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THE RELATION OF PLANT SUCCESSION TO CROP PRODUCTION

A Contribution to Crop Ecology

BY

ADOLPH E. WALLER, PH. D.
Instructor in Botany in
The Ohio State University

PAPERS FROM THE DEPARTMENT OF BOTANY, NUMBER 117

PUBLISHED BY THE UNIVERSITY AT COLUMBUS

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Acknowledgments and Foreword

As in my previous paper on the Crop Centers, I am indebted to Dr. E. N. Transeau for ecological criticism and guidance. The idea of centers of plant and animal life about which certain forms are naturally grouped is originally his and Dr. C. C. Adams's. Its chief advantage, as opposed to the temperature or other "zone" plan of mapping distribution is that it works. It should be clearly borne in mind by the reader that boundary lines as drawn do not attempt to mark divisions in any absolute way, but do show the centers of distribution. For definitions of the biotic center Adams's and Transeau's papers should be consulted. The writer is also indebted to numerous other friends who have aided him in one way or another, and most especially to those who corresponded with him shortly after the publication of the Crop Centers paper.

Due to unavoidable delays in the University publications, the date of the actual completion of the manuscript and the date of going to press shows an interim of two years. In the meantime a number of valuable papers of an ecological nature have appeared, but a discussion of their bearing on the field of crop ecology must be reserved for future work.

A. E. W.

August 24, 1920.

INTRODUCTION

The present paper is a study in one of the recent phases of modern botany as applied to the nation's greatest commercial asset, agriculture. The audience for which it is intended is a large one, for the discussion is mainly directed toward farmers, albeit they may be a special group of farmers. Some perchance are not acquainted with the art of agriculture or the business side of it; some may never have lived on a farm; while most of the members of this group will be interested in the scientific aspects of plant life. The last named constitute the special group who are to be reached by the following series of investigations. For at this time more than ever before in the world's history are the scientists looking in on gatherings where business men meet. This predicates their appearance at farmers' meetings. In the crowded places the man of science learns the things most needful for human welfare. The "pure scientist" who studies the fundamental principles and the "applied scientist" who develops these principles can then work in harmony for the betterment of civilization. The "pure botanist" and the agriculturist, one of the many workers in different fields who draws his fundamental facts from the botanist, can do team work with benefit to each other and humanity.

The purpose of the paper is to show the relation of ecology to agriculture and to introduce ecology to agronomists. In order to do this the general ecology of plants must be discussed first. For the working principles of the ecologist have been derived from studies of the native vegetation. There is much good work in this field which may be taken over verbatim for the use of the practicing agronomer. There is also a good deal which may be derived from experimental and laboratory work. Whenever it has seemed possible to the author, the accumulated facts of agriculturists have also been grouped so that they may be of use to the ecologist in widening his principles and working generalizations, for it is believed that the mutual assistance to be derived from such cooperation may in some cases prove to be a revelation to plant ecologists and agriculturists.

A consistent and wilful attempt is made throughout the paper to avoid the older, though still widely accepted, static ideas of the distribution of vegetation. This is in agreement with the trend of thought developing in botany in the last twenty years. A static classification recognizes that the plants in swamps and lowland forests are different from plants in upland forests, yet no relation between the two is shown. A genetic classification on the contrary would emphasize this relation: it would show the floating aquatic herbs, grasses and sedges gradually filling the swamp with debris until more permanent shrub thickets and young trees could find a foothold. Later as the vegetable debris accumulates and soil is formed, a complex swamp forest would develop. In the uplands, from a dry rock surface covered with a tenuous coating of lichens a denser plant cover gradually accumulates, and as soil forms, an increase in the water content of the substratum results. In time then, starting from bare rock a forest would develop. From the extreme conditions, a fresh water surface, and a rock cliff, a converging tendency would be noted as the development of a richer, denser vegetation cover progressed. This change in the plant associations as the conditions change is the keynote to plant successions. The later plant societies and associations inherit much from the earlier ones; not in a morphological sense of course, but in an ecological sense. There were no transferances of characteristics from the earlier generations to the later ones. The inheritance is in the environment; as in the human race, one civilization may inherit something of the art, poetry, music and ideals of an earlier civilization. The superiority of the genetic classification lies in the completeness of the picture presented.

A second advantage is in the economy of thought in placing a group of plants in a definite relation to the whole vegetation as a unit, instead of attempting to remember the vagaries of individual distribution which many species often present. This is essentially good geography as well as good ecology. We learn to associate certain groups of plants with peculiarities of locality and larger groups with greater regions. By this process of mental association we come to have a good understanding of a chain of perceptions which are included in the underlying conditions of social and economic development of a region.

The factors involved in the development of our native vegetation are climatic, edaphic, and biotic. The climatic factors deal with the absorption and dispersal of the sun's energy and the circulation of water and gases in the atmosphere. Viewed as a physical machine the efficiency of the vegetation is not high. Due to reflection from the leaves during insolation only about 60% to 75% of the total incident energy is absorbed. Of this amount a small fraction, say 1%, is used in photosynthesis and a still smaller amount is released by respiration. The evaporation of water from the internal surfaces of the leaves, or transpiration uses up a large amount of the energy absorbed. Yet transpiration is by no means an unmitigated evil, simply dissipating energy. Heating large quantities of water serves the plant in much the same way that it serves an internal combustion engine, it reduces the temperature. With living plants the process is carried on to the evaporation of water, but without large increase in temperature. Brown and Escombe have shown that the leaf exposed to full sunlight is receiving energy fast enough to raise its temperature almost 30° C. per minute. At this rate two minutes of strong sunshine would result in the coagulation of protoplasm and the instant death of the plant. Clearly then the rôle of transpiration is in keeping the plant alive. Though the efficiency of vegetation may not be high, the balance is in favor of absorption, and this small percent of energy assimilated and stored by green plants is the foundation upon which all the superstructure of organic life is built.

The second, the edaphic factors include in a broad general way the influence of soils upon plant growth. It is from the soil that plants receive the minerals necessary for life in raw form. These are built up into organic compounds in the plant and are assimilated as food after being combined with the products of photosynthesis. Water taken in by green plants also comes for the most part, if not entirely, from the soil. Soil temperature and its oxygen supplying power are still other factors important in the life of the plant. The physical and chemical nature of the soil then is included in the term edaphic.

The last, the biotic factors, include the effects of plants and animals upon the development of the vegetation. The chestnut bark fungus has already destroyed large forests of the Allegheny Mountain region and the white pine blister rust is menacing not only the white pine forests of the east but some of our most important timber pines of the western part of North America. Leaf eating insects often destroy enough foliage to kill or seriously weaken green plants. It has been stated by Professor Herbert Osborn that grass hoppers and leaf hoppers consume as much of the vegetation in a pasture as the cattle. Sap sucking insects are often as destructive. Rodents and grazing animals alter the aspect of vegetation.

Man is by far the most important of the biotic agencies in altering the appearance of the landscape. Earthworms, burrowing beetles, snails and plants with tap roots favor the circulation of air in soils and its consequent more rapid oxidation to humus. Nitrogen gathering bacteria are also to be included among the favorable organisms whose effect can be recorded.

In any of the broader groups of factors are a number of smaller sets of factors. For example rainfall and humidity, (or saturation deficit) of the air would be in the climatic group. Soil moisture and water available for plant growth would be in the second group. In the geographic distribution of plants the climate or the soils may prove to be limiting factors which definitely determine areas beyond which certain plants are unable to advance. It is an abuse of the word edaphic to suppose that it has reference to local conditions. The effect of soils upon plant growth may be limited to certain regions, however, since edaphic refers to the soil conditions. The importance of the edaphic factors is often as great as the climate group in determining the success or the failure of certain species.

In the crop plants a fourth set of factors; namely, the economic group, is fully as important in determining geographic distribution as the other three. For in addition to being limited to regions where soil and climate are suitable or can be controlled to a certain degree, such economic conditions as improvement in transportation facilities, increase in population, land values and intensiveness of utilization of land all affect crop production. Thus we see at once the importance of removing the discussion from all static considerations and using genetic and dynamic ideas of the development of our agriculture. In the natural vegetation the changes in conditions give rise to successions or changes in the types of vegetation. In the crop plants conditional control gives rise to changes in type of farming. This analogy between vegetation and crops does not refer to rotations. In rotations an attempt is made to prevent conditions from retrogressing. The change in the type of farming is historical just as successions are historical.

The disappearance of plants from the vegetation as conditions change may be referred to the operation of limiting factors. Sometimes moisture is the limiting factor, as with the desert vegetation. Or, it may be temperature as we progress northward. Two or more limiting factors may work in combinations. With the crops the limiting factors may easily be from the economic group as well as from the physical group. Accordingly, depending on whether we are interested in the problems from a botanical or an economic aspect we are inclined to minimize the preponderating influence of the economic or the physical factors.

Crop ecology may be viewed from two distinct angles. It is a natural center from which the various phases of the scientific sides of agriculture radiate. This is because the basis of crop ecology is in plant physiology. An increase in the yield of crops is the result of changes in controlled conditions. These may be in the soil or in the plant, and if in the latter the favorable variations are made permanent by selection and plant breeding. If in the former, we have the agronomists and plant physiologists to experiment for certain definite ends and to explain why we arrive at certain results.

In the second place, crop ecology should be regarded as an experiment in organization. It tries to show how the various aspects of plant life, the adaptations, the growth habits, the disease resistance must be unified and brought to a focus for further progress in agriculture. Success in the future rests, not in allowing the pathologist and the geneticist and the agronomist to jog along independently, but in combining their forces. And for the business end of farming the economist must also be invoked so that a complete chain stretches from the producer to the consumer. At present our agriculture is somewhat like a partly organized machine. All the parts have been assembled and can be made to work separately, but for the machine to be in smooth-running order, the operation of all of these parts must be synchronized. Furthermore, increasing the speed of one part of the machine, is likely to result in nothing more than a few broken cogs and stoppage of the output, unless this speeding can be compensated in the different parts. In a cotton yarn factory, for instance, unless all the wheels upon which the spools turn revolve at the same rate the threads are not held at the same tension and develop weak spots or the skein may even break and have to be started over. The moral is that our agricultural threads must all spin together at the tension necessary to make a smooth, straight cord, capable of withstanding the strain of our ever increasing population. Strange as it may seem after so many years of our experimental stations and colleges of agriculture, the living plant has not yet been seriously considered the logical starting place about which agricultural instruction is to be grouped.

Whether or not genetic ideas may be applied to the classification of soils remains to be proved by experiment. It seems reason-able to believe that a study of the relation between soils and the plants growing in them based on the conceptions of the development of the vegetation would be of great benefit. There are already studies in progress in several parts of the country on the indicator significance of the vegetations to such practical ends as the location of future forest sites and the possible crops yields of the future. These investigations mark an important, if thus far only a slight, step in the advance of learning. They indicate a new cooperation among scientists as well as unification of the results of studies in scientific theories and the adjustment possible between these and human welfare.

PART I

PLANT SUCCESSIONS

The study of plant succession is an analysis of the developmental process of vegetation. It is a recognition of the causes of plant distribution. The tracing of the development and the study of the causes have always gone hand in hand. The former leads finally to the classification of vegetation on an ecological basis, the latter to experimental physiology.

The broad concepts of plant distribution formulated from time to time may be regarded as steps in the progress of ecological development, each step bringing one closer to the complete classification. Discovering the causes of plant succession involves changes in methods of study, but does not necessarily alter the concepts.

The advance of the study of the causes of plant distribution depends upon progress in the invention of new instruments, and better ways of operating the existing ones, to measure the plant environment; that these two ways of examining plant distribution have always been employed by the ecologists who have contributed most toward the advance of the science is apparent from the literature. It is quite likely that these two methods will always be used together.

Plant succession represents our most advanced trend of thought in ecology. In its simplest form ecology is the observation of plants and animals in relation to their surroundings and to one another. The genesis of the vegetation from bare areas to highly developed associations of plants is the basis of the examination of successions. Ecologists taking advantage of the point of view of successions are able to use shorthand methods for studying the plants in the field. They thus make descriptions which are concise as well as complete. By using shorthand descriptions of field conditions and measuring these conditions carefully with the various instruments designed for the purpose, the ecologist takes his laboratory out into the field with him.

In most sciences, as time goes on, a broad generalization gives way to one that is still broader, still more daring, more inclusive.

So with plant ecology, the earliest concepts of plant associations have become enlarged and more flexible as it was found necessary to make them more inclusive. The first ecologists perceived a relation of certain plants to dry situations and certain others to moist ones—a most natural sort of grouping. Theophrastus (B. C. 370-286) recognized this in the following words: "All (plants) are distinguishable as either terrestrial or aquatic, just as we primarily distinguish animals; for there are some plants which grow nowhere but in the sea; others affect only marshes or other very wet places. Some cannot live in wet ground, but restrict themselves to dry ground. Certain others are littoral only. A few trees thrive in either moist land or dry, such are the myrtle, alder, and willow." Except for the implication that plants are endowed with will by the use of the word "restrict," this sounds fully as modern as any ecological remarks could be which have been written without the inspiration of the point of view of succession.

Plant succession has progressed in making an ecological classification understandable, because it consists essentially in a genetic conception of vegetation. As the name indicates, succession is the sequence of plant associations which dominate a locality as the development of the vegetations proceeds. In the sequence each stage is made possible because of the next or remote preceding stages. As the term genetic suggests, one stage in the development *grows out* of the preceding stages. A habitat then does not so much consist in rocks or hills or lake, as it does in so much moisture, so many degrees of heat, such an amount and quality of light. A habitat is not viewed dynamically until it is placed on a strictly factorial basis. The field worker *sees* plants growing in sand along the seashore. He must *think* of them in terms of the water balance of the plant, the abundance of light, temperature, and so fortth.

Obviously, the ecologist does not attempt to control the conditions of plant growth and vary them one at a time as one might in a laboratory. The best that he can hope to do is to measure and record the conditions he sees as carefully as his needs require. He may even prove that succession is taking place by photographs made at different intervals. The complete series of stages in most successions are far beyond the space of an individual's life so his records must be capable of interpretation by his successors. But it is not necessary to see a complete succession in one place. One may piece together the whole fascinating story of succession from stages at a distance from one another. It is this careful factorial analysis of the progressive changes in the vegetation which has been the key to the modern ecologist's ability to get ahead.

Succession, then, is only a phase of ecology, but a most important phase. In order to have a clear notion of the relation succession bears to the general subject of ecology, a brief review of the subdivision of the general subject seems in order.

The Orientation of the Field of Ecology

Ecology falls quite naturally into two principal subdivisions, depending upon whether the plant responses to be studied are of individual plants or of groups of plants. This division separates ecology into a section which is related closely to plant physiology and a section related to plant geography, or into individual and associational ecology. Following the names suggested by Schroeter, these are called autecology and synecology.

A. *Autecology*

Autecology is the study of the responses of an individual plant to its environment. It considers the general results of the plant processes with respect to the life of a single plant. This is purely a physiological study; when carried on out of doors it becomes ecological. Autecology represents to a certain extent a reaction from studies which are of a laboratory nature purely. Nevertheless it is in close relation to physiology which has put plant geography into its proper place among sciences. On any other than a physiological basis, plant geography is what it was in the past, pure empiricism. The study of the processes and the factors which determine the activities of an individual plant may be subdivided in many different ways. A convenient way is to consider: (1) the factors relating to changes in the growth activities of plants, (2) the factors usually a part of the sequence of changes called "adjustments."

Changes in the growth activity of plants are measured by computing variations in the water loss, variations in amount of carbon absorbed and in the total mineral absorption. The work in this field is of such magnitude that only the least mention of it may be made here. The influence of water, light, salts, and their concentrations must all be investigated and the results integrated. As the experimental field is opened more extensively the many additional facts unknown or overlooked postpone the final rounding up of the field into a completed work. This is as it should be with any good subject. If we try to classify the experimental work in this field we may at present say no more than that the experiments always take one form, namely, the observation and analysis of the factors causing an increase in activity, and those which diminish it and finally stop it entirely as limiting factors become operative.

The external and internal changes in structure may be summarized as ephemeral and continuous. The former continue only as long as the control conditions last. These affect only the most plastic tissues and organs of the plant. The continuous variations produce permanent effects upon the plants or upon the functioning of the tissues and organs. In a rapidly varying stock such permanent variations, no matter how induced or perpetuated, are called mutants. This brings one to the verge of physiological ecology, the adjoining field in this direction being genetics.

B. *Synecology*

Synecology deals with groups of plants and studies their developmental activity in mass. It is more geographic than physiological. The mass responses are rarely, if ever, the simple sum of the changes of activity of individuals, but more likely a ratio or a quotient. The results of field studies of plants in mass are for this reason different from the results of studies of individual plants. In synecology the plant association as a whole is treated with relation to the factors of the environment which influence its development. Studies in associational ecology are largely in the observation stage still. Accurate records, according to the strictest methods of research, are made in several ways. The progress of the development of the vegetation, or the plant successions, may be recorded by means of photographs, soil and water analyses, besides various instruments for keeping constant records of temperature and light changes. These records, when properly put together, tell the story of plant development in detail. The proof of plant successions, while not at all necessary to the hypothesis, may be seen by revisiting reserved areas where intensive studies have been made. After the lapse of sufficient time, the changes in the appearance of the landscape is marked, but without the use of photographic records is not nearly so convincing.

The Factors in Plant Succession

The most concise grouping of the factors of plant succession that can be made is: climatic, edaphic, and biotic.

1. *Climatic Factors*

In the climatic factors the air environment of the plant is studied. There is no intention of raising the old metaphysical question of "Where does the sky begin?", and it is not likely that the statement will cause confusion. The air is that which begins at the soil surface in the climatic factors and envelopes the above-ground portions of the plant. In water plants it would be whatever portions are not submerged. The atmosphere contains carbon dioxide, water, and oxygen, materials needed by the plant. In addition, the duration and quality of light, the amount of heat, and the velocity of wind are sources of energy for the plant. Animals or plants affecting the above-ground portions of plants are grouped among the biotic factors. The processes of absorption and distribution of materials and energy taken in and released by plant activity have no place in this discussion, rightly belonging to a text on physiology or experimental ecology.

From our viewpoint of the development of the vegetation, extremes of temperatures are the most important factors in limiting plant growth; for the extremes, and not the means, determine which species may become a part of the vegetation and which may be killed from too great cold or too intense heat. Once species become established, the mean temperatures are important because they determine the average rate at which plant activities proceed. The rate may double or treble within certain narrow limits for each rise of ten degrees Centigrade, but Blackman ('05) and Blackman and Tansley ('05) have shown that beyond a set limit further rises do not accelerate growth. To regard temperature means as anything more than a condition for photosynthesis is to put too much weight on the wrong factor.

What has been said for temperature applies largely to light also. The minimum and maximum amounts of light in which a species may develop are the important factors in the distribution of plants. As with the temperature light intensity, varies with the season, the altitude, and the latitude. While some plants are active photo-synthetically at 2° C., their common range is from 20 to perhaps 40 or 45° C. Light less intense than full sunlight is sufficient for growth so that as with temperature, light is not of supreme importance in plant distribution. There are few if any places upon the surface of the earth where the light and temperature requirements of plants are not satisfied at least during some season of the year. Moisture, therefore, remains the important factor in determining plant distribution.

The importance of water as compared with light and temperature is easily shown. Our climatic zones, torrid, temperate, and arctic, are east and west in their bearing, and one crosses them in a journey from the equator to either pole. Desert and arid regions are by no means restricted to any particular climatic zone. Desert and arid regions are the extreme, but we may have dry, grassy plains extending far northward beyond the tree formations. Looking at it another way, we can see that water is irregularly distributed on the earth's surface, while temperature and especially light tend to be somewhat regularly distributed. The water is the unbalanced factor and is therefore the limiting factor. It is the unequal distribution of water, both in amount and during a given period of time, which is the cause of our distribution of various types of vegetation. In order to fully understand this, the variations of climate should be examined in detail.

The Relation of Climate to Plant Distribution

Although the sun's rays strike the different parts of the earth's surface in about equal amounts, yet the total energy derived from them is quite unlike in different regions. What then happens to prevent equal distribution of energy?

In the first place, the land surfaces and the water surfaces absorb heat at different rates. If we call the specific heat of the water surface 1, then the specific heat of the land surface is approximately 4, for the land surface takes up and again gives off heat about four times as fast as the water. Large land masses, *e.g.*, continents, have dry regions toward their centers where the summer temperatures are extremely high and the winter temperatures extremely low. The day and night temperatures also fluctuate greatly. The loss of water from the centers of continents by evaporation tends to intensify the variability of the climate. The sea surface, on the other hand, or a small island in the center of the ocean, has, at sea level, an equable climate in which the summer extremes and the winter extremes are much closer together than in an interior region. In the second place, elevation above sea level produces a local climatic effect in some ways like the climate of the central portions of continents. The sunshine intensity is great, and the water loss rapid. On the windward side of the mountain range, however, the precipitation is heavy, since the air containing moisture deposits its load as it rises and cools in passing over the summits. The influence of the mountains in catching water is felt in all the territory on the windward side between them and the ocean, even in essentially dry regions, since they contribute to stream flow.

More important as reservoirs of water than the oceans even are the land masses. It is not difficult to see that if an air current loaded with moisture from an ocean reservoir reached a land area and deposited some of this water, the air current would become rapidly dry as it passed over the land. Very little moisture would, under these conditions, ever be transported inland for any great distance. An examination, however, of the continents of the earth shows that a good deal of water falls on the land at some distance from oceans, leading up to the obvious conclusion that a current of air is picking up water vapor and precipitating water all the time as it passes over a continent. The amount of water evaporated from oceans and evaporated from the land has been compared. Brueckner has calculated that the land supplies from its own area seven-ninths of the precipitation which falls upon it. This means that the land is a much more abundant source of the moisture carried by winds than the oceans are. A current of air moving over the land and precipitating moisture would be continually having more moisture added to it, a re-enforcement of the supply so to speak, from the evaporation of water from the land surface.

Zon has constructed a balance sheet showing the circulation of water on the earth's surface. The study of Zon's figures lead to the following conclusions: (a) that the bulk of the water evaporated from the oceans is reprecipitated into the oceans, (b) the bulk of the water evoparated from the land is reprecipitated on land, that the precipitation falling upon land is nearly all (four-fifths) furnished by the land area. The examination of Table 1 explains these statements in statistical form.

TABLE 1[1]

CIRCULATION OF WATER ON THE EARTH'S SURFACE

	Cubic Miles
Volume of ocean vapor escaping to the land	5,997
Continental vapor over the land	20,870
Total volume of vapor from which land precipitation is derived	26,868

The present discussion is not concerned with the amount of precipitation into the oceans. The precipitation and evaporation of closed basins in the interior of continents is regarded as equal and therefore omitted. The volume of ocean vapor escaping to the land, 5,997 cubic miles, is 7 percent of all the water evaporated from the oceans. The volume of continental vapor furnishes 98 percent of the continental precipitation.

THE SOURCE OF LAND EVAPORATION

Evaporation is a surface phenomenon. A surface which is rough and which absorbs heat will give off vapor more rapidly than one which reflects heat. Therefore, with equal insolation and equal wind velocity a bare surface of moist soil will give off more water per unit of time than will a water surface. This will continue during a warm season as long as water rises through soil pore spaces to resupply evaporation. A soil surface with only dead vegetation as a cover does not evaporate as much moisture as a bare soil. A soil area with a living cover of vegetation, however, evaporates much more rapidly. Every living plant has an uninterrupted stream of water passing through it. In the case of the flowering plants with the leaves borne on elongated stems some distance above the soil, there is a complicated mechanical structure and a series of interrelated physical processes by which water is absorbed and lifted to the heights of the tallest trees. Plant communities are composed of individuals of different water requirements and capable of absorbing water from different soil levels. In the most highly developed plant communities, the forests, evaporation as well as absorption is taking place at different levels. For example, there is a certain amount of evaporation from the ground cover vegeta-

[1] The relation between continental vapor and continental precipitation.

tion, a certain amount from the shrubs and short vines taller than the plants forming the ground cover, and a still greater amount from the trees and large lianas with their crowns exposed to full sunlight and the more rapidly moving air currents found at this distance above the soil. The forests are for this reason, therefore, the greatest dessicators of the soil. Next in order of amount of water evaporated would doubtless be a tall-growing cultivated crop, corn, tobacco, sorghum, sunflowers, or castor beans, for example. The evaporation would be increased if the weeds were allowed to grow beneath these crops or if, as is commonly practiced, another crop, a legume for example, were seeded in the field when tillage ceased.

The part that forests play in the control of climate, especially in the amount of rainfall in the regions near great forests, has long claimed the attention of intelligent observers. The influence of mountains upon precipitation, as set forth in the preceding section of this paper, is markedly increased if the mountains are clothed with a forest cover. The effect of the forest upon local precipitation may not be very great, but its influence is noticed in drier regions in the paths of winds coming from over forested lands. Hamberg says of the forests of Sweden: "The excess of evaporation which the forest vegetation furnishes to the atmosphere above what the same area would furnish if it were covered with herbaceous vegetation merely, must of course be very considerable. If this aqueous vapor were received in the forest and returned to the land in the form of rain it would be extremely beneficial. But winds carry it off and spread it in all directions with such rapidity that its beneficial influence for our country (Sweden) remains very doubtful." The cultivated lands in Sweden, especially its dairy farms, obtain the benefit of the moisture evaporated from the forests and continental countries east of Sweden also feel its beneficial influence, since they are in the paths of the winds blowing over Swedish forests. In the United States the Ohio Valley receives the benefit of the Appalachian forests when the winds are from the south. Much of the increased moisture of the prairie region of the central states over that of the plains states farther westward must also come from this source. The digest of the present writer's opinion on this point as given in a previous paper may be summarized as follows: (a) The coincidence of precipitation in the United States and prevailing southerly winds, (b) the amount of evaporation from a land surface as compared with a water surface, and (c) the greater efficiency of a vegetative cover, especially a forest, as an evaporating surface when compared with a water surface or a bare soil surface.

Movements of Air Currents

One of the most fundamentally important set of facts in aerography deals with temperature and pressure changes by which currents of air are moved horizontally and vertically over the earth's surface. We know that at sea level air is more compressed than on the tops of mountains, and we consequently obtain barometric registers of greater pressure at lower altitudes than at higher ones. By simple gravity air tends to collect right at the surface and air particles are here crowded and compacted. Higher up the air particles are farther and farther apart, and finally we may get to a region where air no longer exists.

Above the polar regions of the earth the air is less heated than above the equatorial region. Warm air rises and expands, while cool air tends to settle. There is a general tendency then of air to move inward from the polar regions toward the equator. This tendency is considerably offset by another factor, however, the matter of the unequal heating of land and water masses. The difference in the rate of heating was touched on in the previous section. The air over a land mass in summertime will become warm and ascend much more quickly than the air over a mass of water. In winter the air over a body of water is likely to have the higher temperature. With the changes of season there come to be established permanent areas of high or low temperature. The high-temperature areas of ascending air are areas of low barometric pressure. The low-temperature areas may be regarded as areas of high barometric pressure. Simple convection movements and tendency to stabilization and equilibrium would lead to horizontal movements as well as the vertical ones of the rising and descending columns of air.

The centers of action have come to be regarded by meteorologists as the essential factors in the control of climate. Buchan many years ago prepared maps of winds, temperatures, and pressures at sea level for practically the entire globe. It was Teisserenc de Bort at the International Meteorological Conference held in Chicago in 1893 who called special attention to the controlling influence which the centers of high and low pressure exerted upon circulation. He had named them more than ten years previously "the grand centers of action" of the atmosphere. They are understood to be closed areas of high and low pressure, or hyperbars and infrabars as they are commonly called, which have a certain permanence in a given season and give the leading features to the general circulation. In fact, the flow between these centers exerts the dominating influence on the circulation of the entire atmosphere.

FIG. 1. Chart showing the grand centers of climatic control. After Buchan. See also Adams's, "An Ecological Study of Prairie and Forest Invertebrates." Ills. Bull. Nat. Hist, 9 :70.

The centers of action come to have a motion of their own, due to the earth's rotation. In the northern hemisphere the cyclones or columns of ascending air have a counter-clockwise rotation. In the anticyclones or descending air streams the motion is clockwise. In the southern hemisphere the rotary motion of the cyclones and anticyclones is just the opposite of the motion in the northern hemisphere.

The accompanying diagram (Figure 1), modified from Buchan, shows the position of the permanent centers of action which exert a controlling influence over the summer climate of North

America. The hyperbars or anticyclones are marked "high" and the cyclones or infrabars "low." The arrows indicate the direction of rotation of the air flowing into or away from centers of action.

In midsummer there is a large area of low pressure over the central part of the North American continent. On the surface of the earth it is warmer east of a low-pressure area, because the winds blowing spirally, counter-clockwise, inward toward the low are coming from the south, which is usually warmer. Mr. J. Warren Smith of the United States Weather Bureau, in some private correspondence, has kindly pointed out the two laws which are operating:

1. The pressure controls the surface winds.
2. The surface wind controls the temperature.

The converging air is warm at the surface and remains so until it ascends, when it expands and cooling adiabatically, precipitates its moisture. It is to the east of the high that the warm weather and sometimes dry weather exists. The amount of rainfall would depend on the rapidity of the cooling and the total water vapor content of the inrushing air. As far as vegetation is concerned, though there might be rainfall, the final effect of the eastward migration of the low would be unfavorable, since in summer the drying effect of the warm air at the surface would not be balanced by the scattering showers.

Another shifting in the position of a great center of action which would be even more unfavorable in its effect on the vegetation of eastern United States is the westward migration of the Atlantic high shown in the diagram. Where the air is descending it is being warmed adiabatically as it reaches the surface of the earth and is taking up moisture. This air would then have a drying effect on the vegetation and the crops, and since it would be accompanied by clear skies the water loss from living plants would be extremely rapid. There would be no compensating showers brought in by this type of distribution of the centers, and if the positions were assumed for any considerable length of time the ensuing drouth would be followed by a failure of the plants to maintain a water balance. Wilting and even death would be the effect of a protracted drouth. Besides the continental low and the Atlantic high, there are three other region circulation centers, all of which have an effect on the climate of North America in summer. Their action is indicated in the diagram.

Thus the interplay of air currents plowing into and out of the grand centers of action can be seen to influence greatly all the living vegetation. Wind, from the standpoint of plants, is a moisture-temperature-relation factor. Increased wind velocity and increased temperatures both accelerate transpiration. In full sunlight the cooling effect of transpiration is the greatest possible benefit to the plant in preventing coagulation of protoplasm. Rapid transpiration probably also aids the plant greatly in the transfer of minerals after absorption from the soil. But rapid transpiration in the absence of equally rapid water absorption is undoubtedly a constant menace to the life and rapid growth of plants.

2. *Soil Factors*

In dealing with the soil factors which influence plant succession, the only measure which we may use for comparing different soils is plant growth. Obviously, it would be incorrect to talk of "fertile soils" or "barren soils" unless we had the climate as well as the soil expressed in some way. We cannot say that a soil will or will not support a dense cover of vegetation if we consider the soil simply inert mineral material or if we base our notion of productivity on the physical structure of the soil alone, or upon the chemical nature of the soil alone. The temperature and the moisture must both be included in our notion of soils. In the arid southwestern regions of the United States the soils contain salts in more than the amounts required for plant growth and the temperatures are high enough to support a subtropical vegetation. Water is, however, the limiting factor. In the sandy barrens of southeastern United States, the rainfall is high, the temperature high, and the growing season long, but mineral salts and available water seem to be the limiting factors.

The mineral portions of soils formed under arid or humid conditions are entirely different. In arid regions the mineral parts of the soil are formed through mechanical processes of weathering or by disintegration. Soluble materials are found in abundance in the soils of arid regions. In humid regions the mineral portion of the soil is the insoluble or only sparingly soluble material, since the most soluble portions have been carried off in the surface streams and ground water. The mineral portion of the soil in a humid region represents a chemical residue, and like the residue on a filter paper, it is frequently washed clean.

Plants need such small amounts of soluble salts for their development that the surprise is not that they are able to secure these raw materials in most soils, but that there may be found soils in a humid region which do not support abundant plant growth. The pine barrens are apparently an example of this. If a plant cover sufficient to accumulate salts, especially nitrates, in excess of what is carried away in solution and by oxidation, could be started on these barrens, there is little doubt but that a rapid cycle of succession would be initiated.

The mineral portion of a soil is also of importance ecologically because of the fineness of the particles and the nature of their arrangement. These properties are known as the texture and structure of the soil, respectively. The former is a relatively permanent property of the soil, that is, the size of the particles is not materially reduced in a short time. Certainly, cultivation and tillage produce no alteration in the size of the soil particles. The technical classification of the soils has been made largely on the basis of the texture. The structure of soils, the arrangement of the particles, is undergoing constant change. Frost, rain, plant roots, and burrowing animals are a few of the agencies which effect a change in the structure of soils.

The humus portion of the soil is rich in colloids, which are highly retentive of water. For this reason humus soils, or soils in which the humus portion predominates over the mineral portion, are proverbially productive soils. The old evolutionary idea, "all life from pre-existing life," may be translated to the environment when we speak of humus soils, for a soil full of humus contains the accumulated remains of previous generations of plants, and the future generations have this as their heritage. The humus furnishes the energy to bacteria, which in turn leave a newly molded form of energy for green plants.

The nitrifying bacteria do not add to the total soil nitrogen, however. They are unable to use free nitrogen and live solely upon dead organic material, converting the nitrogen into a form useful for the green plants. Some soil bacteria can draw on the free nitrogen supply, but the nitrogen thus accumulated must be converted into organic nitrogen compounds before it is available to green plants. This is discussed in the following section on the biotic factors.

The most important chemical fact about humus soils is that they are, under certain conditions, capable of supplying organic substances to growing plants. In addition to this, in humid regions, soils with a high organic content also have a high mineral content, since the growth of plants tends to prevent the normal amount of leaching which otherwise would take place. The prairie soils of North America and the chernoziom (black earth) of Russia are rich in both organic and soluble salts. If the color can be used as a guide to the lime content, (Coffey '09), then the order in which the soils of the United States rank is (1) the prairies, (2) the forests of eastern America. This accumulation of mineral salts in the soil is in agreement with the distribution of total rainfall throughout the year. It is greater in the forests and less in the prairies. In the prairies there has not been enough rainfall, or its distribution has not been such as to leach the lime from the soils at the rate that this is occuring in the light forest soils. Yet the rainfall in the prairies has been sufficient to induce a heavy growth of vegetation, which is only partly decomposed. This is because water standing during a portion of the year in prairie sloughs prevented as complete oxidation of the organic material as occurs in forests. The vegetation acted as a series of dams in a country of rolling topography made level by glacial action. These lakes or water-bottomed sloughs kept the forests out until man hastened the gradual drainage process. Thus we can see how climate and topography acting in unison formed soils in the east north-central states which are entirely different from the soils of the forested regions, though in many instances they have been derived from similar geological formation.

3. *Biotic Factors*

The influences of plants and animals upon the developing vegetation are known as the biotic factors. These are assigned various degrees of importance by different authors. Clements ('05) classified habitat factors into physical and biotic and ('16) he consistently eliminated an edaphic group while admitting its convenience. It is true that edaphic factors may be further resolved into topographic, or physiographic, yet this does not detract from the importance of having all the subterranean plant environment in a single group. If the resolution be carried out far enough, the last result will be something like Shreve's ('16), in which all the factors are physical. Cowles ('01, '11) has carefully distinguished the biotic factors and presents them in their true rôle of a source of the influences separate from the climatic or edaphic influences. The importance of biotic factors is seen nowhere so well as in the formation of soils, which in the majority of cases are due to the action of plants.

Among the various biotic factors the bacteria are of prime importance, especially the bacteria of the Nitrogen Cycle.

The first group are saprophytic, that is, they live upon plant and animal residues after the death of the individual. Their reactions reduce the plant and animal proteins to ammonia, hence the process is known as ammonification. The chief micro-organisms are Bacillus subtilis and B. mycoides. Ammonification is followed by rapid decay of the plant or animal residue. The ammonia remaining in the soil is commonly ammonium carbonate $(NH_4)_2CO_3$. Decay is followed by nitrification, an oxidation process carried on by the Nitrosococcus and Nitrosomonas bacteria. The ammonia or ammonium salts are oxidized to nitrites of the composition $(R)\ NO_2$. Further oxidation carried on by the Nitrobacter changes the nitrites, $(R)\ NO_2$ to nitrates, $(R)\ NO_3$.

The nitrates are useful for green plants and with the exception of some of the ammonium compounds, are the only form in which nitrogen can be absorbed by most green plants. At this stage denitrification by bacteria of the denitrifying group may liberate the nitrogen of nitrates into the free nitrogen of the air. The presence of these organisms is unfavorable to the growth of green plants therefore.

The completion of the nitrogen cycle is found in one direction by the building up of nitrates in the body of green plants into, first, the amino-acids, then the plant proteins, and finally animals subsisting on the plants build up the amino acids and proteins of plants into their own protoplasm. The cycle begins again with the death of animals and plants.

Free nitrogen of the air may under some conditions be fixed by groups of soil bacteria which derive their energy from carbon-material found in the soil or by living somewhat parasitically on green plants· Azotobacter and Clostridium sp. are the chief of these organisms. The former requires the presence of abundant oxygen and so works only close to the surface of the soil, while the organisms of the Bacillus radicicola group upon living roots of legumes, furnish an example of another kind of organism capable of extracting free nitrogen from the air. The bacteria are parasitic upon the legume which furnishes food in the form of compounds of carbon of its own manufacture. As the tubercles produced by the bacteria grow older, the appearance of the bacteria themselves is altered. They become larger, sometimes branching, and in this form are known as "bacteroids." Active nitrogen assimilation by the green plant coincides with the appearance of the bacteroids in the root nodules of the legume. If a large enough portion of the legume is then allowed to remain in the soil to offset nitrate nitrogen absorbed by the plant, there results a corresponding gain in soil nitrogen.

The reciprocal symbiosis of Phoma an endotrophic mycorhiza should also be mentioned as a relation which nets a gain in the nitrogen supply for the host plant upon which the fungus lives. The mycorhiza as a class are so important to many of the green plants that the latter are unable to grow except in the presence of the fungi.

Protozoa are also important, though mainly unfavorable, as they destroy the beneficial bacteria. Brown ('16) has described the importance of mold action and in addition there are other fungi—all the saprophytic ascomycetes and basidiomycetes.

The white pine blister rust and the chestnut blight are examples of biotic factors which cause certain plants to drop out of the native vegetation as surely as changing climatic or soil conditions cause them to disappear. Chestnut trees in New York and Pennsylvania have already been killed in such numbers as to alter entirely the nature of some of our finest forests. If the disease goes on unchecked it would not be strange to have inhabitants of these states inquiring in a hundred years from now if the chestnut actually grew in these portions of Eastern America. And yet the chestnut bark disease was noted as a menace on Long Island for the first time about the year 1905.

The white pine blister rust, as it has been named, has not yet done any considerable damage and it looks as though this disease will be checked, thanks to the efficient service of our forest pathologists. Yet in those small localities which were infected the white pine was completely destroyed. This disease is not only a menace to the white pine of Eastern United States, but likewise attacks the western yellow pine, another of our valuable timber woods.

Among all the chlorophyll-bearing plants there is competition for light as well as competition for moisture and nutrient materials in the soil. Thus, we see that the influence of the green plants themselves upon the vegetation must be greater than the influence of the non-chlorophyll-bearing plants, since there is active competition going on among the members of an association in addition to the action of the micro-organisms. A plant association cannot be regarded as completely closed until all the levels for abstracting water, minerals, light, and air are filled with sets of species of dissimilar habits and requirements.

The animals are as important in the mixing of soil materials as are plant roots. The importance of earthworms has been known since Darwin's classic work on the subject. Snails, ants, beetles, spiders, rodents, all contribute their quota toward mixing the minerals with vegetable mould and allowing air and water into the substratum. Insects are important in cross pollinating plants and in many species are essential to seed production. Insects may also act injuriously in destroying plants and may even effect complete destruction of a pure stand. The locust borer, to name only one example, has almost eliminated the black locust from farm wood lots and forests of the central states where it was long the favorite wood for fence posts. Birds are agents in the dispersal of seeds and spores. Rodents, rabbits, rats, and mice may destroy trees by pruning the bark, and prairie dogs destroy grasses. Sheep and cattle have been known to prevent the reproduction of some of the timber trees in the grazing region of the National Forests of the Southwest and West (Hill, '17), while the bison has been credited as being one of the agents to delay the invasion of forest upon the plains. Of all the animals, the destruction by man has been the greatest. There are almost no virgin forests left in the United States, due to man's activity.

4. *Summary of Climatic, Edaphic, and Biotic Factors*

It will doubtless have occurred to the reader that any classification of factors of the environment will present certain difficulties in the way of sharp distinctions between the subjects to be classified. The attempt made by the writer shows that the biotic factors cannot be escaped in talking of the other two sets, viz., in the climatic factors the influences of forests upon climate are featured, while the relations of soils and the micro-organisms are discussed under the edaphic factors. The climate and the soil are distinct enough in themselves; the difficulty of classification lies in the degree of modification which they undergo in reactions with each other and with the organic universe. For the present discussion the writer believes that he has carried the resolution of factors far enough. More rigid separation would destroy the continuity of the story of the facts in relation to one another.

5. *Examples of Succession*

Now that the factors contributing to succession have been thus briefly reviewed, some examples of successions which show how the vegetation gradually builds up soils and alters conditions for plant growth, should be included. For this reason two extreme areas have been chosen in order that the effect of plant growth in each case may be brought out. The two areas are a swamp and a dry rock surface. The effect of the changing conditions induced by the vegetation can be noted in the change in plant population shown in the following diagrams.

In the swamp series the open water surface is partly covered by floating aquatics which gradually deposit debris on the bottom of the swamp. This material slowly decomposes into the soil, which in time reaches near the surface. Here and at the shallower margins, rushes and sedges enter and occupy the soil until the shrubs typical of a button bush swamp, *Cephalanthus, Rosa carolina, and Alnus rugosa,* enter. These are succeeded by a willow stage, a red maple stage, a swamp oak stage, and finally an oak-hickory forest, in which beech and hard maple gradually appear. There has been a tendency toward drier conditions continually during this succession. The swamp gradually becomes filled and drained as the vegetation accumulates. The last stage of the swamp is a forest, with all but a few undrained patches occupied by a beech-maple forest. Wherever the conditions remained but slightly changed by the vegetation, the vegetation is itself much as it was formerly. There is, in other words, reaction between the vegetation and the environment.

In the cliff series we start with bare rocks on which only lichens grow. The action of these plants is to decompose slightly the rock surface and to add their own remains to the finely parted mineral material. Some of this soil sifts into crevices and here the action of the larger plants becomes effective in widening and deepening the crevices. By the time a heath stage has been reached the cliff is usually well covered. This stage is succeeded by a shrub stage and often by a coniferous stage. Gradually oaks come in, increasing the shade and lowering the water loss from the soil as well as the oxidation rate of humus. The oaks are succeeded in time by more mesophytic trees—beech and maple, which are again the culmination of the successions. In all of this series the action of the plants has been toward an increase in soil and moisture until the conditions became suitable for plants like beech and maple.

These successions teach the lesson of soil formation and bring out the importance of the biotic factor in soil building. They also show the importance of the genetic conception and the inadequacy of a static or even a merely dynamic system of classification, for the plants become a cause of subsequent change. Successful invasions are of course in the beginning the effect of certain conditions of the bare area into which they migrate. Chance is the sole criterion of the original seed or spore introduction, but the life of the seedling after introduction depends upon its inherent ability to meet the conditions of the environment.

PART II

FACTORS INFLUENCING CROP DISTRIBUTION IN THE UNITED STATES.[1]

That the crop plants are bound by the same laws of physiology as other plants is an obvious truism. They respond in the same way to changes in the environment. They become adjusted to the conditions which they encounter. From the point of view of the crop grower, this response is indicated by an increased yield. There are well known physiological strains and races of cultivated plants just as clearly distinct as morphological races. Examples are: Sixty Day Oats, rust-proof asparagus and anthracnose resistant varieties of beans.

It is important to determine how far the analysis of the relationship of the plant to its environment can be carried in the crop plants. Are the methods of study used in ecology useful here? Can a relationship be established between plants under cultural conditions and the natural vegetation? The study of the indicator significance of the natural vegetation is just beginning, and offers to lead the way to possible future crop production. It has been applied to cropping in the Great Plains by Shantz (1911), Kearney (1914), and to locating forest sites by Korstian (1917), and others. The results indicate how much can be done by the intelligent application of the methods for studying plant associations to problems of culture. It also seems possible that very slowly a scheme of ecological equivalents might be worked out. For example the statement is generally accepted that where sassafrass grows peaches can be successfully produced. This statement is misleading. For sassafras can be found growing under a great diversity of conditions, and there are many varieties of peaches. It is useless to spend much time in looking for individual ecological equivalents, unless they can be grown under controlled or at least measurable conditions.

In the present discussion an attempt is made to indicate some of the relationships between great plant formations and certain crop centers. The studies are, entirely, generalizations. Only the broad-

[1] Presented at the Pittsburgh meeting of the Ecological Society of America, Jan., 1918.

est groups of factors limiting plant distribution can be discussed in such a study. The climatic, the edaphic, and biotic factors are given a brief treatment with respect to the endemic vegetation. Later for the crop studies, a fourth group of factors is added. The rainfall-evaporation ratio, (Fig. 2) successfully employed by Transeau ('05) in delimiting the forest centers, has been used as a basis for this study. This was secured by dividing the total rainfall for a given station by the evaporation obtained from Russell's (1888) data on evaporation.

The centers of vegetation of North America are as strongly differentiated in the United States by the common crop plants as by the native plants of the forest centers. Timothy, spring wheat, rye, buckwheat, and potatoes occupy the same region as is dominated by white pine, spruce, hemlock, balsam fir and white birch—in other words the northeastern evergreen forest. The region occupied by corn, winter wheat, oats, red clover and beans is related to both the central deciduous forest and the prairies. This emphasizes the importance of edaphic factors in plant successions and the relation of the crop to edaphic conditions.

For although the grain belt extends eastward into Ohio, it does not reach far from the edaphic prairies. Tobacco occupies a median position between the central deciduous forest and the southeastern mixed forest. Cotton, yams, cowpeas, and peanuts center in the southeast.

The criteria which have been applied in delimiting the forest centers hold for the crop centers as well. There is first of all dominance. The evidence that one is approaching the center for a given crop is the number of farms upon which it is being grown. In this connection it is interesting to note that while central Illinois is for very special reasons, the center of production of corn, yet in point of acreage devoted to it in proportion to cultivated lands, corn is the most important crop of southeastern Kentucky. No hills seem too steep or too high for the farmers to attempt to grow a corn crop. Compared with production in Illinois, the results on these hills seem far from encouraging. The production and total acreage can be used in determining this center. (Fig. 3).

In the natural vegetation next to dominance come maximum size for the species, greatest differentiation of type and widest range of habitat as criteria of the biological centers. These are all corollaries of general well being, the result of the limiting factors being fewer and less effective. In the crop plants we can see that

FIG. 2. The ratio of rainfall to evaporation in percentages. Data for the Pacific Coast are not available. The desert lies west of the 20 percent line, the drier grasslands from the 20 percent to the 60 percent line, the prairies and their eastward extensions between the 60 percent and the 80 percent lines. Where the ratio is greater than 1 there are forests. After Transeau, with slight modification.

in the centers even the rough, hilly land produces a fair yield. Then it will be noticed that more varieties of a given plant are known. For example it is at the Cornell Station that work in selecting and improving timothy can best be carried on, because of the ready access to timothy variations. At the Minnesota station the collection of wheat varieties and improved strains of wheat is very large. The same is true for corn at the Ohio, Nebraska, and Illinois Stations.

There is another analogy still to be drawn. In the endemic vegetation the center of distribution, that is, where a species dominates, is not necessarily the center of dispersal, the place from which the species is spreading. Rather it is implied that in the center the limiting factors are fewest, and least effective. As one recedes from a center the limiting factors increase in number and in intensity. In the crop plants it can be shown that the regions of greatest yield per acre—which correspond to the centers of dispersal of the vegetation—are frequently separated from the regions of maximum production. For instance in the case of wheat, the yields are higher in the humid section where the rainfall is eight-tenths or more of the evaporation called for. Yet the maximum production of wheat centers in the region where the rainfall is only six-tenths or less of the evaporation called for. An attempt to correlate crop centers and vegetation centers considering only the climatic and edaphic factors would present many strange anomalies. These explanations alone would not support the facts of the distribution. It is necessary to go outside the field of physiology to discover the basis of crop distribution.

The fundamental difference in the occurrence of plants belonging to the natural vegetation and the crop plants lies in culture. In the vegetation invaders from another center are frequently restricted to one habitat, often a poor one. Arbor vitae in central Ohio is confined to the rock terraces of stream gorges and to bogs. The white pine and the scrub pine meet on rock cliffs east of the glacial boundary. On Lake Michigan sand dunes the jack Pine and the cactus meet. Yucca extends northward along the sand plains of the Atlantic seaboard. In the better habitats competition with the plants belonging to the center would be too keen for the invaders. With the crop plants the case is almost the reverse. When they are beyond their climatic optima they are generally to be found on the richest lands of the farms. In New York and eastern

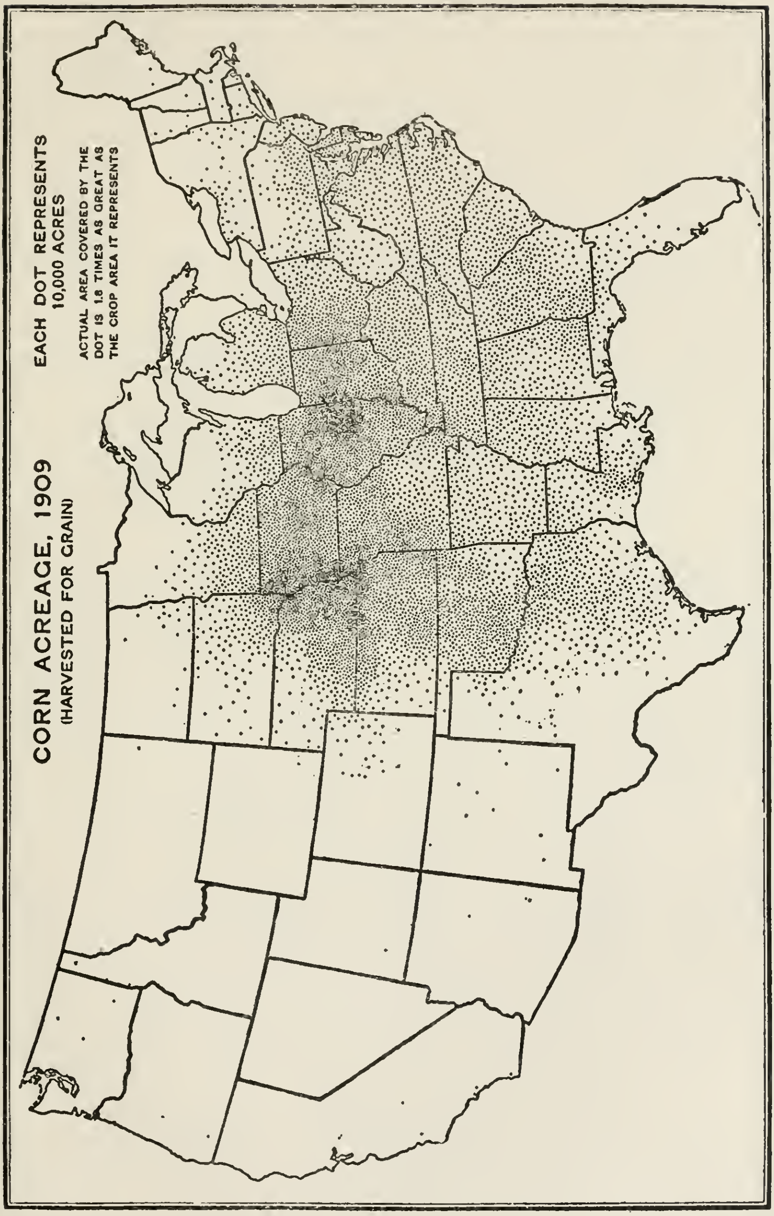


FIG. 3. The corn acreage of the United States. Note the acreage in Eastern Illinois and the Missouri River valley and compare with southeastern Kentucky. Compare Eastern and Western Ohio. From 1915 Yearbook, U. S. Dept. of Agriculture

Pennsylvania only the best fields are ever used for growing corn. These are reinforced and amended by a liberal use of manures. This coddling is carried out to a greater degree in the Connecticut River Valley where tobacco is grown. Not only are the soils treated, but the plants are sheltered under cloth. This cuts down the transpiration rate during the day and at night prevents loss of heat. The climate thus produced is more like that of the center of the tobacco industry.

With the crop plants then, climatic optimum is not the factor which determines the center. The soil conditions are not always the controlling factor. It is the profits.

It is profit which causes the potato crop to center, (Fig. 4) near each of the thirty largest cities of the United States without much indication of climatic or soil preferences. It is profit which links the corn belt with the center of oats production, though the former is pushed upward from the south and the latter down from Canada. Profits makes New York and New England a large meadow of imported cultivated grasses, while the native prairies and plains grasses only come to market if pastured.

An economist attempting to minimize what he regards as an undue preponderance of the physical factors would explain these distributions on the theory of rent. He would imagine a hypothetical state. This state would be circular in outline and present no differences in climate, topography or soils. All transportation problems that existed would be equally distributed over the state. Under such conditions, the state would be divided into many concentric zones. Around the city would be truck gardens; next to these, a dairying community; next, grain farms; and in the outmost circle pasturing would be the chief agricultural endeavor. (Fig. 5). The explanation of the zonation of this unusual state would be that the grain farmer, making more profit than the shepherd, could afford to pay more rent than the latter and so live closer to the city and his market. The dairyman's rent would be higher than the grain farmer's, and so on into the city. The economist has a good case and there is no way of circumventing his argument. We see examples of the working out of this hypothesis on every side.

Now the truth of the matter of crop production and the centering of crops in certain localities lies somewhere between the geographic considerations of climate and soils and the purely hypothetical proposition of the economists. They cannot escape, under

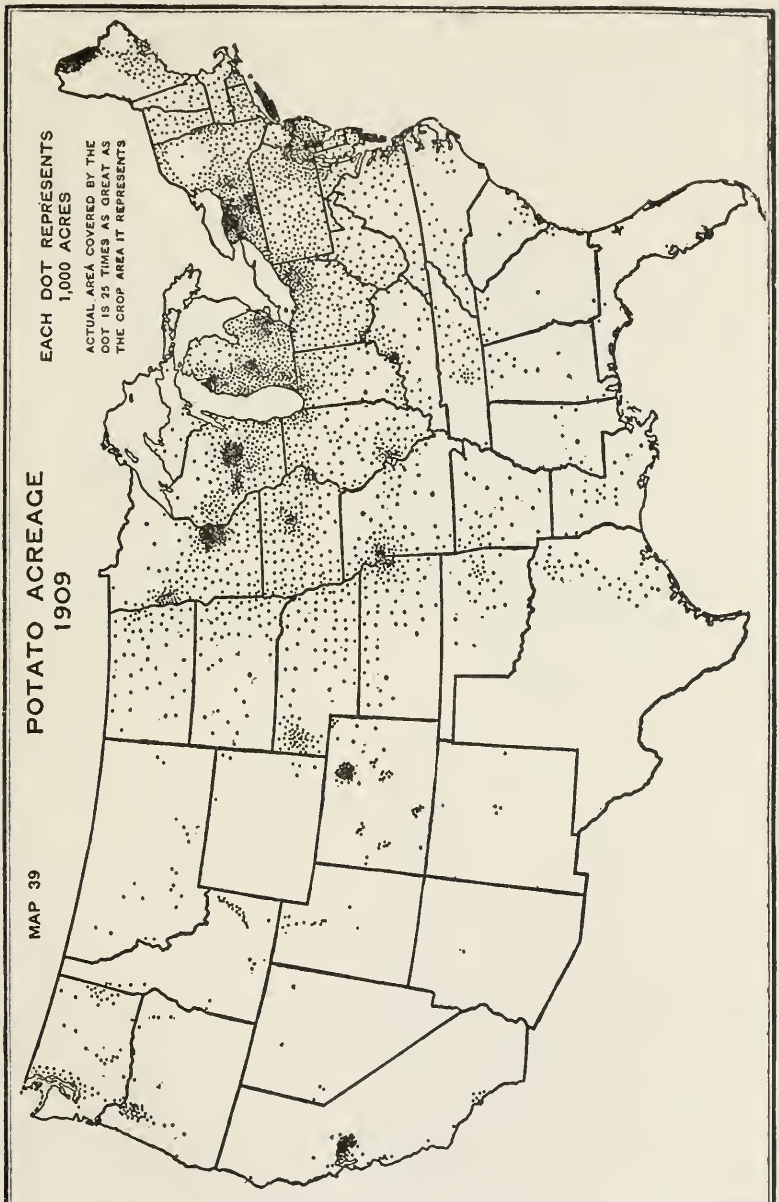


FIG. 4. The potato acreage. Note that except for Northeastern Maine the centers are not far from centers of population. From 1915 Yearbook U. S. Dept. of Agriculture.

actual conditions, the influence of soils and climate. The factors are like the legs of a three-legged stool.

The economist can never avoid the fact that it is sometimes the edaphic group and sometimes the climatic group of factors which stand back of this very profit he is studying. Climatic

Fig. 5. Zones of production on a purely hypothetical economic basis.

conditions determine the physiological limits of the cotton crop. (Fig. 6). It is the climatic conditions and not the economic only that determines the dominance of cotton. Corn is not and never can be a serious competitor of cotton. In the case of spring wheat, edaphic factors limit its distribution to the Dakotas and to Western Minnesota. Here is a level tract of land with rich productive soil, a bequest of the long-deceased Glacial Lake Agassiz.

Finally it would be well to point out an economic factor, not a part of the theory of rent, which is intimately related to the pro-

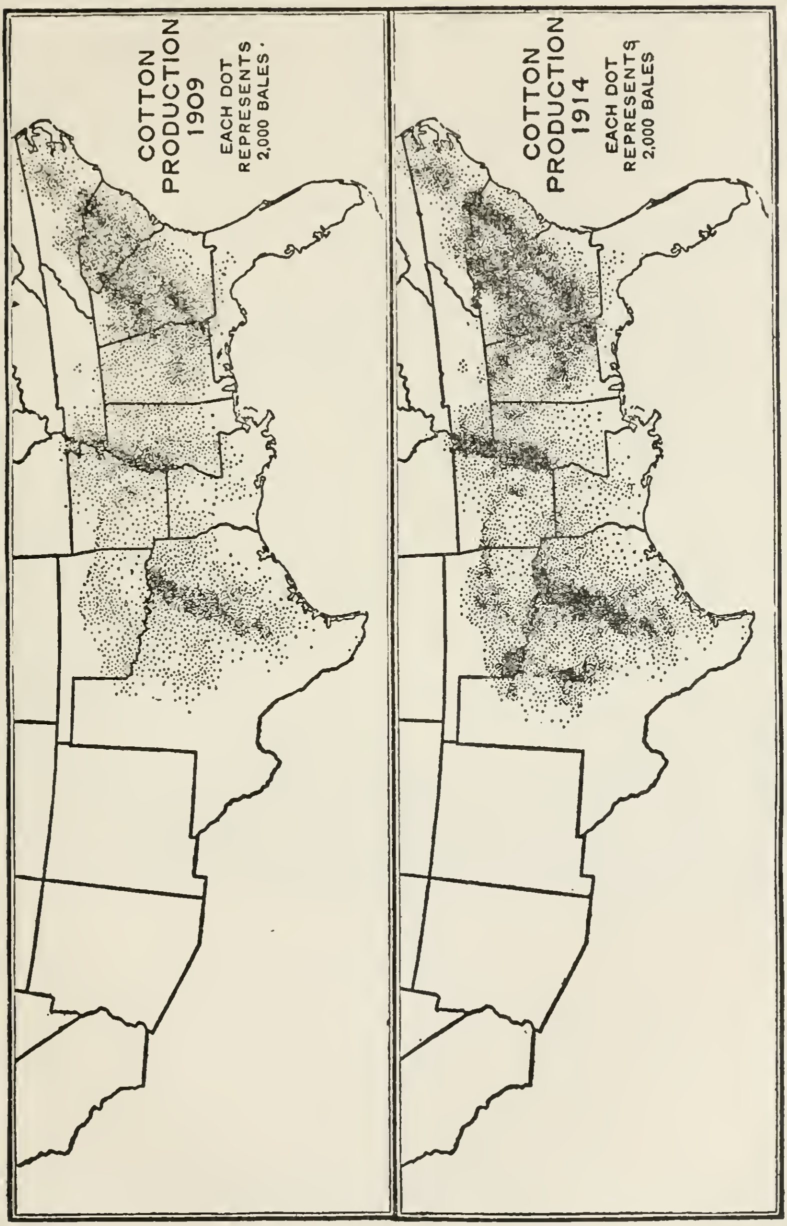


Fig. 6. Cotton production in 1909 and 1914 compared. Note the geographic relation of the cotton-belt States to the corn-belt States. Compare with figure 5. From the 1915 Yearbook of the U. S. Dept. of Agriculture.

duction of spring wheat. It is the invention of a milling device which made possible the manufacture of a handsome white flour from spring wheat. This device called the purifier, separated the bran and endosperm better than any previously known machine had done. But this machine, invented a generation ago, did not establish the spring wheat center. It only intensified the already increasing production. This helps one to understand how the economic factors operate in crop distribution. They do not create the conditions for plant growth, but profit is largely the determinant which carries on or halts crop production.

In the ecological study of the vegetation, climatic conditions are put down as the broad general determiners. The edaphic factors modify the effect of climate. In favorable soils, the center is extended. In unfavorable soils, even well within the center, the occurrence of certain plants is prevented.

In the crops the economic factors increase or diminish production. The physical factors determine whether or not a certain plant may grow, but the profit determines whether or not production will increase. This is the problem of the food administrator; to make the price of wheat, say, high enough to tempt the farmer to increase production, and at the same time not to put it out of reach of the majority of consumers. The relation of the economic factor to crop production is analogous to the relation of the edaphic factors to the climatic in the natural vegetation. The edaphic factors have such an influence in modifying the climatic that the occurrence of a certain plant is the direct result of the edaphic influence. The economic factors have such an influence in modifying crop production, that even though the underlying climatic and soil factors are suitable, production is still limited by the profits.

PART III

THE CROP REGIONS OF OHIO AND THEIR SIGNIFICANCE

A. Topography and Drainage

Ohio lies at the western edge of the Allegheny plateau. This extends partly within the state, and constitutes the eastern and southern three-fourths of it. The northwestern one-fourth is in the Erie Plain. Southwest, the Allegheny plateau merges without a definite line of separation into the Lexington Plain extending northwest from Kentucky (see Fig. 7). In the extreme northwest corner of Ohio is a low escarpment, separating the Erie Plain from the Thumb Upland of Michigan. Thus the Erie Plain forms a trough tilted toward Lake Erie. In Ohio the Erie Plain ranges in altitude from 575 to nearly 1000 feet above sea level. (Geologic Atlas, Columbus Folio pp. 1 to 4). The relief is, however, slight, and it is on the whole a gentle rolling plain interrupted only by low swells and morainic ridges. The Allegheny Plateau in Ohio stands between 1000 and 1500 feet above sea level. It is tilted southwestward and westward. The highest point in Ohio is at the western edge of the plateau, near Bellefontaine in Logan County, and is 1550 feet above sea level. In the eastern and southeastern parts of the state, the plateau is so much dissected by valleys from 200 to 800 feet deep that but little of the plateau nature is discernable. The escarpment separating the plateau from the Erie Plain is well marked in the northeastern and central part of the state. The western ends of the escarpment are, however, obscure and broken in two places by gaps which extend southward in the broad valleys of the Scioto and Miami Rivers.

The drainage of the Erie Plain and its immediate boundary in Ohio, about 12,000 square miles, is into Lake Erie and so on into the Gulf of St. Lawrence. The rest of the state, about 30,000 square miles, is drained into the Ohio River and through the Mississippi to the Gulf of Mexico. Ohio thus lies on the divide of the two great continental drainage systems of Eastern America. The divide between these systems is on the whole rather level and inconspicuous, resembling a rib of an enormous umbrella rather than the ridge of a roof. Lake Erie is about 140 feet higher above sea level than the Ohio River. The plateau is better drained than the plain, except near the edge where the drainage is rather poor and there are a number of small lakes, swamps, and prairies. The narrow belt of the Erie Plain along the lake shore is also well drained,

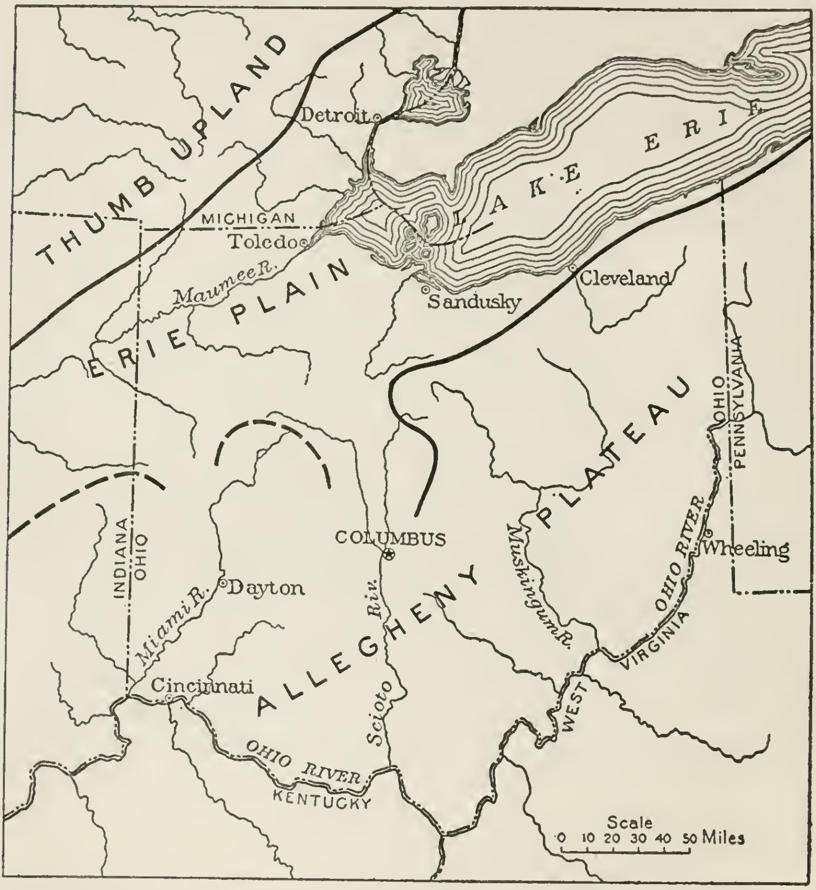


FIG. 7. Outline map of Ohio showing the physiographic divisions. From the geologic Atlas, Columbus Folio 197.

but in the broad, nearly level area of the northwestern part, the drainage is somewhat obstructed by glacial deposits. (Fig. 8). These were formerly lakes and swamps. Later, they became prairie areas. In recent years, however, drainage and cultivation have effaced these except for the rich humus soil and a few relict plants in undisturbed patches.

There are some interesting features of the drainage of the state which should be emphasized because of their bearing upon the biota. From a biological point of view all of the valleys are regarded as special means of ingress of animals and plants. It is

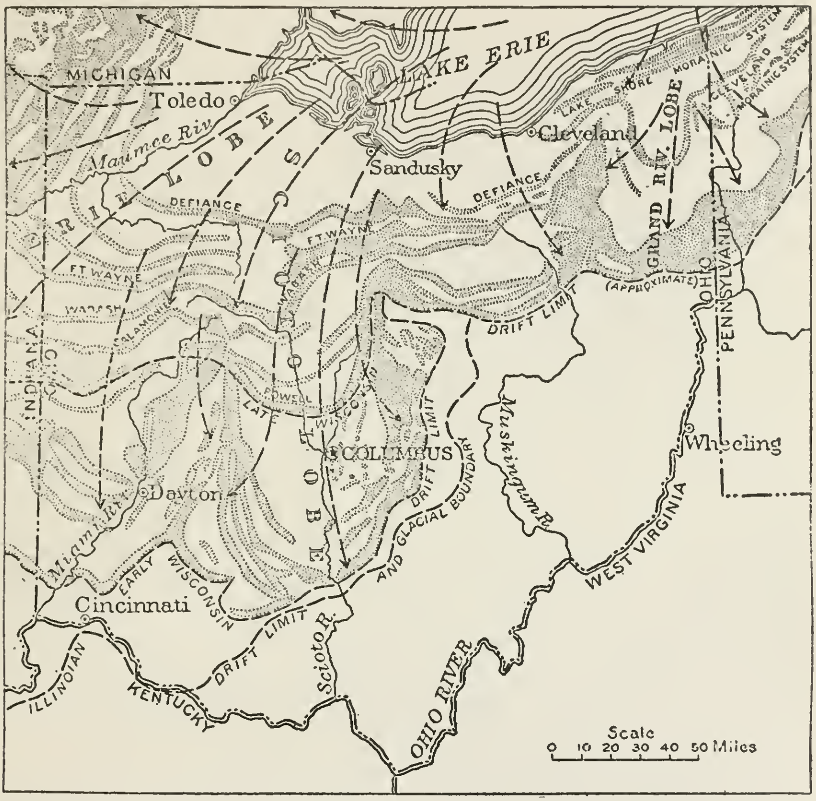


FIG. 8. Map of Ohio showing glacial moraines and the limits of the drift left by the ice at its several stages. The arrows indicate the direction of the ice movement. After Leverett, in Geologic Atlas, Columbus folio 197.

not surprising then that many plants of the northeastern evergreen forest have found their way into Eastern Ohio from the lake and southward along the valleys which drain into the St. Lawrence basin. Furthermore, a number of strictly southern species have made their way into Central Ohio by progressing northward along the valleys which are tributary to the Ohio. The state which lies within the deciduous forest then, serves as a meeting ground for both plants and animals of the northern and southern evergreen forest, many of which are on the edge of their ranges. The drainage systems are to a large degree responsible for this condition.

B. The Soils

Soils represent the action of plants upon finely divided mineral materials. In the broadest sense the term soil means the unconsolidated mixture of mineral and organic substances in which green plants grow. This forms a covering, varying from a few inches to many feet in thickness, over the rock surface of the earth's crust. In a more restricted agricultural sense the *soil* is only the surface eight or ten inches of this material. It is the upper part which contains the largest proportion of the roots of plants and which has become dark in color from the organic content. All strata below this surface layer are termed *subsoil.* After the mineral matter of the subsoil has been exposed to the action of the weather and has become the home of plant and animal microorganisms, it gradually becomes transformed into soil.

The mineral part of Ohio's soils were, for the most part, derived from the geological formations underlying them. (Fig. 9). One of the results of glacial action was the transportation of material from north of Lake Erie. As the ice melted, the stones, clay, and sand thus transported were left in a great mantle of drift on top of similar finely ground material. Part of this transported material became mixed with the soil existing at that time. Since then much of the original drift has been carried away by stream erosion, first as the ice melted, and second after it entirely disappeared, by the normal stream flow. Some streams have cut through to the original bedrock in many places. Others have been forced by the accumulation of drift material, to cut entirely new channels. The soils then, in the glaciated region, consist of bedrock material, surface and subsoil, plus a little transported soil material and the organic remains of plant life which has not been washed away since the beginning of post-glacial time. Coffey (1912) gives a full discussion of the soil types of the state.

In the unglaciated region of southeastern Ohio, the mineral part of the soils has been derived from the underlying bed rock exclusively. Since the mixing effects of glaciation were lacking, the composition of the soil material corresponds closely to the composition of the rock except as weathering and organic action have altered it. The dissection of the Allegheny Plateau by streams has left many steep slopes and deep valleys. The leveling action of the streams, that is, the lowering of the hills and filling of the valleys has been slight as compared with the leveling in the

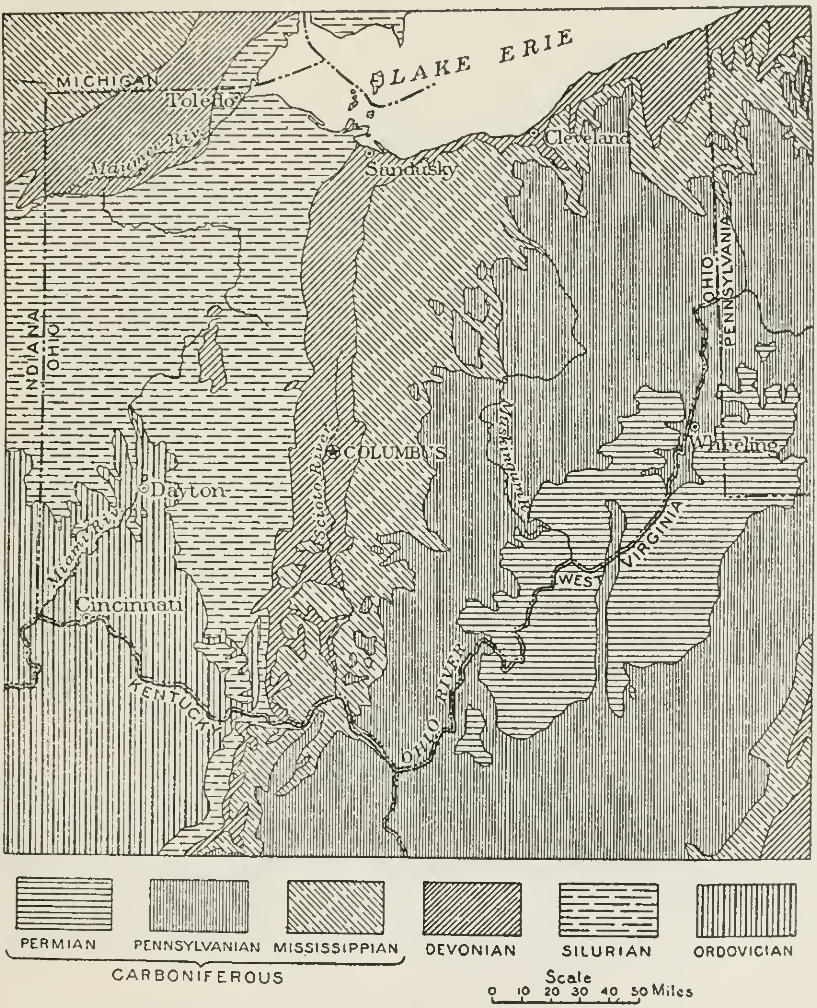


FIG. 9. Geologic map of Ohio. From the geologic map of North America in U. S. Geol. Survey Prof. Paper 71.

glaciated sections of the state, where the deposits of till have filled and blocked many of the valleys. On the steep slopes subject to rapid erosion, good soil is not formed unless the plant cover is left entirely undisturbed. The best soil in southeastern Ohio is to be found in the stream bottoms where the surface material washed down from the slopes has accumulated. With the cutting of the forests, however, many acres of fine bottom lands have been, for a time at least, ruined since the erosion of the hills was rapid enough to wash down sandy subsoils. Instead of leaving a fine deposit of rich organic matter as is usually the case, floods frequently drop a load of coarse sand and gravel and bury the best soil of the farm several feet below the surface.

From the standpoint of plant successions, the original composition of the soils has not had a great deal of influence upon the plant life. Succession on clay soils and upon sandy soils is much the same, though on the sandy soils the cycles require a longer time from the initial stage to the completion of the cycle. The structure of the soil, since it greatly influences the water content, has, on the other hand, a most important influence. In the glaciated region of the state the soils were mixed thoroughly and a good deal of material was clay. In the unglaciated regions the soils are not mixed, except the alluvial soils, and have been derived *in situ* largely from the underlying rock. The successions in the glaciated regions have, except for the lake and swamp areas, advanced as far in the cycle in postglacial time as the succession in the sandy and over-drained unglaciated region. In the latter area the development of the vegetation has not been in any broad way interfered with for ages preceding the advance of the several ice sheets.

C. The Climatic Conditions

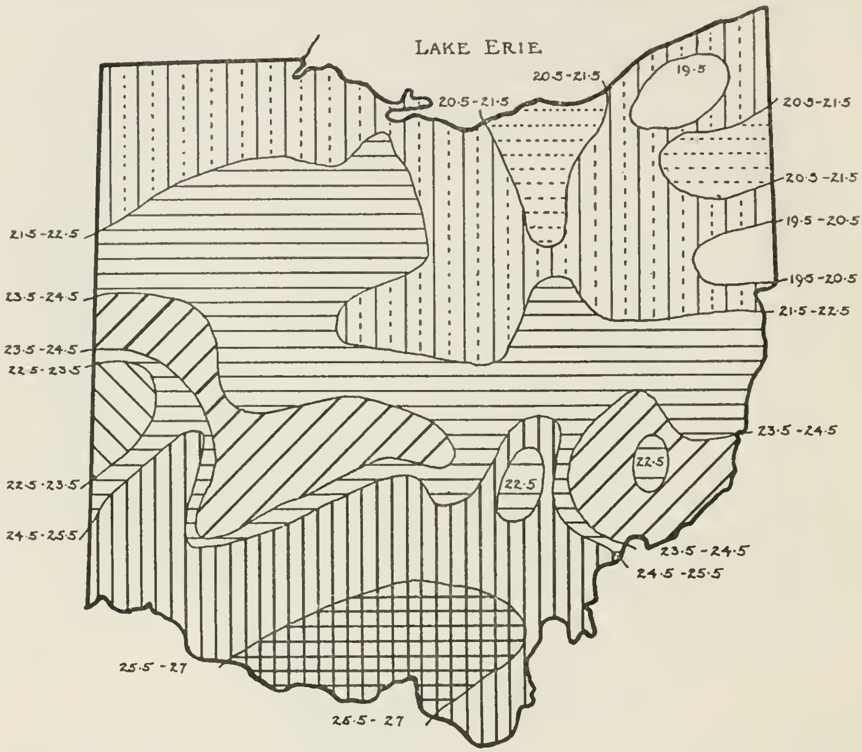
The influence of climate upon plant and animal is everywhere considered to be of fundamental importance. In the broader geographic sense climate is more important than soil conditions. The latter, however, frequently limit the local distribution. Elevation above sea level, latitude, relation to large bodies of water and the direction of prevailing winds are all factors which exert a controlling influence upon the climate of a region.

The effect of land relief and of elevation is to be seen in the precipitation and in the length of the growing season, i. e., the number of days between frosts in spring and fall. The least precipitation occurs in the flattest portion of the state—a part of the Erie Plains (see Fig. 10), and in a narrow band southwest of Lake Erie. Here the annual precipitation averages from 30 to 34 inches. The greatest precipitation occurs in eastern and southeastern Ohio, one region being a band covering the Ohio River counties from Brown to Mahoning and another being a center southeast of Lake Erie in Lake, Ashtabula, and Geauga counties.

FIG. 10. The average annual precipitation for the different sections of Ohio shown graphically by means of shaded areas. The total fluctuation is eight inches. The least rainfall is near the western end of Lake Erie, averaging about 32 inches. There are large areas in the western portion of the state having an annual rainfall of less than 34 inches The heaviest rainfall occurs along the Ohio river, where, in the most heavily shaded part of the diagram the precipitation is more than 40 inches.

Here the precipitation averages 40 inches. The reader is referred to the charts appearing in the Ohio Agricultural Experiment Station Bulletin 235, one of which is here repeated in a modified form. Elevation also shows an influence in the length of the growing season. In southeastern Ohio stations only a few miles apart horizontally, but with a difference in elevation of several hundred feet, may be twenty days apart in the length of the growing season. For example, at Milligan twenty-three years of frost records give an average of 145 days in the growing season. Eighteen years of records give Somerset 174 days.

More important than the length of the growing season, how-



MEAN EFFECTIVE HEAT

MEAN TEMPERATURE ABOVE 42° FROM APRIL 1ST TO OCTOBER 1ST

Fig. 11

ever, is a chart of the mean effective heat (Fig. 11). The data for this chart were obtained through the kind cooperation of Mr. W. H. Alexander, meteorologist and section director in the U. S. Weather Bureau, who allowed the writer to examine the records on file in the Columbus Weather Bureau office. The temperature normals from all the weather observation stations in the state were obtained and the average temperature from April to October found. From this average 42 was subtracted, since 42° F. can be regarded as an average temperature below which plants do not grow very actively. In other words, it is the threshold of our spring season as far as the temperature is concerned. Although the station's records used in the chart are rather scattered in the southeastern portion where temperature varies most and where therefore the stations should have the highest distribution frequency from our point of view, some allowance has been made for elevation. This chart will be modified in the future as increased data seem to warrant it.

Columbus, on the fortieth parallel of latitude is slightly south of the center of the state. The extreme southern portion of the state extends a little south of 38° 30′ N. latitude. The northernmost point almost touches latitude 42°. This position of Ohio affects the seasons and the total amount of energy received from the sun. At Columbus the length of the day varies from nine hours and twenty-one minutes on December 15th to fifteen hours on June 15th.[1] During the longest days of summer the average length of the day is almost eighteen minutes longer in the northern part of the state than in the southern. Reference to Part I is sufficient to inform the reader that the dispersal of the energy is of greater importance in plant and animal geography than the total absorbed, so we may pass this point without further comment. Smith ('12) loc. cit. has described the general climatic conditions of Ohio as follows:

"Ohio is in the path of the general low pressure or storm areas which move across the United States from west to east. These areas move at an average speed of 600 miles in twenty-four hours and are preceded by southerly winds and high temperature, and followed by northerly winds and lower temperature. They are usually accompanied by cloudy weather and precipitation and each storm causes an average of from one to two rainy days at each place as they pass across the state.

As there is an average of two of these storm areas each week with fair weather periods between them, it follows that the change in weather conditions is rather rapid.

Yet Ohio is far enough from the coast so that the damaging Gulf and Atlantic storms lose very much of their severity before reaching our borders."

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1 These figures are for the year 1917. There is a slight variation, a few minutes per day, from one leap year to the next. This is not of any significance in the present work.

No comprehensive detailed studies of evaporation in this state which can be correlated with plant growth have been made. Dickey ('09) and Dachnowski ('11) have studied the evaporation at Buckeye Lake, using the Ohio State University campus lawn as unity. Sears ('16) has shown the evaporation in the plant zone at the edge of a marsh in the Lake Erie region. There are no other data available at present.

For a comprehensive idea of evaporation and rainfall there is the map of rainfall—evaporation ratios of Transeau (Figure 2, p. 35), however. This gives a generalized picture of the effect of air temperature, wind velocity and evaporation power of the air in their effect on plant life. It was made by examining the forest and prairie centers and finding a moisture index which best described their climatic peculiarities. This chart shows that the northeastern corner of Ohio, where *Pinus strobus* and other plants of the northern evergreen center are known, has a rainfall evaporation ratio of 100 to 110 percent. The greatest portion of the state is covered by the deciduous forest and has a general ratio of 80-100 percent, while in the edaphic prairies of Ohio the ratio is between 60 and 80 percent. Further work on evaporation and its relation to the vegetation centers is in progress. As soon as this is published our understanding of the relation of forests and prairies in Ohio will be greatly enlarged. The Erie Plain has uniformly less than 34 inches of rainfall, the Ohio River region 40 inches. The heaviest rainfall occurs during the summer months. June, July, and August. June has the greatest average rainfall with 4.13 inches. July is only slightly less rainy. The least monthly rainfall is in October, averaging only 2.52 inches.

The path of the storm track has an influence upon the direction of the prevailing winds. Over most of the state the prevailing winds are from the southwest. Two notable exceptions, however, are Cincinnati and Cleveland where the prevailing winds for the year are from the southeast. The average hourly wind movement is nearly nine miles. It varies with the season, being greater in the winter and spring months than in the summer and fall months. Near Lake Erie the average velocity is greater than in the central and southern portions of the state.

The humidity or the saturation deficit of the air is one of the most important climatic influences upon plant and animal life. In a state as large as Ohio and with such varied topography, the rate of evaporation differs widely under various conditions. The southern boundary of Ohio, along the river, is in approximately the same latitude as Washington, D. C., while the northernmost point approximates Cape Cod, Massachusetts, in latitude. The summer temperature at these extremes would influence greatly the evaporation rate. There is a difference of approximately a thousand feet in elevation from the lowest part of the Erie Plain to the highest point of the Allegheny Plateau. This would also affect evaporation to a marked degree how, while the wind velocities would vary in the level regions and "cold waves pass across the state with sufficient intensity to ventilate and invigorate the towns and cities and send their health-giving winds into all parts of the state, and yet the cold waves are not so severe in Ohio as in corresponding latitudes in the Mississippi and Missouri valleys." The fact of great significance is that Ohio lies directly across the path of one of the main storm tracks, and there is rapid alternation of areas of low and high barometric pressure. The writer ('18 p. 55) has discussed the influence of this feature of climate upon crops.

The state is 205 miles long from north to south and the effect of latitude is seen in the climatic difference in the northern and southern extremes of Ohio. The influence of Lake Erie is to counterbalance the effect of latitude in a narrow strip just southeast of the lake. Lake Erie is an inland sea, giving an oceanic climate to a narrow strip of land bordering it. The work of Miller, (1917), in Wisconsin shows the climatic effect of the lakes over territory comparable to the Lake Erie region of Ohio. The mean annual temperature in the northern part of the state is 48° F., in the central portion 51°, and in the southern portion 54° to 55° (Smith '12). The coolest sections of the state are in the northeastern and northwestern districts, while the warmest are in the extreme southern and southwestern counties. Isothermal lines show the influence of elevation. From Champaign to Ottawa counties, a distance of over 100 miles across the Erie Plain, the average temperature varies less than one degree. The lowest mean annual temperature is in Portage County, 47.2°. The highest, 55.5°, is in Scioto County. The precipitation shows similar differences, increasing southward. The least precipitation is near the western end of Lake Erie, and the greatest along the Ohio River.

D. The Vegetation Centers Entering Ohio

When the climatic features of a region are studied it is necessary to correlate these features with the climatic conditions surrounding it. We cannot understand the vegetation of Ohio as it exists today without having something of the nature of the vegetation of Eastern North America in mind.

Adams ('02) has pointed out the ideas of centers of flora and fauna which have been accepted and amplified by ecologists. Since plants migrate into and multiply in regions where the soil and climatic conditions are favorable, we can regard the native vegetation as a criterion of the climatic and soil conditions. We must not overlook the fact that after the plants are once established they are themselves agents in altering climatic and soil conditions, especially the latter, and they pave the way for the spread of other species. From our point of view then, the plants are both passive and active, are effect and cause.

For the existing plant cover, it is not necessary to go back any farther than post-glacial time following the last glaciation. The vegetation in southeastern Ohio is much older than that, however. During glacial times southern Ohio became the refuge of northern plants, retreating before the advance of the ice sheet. Along the margin of the advancing ice was a series of bands which from the ice outward were: (1) Arctic tundra, (2) a bog-shrub zone, (3) northern evergreen forest. Beyond this the central deciduous forest was little disturbed except for the advent of the northern species. In the southeastern part of North America the southern evergreen forest was not at all disturbed by the ice cap of the northern part of the continent. These conditions were discussed by Transeau ('03), Chamberlain and Salisbury ('06), and by Clements ('16, p. 372). The climatic changes as recorded in the peat bogs at that time have been discussed by Penhallow (1896, '98, '00) and Harshberger (1911) and Dachnowski (1912, p. 209).

There were several advances and retreats of the ice sheet, and according to Leverett ('02) the glacial boundary is a combination of four invasions, but when the ice finally made the retreat which carries us into the present time, there was a gradual migration of the vegetation northward. The shrub-bog zone advanced into the tundra, the northern evergreen forest into the shrub, and the deciduous forest regained its former terrain. There is no definite information as to whether the movement is still going on or has come to a full stop. However, we can still see in Ohio the advances of the deciduous forest into regions held by northern evergreens, as for example, the capture of the arbor-vitae bogs by deciduous plants. This movement has been hastened by agricultural activities. The bogs existed only as biological islands. Their destruction means extermination, since the conditions which led to their preservation are rapidly passing.

Ohio has been divided into four vegetation regions by Selby (1899). This had the approval of Dachnowski (1912) p. 203. These four divisions are: 1. The Lake Region; 2. The Western Plain or Calcareous Region; 3. The Scioto Valley Region; 4. The Appalachian Region. This *static* classification has for its chief convenience the fact that it divides the state into regions of approximately equal size. It has on that account been followed by the United States Weather Service. As a matter of fact it is not very closely related to the biotic centers which traverse Ohio. Following the physiographic divisions already made in this paper, we have the Allegheny Plateau and the Erie Plain. The plateau is occupied by the deciduous forest, which has its center in the Ohio and Wabash valleys, except as the plateau is held by plants of the two evergreen centers. *Pinus strobus,* from the northern center and *P. Virginiana* and *P. rigida* from the southeastern center are both present in the eastern part of the state. The northern evergreen center is better represented than the southern evergreen center. Then there are on the Erie Plain and in a few scattered spots south of the plain, typical prairie plants. The four vegetation centers represented in Ohio are: the deciduous center, the two evergreen centers, and the prairie center.

The deciduous center, the most important one in Ohio, is represented by such trees as *Fagus Americana, Acer Saccharum,* which are the principal elements of the climax beech-maple forest; *Castanea dentata, Quercus alba,* and *Liriodendron tulipifera.* There are many other trees and shrubs and a large number of herbaceous plants. Trees from the northern evergreen center are *Pinus strobus, Tsuga canadensis, Thuja occidentalis, Taxus canadensis,* and *Larix laricina.* The firs and spruces are missing, but the flora is enriched by many northern shrubs and herbs. These are on the edges of their range in northern and northeastern Ohio. The northern species gain their entrance, or rather have not been driven out, through the hills of the eastern section of the state and more northern species are known in the eastern than in the western section of the state. The southern evergreen trees are *Pinus echinata, P. rigida, P. virginiana,* and *Juniperus virginiana.* In addition should be mentioned the bear oak, *Quercus ilicifolia,* which reaches the northern edge of its range in Ohio. There are also numerous shrubs and herbaceous plants of the southern center which reach the limit of their ranges. These perhaps belong more fairly to the deciduous center and are simply its southern species, rather than species of the southern center reaching up into the deciduous center. The prairie center is rapidly disappearing and is being replaced largely by cultivated lands. The prairies if planted now with trees would undoubtedly support the vegetation of the central deciduous forest. The bogs and the prairies both belong in the glaciated portion of the state and were most numerous in the western part. One of the best evidences of the northward migration of plants since glacial times is to be seen in the plants which were left in the undrained depressions. They became established in early post-glacial times, and the deposits of peat since have tended to keep a cool substratum, which led to the preservation of these species.

E. The Crop Centers of Ohio

The crop statistics of Ohio have been faithfully compiled by the Ohio Board of Agriculture and published for its citizens. This constitutes a valuable annual record which indicates the scope and magnitude of one of Ohio's greatest businesses. These records have been drawn upon freely in gathering the present data. The statistics are published by counties so that each community may see what it is doing and what its neighbors are doing. For convenience, the compilers have divided the state into four sections—northeast, southeast, northwest, and southwest—and the county totals are summed in accordance with this division. For our present purpose this will not always show that crops center in a certain area. The political divisions do not all correspond with natural physiographic and geographic ones. *The writer has not hesitated therefore to add or substract county totals from one district where the geographic data warrants, and place these in another group.* Wherever this is done attention is called to the fact that the names of the counties specifically mentioned. This rearrangement of data is in accord with the plan of the whole line of investigation here recorded, namely, the genetic point of view, which aims to show the relation of the natural vegetation and the cultivated crops to fundamental soil and climatic conditions. In the case of the cultivated plants, economic conditions must be included as well, as has been shown in Part II of this paper.

(a) *Corn*

Ohio is one of the seven states which constitute the corn belt of the United States. (See Chart in Part II.) There is in Ohio a plainly marked corn belt which corresponds in many ways to the corn belt of the United States. It is located in level soils with a high humus and lime content. All of the western half of the state may be regarded as a part of the corn belt. The center of population is in the northwest. Production is cheapest on the level, frequently prairie, soils of northwestern Ohio and the corn center has settled here. This was not the original corn belt of Ohio. The northwest was the last section of the state to be settled, and its development waited on the opening of the Erie Canal. During the last fifty years production has increased in the northwest section so that it outstrips all the older sections. Perhaps poor farming methods of a half and a quarter century ago had something to do with a decrease in the southeastern section, but even with the newest and best farming methods the southeastern part of Ohio is not so well adapted for corn cultivation as the northwestern. The centering of corn in the northwest seems to be a normal, healthy migration of a crop into a region to which it is well adapted. In 1916 the total state estimated production of corn was 82,953,943 bushels. This was divided among the sections of the state as follows:

Northwestern	section	35,101,566
Southwestern	"	29,153,460
Northeastern	"	10,571,956
Southeastern	"	8,126,961

When the production of the two western sections of the state is summed we find that 78 percent, or nearly four-fifths of the corn grown in Ohio was produced in the western part of the state. This clearly indicates the dominance of corn in the western part. If we wish to make a picture of corn production on a map, we will find that there are three highly productive centers in the corn belt. The first includes Seneca, Wood, Henry, Putnam, Allen, and Hancock Counties. The second includes Franklin, Madison, Clark, Green, Clinton, Fayette, Highland, Pike, Ross, and Pickaway Counties. The third includes Darke, Preble and Butler Counties.

(b) *Wheat*

Brigham (1910, pp. 44 and 45) has shown in the yield of wheat of the United States by decades, 1839 to 1899 inclusive, that six times out of the possible seven Ohio has been within the first four states in production. The rapid westward progress of the center of wheat production is shown in the fact that Illinois was not mentioned in the group of four until 1859. It took first place and held that for three years before dropping out of the lists as suddenly as it entered. In forty-one years, 1866 to 1906, Ohio has produced 1,247,082,674 bushels of wheat, an average of thirty million bushels per year. It has eight times exceeded forty millions.

The following table from the Twelfth Census gives the location of the wheat centers of the United States for the period 1850 to 1900.

WHEAT CENTER, U. S., 1850 TO 1900 (Seconds Omitted)

Census Year	N. Lat.	W. Long.	Approximate Location by Important Towns
1900	41° 39′	94° 59′	70 miles west of Des Moines, Ia.
1890	39° 33′	93° 9′	138 miles south by east of Des Moines. (In Missouri.)
1880	40° 36′	90° 30′	69 miles northwest of Springfield, Ill.
1870	40° 39′	88° 48′	82 miles northeast of Springfield, Ill.
1860	39° 59′	86° 1′	18 miles north by east of Indianapolis, Ind.
1850	40° 14′	81° 58′	57 miles east northeast of Columbus,O.

In Ohio, as in all humid climate states, the average yield of wheat is moderately high and is above the average for the whole United States. The average yield for Ohio is sixteen and a fraction bushels per acre. The average for the United States is something like twelve bushels per acre. According to Thorne (1917, pp. 48-50) the average for Wayne County is nineteen bushels. In spite of these higher yields per acre and therefore better returns per acre, wheat is found centering in that part of the United States just west of the corn belt. This is a region of less moisture than in the corn belt and where corn production consequently is not at its highest development.

The reasons for wheat being grown in this center are not difficult to see. Where corn can be grown to its greatest advantage it is the dominant crop. The returns per acre in grain and fodder are greater than from wheat and the money returns are also greater. Why is wheat grown at all in the humid sections, if corn gives it such competition? There are several reasons. A farmer can grow wheat and even in normal times make a return on his investment. He has also found out that to grow corn continuously does not pay. Clover or clover and timothy usually enter into a scheme of crop rotation. Wheat serves as a crop to sow with the hay crop which will return a yield for the use of the land while the hay plants are becoming established.

It is not surprising in the light of the above reasons for wheat culture in humid regions, that we find wheat centering in the same part of Ohio in which corn centers. It is found in the western part of the state. Wheat suffers more from disease, from insects and unfavorable weather conditions than corn does, so it is not surprising to find that the yield from year to year varies widely. In Ohio June and July are the months of heaviest rainfall. This rain is usually too late to help the growth of wheat much and is often the cause of damage. The wheat yield in 1913 was 27,825,105 bushels and in 1915, 35,624,381 bushels. In 1913, the southwestern section led. In 1913 the two western sections produced 63 percent of the crop; in 1915 the same sections produced 60 percent of the total wheat. This shows in spite of variation in yield that the wheat centers in the western half of the state.

There is another way of locating a center if there is some doubt as to its exact location and that is by examining the acreage sown to a certain crop rather than the actual production. This has the advantage of showing what the farmer intended to produce. What he is actually able to grow depends on a number of circumstances, many of which are beyond his control. In 1915, there were 1,888,642 acres in Ohio from which wheat was harvested. This was distributed in the state as follows:

Southwestern section	599,704
Northwestern "	587,979
Northeastern "	466,750
Southeastern "	234,211

When the two western sections are summed, we find that 62 percent of the wheat crop came from the western section of the state. It is also interesting to note that while the southwestern section led in acreage, the northwestern section led in yield that year. This bears out the contention that in a crop subject to damage from conditions beyond the farmer's control, the acreage is frequently a better way of locating the center than is the yield. In a paper recently published the writer (1918, p. 62) discussed the criteria for locating a crop center based upon production. For most purposes the use of production is the method favored. The above example shows how acreage may be used to advantage.

(c) *Oats*

In the United States, the center of oats production is only slightly north of the corn belt. This is the case in spite of the fact that oats are proverbially a cool climate crop with a high moisture requirement. Under such conditions it would be expected that the center of oats production be found much farther north than it is. Oats are grown in rotations into which corn enters as the most important plant. On farms following such rotation schemes, there is need for much horse labor. Oats are ideal for horses and oat straw is much prized for bedding, besides furnishing a certain amount of bulky feed. It is obvious then, that to bring the oats center near to or within the corn center is desirable. The difficulties have been partially overcome by the use of early maturing varieties, which have escaped the summer heat, rusts and smuts. There still remain plenty of opportunities to originate new varieties or strains of oats which are better adapted to corn belt conditions than any of the varieties now grown.

In Ohio we find that the production of oats centers strongly in the northern part of the state and that the heaviest production is in the northwest, where corn production centers. For 1915 the total production of oats for the state was 57,087,410 bushels. The sectional yields were as follows:

Northwestern section	31,380,518
Northeastern "	19,592,053
Southwestern "	4,414,773
Southeastern "	1,700,066

In the northern part of the state 89 percent of the oats crop was produced in 1915. It is not difficult to see where the center of oats production is located.

(d) *Hay*

Timothy and Clover Hay.—The northeastern section of the United States is known to agronomists as the hay and pasture province. To ecologists this is southern edge of northeastern evergreen forest. Both the cultivated plants and the natural vegetation are responses to the climatic conditions of this part of our country. Northeastern Ohio contains the southwestern limit of the northern evergreen forest. This is Ohio's hay and pasture belt.

The total hay production for 1915 in Ohio was 2,240,761 tons. This was divided as follows:

Northeastern section	....	842,223 tons
Northwestern "	....	646,898 tons
Southeastern "	....	454,611 tons
Southwestern "	....	297,029 tons

The northern half of the state with lower summer temperatures and lower evaporation making its rainfall more effective for continuous growth of untilled plants, has the higher production. In grass hay, the eastern half of the state leads, but in clover hay the western half is in advance as can be seen from the following table:

Northwestern section	....	387,497 tons
Northeastern "	....	120,500 tons
Southwestern "	....	144,318 tons
Southeastern "	....	43,901 tons

The total clover hay production for 1915 was 746,226 tons. The difference in clover production in the eastern and western half of the state is doubtless due to limestone. All of the soils of the western half of the state are naturally underlain with limestone bedrock. A good deal of the limestone material was brought near the surface by glacial action and subsequent weathering has not yet leached away all of it. It is a well known fact that clovers grow best when inoculated with the nitrogen gathering bacteria. These bacteria grow best in non-acid soil medium. The grasses are not dependent upon these bacteria. Furthermore, a meadow of timothy will be productive of compact clay soils where clover would be only moderately productive. This again shows the importance of the bacteria to clover production. In the tight clay soils the air circulates less freely, so the growth of bacteria is limited. The soils with a high lime content and a high humus content, as many of the farms in the northwestern section are on former prairies now drained, seem more suitable for clover production. In southeastern Ohio the soils are porous enough for the growth of the nodule forming bacteria and clover could be doubtless grown with the liberal use of lime and a crop occasionally plowed under for green manure.

(e) *Potatoes*

Potato production in Ohio also centers in the northeastern part. In the United States the potato crop seems to follow population more than any special climatic or soil factor. We find a small center of potato production near each of the thirty largest cities of the United States. The east coast of Maine, however, is a famous potato center. This points to a northeastern center for potato production. In Ohio the total production of potatoes in 1915 was 7,757,169 bushels. The sectional production can be seen from the following:

Northeastern section	4,039,487 bushels
Northwestern "	1,499,446 bushels
Southwestern "	1,351,122 bushels
Southeastern "	867,114 bushels

(f) *Tobacco*

Tobacco is in many ways one of our most interesting crops. It is extremely susceptible to the environment and assumes many variations in growth form according to the treatment it has received during cultivation. In the United States, it centers in Kentucky, Virginia, and North Carolina between the corn and cotton belts. Ohio, Pennsylvania, Wisconsin, and Connecticut also engage in tobacco production. In Kentucky while given more attention in cultivation than corn receives, it is grown nevertheless on an extensive system of farming. Farther north it receives a good deal more care, as much often, as vegetables grown on an intensive system would get. In some places in Connecticut it is grown under cloth shelters. These shelters lower the transpiration rate in the daytime. They also decrease the radiation of heat at night, thus maintaining more equable climatic conditions. The shading increases the size and decreases the thickness of the leaf thus making a product more suitable for cigar wrappers.

The Ohio tobacco center is in the southwestern part of the state—a continuation, as has been pointed out, of the Lexington

Plain. The counties along the river grow and cure Burley tobacco in the same manner as it is grown around Lexington, Kentucky. Near Dayton the tobacco is grown for cigar fillers. In southeastern Ohio the tobacco is grown for export trade, as in Maryland. The small northeastern Ohio center produces cigar fillers. The writer (1916) has reviewed the methods of growing and handling Ohio's tobacco crop.

In 1915 the total tobacco production was 42,354,308 pounds. This was distributed as follows according to the statistics of the Board of Agriculture:

Southwestern section	......	26,613,759 pounds
Northwestern "	......	12,766,556 pounds
Southeastern "	......	2,719,394 pounds
Northeastern "	......	254,563 pounds

If, however, we substract from the production credited to the northwestern section the amount produced in the four counties, Champaign, Darke, Mercer, and Shelby, there is less than 3,000 pounds, a negligible amount, produced in Northwestern Ohio. Darke county alone produced the bulk of this yield, 12,614,956. The type of tobacco and method of handling show that it is essentially the same as that produced near Dayton. Our centers then should rank as follows: (1) Southwestern, (2) Southeastern, (3) Northeastern. When the production of Darke County is added to the southwestern counties it is seen that this center produces 90 percent of the total crop.

(g) *The Centers of Livestock Production*

The dependence of animals upon plants, often specific ones, for their food, is a well known fundamental fact which needs no amplification here. However, when detailed information showing how this relationship operates in determining the distribution of animals is presented, plants are brought out in their true rôle as the basis of all agriculture. While no claim for novelty is made for any of the material here presented, it is hoped that the method of presentation will offer a new insight into agriculture even for those who are best acquainted with it.

(h) *The Dairying Industry*

The number of milch cows in 1915 was 748,526. These were distributed over the state in the following proportions:

Northeastern	section	254,050
Northwestern	"	225,090
Southwestern	"	152,560
Southeastern	"	116,826

This distribution makes the northern half of the state the dairy cow center. This agrees with the hay and pasture provinces both in the United States and in Ohio. A region in which summer pastures are most productive is adapted to dairying. The conditions making for productive summer pasture insure a good hay crop for winter feeding, and with silos green feed can be had in winter. Milk production, butter and cheese production, both that made in home dairies and in factories and creameries follow the general trend of this distribution. Space does not permit the detailed recital of these accounts. The northeastern section contains 50 percent of the creameries of the state and 54 percent of the cheese factories. The home production of butter and cheese greatly exceeds the factory production of both of these commodities.

(i) *Horses and Fat Stock*

The corn belt—the northwestern part of the state shows the dependence of the fat stock upon grain. The horses are there because their work is needed for the production of this grain. Forty-four percent of the beef cattle are in the southwestern section of the state, where the most dissected part of the glaciated region permits corn cultivation and has produced land suitable for winter feeding of beef cattle on corn roughage. Twenty-six percent of the beef animals are in the northwestern part of the state. Thus the western half of the state supports sixty-eight percent of the beef production. The southwest has thirty percent of the state's production of hogs. The hog center is in the northwest which has forty-four percent of the production. Seventy-four percent of the hog production is located in the corn belt.

(j) *Sheep*

There is an important sheep raising center located in southwestern Pennsylvania and southeastern Ohio. This the writer (1918 p. 79) has described as an edaphic center or one related to soil and physiographic conditions. There is, in contrast with this, a climatic center of sheep production in the semi-arid districts of the West which extend from Arizona northward to Montana.

The grouping of the statistical data as published by the Board of Agriculture does not show the relation of the production of sheep to the Ohio-Pennsylvania edaphic center. For our present purpose this data is slightly differently arranged. The production of Jefferson, Harrison, Knox, Tuscarawas, and Coshocton counties, although listed with the northeastern production, is credited to the southeastern part of the state. These counties are the border counties between the northeastern and southeastern sections, so that the statistics cannot really be considered distorted by this transfer. The state and section totals as recorded are:

Northeastern	section	462,354
Northwestern	"	400,407
Southeastern	"	397,262
Southwestern	"	131,576
Total		1,391,599

The totals from counties above named are in round numbers 250,000. When this is added to the southeastern section it gives to this section about 650,000 or forty-six percent, to be exact. This leaves 150,000 to the northeastern section and it is transferred from the first to third place in rank. The correctness of this transfer can be seen from the figure showing the distribution of sheep in Ohio and Pennsylvania (Fig. 12).

Sheep can be kept on pasture less continuously productive of the best forage than is required for dairy cattle. Southeastern Ohio is for this reason admirably adapted to sheep raising. Also since the rough topography makes a permanent plant cover better for the light easily eroded soil than cultivated crops, sheep raising should be encouraged for this section of the state. It is a part of the system to winter the sheep in sheds and to feed them grain. The bottom lands of southwestern Ohio can produce sufficient grain to feed the sheep and other livestock and leave some for local human consumption. Feeding the sheep in winter makes the dual purpose sheep, that is, those which produce both wool and mutton, the most economical. There is no fundamental reason why a local demand for mutton could not be developed in this country as has been done in England.

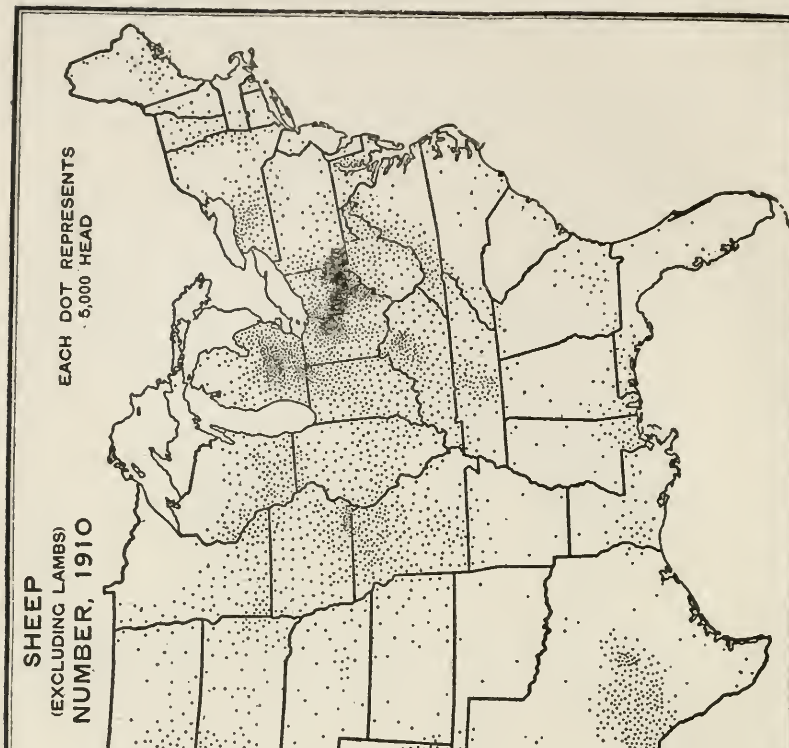

FIG. 12. The production of sheep in the United States. Note the relation of sheep production in Ohio and Pennsylvania to unglaciated regions of rough topography. For further explanaton see text. From 1915 Yearbook U. S. Dept. of Agriculture, from unpublished census data.

(k) *Fruit*

Apples are the most valuable of Ohio's fruit crops, though the peach and grape producing region near Lake Erie is well known. It is not necessary to repeat the reasons for the existence of the Lake Erie fruit belt, since these have been several times discussed. Nor is it necessary to give the peach and grape growing industry more than passing mention though both are important. It is the apple industry which at present solicits attention.

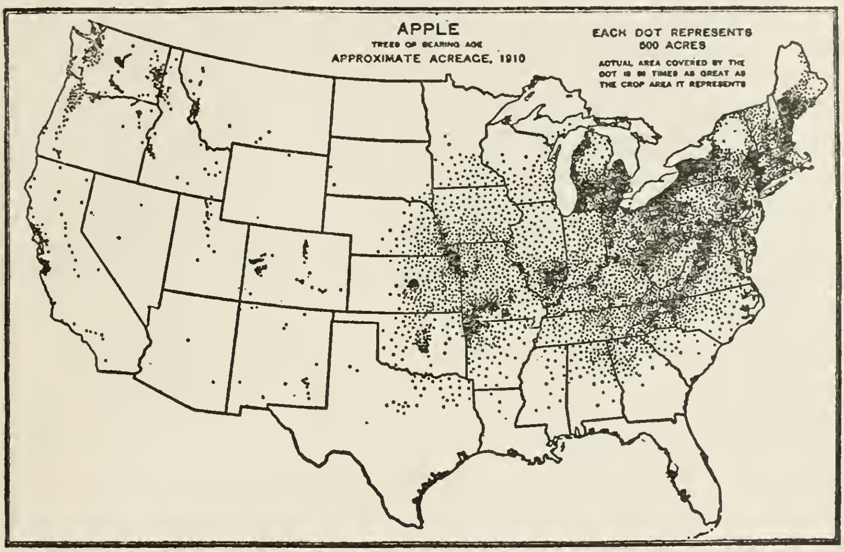

Fig. 13. Ohio's apply industry. In acreage the states rank, New York, Ohio, Pennsylvania, Michigan. Compare the eastern and western states. From 1915 Yearbook U. S. Dept. of Agriculture.

The conditions for apple production in southeastern Ohio are ideal. Sheltered valleys in which both the soil and air drainage are good are common. The rough topography, little suited to cultivated crops, is a genuine advantage in tree crops. It is not surprising then that we find the greatest apple acreage in Ohio in the southeastern part of the state. If the industry were encouraged and advertised, southeastern Ohio could market its apples as well as the Oregon and Washington and New York orchardists market theirs. Some capital and a great deal of cooperation are both needed to develop this enterprise.

The total apple acreage for 1915 was 211,463 acres.* The sections are as follows:

Northeastern section	....	77,105 acres
Southeastern "	....	56,062 acres
Northwestern "	....	54,952 acres
Southwestern "	....	23,344 acres

If, however, we substract the acreage of Jefferson, Harrison, Tuscarawas, Knox, and Coshocton counties, the northeast-southeast border counties, from the northeast section, and add it to the southeast section, it gives some 72,000 acres for the southeast and 61,000 in the northeast. There is, however, no sharp break in the topography in the eastern part of the state north and south of the glacial boundary. It is all part of the Allegheny Plateau. The eastern half of the state contains sixty-three percent of Ohio's apple acreage in spite of the fact that all over the state almost every farm has a few trees. The chart (Fig. 13) shows the relation of Ohio's apple acreage to Ohio's conditions and to the acreage in the United States.

*Acreage is a better guide to tree crops than a single year's production.

Summary and Conclusion

There is no better way of summarizing the foregoing discussion on the effect of climatic and soil conditions upon agriculture than by showing a chart of land values. This was made from the state tax commission figures and while it does not give actual price of land or show the changes in prices since the figures were collected, yet the relative values are plainly discernible, and for our purpose this is what is wanted. At first, the writer tried dividing the land values into eight classes and using a large scale map. While this gave much detailed information, the map appeared "patchy." Six classes and two classes were subsequently tried and discarded. The present chart (Fig. 14) was obtained by using the eight-class chart but combining the classes 1 and 2, 3 and 4, 5 and 6, 7 and 8, making a new chart of four classes. This chart, obtained entirely independent of physiographic, climatic or geological conditions, nevertheless brings out some of these quite strongly, thus emphasizing their bearing upon agriculture.

In the first place, the glaciers have the most important influence upon present day values of farm land. The Illinoisan (earliest) glaciation was the most extensive. All of the land of lowest value, (lightest shading) lies south or east of this glacial line, except for the undrained bog land in the extreme northeast corner of the state. The bog land probably has more potential farm value for cultivated crops than most of the unglaciated territory. Except where cut by the Miami Valley in the southwestern part of the state, the once-glaciated terrain is separated from the several-times-glaciated. The boundary of the Wisconsin drift is seen in the southwestern part of the state and between it and the Ohio River, the land is in the second class of values. The two glacial boundary lines meet somewhere near Chillicothe. Running south from Lake Erie through the central part of the state is the line separating the Waverly formation on the east from the Devonian and Silurian on the west. Some of the Ohio river counties in eastern Ohio show the influence of limestone outcrops in raising land values, for the second-class values appear in a region of lowest values. The third class constitutes our average or better farm values. This class makes up the bulk of the state's area. The fourth class, the highest values, show the influence of the cities and towns upon farm land in the spread of the deep shading around the area within which the city is located. It also shows

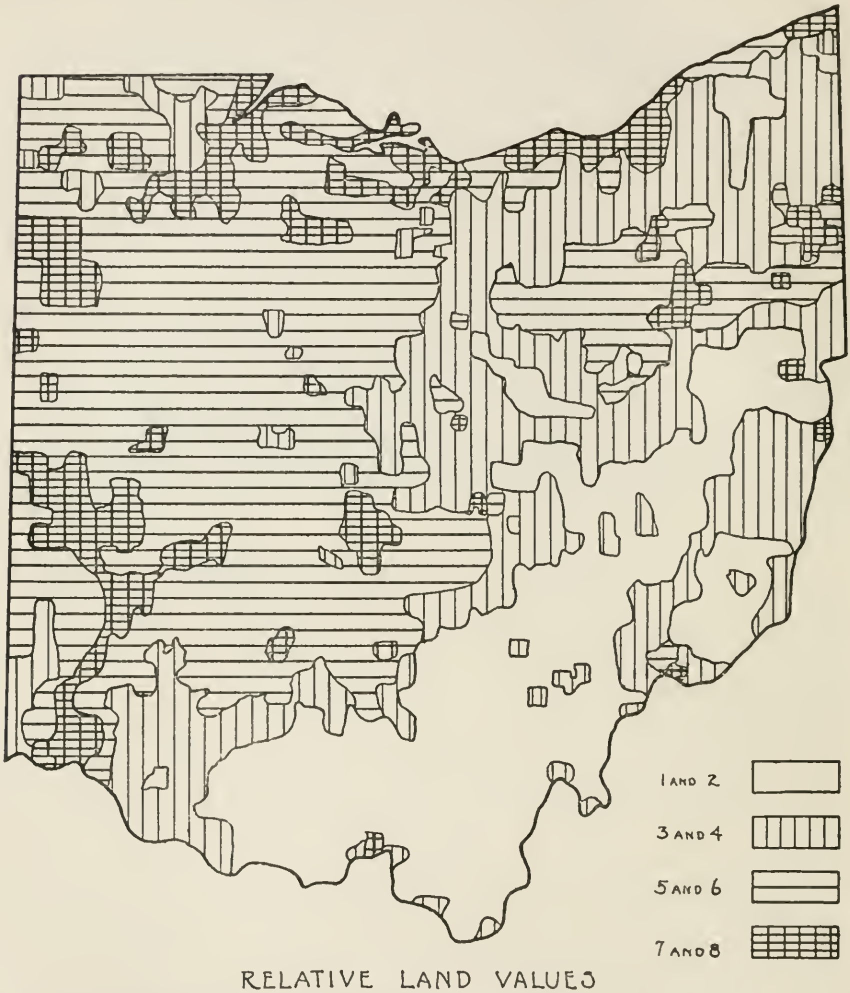

Fig. 14. Chart of the relative land values in Ohio. Compare with the physiographic and the two geological maps.

the farm land not near large communities which takes its values from the productions of the farms. Darke and Miami counties, for example, near the Indiana line in the southwestern part of the state, and Paulding, Van Wert, and Allen counties, are also shown as having high agricultural values. The spread of Cleveland and the fruit belt along Lake Erie stand out. The city of Toledo and the flat land of the Maumee River are both included in the heaviest shading.

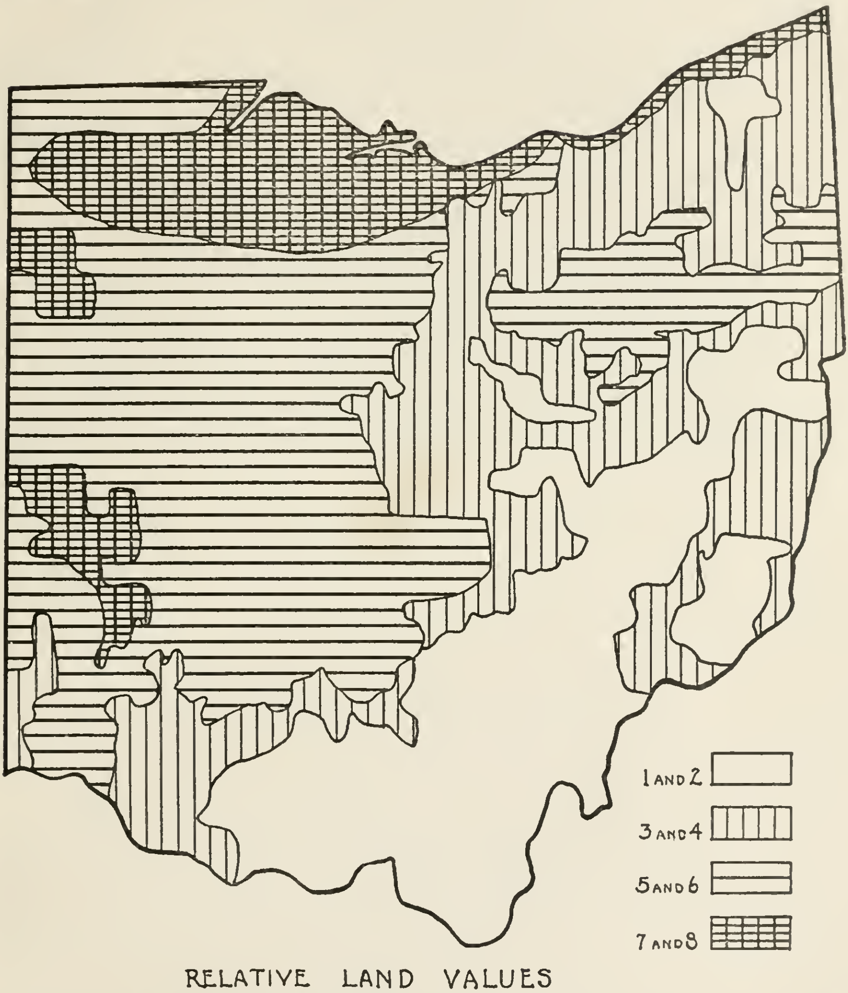

FIG. 15. The relative value of farm land. Derived from the preceding chart by eliminating the infliuence of centers of population. Compare with the glacial map and the climatic maps.

There is still another extremely interesting feature. A pencil line drawn from the southern part of the heaviest shading just south of Cleveland, curving southwest around the curves of Lake

Erie and then northwest, north of Paulding County toward Indiana and Michigan, and touching all the southern boundary lines of spots of heaviest shading, will outline the old glacial Lake Maumee. This is indicated on the Moraine chart (Figure 9, p. 47) by the total absence of drift deposits since the land was covered with water long enough to allow settlement and covering of coarse material with a finer deposit from the lake. In post-glacial time this territory has emerged. The finer soil deposits under water, and the organic deposits of plants as the lake line retreated northward to the present Lake Erie, are still of interest and importance to us when we see in them a cause of increased land values.

The second chart of land values as shown in Figure 15, is made by eliminating the areas in which tax evaluation comes from the accrued value of population in the cities. Since the farm land would have no value if it were not for population, and since on the other hand the climate and soils are underlying fundamental factors in the values, to be fair, both charts must be shown. The second chart is our real summary and illustrates the ecological conditions.

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