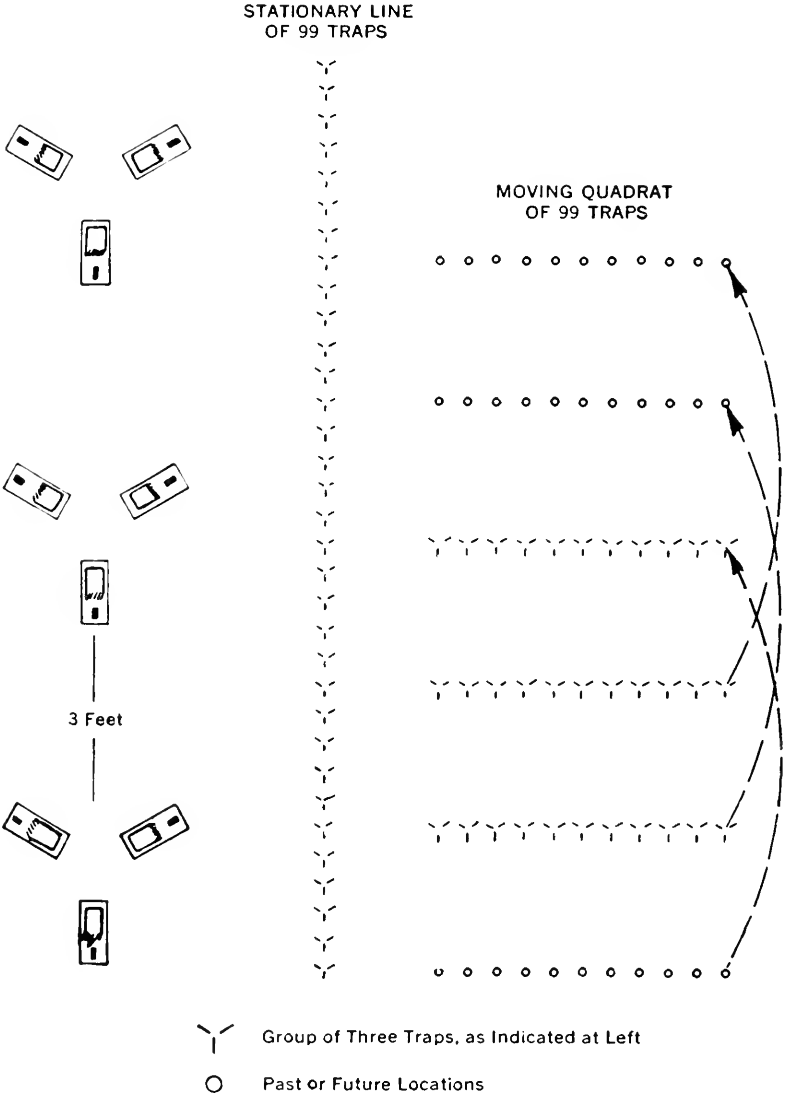

FIG. 85.—Showing the Townsend (1935) method of trapping of mice to secure all the regular population.

The trapping of small animals has also been given attention. Townsend (1935) has worked out a plan for such trapping. The Illinois Natural History Survey has used a unique method in estimating fish populations. Numbers of fishes are caught and marked, and the proportion of these that enter into subsequent catches is used to estimate total populations. For example, if 10 per cent of the subsequent catches were made up of marked individuals, it would be assumed that the number marked was 10 per cent of the total population.

The numbers of birds and larger mammals are usually ascertained by cruising. Only experts are really effective in estimating numbers of birds. The person generally best at field identification usually reports most birds. The general impression is that most of the figures published are underestimates. All observations should be made at the hour of maximum activity, often early morning, but different for different species.

Methods of preserving these animals in natural numbers in public reservation areas too small for their proper support are discussed by Hall (1929) and Shelford (1933, 1936). This consists in surrounding the small sanctuary area by buffer zones or zones of protection of animals traveling out of the sanctuary in course of food-getting, seasonal migration, etc. Such areas are of the greatest value to science. They constitute check areas for reservations under management.

In dealing with the more strikingly influent animals, for example, mammals and birds, one is confronted with the fact that they have commonly been exterminated or suppressed in most of the places where it is desirable to know what their effects may have been under primeval conditions. In order either to reconstruct a former condition or to determine an existing one in regard to these animals, the following operations are necessary:

1. The species of influent animals occurring in a biome should first be listed for several points not too near the biome periphery.

2. The range of these species in and out of the biome areas must be ascertained as completely as possible.

3. The relative abundance of a species in the parts of its range must be ascertained from literature. The records are fragmentary and in obscure publications.

4. The breeding, shelter, and feeding preference must be determined in relation to daily and seasonal cycles. Home range should be ascertained.

5. These habitat preferences must be interpreted in terms of the various seral stages and the climax.

a. Water.
b. Water margins.
c. Bare areas of all kinds.
d. Early seral stages.

6. The distribution of the habitat type occupied or utilized by the animal must be determined. Its local occurrence in other biomes as bare areas, devel-

opmental stages, and relicts should be used to interpret extension of range beyond the limits of the biome.

7. The distribution of the principal food plants or animals must be ascertained.

The greatest importance is to be attached to habitat relations. This must be learned particularly with reference to early seral stages or climax and late subclimax stages of vegetation, as the primary classification of influents has practically to be based upon these considerations.

The quantitative methods used in water are numerous, and the reader should consult Abderhalden's Handbuch; Juday (1916, 1926); Ward and Whipple (1918); Reighard (1908); Ekman (1911); Needham and Christensen (1927); Moon (1935); and Williams (1936).

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