

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

CENTENNIAL YEAR 1913–2013



CONTENTS

INTRODUCTION TO THE CENTENNIAL ISSUE <i>Matt Ritter and the Council of the California Botanical Society</i>	265
REPRINTED CLASSIC MADROÑO ARTICLES <i>Various Authors</i>	267
PRESIDENT'S REPORT FOR VOLUME 60 <i>V. Thomas Parker</i>	360
EDITORS' REPORT FOR VOLUME 60 <i>Matt Ritter and Richard Whitkus</i>	362
REVIEWERS OF MANUSCRIPTS FOR VOLUME 60.....	362
INDEX TO VOLUME 60.....	363
DEDICATION <i>Staci Markos and Brent D. Mishler</i>	365
TABLE OF CONTENTS FOR VOLUME 60	367



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INTRODUCTION TO THE CENTENNIAL ISSUE

This year the California Botanical Society is celebrating its 100th year. To commemorate the occasion we are devoting this issue of *Madroño* to reprinting selected classic and seminal articles from the journal. We have chosen papers that we consider important to the understanding of California's plant life published by prominent figures in the history of botanical discovery.

Many of these articles will be new to the younger generation of California botanists. For those of you who have been with the Society for many years, we hope these articles will remind you of the interesting history that has been captured in *Madroño*. The selected articles contributed new insights and directions for research that fundamentally shaped botany and botanical institutions in western North America. They remain important today. Whether you're reading them for the first time or finding a new source of inspiration in the familiar, we hope you enjoy them.

Selecting the articles to include in this issue was not easy; many important papers have appeared in the journal over the decades. We encourage you to explore both recent issues of *Madroño* and the archives to discover additional favorites and classic articles. Printed back issues of *Madroño* can be ordered from the Corresponding Secretary or online (<http://www.calbotsoc.org/payment.html>). Recent issues are also available online through BioOne, and archived back issues may be accessed digitally through JSTOR. The 80-year index to *Madroño* is online at http://www.calbotsoc.org/madrono_index.html. We encourage you to work with your libraries and institutions to request access to recent and archived issues of *Madroño*.

In the first section of this celebratory issue we reprint articles by California's early ecologists and evolutionary biologists. Arthur Kruckeberg (1969) established the critical importance of variation in soils in relation to plant diversity and distribution. Herbert Mason (1954) discussed plant migration and the effect this has on evolution. And finally, G. Ledyard Stebbins (1942) laid the foundation for our understanding of the genetics of small populations of rare plants.

In the pages of *Madroño*, we have learned of new genera and species from different habitats across western North America. As botanical discovery has progressed over the last one hundred years in the region, new species descriptions have appeared in nearly every issue of *Madroño*. Here we revisit two wonderful discoveries: the descriptions of *Calochortus tiburonensis*

by Albert J. Hill (1973) and *Sanicula deserticola* by Peter Raven and Mildred E. Mathias (1960).

Madroño has also served as a place to publish natural history observations and studies. In the third section of this issue we reprint an article from the very first volume of the journal in which Willis Lynn Jepson described the results of studies of regeneration in manzanita. The article is the first discussion of obligate seeders versus facultative sprouters in the genus. A great deal of work would follow these initial studies, including Jepson's own studies in *Arctostaphylos*, chaparral communities, fire adaptations, vegetative diversification, radiation and hybridization, and co-occurring and edaphically restricted taxa. We also reprint an article on our state flower, *Why the Eschscholtzia?* by Edward Lee Greene, California's first professor of botany. This article was originally written for the California Floral Society's 1890 selection of an official California State flower, and was published posthumously (Greene died in 1915). Notice Greene's spelling of the genus, in which he includes the "t" from Johann Friedrich Gustav von Eschscholtz's correctly spelled last name. Eschscholtz's companion and fellow naturalist, Ludolf Karl Adelbert von Chamisso published the genus name without the "t" and so, to the displeasure of Greene, this scientific name and its misspelling stands.

In the fourth section, we reprint two articles on California vegetation. James W. Bartolome, S. E. Klukkert, and W. James Barry presented an early, evidence-based study of climate change in California's grassland communities during different anthropogenic regimes. The second article announced and summarized the efforts of the [then] forthcoming publication of the California Vegetation Type Maps (VTM). The foresight and leadership of Albert Everett Wieslander is evident in this article, in which he described the goals and potential utility of the large scale and long term VTM project. The impact of Wieslander's study is clear today; the VTM dataset is now digitized and continues to contribute to our understanding of vegetation types, soils, and climate change in California.

Finally, botanical discoveries in California have been made by a colorful cast of characters. Over the last 100 yrs, *Madroño* has been used as an outlet for personalities, accomplishments, and failures of the most prominent California botanists. Here we reprint a summary of the role that Willis Lynn Jepson played in the California Botanical Society and California botany by David D. Keck. To demonstrate the humor and eccentricity present in the journal we are reprinting

what is likely one of the shortest articles ever published: Reid Moran's five-word Noteworthy Collection.

During his address at the 1938 California Botanical Society Banquet, Professor Jepson stated, "The future of the Society lies fair and bright before it. There is every hope that it will extend its usefulness to all parts of California and that its days will be days of inspiring growth and days of true felicity. Its friends will be multiplied

and it will in this, our California, live long in the land." His words still ring true 75 yrs later. We hope this issue will make you laugh, remind you of the significance of scientific legacy of *Madroño*, and inspire your future work on the California flora. It has been a wonderful 100 years!

Matt Ritter and the Council of the California Botanical Society
December, 2013



Thanks to JSTOR for providing scans of these historic MADROÑO articles.

SOIL DIVERSITY AND THE DISTRIBUTION OF PLANTS, WITH EXAMPLES FROM WESTERN NORTH AMERICA

A. R. KRUCKEBERG

Discontinuity of pattern and form is an ubiquitous feature of living things. All along the scale of organizational complexity, from cell to ecosystem, some degree of environmental hiatus separates the elements of a system. Mitochondria are discreet entities separated from one another by the microenvironments of dissimilar subcellular phases. At a higher level, individuals of the same population are not confluent; time, space, chance and inhospitable habitats contrive to maintain temporary or partial discontinuities. But it is at the level of the species that isolation is most apparent and evolutionarily significant. The modern Darwinist sees the immense diversity in the organic world as resulting from the interactions over geological time of the variant heredities of organisms, the natural selection of adapted variants, and the manifold factors which promote the isolation of those adapted variants. Evolution of our present diverse biota without discontinuity is unthinkable.

The discontinuities in the physical environment which isolate populations and species, though richly unlimited in degree and permuting interaction, can be reduced to but two broad groups: climatological and geological. In other words, the limits to distribution of kinds of organisms are largely imposed by differences in climate or geology, or both. That climate is primary in controlling the broad distribution of organisms is undisputed. Tolerance spans of terrestrial organisms are chiefly limitations in reaction to stressful levels of moisture and temperature. Within areas of broad climatic similarity, though, geological variability provides the major source of regional biotic diversity. The contribution of geological phenomena to vegetational discontinuity takes a number of forms. Variations in topography, in mineral content and physical properties of parent rock account for most of the regional differentiation brought about by geological processes. When microclimatic and biotic features act in concert with geology, the mosaic of habitats is greatly enriched.

The soils derived from parent rocks owe their distinct qualities to a set of interacting factors. Hans Jenny (1941) characterizes the soil formation process as a set of variables in a functional array. In Jenny's formula, $s = f(c, o, r, p, t)$, there are five independent variables that define the soil system: climate (c), organisms (o), topography (r), rock type or parent material (p), and time (t). If all but one factor, say p (parent material), remain constant, then variations in the end product (soil) are due to differences in parent material.

It is this one variable, parent material (p), that will be the central theme of this review of soil diversity and plant distribution. The Jenny

formulation, however, reminds us that the biological properties of soils cannot be analyzed one factor at a time. When we abstract just parent material from the total soil ecosystem, we achieve manageable simplicity only at the expense of setting aside the interacting whole system. Our primary concern will be to examine the possible effects of chemical variations of parent material and soil on plant distribution. Such chemical diversity will condition the kind and amount of mineral nutrients available to the vegetation. To paraphrase Jenny's factorial approach, we can ask: Other factors being equal, what effects do differences in soil mineral content have on the distribution of plants?

Soils can control the distribution of plants in other ways, however, and we will look briefly at some of these. The physical properties of soil and parent material, weathering processes, soil microclimate, and those properties uniquely induced by the biota are also the domain of the edaphic factor complex; they will be touched upon wherever appropriate.

Though we may be operating at a microcosmal level where other environmental influences might vastly overshadow the effects of soil chemical differences, such differences can be dramatically effective in altering plant distribution. Examples to follow will support this contention. I will offer evidence to support two general hypotheses that bear on the probable interactions between mineralogical composition of parent material and discontinuities of plant distribution.

First Hypothesis: Given a regional climatic framework, much of the plant species diversity and discontinuity in the region is governed by variations in soil chemistry, and thus by specific variations in the mineralogy of rock substrates.

Second Hypothesis: Speciation within a regionally contiguous genus is largely a response to environmental discontinuity within the confluent area. Sharp discontinuities in soil chemistry can serve as isolating phenomena to bring about species diversification.

HISTORICAL BACKGROUND

We can scarcely doubt that discerning humans through the ages have been aware of sharp vegetational discontinuities arising from differences in soil. Geological and vegetational diversity go hand in hand in regions around the Mediterranean and the near east, the scene of Man's agricultural beginnings. A much later record from the Age of New World Exploration specifically ties vegetation to soil. Columbus is said to have capitalized on a specific soil-plant association when he had to replace a mast on a ship of his first fleet (Buck, 1949). The story goes that he was counselled to choose a log of pine growing on red soil in nearby Cuba; the red limonitic soils of Cuba are known to be high in iron and to have furnished durable timbers.

Correlations between substrate and vegetation really became a part of botanical science much later—in the 19th century. It was the young and alert Austrian botanist, Franz Unger, who first emphasized the signif-

1969]

KRUCKEBERG: SOIL DIVERSITY

131

icance of geological formation for plant distribution. From the pen of the master botanist-naturalist, Anton Kerner von Marilaun, we get an intriguing account of the patterning of vegetation that set Unger to develop his concept of the chemical concept of plant distribution. I quote from the English version of Kerner's *Natural History of Plants*, (Kerner and Oliver, 1902): "The little town of Kitzbuhel, in the Northeast Tyrol, has a very remarkable position. On the north rises the Wilde or Vorder Kaiser, a limestone chain of mountains with steep, pale, furrowed sides, and on the south the Rettenstein group, a chain of dark slate mountains whose slopes are clothed far up with a green covering. The contrast presented by the landscape in its main features is also to be seen in the vegetation of these two mountain chains. On the limestone may be seen patches of turf composed of low stiff Sedges, Saxifrages whose formal rosettes and cushions overgrow the ledges and steps of the rugged limestone, the yellow-flowered Auricula, the Rock-rose-flowered Rhododendron, and white-flowered Cinquefoil adorning the gullies, dark groups of Mountain Pines bordered with bushes of Alpine Rose; and opposed to these on the slate mountains are carpets of thick turf composed of the Mat-grasses sprinkled with Bell-flowers, *Arnica montana* and other Composites, groups of Alpine Alder and bushes of the rust-colored Alpine Rose—these are the contrasts in the plant-covering which would strike even a cursory observer, and would lead a naturalist to ask what could have been the cause. No wonder that the enthusiastic Botanist, Franz Unger, was fascinated by this remarkable phenomenon in the vegetable world. In his thirtieth year, furnished with a comprehensive scientific training, he came as a doctor to Kitzbuhel, and with youthful ardour he used every hour of leisure from his professional duties in the investigation of the geological, climatic and botanical conditions of his new locality, devoting his fullest attention to the relations between the plants and the rocks forming their substratum. The result of his study was his work, published in 1836, on the Influence of Soil on the Distribution of Plants as shown in the Vegetation of the North-east, Tyrol, which marked an epoch in questions of this sort. The terminology introduced in the book found rapid entrance into the botanical works of the time. Unger divided the plants of the district accordingly to their occurrence on one or other of the substratums—in which lime and silica respectively predominated—into (1) those which grow and flourish on limestone only; (2) those which prefer limestone, but which will grow on other soils; (3) those which grow and flourish on silica only; and (4) those which, whilst preferring silica, will grow on other soils."

Until the advent of modern soil science, arguments pro and con for Franz Unger's chemical theory of plant-soil relationships persisted without the full understanding of the nature of plant mineral nutrition. The essence of Unger's view—that mineral content of soils is the primary edaphic influence on plant distribution—is vindicated by contemporary soil chemistry. Qualitative and quantitative differences in elemental

(ionic) content of both the exchange complex and the soil solution do cause selective responses in the composition of vegetation cover as I will relate shortly.

Parent material of whatever sort, igneous, metamorphic, sedimentary rocks, and organic materials, become soil by weathering. Through the action of temperature changes, wind abrasion, water and other chemical agents, as well as biological influences, rocks weather to those textural and particle size classes of materials that constitute mineral soil. Mineral soil, then, is a mixture of particles ranging downward in size from rock fragments through gravel and sand to silt and clay. The most reactive phase for plants is the colloidal clay fraction. Ionic exchange between root systems and the soil is mediated by clay colloids. Major and minor elements required for plant growth are adsorbed on clay colloid surfaces. Since weathering frees primary minerals to generate secondary clay minerals and to participate in ion exchange, it is to be expected that the mineralogical composition of the weathering parent material will determine the quality of the reactive mineral content of soils.

The diversity of the geologic parent materials available at the earth's surface for soil formation is vast and rich. The range of rock types is derived from variations in both mineralogical content and mode of origin. Thus, at one end of the spectrum are the acid rocks, rich in feldspars (silicates of K, Na, Al and Ca). Acid rocks exist as granites (batholithic or intrusive igneous), rhyolites (volcanic surface flows), or as schists and gneisses (metamorphics), or as consolidated sediments (sandstones, etc.). Omitting the broad range of transitional members along the scale from acid to basic rocks, we come to the other end of the spectrum. Here are the ultrabasic rocks, chiefly of iron-magnesium silicates, plentiful and worldwide in distribution. Both igneous and metamorphic types occur; common examples of ultrabasics are peridotite and serpentinite.

PLANT RESPONSES TO DIFFERENCES IN CHEMICAL COMPOSITION OF SOIL AND UNDERLYING PARENT MATERIAL

How sensitive is the plant to variations in chemical content of soils? For cultivated plants, man's agricultural experience is rich and his skillful manipulations of crops and soils have had bountiful returns. Application of macro- and micronutrient fertilizers is a cornerstone of good farm practice. But what of natural vegetation and its response to chemical variations in soil? Positive evidence is clear for peculiar vegetational and floristic displays on a number of truly abnormal soils. The term "abnormal" signifies 1, the abundant occurrence in soils of one or more elements rarely found in such excessive amounts in agricultural soils, or 2, the absence of one or more of the essential plant nutrients usually available in cultivated soils, or yet 3, some combination of these exceptional elemental constitutions. However, I would repeat my earlier "disclaimer". Soil as a part of the living ecosystem is the product of many interactions, both biotic and environmental. To say that a soil is abnormal

1969]

KRUCKEBERG: SOIL DIVERSITY

133

and gives rise to exceptional vegetational responses due to mineral composition is valid to the extent that of all the soil forming influences, the quality of parent material is primary in its effect on plant growth.

I will present examples largely from the "abnormal" group of soils. Not only are the vegetational responses so striking, but their careful study may reveal guidelines for determining the chemical effects that may exist for plants on more normal, yet chemically variable, soils.

"ABNORMAL" (AZONAL) SOILS

Soils and Vegetation of Limestone and Dolomite

It was the stark contrasts in vegetation between limestone and slate slopes in the Tyrolean Alps that led Franz Unger (1836) to his chemical theory of edaphic restriction. Striking differences in physiognomy, species composition, and plant morphology are associated with rocks rich in calcium carbonate. Examples of contrasts between calciphile and calciphobe elements of a regional flora abound in the early European literature. Plants favoring limestone soils are *calciphiles* or *calcicoles*; plants avoiding limestone soils are *calciphobes* or *calcifuges*. The occurrence of vicarism (selective replacement of closely related species or varieties on contrasting soils) is frequent. It will suffice to give one or two examples of contrasts in floristic composition to reveal the nature of the vegetational discontinuity caused by limestone.

The remarkable flora on vast outcrops of limestone and chalk in Great Britain has fascinated botanists and naturalists for decades. This sustained interest is delightfully recounted in two modern books, "Wild Flowers of the Chalk and Limestone," by J. E. Louseley (1950), and "Downs and Dunes, Their Plant Life and its Environment," by E. J. Salisbury (1952). Only a fragmentary account of the rich chalk and lime floras can be given here. The gamut in degree of constancy of species to soils derived from rocks rich in calcium carbonate begins on the side of the rare and obligate lime inhabitants such as the two orchids, *Orchis simia*, monkey orchid, and *O. militaris*, military orchid, and *Helianthemum polifolium*, white rockrose. Franz Unger (1836, p. 168) would have called such exacting plants "bodenstet" (or "soil-fast"). The other extreme, plants common not only on limestone, but on other soils, he referred to as "bodenvag" (or "soil-wanderer") species. In addition, limestones and chalks in Britain have their share of calcifuges—plants that avoid the calcareous substrates. Foxglove, *Digitalis purpurea*, and broom, *Sarothamnus scoparius*, though widespread, are conspicuously absent from these soils. Louseley says of the two species, ". . . (they) are such excellent soil indicators that on train journeys it is often easy to tell immediately when the railroad line leaves chalk or limestone by their presence on the railway banks." Ericaceous species, long known to gardeners for their aversion to limestone, are equally discriminating members of the natural vegetation. Only where the chalks are surface-leached and an

acid humus has developed can species of the heath family get a local toe-hold on lime.

Limestone vegetation in other parts of the world is no less remarkable for possessing a high proportion of indicator species. For example, the geology of Japan and Taiwan is especially rich in calcareous deposits. The botanical composition of 63 limestone outcrops (Shimizu, 1962), were categorized in grades of fidelity, the degree to which a species is restricted to a particular community type. There are 75 species in Fidelity Class 5 ("exclusives"—high restriction to limestone); this class contains a large number of ferns, shrubs, and herbaceous perennials, but few trees. The next Fidelity classes, 4 and 3, ("selectives" and "preferents") with 48 and 112 species respectively, add considerably to the total floristic richness of the calcicolous floras.

There is no question, then, that limestone parent materials have exerted a profound selection on regional floras, resulting in unique vegetational composition, physiognomy, and soil formation. It remains now to look at possible physiological explanations of accommodation to limestone.

Physiological explanations of preference for, or avoidance of, limestone soils are not wholly satisfying. Obscuring the search for answers are a number of complicating ecological and soil chemistry factors. Do calcicoles require a medium high in calcium or are they merely able to tolerate high calcium in exchange for a release from greater competition stress on non-calcareous soils? Is the limestone effect one of pH preference or more fundamentally a nutritional problem? The high pH values generated by some limestone soils no doubt exert strong side effects on the availability of other elements, e.g., iron, aluminum, manganese, phosphate. A physiological approach has been fruitful in the case of differences in calcium preference of grasses in the genus *Agrostis* (Clarkson, 1965). Of four species of *Agrostis* grown in controlled solution cultures of various calcium regimes, the well-marked calcifuge species, *A. setacea*, has a significantly different capacity for calcium uptake. The results for the three calcicole and one calcifuge species appear to be related to differences in the capacities of their active transport system—the metabolically controlled mechanism for moving ions from soil to root interior. The calcifuge species, *A. setacea*, seems to have a calcium transport system of lower capacity than the other three. The ecological assessment of these results would appear to be that a calcifuge species may have an inherently lower threshold to calcium uptake.

A now classic study of a calcicole-calcifuge species pair by A. C. Tansley, pioneer British ecologist, has a timely and contemporary message for anyone studying the effects of a single soil variable on plant distribution. Tansley (1917) demonstrated that species interactions greatly altered the effect of soil type on plant growth. The two bedstraws, *Galium saxatile* and *G. sylvestre*, were grown in pure and mixed stands on acid peat and calcareous soils. "Both species can establish and maintain

1969]

KRUCKEBERG: SOIL DIVERSITY

135

themselves—at least for some years—on either soil,” but “the calcicole species is handicapped as a result of growing on acid peat and therefore is reduced to subordinate position in competition with its calcifuge rival, which is less handicapped,” and “. . . the calcifuge species (*Galium saxatile*) is heavily handicapped especially in the seedling stage, as a direct effect of growing on calcareous soil, and is thus unable to compete effectively with its calcicole congener, *Galium sylvestre*.” Tansley’s work emphasizes the obvious but often overlooked danger of reading too much ecological significance into results obtained from plants studied in artificial isolation. The current research on plant competition by John Harper (1967) and his associates in Britain underscores the importance of variability in plant response as influenced by biotic interaction.

Lists of species pairs, calcicole versus calcifuge, imply that taxonomically recognizable kinds of plants have different tolerances and that the members of a given pair may be closely related. Though there may be some question as to the advisability of giving such vicariads taxonomic recognition, there is no doubt that there are interpopulational differences to an edaphic factor such as limestone. In pursuit of this possibility, it has now been amply demonstrated that species occupying a diverse array of edaphic habitats have responded genetically to variant selective agents of the soil; i.e., such species exhibit ecotypic differentiation. Working with *Trifolium repens*, a species with wide edaphic range, genecologists in Britain have found intraspecific variation in tolerance to calcareous and acid soils. Snaydon (1962) concludes that, “. . . the wide edaphic range of *T. repens* is due, at least in part, to the presence within the species of specifically adapted physiological types.” When such intraspecific but interpopulational differences include morphological characters, and when the contrasting edaphic factors act as isolating barriers, both taxonomic separation and microevolutionary divergence are demonstrable.

It is too simple to hope for a one-to-one correspondence between the chemical nature of a calcareous substrate and a selective action on the potential flora the rock may support. Species which may be highly restricted to limestone in one area may be indifferent to such substrates elsewhere along their range. This is likely the case for the peculiar floristic composition of the Convict Creek basin in the Sierra Nevada of California. Major and Bamberg (1963) describe a remarkable aggregation of geographically disjunct species in the basin. Several taxa, otherwise found only far to the east or north, occur on a narrow band of marble in the basin; this highly distinctive calcareous substrate intrudes locally at Convict Creek, the monotonous granodiorite of the Sierras. It appears that the locally arid outcrops and the contrasting moist seeps provide habitats not otherwise available on the high eastern slope of the massif. The high calcium content of the marble is thus only secondary or even irrelevant to the local occurrence of the disjunct species.

The end result of interactions between substrate and floristic composition can be clearcut: the patterning of vegetation we see can then be di-



FIG. 1. Mosaic of vegetation types in the White Mountains, California. Sagebrush on sandstone and bristlecone pines on dolomite. Photograph taken by Albert Hill and furnished by Harold Mooney.

rectly related to the distribution of the parent materials. But when one is led to sort out the properties of the environment which yield the floristic end product, the story becomes complex. Take a recent case, that of the clearly substrate-oriented distribution of bristlecone pine, *Pinus aristata*, of the White Mountains in eastern California. The pines, now acclaimed the real patriarchs of the plant world, occur chiefly on dolomitic limestone, whereas sagebrush is dominant in adjacent granitic and sandstone soils (fig. 1). Physiological ecologists (Wright and Mooney, 1965) find that it is the interaction of physical, nutritional and biotic factors that lead to the complementary distribution of the pine and sagebrush (*Artemisia tridentata*) dominants. The light-colored dolomitic soils are moist and cool, and yet are highly deficient in phosphates. Sagebrush is excluded from the dolomite by the phosphorus deficiency, and reciprocally the pines prefer the cooler, moister dolomites, while tolerating the low phosphorus status. The temperature-moisture difference and the phosphorous deficiency thereby effect a competitive relationship which results in the visible substrate-oriented patterning of vegetation.

Vegetation on Acid Soils

The story of vegetation on limestone tells us that the plant response runs the gamut from narrow calcicolous restriction through broad toler-

1969]

KRUCKEBERG: SOIL DIVERSITY

137

ance or indifference to clear avoidance of the substrate. Such an array of responses largely repeats itself whenever exceptional chemically limiting edaphic responses occur. At the risk of being too inclusive, I want to examine this range of plant response for other chemically unique substrates. For most of them only limited discussion is possible. The mere catalog of other unusual substrates is intriguing in itself. Thus, to use low pH as a crude basis for compilation, there are the highly acid soils induced by a variety of exceptional parent materials: Aluminum-rich bauxites or terra rossa soils of the tropics, silica-rich soils (sands, diatomaceous earths, slates, laterites, etc.), hydrothermally altered volcanics (rich in sulfates), and the soils of lead mine tailings and zinc deposits.

Studies prior to 1957 on the effects of aluminum on plant life led to the generalizations, 1, that soils with high Al may restrict dicot weed competition in grass pastures, 2, that on Al-rich soils there are three levels of Al uptake: a, plants requiring aluminum ions in their metabolism, b, plants known as "aluminum accumulators," which concentrate Al ions in plant tissues with visible but non-lethal effects, and c, plants which are tolerant of Al but collect little or only small percentages of Al in their tissues, and 3, that certain plant families or genera either require Al for normal growth, e.g., Ericaceae, Moraceae, Ferns, and Lycopodiaceae, or are accumulators of Al (*Carpinus*, Rubiaceae, and Melastomaceae). Several of these generalizations have now been put to the test of careful field observation by Howard and Proctor (1957). A major portion of the lowland land surface of Jamaica contains aluminum-rich bauxite deposits. Although agriculturally poor, the bauxitic areas do support a mixture of cultivated crops and a native vegetation in varying stages of secondary succession. Since undisturbed vegetation on bauxite is in remote areas and as yet unsampled, studies on the effects of Al on vegetation were restricted to disturbed sites. The authors concluded: "it appears that the bauxite flora of Jamaica consists of plants which are unaffected by aluminum and tolerant of its presence . . . to the present we have found no species characteristic of bauxite soils, nor have we demonstrated that the vegetation of adjacent areas currently not found on the bauxite deposits will not grow on the bauxite soils. To the contrary, the invasion of plants from adjacent areas on barren, mined-out pits and the plantations established in these pits indicate that factors other than the concentration of aluminum will control the success or failure of these species on bauxite." At this point we would have to conclude the effects of Al on floristic pattern and vegetation are unresolved.

Highly acid and infertile soils underlain by sands and other siliceous substrates often support unique plant assemblages. The pine barrens of New Jersey, the shale barrens of the Appalachians, and possibly the coastal sands of the Carolinas are eastern representatives of the type. Notable in the West are the Mendocino barrens and the laterites-sericitic schists in the Sierra Nevada foothills of California, while in the

Great Basin's desert and mountain country the hydrothermally altered volcanics create local vegetational discontinuities.

Just back of the Pacific coastline in Mendocino Co., California, is a dissected sandstone plateau which supports that most remarkable vegetation, the "pygmy forest" (Jenny, et al., 1969). In its most extreme representation a dense growth of cane-like dwarfed individuals of *Cupressus pygmaea* and *Pinus bolanderi*, not over eight feet tall, cover the ashy gray podsolic soils. Notable associates of the pygmy conifers are several ericaceous shrubs. Of the latter, *Arctostaphylos nummularia* is endemic to the pygmy forests and is one of the three rare acid-soil endemics in the section Schizococcus. Since other species of conifers occur on exceptional soils, the possibility exists that there are features in common among several atypical (non-zonal) soil types in California that yield unusual floras. The general conclusions from thorough field study, greenhouse culture work (mineral nutrition) and laboratory analysis of soils and plant material (McMillan, 1956) merit our attention. Two problems needed explanation: 1, the restricted distribution of *Cupressus* species on a variety of exceptional soil types including the Mendocino acid barrens, and 2, the anomaly of good growth of cypress seedlings on fertile and infertile soils in greenhouse culture. McMillan suggests 1, that edaphic restriction of native plants is not tied to a particular nutritional requirement provided solely by the unique substrate; 2, some common physiological tolerance, e.g., to low calcium availability, may be the basis of generic differentiation in *Cupressus* but not so for other genera of similar edaphic predisposition, and 3, that the pine barren plant community is an array of species that results from "the overlapping of different tolerance ranges of the component individuals for environmental conditions presented by a particular habitat."

In the Great Basin region of the West, broad expanses of sagebrush, juniper, and saltbrush desert are occasionally interrupted by isolated stands of yellow pine and other disjunct subordinate species. These remarkable floristic islands are usually found to be growing on local non-zonal soils of exceptional nutrient characteristics. In both Nevada and Utah, such restricted isolates of vegetation occur on highly acid soils derived from hydrothermally altered lavas and volcanics. Billings (1950) found that the altered andesites northwest of Reno were "very deficient in exchangeable bases, phosphorous, and nitrogen as compared to" adjacent zonal soils supporting pinyon-juniper and sagebrush. Billings concluded that "the pine stands are relicts which have remained because of the inability of sagebrush zone dominants to invade these mineral-deficient soils."

The vegetation of desert "islands" of altered volcanics in Utah substantiate Billings' views on the casual nature of the floristic isolation. Salisbury (1964) adds to the total picture by suggesting that succession to zonal soils typical of the regional climate can occur under the influence

1969]

KRUCKEBERG: SOIL DIVERSITY

139

of the vegetation itself especially through humus accumulation and eventual plant succession . . . even on these altered volcanics of low pH. The soil profiles from extreme (non-zonal) to zonal sites show an amelioration of the pH and nutrient status of the soil. Leaching of the undesirable elements and the biological addition of essential nutrients appears to achieve the successional change. We would predict, however, that succession to zonal status could be achieved only under ideal conditions of topography, moisture and vegetation cover. Steep slopes of altered andesite with high runoff would undoubtedly persist as non-zonal, sterile soils. In fact, we could generalize to say that severe topography coupled with exceptional parent material will permanently arrest soil formation at the azonal or skeletal state; the biological consequence would be the persistence of a pioneer, edaphically specialized endemic flora.

The last example of non-zonal acid soil and its influence on plant distribution is not only fascinating in its own right, but fosters some far-reaching generalizations. The remarkable restrictions of *Arctostaphylos myrtifolia* in almost pure stands to Eocene laterite and to sericitic schists in the Sierra Nevada foothills of California has been thoroughly studied by Gankin and Major (1964). Near Ione and San Andreas a non-zonal acid heath association abruptly interposes itself within the regional climax vegetation. The Ione manzanita occurs often in dense heath-like stands on substrates of low base status, low fertility, of exceptionally low pH values, 2.0 to 3.95, and of high soluble aluminum values. It is contended that it is the high soil acidity and high aluminum content which exert such a strong selective inclusion-exclusion effect on the regional flora. After citing a number of other examples of edaphically controlled endemism and disjunct distributions, the authors seek a common cause (p. 803): "The above examples could be expanded, evidently indefinitely. Once this principle of disjunct and endemic plant occurrence on non-zonal sites is accepted, examples become almost too numerous. In all these cases,, explanations of why the rare plants occur where they do in terms of plant physiological reactions are completely lacking. Judging from the cases cited, they would have to be conflicting. The only explanation which fits the diversity of facts—that is, plants occurring at higher or lower altitudes than normal, in wetter habitats or drier, with less calcium or more—is in terms of plant competition. All the cases fit the conclusion that rare or disjunct (non-zonal) plants can occur in a given area where competition is decreased by some kind of extraordinary soil parent material or other continuously effective disturbance of climax vegetation development." With that conclusion I would concur, but would at the same time suggest that the competition hypothesis opens up still another "Pandora's Box" of complex biotic interactions. Competition, like endemism, soil infertility, and pH, is as yet a rather vague concept, at least in contemporary plant ecology. Attempts to analyze "competition" and to test its complex nature are only recently gaining fruitful momentum.

Soils and Vegetation on Serpentine and other Ultramafic Rocks

The last and certainly most spectacular "abnormal" (azonal) soil to be discussed is that derived from serpentine and other ferromagnesian rocks. The plant life on such soils has held particular fascination for generations of botanists. On nearly every major land mass of the world, ferromagnesian (ultramafic) outcrops weather to soils that exert a profound selective influence on the regional flora. Stark contrasts between the barrenness of ultramafic and the comparative luxuriance of adjacent non-ultramafic sites, as well as the pronounced differences in species composition are familiar and striking features of this discontinuity in vegetation dominated by geology. Although the most celebrated manifestations of ultramafic vegetation are in Europe (the "dead" Alps, the Balkan Peninsula and northern Sweden) and North America (central California to Oregon and Washington, and the Gaspé Peninsula) other areas, both tropical and temperate, show tell-tale vegetational responses to these soils. Cuba, New Caledonia, New Guinea, New Zealand, and Japan also have notable areas of serpentine and related rocks which in turn support unique floras (Krause, 1958; Whittaker, *et al.*, 1954).

Before turning to the floristics and ecology of serpentines, we should set the scene. I propose to use the word "serpentine" broadly to encompass all ultramafic rocks and soils weathering from them. The term "ultramafic" (or "ultrabasic") embraces those rock types in which the mineralogical composition is largely in the form of silicates of iron and magnesium, as exemplified by the mineral, olivine. The commonest ultramafics are the igneous rocks, peridotite and dunite, and their metamorphic derivative, serpentine. Soils weathering from such rocks are high in magnesium and low in calcium; because of other minerals, pyroxene, amphibole, chromite, etc., in addition to the crucial olivine, the soils may also contain unusually high amounts of nickel and chromium. A secondary biological effect during soil genesis is the common deficiency in nitrogen and phosphorus. Serpentine soils are both unfit for most agriculture and highly selective for native plant species. The calcium-magnesium ratio of much less than 1.0 is considered to be a crucial selective soil factor for the distribution of plant species. Serpentine usually has both a physiognomic as well as a taxonomic effect on plant life. Serpentine vegetation is sparse, with much intervening barren ground; dwarfing and xerophytism are common. Species composition is both depauperized and often unique; endemism and range disjunction are frequently the most outstanding floristic attributes.

Both because they are spectacular samples of serpentine vegetation and are reasonably representative of temperate zone ultramafics, I will confine my discussion to the serpentines of western North America. For convenience, we can distinguish three physiographic regions in which serpentines abundantly occur: 1, the Central California Coast Ranges—Sierra Nevada foothills area, 2, the Klamath-Siskiyou area, and 3, the Northern Cascades—Wenatchee Mountain areas. We will look first at

1969]

KRUCKEBERG: SOIL DIVERSITY

141



FIG. 2. Outcrop of serpentine overlooking meadow of mixed alluvium, three miles northeast of Middletown, California.

the vegetational and floristic responses, then at the genotypic reactions of populations to serpentine, and finally develop hypotheses to account for the evolution and adaptation to the serpentine habitat. All along the north-to-south transect, especially from Douglas Co. in Oregon, to San Luis Obispo Co. in California, abundant and often extensive ultramafic outcrops serve to further complicate the already intricate environmental mosaic. The North Bay counties (Napa, Lake, Marin and Sonoma) of central California afford an ideal locale in which to sample the central Californian version of the vegetational discontinuities associated with serpentine outcrops (fig. 2). The serpentines here stand in sharp contrast to the adjacent non-serpentine sites which support largely wide-ranging woody dominants of either the oak woodland, mixed conifer, or chaparral type. Such sclerophyllous shrubs as *Quercus durata*, *Ceanothus jepsonii*, *Garrya congdonii*, and even the small coniferous trees, *Cupressus sargentii*, and *C. macnabiana*, are unmistakable "indicator" species because of their typical restriction to and numerical dominance on serpentine soils. It is not these dominant woody species, however, which have made

Californian serpentines celebrated as a source of rare and endemic plants. The transient spring flora of the dry serpentine hills still continues to be a source of "new or otherwise noteworthy" additions to the California flora. From the time of E. L. Greene and W. L. Jepson to recent collecting by Freed Hoffman, John Thomas Howell, John Morrison, Helen Sharsmith and others, the list of herbaceous rarities endemic to serpentine has grown and continues to grow. A genus of crucifers, *Streptanthus*, is particularly rich in serpentine forms and well serves as an example of wholesale evolutionary diversification on this selective substrate. At least 12 species in California and southern Oregon occur on serpentine: for example, *S. niger*, Tiburon Peninsula; *S. batrachopus*, Mount Tamalpais; *S. insignis*, San Benito Co.; *S. polygaloides*, Sierran foothills; *S. hesperidis* and *S. brachiatus*, Lake Co.; and *S. morrisonii*, upper Austin Creek, Sonoma Co. A few are just as obligate on serpentine but of wider range: *S. howellii*, Siskiyou Mts.; and *S. barbatus*, *S. breweri*, *S. barbiger*, and *S. drepanoides*, Napa to Trinity counties. Still others have a broader edaphic tolerance and occur both on and off serpentine: *S. glandulosus*, San Luis Obispo Co. to southern Oregon; and *S. tortuosus*, Sierra Nevada—Coast Range-Siskiyou triangle, though some named intraspecific taxa appear to be local serpentine endemics. Populations of *S. glandulosus* when grown on test serpentine soil proved to be most instructive in the quest for an explanation of serpentine restriction (Kruckeberg, 1951). Collections from non-serpentine sites were clearly intolerant of serpentine soil, while morphologically indistinguishable serpentine samples grew vigorously on the same test soil. Intraspecific variation in physiological tolerance is clearly demonstrated here and expands the idea of ecotypic differentiation of species beyond climatic response to that on soil differences. *Streptanthus glandulosus* is therefore interpreted as a species originally possessing several edaphic biotypes and that through time non-serpentine biotypes have been gradually eliminated. Ultimately its fate may be that of its obligate serpentine endemic relatives, restricted to serpentine. I would concur with Gankin and Major (1964) that it is the 'pressure' of competition—though its action unspecified as yet—that reduces biotype diversity and forces ultimate confinement to serpentine. In this sense then, some of the narrow endemics of *Streptanthus* appear to be "depleted" species. Biotype depletion need not be the prelude to extinction, however. Having found refuge as edaphic specialists on serpentine, diversification within the serpentine environment may ensue. This seems to have been the speciation history in at least three subsections, *Insignes*, *Pulchelli*, and *Hesperides*, of the genus.

When we move from the xeric chaparral-covered serpentines of California to the more mesic serpentine habitats in the Siskiyou Mountains to the North, we find a definite shift in composition of vegetation. Though the contrast between serpentine and non-serpentine plant associations is often as striking as those to the South, both species and life-form composition are clearly different. Annuals and chaparral shrub spe-

1969]

KRUCKEBERG: SOIL DIVERSITY

143

cies no longer dominate the ultrabasic landscape. Rather, it is the particular blend of widely spaced conifers and intervening broadleaved shrub and herbaceous layers that characterize the mountainous serpentines the Siskiyou. The forest-shrub complex on serpentine (Whittaker, 1960) gives way abruptly to climax (?) montane mixed coniferous forests on neighboring non-serpentine soils. Repeating the character of the highly acid non-zonal soils discussed earlier is the occurrence of open mixed stands of conifers, often stunted, composed in part of species not common on adjacent "normal" soils. The occurrence of certain conifers on serpentine appears to be the result of altitudinal and/or geographical extensions of more typical ranges of the species. *Pinus jeffreyi*, Jeffrey pine, and *P. attenuata*, knobcone pine, fit this category of disjunct distributions, repeating here in the Siskiyou what is notable about their distributions elsewhere in the far West.

Most remarkable is the shrub cover of Siskiyou serpentines. Nearly every taxon of the sclerophyllous shrub layer is a varietal xeromorph of a species more typically of mesophytic and arborescent habit. Whittaker has observed example after example of these "trees-turned-shrubs," or mesic-turned-xeric shrub. "*Quercus chrysolepis* is represented on serpentine by var. *vacciniifolia*, the most abundant single shrub species there; *Lithocarpus densiflora* is represented by var. *echinoides*, *Umbellularia californica* by an unnamed shrubby variant, and *Castanopsis chrysophylla* by var. *minor* (uncommon in the study area). *Quercus garryana* occurs on serpentine as the shrubby var. *breweri*. Among other trees and shrubs a series of congeneric pairs appear in non-serpentine and serpentine floras with the serpentine species in each case of smaller stature: *Amelanchier florida* and *A. gracilis*, *Garrya fremontii* and *G. buxifolia*, *Rhamnus purshiana* and *R. californica occidentalis*, *Holodiscus discolor* and *H. dumosus*, *Ceanothus integerrimus* and *C. pumilus*, and *Berberis nervosa* and *B. pumila*."

Local moist seeps at the base of serpentine-peridotite slopes are havens for some of the most spectacular of the Siskiyou endemics: *Cypripedium californicum*, *Rudbeckia californica*, *Darlingtonia californica*, *Trillium rivale*, *Lilium bolanderi*, and *L. occidentale*. There is no doubt that the rich endemism of the Siskiyou Mountains can be correlated in large part to the "insular" occurrence of ultrabasic rocks.

Contrasts between serpentine plant life of the Siskiyou and that of western and central Washington are muffled by the presence in both of a coniferous forest cover. Yet species differences between the two areas are truly sharp. The most telling contrast is in the reduction in species diversity on the Washington ultrabasics. Though there are remarkable species discontinuities and edaphic restrictions in the state, the serpentine flora is markedly depauperate compared to that on the Siskiyou and Californian serpentines. But before we deal in specifics, let me set the physiographic scene for display of plants on ultrabasics in Washington.

Ultramafics in the state occur in two major settings (Kruckeberg,



FIG. 3. Barren serpentine slopes within coniferous forest type, headwaters of Boulder Creek in Cle Elum River drainage, Wenatchee Mountains, Washington.

1969). The largest exposure is in montane portions of Kittitas and adjacent Chelan counties. The sites are all in the Wenatchee Mountains which form an easterly extending spur of the Cascade Range. The outcrops occur either as peridotite, dunite, or serpentine; exposures of the rock may be massive, of many square miles in extent, or very local (fig. 3). Old altered volcanics (greenstones), sedimentary rocks, gneisses and schists, as well as acid igneous granodiorite border or even interfinger with the ultramafics. The region is thus lithologically rich and complex. The terrain is rugged, with steep slopes and high ridges that culminate in the ultramafic peaks, Earl, Navaho, and Ingalls, from 5000 to 7000 feet altitude. The clearest and most spectacular contact between ultramafic and non-ferromagnesian rock types is along upper Ingalls Creek where the east boundary of peridotite at the creek abruptly gives way to the massive granodiorite of the Stuart Range.

All of the Wenatchee Mountains ultramafics occur in areas of coniferous forest. At altitudes from 2400 to 4000 feet, the forest consists of open stands of Douglas fir, yellow pine, and western white pine; this forest type grades insensibly upward into a mixture of subalpine fir, mountain hemlock and whitebark pine. The stand are invariably open, the barren slopes between the scattered trees lightly populated with

1969]

KRUCKEBERG: SOIL DIVERSITY

145

grasses and forbs, some of which are highly characteristic of ultramafic soils.

The next largest series of ultramafic occurrences in Washington is in the northwestern counties of Snohomish, Skagit, San Juan, and Whatcom. The most outstanding of these is Twin Sisters Mountain, a westerly outlier of the northern Cascades; it is pure dunite, an igneous ultramafic composed primarily of the mineral olivine. Rock of similar origin occurs locally at low elevations to the west; Fidalgo Island and Cypress Island have the most extensive of this series of ultramafic outcrops.

The vegetation on the Twin Sisters dunite contrasts strikingly with that on the adjacent non-ferromagnesian parent materials. The luxuriance of the Humid Transition forest abruptly gives way to stunted Douglas fir, lodgepole pine, western white pine and shrubby *Juniperus communis*. The insular ultramafics also support conifers, largely Douglas fir, *Pinus contorta*, and *J. scopulorum*.

The coniferous forest on ferromagnesian substrates is by no means dense and continuous. The trees are largely stunted and widely spaced; often on steep, stony serpentized outcrops there are no trees present. On such barren, continuously eroding slopes, as well as on talus, in rock fissures and on sparsely forested slopes, one is almost sure to find a representation of species restricted to the ferromagnesian soils and rock.

The flora of the Wenatchee Mountains has received the lion's share of my attention. The serpentines of this rugged range support a depauperate flora, a shifting, variable mosaic of both indicator-endemics and wide-ranging edaphically indifferent ("bodenvag") species. The ultramafic rocks at the same time exert a pronounced exclusion effect on much of the regional flora on adjacent non-serpentine habitats. From field records of observations on 36 serpentine and 30 non-serpentine sites a picture of partial floristic discontinuity has emerged and yields fruitful generalizations on the effects on the flora of these northern ultramafic soils. 1. Extreme barren serpentine habitats are depauperized in species number, especially in species of the tree and shrub life form. Such serpentine barrens within the coniferous forest biome appear as though the alpine and timberline zones have been eccentrically displaced downward in altitude. 2. There are indeed endemic and indicator species on Washington serpentines. These are: *Polystichum mohrioides lemmonii*, *Cheilanthes siliquosa*, *Poa curtifolia*, *Eriogonum pyrolaeifolium coryphaeum*, *Arenaria obtusiloba*, *Claytonia megarhiza nivalis*, *Anemone drummondii*, *Thlaspi alpestre*, *Ivesia tweedyi*, *Lomatium cuspidatum*, *Douglasia dentata nivalis*, and *Chaenactis thompsonii*. These twelve species are strong indicators of serpentine; all are herbaceous (two ferns, a grass and nine dicot forbs). 3. Conifers for the most part do not show any marked edaphic preferences. I have observed certain low to mid-montane coniferous species to occur at higher altitudes on serpentine: *Pinus contorta latifolia*, lodgepole pine; *P. ponderosa*, yellow pine; *P. monticola*, western white pine; and *Taxus brevifolia*, western yew. On massive dunite of the more west-

erly Twin Sisters Mountain, lodgepole pine is the dominant timberline tree; it is unknown in this role elsewhere in the Pacific Northwest. A reverse displacement occurs for the three other conifers. *Pinus albicaulis*, whitebark pine; *Abies lasiocarpa*, subalpine fir; and the shrubby *Juniperus communis* occur at lower than normal elevations on serpentine.

With respect to the flora on nearby non-serpentine soils, it is clear that a large number of species (35) avoid serpentine. This "serpentinophobia" is most evident where serpentine rocks contact other rock types such as granite, greenstone, sandstone, etc. For some plants, avoidance of serpentine becomes a family or generic matter. Though rich in species in the Pacific Northwest, the genus *Penstemon* fails to occur on serpentine. The Ranunculaceae, Saxifragaceae, Leguminosae, Rosaceae, and Ericaceae are conspicuous by their scarcity or absence on serpentine.

In Washington as in other parts of the world, some elements of the regional flora appear to act indifferently to serpentine. The soil-wanderers (bodenvag species) in Washington form a conspicuous element of the flora, especially since most are conifers. There is no doubt though that species of this category often are responding genetically to the serpentine habitat. Ecotypic differentiation into serpentine tolerant strains has been demonstrated for Washington serpentine flora just as clearly as for the Californian examples (Kruckeberg, 1967). Nine of the 18 bodenvag species tested clearly showed differences in serpentine tolerance. Six showed signs of the same phenomenon, while only three species failed to show ecotypic variation. The clearest responses were with herbaceous perennials, e.g., *Achillea lanulosa*, *Fragaria virginiana*, *Prunella vulgaris*, and *Rumex acetosella*. The two latter species are especially noteworthy inasmuch as they are introduced species on serpentine. They have responded adaptively to selection for serpentine tolerance probably within the last 50–75 years. At first it appeared that coniferous bodenvag species were not ecotypically differentiated. Only after a long period of growth (2 years) has it been possible to detect ecotypic response in lodgepole pine, *P. contorta latifolia*.

The most faithful indicators of Washington serpentines are two ferns, *Cheilanthes siliquosa*, rock brake, and *Polystichum mohrioides* var. *lemonii*, (Kruckeberg, 1964). The *Cheilanthes* rarely fails to appear on even the most isolated and smallest ultrabasic outcrop, and at all altitudes from sea level to timberline. Though restricted to higher altitudes the *Polystichum* is just as reliable an indicator. One is led to assume that spores of these serpentinophytes are widely dispersed or at least in a regionally chain mail fashion, but only do they establish populations following germination on soils of ultramafic origin. The distribution of *C. siliquosa* spans the North American continent from the Gaspé of Quebec to British Columbia and thence to central California and nearly always its discontinuous range coincides with the outcropping of ultramafics.

"Normal" (Zonal) Soils

Admittedly arbitrary is the antithesis—normal versus abnormal soils.

1969]

KRUCKEBERG: SOIL DIVERSITY

147

Yet to the extent that climate or parent material are primary in determining the quality of a soil, the distinction is justified. We would, therefore, expect that normal soils will be characterized by properties derived from other parent materials. In other words, given a range of unexceptional parent materials in a region of similar climate, all normal soils would be nearly alike, converging on common properties due to the overriding effects of the regional climate. The vegetational response to a single soil type on differing parent materials should be homogeneity, other factors being the same.

Does this in fact ever occur? A test of this progression to sameness of soil from different parent materials could only be made under ideal conditions. For example, chemically similar and "normal" parent materials of varied origin, e.g., volcanic, intrusive, metamorphic and sedimentary rocks would be expected to have weathered over the same periods of time, would have to be subjected to the same succession of biota and would have to be compared under similar topographic sites. The concurrence of all of these seems unlikely. Even where the properties of the differing parent materials are not extreme, physically or chemically, soil and vegetation differences are likely to exist. Two of the examples cited earlier can be brought to bear on this point. According to Wright and Mooney (1965), it is the dolomite which is the preferred substrate for the White Mountain bristlecone pine. The sandstone and granite both support the sagebrush dominant and much of the subordinate vegetation. Yet the species composition on the two latter substrates does differ: between the two more normal rock types there are substrate preferences by the flora.

Whittaker's (1960) study of soil preferences by the flora of the Siskiyou Mountain included comparisons between two rock types, diorite and gabbro, less extreme than serpentine-peridotite. Soils derived from diorite and gabbro are much alike chemically. Assuming uniform soil forming factors other than parent materials, the two parent materials should support rather similar vegetation. On the contrary, differences in vegetational composition still do occur and are substrate-dependent. Even dominant tree species show differential responses; species on the gabbro occur with greater frequency on more mesic sites. Whittaker generalizes this "shift toward the mesic" as a common trend associated with change toward substrates higher in ferromagnesian minerals.

It is therefore likely that whenever geological diversity exists in mountainous regions there will be corresponding floristic diversity. The more extreme the lithological differences, the greater the differences in flora. Substrate dependence will more likely be minimal in areas of minimal topographic relief and/or on alluvial substrates. The latter condition appears to hold for the Pacific Northwest where valley alluvium from volcanics, sedimentaries, or granodiorites supports the same climax coniferous forest—including much the same species in the subordinate vegetation. Still another possibility exists: several vegetation types on a single and local substrate. Wells (1962) finds this to be true in the cen-

tral Californian coastal vegetation. He attributes this kind of vegetational heterogeneity to a history of fire, grazing and other disturbances.

Other Soil Properties Affecting Plant Distribution

Once formed from parent material by the processes of weathering, soil comes into its own as a substrate which can develop unique properties independent of its mineralogical origin. The interplay between organism and soil introduces new dimensions and creates new properties. Two significant attributes of soil that affect plant distribution in remarkable ways are currently under vigorous and fruitful scrutiny. The first of these, soil microtopography, is usually intrinsic to soil and can vary apart from the activity of associated biota. The other influential soil property is the presence in soils of substances of biological origin that promote or inhibit growth. Studies of these two properties are providing unexpected insights into the basic ecological problem of competition (interference) and evoke possible mechanisms for such ecological phenomena as a succession, spatial pattern, endemism, etc.

Soil Microtopography

The fate of seed, once shed from the parent plant, is largely a matter of chance. Where a seed is deposited will be a primary determinant of germination. Even dispersal to a suitable soil or organic substrate is not enough to ensure success. From the "ant's eyeview" the surface of the substrate can be mountainously irregular; and to the seed, major differences in soil microtopography may spell the difference between a favorable microenvironment for germination and failure. Harper, *et al.* (1965) has studied the effect of microtopography on germination and has emphasized germination on "safe" versus "unsafe" germination sites as a potent control of plant populations. Their earlier experiments (Harper, 1961) were done with seed of annual grasses, *Bromus* species, sown on two contrasting soil surfaces. On a uniformly rough surface, irregular clumps of soil about $\frac{1}{2}$ inch in diameter, there was a linear increase in germination with increase in sowing density. But on a soil of regular surface, checked by drying into smooth sectors bounded by cracks, germination failed to increase beyond a rather low density. Clearly the rough surface provided "many more potential germination sites" than did the smooth one. Only those seed that landed in the crevices germinated and there the number of "safe" sites was limited! Harper, *et al.* (1965) greatly elaborated on this theme by using a variety of species of differing seed size and increasing the variety of soil surfaces. There is no question but that the physical heterogeneity of soil surfaces provides a range of microhabitats both suitable and unsuitable for germination. The probable effect of "safe" microsite may be to provide suitable moisture and temperature conditions for germination. The effectiveness of soil pathogens on reducing seedling survival must also depend on the quality of the particular microsite.

1969]

KRUCKEBERG: SOIL DIVERSITY

149

Variations in soil microtopography are the product of soil-forming factors. This idea can be formalized in terms of Jenny's soil-forming factor equation ($s = (cl, o, r, p, t)$) where "s" now is "soil microtopography." We can draw from Harper's work some rather far-reaching inferences which bear upon competition, succession and plant distribution. 1. Different species will respond uniquely to different configurations of soil microsites and thereby create local differences in species distribution. 2. Microsite variations decrease the pressure of interspecific interference, if the species have distinct safe site preferences. 3. Changes in microsite through time from bare mineral soil through various successional stages will result in the selection for different species at each stage of the seral sequence. The concept of "safe" site thus is pregnant with experimental stratagems for studying a species niche, plant distribution, and the dynamics of vegetation.

Soil Inhibitors

The effect of a metabolite of one species on the survival and/or competitive ability of another is well known to the protistan (microbial) and aquatic animal ecologist. That an equivalent interaction mediated by soil intake-output of metabolites can occur in higher plants thus appears most reasonable. Though repeatedly suggested ever since the time of Liebig, the possibility of promotion or inhibition of growth by metabolites which pass from plant to plant via the soil has only occasionally been given serious attention. Paradoxically the botanist who now finds good evidence for the phenomenon was in the position of having to deny the ecological effectiveness of the first modern case of allelopathy, the effect of plants on each other through their metabolites. Muller (1953) could not substantiate under field conditions the inhibitory effect of metabolites of *Encelia*, a desert shrub, on other plants which had been found in laboratory tests of leachates. The inconclusive nature of antibiotic effects of plant-on-plant is attributed to the differences between natural conditions in the field, dilution, microbial decomposition, soil sequestering of leachates, etc., and the more concentrated doses combined with ideal though artificial conditions in laboratory experiments. More recently Muller and his associates (1964; 1965), have developed incontrovertible evidence for the inhibition of vegetation by volatile terpenes given off by species of *Salvia* and *Artemisia* in the California coastal sage community. The causal basis, toxicity of terpenes, for swaths or perimeters of sterile ground around the sage species has been confirmed in laboratory studies. The suppression is greatest against annual grassland species. Moreover the toxic effect of the terpenes can be retained by the soil for several months. Natural inhibitors can have a far-reaching effect on floristic composition. A substance produced by the shrub by chamise, *Adenostema fasciculatum*, excludes species of grass, which in turn would otherwise exclude *Dodecatheon clevelandii*, a shrub-tolerant herb. Thus this two-step biochemical exclusion creates an in-

hibitor-induced association of the chamise with the *Dodecatheon*.

The deposition in soil and recycling of organic metabolites is now well established. A wide range of secondary metabolic products of plants, carbohydrates, amino acids, organic acids, volatiles, alkaloids, etc., can be recovered in the tissue of plants grown on substrates, soils or culture solutions, that contain the substances (Grummer, 1961; Tukey, 1962; Winter, 1961). Evaluation of the ecological role of such exogenous substances confronts the same problem of complex factor interaction that persistently vexes the ecologist. A laboratory test of toxicity may not be complemented by positive evidence of toxicity in the field. Differences in concentration, unavailability of exudate-leachate due to adsorption or microbial activity, rainfall-temperature effects, all may lessen or negate the influence of the metabolite. Despite these reservations, it is becoming increasingly clear that interference phenomena, and in turn, pattern and distribution of species in communities, even the effective niche of a plant species, can be importantly influenced by organic compounds cycled through the plant-soil-plant system.

Evolutionary Consequences of Variations in Soils

Plants are ever responsive to differences in their environment that occur over spans of time and space. The effective level of response is the population. The outcome of organism-environment interaction is either adaptive response through natural selection or failure to colonize the habitat, and hence, exclusion or extinction. Variations in soils, then, as significant parts of the fabric in the environmental mosaic, operate as agents of natural selection. Discontinuity of the soil features will further act to isolate adaptive variants. The result of such interactions can be discerned at various hierarchical levels and will be expressed in a variety of modes. Microevolutionary reaction to soil differences will take the form of degrees of ecotypic differentiation, the development of broad genotypic tolerance, or ecological exclusion. The origin of species restricted to edaphically unique habitats is a higher order of evolutionary divergence. Raven (1964) has invoked the concept of catastrophic selection to account for diversification of edaphic specialists. Rapid selection of exceptional genotypes under the stringent environment of azonal soils is presumed to lead to fixation of unique, incipient populations. When soil and biological discontinuities become congruent, isolation and species formation then are promoted. Examples of evolutionary change up to the level of species as occasioned by the selective action of soil differences have been presented above in the section on "abnormal" soils.

Would we not expect some degree of edaphic preference to be expressed in still higher levels of the taxonomic system? Could not sections of genera, entire genera, or even families show in substantial degree singular edaphic restrictions? Such expression of specificity can be induced by climate and is a major ingredient of speciation in the direction of adaptive radiation or extinction. The high incidence of the genus *Streptan-*

1969]

KRUCKEBERG: SOIL DIVERSITY

151

thus to serpentine, many caryophylls to ultrabasics, Ericaceae to acid soils, Cyperaceae to water-logged soils, genera of the Chenopodiaceae and Amaranthaceae to nitrogenous or saline soils are all suggestive of edaphic specialization. We would contend then, that soil, as is climate, is a potent selective agency in securing evolutionary change.

Plants as Indicators of Mineral Deposits

The non-random distribution and abundance of plant populations in a circumscribed habitat is the expression of one or more of a set of environmental controls. It is as though the unique composition of a flora is telling the observer that some factor is having an overriding effect on the composition of the plant cover. Plants which act as assay organisms for some environmental component are called indicator species. The recognition of plant indicators has been a traditional approach to the study of environmental restraints on plant distribution. Ecologists, agriculturalists, foresters and range managers all use the sensitivity of plants to environment in attempting to control or manage vegetation.

Plant indicators have been exploited in yet another way—prospecting for mineral deposits. Deposits of a variety of minerals have been located by searches in the field for the tell-tale displays of eccentric patterns of plant occurrences or equally startling absences of occurrences. It is when the indicator plants are found to contain unusual quantities of some mineral element that the geobotanical prospector strikes it rich. Biogeochemical methods have now become standard practice for search for ore deposits in the United States, Canada, Scandinavia, the U.S.S.R. and elsewhere.

Let me relate a personal anecdote as a prologue to the description of some of the results that the method has produced. During his nightly rounds of our department, a faithful janitor would customarily linger in the herbarium. Our suspicions were aroused by his preoccupation with the contents of the herbarium cases, a conduct most unlikely for one of his limited talents. His predilection for dried plants was, however, genuine. He was scanning the contents of every case with a Geiger counter, in the hope that somewhere in our Pacific Northwest collection, his counter would begin ticking at a runaway accelerated rate. His actions told us that he was looking for uranium, at that time a much sought-after element. The outcome of his effort was, alas, unsuccessful, though the intent was perfectly justified. Uranium deposits could be located by this method!

More systematic and successful have been the operations of the Geochemical Prospecting Methods Division of the U.S. Geological Survey. Helen Cannon of the U.S. Geological Survey has published (1960) a comprehensive review of geobotanical prospecting for ore bodies. Although she points out that the recognition of absences of vegetation, or unusual changes in appearance of plants also can yield "strikes," it is the plant indicator approach that concerns us here.

The list of minerals which plant indicators can disclose reads like a miner's "Eldorado": A conservative compilation would contain boron, copper, gypsum, iron, lead, phosphorus, selenium, silver, uranium and zinc. The copper indicators are both abundant and unusually reliable. They "belong" mainly to three plant groups: the Caryophyllaceae or pink family, the Labiatae or mint family, and the mosses. These copper deposits have been located in Sweden by simply examining localities from which the herbarium specimens of the "copper mosses" had been collected. The copper indicators, *Elsholtzia haichowensis* from China, *Acrocephalus robertii* from Katanga, and *Ocimum homblei* from Rhodesia all belong to the mint family and are very useful in prospecting. The blue-flowered *Ocimum homblei* will not grow in soil containing less than 100 parts of copper per million. The distribution of this plant has led to the discovery of several ore deposits and is currently being mapped in both Northern and Southern Rhodesia by the Rhodesian Selection Trust (Cannon, 1960).

The well-known affinity of members of the loco-weed genus, *Astragalus*, for selenium has led to uranium discoveries, since the occurrence of the two elements is often highly correlated. A good example of the plant indicator method comes from the work of Cannon's group in western United States. Several species, grasses, legumes, and composites, in the shadscale-juniper vegetation of the Yellow Cat area in Grand Co., Utah, proved to be consistent indicators of selenium. In this particular area, selenium and molybdenum are useful pathfinder elements in prospecting for uranium and vanadium. On mineralized soil indicator species contained 6 to 11 times the amount of uranium found in unmineralized ground.

As biogeochemistry becomes more sophisticated in technique, we would predict additional rewarding mineral discoveries. Edaphic plant ecology is certain to contribute to future mineral prospecting and as well, should reap rewards for the student of plant distribution.

Epilogue

It is axiomatic in biology that complexity through factor interactions breeds exceptions to consistent trends and that the analytic approach at the community level must momentarily disregard complex interactions. Our singling out of the soil factor in plant distribution has been just such an over-simplification. The dwelling place of a particular species or assemblage of species is the result of past and ongoing interplay between biota and environment.

In this paper, we have taken the view that soil characteristics can often have the dominating local or even regional impact of determining distribution and/or pattern of plants in associations. Edaphic plant ecology, then, becomes one useful key to the understanding of discontinuity in vegetation.

A condensed version of this paper was presented at the American As-

1969]

KRUCKEBERG: SOIL DIVERSITY

153

sociation for the Advancement of Science Symposium, "Plant Biology Today—Advances and Challenges," Berkeley, California, December, 1965. The author's studies on serpentine vegetation of Washington and on the genus *Streptanthus* have been supported by N.S.F. Grants GS-2792 and GB-4579.

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1954]

MASON: MIGRATION AND EVOLUTION

161

MIGRATION AND EVOLUTION IN PLANTS¹

HERBERT L. MASON

It will be my objective to point out that the dynamics of the genetic elaboration of the plant population over the available habitats is the dynamics of natural selection and that genetic variation and natural selection together provide the dynamics of plant migration. Hence, plant migration and the organic evolution of each genetic lineage involved are concomitant.

THE CONCEPT OF MIGRATION

There are at least three different types of movement of natural populations, each of which may be spoken of as migration. There is the oscillating phenomenon such as the back and forth movement of ducks and geese wherein these animals migrate closely in tune with the seasonal progression of climate. This we may speak of simply as *seasonal migration*. Although these animals are adapted genetically to this mode of life, the dynamics of seasonal migration do not involve the simultaneous and oblige genetic elaboration of the population over area.

A second type of migration is the impulsive or sporadic movement of organisms possibly related to overpopulation phenomena. Here we have such phenomena as the curious suicidal migrations of the arctic lemming and the occasional mass migrations of excessively large populations of rodents such as the migration of mice in the San Joaquin Valley of California a few years ago. Such *sporadic migrations* do not necessarily involve the genetic elaboration of the population, although with the increase in density of the population there is probably a concomitant increase in its genetic variability.

A third type of migration is not seasonally oscillatory, but it may at times appear as though sporadic. It is often persistently directional through long time, and always involves the lineal succession of individuals. It may be either a response to secular environmental changes or to the local environmental selection of fortuitous adaptive changes that are products of genetic variation. More commonly, these changes operate together. Because such changes usually include occurrences on a scale of very long time periods even in terms of geological time, we may speak of this type of migration as *secular migration*.

Both seasonal and sporadic migration are known only in animals. Secular migration may occur in both animals and plants. For instance we have fossil evidence that both the camel and the horse originated in North America, where they are now extinct, and migrated to the old world, where they still persist in the form of changed modern descendants. We have

¹ Presented as a semi-popular lecture in the "Symposium on Evolution" commemorating the Centennial of Mills College, Oakland, California, April, 1952.

similar evidence of the migration of plants which we are able to trace through the "flashes" of the fossil record and through which we may interpret the evolutionary changes that have taken place during this migration.

The important difference between secular migration and seasonal and sporadic migration is that secular migration, because it is involved with the linear reproductive succession of individuals through time, is obligately concerned with the genetic elaboration of the population over environments. Such genetic elaboration of the population over environments is a significant part of the migrational dynamics. This need not be the case with either seasonal or sporadic migration.

It is necessary that I make clear that migration and dispersal are not synonymous. Dispersal is the movement of an organism in any form from one place to another (Ridley, 1930). If, however, after dispersal, the individual is unable to survive and reproduce, there is no migration (Clements, 1916). At any given time with any species population the potential scope of dispersal is infinitely greater than is the potential scope of migration. Seeds regularly find their way into many habitats in which there is no chance of their survival. Perhaps the best examples are the hundreds of cultivated plants dispersed by man through cultivation which are unable to survive in the areas into which they are introduced except through the care given them by man. Assuming that activities associated with man's culture are artificial, such introduced plants are not regarded as part of the natural plant population. On the other hand, many of our weeds, dispersed through man's carelessness, became established and now are self-perpetuating populations. These are examples of effective steps in migration.

Dispersal beyond the habitat of the population provides that genetic variants, initiated in the population, may reach a new environment to which they may be adapted and by which they may be selected for survival. If the new area is contiguous to the old, the area of the population is extended, and the survival of the new variant may, through gene exchange, serve to stimulate the pattern of genetic variability of the population as a whole. If the new area is not contiguous a new, isolated or semi-isolated race is established.

It is also important that I point out that we have traditionally thought of secular migration in terms of the migration of floras and faunas (Chaney, 1936). Such apparent mass migrations are strictly coincidental insofar as dynamics are concerned. If we are to study and interpret migrations in terms of dynamics we must concern ourselves solely with the activities of successive individuals within interbreeding populations functioning under the influence of environmental conditions.

THE DYNAMICS OF MIGRATION

In a previous paper (Mason, 1946) I have pointed out that there are three aspects to the scope of the dynamics of any problem in plant geog-

1954]

MASON: MIGRATION AND EVOLUTION

163

raphy. First, there is the individual organism carrying on the vital processes that insure its survival and provide for the continuity of the population. These vital processes are physiological in scope and they operate in accordance with the theory of physiological limits and the principle of limiting factors, and they are influenced by the conditions of the environment. Secondly, there is the genetics of the population which is concerned with the actual gene exchange between individuals and the genic changes that may result from any of the mutagenic agencies that may operate in the populations. These may set the physiological capacity of the individual with respect to its various functions. Thirdly, there is the environment as it varies over area and through time. The conditions of the environment may function as barriers to migration or they may serve as migration lanes. Through environmental control over physiological function the environment selects its plant population. This is, in effect, natural selection.

THE PHYSIOLOGY OF THE INDIVIDUAL. The functioning of plants is conditioned by the factors of the environment as they operate to control physiological processes. The relationship between environment and precise physiological process is probably genetically fixed within each individual plant as to the nature of the span of tolerance of the particular environmental factors concerned. The fixation of the tolerance span may result from any of the gene assorting and gene modifying mechanisms of cytology and genetics as these operate to allocate a given set of genic materials to each individual plant. Physiological characters, as imparted by gene combinations, vary among the individuals of the population in the same way that morphological characters do. They might and probably do vary to the extent that many of the seeds produced are incapable of functioning under the environmental regime in any of the available habitats. However, they could function in some other habitat should chance dispersal enable the seed to reach that habitat.

It is especially important to our thesis that we emphasize the role of variation in physiological capacity of individuals of a population. The vital physiological processes that go on within each individual plant operate within the basic structure of the theory of tolerance and the principle of limiting environmental factors. It is because of this that there is a close relationship between the plant and the environment. It is because of the variation in physiological capacity and the role of limiting environmental factors that different kinds of plants occur in different kinds of habitats. We can speak broadly and say that some kinds of plants grow only in the tropics while others grow only in the arctics. Or, as research in this field advances, we can speak in increasingly precise terms. We now know that species become elaborated over area in direct proportion to their genetic diversity with respect to physiological characters on the one hand and, on the other, to the degree that these variants become dispersed into suitable habitats. The experimental work of Clausen, Keck and Hiesey (1948) on *Achillea* gives ample evidence of this. Thus, individuals

comprising a species may be aggregated into populations that differ from one another to a greater or lesser degree. Today, facts discovered during the research of some of my students enable us to carry this even further. We may now state that the precise distributional pattern, even within some small interbreeding populations, reflects a pattern of genetic diversity in the physiological capacity of the individuals that have been selected by a pattern of local habitat variation. Some members of the same interbreeding population can survive through selection in one part of the area of the population, but would be rejected and perish in another part of the area of this same small population. It is because the physiological processes that they are important in determining the area in which species can live. Since the range of tolerance is subject to the laws of evolution and genetics and is as characteristic of the plant as are its morphological characters, it is to be expected that there will be variation from one individual to another within the interbreeding population. Variation in tolerances thereby becomes the basis of explaining how the members of a species become elaborated over a complex set of environmental conditions, the total range of which is beyond the capacity of any one individual. Each individual is but an increment in the total range of the species. One individual may extend the tolerance of the species population in the direction of one environmental extreme while another individual will extend it in the direction of another extreme.

Thus the physiological processes of the plant, whether they involve nutrition, respiration, growth, or reproduction operate under the influence or sanction of the environmental conditions. The environmental condition circumscribes the area in which the function can operate. Variation in physiological capacity among individuals almost certainly demands that the plants will occupy different kinds of habitats.

THE GENETICS OF INDIVIDUALS IN POPULATIONS. The interbreeding population, through the physiological functioning of individuals and the mechanism of gene exchange, sets up a self-perpetuating dynamic system so that functioning individuals continually are being produced as old ones die. Because there are always individuals present, the population is said to persist. Persistence of the population and of the species is thus vested in the reproductive process of individuals of the population. For the most part, these processes are sexual processes which, because of their attendant cytological phenomena, set in motion the mechanics of population genetics. Persistence of the population is not guaranteed through population genetics, but no better device has as yet been produced to insure opportunity for survival in the face of fluctuating and changing environmental conditions. In meeting these situations, some populations have both migrated and undergone evolutionary changes. Other populations have not been genetically adaptable and have perished. I have previously pointed out (Mason, 1946) that genetics, by whatever mechanism it may operate, in each individual case functions to set the capacity of the plant to tolerate

1954]

MASON: MIGRATION AND EVOLUTION

165

the conditions of the environment. Once the zygote is formed, the potential individual will be capable of carrying on all of its vital functions only under the environmental conditions to which it may be thus preadapted. Usually seed grow only in an environment similar to that in which the parents grew, but genetic processes may result in production of seed having somewhat different capacities than those of the parents, capacities that enable the progeny to become established and survive in slightly different or new environments. Such new environments have nothing to do with the *preadaptation* of these seeds that become established there. They can only select or reject an already adapted individual. The role of genetics, so far as the potential characters of this individual are concerned, is ended with the formation of the zygote. Since reproductive processes continue in the population, we may think of the population as thereby being continuous beyond the life span of any single individual member. The continuity in reality is the many successions of individuals, overlapping in their duration.

That the relation between function and conditioning environmental factors is genetically fixed within each individual plant has been established through considerable research (Turesson, 1922; Clausen, Keck and Hiesey, 1940, 1948). However, no individual represents the total span of variation exhibited by the population as a whole. Breeding programs for earliness or lateness in agricultural crops in local situations are dealing essentially with the genetics of physiological characters. The fixing of the tolerance spans within individuals may result from any of the mechanisms operating in genetics which function to apportion gene materials among gametes.

Out of the mass of preadapted seed received, the environment permits the survival of only those which are capable of carrying on all of their vital functions under the conditions prevailing in that environment. This repeated selection, generation after generation, tends to fix the form and the physiological capacity of the mass of individuals that constitute the species population in that environment, and it tends to control the range of genetic variation within the species population. Thus any mutant in the population which has the potentiality of affecting physiological relations will soon be eliminated should it produce an effect that is not selected by the environment. On the other hand, should the mutant produce a better relationship with the environment, or should it enable the population to expand its area into new habitats, it will be favored and will tend to increase the genetic diversity of the population and thus increase the survival chances of the population in the face of environmental fluctuation and change. This is essentially the mechanism of natural selection.

Thus the genotypes within the species population become modified by environmental selection. This is what Turesson (1922) called, "genotypical response of the plant species to the habitat." Such selection results locally in a genetic race thoroughly in adjustment with its environment. It involves the pattern of interaction between the various factors of the

environment, the physiological processes of the plant concerned with germination and establishment and the various functions of individuals.

It is through these processes that the species is able to persist in a given environment through normal fluctuations of environmental conditions. Likewise it is through these genetic processes that variation develops, thus enabling the species to extend itself into new habitats. Only in this way can a migrating plant species overcome the diverse environmental conditions that it would encounter in its migration. Only in this way can we explain the habitat diversity between the species of a genus. In recognizing the role of genetics in plant migration, it is important to reemphasize the point that the seed destined to survive in a new environment arrived in that environment already adapted. Also it is important that we realize that the new environment played no part in this preadaptation. All of this happened through those genetic phenomena that are inherent in the reproductive process under the influence of the environmental relations of the parents.

THE NATURE OF ENVIRONMENT AND ENVIRONMENTAL RELATIONS. The medium in which the plant grows, involves chiefly the climate and the soils, but it may also include the direct and indirect effects of other organisms. The interaction of climate, soils, and organisms is very complex.

Climatic factors in any given region function within a general pattern of diurnal and seasonal rhythm, such as the daily fluctuations of temperature, or as temperature and rainfall follow a seasonal sequence, or as length of day and length of growing season follow a rhythmic sequence. Often these rhythmic sequences impose a rhythmic sequence on other environmental factors such as the position of the water table, or the salinity of lakes in seasonally arid regions. The nature of such sequential events may be limiting factors to some species of plants. Climatic factors usually occur over area as directional gradients of intensity or amount and no sharp boundaries exist. Where these appear to exist they are usually evidence of a local steepening of the gradient. The nature of these gradients in their effect upon plant populations often becomes selective locally to produce clines within the population with respect to the tolerance of these conditions. Each local race is adapted to the local area of the gradient. This is often evident in the gradient of length of season on the slopes of a mountain of sufficient height where a species occurs throughout. Those plants at low altitudes will be adapted to a long season while those at high altitudes will be adapted to a short season.

Edaphic factors are those pertaining to soil composition and condition. They operate within a situation imposed by local climate and to some extent they may be a product of that local climate. They may be relatively persistent features, expressible in terms of presence; they may vary locally in their intensity or amount; they may fluctuate as a result of chance climatic, biotic or diastrophic events; or they may follow a rhythmic pattern in tune with the rhythm of climate. The edaphic situation often has persistent features of large area such as may be determined by litho-

1954]

MASON: MIGRATION AND EVOLUTION

167

logic conditions, or by the position of the water table. Such features in turn produce effects upon soils to which they contribute. In conjunction with local climate, soils may be significantly altered and characterized by accumulations of salts at the surface. There are many ways in which edaphic situations may vary either within themselves or through their interactions with other environmental conditions. In any event, the areas occupied by given sets of edaphic conditions constitute the areas available to plants, and the mosaic of edaphic factors across area provides a significant set of variants for the operation of selection.

Biotic factors present many interpretational problems because the organism itself is subject to climatic and edaphic situations. Furthermore biotic effects may be either direct or indirect. When the influence of an organism is indirect, the organism creates a condition in another factor to which a second organism reacts. For instance a rodent may loosen the soil. The reaction of any plant that might be affected is to the loosened soil rather than to the rodent directly. Loosened soil due to other causes might produce the same effect in the plant.

It should be made clear that because they are often interrelated the problems of environmental factors and their conditioning effects are not simple. They are not solely matters of presence or absence of fluctuating intensities and demands, nor are they the simple problems of gradients between extremes. They may involve coincidences between two or more rhythmic cycles of fluctuating conditions, or fluctuating physiological demands, or of rhythmic sequences in the ontogeny of the plant. Often they serve to condition one another and in so doing, they may alter the physiological response.

When we consider all aspects of the environment, it becomes clear that much of its significance to our problem is the fact that environmental condition occupies area independently of whether or not the precise condition or combination of conditions may influence a particular organism. Thus area is subordinate to environmental condition in determining where a given species can grow. Of equal significance is the fact that environmental condition varies enormously over area, thus presenting a mosaic of conditions sometimes locally rather uniform, sometimes locally very complex. Each such local habitat is either the potential habitat of some chance genetic race of the species population, or it may present a barrier too great for a genetic race to cross by occupancy and successive seed dispersal.

It should be clear that environmental conditions as they occupy area present problems to any migrating species. The magnitude of some of these areas is such as to make it mandatory that the species cross by occupying the area. One individual seed may, by preadaptation and fortuitous dispersal, reach a suitable habitat in the area and become established. Before a second step can be taken normally, the reproductive process must take place to produce additional migrules. These, if they succeed, build a local interbreeding population.

In the process of migration, environmental diversity must be met and overcome through the development of individuals and races of the species population preadapted to the new environmental situations that are encountered in the migration. Although in general the population must cross such areas by inhabiting them, some fortuitous long-jump dispersal may at times occur. The greater the genetic diversity of the population, the greater are its chances of survival in the face of the hazards of migration. A genetically stable species has little chance of success as a migrant. We must bear in mind that migration is possible through successive genotypic changes which meet the pattern of the environment encountered. Climatic change usually makes it mandatory that the species population either migrate, become adapted to the change, or perish. Under conditions of climatic change, the species population may remain within range of the same climatic conditions by migrating in pace with the change. In so doing, however, it encounters very great edaphic diversity to which it must become accommodated or it will perish. Such a migrating population may leave behind descendant populations capable of adjustment to further climatic changes. These populations may become points of origin of further evolutionary diversification.

In conclusion, we may say that simultaneous with migration we usually find evolutionary diversification by means of genetic elaboration of the migrating lineages. Thus, the population is accommodated to the environmental diversity that it encounters. The interbreeding population provides the necessary reservoir of genic materials for recombination in varying manner. It thereby provides for the persistence of the species through adjustment to environmental fluctuation and change and for extending the area through genetic change. At length these changes may be of profound scope and be spoken of as evolution.

It is doubtful if any extensive long-term migration is possible without significant evolutionary change in physiological capacity. It seems probable that only plants undergoing active speciation are capable of extensive migration. It would seem therefore that an elaborate taxonomic and geographic pattern in any group of plants would stand as testimony of a former highly vigorous genetic nature.

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1954]

BEAMAN: TOWNSENDIA

169

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THE GENETIC APPROACH TO PROBLEMS OF RARE AND ENDEMIC SPECIES

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One of the questions that every field botanist with an inquiring mind is bound to ask is: Why are some plant species widespread and common, while others are rare and local? The problem of rare species has a twofold fascination; their discovery never fails to provide a thrill, while the analysis of their affinities and distribution often gives valuable clues to the history of floras. It is natural, therefore, that many botanists have given their answer to this question, and that these answers have been as diverse as are the minds of their proponents. Among these answers there have recently appeared a series which has emphasized the genetic constitution of the species involved. The object of the present article is to review the available evidence upon which these concepts are based, to suggest ways in which new experimental evidence for them may be obtained, and to follow out some of their implications when applied to problems of the history of floras and plant evolution.

The word "rare" may not always mean the same thing. Some plants are regarded as rare because throughout a large part of their range they are found only as scattered individuals or small groups, separated by miles from their nearest neighbors. Such is the case with many species of orchids, such as *Calypso bulbosa* (L.) Oakes, *Cephalanthera Austinae* (Gray) Hel., *Cypripedium arietinum* R. Br. and *Aplectrum hyemale* (Muhl.) Torr. In most of these cases, however, there are some regions where the species concerned are abundant. *Calypso*, for instance, is common enough in the northern Rocky Mountains, as is *Cypripedium arietinum* in parts of southern Ontario, while the rarity of *Aplectrum* is due largely to extermination by man. Another type of rarity is extreme localization. A species may occur in only a few widely separated localities, but may be abundant enough where it is found. This is notably true of *Phyllitis Scolopendrium* (L.) Newm. var. *americana* Fernald, the hart's tongue fern in eastern North America. Many species of serpentine barrens in California, such as *Cupressus* spp. and *Streptanthus* spp. are similarly distributed. Still a third type of rareness is extreme endemism. A species may occur only in one or two spots on the entire globe, but in this case it is almost always represented in these spots by hundreds of individuals. These three types are, of course, connected by innumerable intermediate cases. In the writer's opinion, the concepts set forth below will apply with modifications to all of them.

As a necessary background for this study, let us review briefly the most widely current answers to this question of why certain

species are rare. Perhaps the most direct and simple answer is that of Willis (34, 35), who maintains that in general rare and endemic species are beginners, which have not yet had time to spread. The weaknesses and fallacies of this hypothesis have been fully exposed by Fernald (16), Wright (38), and Hubbs (23), so that they need not be dwelt upon here. It will be pointed out below that our present concepts of the genetic structure of species, which have been developed as a result of many painstaking experiments, throw into glaring relief the fallacies of Willis's reasoning. In addition, recent paleobotanical research has added greatly to the number of rare modern species whose fossil ancestors are known to have been common and widespread, and this is particularly true of the endemics of the California flora (Chaney, 7, Axelrod 2, 3).

A second answer was given by Fernald (15, 17, 18), as a result of his keen observations in the field and his careful analysis of the distribution of many rare species in the flora of eastern North America. This is the concept of senescence; that most rare species were once common, but that their great age and the vicissitudes to which they have been subjected have made them "conservatives," and unable to spread. This concept, based as it is upon extensive observations of rare plants as they actually grow in the field, has much to recommend it. Most field botanists will agree with Professor Fernald that conservatism rather than aggressiveness is characteristic of rare plants. In fact, the genetic concept to be reviewed below is based primarily upon this assumption. The weakness, however, of the concept of senescence is the implication that conservatism results directly from the age of a species. There are two large objections to this implication. In the first place a number of species, such as *Sassafras variifolium* (Salisb.) Ktze. *Liquidambar styraciflua* L. and *Ulmus americana* L. are known to have close relatives that go far back into the fossil record, and yet the present species are still widespread and common, having invaded much of the region that was covered by the Pleistocene ice sheet. The other, and perhaps more serious objection is that the same species may be rare and conservative in one part of its range and common and aggressive in another. *Erigeron compositus* Pursh is cited by Fernald (15) as one of the "senescent" species composing the relict flora of the Gaspé Peninsula. In the Sierra Nevada of California, and presumably also in the Rocky Mountains, this species is far from conservative. The variety of habitats which it occupies is matched by the morphological variability of the species itself. *Adenocaulon bicolor* Hook. was considered a "senescent" species (Fernald 18) on the basis of the disrupted range and obvious great age of the genus and the rarity of *A. bicolor* in the Great Lakes region. In California this species grows under redwoods, as Fernald has pointed out, but it is also common under *Pseudotsuga*, *Abies*, *Pinus ponderosa* and other conifers. In the Sierra

Nevada at middle altitudes, however, *Adenocaulon* is far from conservative. It is one of the commonest and most aggressive weeds about cabins, being often the first species to occupy disturbed ground, if sufficiently shaded. From the hypothesis of senescence one would be forced to conclude that *Erigeron compositus*, *Adenocaulon bicolor*, and similar species are old in the east and young in the west. This conclusion seems illogical in the extreme. And in one genus, *Antennaria*, there is direct evidence that the conservative, "senescent" species of the Gulf of St. Lawrence area are actually younger than their common, widespread western relatives. With one exception these Gaspé and Newfoundland antennarias are exclusively apomictic; staminate plants are unknown in them. They therefore are "dead ends" from an evolutionary point of view, and must have originated from sexually reproducing species (cf. Stebbins, 29). Their only close sexual relatives, and therefore their presumable ancestors (*A. umbrinella* Rydb., *A. microphylla* Rydb., *A. reflexa* Nels., *A. media* Greene, *A. monocephala* T. & G., etc.) all occur in western North America, and are for the most part widespread, common, and aggressive enough to have colonized extensively areas vacated by the Pleistocene glaciers. Therefore, the conservatism of the relict *Antennaria* species cannot be due to age alone, since their ancestors have still retained "youthful" characteristics.

The third answer to this problem of rare species is the genetic concept which is to be reviewed in the present paper. It is based upon the realization, as a result of the experiments of Turesson and others (cf. Turesson, 31; Hiesey, 22; Clausen, Keck and Hiesey, 8), that most widespread and common plant species consist of a large number of genetically different biotypes, many of which differ widely in their ecological preferences. This is, of course, the basis of the ecotype concept, which conceives of these widespread species as consisting of several clusters of similar biotypes, each cluster, or ecotype differing from other ecotypes in its ecological preferences. On the basis of this concept, the range of ecological tolerance of a species, in the sense of Good (20), embraces the tolerance ranges of all of its component ecotypes and biotypes. Naturally, therefore, a species with many ecotypes and biotypes will be widespread and common. And conversely, a species which is poor in biotypes, and has only one ecotype, will be rare, unless its individual biotypes have a wide range of ecological tolerance, or unless the particular conditions to which they are adapted are widespread. A rare species, therefore, may be conceived of in genetic terms as one poor in biotypes, and with its biotypes so specialized that they can grow and compete with other species in only a limited area. Aggressiveness, or the ability of a species to colonize new areas, and to crowd out other species, is the result of the possession of a great store of genetic variability either evident or concealed. This consists of genetic heterozygosity, of biotypes preadapted to new conditions

which the species might encounter, or of a rapid mutation rate, by which new biotypes may be produced. A species is conservative, on the other hand, if it contains few biotypes, most of which are homozygous or nearly so, and has a low mutation rate.

This concept was foreshadowed by Darwin's classic statement that "wide ranging, much diffused, and common species, vary most." It was hinted at some time ago by Turesson (31), but so far as this writer is aware was first clearly stated by Anderson (1, p. 496). Hultén (24) made it the cornerstone of his brilliant analysis of the history of the Arctic flora, while Camp (6) used it to explain the relative constancy and limited distribution of some species of the interesting genus *Befaria*. Cain (5) pointed out the advantages of this concept over that of senescence, while Raup (28) recognized it as an important factor in the distribution of species of boreal America. Fassett (14) made the determination of genetic constancy in certain areas a major objective of his interesting and valuable study of variation in *Rubus parviflorus*.

The main difference between this genetic concept and that of senescence is that it aims to interpret the rarity of species primarily as a result of their present constitution, without implying anything about the past history or future fate of the species concerned. Many, and perhaps most rare species were once more common and aggressive, but not all. The phenomenon of insular species, many of which have always been rare, will be discussed below. The rare conservative species which were once common have been characterized by Turesson (31) and Hultén (24) as having been "depauperated with regard to their biotype contents" (Turesson 31, p. 97). Since the word depauperate is generally applied to plants of small size, its use in the present sense seems inadvisable. The word depleted expresses the situation more precisely and has no other connotation. To those who accept this genetic hypothesis, therefore, the writer suggests that the term "depleted" be used for those rare, conservative species which appear to have been formerly more common and aggressive; i.e., the "senescent" species of other authors.

Griggs (21) has recently sought to explain the rarity of plant species on the basis of competition. He states that (p. 592) "a species is rare because it cannot compete successfully with the common plants," and that "most rare species find their habitats in the early stages of the ecological succession." These statements are supported by a wealth of evidence derived from a study of rare plants in eastern North America. They lead to a conclusion similar to that implied by the term senescence, namely that those rare species which have ranges at present disrupted, but formerly continuous, "are therefore slowly dying out." On the basis of this hypothesis Griggs admittedly has difficulty in explaining the fact that many of the plants which are rare in eastern North America are common in the west. And if one examines the plants which are rare in western America, particularly those of

California, one finds that Griggs' hypothesis does not apply to a large number of them. The most famous rare species in California is the big tree, *Sequoiadendron giganteum* (Lindl.) Buchholz. Others, almost equally famous to botanists, are *Cupressus macrocarpa*, *Pinus Torreyana* Parry and *P. radiata* Don, *Picea Breweriana* Wats., *Abies venusta* (Dougl.) Koch, *Quercus Sadleriana* R. Br., *Crossosoma californicum* Nutt. and *Lyonothamnus floribundus* Gray. None of these species can be said to "find their habitats in the early stages of ecological succession." They are sub-climax, climax, or post-climax types. Furthermore, such observations as have been made indicate that in restricted areas and under certain conditions these species can compete very well with their common associates. Mr. Woodbridge Metcalf of the Division of Forestry, University of California (unpubl. bulletins and oral comm.), has found that seedlings of the big-tree may under certain conditions become established in great numbers. Once established, they grow very rapidly and in one forest, started through natural re-seeding in the early eighties, "none of the associated species have been able to keep pace with the sequoias in height, though there are some excellent specimens of sugar pine, *Pinus Lambertiana*, and white fir, *Abies concolor*, in situations where they have not been too much crowded by the big-trees." Apparently the limits to the spread of this most famous of rare plants, are the specialized conditions necessary for the successful establishment of seedlings. These are chiefly a disturbed mineral soil, and a sufficiently early onset of the fall rains during the early years of growth. In these respects the seedlings of the common species of Sierran trees are much less particular. Another rare Californian, *Pinus radiata*, the Monterey pine, is a very good competitor in the regions where it grows naturally. Last spring the writer led a class through a clearing in a grove at the northernmost of its three natural localities, Ano Nuevo Point. Although this clearing had gone over completely to grassland (the predominant plant formation for miles along the coast both north and south of the four mile stretch of pine forest) it was filled with vigorously growing pine seedlings, which will soon crowd out the grass, and restore the area to its natural cover of pines. Furthermore, there were abundant seedlings of *P. radiata* throughout the stand, and in some places beyond its edges, so that one could not possibly draw the inference that the species is dying out. Mr. H. A. Jensen, of the California Forest Experiment Station has informed the writer that the southernmost grove of *P. radiata*, at Cambria, was once extensively lumbered, and has since restored itself. Hence neither the statement that rare species occupy chiefly pioneer habitats nor that they are slowly dying out applies to the most famous of Californian rarities.

Griggs' hypothesis, however, still is of great value in interpreting many of the rare plants of eastern North America. Furthermore his emphasis upon ability to compete as a major

factor in the distribution of both rare and common plants is fully justified and is an important part of the concept of genetic homogeneity as here presented. This seems evident from the writer's preliminary observations of one of the most interesting endemics of the San Francisco Bay region, *Dirca occidentalis* Gray. This species is restricted to an area about ninety miles long and twelve miles broad, being most abundant in the Oakland and Berkeley hills. Its nearest relative, which it resembles rather closely, is the wide-spread eastern American *D. palustris* L. (fig. 1). In contrast to the swamp habitat of the eastern species, *D. occidentalis* occurs principally upon well-drained hill slopes, where its chief competitors are other shrubs, such as *Toxicodendron diversilobum*

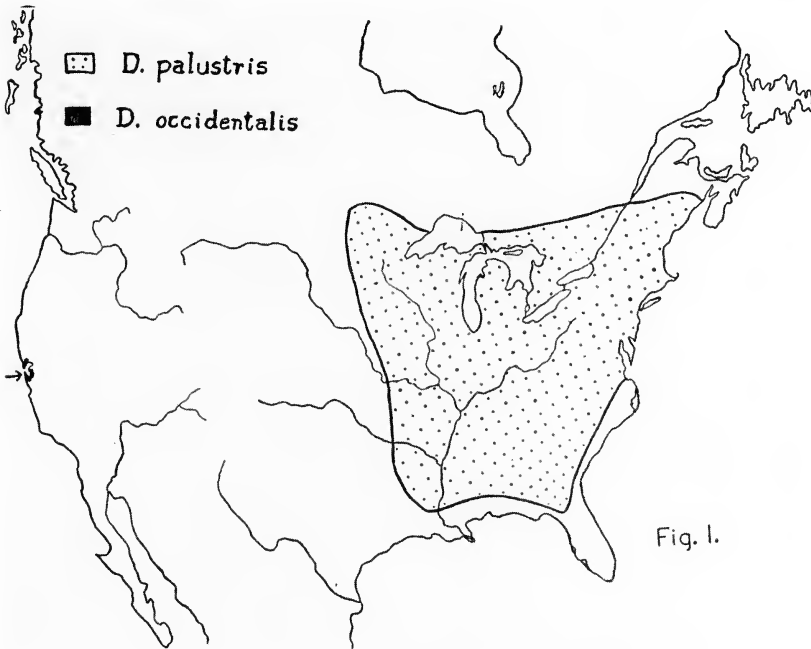


FIG. 1. Ranges of *Dirca palustris* and *D. occidentalis*.

(T. & G.) Greene, *Baccharis pilularis* DC., *Rhamnus californica* Esch., and *Osmaronia cerasiformis* (T. & G.) Greene. In Wildcat Canyon, just east of Berkeley and still within the summer fog belt, *Dirca* is rather common, and in a few places forms almost pure stands. Here the writer has observed several clearings in sheltered north and east facing slopes, where *Dirca* seedlings were more abundant than those of any other shrubs, and were competing on equal terms with *Toxicodendron*, and doing better than *Baccharis* or *Rhamnus*. On such slopes young *Dirca* seedlings can be found everywhere under the other shrubs, so that there seems no more reason to suppose that it is dying out than that *Rhamnus*, *Osmaronia*, or *Symphoricarpus albus* are disappearing from this

1942]

STEBBINS: GENETICS AND RARE SPECIES

247

area. On the sunnier west and south facing slopes, however, adult *Dirca* shrubs are sometimes found, but no seedlings have been observed. *Toxicodendron* and *Baccharis*, on the other hand, are equally vigorous and self-perpetuating in both sites. If one travels two miles east from Wildcat Canyon, crossing a ridge 1500–2000 feet high, one reaches the inner edge of the fog belt, where the summer weather is considerably drier and hotter. Here *Dirca* is rather local, and occurs only in shade. The only extensive stand seen by the writer was in dense shade under a grove of live oaks (*Quercus agrifolia* Nee), a habitat which it never occupies in Wildcat Canyon. Here it was accompanied, as usual,

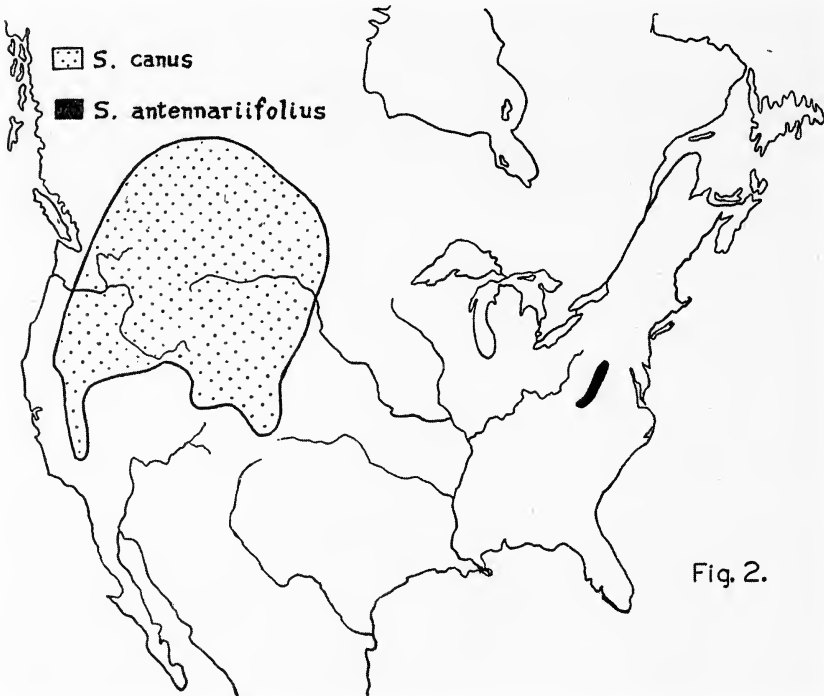


Fig. 2.

FIG. 2. Ranges (generalized) of *Senecio canus* (*sens. lat.*) and *S. antennariifolius*.

by poison oak (*Toxicodendron*), but the latter species was also abundant on the open, sunny slopes away from the oaks. Going eastward from Orinda, one would have to travel 1500 miles before he would see *Dirca* again. The logical inference from these observations is that *D. occidentalis* contains only a few biotypes, with a limited range of tolerance. These are successful only in sheltered spots, and may require the rather heavy type of soil characteristic of the Berkeley Hills. In the fog belt, they are only moderately tolerant of shade, while in the warmer regions east of the fog the seedlings can compete successfully only in deep shade, where they are met and surpassed by the more vigorous

competition of such undershrubs as *Rhus*, *Osmaronia*, *Symphoricarpos albus* (L.) Blake and *Corylus rostrata* Ait. var. *californica* A. DC. These more common competitors, on the other hand, appear to possess biotypes which can withstand a variety of sun and shade conditions in both Wildcat Canyon and Orinda.

The above argument may be summed up by a definition of the concept of *genetic homogeneity*, as follows. In continental areas, most rare or narrowly endemic species are genetically homogeneous, and may therefore be termed *homogenic*. They consist of relatively few biotypes which are themselves relatively homozygous. In contrast, the common and widespread species are usually heterogeneous in their genetic makeup. They include many biotypes, often grouped into more or less distinct ecotypes, and a large proportion of their individuals are genetically heterozygous, possessing a store of genetic variability beyond that which is evident from the appearance of their phenotypes.

This concept of genetic homogeneity, however plausible it may seem, is nevertheless only a working hypothesis. It should be put to the acid test of experimentation. Two lines of attack occur to the writer. In the first place, the genetic variability of typical rare species should be tested by growing under constant, controlled conditions progenies from all parts of their ranges. This variability should then be compared with that found in a series of progenies of their most common competitors, taken from various parts of the range of the rare species, as well as from beyond that range. Finally, in the case of species that are rare in one part of their range and common in another, or of those rare species that have close relatives elsewhere it should be possible to inject new variability, and therefore new aggressiveness into them by means of hybridization. In other words, if the concept of genetic homogeneity as the cause of "conservatism" is valid, wide intervarietal or interspecific crossing should replenish the biotype supply, and make for increased aggressiveness. Some of the new hybrid derivatives should then be easier to establish in new sites than the original rare species.

While recognizing that this hypothesis needs experimental confirmation, we can nevertheless follow out some of its implications. In the first place, it is entirely incompatible with the hypothesis of "Age and Area." The concept of genetic homogeneity is based partly on the assumption that in terms of the geological time-scale the migration of young species into new territory is rapid or at least fast enough to keep up pretty nearly with the prevailing rates of climatic change. The distribution of a species will be a reflection of its store of genetic variability only if each ecotype can occupy all of the contiguous territory to which it is suited in a relatively short period of time. This assumption, diametrically opposed to Age and Area, was emphasized by Gleason (19) and explains the facts of distribution as the present writer has observed them. Many species whose seeds have no

obvious means of rapid dispersal are widespread in new territory. The lupines of California are good examples. On the other hand, many species with apparently excellent means for dispersal are highly restricted. To cite just one instance, there are in California a number of native species of thistle (*Cirsium*), all with presumably equally efficient methods of seed dispersal. Some of these, *Cirsium fontinale* (Greene) Jepson, *C. campylon* Sharsmith, *C. Andrewsii* (Gray) Jepson, and *C. Vaseyi* (Gray) Jepson are more or less rare and local. One cannot ascribe this localization to the recent origin of the forms in question and the consequent lack of time for their distribution, since various European thistles, such as *Cirsium lanceolatum* (L.) Scop., *C. arvense* Scop., and *Silybum marianum* Gaertn., with apparently no better methods of seed dispersal than the native species mentioned, have become common in various parts of California within the past hundred years or less. These rare California thistles have failed to spread because they are not adapted to any of the areas adjoining their present ranges.

Furthermore, the genetic concept of intraspecific variability offers an entirely different, and in the writer's opinion more satisfactory, explanation of the facts upon which Willis has based his hypothesis. Willis's two main lines of evidence are first that endemic species are in general rarer even in the places where they occur than are widespread species in the same area, and second that the ranges of related species often overlap in "chain-mail" fashion, so that at the limits of their ranges they may intermingle with each other. The first point, which is borne out by most rare species, is entirely compatible with the concept of the genetic uniformity of rare species. These species are adapted to only a few ecological niches, and these niches are not only restricted geographically, but are in general of small extent even in the regions where they do occur. To use a simile: a physician belongs to a widespread and common profession. Not only is there room for physicians in every town in the world, but in addition a city can absorb a large number. A botanist, on the other hand, belongs to a profession which is rare and local. There are only a few cities, those which possess a large institution of learning, in which a professional botanist can survive at all, and in these botanists are much rarer than physicians, because there are many fewer places which they can occupy. Similarly a plant species with a narrow range of tolerance will tend to be not only localized geographically but also rare where it does occur.

The "chain-mail" pattern of distribution can be explained equally well upon the genetic concept, without resorting to "Age and Area." Willis argues that if two related species are found together in the same forest one cannot assume that they have different ecological preferences. This may be in part true, although one cannot help remarking that every forest or meadow has inequalities, however slight, of topography, exposure, soil,

moisture, etc., which would permit individuals with unquestionably different ecological preferences to grow near each other. But even if we grant that two groups of individuals belonging to different species have the same genetically conditioned ecological requirements, we need not conclude from this fact that the two species as wholes have the same range of tolerance. The biotypes which are ecologically equivalent may represent opposite extremes of the ranges of genetic variability of the two species. The normal or average biotypes of the two species may be very different from each other. For instance, *Pinus ponderosa* (*sens. lat.*) and *P. contorta* var. *Murrayana* overlap in the Sierra Nevada in typical "chain-mail" fashion, so that forests exist where the two species grow side by side, although in general *P. ponderosa* grows at lower altitudes and in drier situations than *P. contorta* var. *Murrayana*. This overlapping may mean that the hardiest, most moisture tolerant individual biotypes of *P. ponderosa* are nearly or quite equivalent to the least hardy, most drought resistant ones of *P. contorta* var. *Murrayana*, but it certainly does not mean that the two species as wholes are ecologically equivalent. In fact, the only reasonable conclusion which one can draw from the ranges of these two species, which occur separately over enormous stretches of territory, at very different altitudes and latitudes from each other, is that they have very different ranges of tolerance. And there is no case of "chain-mail" distribution known to the writer to which the same explanation cannot be applied.

When "Age and Area" has been eliminated, there remain two possible conditions of the past history of a rare species. One is that the species was once more common, widespread, and richer in biotypes than now, so that its present rarity is due to depletion of the store of genetic variability. The other is that the species never was common, but diverged from a small group of individuals of a widespread ancestral species, following the establishment of these individuals upon a small insular area. There are thus two types of homogenic rare species, *depleted species* and *insular species*.

The evidence from both paleontology and present distribution indicates that depleted species are frequent, and constitute a large proportion if not a majority of rare species (Fernald, 16, Axelrod, 2). The process of depletion has two stages. First, the widespread, common species becomes reduced in geographic distribution and in numbers through climatic or geological changes which eliminate many of its original habitats. During this process many biotypes and ecotypes are automatically destroyed, both through the complete elimination of the species from many areas and through more rigid selection in the few regions where it can survive. After this reduction in numbers, the species may still preserve a considerable amount of individual genetic variability, as well as a store of potential variability in

the form of recessive genes for which the individuals are heterozygous. Its continued existence as a series of small, completely isolated populations will, however, automatically lead to the further depletion of each population. As Wright (37) and Dobzhansky (12, p. 334) have pointed out, such small populations become more uniform genetically on account of inbreeding. Recessive genes tend to express themselves phenotypically, and thus become eliminated through adverse selection. Furthermore, the process known as random fixation takes place, so that purely by the vagaries of chance each population becomes uniform for a series of non-adaptive characteristics which in the larger population varied from individual to individual. This, of course, leads to the divergence of the isolated populations. It explains the fact that depleted species are usually sharply defined, that is morphologically very distinct from their nearest relatives, as well as being relatively uniform.

In addition to the depleted species, there is also a large body of rare species which have always been so because they have never had an opportunity to spread. Since such a condition is most characteristic of islands, rare species of this type can be termed *insular species* (Kinsey, 25). If through some accident a small group of individuals of a continental species becomes established upon an island, they will carry with them only a small part of the genetic variability of the original species. Furthermore, inbreeding and random fixation will tend further to make this insular population more uniform and more different from its continental ancestor as the years of its isolation progress. Thus the genetic structure of a restricted insular species becomes homogenic as does that of a depleted one.

There is, however, one way in which insular populations can maintain a certain degree of variability. If the insular areas are near enough to the continental ones or to other islands so that the migration of individuals to the island can occur repeatedly, the insular population can periodically be enriched with a new infusion of genetic variability. It becomes the semi-isolated population which, according to Wright (37), has the best potentialities for evolutionary progress. If the insular area or areas are small, the species will remain rare, but it will have an unexpected amount of variability. Thus a rare species confined to several small, insular areas partly isolated from each other is an exception to the hypothesis stated above of genetic uniformity for rare species. It has a potential aggressiveness, but cannot spread because it has no place to go.

Insular species are most easily recognized when they occur on actual islands, but they also exist within continental floras. Any species which occurs in a small area of favorable territory surrounded by extensive areas which neither it nor any of its close relatives could possibly occupy is as isolated as if it were on an island (cf. Kinsey, 25). This is true of the species of isolated

mountain tops which contain an alpine flora but are surrounded by great stretches of temperate or tropical lowland; of those found in oases in a desert, whether the oases are associated with streams, springs, or isolated mountain ranges, and of those in many types of habitats which are radically different from their surroundings.

It is on one of these terrestrial "islands" that there occurs the example best known genetically of a plant species which, though rare, has an unexpected amount of variability due to its existence in a series of semi-isolated colonies. This is *Oenothera organensis* Munz (*O. macrosiphon* Wootton & Standley) endemic to the Organ Mountains of New Mexico, which occurs in a series of small colonies along the only living streams found in this arid range of mountains completely surrounded by desert. It is a mesophyte living in the only mesophytic habitats available to it. Emerson (13) found that *O. organensis* has an unexpectedly high number of genes for self-incompatibility. Wright (36) on the basis of his mathematical deductions, could explain this situation only by assuming that the total number of about five hundred individuals found in the species was divided into a series of small, semi-isolated colonies, an assumption fully warranted by its distribution. *Oenothera organensis* may have a good deal of potential aggressiveness, which might result in a spreading of the species if an increasingly moist climate should open up new habitats to it.

In discussing the flora and fauna of actual islands, the distinction is often made between continental islands, which were formerly connected with some large land mass, and oceanic islands, which have never been so connected (Baur, 4). The flora and fauna of the former are said to be harmonious, since they are derived entirely from one continental area, while those of the latter are termed disharmonious, being derived from two or more different continental areas, and by several different migrations from each area at widely separated intervals. Terrestrial insular areas may be similarly classified as to their origin. Many, such as most of the alpine regions in mountain ranges of the north temperate zone, were once connected with extensive continental areas of similar ecological conditions; others were never so connected. The latter nearly always provide striking cases of endemism.

One such area in the eastern United States is the famous series of shale barrens in the Appalachian Mountains, extending from southern Pennsylvania to southwestern Virginia and eastern Tennessee. These barrens occur wherever rocks of certain geological formations outcrop on steep slopes. They are mildly arid as well as poor in mineral matter, so that they support a flora more xerophytic than that in the surrounding hills (Core, 11). Although each slope is obviously a pioneer habitat, destined to disappear as soil accumulates on it, new barrens are constantly being created by weathering and stream erosion, so that the shale barren habitat has probably existed continuously ever since the

uplift of the Appalachians began early in the Tertiary period, and will continue to exist as long as these mountains stand. They thus represent, like the seashore, a "pioneer" habitat of permanent duration, at least so far as present-day species are concerned. Although the climate of the Appalachian region may at times have been drier than it is now (Gleason, 19, Core, 10), there is no reason to believe that it was ever arid or even semi-arid, so that the possibility that the shale barrens were ever joined to the large semi-arid areas in the central and western United States by a continuous stretch of territory similar to the present barrens is rather remote. Hence they represent semi-xerophytic islands in a region dominated by a mesophytic forest. The flora of these shale barrens, as analyzed by Wherry (32, 33), contains species of rather diverse affinities. Some like *Senecio antennariifolius* Britton, are closely related to xerophytic western species. Others, like *Oenothera argillicola* Mackenzie, show certain characteristics in common with western species, but no close relationship. Cleland (9) has pointed out that *O. argillicola* resembles the western *O. Hookeri* alliance in its large flowers, self-incompatibility, and in forming pairs of chromosomes rather than rings at meiosis. In other morphological characteristics, however, it is more like some of the eastern species, and the arrangement of its chromosome segments is somewhat different from that of any other species. Still other shale-barren species, like *Pseudotaenidia montana* Mackenzie, are of very obscure affinities. Finally there is a series of shale barren species which have obviously evolved from mesophytes of the surrounding flora. Some of them are specifically different from their mesophytic relatives, others are apparently only ecotypes, while still others are of doubtful status. In view of this diversity of affinities, the hypothesis of Wherry (32, 33) that all of the shale barren plants originated somewhere to the northwest, seems unlikely. The plant association of these barrens appears rather to have been gradually built up over a long period of time through the addition at widely separated intervals of plants derived from very different sources.

In the west, such permanently isolated areas are more common. The mountain ranges of the southern Great Basin are excellent examples. They were uplifted during the latter part of the Tertiary period (Louderback, 26), and it is very unlikely that the forest and alpine areas of their higher slopes were ever continuous with those of other mountains. The best known of them floristically is the Charleston Range of southern Nevada. The enthusiastic and thorough explorations of Mr. Ira W. Clokey have uncovered a large number of endemic species of diverse affinities, and the high montane flora as a whole differs from all others in the world.

Another series of examples on a much smaller scale are the serpentine barrens of central California. Species of certain genera, like *Streptanthus*, will grow in this region only on serpen-

tine, so that these barrens for them are and probably have always been islands. Some of these *Streptanthus* species are endemic to only one or two barrens (Morrison, 27). These have probably always been rare, and may have been derived rather recently from the more widespread species by the establishment and divergence of an insular population as described above. So far as the writer is aware, no study of the geographic affinities of the serpentine barren endemics has been attempted; on the basis of the present discussion, these affinities should be diverse.

Not all species now endemic to islands are insular in the sense that their present population has been derived from a few individuals of an existing continental species. Relict, depleted species have been preserved on many islands, as well as on terrestrial insular areas (Baur, 4). This is particularly true of islands of continental derivation, and may be due to the lower intensity of competition as compared with continental areas. The Channel Islands off the coast of southern California, for instance, have preserved the last remnants of such species as *Lyonothamnus floribundus* Gray, *Prunus Lyoni* (Eastw.) Sarg. and *Quercus tomentella* Engelm., which are known through fossil evidence to have been formerly more widespread, and very likely consisted of several ecotypes (Axelrod, 2, 3). Even on oceanic islands or those with remote continental connections there are often found species which are apparently either the last relics or the immediate derivatives of ancient genera now extinct elsewhere. This is well illustrated by some of the arboreal Compositae of the Pacific Basin. Two of the archipelagoes west of South America, namely Juan Fernandez and the islands of San Felix and San Ambrosio contain endemic genera of the tribe Cichorieae; *Dendroseris* on Juan Fernandez and *Thamnosericis* on San Felix and San Ambrosio, which are related neither to each other nor to any other genus found in the Southern Hemisphere. *Thamnosericis* appears to be nearest to *Stephanomeria* of western North America, particularly *S. Blairii* Munz & Johnston, an anomalous endemic of San Clemente, one of the Channel Islands. *Dendroseris* is of more obscure affinities but is also most nearly related to North American genera. The modern species of both *Thamnosericis* and *Dendroseris* therefore, must have had more widespread ancestors, and are to be considered as relict, depleted genera. Another case is *Hesperomania*, endemic to Hawaii, where it is very rare. Its nearest relatives are *Augusta* (*Stiffia*) of Brazil and *Nouelia* of southwestern China. All three are apparently the last remnants of a group which must have been widespread in the Northern Hemisphere in Cretaceous or early Tertiary time (Stebbins 30). *Fitchia*, endemic to two islands of Polynesia, is an extraordinary genus which combines the characteristics of the tribes Mutiseae, Heliantheae, and Cichorieae, but has no close relatives in any of them. It is obviously a relict genus, perhaps a survivor of an ancient stock of

Compositae which existed before the present tribes became differentiated from each other.

Since both insular and depleted species may occur on insular areas, terrestrial as well as actual islands, the differentiation between the two types in such areas is a difficult problem. No set rule will hold for all species, but two criteria can be considered as valuable. First, if the endemic is closely related to a widespread species which occurs on an adjacent continental area, it is probably a strictly insular species, while if it is closely related to no other living form, or has its relatives in some remote corner of the globe, it is more likely a depleted species or a derivative of one. Second, if the endemic is morphologically a highly specialized type in relation to its continental relatives, it is probably an insular descendant of these; while if it is less specialized it may be their depleted ancestor.

Finally we must consider the future of these homogenic rare species. The most obvious fact is that they are more at the mercy of climatic changes than are the common, variable species. Just as their genetic rigidity prevents them from occupying new habitats, so it must also reduce their power to adapt themselves to climatic changes. Hence if the climate remains the same they may persist as rare species indefinitely. If it becomes more unfavorable to them, they are likely to disappear. This is the fate awaiting many Californian trees and shrubs, notably *Pinus Torreyana*, *P. radiata*, *Abies venusta* and *Cupressus macrocarpa*, if the progressive desiccation of our climate continues. On the other hand, if conditions become more favorable for the spread of their few remaining biotypes, they may become more common. Then, if two or more isolated colonies of a depleted species are enabled to spread until they meet, a partial replenishment of the store of genetic variability may take place. During their isolation the disjunct colonies must have acquired some different genetic characteristics, both by mutation and by random fixation (Wright, 37, Dobzhansky, 12). Thus when two such colonies reunite, hybridization between genetically different individuals is made possible. By this means, a large number of new genetic combinations may arise, replenishing the store of genetic variability, and opening up new possibilities for the spread of the species.

Examples of species that have apparently been replenished in this fashion are provided by relatively widespread and common members of mono- or ditypic genera which occur in the same region and appear to be somewhat related to each other, but are very sharply set off morphologically and have no close interrelationships. Such a group is found among the Compositae, tribe Cichorieae of the Sonoran desert of western North America. Here there are two monotypic genera, *Anisocoma* and *Atrichoseris*, and three ditypic ones, *Rafinesquia*, *Calycoseris*, and *Glyptopleura*. These are all related to each other and to the larger genera *Stephanomeria* and *Malacothrix*. Together with *Pinaropappus* of

Texas and Mexico as well as the insular *Thamnoseis* mentioned above, they form a natural group, not closely related to any other Cichorieae. The small size and remarkable distinctness of the genera and most of the species of this group is in sharp contrast to the situation in the Cichorieae of the Old World, where most of the genera are relatively large and are so closely interrelated that generic boundaries are very difficult to define. Supposing, however, one were to select a dozen species from each of the large Old World genera *Lactuca* and *Crepis*, and one or two each of *Hypochaeris*, *Leontodon*, *Sonchus*, *Launea*, *Ixeris*, and *Youngia*, choosing the more xerophytic members of each genus and should then deposit these species upon a semi-arid or desert area completely devoid of Cichorieae, and they all became established in this area, the resultant pattern of variation would closely simulate that now found in the western American Cichorieae mentioned above. This suggests the hypothesis that exactly such a process of selection has taken place in the history of the latter. Their history may have been somewhat as follows. Once the entire group consisted of a few fairly large closely interrelated genera, or of one genus divided into several sections. Then the group became much reduced in numbers, due to the reduction in extent of the habitats which it occupied, and was broken up into many partly or completely isolated populations. The larger of these retained their store of genetic variability throughout the period of reduction. The smaller ones, being subject to intense selection and random fixation diverged sharply from the ancestral stock, and at the same time became much depleted genetically. Then with the restoration of conditions favorable to the group, all of the remaining species were able to spread again. Those less completely isolated then gave rise to the more closely interrelated species of the larger genera *Stephanomeria* and *Malacothrix*, while the descendants of the strongly isolated and depleted small populations became the distinctive mono- and ditypic genera. This history may be greatly oversimplified; perhaps several cycles of depletion and replenishment were necessary to produce the pattern of variation found in this group. Nevertheless, the occurrence of such cycles in the evolutionary history of this and other groups is a very likely possibility, and may have been of considerable importance in the differentiation of species and genera throughout the plant kingdom.

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SUMMARY

The concept of age and area and that of senescence of species in the stricter sense is not considered adequate to explain the occurrence of rare and endemic species. Instead the writer regards as most important the concept of genetic homogeneity.

This assumes that most common and widespread species are genetically diverse, while rare and endemic ones contain relatively little genetic variability, that is relatively few biotypes. They are therefore termed homogenic. This homogeneity reduces the number of ecological niches in which the rare species can compete successfully with other species, but if the climate is a stable one, does not necessarily cause their extinction. From the historical point of view there are two types of homogenic species. Depleted species are those which formerly were widespread and genetically diverse, but have lost many or most of their biotypes. A species may become depleted in only one part of its range, remaining common and variable in another. Insular species are those which have developed on an island or an isolated ecological habitat on a continent. They have originated from a few individuals or a single individual of the ancestral species, and have never possessed great genetic variability. The distinction between depleted and insular species is often hard to recognize, because depleted species often find their last refuges in insular areas. The future of rare, homogenic species depends upon the future of the ecological niches to which they are adapted. If the environment remains stable, they can persist indefinitely as rare species. If changes occur which obliterate their restricted habitats, they will become extinct. If, however, environmental changes result in an increase of the particular ecological conditions to which the species is adapted, it can spread. Then if this spreading permits the coming together of two isolated colonies of a homogenic species or of two such species which are still capable of interchanging genes, the populations thus united will both acquire new genetic variability. By this means a homogenic species may become diverse and widespread. If it is a depleted species, part or all of its original diversity may be restored.

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A DISTINCTIVE NEW CALOCHORTUS (LILIACEAE) FROM
MARIN COUNTY, CALIFORNIA

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While it is not unusual for a new species of plants to be described from a state as well collected as California, it is remarkable that a plant as distinctive as the species of *Calochortus* described herein has escaped discovery for so long, since it is from an area that has been given considerable attention (Howell 1970, Peñalosa 1963). In overall appearance it is easily recognized and in detail it shows a combination of characteristics unique in the genus. It is in fact so distinctive that its existence challenges the currently accepted infrageneric classification.

Calochortus tiburonensis A. J. Hill, sp. nov.

Bulbi tunica, saltem apud bulbos maiores, fibroso-reticulata; folium basale unicum, planum, usque ad post anthesin tempum viride: flores late campanulati, erecti; petala pallida flavo-viridia, fimbriata, maculis

1973]

HILL: CALOCHORTUS

101

guttisque badiis ornata, maxima parte centrali deltoideo-ovata, apice acuta vel acuminata, late unguiculata, glandula infra medium posita, superficie nuda, pilis gracilibus proxime supra atque utroque et lateraliter fere usque ad apicem barbata, profunde lunata, versus petali apicem arcuata, depressa, margine inferiori membrano lato, ea superiori seriebus duabus vel pluribus processibus applanatis instructa; ovarium lineare, non alatum; fructus fusiformi-prismaticus, in transectione triangularis, erectus; semina parum compressa, asymmetrica vel plus minusve rhomboideo-prismatica, atropurpurea, testa sexangulariter reticulata.

Bulb ovoid, with coat membranous or fibrous-reticulate in larger bulbs; stems slender, to 5 dm or more in height, usually branched, not bulbiferous; basal leaf single, linear-oblong, to 17 mm or more in width and to 6 dm or more in length, usually green at anthesis; cauline leaves linear, involute, reduced upward; inflorescences bracteate, the bracts similar to the cauline leaves, the flowers usually in pairs or less frequently three from the ultimate axils; flowers broadly campanulate in outline, erect, the petals light yellow-green, flecked to varying degrees with purplish-brown and with more or less conspicuous transverse arching bands of the same color, the most prominent of which is near the mid-point; sepals about equalling or slightly longer than the petals, lance-oblong, attenuate, glabrous, pale yellow green, flecked, streaked, and veined with purplish-brown; petal blade deltoid-ovate, rounded laterally, acute to acuminate above and very broadly clawed below, with a conspicuous complex glandular area below the middle; basal portion of petal, including the glandular region, extending outward more or less at a right angle from the vertical axis of the flower, the apical portion curving abruptly upward to an erect position; petals long-fimbriate from above the claw to near the tip with long, slender hairs similar to the lateral fimbriations; gland deeply crescent-shaped, about one-half the width of the petal, depressed, the surface naked, bordered below with a broad, erect, upward arching, erose and minutely papillose membrane, bordered above with two or more indistinct rows of transversely flattened processes, which are often engaged and sometimes divided apically, the processes similar in appearance to the lower membrane, but less broad with respect to the vertical dimension of the lower membrane; stamens about equal to or slightly shorter than the petals, the filaments parallel to the flower axis to near tip, then divergent; anthers slightly longer than the filaments prior to shedding of pollen, narrowly lanceolate, short acuminate, divergent from the flower axis; ovary linear, not winged, tapering to a persistent trifold stigma; stigma-branches linear, strongly divergent and curved; fruit fusiform-linear, acute, triangular in cross-section, several times the length of the pistil at anthesis, erect; seeds in two closely appressed rows in each locule, slightly compressed, irregular or roughly rhomboid-prismatic in shape, dark purplish, with a hexagonally reticulate coat. Figure 1.

TYPE. *A. J. Hill 51239.4A*, north slopes of Ring Mt., Tiburon Peninsula, Marin Co, California, elevation ca 110 m, June 19, 1972 (UC 1393720—holotype; isotypes to be distributed to US, UCLA, and RSA).

Known only from the vicinity of the type locality in an area about 0.8 kilometers across. It is found on rocky slopes of serpentine and serpentine derived soils. The area is open, with a variety of grasses and other annual and perennial herbs. There are limited areas of shrubs and wind-swept trees, but no plants of this *Calochortus* were seen growing in these areas. The site of the type locality is privately owned and there is considerable interest in including it in an adjacent open space area slated to be purchased by the city of Tiburon.

In its combination of morphological features *Calochortus tiburonensis* is unlike any other species of the genus. It does not fall within any of the three sections of the genus as delimited in the most recent monographic treatment (Ownbey 1940), but shows features that are normally found in two of these sections. The flat, usually single, rather persistent basal leaf would place it among the species of sections *Calochortus* (= *Eucalochortus*) or *Cyclobothra* and make it rather distinct from those of section *Mariposa*.

The fibrous-reticulate bulb coat, although not as reticulate as in many species of the section, and non-winged capsule could be considered sufficient evidence to place *Calochortus tiburonensis* in section *Cyclobothra*. The general coloration and shape of the flower, the petal margin and vestiture, and the habit of the plant also give the general appearance of some species of this section, such as *C. weedi*. However, the glandular area of the petal, which is prominently developed in the genus and appears to be of considerable diagnostic value, is definitely unlike that found in the species of section *Cyclobothra*. Moreover, it is quite similar to a type of gland found in species of section *Calochortus*, such as *C. tolmei*. The darkly pigmented, reticulate seed coat and only slightly compressed seeds are also typical of species of section *Calochortus*, although this type of seed may also be found among species of section *Cyclobothra*, the seeds of many of which have not yet been described.

Geographically, *Calochortus tiburonensis* also seems to occupy an intermediate position between the two sections. The nearest representative of section *Cyclobothra* is found 250 kilometers to the south of the Tiburon area, with the remaining species further to the south in California and in Mexico and Guatemala. The greatest species diversity in section *Calochortus* is in the Pacific Northwest with the number of species decreasing sharply south of the San Francisco Bay area. *Calochortus tiburonensis* occupies a position distinctly to the south of the center of diversity of section *Calochortus*.

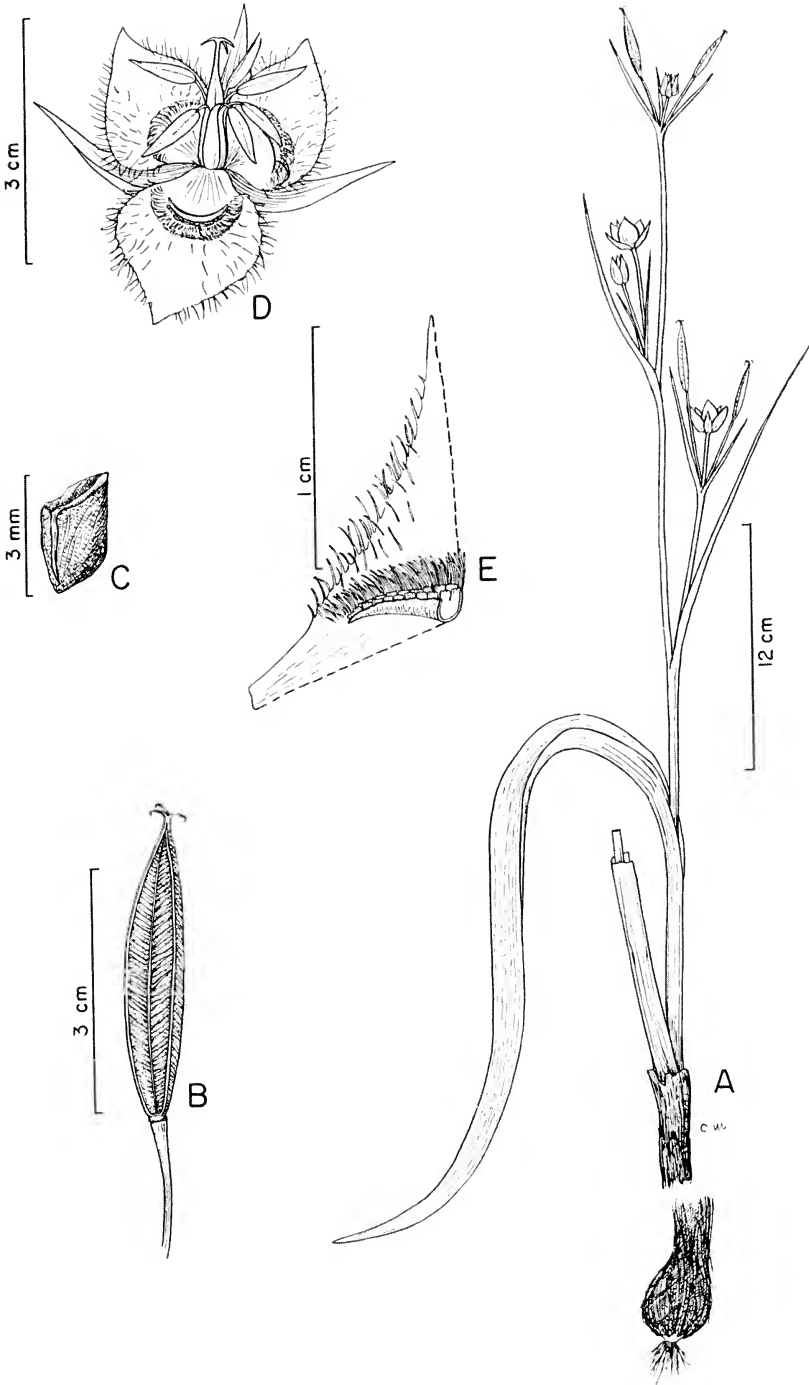
The highly unusual combination of characteristics, geographic position, and localized occurrence of *C. tiburonensis* suggest the possibility, although remote, that it may be the result of hybridization. However,

FIG. 1. *Calochortus tiburonensis*: A, habit with portion of persistent previous year's stem and leaf shown on the left; B, mature fruit; C, seed; D, flower with forward petal bent down and forward for clarity; E, side view of one-half of petal in longitudinal section. (From collection A. J. Hill 51239.4)

1973]

HILL: CALOCHORTUS

103



aside from variations in the depth of the purplish pigmentation in the flowers and general size of the plants, the population appeared to be quite uniform on field examination and without any variations that would suggest hybridization. Examination of a scattered sample of immature capsules in the field did not reveal any with reduced seed set. Pollen fertility, as judged under the microscope when stained with cotton blue in lactophenol, was 96, 98, and 99 per cent in samples of 600 grains from a single flower each of three plants, which compares favorably with observations on other *Calochortus* species. In these preliminary studies, then, there is nothing to support the idea of hybridization, at least of recent occurrence.

The occurrence of this intermediate species does establish a closer relationship between the two sections than was previously recognized and challenges the concept of placing the two species groups in separate sections on a par with the third species group in the genus. It also challenges the idea of Hoover (1944) that they should possibly be placed in separate genera.

The existence of an unidentifiable *Calochortus* was apparently first noticed by Dr. Robert West and was subsequently seen by Mrs. J. C. Youngberg, Miss Annetta Carter, and Mrs. George Ellman. Miss Carter reported the occurrence of the *Calochortus* to the author. The credit for the actual discovery belongs to these persons whose interest in protecting the open space of Marin County was probably the most significant factor in their making the discovery.

That a previously uncollected new species, and one of potentially great significance in interpreting relationships within the genus, was discovered in such a botanically well known area suggests the need for a very careful look at any areas that are threatened by development or other disturbance, especially near expanding population centers. Had this species not been noticed soon, it might very well have become extinct without ever having been recorded.

In addition to those persons already mentioned I acknowledge with thanks the assistance of Dr. Rimo Bacigalupi and Dr. Lawrence R. Heckard in reviewing portions of the manuscript and translating the diagnostic description into Latin; Ms. Charlotte Mentges in preparing the illustration; other staff members of the University of California Herbarium and the University of California Botanical Garden in providing research space and time; and Dr. and Mrs. H. G. Baker in providing research materials and space.

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1960]

RAVEN & MATHIAS: SANICULA

193

SANICULA DESERTICOLA, AN ENDEMIC OF
BAJA CALIFORNIA

PETER H. RAVEN AND MILDRED E. MATHIAS¹

One of the more restricted species of northern Baja California is *Sanicula deserticola* Bell, known from a few disjunct populations at the northern margin of the Sonoran Desert. One population is known from near El Mármol at the headwaters of the Arroyo de San Fernando, while others are in the yellow hills northwest of Rancho Arenoso and near Rancho Aguajito, both in the drainage of the Arroyo del Rosario. At the last-mentioned locality, it was found growing abundantly on the northwest-facing slopes of a yellow conglomerate hill, 3.6 miles west of Rancho Aguajito (Raven, Mathias, and Turner 12,678), associated with *Rosa minutifolia*, *Euphorbia misera*, *Yucca whipplei eremica*, *Idria columnaris*, *Eriogonum fasciculatum*, *E. scalare*, *Encelia californica* var. *asperifolia*, *Calandrinia maritima*, *Harfordia macroptera*, *Brodiaea pulchella*, *Layia platyglossa*, and *Filago californica*, as well as two species of *Agave* and one each of *Dudleya*, *Mammillaria*, *Echinocereus*, *Echinocactus*, and *Opuntia*. This curious mixture of characteristic members of the California flora and such species as *Idria columnaris*, restricted to the Sonoran Desert, clearly demonstrates the unique ecological position of *Sanicula deserticola*.

The subfamily Saniculoideae of the Umbelliferae, with some 260 species, like the other subfamilies Hydrocotyloideae and Apioideae, has apparently had a long and independent evolutionary history. The distribution of the extant genera of Saniculoideae shows clearly that they have developed within the Arcto-Tertiary Geoflora and have been associated with it for a long time, perhaps since late Mesozoic time when this Geoflora is first recognized in the fossil record. Several of the genera in this subfamily are restricted to areas of Arcto-Tertiary-derived deciduous forest in eastern Asia. Others range south along mountain chains to Africa. The genus *Eryngium* is world-wide in distribution, whereas the genus *Sanicula* is exceedingly widespread in the Northern Hemisphere, with some of its species occurring also in the Southern Hemisphere. Shan and Constance (1951) considered the section *Sanicula* (*Sanicla*), with about one-third of the species of the genus *Sanicula*, the main trunk of the genus. Some species of this section are widespread in Eurasia, and their present distribution suggests development of the section from a northern stock with subsequent southerly migrations. In North America *S. mairlandica* L. and *S. trifoliata* Bickn., which Shan and Constance considered probably the least advanced species, occur as common associates of the eastern deciduous forests. The distribution of this section is therefore closely related to that of the Arcto-Tertiary Geoflora.

¹ The authors would like to acknowledge the helpful suggestions of Dr. Harlan Lewis in the preparation of this paper.

In western North America, the genus *Sanicula* is represented by section *Sanicoria*, which Shan and Constance showed was probably derived from members of section *Sanicula*. *Sanicula deserticola* is one of fourteen species comprising section *Sanicoria*, which is the most diverse within the genus in vegetative and reproductive characters. The development of the Madro-Tertiary Geoflora in early Tertiary time in western North America involved a segregation of species from the dry margins of the tropics and from the Arcto-Tertiary Geoflora,—a segregation fostered by the ever-increasing influence of aridity, particularly the loss of summer rain, and of more extreme temperature variation over much of the West (Axelrod, 1958). Increasing environmental diversity in this area has resulted in large measure from the continuation of this process of progressively increasing aridity, and the evolution of section *Sanicoria* was doubtless correlated with the development of this climatic and topographic diversity. Bell (1954) showed that the different diploid species of section *Sanicoria* differ in their environmental preferences. The existence of localized species in specialized environmental situations is unique to this section. Thus *Sanicula peckiana* F. Macbr. occurs only on serpentine, *S. saxatilis* Greene occurs only on volcanic or serpentinized rocks, *S. arctopoides* H. & A. occupies coastal bluff and dune habitats, and *S. maritima* Kell. is a local species confined to moist adobe soil near the coast. Although some species of the section are less sharply differentiated ecologically, they are, as a class, plants of relatively xeric habitats in chaparral and various oak-conifer woodland associations derived from the Madro-Tertiary Geoflora. One species, *S. graveolens* Poepp., ranges widely north and east, and others occur in suitable sites north along the Pacific Coast, but most of the species of section *Sanicoria* are members of the California flora in the broad sense as delimited by Howell (1957). The occurrence of two mesophytic species of *Sanicula* on the western coast of South America is, we believe, the product of relatively recent long-range transtropical dispersal of the type discussed by Grant (1959) and by Raven and Lewis (1959).

On morphological grounds, the species most closely related to *Sanicula deserticola* is *S. bipinnatifida* Dougl., but nevertheless the two are amply distinct. *Sanicula bipinnatifida* is found colonially in open rocky grassland from Washington south to the northern edge of Baja California, in regions with average annual precipitation ranging from about 12 to 40 inches. The populations of *S. deserticola* are about 150 miles south of the range of *S. bipinnatifida* in a region with an average annual precipitation that ranges from perhaps 2 to 7 inches (fig. 1). It is therefore found in a habitat which with respect to aridity is very extreme for members of section *Sanicoria* and for the genus *Sanicula* as a whole. In its native habitat *S. deserticola* probably flowers whenever it has sufficient water. This is suggested by its flowering response when grown at the University of California, Los Angeles, where it flowered twice a year when supplied with abundant water.

1960]

RAVEN & MATHIAS: SANICULA

195

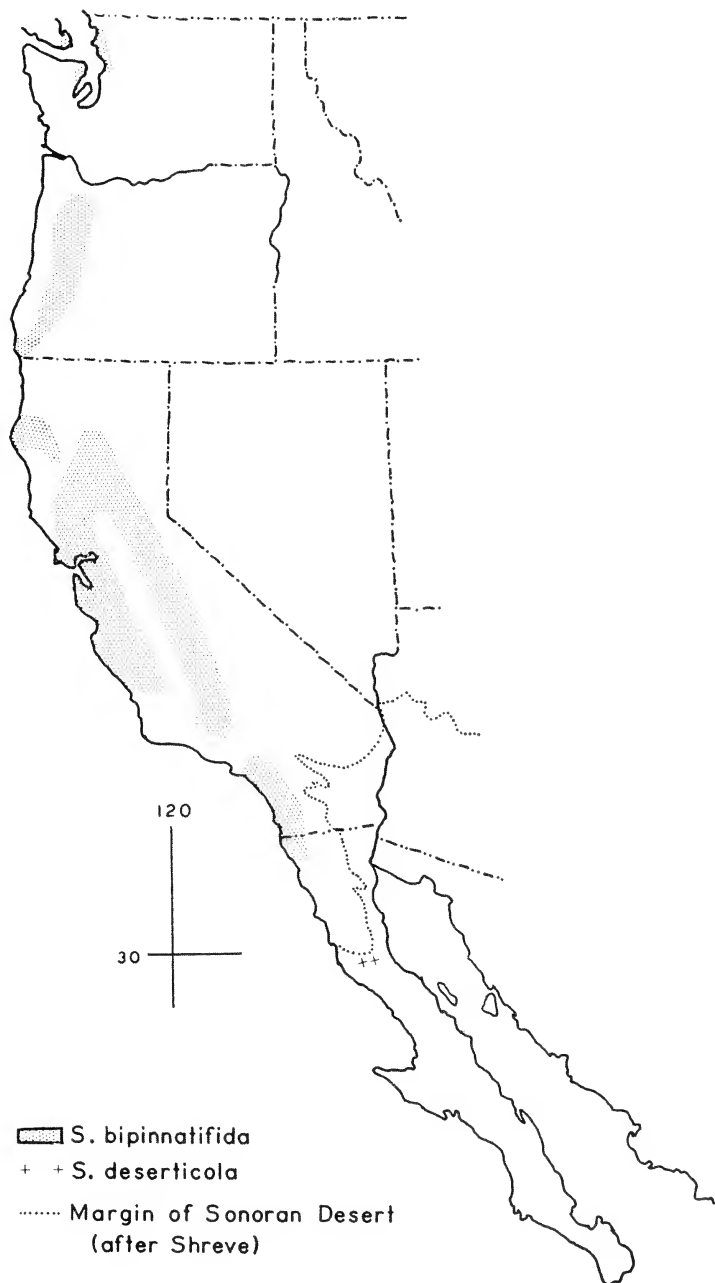


FIG. 1. A portion of western North America, showing ranges of *Sanicula deserticola* and *S. bipinnatifida* and approximate line of demarcation between desert and chaparral in Baja California.

Rodríguez (1957) found that the vessels of *Sanicula deserticola* have the smallest mean length for any member of the family that he examined; this, together with its long taproot and clumped habit, indicate its advanced position compared with *S. bipinnatifida*. One may reasonably infer that populations ancestral to both became differentiated at the southern margins of their distribution in response to an arid climate. The disjunct populations of *S. deserticola* may have been somewhat more continuous during pluvial periods of the Pleistocene, but at which time period this species became spatially and genetically isolated from *S. bipinnatifida* cannot be demonstrated.

The area of *Sanicula deserticola* lies along the southern margins of the transition area between the Californian chaparral and the Sonoran Desert, as defined by Shreve (1936). Shreve noted that species which are endemic in the transition area are preponderantly of northern relationship, while the plants of the desert area are more sharply confined to their own formation. He explained this relationship by the fact that the only requirement for the long southward extension of a chaparral species is a relatively moist habitat, however restricted in area this may be, while the requirements for northward extension of desert species are more complex. The approximate boundary between the two areas is shown in figure 1. *Sanicula deserticola* is certainly such a species of northern affinities. A parallel distributional pattern and relationship are found in the shrubby *Salvia chionoeplica* Epling; this species also consists of a few disjunct populations in north-central Baja California, and it is closely related to other species of section *Audibertia*, such as *Salvia leucophylla* Greene. The distribution of most species of *Salvia* sect. *Audibertia* is associated with the California flora and therefore similar to that of *Sanicula* sect. *Sanicoria*.

Within the genus *Sanicula*, the section *Sanicoria*, apparently stemmed from ancestors adapted to relatively mesic sites within the area of the Arcto-Tertiary Geoflora and occupied successively drier and drier habitats offered by the expansion and differentiation of the Madro-Tertiary Geoflora. The species of section *Sanicoria* that occupies the most xeric habitats is *Sanicula deserticola*. Relatively few perennial Umbelliferae occur in such habitats, and most of those that do are members not of Saniculoideae, but of the larger and more diverse subfamily Apioideae.

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197

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1916.]

JEPSON : REGENERATION IN MANZANITA

3

REGENERATION IN MANZANITA.

WILLIS L. JEPSON.

In the Oakland Hills there may be found two manzanitas that are species of *Arctostaphylos* growing in localized areas. *Arctostaphylos andersonii* Gray grows on the main ridge a mile south of the summit of the Snake Road which leads into the headwater basin of San Leandro Creek. *Arctostaphylos glandulosa* Eastw. grows on the same ridge on yellow shale, and also abundantly on Moraga Ridge on the same formation. A number of years ago while making field studies of these shrubs, my attention was directed to the rather striking fact that individuals of *Arctostaphylos andersonii* had been killed outright by fire, and that *Arctostaphylos glandulosa* was stump-sprouting abundantly from heavy root-crowns. No root-crown or tabular development at base of the stem could be found in the former species, nor even any attempts at root sprouting at all, while in the case of the latter species the root-crowns became very heavy, globose, or turnip-shaped, or even eventually forming broad tabular areas of irregular shape at the surface of the ground. Since then many further observations have been made upon the species of this genus in various parts of the state to determine if reaction to fire ran parallel with the specific limitations.

Arctostaphylos andersonii is a larger shrub, eight to twelve feet high. One individual within a few feet of the bridle-path along the eastern brow of the Oakland Hills, and about half-mile south of Snake Road summit, is sixteen feet high, with a trunk circumference of three feet nine inches, at six inches above the ground. As said above, this species is killed by fire. Trunks decapitated four feet high failed to regenerate. This species may be recognized by its densely set leaves, which are heart-shaped at base, and by its very close flower-clusters. (Pl. I.)

Arctostaphylos glandulosa. This is a rather low-growing species of the immediate coast region, occurring in formations of considerable extent on slopes of yellow shale. It is perhaps the most remarkable species in California in the matter of its behavior under repeated fire devastation. After the stems are fire-killed, young plants begin to form a root-crown which becomes turnip-shaped or globose (Fig. 1) and lies immediately at or below the surface of the ground. As the plants increase in age and fires continue to run, as characteristically in chaparral, the root-crowns increase in size (Pl. II, A) and give rise to many stems. While at first small, root-crowns often become two to five, or indeed ten to thirteen, feet broad.

The very large ones form irregular circles or crescent-shaped areas, and are truly remarkable structures. (Fig. 2) Such crowns can be studied to advantage upon the southeastern slopes of Mt. Tamalpais or in the Oakland Hills just south of the low wagon pass

4

MADROÑO

[Vol. 1,

PL. I.



ARCTOSTAPHYLOS ANDERSONII

1916.]

JEPSON: REGENERATION IN MANZANITA

5

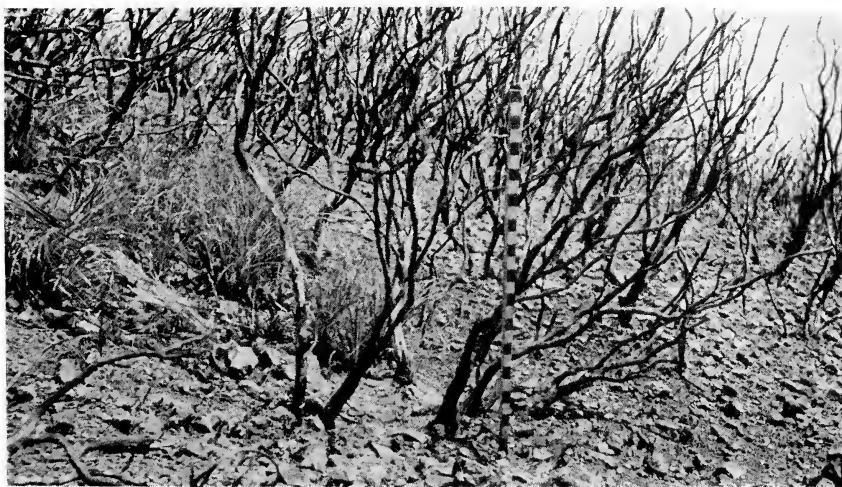
at the headwaters of Kohler Creek, and along the summit of Moraga Ridge, where the species is associated with Knob-cone pine in a characteristic habitat. The vitality of the species must be normally very great. After the Mt. Tamalpais chaparral fire of early July, 1913, sprouts began to appear within four weeks, and in two months made an abundant showing. Two of my students, Wieslander and Herbert, counted forty-eight sprouts in a square inch from the crown of an individual of this species occurring on Mt. Tamalpais in the area subject to the fires just mentioned.



FIG. 1.

Arctostaphylos vestita. This species occurs on the Monterey Peninsula in company with the Monterey pine, and on the mesa east of Del Monte in the chaparral. It exhibits habits exactly similar to *Arctostaphylos glandulosa* and forms heavy root-crowns. These Monterey shrubs do not seem to be specifically, although they may be varieties, different from the shrubs of Mt. Tamalpais, which are taken as *Arctostaphylos glandulosa*.

Arctostaphylos tomentosa. This species is well developed along the Washington and Oregon coasts, and extends southward in typical form to the Mendocino coast. Within the limits of this range it is well characterized by the long, somewhat scattered bristles of its branchlets, in addition to a fine tomentum, which is rather close and dense. It also occurs in Marin County, especially about Point Reyes, and in the Santa Cruz Mountains, but within this portion of its distribution—that is at its southern limits—it becomes difficult to distinguish from *Arctostaphylos glandulosa*. There is however a fundamental difference between the typical forms that, so far as observed, is invariable—namely, as to their reaction to fire. *Arctostaphylos tomentosa* on the Mendocino coast is quite killed by fire,

A.—*ARCTOSTAPHYLOS GLANDULOSA*B.—*ARCTOSTAPHYLOS NUMMULARIA*

1916.]

JEPSON : REGENERATION IN MANZANITA

7

and, so far as observed, reproduces entirely by seed. Mr. W. C. Mathews, one of my students, who has also observed it on the coast region of Mendocino, has given me the results of identical observations on this species. *Arctostaphylos glandulosa*, on the other hand, as noted above, flourishes under fire, and establishes heavy sub-hypogeous platforms from which sprouts freely rise after fire.



FIG. 2.

Arctostaphylos nummularia is another coast species. (Fig. 3.) It is very erect, with the branchlets crowded with small round leaves. While locally abundant, and even gregarious (Fig. 4), it is in general a rather rare species, and my observation of its behavior on Mt. Tamalpais shows it to be killed outright by fire. (Pl. II, B.) One of my former students, Miss C. M. Hoak, makes a similar observation for the Mendocino White Plains. It may be that the restricted occurrence of this species is due to its inability to respond vegetatively from the root after chaparral fires, a fact which may perhaps be connected with the character of its root-system, which is spread out near the surface of the ground like an inverted umbrella. In any event, the roots lie so near the surface of the ground that they must suffer directly from the heat of chaparral fires (Fig. 5.)

Arctostaphylos stanfordiana is a species of the Mt. St. Helena range. It is remarkable for its deep-green glabrous leaves, and clean, trim habit, and is susceptible of field recognition in this way by those who notice manzanitas. This species, according to the available evidence, does not reproduce vegetatively. This testimony I had first from Mr. Carl Purdy, who lives in its region, and Miss

Hoak, on her own initiative has confirmed this observation, although further field notes on this species are desired. I have seen it many times in the field, but never where the fire evidence was very clear.

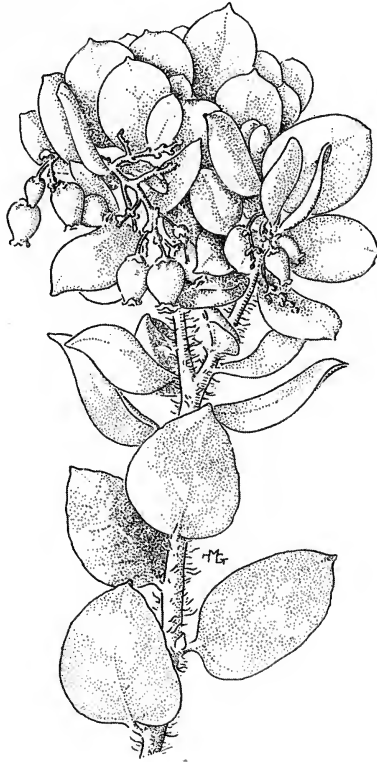


FIG. 3.

Arctostaphylos patula is the common species of the main coniferous belt in the Sierra Nevada from the south to the north, and west to Mt. Shasta and Trinity Summit. It is a shrub four to six feet high, and is remarkable for its rather dark but lively green and shining foliage. Under fire killing of its crown, or even apparently in advance of such killing, this species forms a turnip-shaped or globose root-crown that continues to increase in thickness and persistently sprouts under the successive conflagrations that run through the chaparral. Winter snowfall is heavy in this region. Its branches in consequence often lie along the ground, at least as to their lower part, and so take root. Spreading of the species in a given area may occur only in this way—that is, by the rooting of ascending or horizontally spreading branches.

1916.]

JEPSON: REGENERATION IN MANZANITA

9

Just here I may revert for a moment to *Arctostaphylos stanfordiana*. In the character of its branchlets, and in its inflorescence, this species is so similar to *Arctostaphylos patula* that the two can scarcely, it would seem, be held as distinct, or in any event it is plain that they lack sufficient differentia. Their difference in behavior under fire, however, helps to make good this lack of technical distinction.

Arctostaphylos manzanita, as to regeneration, is one of the vaguest of the earlier published species with which we have to deal. As to its reaction to fire, a definite report is not yet ready.

Arctostaphylos viscida grows in the Sierra Nevada foothills. The southern form of it has very viscid berries, and is known as *Arctostaphylos mariposa*. Without for the moment going into the matter of the exact status of *A. mariposa*, one may safely say that this white manzanita of the Sierra foothills is in hue the most sharply defined manzanita in California. Its foliage is very glaucous, or even quite silvery, and presents a most striking yet most pleasing contrast to the deep-red bark. My experience is that this species is killed under fire, an observation which has ample confirmation from the experience of settlers in the southern Sierra Nevada in clearing land of chaparral. In an area where, as the saying is, "everything sprouts," they have noticed that this white manzanita does not do so. Mr. Ralph Hopping, Insect-control Expert of the United States Forest Service, also confirms the non-sprouting of *Arctostaphylos viscida*, or in any event its southern form.

To fix the limit of species of *Arctostaphylos* in California has always been difficult, and those who have studied the genus as it occurs with us have recorded widely divergent judgments as to the number of species that are to be recognized. The discrimination of proposed species, however, by all authors, rested upon differences of pubescence, glandulosity and habit. The character of the nutlets and their degree of separation or coalescence has also been used,

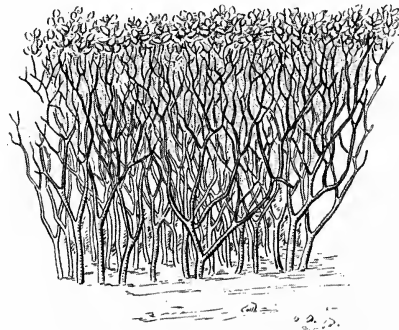


FIG. 4.

but is, on the whole, so variable that only slight importance can be attached to it, except in one or two species.

Search for technical characters for the separation of species has been carried on by the writer, but has been to a large degree unsatisfactory in results. Experience, both in field and in herbarium, determines that habit, general aspect, and hue must be taken as of first importance in segregation, although pubescence and glandulosity would have practical value in the construction of diagnoses. Now, if the Californian species be segregated on this basis, one obtains about twenty species. These species, I may say, fall into five or six fairly natural groups, the species in each group being very closely related. In successive attempts to determine the most satisfactory criteria for separating the species within each group, all possible information regarding the life history was sought. As a result, it was found that within the limits of a group the differential mortality of two species very closely related is markedly decisive. As this cleavage is largely between closely related species rather than between groups, the difference in reaction to fire is highly interesting, and is also, evidently, of taxonomic value. In other words, the working conception of species above outlined seems to be unexpectedly fortified by their habits in relation to fire—that is, of root-crown sprouting or of failure to do so.

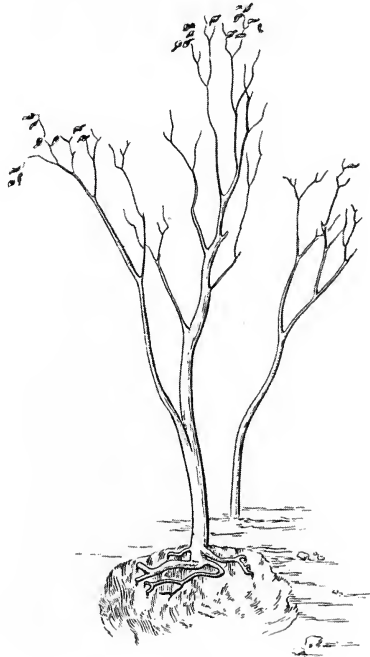


FIG. 5.

1916.]

JEPSON: REGENERATION IN MANZANITA

11

While the number of observations that have been made are not sufficiently large or geographically extensive to warrant final conclusions, the results so far are interesting, and are here put on record to draw out criticism and to stimulate further observations. One set of observations in a given locality, however faithful and accurate, cannot be regarded as entirely sufficient, because in other genera of the chaparral stump-sprouting varies within a species. This variation may be related to the age, vitality, soil situation of the individual, or to some other cause, such as variation in the mutilating or destroying agent, fire or the axe. An excellent example of such variation may be had from *Ceanothus sorediatus*. *Ceanothus* is a favorable genus for comparison in the matter of stump-sprouting, as many of its species are typical chaparral shrubs. In the Oakland Hills *Ceanothus sorediatus* (Jim brush) has been observed to stump-sprout freely; on Mt. Tamalpais we have found it killed outright by fire. While this difference in behavior in a single species has thus far not been observed in any species of manzanita, ampler records based on a wider range of observations, are desired.

1929]

WHY THE ESCHSCHOLTZIA

195

WHY THE ESCHSCHOLTZIA?

EDWARD LEE GREENE

Doubtless our sunny plains, shady cañons and mountain forests yield types of floral beauty more delicate than the *Eschscholtzia* and some of them equally characteristic of California; why then should this poppy-like flower have been selected as the State's floral emblem?¹ The snow plant of the Sierra—stem, leaves, flowers and all of the richest crimson—is peculiar to California and the subject of universal and unbounded admiration. The lily family, an alliance of plants abounding in flowers of signal beauty and elegance, has plenty of distinctly Californian types not excelled by their relatives of other parts of the world. The lilies themselves, as they adorn our mountain woods and stream banks, might have furnished a State flower; or, even more appropriately, their near ally, the *Calochortus*, or butterfly tulip, or Mariposa lily, as it is popularly called. These, with our *Brodiaeas* and other lily-like flowers, are coveted throughout the world by flower growers as among the most surpassingly beautiful of all the plants indigenous to California. Even the blue and white and purple-flecked *Nemophilas*, or their kindred, the *Phacelias*, whose masses of bloom impart to our wheat fields in March the hues of the sky overhead, might have furnished a good floral emblem.

But the State flower must be that of a plant more generally disseminated throughout our commonwealth, more conspicuous—in a word, more popular than any of these. The *Sarcodes*, or snow plant, gorgeously beautiful though it be, is limited to the woods of the upper Sierras, where in its native vigor and freshness, perhaps not more than one in a thousand among us will ever behold it. And it steadily refuses to be cultivated; moreover, it is after all only a splendid parasite, and California is not a parasite State. The delicate yet brilliant *Mariposas* put forth their white, or red or yellow pendants in the shade of thickets, or among the more inaccessible places of the mountains. They are matchless among our wild flowers, in both form and coloring, but they are too select and retiring for popularity. The grain field flowers of spring, painting whole landscapes, are both short lived and local. They are of the great interior valleys but not of the whole State.

All the prerequisites of an acceptable floral emblem for California meet in the *Eschscholtzia*. It is a plant of singular beauty. The delicately-cut foliage, the graceful stem, the satin-like luster of the golden petals—all these combine to make such a plant as flower lovers in all parts of the world have prized highly ever since the

¹This article was written to serve as part of the general observance which took place in 1890 on the occasion of the adoption of the *Eschscholtzia* as the state flower of California by vote of the California Floral Society and other public organizations. By act of the legislature of California in 1903 the *Eschscholtzia* became officially the state flower of California. So far as we know this article has never been printed in any magazine of botany or horticulture.—W. L. J.

MADROÑO, vol. 1, pp. 195-202, Apr. 22, 1929.

time of its first discovery. It is distinctively Californian. There is no *Eschscholtzia* indigenous to any island of the sea or any continent but North America; and even here it is confined to the Pacific Coast, where it is well-nigh exclusively Californian. While a single species illuminates the plains of northern Mexico in early spring, and another extends northward to the valley of the Columbia, all the rest are strictly Californian. And within the State they are of more universal distribution than almost any other of our native flowers. The great desert of the Rio Colorado has its peculiar *Eschscholtzia*, and that quite different physical region, the Mojave, has two species, one of them with flowers so small that none but a botanist would be likely to recognize it at first glance as of this genus. Another sort adorns the San Diego seaboard hills; and still another—and this is the original *Eschscholtzia* Californica—enlivens our northern coasts from Monterey to San Francisco. Both the plains and the foothills of our great interior valleys present in many places in the month of April vast landscapes largely orange-colored by the profusion of the handsomest of all the species, *Eschscholtzia crocea*. Still another sort, a small and close-tufted plant with flowers of lighter yellow, occupies the hill country of our more northerly districts; and this species drew the attention of the mining pioneers of forty years ago, springing up as it did and unfolding its yellow flowers abundantly on every dump newly made by the pick and spade of the gold-seekers. And men pressed the brilliant corollas and sent them in letters home to the east and called them the “California Gold Flower”. It was a name most naturally suggested to their minds by both the habitat and the hue of the petals which might well have been retained as a popular one for these plants. It was at a later period, and only by help of the botanists, who knew the plant to be of the poppy family, that the name of California poppy came into use. It is not a very good name, inasmuch as it is hardly a natural one. The affinities of the *Eschscholtzia* are with the poppies, no doubt; but the external resemblance is so slight that none but a professional botanist would have been likely to detect the relationship.

As a popular name *Eschscholtzia* will, perhaps, always continue to be objectionable; a college course in German seeming to be almost necessary to either an understanding or a correct pronunciation of it. But this, like every other scientific plant-name, has a history; and, to those who know the history, a fitness. A brief sketch of the origin of this name *Eschscholtzia* may, perchance, commend it to the scorner of Teutonian polysyllabics in general.

Seventy-five years ago our State floral emblem had neither a name nor place in the lists of either botanists or florists. Two years since at the German capital they unveiled to the public a statue of an eminent traveler, botanist and man of letters, Adelbert von Chamisso; and it was he who had the happiness of discovering in California, and of introducing into Europe, this most characteristic of our California plants. In the year 1816 this man, then a youth, in company with his intimate friend, John Frederic Eschscholtz, during

1929]

MONTEREY CYPRESS

197

successive October days rambled over what must have been bleak and desolate hills where now stands the city of San Francisco. They were both fresh from university halls, and, as young men of promise, had received appointments from the Russian Emperor to accompany Lieutenant Kotzebue on his voyage of discovery. Eschscholtz was surgeon and zoologist to the expedition, Chamisso was botanist, and upon their return from the voyage, Chamisso made known to the botanical and floricultural world the most beautiful of their new acquisitions, the California poppy-like flower, dedicating it to his friend and companion of the voyage, the young Dr. Eschscholtz.

Berkeley, Dec. 3, 1890.

OPAL PHYTOLITHS AS EVIDENCE FOR
DISPLACEMENT OF NATIVE
CALIFORNIAN GRASSLAND

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ABSTRACT

Opal phytoliths are produced by plants and persist in soils as microfossils with taxonomically distinct morphology. We found phytoliths produced by the original native perennial species in soil under an annual grassland, thus providing the first direct evidence that the Californian grassland was formerly dominated by panicoid opal-producing grass. The most common panicoid-type opals were probably produced by *Stipa pulchra*. Frequencies of opal phytoliths from native grasses were greater at 10 cm depth than at the soil surface beneath the annual grassland. Comparison of opal phytolith frequencies from 10 cm deep at the annual site and an adjacent relict perennial grassland site suggested that the density of panicoid opal-producing native grasses on the annual site was once similar to the relict grassland.

Reconstruction of pristine plant communities in California is constrained by limited techniques for establishment and maintenance of natural vegetation, and by a lack of recorded knowledge about the composition of those historical communities. The evidence for previous vegetation includes results from pollen studies, macrofossils, observation of succession, and the composition of present vegetation on selected relict sites. One technique, which has not been applied to any California plant community, uses opal phytoliths to identify historical species assemblages.

Plant opals are microscopic, translucent particles that occur in plants and persist for long periods in soil as opal phytoliths. They are formed within plant cells and cell walls through the passive uptake of monosilicic acid by way of the transpiration stream from soil solution (Jones and Handreck 1967). They are composed of amorphous silica, which also contains some additional carbon, water, and cations (Wilding et al. 1975). Opals are most common in leafy portions of plants but are also present in stems, roots, and other parts. Biogenic opal particles range in size from less than one micron to over 500 microns; however, the majority of diagnostic forms range from two to 50 microns.

Research on opal phytoliths initially emphasized investigations of biogeochemical processes, genesis of paleosols and of catenas, and loess deposition, in which phytoliths were studied as components of soil (Wilding et al. 1975, Twiss et al. 1969, Moore 1978). Plant ecologists and paleoecologists have now begun to use phytoliths to document vegetation change, post-glacial succession, type distributions, and shifting ecotones such as grassland-forest boundaries (Wilding et al. 1975, Moore 1978, Rovner 1983, Palmer 1976).

Plant anatomists refer to opals as "silica bodies" or "silica idio-blasts." They are useful in taxonomic descriptions and have been useful in classification of monocots (Metcalf 1960). Members of the Poales (grasses and sedges) have a significant propensity to form opals. In the Poaceae (Gramineae), silica body morphology is considered diagnostic at the subfamily and tribal levels. There are at least three recognized types of silica bodies in grasses: festucoid, panicoid, and chloridoid (Twiss et al. 1975), which suggests a correlation between opal cell morphology and C3 and C4 type photosynthesis (Rovner 1983, Palmer 1976).

These taxonomic affinities are useful to differentiate Californian grasses. The common grasses that now dominate the Californian grassland are festucoid species introduced from the Mediterranean (Heady 1977). Native perennials assumed to have dominated the pristine grassland, *Stipa* spp. and *Danthonia californica* Boland., contain significant amounts of panicoid opals (Barkworth 1981, DeWet 1956, Bartolome and Gemmill 1981); others, including the genera *Deschampsia* and *Distichlis*, are exclusively festucoid. The typical "dumbbell" or "hourglass" shape of panicoid opals is readily distinguished from the elliptical disc or "hat"-shaped festucoid types and from silicified, dumbbell-shaped, stomatal guard cells (Figs. 1a, 1b). Several distinctive types of silicified trichomes (unicellular or bicellular hairs) also are associated with particular tribes or genera (Metcalf 1960, Barkworth 1981, DeWet 1956).

This paper describes the use of opal phytoliths from two soil depths to document replacement of native vegetation by exotics on Jepson Prairie Reserve in Solano County, California (Lat. 38°N, Long. 122°W), 75 km northeast of San Francisco. The Prairie contains a small remnant of the California Valley Grassland or California Prairie, which may have covered much of the Central Valley (Heady 1977). The vegetation on all but a few hectares of the 1000 ha reserve, described in detail by Barry (1972), is now dominated by annual grasses from the Mediterranean region.

STUDY SITES

The study contrasted two locations. One location is dominated by native grasses and forbs, including *Stipa pulchra* Hitchc. and

1986]

BARTOLOME ET AL.: OPAL PHYTOLITHS

219

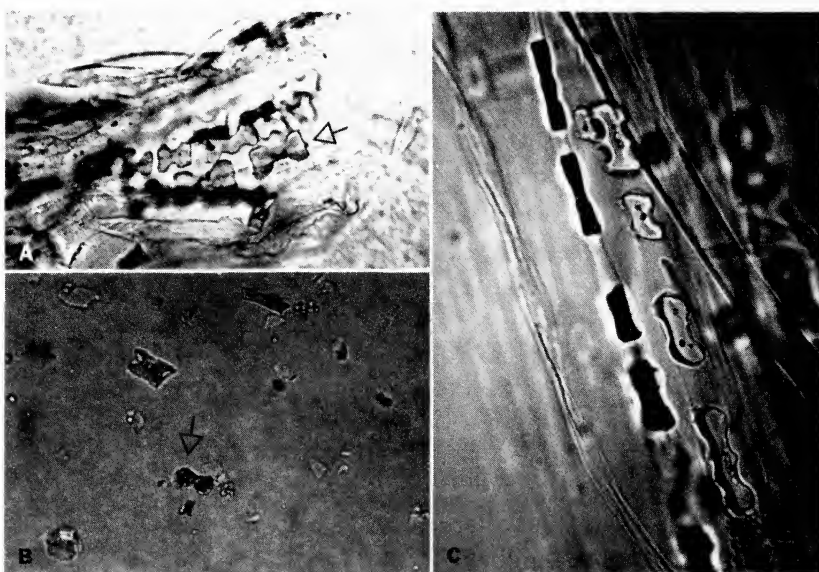


FIG. 1. Photomicrographs of opal phytoliths. a. Dumbbell-shaped panicoid opals (length = 25 microns), isolated from leaf tissue of *Danthonia californica*, are visible in the center of the photomicrograph. b. Opal phytoliths isolated from annual grassland soil, 10 cm depth (480 \times magnification). The arrow points to a phytolith produced by a perennial, *Stipa pulchra*. c. Linear arrangements of panicoid opals (length = 20 microns) in leaf tissue of *Stipa pulchra*. Dark rectangular shapes are opals viewed on edge.

Deschampsia danthonioides (Trin.) Munro ex Benth. This pasture has been grazed lightly by sheep for at least the last 100 years. Stands of *S. pulchra* averaged 4.2 plants/m² when sampled in the spring of 1985 on 30 permanently marked 25 cm \times 25 cm plots (B. Leitner, pers. comm.). Frequency of *S. pulchra* measured 23.3 percent on these same plots, with the remainder of the vegetation exotic and native annuals. This density is typical of relict non-coastal sites (Bartolome and Gemmill 1981).

The second pasture also is part of the Reserve and is less than one km away, but it has been in different ownership and grazed by cattle. Annual grasses of Mediterranean origin, including the genera *Bromus*, *Avena*, *Vulpia*, and *Hordeum*, dominate the second location. It contains no native tussock-forming bunchgrasses and only a few scattered plants of rhizomatous *Distichlis spicata* (L.) Greene. The nearest native bunchgrasses are 200 meters from the second sample location. The soils are similar, sandy loam or loam derived from sedimentary alluvium, and classified as Palexeralfs or Natrixeralfs. "Hogwallow" or mima-mound topography with vernal pools typifies undisturbed portions of both the sites.

220

MADROÑO

[Vol. 33

TABLE 1. RATIO OF DUMBBELL OPAL PHYTOLITHS PRODUCED BY NATIVE PERENNIAL GRASSES TO TOTAL OPAL PHYTOLITHS FOR SOIL SAMPLES FROM THE JEPSON PRAIRIE AND FREQUENCY OF FIELDS WITH DUMBBELL OPAL. Sample size numbered 400 from each depth and location. Numbers in parentheses are 95 percent confidence intervals for each value from binomial distribution.

Depth	Annual grassland		Perennial grassland	
	Ratio	Dumbbell opal freq.	Ratio	Dumbbell opal freq.
Surface	0.056 (0.03–0.08)	0.45 (0.39–0.51)	0.154 (0.10–0.19)	0.89 (0.85–0.92)
10 cm	0.144 (0.10–0.18)	0.75 (0.70–0.80)	0.169 (0.13–0.22)	0.80 (0.75–0.84)

METHODS

In August 1984, we collected soil from the surface (0–1 cm) and from 10 cm depth at ten randomly located sites in each of the two locations. Collected samples were air-dried, and the gravel and organic debris removed. The five to 10 g of fine material remaining was sieved through 240 micron mesh plankton netting (Cwynar et al. 1969). Organic matter was removed using 30 percent hydrogen peroxide. Mechanical shaking in a sodium hexametaphosphate (0.5–1 molar)–sodium pyrophosphate (10%) solution dispersed aggregates. Dispersed soil was then wet-sieved through 107 micron mesh plankton netting. Microscopic inspection of coarser material verified that essentially all the opal had passed the sieve.

Particle sizing was performed by sedimentation and decantation using standard procedures (Jackson 1979) adjusted for specific gravity of opal (2.2 g/cc). Soil smears were prepared from a dilute, ammoniated soil/water suspension (Smithson 1961) and placed onto a standard microscope slide and mounted in cedarwood oil. Separate microscope counts were made on the medium silt (5–20 microns) fraction, at 400× magnification using a 0.2 × 0.4 mm grid system. A maximum of 50 fields/slide were used to record frequency of distinctive dumbbell phytoliths, tallied as ratio of dumbbell to total phytoliths.

RESULTS AND DISCUSSION

Dumbbell opal phytoliths, which could have been produced only by native grasses, were, as expected, more frequent in the surface soil of perennial grassland than of the annual grassland (Table 1). Dumbbell opals were nearly as frequent in the annual site subsurface soil as in the perennial site subsurface. Most of these opals are probably from *Stipa pulchra*. The low density of panicoid phytoliths in the surface of the annual grassland site apparently resulted from

the replacement of native perennials by introduced annuals and the influx of non-panicoid opal.

Although the replacement of the native grassland by introduced species has been widely hypothesized (Heady 1977), using circumstantial sources of evidence such as the presence of relict stands of natives in presumed undisturbed sites, this study has produced the first documentation of replacement based on more direct evidence. The annual site apparently had a cover of native perennial bunchgrass vegetation. Since settlement by people of European origin, the bunchgrasses were replaced by introduced annuals on the present annual grassland site. Number and composition of panicoid-type phytoliths (Fig. 1c), including some "fan"-or "keystone"-shaped forms (Wilding et al. 1975, Metcalfe 1960) at 10 cm depth, suggests that the present perennial grassland site is similar to the original grassland in density of panicoid opal-producing native bunchgrasses.

Phytoliths show much potential as a tool to study historical changes in vegetation. At the Jepson Prairie, we were able to characterize vegetation change from a grassland dominated by perennial species, which produce panicoid-type phytoliths, to an annual grassland without panicoid opals. We were able to take advantage of a situation ideally suited to the use of opal phytolith characteristics. In other vegetation types, the changes will be more difficult to detect. However, even where the types of opal phytolith produced do not change at detectable levels, the relative abundance of opal in soil can be a useful diagnostic aid. Changes most likely to show large differences in the quantity of opal in the soil occur on grass/shrub or grass/tree boundaries because of the great difference in opal production between grasses and woody species. The invasion of meadows by trees, for example, should be readily detectable with opal phytolith studies. Because of the complementarity of pollen and opal phytoliths (the two tend to differentiate into taxonomic categories differently) and the different dispersal potential of phytoliths, the dual use of phytoliths and pollen for studies of vegetation history should increase.

ACKNOWLEDGMENTS

We thank representatives of the University of California Natural Reserves System and the Nature Conservancy for permission to work on the Jepson Prairie. Emeritus Professor Hans Jenny suggested this study and contributed his inspiration and advice. Professors Roger Byrne, Don Erman, and Paul Zinke lent use of their laboratories and equipment. Funds were provided by the California Department of Parks and Recreation.

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A VEGETATION TYPE MAP OF CALIFORNIA

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Those interested in the California flora will be glad to know that published units of a vegetation type map of California will soon be available for distribution. This map is being prepared as a part of a forest survey of California conducted by the United States Forest Service in cooperation with other federal and various state and county agencies. The survey embraces a total area of nearly seventy million acres and will cover the entire state exclusive of the deserts and the larger valleys devoted mainly to agriculture. When complete there will be a total of 220 map units. These units consist of the standard United States Geological Survey 15 and 30 minute topographic sheets upon which the vegetation types are shown in color and symbol legend. To date, field work has been completed on forty-eight units of which eight are now off the press and fourteen additional are in the process of publication.

The vegetation types are mapped in the field directly upon Geological Survey topographic quadrangles by direct observation and sketching from ridges, peaks, and other vantage points, supplemented by frequent sample-plot checks. The major types which are shown by color legend are further subdivided into pure and mixed stands in which species composition is indicated by symbols. A pure stand is defined as one in which a single species forms more than 80 per cent of the vegetation cover;

1935] WIESLANDER: VEGETATION TYPE MAP OF CALIF. 141

while a mixed stand is one in which neither of the two or more species composing it exceeds 80 per cent.

On the map, a pure stand is designated by the single important dominant. Ordinarily a mixed stand is designated by those dominants individually forming 20 per cent or more of the cover and they are listed in so far as practicable in order of relative abundance. However, in a composite formation, which is neither distinctly herbaceous, shrubby, nor arborescent, but a mosaic of two or more of these elements, this percentage is applied to each class of vegetation separately. For example, in a tree-shrub formation, the tree and shrub species forming 20 per cent or more of the aggregate area occupied respectively by trees and shrubs are designated, prior place in the designation being given to the trees. In this classification understory vegetation is not considered, but only those elements of vegetation cover visible from above as from an airplane. In shrub types, an estimate is made of the percentage of cover formed by the various species, but in tree types it is frequently easier to approximate this by tree counts. These percentages serve more accurately as guides for the major types and for pure subtypes which stand out in fairly bold relief, than for mixed stand subtypes. Where the latter merge from one subtype to another so gradually that there are no visible dividing lines, the sample plots serve as a basis for a delineation which gives at least close altitudinal and slope exposure relationships.

Each of the major types or plant associations represents an attempt to group subtypes having fairly similar fire hazard characteristics, and uses or qualities of economic importance. Thus, these broad plant associations in color legend serve to make the maps of ready use to engineers, foresters, and others charged with the management of so-called wild lands, while the more detailed subtype units provide the basic information on vegetation cover desired by the research worker in various fields such as botany, ecology, and forestry.

A great wealth of material in addition to the vegetation type map itself is being procured in this survey. Sample plots cross-sectioning all types mapped supply such details as species composition, stand density, size of trees and shrubs, and depth of leaf litter. On a supplementary map such information is shown as (1) occurrence of tree species not abundant enough or too restricted in area to be designated on the type map; (2) occurrence of shrub species of especial importance, the range of which would otherwise not be indicated either by the type map or the sample plots; and (3) visible boundaries of burned-over areas. Herbarium specimens are collected from every species recorded upon the map or in the sample plots of each quadrangle mapped. Photographs illustrative of various vegetation conditions are taken and are so referenced that they may be duplicated at a later time for the purpose of recording vegetational changes.

The Vegetation Type Map Herbarium, housed on the fifth floor of the University Herbarium in the Life Sciences Building, University of California, Berkeley, should be of increasing interest to California botanists. This collection now contains about 7,500 mounted specimens and it is expected that between 3,000 and 4,000 will be added yearly. It includes many plants in addition to those required for authenticating the maps and sample plots. Very complete field notes accompany each specimen, comprising information as to collector, date, elevation, location, also notes as to size and character of the plant, the slope exposure, the formation in which it grows, and the names of the more common associated species.

The primary purpose of the herbarium is to serve as a check upon field identifications, and to afford a permanent record of the plants collected in each quadrangle. Probably its greatest value, however, will lie in the wealth of material from all parts of the region, and in the detailed information, as to the range, habitat, and associated plants that will be available for each species. It is planned also to include in the herbarium characteristic photographs of many of the plants together with notes on their ecology and their economic importance as grazing or browse plants, or for erosion control.

The survey not only provides information about the present vegetation cover, but also discloses that in many localities its character has been profoundly changed since the advent of the white man. The most striking and significant of such changes are those representing a progressive deterioration from higher and more valuable to lower and less valuable types of vegetation as a result of such land abuse as destructive logging, accidental and wilful summer fires, the practice of annual burning in many foothill and mountain localities, and excessive grazing. As a consequence of such treatment, there have been extensive replacements of commercial timber stands by woodland, chaparral, or sagebrush; of big-cone spruce and Coulter pine by chaparral or woodland; of piñon by chaparral; of grasslands by chaparral or sagebrush; of chaparral by sagebrush.

A compilation of the information obtained in the western or foothill portion of El Dorado County affords an example of the character and extent of the change that has taken place along the western slopes of the Sierra Nevada. Of especial interest in this county is an area of about 162,000 acres, most of which lies between the 1,000-foot and 2,500-foot contour levels and adjacent to, but below, the present belt of yellow pine (*Pinus ponderosa*).¹ The type map shows that this area embraces about 30,000 acres of woodland, 45,000 acres of woodland-chaparral, 5,000 acres of chaparral, 43,000 acres of woodland-grass, 22,000

¹ "Ponderosa pine" is the name now officially recognized by the U. S. Forest Service for *Pinus ponderosa*, probably more widely known as "western yellow pine."

1935] WIESLANDER: VEGETATION TYPE MAP OF CALIF. 143

acres of grassland, and 17,000 acres of cultivated land including urban areas, and that most of the tree and shrub species occurring as important dominants in this area are mainly characteristic of the Upper Sonoran Life Zone. Study of the soil in conjunction with growth measurements of scattered second-growth individuals and groups of yellow pine show that this area is capable of growing excellent stands of this conifer. That old-growth stands of yellow pine formerly existed in this area and that lumbering operations had no small part in their disappearance is evidenced by such names as Sawmill Creek, Sawmill Ravine, Shingle Springs, as well as by known locations of early day sawmills including the famous Sutter Mill at Coloma, where the discovery of gold led to the mining rush of 1849.

Other interesting evidences of former pine forests were supplied by survivals of various sorts. Two cemeteries have preserved excellent stands of second-growth pine which would obviously have continued beyond these boundaries if not destroyed. In several localities boundary line fences between forest and non-forest cover coinciding with property line fences also indicate the artificial restriction of range. Still other evidence is provided by the general occurrence of California black oak, a species commonly associated with yellow pine and with much the same habitat requirements. The oak usually survives by sprouting when the pine succumbs to ax and fire.

From the facts accumulated in the survey of El Dorado County, the conclusion seemed warranted that, since the white man settled here, the yellow pine belt has retreated up the Sierra slopes an average distance of ten miles on a thirty mile front. This leaves a deforested area of 162,000 acres much of which has been invaded and occupied by tree and shrub species from non-forest areas below.

Obviously it is possible to present upon the published maps only a fraction of the information accumulated in this survey. Therefore, in order to increase their utility and interest, there is planned a further interpretation of the vegetation types by analysis of the supplementary sample plots and other data. This will be published as regional studies which, upon the completion of the survey, will be combined into a comprehensive whole. The first of these, for which the field survey has already been completed, will cover the Southern California region as embraced by the six counties of Ventura, Los Angeles, San Bernardino, Riverside, Orange, and San Diego. This study will attempt to correlate existing vegetation with various climatic and physical factors. The influence of man on the vegetation, with particular reference to the effect of fire, will be taken into account. The results to be expected from such a study might include among others the following:

1. A partial explanation of the present distribution of vegetation types and dominant species.

2. A better understanding of vegetation changes that have occurred in the past, those now in progress, or those to be expected to occur in the future.

3. Further contributions to our knowledge of the value of certain plants and vegetational types as indicators of particular soil and climatic conditions. These should have an important application in many fields, both in pure research and in applied fields such as game and land management.

4. Suggestions for future investigations and also a foundation for further research.

The projected study is in too preliminary a stage for present discussion other than to mention briefly two first steps which, in addition to the field work, are already under way. One of these is the preparation of maps of the Southern California region on a scale of one-quarter inch to one mile, each showing the distribution of one of the forty-two more important trees and shrubs. Both the dominant and scattered occurrence of the species are indicated on these maps, which are on tracing linen and will be superimposed on maps showing geologic formations, the various climatic factors and fire history. Thus, by these and other means, such as a statistical analysis of the sample plots, it is hoped to determine the rôle of the various factors controlling the distribution of these species. The other step is a systematic search of the literature for references to the character of the vegetation found by the early Spanish explorers and other pioneers in California, also to sawmill and logging operations, fires, and other destructive activities of man. Considerable progress has already been made in this compilation and from the information thus obtained it should be possible, in conjunction with evidence procured in the field work, as illustrated by the El Dorado County survey, to reconstruct a partial picture of former vegetation for comparison with that existing today.

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January 31, 1935.

1948]

KECK: WILLIS LINN JEPSON

223

THE PLACE OF WILLIS LINN JEPSON IN CALIFORNIA BOTANY

DAVID D. KECK

For three-score years Willis Linn Jepson, 1867–1946, was actively connected with the Department of Botany of the University of California as student, professor, and professor emeritus. Throughout this long period he was thoroughly devoted to the study of the flora of his native state and to furthering its interpretation and appreciation. To this end he founded the California Botanical Society in 1913, which he served as president, with the exception of three years, until 1929. In 1916 he launched the organ of the Society, *MADROÑO*, which he edited continuously through 1934. Much earlier, with the aid of E. L. Greene, he had founded and edited the journal *Erythea*.

The botanical writings of Jepson are both extensive and profound, and they have exerted a lasting influence upon our knowledge of the botany of California. The present account attempts to evaluate Jepson's lifework, as made known by these contributions, on the historical background.¹ A bibliography of authors who have named flowering plants occurring in the wild in California now includes well over 900 names! Where does Jepson stand among these?

Three stages can be recognized in the study of the California flora: (1) its study by Europeans; (2) by Americans along the eastern seaboard; and (3) by Californians. The first stage dates back to the late eighteenth century, when European explorers began to collect the objects of natural history that they found on these shores. By the early nineteenth century people in England had become greatly interested in horticulture, and expeditions were sent out to the four

¹ For sketches of Jepson, the man, giving more details of his active life, refer to (1) Herbert L. Mason in *Madroño* 9: 61–64, 1947; (2) Lincoln Constance in *Science* 105: 614, 1947; (3 & 4) Emanuel Fritz in *California Forester* 14: 6–8, 1947, and in *Jour. Calif. Hort. Soc.* 9: 23–26, 1948; (5) Marion R. Parsons in *Sierra Club Bull.* 32: 104–107, 1947; and (6) Joseph A. Ewan in *Jour. Wash. Acad. Sci.* 37: 414–416, 1947.

corners of the earth in search of plants to enrich British gardens. Bent on this purpose and showing amazing activity, David Douglas alone, Scotch collector for the Horticultural Society of London, now the Royal Horticultural Society, in his single season in California provided the material from which some 300 species were to be described.

The second stage, led by Thomas Nuttall, began around 1830, when the botanical exploration of the West by American botanists was under way. Soon John Torrey and Asa Gray were vying with the British botanists, W. J. Hooker and George Bentham, in the volume of West American species that they were bringing to light. During much of the latter half of the century, collectors by the dozen were sending West American plants to Dr. Gray, the highest authority of the period on the flora of this region. As a culmination of this stage there appeared the monumental two volume *Botany of California* by W. H. Brewer and Sereno Watson, with a large section contributed by Gray (1876, 1880). This invaluable work, based principally on the large accumulations of western material that had gravitated to Harvard and also the collections of Brewer and others made in connection with the Geological Survey of California, has been the starting point for all subsequent floras that have been produced in the state.

Gradually, as the third stage in the elucidation of the California flora, the West developed its own botanical authors. The first to publish a number of native species new to science was Albert Kellogg, a San Francisco physician. His contributions appeared particularly from the 1850's to the 1870's in the *Proceedings of the California Academy of Sciences*, the institution of which he was a founder.

By 1880 the botanical activities of the Reverend Dr. E. L. Greene had begun. His contributions through the years were very large, but were so rarely of a monographic nature that the proportion of his specific proposals that were to be widely accepted is not to be compared with that of Gray, Watson, or Jepson. Yet, as a pioneer worker in a region outstanding for the richness of its flora, and having a keen eye for small variations, which he named, it was inevitable that Greene's name should be associated with a goodly percentage of our California species. He contributed two local floras of value: *Manual of the Botany of the Region of San Francisco Bay*, 1894, and *Flora Franciscana*, 1891-97.

The first of the major botanical works produced by Jepson, who was a student of Greene, was *A Flora of Western Middle California*, 1901, second edition, 1911. He usually had several manuscripts in preparation simultaneously. His work on one yielded information or suggested ideas applicable to another. About the time he finished work on this book he projected *The Silva of California* (1910), *The Trees of California* (1909, second edition, 1923), and *A Flora of California*, which from the first he looked upon as his greatest life's work. Jepson himself says² the *Flora* was planned in 1894. The first two parts ap-

² *Flora of California* 2: 7, 1936.

1948]

KECK: WILLIS LINN JEPSON

225

peared in 1909, the twelfth part in 1943. Work was actively progressing on the thirteenth part until illness interrupted, and the author's death a year later in 1946 found the Flora about three-fourths completed and published. Volume I starts on page 33, the first 32 pages being reserved for an introduction that was to have appeared upon the completion of the whole work. Its seven parts, otherwise complete, are not indexed. Volume II is complete, but the index is to families and genera only. The two completed parts of volume III are not indexed.

Jepson was thoroughly aware of these deficiencies and was almost reticent in advertising the parts of the Flora that were available. As in the case of *A Manual of the Flowering Plants of California*, which was also issued in parts, from 1923 to 1925, he preferred to withhold advertising of the parts as they appeared individually, because for the general user the completed work would prove more useful, and it was desirable not to deplete the stock of any one part before the entire volume could be bound. Because of these shortcomings, Jepson's Flora is definitely less convenient than his Manual, particularly for use in the field, and therefore has not received the general recognition and use that it deserves, but the quality of workmanship in the later parts is unsurpassed in any similar American work.

Jepson's major projects built progressively upon one another. As the Flora of Western Middle California built upon Brewer and Watson's Botany of California, Gray's Synoptical Flora of North America, and the works of Greene, appreciably advancing our knowledge of the plants of its area, so the Manual drew upon this work and the portions of *A Flora of California* then completed to become one of the finest botanical handbooks extant. Similarly, succeeding parts of the Flora mark a distinct advance over the Manual. As would be anticipated in a work that was to appear in parts over more than a third of a century, *A Flora of California* is uneven in treatment. The progressive improvement noted in volumes II and III as compared with volume I reflect not only the scientific growth of the author, but also the growth of botany in the West.

At a very early time Jepson had to decide whether to use the system of measurement based on the foot, inch, and line, used by the English botanists and the Harvard school, or to adopt the metric system coming into vogue on the Continent. He chose to follow the former, and, having committed his Flora to this system, was forced to continue, even though it was soon evident that the English system had been becoming obsolete from the turn of the century. By the time his Manual appeared in 1925, Jepson was originating the only major flora in America that did not follow the metric system.

This relatively minor fault, if fault it be, is nevertheless one of the few mechanical details to which exception can be taken in the works of one who put mechanical perfection very high indeed among the obligations of an author. Jepson's works are freer from typographical error than those of almost any other American botanist due to the fact that he

meticulously read proof himself and left no mechanical detail to the discretion of his printer.

Jepson strove for a uniform treatment and avoided introducing chromosome numbers, genetical data, and other experimental results that, by the time the later parts of the Flora were appearing, were becoming a determinative influence in taxonomy. It is well that he stayed on wholly familiar ground, continuing to rely on those tools which he handled as an adept—accurate descriptive morphology and analysis and a keen perception for the place of the plant in its natural environment. The story that he wrote he was perhaps better prepared to write than any other person.

The inclusion in later parts of the Flora of excerpts from Jepson's very extensive field notebooks on the ecology, physiology, and morphology of many species is of great value. The reader finds much interesting and original information under such a variety of titles as: geographical note, field note, leaf variation, taxonomic note, note on relationship, biological note, etc. Jepson was not only an astute observer; he was a facile writer whose written word was forceful, clear, and often of great beauty.

His appreciation of the historical precedent and the classical style stemmed not only from his teacher, E. L. Greene, who valued these especially highly, but also from his study of the works of the greatest systematists and from a reading of the classics. He urged upon his students the desirability of becoming familiar with great works on travel and biography as a proper foundation for work in taxonomy.

Students of west coast botany are fortunate that the principal task of organizing their flora has been done by one with the sound botanical judgment of Jepson. This he did not learn from Greene, nor from other contemporaries in California, but from a devoted study of the artistry of the great British systematists of the nineteenth century. That he profited much from this study is evident from the quality of his work, which has made an impress on the writings of others.

Jepson, with an intuitive grasp of what are good species and genera, organized the scattered knowledge of the complex California flora in a remarkable way. He introduced the Englerian system of phylogeny to California, but here and there made his own appraisals of the proper positions for the families. His species concept was grounded on so sound a morphological basis that, on the whole, it has been widely accepted, and the present-day methods of the experimental gardens and the cytological laboratories usually substantiate rather than displace Jepson's judgments. Relatively few of his contemporary authors have found their work so generally acceptable.

In gauging Jepson's place in California botany, the writer was prompted by curiosity to tabulate the number of species in the state named by each author, using unchanged the data as given in Jepson's Manual, our last complete list. Despite the shortcomings of the Manual data, such as the incomplete synonymy, the resulting list is of some interest. Here are the top 15 names, including all those who

1948]

KECK: WILLIS LINN JEPSON

227

have named 50 or more species in the Manual, together with the number of names contributed by each.

1. Asa Gray	717	9. Willis Linn Jepson	154
2. Carolus Linnaeus	431	10. David Douglas	86
3. Edward Lee Greene	365	11. George Engelmann	74
4. Sereno Watson	283	12. A. P. de Candolle	68
5. Thomas Nuttall	266	13. Frederick T. Pursh	64
6. John Torrey	245	14. George A. W. Arnott	58
7. George Bentham	188	15. Joseph Nelson Rose	51
8. William J. Hooker	160		

The only Californians among the first 15 are Greene and Jepson, and these are grouped among the classical students of the California flora. Albert Kellogg, however, with 48 species, is in sixteenth place. Other Californians among the first 50 are A. A. Heller, T. S. Brandegee, Alice Eastwood, H. M. Hall, Katherine Brandegee, and S. B. Parish, in that order.

Jepson worked in that transitional period between the time of Greene, when new species were yet to be found on almost every mountain range and valley floor, and the present, when even monographic researches uncover relatively few acceptable new species. Considering the conservative stand that he took on the matter of describing new species, it is interesting how high in the list his name is found. Jepson preferred to evaluate critically his own proposals before offering them to the world. This is one reason that his work has attained a lasting character.

The influence of Jepson does not rest wholly upon his writings. The relatively small number of graduate students that he found time to encourage came impressionably under the influence of his strong character. Their training would doubtless be considered unorthodox and irregular, but certain fundamentals about meticulous detail in observation of the plant, whether in the field or in the laboratory, and a broad appreciation for the contributions from related fields were drilled into the memory. His graduate student seminars were often his sole contact with the student. These were broadening and often dramatic experiences that challenged the imagination to reach out; they served to turn the student's attention from the local flora, with which Jepson's life would seem to be engrossed, to the far corners of the earth and to many fields untouched by Jepson's writings. The beneficial influence of this training is apparent from the sound taxonomic practices of those trained by him and, in turn, of their students.

Jepson succeeded in imparting to his public, which consisted in good part of laymen as well as of students, his deep feeling for nature. He looked upon the plant not only with the discriminating eye of the master systematist, but also with the enthusiasm and reverence of the naturalist and woodsman. Perhaps most beautifully expressed was his love for trees, so obvious in the *Silva*. One's love of nature is apt

to govern in direct proportion one's concern for conservation, and so it was that Jepson was a founder and prominent spokesman for the Save-the-Redwoods League and a staunch advocate of forest conservation measures and such other endeavors as the Point Lobos Reserve. All in all, it has been through many channels that the works of Jepson the botanist have become known, not only to his California audience, but to the world at large.

Carnegie Institution of Washington
Division of Plant Biology
Stanford, California

CNEORIDIUM DUMOSUM (NUTTALL) HOOKER F. COLLECTED MARCH 26, 1960, AT AN ELEVATION OF ABOUT 1450 METERS ON CERRO QUEMAZÓN, 15 MILES SOUTH OF BAHÍA DE LOS ANGELES, BAJA CALIFORNIA, MÉXICO, APPARENTLY FOR A SOUTHEASTWARD RANGE EXTENSION OF SOME 140 MILES.

I got it there then (8068).

I wish to express my sincere thanks to the San Diego Museum of Natural History and particularly to its director, Dr. George E. Lindsay, for making possible the trip on which this interesting specimen was collected; to my companion of the trip, Mr. Glen Ives, then staff artist of the Museum but functioning on the trip as collector of birds and mammals, for much help and encouragement during the field work; to Señor Ricardo Daggett of Bahía de los Angeles, majordomo of the Vermilion Sea Field Station of the San Diego Museum of Natural History, for help in planning and arranging the trip; and to Señor Pepe Smith and his 14-year-old son Favian, both of Bahía de los Angeles, who packed us into the mountains, for many courtesies extended. I am very grateful to Miss Anita Carter, Principal Herbarium Botanist of the University of California, Berkeley, for graciously verifying my determination of the specimen. I also wish to extend my thanks to the editor of the publications of the San Diego Society of Natural History for his many helpful suggestions during the compilation and processing of the data and the writing of the manuscript; to Dr. Helen K. Sharsmith, Señora Herbarium Botanist of the University of California, Berkeley, for her valuable suggestions on expanding the discussion and making the title more precise; to Mrs. Jerry Heller of the Museum staff for her very careful and accurate typing and retyping of the manuscript; and to Mrs. Rosemarie Fiebig of the Museum staff for taking the final manuscript to the post office for mailing. I must also express my deep gratitude to all my former mentors, to whose excellent instruction and training must ultimately be attributed any merit that this unworthy contribution may possess, although, needless to say, any errors are my own: in particular, I would name Professor Ira L. Wiggins and the late Professor LeRoy Abrams, of Stanford University; Professor Robert T. Clausen, of Cornell University; and Professors Lincoln Constance, Herbert L. Mason, and G. Ledyard Stebbins, of the University of California, Berkeley. Last but not least, I cannot fail to mention my deep indebtedness to my parents, without whose early cooperation this work would never have been possible.—REID MORAN, Museum of Natural History, San Diego, California.

PRESIDENT'S REPORT FOR VOLUME 60

The Centennial Year 2013 has been a fantastic year for the Society. We reached our 100th birthday as a Society on April 13, 2013. To celebrate the achievement of this milestone, we held a symposium in Berkeley on Saturday, April 14, hosted a special celebratory banquet that evening, and held the symposium in conjunction with the 23rd graduate student meetings on Sunday, April 15. We published an article in *Fremontia* (the Bulletin of the California Native Plant Society, 40:7–10) highlighting the history of the Society and contributions to California botany. We also conducted a series of field trips in honor of the 100th birthday. Brent Mishler led a bryology foray to the Cobb Mountain Region (March 2012), Dave Keil and Matt Ritter led a field trip to Fort Ord (May 2012), Tom Parker and Mike Vasey led a field trip to the Gold Lake Region (July 2012), and Jen Beck and Calvin Farris led a field trip to Desert Creek Natural Research Area (July 2012). For the Centennial weekend, on Friday, April 13, field trips went to Mt. Tamalpais (led by Dean Kelch with Brennan Wenck-Reilly) and Mt. Diablo (led by Barbara Ertter with Ingrid Jordon-Thaden). That Friday evening, we also enjoyed a mixer attended by over a hundred participants who renewed old acquaintances and made new ones. Our symposium linked our botanical past with the future through a series of talks led by Todd Keeler-Wolf (Cal Dept F&G), Aaron Liston (Oregon State), Bruce Baldwin (UCB), and Dave Peterson (U. Washington and USFS Western Mountain Initiative) in the morning, followed by Anna Jacobson (CSU Bakersfield), Ray Callaway (U. Montana), Carla D'Antonio (UCSB), and Richard Hobbs (U. Western Australia) in the afternoon. Kent Holsinger (U. Conn) provided an entertaining and informative banquet talk to wrap up this amazing day. On Sunday, more impressive talks were delivered, this time by three concurrent sessions of graduate student presentations. The graduate student meetings were supported by a number of volunteers, graduate student panel chairs, and judges. Awards were provided in several categories, always a difficult process. Ayla Mills, California State University, Chico, won for Proposed Research. Tommy Stoughton, Claremont Graduate University, won for Research in Progress. Diana Gamba, San Francisco State University and California Academy of Sciences, won for Completed Research. And finally, Jenn Yost, University of California, Santa Cruz, won for Best Talk. Please see www.calbotsoc.org for more information about the Centennial and links to or our Facebook page for photographs by Centennial photographer Brennan Wenck-Reilly and Centennial Symposium talks on YouTube by Lockyer Video Productions. Special thanks go to Genevieve Walden from UC Berkeley for her outstanding effort at organizing the graduate student meeting.

The Centennial was made possible by the generous sponsorship by the following individuals and organizations: East Bay Regional Parks District, RECON, Marin Municipal Water District, Golden Gate Parks Conservancy, Stillwater Sciences, Claremont Canyon Conservancy, WRA Environmental Conservancy, BOTANY and Rainbows, V. Thomas Parker and Alison Sanders, Northern California Botanists, Lawrence Janeway, GANDA, Heath Bartosh, Dean G. Kelch, Calflora, University and Jepson Herbaria, Michael C. Vasey and Patti Papeleux, Thomas J.

Rosatti, Steven Timbrock, Taylor Crow, Kristina Schierenbeck, Michael Williams, and an Anonymous sponsor. Thank you.

The Council's work this year has been busy and exceptionally productive. We finalized an agreement with JSTOR (an online archiving system) to place all of our *Madroño* back issues online and they are now available (since April, 2013). Current issues are already online through BioOne.2. We are moving toward having the current online issues easily available through individual member subscriptions, so look forward to that. One of the journal's editors, Richard Whitkus, has announced that he is stepping down after several pivotal years. We all are thankful to have had Rich during the time the journal converted to an online manuscript submission and tracking process and he also was instrumental in our rapidly catching back up on schedule. The Council has worked particularly hard this year because of the Centennial and I would especially like to thank Andrew Doran, Dean Kelch, Kim Kersh, Anna Larsen, Staci Markos, Matt Ritter, Tom Schweich, Michael Vasey, Genevieve Walden, and Rich Whitkus. We all owe them a great deal of thanks for their outstanding efforts. Our staff members, Lynn Yamashita and Bier [Ekaphan] Kraichak, also played crucial roles in the Centennial and deserve equal recognition for their efforts. Finally, the Council drafted an outsider to help with organizing details of the Centennial and to make sure we stayed on track in a timely fashion; accordingly, the Council especially thanks Alison Sanders for her role.

What does it mean for a Society to reach the age of one hundred years? Almost 300 botanists came from great distances for all or part of our three-day Centennial celebration. I think this suggests that the Society continues to provide an important resource for plant-oriented biologists in California and the western United States. The central objectives of the Society when it was established were to promote the collection of new information about the flora of the West, to provide a vehicle for disseminating that information, and to educate the public about the value of conserving plant species and habitats found in wild areas throughout our region. Clearly the Society has achieved these objectives in large measure. Nonetheless, over time, the membership has evolved and our interests overall have shifted as our science has matured. A Society is only as healthy as its membership and the engagement of that membership in the mission of the Society. We must continue to grow our membership, including its leadership, and be ready to respond to new opportunities. Advanced technologies now make it possible for us to broaden our reach and the challenge will be for us to do so over the next hundred years. Certainly, and unfortunately, the need for our science to help conserve plant resources is not diminishing but rather becoming more critical every day.

This issue of *Madroño* reprints a small selection of articles from the past century as a way of reminding us of the central role the California Botanical Society has played in the development of concepts about plant evolution, ecology, systematic relationships, paleohistory, biogeography, conservation management and ecological restoration. Take the opportunity to read not only this collection, but to explore the prior sixty volumes (an index is found online

at our website). You will be rewarded by a diverse array of articles about the history of botanical exploration in the western United States and Mexico in the 18th and 19th centuries, early floras of a variety of places (including an early one of the Swiss Alps!), and arguments about the concepts on which we base our sciences. You will also see that our Society has been a critical source of creativity and

innovation for plant sciences. Now it remains for the membership to continue the impressive traditions of this past century.

V. Thomas Parker
December 2013

EDITORS' REPORT FOR VOLUME 60

We are pleased to report the publication of volume 60 of *Madroño* by the California Botanical Society (CBS) in 2013. With this volume we are celebrating 100 years of the CBS.

The publication of *Madroño* remains on schedule with an average time between initial submission and publication of about 8 months. We hope that *Madroño* continues to be viewed as the best outlet for western botanists to publish their work in a timely fashion, while reaching an interested and relevant audience. This year, all the past issues of *Madroño*, from volume one on, have become available online through JSTOR. Special thanks are due to JSTOR, especially to Barbara Chin and Katherine Harto, who were extremely helpful in providing PDFs of articles on short notice for the use of the editor and to produce this issue.

The efforts of numerous individuals are critical to the continued quality of the journal. Among these are our Noteworthy Collections editor, Dieter Wilken; Steve Timbrook who has long provided the volume Index and Table of Contents; Annielaurie Seifert at Allen Press; and the CBS executive council. We are also grateful to our contributors for their interesting and insightful manuscripts, and our reviewers who take time from their busy schedules to assess the quality of submitted work.

Dieter Wilken will be resigning after this volume as Noteworthy Collections editor. Dieter served the readers of *Madroño* in that position for more than 15 years and we are extremely grateful for all his efforts. David Keil of Cal Poly, San Luis Obispo will become the next Noteworthy Collections editor. Genevieve Walden is our new editorial assistant and has been doing great work in the position. Finally, Richard Whitkus has been the copy editor for *Madroño* for the past 5 years. In his time Dr. Whitkus

presided over *Madroño's* move to an online submission process, and was critical in getting the journal back on schedule. The CBS executive council is extremely grateful for all the work he has done for the journal.

This year we received 26 new manuscripts and 22 were accepted for publication. Several manuscripts were also carried over from the previous year. The 60th volume includes two special issues: *Tanoak: ecology, botany, history, and values* (guest edited by Susan Frankel of the USDA Forest Service), and this issue that celebrates nearly 100 years of *Madroño* by reprinting articles by prominent people in the history of California botany as well as seminal and important papers that strongly influenced later botanical work in California.

As Editors, we have enjoyed our interactions with contributors and reviewers this past year and anticipate continued submissions of novel and exciting work.

This volume represents the last one of which I (Whitkus) will be an editor. I have enjoyed the opportunity to work with the California Botanical Society in bringing forward articles and reports of interest to plant professionals and enthusiasts. I have been honored to work with the Board members over the past several years and to have their trust in producing the journal. The two co-editors I worked with, Tim Lowery and Matt Ritter, have been extremely supportive of my quirkiness and tardiness. In truth, I will not miss the work, but I will miss the professional and collegial interactions of everyone who has contributed to the production and distribution of a singular botanical journal.

Matt Ritter
Richard Whitkus
December 2013

REVIEWERS OF MADROÑO MANUSCRIPTS 2013

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Marti Witter
Dorde Woodruff
Jenn Yost

INDEX TO VOLUME 60

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

Adenostoma fasciculatum, seed dormancy, 165.

Ambrosia chamissonis, effect of trampling on CA beaches, 4.

Apiaceae (see *Lomatium*)

Arizona (see *Monardella*)

Asteraceae: *Ambrosia chamissonis*, effect of trampling on CA beaches, 4; *Centaurea melitensis*, fire effects on, 173.

New taxon: **Lagophylla diabolensis**, from CA, 249.

Noteworthy collections: *Centaurea macrocephala*, *Lactuca muralis*, *Psilocarphus tennellus*, from MT, 262.

Beach vegetation: Effect of trampling on *Ambrosia chamissonis* and *Cakile maritima* in CA, 4.

Bergia texana, noteworthy collection from MT, 262.

Boraginaceae (see *Cryptantha* and *Phacelia*)

Brassicaceae (see *Cakile*)

Cakile maritima, effect of trampling on CA beaches, 4.

California: *Ambrosia chamissonis* and *Cakile maritima*, effect of trampling on CA beaches, 4; CA Phenology Project: tracking plant responses to climate change, 1; fire effects on chaparral, 173; *Phacelia cookei*, habitat, seed dormancy and allozyme variation, 11; rare plants, climate change vulnerability assessment, 193.

New taxa: **Lagophylla diabolensis**, 249; **Limnanthes douglasii** subsp. **ornduffii**, 229; **Mimulus filicifolius**, 236; **Polemonium eddyense**, **P. pulcherrimum** var. **shastense**, 243.

Noteworthy collections: *Calyptidium pygmaeum*, 56; *Eriogonum heracleoides* var. *heracleoides*, 261; *Gracilariopsis chorda*, *Grateloupia asiatica*, 57; *Lewisia triphylla*, 56; *Sphaeropteris cooperi*, 258; *Trifolium suffocatum*, 260; *Ulva clathratioides*, and *U. pertusa*, 58.

Calyptidium pygmaeum, noteworthy collection from CA, 56.

Ceanothus cuneatus, seed dormancy, 165.

Centaurea: *C. macrocephala*, noteworthy collection from MT, 262; *C. melitensis*, effects of fire on, 173.

Chaparral: Fire effects in so. CA ecological reserve, 173; mimicking fire for restoration, 165.

Claytonia saxosa, noteworthy collection from OR, 264.

Climate change: CA Phenology Project, tracking plant responses, 1; rare plant vulnerability assessment in CA, 193.

Compositae (see Asteraceae)

Conservation (see *Notholithocarpus densiflorus*)

Cryptantha martirensis, new sp. from Sierra de San Pedro Martir, Baja California, MEXICO, 35.

Cryptantha wigginsii rediscovered, 24.

Cyatheaceae (see *Sphaeropteris*)

Datura arenicola, new sp. in new sect. **Discola** from Mexico, 60.

Editors' Report for Vol. 60, 362

Elatinaceae (see *Bergia*)

Ericaceae (*Pterospora*)

Eriogonum heracleoides var. *heracleoides*, noteworthy collections from CA and NV, 261.

Fabaceae (see *Senegalia* and *Trifolium*)

Fagaceae (see *Notholithocarpus*)

Fire: Effects on plant community in so. CA ecological reserve, 173; mimicking for chaparral restoration, 165.

Foods from forest ecosystem (see *Notholithocarpus densiflorus*)

Gibberlic acid (see *Pterospora*)

Gracilariaceae (see *Gracilariopsis*)

Gracilariopsis chorda, noteworthy collection from CA, 57.

Grateloupia asiatica, noteworthy collection from CA, 57.

Halymeniaceae (see *Grateloupia*)

Invasive plants (see *Centaurea*)

Juncaeae (see *Luzula*)

Keys: *Cryptantha martirensis* and vars. of *C. muricata*, 44; *C. wigginsii* added to key of *Cryptantha s.l.* of Kelley et al., 33; *Datura arenicola* and comparable spp., 225; *Monardella* spp. of e. Mojave Desert, 53; *Senegalia*, selected spp. and hybrids, 183.

Lactuca muralis, noteworthy collection from MT, 262.

Lagophylla diabolensis, new sp. from CA, 249.

Lamiaceae (see *Monardella*)

Lewisia triphylla, noteworthy collection from CA, 56.

Limnanthaceae (see *Limnanthes*)

Limnanthes douglasii subsp. **ornduffii**, new subsp. from CA, 229.

Limonium vulgare, noteworthy collection from MT, 262.

Lomatium triternatum, morphological and ecological segregation of two sympatric varieties in MT, 211.

Luzula subcapitata, noteworthy collection from WY, 60.

MEXICO: (see *Cryptantha* and *Senegalia*)

New taxa: **Datura arenicola** in sect. **Discola**, 217.

Mimulus filicifolius, new sp. from northern Sierra Nevada, CA, 236.

Monardella eplingii, new sp. from the Black Mts. of nw AZ, 46.

Monotropes (see *Pterospora*)

Montana: *Lomatium triternatum*, morphological and ecological segregation of two sympatric varieties, 211.

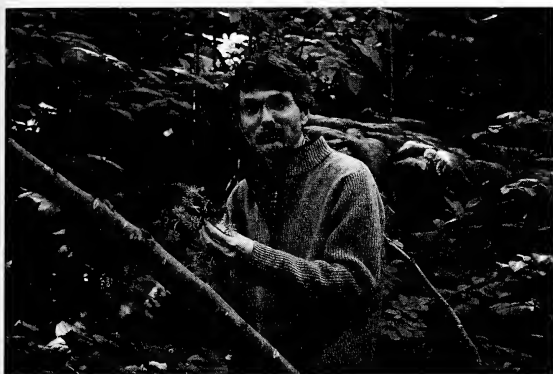
Noteworthy collections: *Bergia texana*, *Centaurea macrocephala*, *Lactuca muralis*, *Limonium vulgare*, *Psilocarphus tennellus*, *Ranunculus sulphureus*, 262.

Montiaceae: Noteworthy collections: *Calyptidium pygmaeum* from CA, 56; *Claytonia saxosa* from OR, 264; *Lewisia triphylla* from CA, 56.

- Mycoheterotroph (see *Pterospora*)
- Nevada (see *Eriogonum*)
- Notholithocarpus densiflorus* (see entire issue Vol. 60(2))
 Conservation, replanting and genetics, 130.
 History, ecology and values, 63.
 Insect pollination and biodiversity, 87.
 Mutant tanoak morphology, physiology, genetics, etc., 107.
 Past, present and future as a forest products resource, 118.
Phytophthora ramorum and ectomycorrhizal fungi, 95.
 Tanoak forest ecosystem foods, 126.
 Tending a native American nut tree, 64.
- Oregon (see *Claytonia*)
- Phenology, CA Project, tracking plant responses to climate change, 1.
Phacelia cookei, habitat, seed dormancy and allozyme variation, 11.
 Phrymaceae (see *Mimulus*)
Phytophthora ramorum (see *Notholithocarpus densiflorus*)
 Plumbaginaceae (see *Limonium*)
 Polemoniaceae (see *Polemonium*)
Polemonium eddyense, new sp., and ***P. pulcherrimum*** var. ***shastense***, new var., from CA, 243.
 Polygonaceae (see *Eriogonum*)
Psilocarphus tennellus, noteworthy collection from MT, 262.
Pterospora andromedea and *Sarcodes sanguinea*, gibberellic acid induces germination of obligate mycoheterotrophs, 186.
 President's Report for Vol. 60, 360
- Ranunculaceae (see *Ranunculus*)
Ranunculus sulphureus, noteworthy collection from MT, 262.
 Rare plants, climate change vulnerability assessment in CA, 193.
 Reviews: *Field Guide to Mushrooms of Western North America* by R. Michael Davis, Robert Sommer and John A. Menge, 55; *Wildflowers of the Mountain West* by Richard M. Anderson, JayDee Gunnell, and Jerry L. Goodspeed, 257; *Woody Plants of Utah: A Field Guide with Identification Keys to Native and Naturalized Trees, Shrubs, Cacti, and Vines* by Renée Van Buren, et al., 255.
- Rhamnaceae (see *Ceanothus*)
 Rosaceae (see *Adenostoma*)
- Sarcodes sanguinea* (see *Pterospora*)
 Sawyer, Dr. John O., Jr., In Memoriam, 61.
 Seed dormancy: Chaparral, 165; *Phacelia*, 11.
Senegalia hybrids in central and northern Mexico, 179.
 New taxon: ***Senegalia X zamudii***, new nothomorph, 182.
- Solanaceae (see *Datura*)
Sphaeropteris cooperi, noteworthy collection from CA, 258.
- Trifolium suffocatum*, noteworthy collection from CA, 260.
- Ulla clathratioides* and *U. pertusa*, noteworthy collections from CA, 58.
 Ulvaceae (see *Ulva*)
- Wyoming (see *Luzula*)

DEDICATION

BRUCE G. BALDWIN



Bruce G. Baldwin with fruiting Elk clover (*Aralia californica*), August 2013. Photograph by Susan Bainbridge.

In this year, the Centennial year of the California Botanical Society, the Council is pleased to dedicate this volume of *Madroño* to Bruce G. Baldwin, Curator of the Jepson Herbarium and Professor of Integrative Biology, University of California, Berkeley.

A native Californian, Bruce grew up in Arroyo Grande, amidst the highly diverse flora of San Luis Obispo County. At a young age, he developed an interest in natural history while on family camping trips and on backpacking trips with friends in California and other parts of the West. He also developed an interest in conservation biology and became a member of the Sierra Club. Biology was his favorite subject in school, especially fieldwork—in elementary school he made an informal plant collection (which he still has).

Bruce earned a B.A. with Honors in 1981 at the University of California, Santa Barbara, where he first learned in detail about the wonders of the California flora. In addition to course work and working as a plant collector for botany labs, he was involved in a National Science Foundation sponsored effort that included a floristic and vegetation survey of the Old Dad-Kelso Mountains region in the Mojave Desert. After his work in the Mojave, Bruce moved to another ecological extreme, Alaska, where he worked for the state geological survey before returning to California for graduate school at UC Davis. There he completed a Master's Degree (1985) and Ph.D. (1989) in Botany under the direction of Donald Kyhos. His dissertation was titled "*Chloroplast DNA Phylogenetics and Biosystematic Studies in Madiinae (Asteraceae)*." After a post-doc at the University of Arizona, Tucson, and a faculty appointment at Duke University (1992–1994), Bruce once again returned to California; this time to the Jepson Herbarium where he has been (working at Jepson's desk) since 1994.

During his academic tenure, Bruce has supervised ten postdoctoral scholars and eleven graduate students and has served on many other Ph.D. and Master's thesis and

exam committees. Students in Bruce's lab (of which there are currently five active students) learn important lessons regarding data collection, data analysis, and publication: be careful, double-check everything, investigate uncertainties, and when you think the work is perfect, it's still not done; good work requires time and persistence. Bruce's emphasis on a well-rounded dissertation project derives from his own distinguished mentors (e.g., Axelrod, Carlquist, Carr, Crawford, Dvorak, Gottlieb, Kyhos, Raven, Stebbins, Strother, Sytsma, and Webster), mentors who positioned him ideally to move plant systematics into the era of molecular studies.

Bruce's research is integrative and brings together traditional biosystematic approaches with cutting edge molecular tools to produce a deep understanding of the ecology, cytology, and morphology of organisms as well as the evolutionary origins of their traits. Bruce's work and that of his students is so varied and wide-reaching, it's hard to imagine what the science of plant systematics or California floristics would be without his continual, persistent, and thoughtful contributions. To date, Bruce has contributed over 115 refereed research publications and edited three books: *The Jepson Desert Manual: vascular plants of southeastern California* (UC Press); *Tarweeds & Silverswords: evolution of the Madiinae* (Missouri Botanical Garden Press); and *The Jepson Manual: vascular plants of California, Second Edition* (UC Press).

He has provided countless hours of service to the Department of Integrative Biology and the Jepson Herbarium as well as to professional societies, academic journals, government agencies, and other academic institutions. He was President (2000–2003) and Past President (2003–2006) of the California Botanical Society and President of the American Society of Plant Taxonomists (2008–2009).

Bruce has been a pioneer in molecular systematics, a field that has transformed evolutionary biology. One of Bruce's early papers, "*The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny*" (Baldwin et al. 1995), is among the most highly cited of his career because it set the stage for so many others to pursue phylogenetic investigations with molecular data. Bruce's innovation didn't stop with ITS, he soon pursued the phylogenetic utility of the external transcribed spacer (ETS), which, together with the ITS region, have become standard regions used in molecular phylogenetic analyses.

Since the early 2000s, Bruce has continued to develop techniques that have allowed for further examination of diversity at ever-refining levels. His work with cryptic species changed the philosophy undertaken by the Jepson Flora Project and has continued to reveal that recognizing fine-scale diversity is critical to understanding diversification and guiding conservation efforts, especially in places like California.

As Convening Editor and contributor of over 40 treatments to the second edition of *The Jepson Manual*, Bruce led five editors, a staff of six, and an author group

of over 300 contributors from around the world to produce a thoroughly revised and updated book and associated resources for the California flora. The project benefited greatly from Bruce's ingenuity and the *Jepson eFlora* (<http://ucjeps.berkeley.edu/IJM.html>) is leading the way as a model in the production and maintenance of modern floras.

Bruce is perhaps at his best when working with a group of students in the field or lab. Many times, we have seen students (undergraduates and workshop participants alike) hang on his every word. Like no other, Bruce can deliver an impromptu mini-lecture full of history and context, interesting facts, and humor. His

endearing spirit and undisputed commitment to conserving the flora of California are attributes that make everyone we've encountered wish they could spend more time with him, learning about and appreciating the natural world.

The world has been enriched with the gifted mind and heart embodied in Bruce Baldwin and for that, we are grateful.

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MADROÑO VOLUME 60
TABLE OF CONTENTS

Alexander, Janice (see Nielsen, Bonnie)	
Anacker, Brian L., et al., Climate change vulnerability assessment of rare plants in California	193
Anderson, John L. (see Elvin, Mark A.)	
Afzal-Rafii (see Dodd, Richard S., et al.)	
Baldwin, Bruce G., <i>Lagophylla diabolensis</i> (Compositae-Madiinae), a new hare-leaf from the southern Diabolo Range, California	249
Bergemann, Sarah E., et al., Implications of tanoak decline in forests impacted by <i>Phytophthora ramorum</i> : Girdling decreases the soil hyphal abundance of ectomycorrhizal fungi associated with <i>Notholithocarpus densiflorus</i>	95
Bowcutt, Frederica, Tanoak landscapes: Tending a native American nut tree	64
Bruns, Thomas D. (see Wong, Valerie L.)	
Buxton, Eva G., A new subspecies of <i>Limnanthes</i> (Limnanthaceae) from San Mateo County, California	229
Chambers, Kenton L. (see Duncan, James T.)	
Christiaens, Bryce (see Lesica Peter F., et al.)	
Clark, John R., and Tony M. Summers, Noteworthy collection from California	258
Cobb, Richard C. (see Dillon, Whalen W., et al.)	
Cobb, Richard C., et al., Biodiversity conservation in the face of dramatic forest disease: An integrated conservation strategy for tanoak (<i>Notholithocarpus densiflorus</i>) threatened by sudden oak death	151
Dillon, Whalen W., et al., Range-wide threats to a foundation tree species from disturbance interactions	139
Dillon, Whalen W. (see also Cobb, Richard C., et al.)	
Dodd, Richard S., et al., Genetic structure of <i>Notholithocarpus densiflorus</i> (Fagaceae) from the species to the local scale: Review of our knowledge for conservation and replanting	130
Dodd, Richard S. (see also Wright, Jessica W., and Richard S. Dodd)	
Duncan, James T., and Kenton L. Chambers, Noteworthy collection from Oregon	264
Ebinger, John E. (see Seigler, David E.)	
Edwards, A. L. (see Patterson, M. E.)	
Eliason, Scott (see Williams, C. Matt, Gina Richmond and Scott Eliason)	
Elvin, Mark A., John L. Anderson and Andrew C. Sanders, <i>Monardella eplingii</i> , A new species from the Black Mountains of northwestern Arizona, USA	46
Evenden, Angela G. (see Haggerty, Brian P.)	
Evens, Julie M., and Todd Keeler-Wolf, In Memorium, Dr. John O. Sawyer, Jr. 1939–2012	61
Ferris, Kathleen G. (see Sexton, Jason P.)	
Filipe, João A. N. (see Cobb, Richard C., et al.)	
Forbis De Quieroz, T. (see Patterson, M. E.)	
Frankel, Susan J., Tanoak: History, ecology and values	63
Frankel, Susan J. (see also Cobb, Richard C., et al.)	
Garbelotto, Matteo (see Bergemann, Sarah E., et al.)	
Garbelotto, Matteo (see Cobb, Richard C., et al.)	
Gerst, Katharine L. (see Haggerty, Brian P.)	
Gilligan, Christopher A. (see Cobb, Richard C., et al.)	
Glass, Catherine E. (see Seigler, David E.)	
Gogol-Prokurat, Melanie (see Anacker, Brian L., et al.)	
Goheen, Ellen (see Cobb, Richard C., et al.)	
Williams, C. Matt, Gina Richmond and Scott Eliason, Noteworthy collections from CA	56
Williams, C. Matt (see Simpson, Michael G., Jon P. Rebman, Kristen E. Hasenstab-Lehman, et al.)	
Haggerty, Brian P., Elizabeth R. Matthews, Katharine L. Gerst, et al., The California Phenology Project: Tracking plant responses to climate change	1
Hanna, Dave (see Lesica Peter F., et al.)	
Hansen, Everett M. (see Cobb, Richard C., et al.)	
Hasenstab-Lehman, Kristen L. (see Simpson, Michael G., Jon P. Rebman, Kristen E. Hasenstab-Lehman, et al.)	
Hayden, Katherine J. (see Cobb, Richard C., et al.)	
Holland, V. L. (see Wilken, Katherine M.)	
Hoyer, William F., III, Noteworthy collections from California and Nevada	261
Hughey, Jeffery R., Noteworthy collections from California	57
Ivey, C. T. (see Patterson, M. E.)	
Keeler-Wolf, Todd (see Evens, Julie M.)	
Keil, David J., Review of <i>Woody Plants of Utah: A Field Guide with Identification Keys to Native and Naturalized Trees, Shrubs, Cacti, and Vines</i> by Renée Van Buren, et al.	255
Keil, David (see also Wilken, Katherine M.)	
Kittelson, Pamela M. (see Lesica, Peter, and Pamela M. Kittelson)	

Kordesch, Nicholas C. (see Bergemann, Sarah E., et al.)	
Larsen, Lisa (see Lesica Peter F., et al.)	
Leidholm, Kyrstal (see Anacker, Brian L., et al.)	
Lesica, Peter, and Pamela M. Kittelson, Morphological and ecological segregation of two sympatric <i>Lomatium triternatum</i> (Apiaceae) varieties in Montana	211
Lesica Peter F., et al., Noteworthy collections from Montana	262
Matthews, Elizabeth R. (see Haggerty, Brian P.)	
Mazer, Susan J. (see Haggerty, Brian P.)	
McConnell, Patrick O. (see Simpson, Michael G., Jon P. Rebman, Kristen E. Hasenstab-Lehman, et al.)	
McDonald, Philip M., et al., Morphology, physiology, genetics, enigmas, and status of an extremely rare tree: Mutant tanoak	107
Meentemeyer, Ross K. (see Cobb, Richard C., et al.)	
Meentemeyer, Ross K. (see Dillon, Whalen W., et al.)	
Metz, Margaret R. (see Dillon, Whalen W., et al.)	
Metz, Timothy A. (see Bergemann, Sarah E., et al.)	
Morgan, Randall (see Styer, David)	
Moroney, Jolene R., and Philip W. Rundel, Effects of fire and fireline disturbance on the plant community in a southern California ecological reserve	173
Nelson, J. K. (see Patterson, M. E.)	
Nettel, Alejandro (see Dodd, Richard S., et al.)	
Nielsen, Bonnie, and Janice Alexander, Foods from the tanoak ecosystem	126
Odegard, Craig (see Lesica Peter F., et al.)	
Parker, V. Thomas, President's Report for Volume 60	360
Patterson, M. E., C. T. Ivey, A. L. Edwards, et al., Habitat, seed dormancy, and allozyme variation of the rare endemic <i>Phacelia cookie</i> (Boraginaceae)	11
Patterson, Robert (see Stubbs, Rebecca L.)	
Quarles, Stephen L. (see Shelly, John R.)	
Rebman, Jon P. (see Simpson, Michael G., and Jon P. Rebman)	
Rebman, Jon P. (see also Simpson, Michael G., Jon P. Rebman, Kristen E. Hasenstab-Lehman, et al.)	
Richmond, Gina (see Guilliams, C. Matt, Gina Richmond and Scott Eliason)	
Ritter, Matt, and Richard Whitkus, Editors' Report for Volume 60	362
Rizzo, David M. (see Cobb, Richard C., et al.)	
Rizzo, David M. (see Dillon, Whalen W., et al.)	
Rundel, Philip W. (see Moroney, Jolene R.)	
Sanders, Andrew C. (see Elvin, Mark A.)	
Schaffner, Andrew (see Wilken, Katherine M.)	
Schierenbeck, K. A. (see Patterson, M. E.)	
Schoenig, Steve (see Anacker, Brian L., et al.)	
Schoenig, Steve (see also Sexton, Jason P., et al.)	
Seiger, David E., John E. Ebinger and Catherine E. Glass, <i>Senegalia berlandieri</i> , <i>S. crassifolia</i> , and <i>S. reniformis</i> hybrids (Fabaceae; Mimosoideae) in central and northern Mexico	179
Senock, Randy S. (see McDonald, Philip M., et al.)	
Sexton, Jason P., Kathleen G. Ferris and Steve E. Schoenig, The fern-leaved monkeyflower (Phrymaceae), a new species from the northern Sierra Nevada of California	236
Shelly, John R., and Stephen L. Quarles, The past, present and future of <i>Notholithocarpus densiflorus</i> (Tanoak) as a forest products resource	118
Simpson, Michael G., and Jon Rebman, A new species of <i>Cryptantha</i> (Boraginaceae) from the Sierra de San Pedro Martir, Baja California, Mexico	35
Simpson, Michael G., Jon P. Rebman, Kristen E. Hasenstab-Lehman, et al., <i>Cryptantha wigginsii</i> (Boraginaceae): A presumed extinct species rediscovered	24
Stubbs, Rebecca L., and Robert Patterson, Revisions in <i>Polemonium</i> (Polemoniaceae): A new species and a new variety from California	243
Styer, David, and Randall Morgan, Noteworthy collection from California	260
Summers, Tony M. (see Clark, John R.)	
Swiecki, Tedmund J. (see Cobb, Richard C., et al.)	
Tobias, Michele M., Effect of trampling on <i>Ambrosia chamissonis</i> and <i>Cakile maritima</i> cover on California beaches	4
Valachovic, Yana S. (see Cobb, Richard C., et al.)	
VanSant-Glass, William (see Bergemann, Sarah E., et al.)	
Vellinga, Else C., Review of <i>Field Guide to Mushrooms of Western North America</i> by R. Michael Davis, Robert Sommer and John A. Menge	55
Vogler, John B. (see Dillon, Whalen W., et al.)	
Watson, D. Robert A., <i>Datura arenicola</i> (Solanaceae): A new species in the new section <i>Discola</i> from Baja California Sur in Mexico	217
Whipple, Clinton, Review of <i>Wildflowers of the Mountain West</i> by Richard M. Anderson, JayDee Gunnell and Jerry L. Goodspeed	257
Whitkus, Richard (see Ritter, Matt)	
Wilken, Katherine M., et al., Mimicking fire for successful chaparral restoration	165

Wong, Valerie L., and Thomas D. Bruns, Gibberellic acid induces asymbiotic germination of the obligate mycoheterotroph <i>Pterospora andromedea</i> (Ericaceae)	186
Wright, Jessica W., and Richard S. Dodd, Could tanoak mortality affect insect? Evidence for insect pollination in tanoaks biodiversity	87
Wright, Jessica W. (see also Dodd, Richard S., et al.)	
Wright, Jessica W. (see also McDonald, Philip M., et al.)	
Zhang, Jianwei (see McDonald, Philip M., et al.)	
Zika, Peter F., Noteworthy collection from Wyoming	60

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