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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, $s = f(cl, o, r, p, t)$, there are five independent variables that define the soil system: climate (cl), 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-

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

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

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-

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-sericitis 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

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

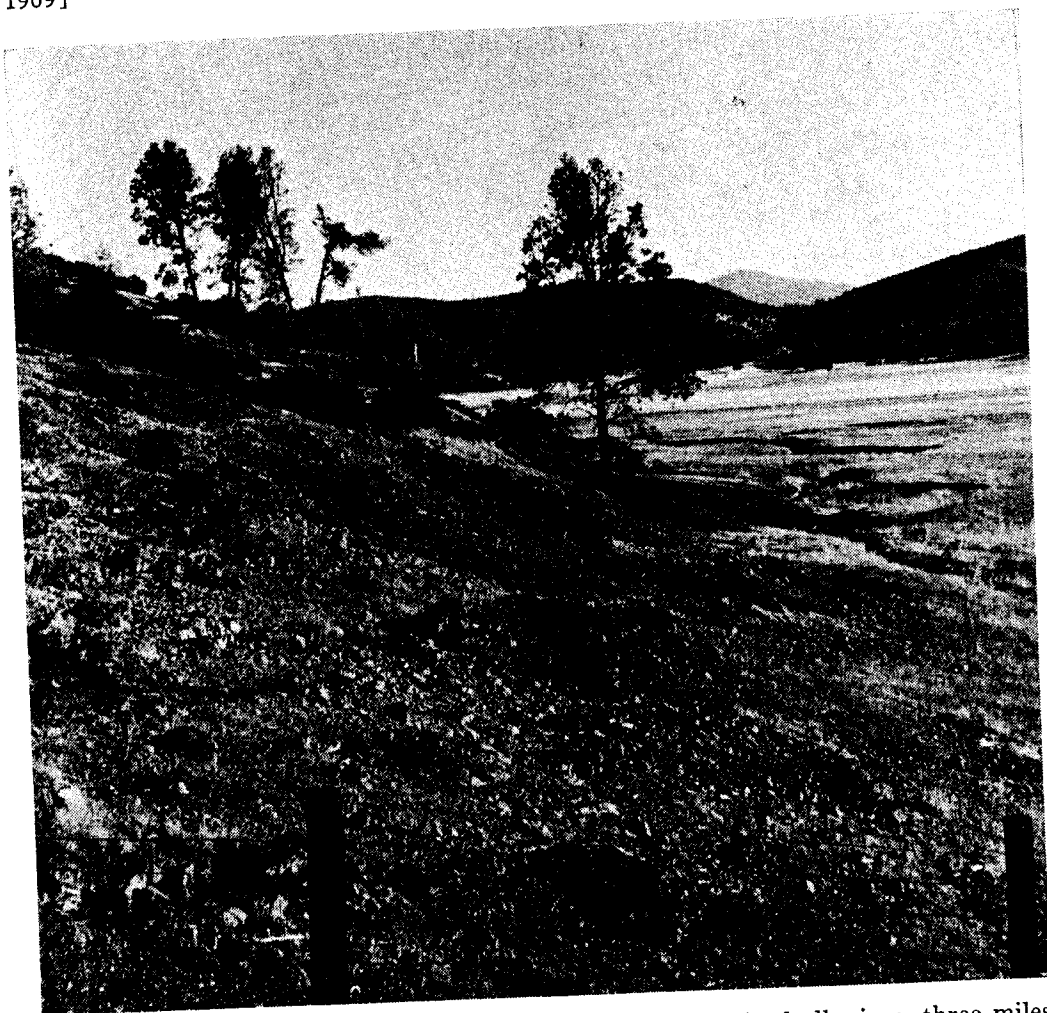


FIG. 2. Outcrop of serpentine overlooking meadow of mixed alluvium, three miles northeast of Middletown, California.

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-

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. *vaccinifolia*, 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 stands are invariably open, the barren slopes between the scattered trees lightly populated with

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 serpentinized 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. *lemmonii*, (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.

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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.

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-*

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 soughtafter 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.

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