Some Vegetation of the California Coastal Redwood Region in Relation to Gradients of Moisture, Nutrients, Light, and Temperature

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SOME VEGETATION OF THE CALIFORNIA COASTAL REDWOOD REGION IN RELATION TO GRADIENTS OF MOISTURE, NUTRIENTS, LIGHT, AND TEMPERATURE

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INTRODUCTION

Great environmental variation and associated vegetation change occur within very limited geographical areas in California. This environmental variation provides a natural laboratory for many types of ecological studies.

One such area is in the Humboldt Redwoods State Park of northern coastal California. Here are magnificent forests of coast redwoods (*Sequoia sempervirens*)[2] in a varied landscape with other kinds of vegetation. Opportunity to study the vegetation and environments in this area was afforded by interest of the State of California Division of Beaches and Parks in preservation of the redwood groves entrusted to their care. A prerequisite for preservation was recognized to be better knowledge of the ecosystems in which the redwood exists. The death of a number of redwood trees, brought about by the unfortunate sequence of poor logging practices, fire, and torrential rains in the watersheds shared with Humboldt Redwoods State Park, brought support for such ecological studies, of which this paper reports some aspects.

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[2] Nomenclature and taxonomy follow Munz & Keck (1959) except where the authority for a name is given.

An attempt is made in this paper to: 1) specify the location of individual species of the redwood region along environmental gradients of moisture, soil nutrients, light, and temperature; 2) to analyze the distribution of recognizable vegetation patterns along these gradients; and 3) to develop simple numerical indexes requiring no field measurements other than a listing of species present in a vegetation sample or stand to position that sample along environmental gradients in relation to other segments of the vegetation. Gradients were quantified.

The approach suggested in this paper lends itself to the interpretation and comparison of ecosystems in the field and, at the same time, provides procedures applicable to physiological studies utilizing controlled environment chambers.

The approach should be valuable in autecological or biosystematic (genetic) studies, in studies of vegetation, in studies of plant physiology which are intended to have relevance to plants as they exist in nature, and in forest and soil classification.

We wish to thank the California Division of Beaches and Parks for sponsoring this project, and Mr. Fred Eggiman and Mr. Carl Anderson of Humboldt Redwoods State Park for providing the field headquarters and cooperating in other ways. At Berkeley the following persons provided facilities,

THEORETICAL CONSIDERATIONS

It is desirable that any approach to the analysis of vegetation be in harmony with presently accepted ecological theories, or at least recognize the existence of such theories and point out where disagreement occurs.

Recognition that all plants reflect by their presence the integrated environment is not very helpful in unscrambling the functional relationships between plants and their environments. To use these plants as indicators one must determine which are the factors to which they are most responsive.

Two approaches to analysis of the factors influencing plant growth and occurrence have been suggested: 1) operational, 2) correlative. They overlap.

The correlative approach, which relies on an assumed correlation of measurable habitat factors with those of direct, effective physiological importance to plants, has the advantage that the environmental factors can be defined as independent and the plant, soil, or microclimatic responses as dependent (Major 1951). Cause and effect complications are thus avoided (Major 1958, 1961a). Also, commonly available measures of environmental factors such as Weather Bureau observations of regional climates can be used. On the other hand, mechanisms are not explained. There is usually no tie in to the data supplied by plant physiological studies.

An operational approach is used in this paper. Mason & Langenheim (1957) have elaborated the useful tautology that only those phenomena which actually affect an organism during its life cycle are important in determining its success or failure. All such phenomena comprise the "operational environment." This differs from the "potential environment" which includes those phenomena that are not at present operational but in time may be. The effects of an ice storm or a deep water table are only potential environmental factors to a seedling growing under a protecting tree canopy. Mason & Langenheim did not believe that the origin of the operational or "effective" factors was important. That is, forms of precipitation and characteristics of a water table would not directly influence a plant, but only modify the soil moisture available to it. However, for convenience in actually measuring the effective factors or in attempting to modify them, some separation as to origin, or at least locus of effectiveness (e.g., to distinguish between temperature effects upon foliage and upon roots) is desirable.

The actual distribution of plants in nature is determined by the combined influence of all environmental factors. Each plant has a certain tolerance for each factor and can only survive and reproduce if all factors are within its range of tolerance during certain critical stages in its development (Good 1931). The factor closest to the edge of a species' tolerance is said to be limiting. The range of tolerance concept implies that either extremes or deficiencies in a factor may be limiting.

Within the physiological limits of a species it is incorrect to speak of a factor as being limiting since the *limits* have already been defined for the growth of that particular plant. The *relative* response of two species to particular levels of environmental factors determines which of the species is better adapted under those conditions. That many species do not occupy the whole of their physiologically potential range (of tolerance) can be explained by one or a combination of the following: (1) insufficient time for migration, (2) physiological barriers to migration, (3) occupancy of the area by better-adapted species.

The often large difference between the potential and actual range of a species has sometimes been overlooked. MacGinitie's (1933) observation of frost damage to redwood in the northern portion of its range may be an example. MacGinitie concluded that the rare occurrence of freezing temperatures probably restricts redwood in its northern expansion. Since none of the redwood were actually killed and natural regeneration from seed is observed in the most northern stands, his conclusions are doubtful. It may well be that an increased frequency of freezing temperatures controls the potential range of redwood expansion to the north, but the difference between the actual and the potential range may be considerable. Douglas-fir, hemlock, and other better-adapted species are now occupying that area, and only with their removal could the actual range of redwood be expected to approach the potential range. Perhaps where vegetation is sparse, such as at timber line or on deserts, the potential and actual range of a species may coincide. Thus, plant competition in general acts to restrict the distributional ranges of species even though their disseminules are more widely distributed.

Since "species" are not physiologically homogeneous but often consist of races having different tolerances, one cannot expect the same reaction of members of a species to their environments throughout the species' area of distribution. The detection of such ecotypes is a series of experimental problems, and a systematic treatment of ecotypes is not yet possible. For no stand of vegetation have the racial divergences of its taxa been explored. The methods developed here can suggest that such ecotypic variations do occur within a species. At any rate, the range of tolerance of that abstract working hypothesis

termed a species is taken to be the range of all its ecotypes, if any.

How are individual species with their individual ranges of tolerance, modified by competition with other plants, arranged into vegetation? Gleason (1926, 1939) in introducing his "individualistic" concept of the plant association recognized that two identical environments in regard to physiography and climate might be occupied by entirely different species. That is, the flora available to a site is an independent factor in determining what vegetation will grow there (Jenny 1941, 1958; Crocker 1952; Major 1951). Additionally, Gleason said that vegetation units were not discrete because each species reacts somewhat differently to the environment, and the interrelationships between species generally do not have the obligate character required for an organized unit. This certainly does not mean that vegetation is independent of its environment, but it emphasizes the fortuity involved in determining just which species occupy an area and the possibility of one species replacing another. As Ponyatovskaya (1961) has shown, this idea of individualistic behavior of species in vegetation has arisen independently many times in many different lands. It has been described as a stage in the ontogeny of plant ecologists and sociologists (Major in Ponyatovskaya 1961:375).

There is no absolute conflict in the two views that vegetation can be studied as units or as continua. Braun-Blanquet, whose name is linked to a successful effort to describe vegetation as units, succinctly defended the individualistic approach to vegetation (1928:271, 1932:315-6, 1951:451, cf. Major in Ponyatovskaya 1961:375). He even earlier endorsed the same view (1919:507), agreeing with Pavillard's textbook of almost two decades earlier.

Ellenberg (1956:36, cf. Major 1958:356) pointed out that similar kinds of vegetation do re-occur repeatedly in widely separated sites where ecological conditions repeat themselves and that the repetitions are amazingly similar, but also that there is always variation between stands. Naturally, abrupt vegetation boundaries will occur where there are abrupt changes along an environmental gradient.

An ideal approach to the study of vegetation should be able to distinguish whether the vegetation forms discrete units or a continuum even if sampling procedures differ, e.g., restricted to homogeneous areas or at random. It may be of course that no real question is posed here. Discreteness and continuity may simply and irrevocably be functions of sampling procedures.

Billings (1952) and many others have recognized that different physiographic combinations can produce equivalent environments. For example, a steep south-facing slope may support vegetation similar to that found on more level topography at a more southern latitude; seepage water or a high water table may offset the low nutrient status and moisture holding capacity of a shallow or coarse-textured soil. The usual multiple regression analysis is unable to account for such physiographic compensation and for this reason, as well as others, is unsatisfactory for studying the relationships between plants and their environment.

Cain (1944) states that since physiological processes are multi-conditioned one cannot speak of a single condition of a factor as being the cause of an observed effect in an organism. Examples of multi-conditioned responses are provided by Went (1957) who found that the optimal temperature for the growth of tomato was strongly dependent upon the light intensity and nutrient supply.

While the effects of a factor may be studied in the laboratory, its significance must finally be evaluated in the field. An ecological approach is desired, therefore, that allows all factors to vary, yet permits study of the influence of one factor upon the vegetation. In most cases the relationship will be expressed as a correlation. The idea of causation offers no advantages. Because of the interrelationship between environmental factors a multi-dimensional form of presentation is necessary.

As an operational framework for this study, measurement, and interpretation of the environment as it affects plant growth and distribution the scheme suggested by Walter (1960:13) is used. The following factors are distinguished: 1) Moisture (atmospheric and available in the soil), 2) Chemical (atmospheric and soil), 3) Light, 4) Heat (measured by temperature), and 5) Mechanical.

The environmental factors ordinarily discussed, such as the independent ones: climate, soil parent material, relief, biota (including the flora), fire, and time (plant succession) (Major 1951), are called by Walter secondary factors. This is a reversal of Fries' nomenclature (1925). The independent factors can be analyzed in terms of Walter's five directly acting or effective factors, although their independent nature is thereby lost. Others have also recognized this division into independent (exogenous, allogenic) and dependent (endogenous, autogenic) ecological factors (Major 1961:169).

Combinations of factors and mixtures of independent and dependent factors such as those related to elevation or physiographic gradients, soils, or non-eclectic vegetation change with time may represent such mixtures of effective factors as to be of little heuristic value.

It would be advantageous that measurements of the effective factors be applicable to both field and controlled environment experiments. Biotic interrelationships are very difficult to study in the laboratory and may be better investigated by carefully designed field experiments. Pathogens for example are not included in usual laboratory experiments designed to elucidate environmental tolerance ranges of plants. However, the influence of pathogens may be already expressed in the distribution of plants

in nature. The pathogens themselves may be studied in relation to environmental gradients.

APPROACHES TO THE STUDY OF ECOSYSTEMS

Numerous investigators have emphasized the importance of considering as one unit the biotic community and its abiotic environment. This unit was called the "ecosystem" by Tansley (1935), but was first named the "biocenose" by Mobius in 1877 (Bakuzis 1959). Evans (1956) very logically proposed that the ecosystem is the basic ecological unit. The origin of such synonyms as cene, microcosm, biogeocenose, nature complex, and biochore is discussed by Bakuzis (1959) as is the significance of various approaches to the classification of ecosystems. Other terms for the ecosystem or biogeocenose are discussed by Major (1951:394, 1958:352, 1961b). The boundaries of an ecosystem are arbitrary, depending upon the purpose of a study.

Matter-energy exchange was suggested as an approach to the study of ecosystems by Lindeman (1942). He termed this approach the "trophic-dynamic" viewpoint and emphasized the importance of energy transport from one part of the lake ecosystem to another and of the energy relationships within the community unit as they affect the process of succession. Closely related to this approach are those involving food chains in animals or mineral cycles in plants.

Comparison of ecosystems may be made on the basis of total energy or matter accumulation or on the rate of change from one state to another within a given space-time unit. Energy and matter accumulation may be expressed in heat, weight, or volume units. Such an approach has merit, but it should be recognized that ecosystems which are quite different qualitatively can have energy and matter accumulations which are quite similar quantitatively. For example, hot desert and tundra ecosystems both represent systems with low energy or organic matter accumulation but for significantly different reasons. The composition, structure, physiology, ecology, genesis, history, distribution, and classification of desert and tundra ecosystems are absolutely different under most standards of measurement other than the drastically simplified ones of productivity (grams dry weight) or energy exchange (calories).

Ecologists often use plant species, or better ecotypes, as Braun-Blanquet suggests (1928:18, 1932:21, 1951:17), as indicators of ecological conditions. Communities of several species are still better indicators. This is so partly because a plant's environmental distribution is modified and often narrowed, by competition or interaction with other plants to a zone well inside its physiological tolerance. Ecological tolerances resulting from competition are thus more precise indicators than physiological tolerances determined from plants growing alone. Ellenberg's (1953) definition and separation of these

two kinds of operationally determinable tolerances is a major step in our understanding of why plants grow where they do. The subject has been treated further by Ellenberg (1956), Knapp (1954), and Walter (1960:16-26) (cf. Major 1958:357,359; in Ponyatovskaya 1961:376).

Theoretical considerations have suggested an approach using effective ecological factors as mentioned above. Different plant species can be expected to show a distribution along the environmental gradients of these factors. The species themselves, then, can predict a position on the gradients, and in particular a community of species can be expected to predict with some precision a particular point of ecologically overlapping tolerances on the gradient.

Once plant species occurrence can be used to predict values of environmental gradients in ecosystems, a new measure of objectivity is introduced into site classification. Botanists can agree on what plants are found in a given stand of vegetation; they usually cannot agree on how to measure any of the environmental variables or at least on what the measurements mean. We do believe that the specific measurements of moisture, soil nutrients, light, and temperature developed in this paper have certain advantages of logic and reproducibility. They may work less well in ecosystems of quite another kind—in a non-Mediterranean climate for example. The use of species calibrated to the factor measurements, however, will immensely speed up the definition of ecosystems properties or at least the classification of sites into similar groups, making possible quantitative comparisons between groups.

Approaches to ecosystems involving habitat measurements or classification by means of or combined with plant indicators have been widely used in studying ecosystems. For example, G. A. Hills has developed an adequately detailed scheme for classifying forest ecosystems in Ontario, Canada (Hills 1959, Hills & Pierpoint 1960). Physiographic features were selected as the basis for the approach, assuming these to be more stable than other characteristics of the ecosystem. Twelve regions were described within which like vegetation could be assumed to respond similarly on equivalent sites.

In each region a "normal physiographic site type" was defined. Usually this was the most common upland situation where neither an excess nor a deficiency in available moisture existed. This "zonal" idea has long been used in Russian soil and vegetation classification (Alechin 1932:363-5) and has recently been advocated for vegetation by Daubenmire (1954:34) and Walter (1954). In Hills' scheme the topographic position, the physical nature of the parent material, soil depth, position of the water table, and soil profile features were considered in determining relative position along three major gradients: moisture, pore pattern (related to drainage), and ecoclimate (local climate influenced by relief). Diagrams illustrating the possible combinations of

soil texture, drainage, and relief yielding equivalent sites were given. Finally, the stable and successional vegetation types were presented for each region within the physiographically defined system.

In California no such system has been devised. The Storie Index (Storie 1959) has been used to classify land on the basis of agricultural productivity. The index is derived from subjective ratings of the importance of: 1) character of the physical profile, 2) surface soil texture, 3) slope, and 4) other features including drainage, soil reaction, erosion, and micro-relief. As one might expect nearly all forest lands are grouped in one class, namely nonagricultural.

A soil-vegetation classification based on soil series-depth class units (Zinke 1960a), has been applied over much of the forested area in California. To each of these units a site index value for the coniferous tree species dominating in the area is usually assigned. For a preliminary approach such a survey has great merit, but much research remains to be done in interpreting the significance of the soil series in relation to one another and to the vegetation. Any classification that is tied to productivity alone is usually too broad for much practical use in land management because dissimilar environments may have similar productivities (e.g., a very dry and a very wet site). Often other features are more important, such as shrub density and ease of natural regeneration in forestry or forage quality and palatability in range management.

In Denmark, Warming (1909) distinguished 10 qualitative units along a moisture gradient in his description of water in the soil as an ecological factor. He cited J. P. Norlin, a Finn, as suggesting the idea of separating vegetation into units in relation to a moisture gradient. Warming also presented a quantified gradient related to depth to the water table on sandy plains in Denmark. More recently Tüxen (1954) used plant sociological units and floristic variations within these units to quantify water table changes in Germany.

Sukachev (1928) used moisture and nutrient gradients to illustrate the genetical interrelationships between spruce communities in European Russia. Wiedemann (1929) studied spruce yield and natural regeneration problems in relation to moisture-nutrient coordinates. The four steps along his moisture gradient and six steps along the nutrient gradient were recognized by the occurrence of various herbaceous and shrub species.

Pogrebnjak (1929, 1955) was one of a number of Russians who used moisture-nutrient coordinates for the study of forest vegetation. He presented the distribution of a number of species within a coordinate system and termed the resulting patterns "ecological figures." The Russians have also used coordinates of heat and light according to Bakuzis (1959). A forest classification by Zlatnik (1961) employed the response of species to these and other gradients to define both environments and the ecological relation-

ships of forest communities to each other and to these environments.

Ramensky (1930) in a theoretical paper suggested that all vegetation be studied along various environmental gradients in a coordinate system that would not break up the natural community, be applicable to continuous phenomena of nature as well as the discontinuous, be objective, and permit all data to be represented without losing their individuality. He termed his approach "series coordination."

In a recent practical application of these ideas Ramensky and his colleagues (1956) provided scales representing the ecological adaptations of some 1400 species occurring mainly on Russian river floodplains to environmental gradients characterizing such ecosystems. Species positions on the scales were derived from their modal occurrences in some 20,000 stand surveys. The gradients employed were for soil moisture, soil nutrients, variability of soil moisture throughout the year, grazing use, and alluviation. Scale values were not instrumentally determined and were recognized mostly by plant community criteria. Diagrams in Ramensky et al.'s introduction illustrate the occurrence of species related to combinations of two gradients.

Ellenberg (1950a, 1950b, 1952, 1956) observed that, although no plant species completely coincide in their ecological behavior, some grouping of species according to their relations to the most important site factors was possible. He expanded upon this premise by assigning species to various "ecological groups" based on their behavior characteristics in relation to moisture, nitrogen, light, temperature, soil reaction, soil tilth, and other physical characteristics. Usually species were placed in one of five groups related to the increasing intensity of a factor as follows:

Group	General Characteristics
1	Species which dominate and occur almost exclusively under the most nearly limiting conditions of the factor.
2	Species of similar occurrence but with wider amplitude than those of Group 1.
3	Species which are especially frequent near the mid-point along the factor gradient.
4	Species which dominate on the gradient where the factor being considered is in plentiful supply.
5	Species which occur almost exclusively at the highest values of the factor being considered.
0	Species which are indifferent to the factor and have a very wide amplitude.

Ellenberg (1956) emphasized that the behavior of a species may differ in a meadow, agricultural field, and forest because competition differs. Ecological groups, therefore, should not be used indiscriminately in quite different vegetation types or over wide geographical areas where the floristic composition

(and possibly the genetic composition too) changes drastically. He utilized his ecological groups in southern Germany for evaluating the relative position of agricultural fields (using weed species, 1950b) and meadows and pastures (1952) along various environmental gradients based on the total species composition excluding the indifferent species.

Ellenberg derived an integrated community measurement for each of the evaluated factors by merely tallying the number of species in each ecological group, multiplying by the group number (1-5), totaling, and dividing by the number of species entering into the calculations. This community number was then used to relate the environment in one location to that in another. For various combinations of community numbers he made suggestions relative to crop production and pasture management.

For evaluating the moisture regime Ellenberg used the depth to water table, infiltration rate, or morphological features of the soil profile depending upon the study and local conditions. In his study of agricultural fields, species were assigned to temperature groups by comparing their geographic distributions with the limits of various agricultural crops (grains and grapes) and tree species (oak and maple).

Curtis and his associates have used a number of different indexes based on characteristics of the vegetation itself to arrange plant communities objectively in relation to one another (Curtis & McIntosh 1951, Bray & Curtis 1957, Curtis 1959, Maycock & Curtis 1960). Ecological considerations have been secondary.

Among the most useful of these indexes was Sørensen's (1948) index of similarity with the following formula: Index of Similarly = 2W/(a + b) X 100. The index is a measure of the degree to which two stands resemble each other. The numerator is twice the sum of the measurements which are common in the two stands (2W), and the denominator is the sum of the total measurements in both stands (a plus b). The index was intended for floristic comparisons. Ecological interpretations follow immediately, but there are difficulties in using Sørensen's index for the study of environmental relationships since similar environments need not have identical species composition. Disregard for the replaceability of one species by another is a major theoretical deficiency.

In practice the Wisconsin workers placed the two stands least similar to each other at opposite ends of a linear axis with all other stands arranged between them on the basis of their average relationship to the two terminal stands. Because many of the stands in the center of this first axis showed low indexes of similarity with each other, a second axis was established using the least closely related stands near the center of the first axis for terminal points. Each stand received two values, one indicating its position on the first axis and the other related to its position on the second axis. Still some of the centrally located stands were dissimilar, with low indexes, so repetition of the process produced a third axis, providing coordinate values for a three-dimensional placement of stands.

What the three axes relate to is difficult to interpret ecologically although Curtis felt (1959) that temperature, moisture, and light gradients were suggested. In the work of Maycock & Curtis (1960) the primary axis appeared to represent a moisture gradient, the secondary axis temperature (represented by pure hardwood stands at one end and pure conifers at the other), and the tertiary axis somehow related to nutrients although the concentration of different nutrients increased and decreased in both directions.

Dahl (1956) calculated Sørensen's indexes of similarity for his Norwegian plant communities. He noted that the groupings of stands arrived at in this way substantiated those already made on the basis of characteristic and differential species. His ecological interpretations were based on phytosociological studies rather than on calculated floristic similarities between stands.

Matuszkiewicz and his colleagues (1955, 1957) also arrange vegetation stands by indices of similarity. Ecological interpretations were based on blocks of characteristic and differential species. Continuity in the vegetation was illustrated by blocks of indicator species cutting across several types of plant communities. A "dendrite" diagram was used to give a multidimensional ordination having both floristic and ecological significance. Similarly in Braun-Blanquet's work can be found ecological gradients expressed by particular arrangements of stand surveys. Examples are mentioned by Major in Ponyatovskaya's paper (1961:381).

Rowe (1956) derived a Vegetation Moisture Index and found it was related very closely to the physiographically defined moisture regime classes developed by Hills. His procedure was similar to Ellenberg's, but differed by the assignment of geometrically increasing weights (1,2,4,8,16) to the 5 moisture groups. In each stand all species, except ubiquists, in each of the 5 groups were summed, and the totals weighted by multiplying by the appropriate number. The figures from all groups were then summed and the total divided by the number of species entering into the calculations. The quotient was multiplied by 10 to eliminate the decimal.

Maycock & Curtis (1960) also used Ellenberg's approach in deriving a five step moisture gradient which was compared with the arrangement of stands determined by the index of similarity method. Whittaker (1960) tested three methods for aligning the vegetation along a "complex moisture gradient" in the Siskiyou Mountains of Oregon and California and found the method based on ecological groups gave better results than those founded on topographic relationships or similarity indexes between character-

istics of the vegetation. Even better results were recorded using the ecological group approach in a study of the Great Smoky Mountain vegetation (Whittaker 1956). Whittaker applied the term "gradient analysis" to the general approach to study of landscape patterns, species populations, and other relations of ecosystems through ecological gradients and multidimensional coordinate systems (Whittaker 1956).

Bakuzis (1959) assigned species to five groups along gradients of moisture, nutrients, light and heat using information from the literature. The literature-derived values were later adjusted to local conditions based on data from 365 stands. Bakuzis investigated not only relatively undisturbed sites but also disturbed situations. In addition, his approach differed from all others mentioned for he did not exclude indifferent species from the calculations; he assumed them to be unresponsive and therefore not to affect average values based on the total species composition of each stand.

With the aid of the vegetation-derived heat gradient and species geographic distribution patterns he divided Minnesota into 10 forest geographical sections. Within each of these sections it was predicted that similar vegetation on equivalent sites would respond uniformly to forest management. The forest site complex, i.e. patterns of available environments within the coordinate systems, differed significantly in each section. Bakuzis chose to call his coordinates "synecological" in order to emphasize the influence of associated vegetation as opposed to relations where species are grown alone.

In a detailed investigation of one of the sections, Bakuzis (1961) presents correlations between the vegetation-derived moisture and nutrient coordinates and actual physical and chemical analyses of the soils. The relationships are by no means simple, and many physiographic combinations appear to yield equivalent sites. Many practical problems relating to natural regeneration, brush invasion, and the potential hazard from white pine blister rust were also analyzed within the framework of the four coordinates (Bakuzis 1959).

Loucks (1962) interpreted the forest vegetation in the Green River Watershed of New Brunswick employing the index of similarity as used by Curtis (1959). He then compared these results with those derived independently through the use of three-dimensional models based on numerical environmental gradients ("scalars") modified from those described by Hills (1959). The correspondence between the two procedures was then used "to assess the predictive value of community ordination for expressing the environment" and conversely "to assess the usefulness of physiographic descriptions for predicting the nature of the forest ecosystem."

The stable features of the environment were considered by Loucks in three groups relating to moisture, nutrient supply, and local climate. Nomo-

grams were constructed for each of these based on a combination of environmental factors. Some of these factors were approached through theoretical means or by using data gathered elsewhere, but as Loucks points out this may be more a strength than a weakness. The presence of a biologically meaningful gradient in species composition substantiated the value of each of his gradients. The procedure allows for compensating physiography and will probably see much use in non-mountainous areas where abrupt changes in parent material and macroclimate do not occur.

To summarize, a gradient analysis approach using ecological groups satisfies theoretical requirements. Such an approach allows for multi-conditioned responses, physiographically equivalent combinations, discrete vegetation units or a vegetational continuum, and the replaceability of one species by another. In addition it permits the use of effective factors for the various gradients, at least so far as present knowledge and instrumentation allow.

The following sections deal with moisture, nutrients, light, and temperature gradients and their interrelationships. In each of these an attempt was made to approach as nearly as possible to the effective factor.

THE STUDY AREA

The major study was in the vicinity of Humboldt Redwoods State Park on the Eel River a few miles inland on the north coast of California near Weott (40° 19′ N. Lat., 123° 55′ W. Long.). Reconnaissance of vegetation extended to the extremes of the natural distribution of redwood, to Brookings, Oregon on the north and to an unnamed canyon on the coast of Monterey County (35° 49′ N. Lat., 121° 23′ W. Long.) on the south.

The Eel River, which empties into the Pacific Ocean just south of Eureka, exerts a considerable influence upon much of the park vegetation through periodic flooding. Also, the entire river valley acts as a pathway for the inland movement of fog from the Pacific, more than 20 mi to the west. From the vantage of a coast range peak, fog can be seen nearly every evening during the summer moving majestically into the valley from the northwest. The importance of this fog cannot be overemphasized. Correlated very closely with its distribution is that of the coast redwood. To the west of the park, nearer the ocean but outside the Eel River drainage, or above 2,500 ft where little summer fog is observed, few redwood occur. Those that do are restricted to sheltered coves or canyons.

Because of these geographic differences three physiographic areas have been recognized in the study. These are labeled on the map (Fig. 1) as Grasshopper Peak, Salmon Creek, and the Eel River Valley. The Grasshopper Peak area lies above 2,500 ft (765 m) in an exposed, relatively fog-free position. Snow is not uncommon in the winter and as much as two fresh feet covered the ground and
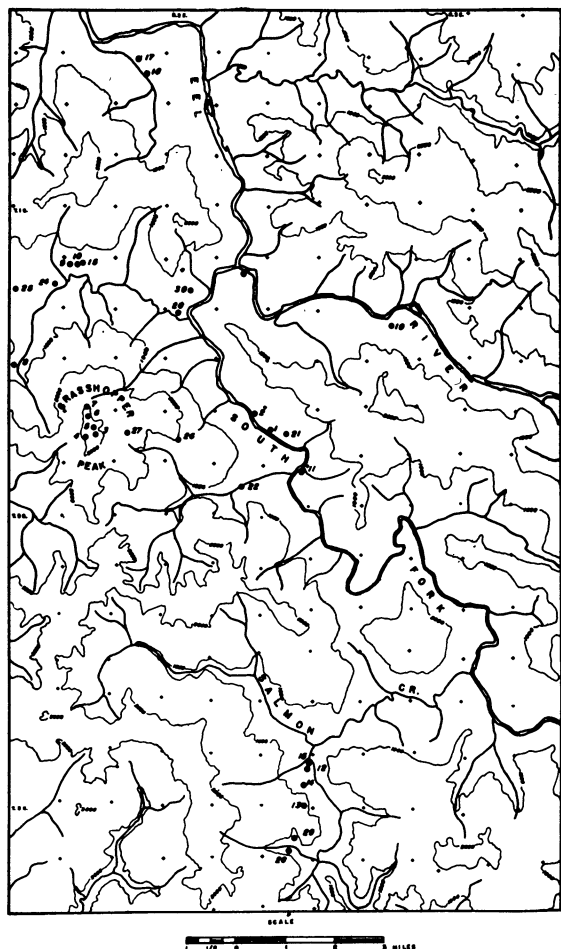
FIG. 1. Distribution of stands within the study area. Grasshopper Peak, the Eel River Valley, and the Salmon Creek drainage represent different physiographic subunits.

added an exotic touch to soil sampling on 22 April 1961. To the south of the park, also outside the influence of the summer fog belt, lies the Salmon Creek area. Although the study there was confined to locations of less than 1,300 ft (400 m) elevation, the climate in general closely resembles that of the Grasshopper Peak area. The Eel River Valley represents the maritime climate most prevalent in the redwood region with moderate temperatures and considerable fog. At Scotia, the nearest meteorological station, less than 1 in. of snow is recorded as an annual average. Rain is very infrequent during the summer, a rather unique feature in a heavily forested region. The annual precipitation, however, ranges from about 30 in. (760 mm) in the park to over 100 in. (2540 mm) in some parts of the region. Data from weather stations, nearly all of which are located in valleys, cannot be used to represent the areas at higher elevations and (or) more exposed situations.

The topography is strongly dissected with some slopes greater than 45°. Elevations range from about 120 ft (37 m) along the Eel River to about 3,500 ft (1070 m). The major streams are swollen tremendously during periods of torrential rains but are reduced to a series of barely-connected pools with sometimes hundreds of feet of exposed river bottom by the end of the summer. Still, nearly all the streams in the area, as well most of the creeks, flow continuously throughout the year, and this is a rarity in California.

The geology of the North Coast Ranges has recently been discussed in detail by Irwin (1960). The principal rocks range from late Jurassic to Cretaceous in age. The absence of granitic intrusions in the North Coast Ranges distinguishes this area geologically from the Klmath Mountain region. The area has been subdivided into three main lithic belts that trend to the northwest: a central belt of sedimentary rocks of the Franciscan Formation, and eastern belt of weakly metamorphosed rocks of the Franciscan Formation, and a western and coastal belt of undivided sedimentary rocks. The Franciscan Formation differs from the coastal series, and also from the Sacramento Valley sequence, by the almost complete absence of potassium feldspar in the dominant rock, graywacke. As shown in Fig. 2, the study area lies in the coastal belt of sedimentary rocks. The central Franciscan Formation lies to the east, with just a few areas of metamorphosed Franciscan material appearing on the map. In all formations ultramafic intrusions are not uncommon. A geologic summary is presented in Table 1.

SAMPLING

An attempt was made to sample not only a wide range of vegetation types in the vicinity of the park, but also the range of ecological conditions over which each vegetation type occurred. Only relatively stable types were investigated (those with no history of fire or logging for at least 40 yrs), under the premise that an understanding of these would provide a foundation for future study of successional types.

During the first two summers of this study more than 60 reconnaissance plots were established throughout the range of redwood. From these and additional areas chosen from Soil-Vegetation survey maps, 30 stands which represented the following 10 cover types were selected:

Cottonwood—Maple—Bay (*Populus trichocarpa-Acer macrophyllum-Umbellularia californica*)
Alder (*Alnus oregona*)
Redwood Flat Ia (*Sequoia sempervirens*)
Redwood—Douglas-fir II
Redwood—Douglas-fir III
Douglas-fir IV (*Pseudotsuga menziesii*)
Deciduous Oak (*Quercus kelloggii-Q. garryana*)
Incense-cedar—Jeffrey pine (*Libocedrus (Calocedrus) decurrens-Pinus jeffreyi*)
Grassland
Chaparral

TABLE 1. Stratigraphic summary of the geologic formations in the study area (after Irwin 1960).

Classification	Periods	Description
Surficial deposits	Pleistocene and Recent	Marine and river terrace gravel and silt, landslide debris, beach and dune sands
Coastal belt	Eocene to Early Pleistocene—chiefly Pliocene	Undifferentiated marine sedimentary rocks
Coastal belt	Upper Cretaceous	Sandstone, shale, and conglomerate
Coastal belt	Upper Jurassic and Cretaceous	Sandstone, shale, and conglomerate
Franciscan Formation	Upper Jurassic and Cretaceous	Sandstone, shale, conglomerate, greenstone, chert, and minor limestone
Metamorphosed Franciscan Formation	Upper Jurassic and Cretaceous	Metamorphosed lithologic equivalents of rocks of the Franciscan Formation
Ultramafic rocks	Jurassic	Peridotite and serpentine

Stands were selected to be ecologically homogeneous and of adequate size. Location of the 30 stands is shown in Figure 1. More information on them is in Tables 2 and 20 (site indices indicated by Roman numerals).

Grassland vegetation was studied on three different soil series; the redwood—Douglas-fir III stands occurred at different elevations and aspects; chaparral was sampled on both shallow and deep soils; incense-cedar stands were located on a ridge top as well as in an area of permanent seepage from a spring. The other types were selected on a similar basis to reflect the full range of conditions found in the vicinity of the park. Such sampling does not allow indiscriminate grouping and averaging of data. It is advantageous because a more realistic picture of the environment and the vegetation results.

Stands were investigated as follows: at a random distance from the edge of each stand (1-3 chains) a 100-ft square was laid off. Within this area a series of 10 sample plots were located, with coordinates selected from a table of random numbers. At each of the 10 points a circular 2m^2 plot was established and the non-arboreous vegetation recorded. At the 3rd, 6th, and 9th points, basal area determinations were made on the coniferous species with a slope-correcting Spiegel Relaskop. Circular plots of 200 m^2 size were laid out for the determination of hardwood basal area. Ocular estimates were made of crown closure, the coverage of shrubs, herbs, bryophytes, litter, and slash. Heights of three dominant trees were taken by means of an Abney level and range finder on those areas supporting forests.

Near one of the three basal area sampling points a soil pit was dug under the canopy of the dominant plant (redwood, Douglas-fir, grass, etc.). Depth of sampling extended to 1 m, where bedrock permitted. This choice is wholly arbitrary, and results should be interpreted in this light. On the upland soils this
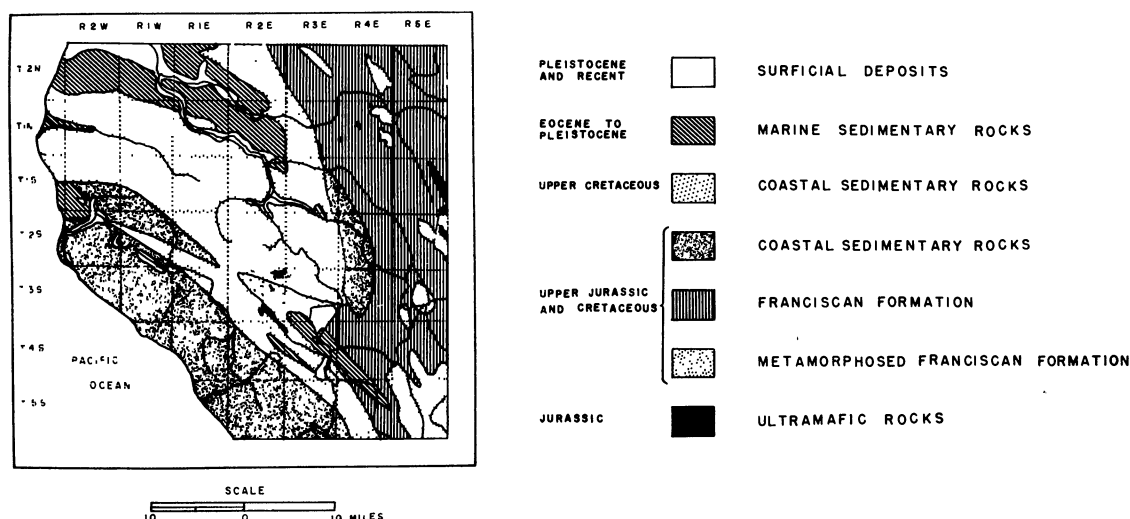
FIG. 2. Geology of the North Coast Ranges in the vicinity of the study area. Field headquarters were located at the Burlington Camp ground in T2SR2E.

TABLE 2. Stand characteristics and locations. Roman numerals refer to site productivity classes; see Table 17.

Vegetation type	Stand No.	Elev. feet	Slope %	Aspect	Topographic Position	Basal area sq. ft./ acre	Volume/ acre cu. ft.	Location
Incense-cedar Jeffrey pine	14	850	70	E.	Crest	170	7,400	SE 1/4, S13, T3S, R2E
Incense-cedar	29	900	20	E., S.E.	Mid-Slope	93	5,500	S24, T2S, R2E
Incense-cedar Douglas-fir IV	13	1,200	55	N.	Lower Slope	110	5,000	SE 1/4, S13, T3S, R2E
Chaparral	4	3,300	35	W., S.W.	Crest	—	—	Center, S8, T2S, R2E
Chaparral	6	3,100	35	W.	Upper Slope	—	—	N.W. 1/4, S8, T2S, R2E
Chaparral Douglas-fir V	5	3,370	1	—	Top	—	—	Center, S8, T2S, R2E
Grassland	3	3,380	35	E.	Top	—	—	Center, S8, T2S, R2E
Grassland	12	550	30	N.E.	Mid-Slope	—	—	NE 1/4, S13, T3S, R2E
Grassland	9	500	35	S.	Lower Slope	—	—	NW 1/4, S29, T1S, R2E
Deciduous Oak Douglas-fir IV	10	500	35	S.	Lower Slope	228	9,700	NW 1/4, S29, T1S, R2E
Deciduous Oak Douglas-fir IV	15	800	30	N.W.	Mid-Slope	170	1,600	NW 1/4, S13, T3S, R2E
Deciduous Oak Douglas-fir III	28	950	50	S.W.	Mid-Slope	342	14,000	S24, T2S, R2E
Madrone Tanoak Douglas-fir IV	27	2,600	65	S.E.	Upper Slope	190	2,600	NW 1/4, S9, T2S, R2E
Douglas-fir IV	7	3,000	1	—	Upper Slope	196	6,500	SW 1/4, S5, T2S, R2E
Redwood IV Douglas-fir IV	30	600	65	S., S.E.	Upper Slope	214	6,800	SE 1/4, S27, T1S, R2E
Redwood III Douglas-fir III	8	750	58	E., S.E.	Mid-Slope	290	17,000	NW 1/4, S6, T2S, R2E
Redwood III Douglas-fir III	25	400	35	N., N.E.	Mid-Slope	318	16,300	SW 1/4, S30, T1S, R2E
Redwood III Douglas-fir III	26	2,000	15	N.	Upper Slope	366	19,800	SW 1/4, S10, T2S, R2E
Redwood II Douglas-fir III	16	500	38	S., S.E.	Lower Slope	376	25,800	NW 1/4, S29, T1S, R2E
Redwood I Douglas-fir II	19	375	65	N., N.E.	Lower Slope	350	29,000	Sec. 32, T1S, R3E
Redwood I Douglas-fir II	21	300	20	S.W.	Lower Slope	370	26,600	NW 1/4, S12, T2S, R2E
Redwood Ia	1	175	1	—	Valley Bottom	460	35,000	NW 1/4, S12, T2S, R2E
Redwood Ia	20	155	1	—	Valley Bottom	825	76,000	NW 1/4, S34, T1S, R2E
Redwood Ia	24	260	1	—	Valley Bottom	855	80,000	SE 1/4, S30, T1S, R2E
Bay Maple Redwood III	23	170	1	—	Valley Bottom	278	9,500	NW 1/4, S26, T1S, R2E
Alder	17	130	1	—	Valley Bottom	134	2,300	NW 1/4, S4, T1S, R2E
Alder	18	135	1	—	Valley Bottom	159	3,000	Center, S4, T1S, R2E
Alder Maple	22	550	12	N.E.	Outcrop in Stream channel	96	2,300	SW 1/4, S14, T2S, R2E
Maple Cottonwood	11	160	1	—	Valley Bottom	86	1,600	NE 1/4, S13, T2S, R2E
Cottonwood Ash	2	150	1	—	Valley Bottom	23	1,000	NW 1/4, S11, T2S, R2E

sampling depth appears to encompass about 90% or more of the total volume of roots. On alluvial soils influenced by flooding or a high water table an arbitrary depth of measurement yields data of questionable value.

The flora was intensively collected during three summers, and determinations were checked in the University of California herbarium at Berkeley. As a result it was possible to identify plants in the field in vegetative as well as flowering condition. Voucher specimens are in the herbarium prepared for the park. The floristic checklist as of March, 1963 con-

tained 557 species of vascular plants found within the boundaries of the park.

THE MOISTURE GRADIENT

A single environmental characteristic that could fully define the plant's moisture regime under all possible situations is not available. Numerous authors have selected variables such as the depth and stability of the water table, soil morphology, and topographic position to classify sites in relation to a moisture gradient (Hills 1959, Whittaker 1960, Loucks 1962).

Fraser (1957) followed the variation in available moisture under Ontario hardwoods which had been grouped into six moisture regime types upon the basis of Hills' methodology. On three of the types a separation was possible based on the storage capacity of the soil to a depth of 9 ft, where bedrock permitted. On the more hydromorphic sites the fluctuation and depth of the water table became important. Wilde & Leaf (1955) also stressed the importance of the water table in influencing plant distribution on some sites in Wisconsin.

A number of European workers have recently approached the study of the moisture regime under different vegetation types in quantitative terms. In Czechoslovakia, Pelisek (1958) followed the moisture content throughout the year under 8 vegetation types. Allowances were made for differences in soil texture and the duration of surface flooding. Graphic and tabular descriptions summarized the moisture regime relationships for each type. During a dry year in Germany, Glatzel (1960) traced at two week intervals the available moisture depletion under 12 stands representing 4 hardwood types. His data showed that whereas all available moisture had been removed under a *Quercus-Carpinus* type by September, the other types still had from 2.5 to 7 cm of available moisture in the surface meter.

The work most pertinent to this study was that done by McMinn (1960) on western redcedar and Douglas-fir types on Vancouver Island, British Columbia. The distributions of a large number of species common to the redwood region are presented in tables characterizing the various forest types aligned along his moisture gradient.

A PHYSIOLOGICAL MEASURE OF SOIL MOISTURE

Total Soil Moisture Stress (TSMS) has been demonstrated by Richards & Wadleigh (1952) to be physiologically significant to plant growth. The TSMS is the arithmetic sum of two factors: the osmotic pressure of the soil solution and the soil-moisture tension. Richards & Wadleigh varied the osmotic pressure and soil-moisture tension in carefully controlled laboratory experiments, showing that fresh weight yields of plants decreased progressively as soil-moisture stress increased up to about 15 atmospheres (wilting point for many plants).

Others believe that moisture is equally available throughout the range from field capacity to permanent wilting point (Veihmeyer 1956, Henderickson & Veihmeyer 1950). This controversy may result partly from a choice of different units of measure and partly from the difficulty of comparing field experiments with laboratory studies. Investigations on fine and coarse-textured soils may give different results as to the availability of water, for the moisture-tension curves on these soils differ appreciably. On coarse-textured soils most of the range of readily available water lies in the flat portion of the hyperbolic moisture-tension curve. Most of the readily available water is removed from coarse-textured soils before the tension of the remainder exceeds 1 atmosphere, and only a small fraction is held with sufficient force to hinder absorption. On the fine-textured soils 50% or more of the available water may be held with tensions in excess of 1 atmosphere. In such soils water becomes less available long before the moisture content approaches the permanent wilting percentage (Kramer 1949).

In non-saline soils, such as occur in the redwood region, the osmotic concentration of the soil solution is very low and may be disregarded. Under these conditions the readily available moisture may be defined as the difference in moisture content between field capacity and the first wilting of sunflower. Richards & Weaver (1943) demonstrated that moisture retained by soil samples placed on a suction plate at a tension of $\frac{1}{3}$ atmosphere agreed with the moisture equivalent (and that with field capacity). They also showed that the 15 atmosphere percentages on the fine fraction, determined by a pressure membrane apparatus, closely matched the first wilting point of sunflower (PWP). The difference between these two physical constants has been called the "Moisture Retention Value" (MRV) to distinguish it from the biological determination of readily available moisture (Gardner 1958:89).

There have been a number of papers published which demonstrate that grasses (Lane & McComb 1948, Ursic 1961), pine (Fowells & Kirk 1945, Stone 1957, Ursic 1961) can reduce the moisture content in soils significantly below the PWP of sunflower. However, the water is held so tightly below the 15 atmosphere point that tensions of over 50 atmospheres normally reduce the moisture content only an additional 1 or 2%. Although this water may be significant to the survival of some plants, our laboratory methods are not refined enough to determine values more accurately than about 1%. Still, this variation in PWP between species presents a strong case for elimination of direct determination of PWP and replacement with physical determinations of TSMS (Slatyer 1957).

CHARACTERISTICS OF SOIL MOISTURE USE AND REPLENISHMENT

Soil-moisture utilization at different rates or amounts by different types of vegetation is important in a gradient analysis. In general, any kind of vegetation completely covering the ground and well-

supplied with water evapotranspires an amount of
water limited only by the radiation energy received
(Tanner 1960, Thornthwaite & Mather 1955:181).
Zahner (1955) found that both hardwoods and coni-
fers removed moisture at similar rates, and con-
cluded that in a given climatic area, evapotranspira-
tion was independent of the type of forest cover.
Metz & Douglas (1959) published similar findings.
Both of these studies were conducted in the south-
eastern United States where precipitation is regu-
larly distributed and conditions for potential evapo-
transpiration usually obtain.

Grasses, however, generally start to deplete mois-
ture early in the season, and in this study did not
utilize sources much below 70 cm depth. Grassland
species are usually dead or dormant in the redwood
region by the middle of July.

Rates of depletion under different kinds of vege-
tation are difficult to compare because variations in
temperature also occur during the growing season.
Changes in temperature affect growth rates directly
as well as reflect variations in radiation energy.
That is, an increased rate of depletion reflects both
an increased transpirational stress and a period
of active growth (as in the grasses).

Liacos (1962), studying depletion rates under
grassland types, concluded that soil-moisture was
utilized by plants at a rate proportional to the amount
of soil water remaining. Liacos' differential equation
integrates to an exponential. Zinke (1959), follow-
ing the depletion of moisture under *Pinus coulteri*
on lysimeters for a 10-yr period, derived a similar
exponential equation to predict the moisture content
in soils at a given date after substantial precipita-
tion. The findings of Liacos and of Zinke had been
predicted by Thornthwaite & Mather (1955:23).
Both Liacos' and Zinke's work was done in California
where summer drought provides a favorable, almost
unique area, for depletion rate studies.

The replenishment of soil-moisture occurs mostly
through saturated flow. This applies to water falling
as precipitation, moving by lateral seepage or rising
by capillarity. The rate of movement of unsaturated
flow or along a vapor pressure gradient is very
slow. Consideration of the principles by which
water moves in soils accounts for the fact that the
horizon beneath the surface few inches of a fallow
field remains near field capacity. Although the sur-
face may be at PWP, the humidity of the soil air
is still 99%. Thus only a slight vapor pressure
gradient will be in operation between the lower, moist
horizons and the drier, surface soil.

FIELD MEASUREMENT OF SOIL MOISTURE

To evaluate soil-moisture in the light of the
previous discussion the following factors were in-
vestigated under the 30 vegetation stands: the storage
capacity of the surface meter, depletion of the avail-
able moisture throughout the growing season, and the
characteristics of the water table if it was within

2 m of the surface. To do this required sampling at
monthly intervals throughout the growing season.

In addition to soil-moisture samples for each of
the 4 depth classes (0-10, 10-30, 30-70, 70-100 cm),
bulk density cores (70 cm³) were collected. Finally,
it was necessary to collect a rock sample, both to
estimate the percentage of rock in the soil and to
deduct the considerable amount of moisture bound
within rocks, unavailable to plants. Coile (1953)
and Reinhart (1961) have mentioned the problem
and suggested procedures to correct for soil stone
contents when measuring soil-moisture.

An auger, shovel, and pulaski were used to obtain
the soil samples which were stored before weighing
in friction-top cans. To hold sampling variation
to a minimum the monthly collections were taken
within a few feet of one another.

The moisture regime, as measured in this study,
represents the net effects of many factors. Because
of the drought conditions that characterize the sum-
mer months in California the procedure is greatly
simplified. On the broadest level (grass vs. forest)
the vegetation must still be considered a variable.
But the effects of aspect, topographic position, fog
drip, wind, evapotranspiration, and subsurface water
supply from seepage or capillary rise are already
accounted for in the experimental design.

LABORATORY ANALYSES AND CALCULATIONS

When the soil-moisture samples were brought into
the laboratory they were weighed, oven-dried (at
105° C for 24 hrs) and reweighed. The stones were
then removed by passing the fine material through
a 2 mm sieve. Stones, after separation, were oven-
dried again and weighed.

The moisture content of rocks in the surface and
subsoil horizons was obtained gravimetrically also.
For soils containing more than 10% rock, some con-
sideration of the moisture held in the rocks must be
made. In this study, moisture contents of the rocks
varied from 3-24%, depending upon the type of rock
and degree of weathering. Disregarding this cor-
rection would have led to errors of up to 300% on
very rocky soils derived from porous sandstone.
Coile (1953) in emphasizing that corrections should
be made for the moisture content of rocks when
doing soil-moisture calculations had recorded mois-
ture contents from 5.0% in acid igneous rocks to
27.0% in slate. He also noted some variation in the
moisture content of similar rock types dependent
upon rock sizes. This is probably a function of
weathering.

Bulk density samples were oven-dried and weighed
to determine dry weight per unit volume. Stones
were then removed by sieving, oven-dried, and
weighed. The weight of stones divided by their spe-
cific gravity (assumed 2.65) gave the volume of stones
in the sample. Following this, the volume and
weight of the soil were computed by subtracting the
volume and weight of the stones from that of the

total sample. The bulk density of the stone-free soil was then computed by dividing weight by volume.

If the percentage of rock in the bulk density sample differed by more than a few percent from the rock content of the general sample collected for nutrient analyses, as it often does in rocky soils where core samples are difficult to take, a correction for this sampling bias was made using the formula given by Crocker & Major (1955:433).

$$B.D. = \frac{F.dr. \, df}{F.dr + R.df}$$

where B.D. = Bulk density of the fine earth fraction (less than 2 mm diam.) corrected for rocks, and expressed in grams per cm^3

F. = Percent fine earth (general sample)

R = Percent rock (greater than 2 mm diam.) in general sample

dr = Specific gravity of rock (assumed 2.65)

$$df = \frac{\text{Weight of fine earth fraction in special core sample}}{\text{Total volume of core — volume of rock in core}}$$

Soil-moisture constants (Table 3) were determined on the fine earth fraction using a $\frac{1}{3}$ atmosphere pressure plate and a 15 atmosphere pressure membrane apparatus (U.S.D.A. 1954).

Knowing the bulk density and Moisture Retention Value (MRV) permits one to calculate the storage capacity. If the field moisture content is determined, then the available moisture percentage may be de-

TABLE 3. Soil analyses.

Depth cm	B.D.[1]	Water Relations				pH	%N	Exchangeable cations (me/100g fine soil)			
		1/3 Atm. %	15 Atm. %	1/3-15 Atm. %	Storage Capacity cm			K+	Ca++	Mg++	C.E.C.
Stand 14. Incense-cedar—Jeffrey Pine on Dubakella Soil Series											
0-10	.59	42.0	24.6	17.4	1.03	6.8	.16	.38	6.1	19.0	22.0
10-30	.35	29.6	21.7	7.9	.55	7.0	.05	.14	1.5	13.4	17.0
30-60	.37	17.0	12.6	4.4	.49	7.1	.02	.08	0.6	7.6	11.8
Stand 29. Incense-cedar on Dubakella Soil Series											
0-10	.62	21.0	11.0	10.0	.62	6.9	.06	.11	3.1	5.8	14.8
10-30	.64	20.3	11.7	8.6	1.10	7.0	.04	.11	2.5	5.6	12.8
30-70	.75	15.4	9.3	6.1	1.83	7.0	.01	.03	0.7	2.3	4.4
Stand 13. Incense-cedar—Douglas-fir IV on Dubakella Soil Series											
0-10	1.10	37.4	21.9	15.5	1.70	6.5	.19	.35	6.3	32.1	35.6
10-30	1.20	37.5	22.2	15.3	3.68	6.5	.14	.25	5.3	33.2	36.8
30-70	1.32	27.1	14.6	12.5	6.60	6.6	.08	.23	6.3	42.1	39.9
70-100	1.34	29.1	15.7	13.4	5.40	6.8	.06	.22	5.8	27.6	30.7
Stand 4. Chaparral on Cahto Soil Series											
0-10	.63	24.4	12.2	12.2	.77	5.4	.11	.87	13.9	6.8	23.8
10-30	.31	22.6	12.5	10.1	.63	5.2	.05	.54	11.7	6.4	21.6
30-40	.12	23.6	13.3	10.3	.12	5.2	.06	.59	13.0	6.9	24.1
Stand 6. Chaparral on Cahto Soil Series											
0-10	.71	28.8	13.2	15.6	1.09	6.1	.24	1.09	17.9	5.7	23.3
10-30	.65	28.9	13.3	15.6	.84	6.0	.19	1.20	14.5	5.4	20.9
30-50	.24	27.4	13.8	13.6	.65	5.7	.16	1.05	15.2	6.3	21.8
Stand 5. Chaparral—Douglas-fir V on Cahto Soil Series											
0-10	.79	26.4	12.9	13.5	1.07	5.2	.53	1.42	6.5	1.5	12.5
10-30	.74	31.0	14.3	16.7	2.47	5.3	.43	1.19	7.4	2.0	13.5
30-70	.72	28.8	13.1	15.7	4.52	5.1	.24	.66	1.4	0.6	7.4
70-100	.92	30.2	11.2	19.0	5.25	5.2	.15	.40	0.9	0.5	7.0
Stand 3. Grassland on Laughlin Soil Series											
0-10	.81	24.4	10.7	13.7	1.11	5.5	.15	.52	7.8	2.9	13.8
10-30	.89	26.0	10.9	15.1	2.69	5.6	.13	.51	7.9	2.9	15.1
30-50	.19	24.5	11.0	13.5	.51	5.7	.13	.50	8.3	2.8	13.0
Stand 12. Grassland on Yorkville Soil Series											
0-10	1.29	27.9	14.3	13.6	1.75	5.7	.13	.55	11.4	16.1	25.8
10-30	1.37	31.2	16.9	14.3	3.93	5.9	.06	.33	12.9	24.4	33.8
30-70	1.21	29.6	15.4	14.2	6.87	6.7	.05	.22	17.7	19.1	34.6
70-100	1.48	28.9	14.8	14.1	6.25	7.8	.04	.18	31.5	18.3	36.3

[1] Bulk density of fine earth fraction (less than 2 mm dia.) in g/cm^3.

TABLE 3 cont.

Depth cm	B.D.[1]	Water Relations				pH	%N	Exchangeable cations (me/100g fine soil)			
		1/3 Atm. %	15 Atm. %	1/3-15 Atm. %	Storage Capacity cm			K+	Ca++	Mg++	C.E.C.
Stand 9. Grassland on McMahon Soil Series											
0-10	.96	28.3	13.2	15.1	1.45	5.3	.12	.62	14.4	5.0	22.0
10-30	.98	26.2	13.8	12.4	2.43	5.4	.17	.69	14.7	4.5	23.0
30-70	.83	23.8	13.5	10.3	3.42	5.9	.10	.47	18.2	5.9	23.0
70-100	.83	20.4	12.0	8.4	2.09	6.4	.07	.33	18.2	5.6	24.1
Stand 10. Deciduous Oak—Douglas-fir IV on McMahon Soil Series											
0-10	.91	31.5	14.6	16.9	1.54	5.4	.21	1.06	14.2	4.7	25.9
10-30	1.12	23.7	14.3	9.4	2.10	5.0	.09	.82	17.5	6.8	24.8
30-70	.91	24.2	14.0	10.2	3.70	4.8	.06	.53	16.3	7.7	25.6
70-100	.86	22.0	13.9	8.1	2.09	4.9	.06	.37	16.9	8.5	26.4
Stand 15. Deciduous Oak—Douglas-fir IV on Hugo Soil Series											
0-10	.77	31.8	13.3	18.5	1.42	5.7	.20	.61	9.3	7.8	19.9
10-30	1.21	26.6	11.0	15.6	3.77	5.5	.11	.42	5.6	8.1	17.0
30-70	1.12	23.4	12.1	11.3	5.10	5.5	.05	.36	4.8	13.8	21.5
70-100	1.20	26.4	14.3	12.1	4.36	5.6	.05	.36	7.4	18.3	28.3
Stand 28. Deciduous Oak—Douglas-fir III on Hugo Soil Series											
0-10	.79	43.0	21.7	21.3	1.68	5.7	.27	1.43	25.5	7.1	36.0
10-30	1.06	35.5	20.1	15.4	3.26	5.2	.14	1.18	18.1	7.8	30.8
30-70	.91	33.4	20.3	13.1	4.76	4.8	.10	.69	16.8	9.3	31.2
70-100	.61	38.4	20.8	17.6	3.22	5.4	.09	.82	19.6	10.6	31.9
Stand 27. Madrone—Tanoak—Douglas—fir IV on Cahto Soil Series											
0-10	.72	46.8	15.5	31.3	2.25	6.2	.33	1.35	14.7	4.7	23.1
10-30	.74	43.9	15.1	28.8	4.26	6.2	.28	1.76	13.0	3.7	20.3
30-70	.88	33.3	11.7	21.6	7.60	6.1	.14	1.20	10.2	2.7	14.7
70-100	.93	28.4	11.3	17.1	4.77	6.0	.08	.82	10.8	3.4	16.4
Stand 7. Douglas-fir IV on Cahto Soil Series											
0-10	.67	46.4	17.1	29.3	1.96	6.1	.44	1.44	8.6	1.7	11.3
10-30	.82	42.7	16.0	26.7	4.38	6.1	.30	1.16	5.7	1.6	11.4
30-70	.85	37.1	14.4	22.7	7.70	5.8	.15	.64	6.2	1.8	12.6
70-100	.96	31.4	14.2	17.2	4.96	5.1	.06	.27	2.2	1.3	15.4
Stand 30. Redwood IV—Douglas-fir IV on Hugo Soil Series											
0-10	.62	26.9	7.9	19.0	1.18	5.0	.08	.40	2.5	1.2	8.5
10-30	.95	27.2	7.3	19.9	3.78	5.5	.05	.40	2.6	1.3	7.2
30-70	.64	19.6	6.5	13.1	3.36	5.5	.04	.40	4.1	1.7	7.7
Stand 8. Redwood III—Douglas-fir III on Hugo Soil Series											
0-10	.64	35.0	15.6	19.4	1.24	5.8	.16	.88	13.7	3.7	23.7
10-30	.74	29.7	13.5	16.2	2.40	5.5	.06	.81	9.1	3.1	16.4
30-70	.83	25.6	14.2	11.4	3.79	5.4	.05	.83	10.0	3.4	17.0
70-100	.61	28.2	16.2	12.0	2.20	5.4	.06	.79	13.1	5.4	19.4
Stand 25. Redwood III—Douglas-fir III on Hugo Soil Series											
0-10	.51	44.0	21.8	22.2	1.13	5.6	.23	.52	26.6	10.3	37.2
10-30	1.03	31.4	19.5	11.9	2.45	5.5	.16	.52	24.4	11.4	33.1
30-70	.80	26.0	16.8	9.2	2.94	5.5	.10	.47	22.4	10.4	29.5
70-100	1.10	24.5	15.6	8.9	2.94	5.4	.08	.44	21.0	10.7	28.5
Stand 26. Redwood III—Douglas-fir III on Hugo Soil Series											
0-10	.84	42.0	23.3	18.7	1.57	5.8	.29	1.39	25.0	6.2	31.7
10-30	1.05	31.8	18.5	13.3	2.80	5.8	.14	1.32	15.5	4.7	26.0
30-70	1.12	28.7	17.0	11.7	5.24	5.5	.11	1.21	15.6	4.8	23.5
70-100	1.18	27.1	15.6	11.5	4.08	5.6	.08	.94	13.7	6.5	23.6
Stand 16. Redwood II—Douglas-fir III on Hugo Soil Series											
0-10	.93	37.9	20.7	17.2	1.60	6.2	.28	1.05	29.7	6.1	33.5
10-30	1.35	26.6	13.6	13.0	3.51	5.6	.10	.72	16.5	4.3	21.4
30-70	1.47	25.4	13.7	11.7	6.80	5.3	.09	.69	14.5	5.5	23.0
70-100	1.16	25.9	14.1	11.8	4.10	5.3	.09	.59	15.4	5.7	25.6

TABLE 3 cont.

Depth cm	B.D.[1]	Water Relations				pH	%N	Exchangeable cations (me/100g fine soil)			
		1/3 Atm. %	15 Atm. %	1/3-15 Atm. %	Storage Capacity cm			K+	Ca++	Mg++	C.E.C.
Stand 19. Redwood I—Douglas-fir II on Larabee Soil Series											
0-10	.67	38.2	23.8	14.4	.98	5.9	.35	1.06	21.2	6.7	29.5
10-30	.55	33.5	22.9	10.6	1.16	6.0	.31	.96	18.9	6.0	30.9
30-70	.56	26.8	18.0	8.8	1.97	5.9	.21	.90	14.1	4.4	24.6
70-100	.61	16.9	9.8	8.1	1.48	5.0	.03	.42	3.7	3.9	14.8
Stand 21. Redwood I—Douglas-fir II on Hugo Soil Series											
0-10	.92	37.9	20.7	17.2	1.60	6.2	.43	1.04	37.2	12.7	53.0
10-30	.93	26.6	13.6	13.0	3.51	5.8	.24	.40	22.7	8.6	31.5
30-70	1.00	25.4	13.7	11.7	6.80	5.8	.13	.50	18.0	8.6	26.8
70-100	1.10	25.9	14.1	11.8	4.10	5.6	.09	.41	19.5	12.4	30.2
Stand 1. Redwood Flat Ia on Alluvium											
0-10	1.00	36.5	13.2	23.3	2.33	5.8	.14	.66	17.1	9.9	26.0
10-30	1.16	29.8	11.6	18.2	4.20	6.0	.11	.44	14.0	8.4	21.4
30-70	1.12	26.0	8.5	17.5	7.84	6.0	.06	.40	9.1	7.0	16.4
70-100	1.11	30.4	9.4	21.0	6.97	6.0	.05	.37	10.6	8.4	15.5
Stand 20. Redwood Flat Ia on Alluvium											
0-10	1.20	40.2	10.8	29.4	3.53	6.2	.09	.41	14.0	6.9	21.7
10-30	.88	37.9	14.3	23.6	4.18	6.0	.16	.39	17.2	7.9	25.9
30-70	1.13	36.2	12.3	23.9	5.10	6.0	.09	.35	12.7	7.7	20.2
70-100	1.20	36.7	11.8	24.9	4.32	6.0	.07	.28	12.7	8.3	20.9
Stand 24. Redwood Flat Ia on Alluvium											
0-10	.95	39.4	19.7	19.7	1.78	5.6	.29	.77	26.9	6.0	38.1
10-30	1.00	39.5	18.5	21.0	4.20	5.8	.22	.69	25.5	4.9	28.9
30-70	1.05	17.8	10.0	7.8	3.27	5.8	.04	.40	10.6	2.8	14.0
70-100	1.18	12.1	5.9	6.2	2.19	5.5	.03	.42	9.8	2.7	12.8
Stand 23. Bay—Maple—Redwood III on Alluvium											
0-10	1.11	21.8	6.8	15.0	1.66	6.3	.10	.29	11.0	3.1	11.7
10-30	1.07	21.6	8.6	13.0	2.78	6.4	.17	.30	10.3	2.7	15.0
30-70	1.24	10.2	4.6	5.6	2.78	6.5	.05	.23	6.3	3.8	9.3
70-100	1.25	9.6	4.4	5.2	1.95	6.6	.05	.21	5.3	3.7	8.8
Stand 17. Alder on Alluvium											
0-10	.95	25.8	13.6	12.2	1.16	5.7	.18	.42	18.7	6.8	23.7
10-30	.96	26.2	13.0	13.2	2.54	5.9	.11	.34	13.9	6.4	21.0
30-70	1.18	24.6	10.4	14.2	6.70	5.8	.09	.24	11.6	5.1	17.8
70-100	1.08	17.0	8.1	8.9	2.88	7.0	.04	.23	10.9	4.9	14.2
Stand 18. Alder on Alluvium											
0-10	.91	28.1	12.3	15.8	1.44	5.2	.24	.34	10.4	6.5	22.2
10-30	.96	13.3	8.1	5.2	1.00	5.4	.10	.33	7.7	5.0	13.8
30-70	1.18	22.2	10.4	11.8	5.57	5.6	.09	.25	8.3	6.9	15.0
70-100	.93	16.1	7.4	8.7	2.44	5.5	.05	.24	6.3	6.1	12.2
Stand 11. Maple—Cottonwood on Alluvium											
0-10	1.07	32.4	8.8	23.6	2.52	6.4	.08	.28	13.2	5.5	18.7
10-30	1.10	33.4	8.9	24.5	5.40	6.8	.08	.27	15.0	6.4	18.4
30-70	1.06	23.9	7.1	16.8	7.10	6.6	.06	.20	11.5	5.6	15.2
70-100	1.10	20.0	7.3	12.7	4.20	6.5	.07	.19	12.4	5.5	16.3
Stand 2. Cottonwood—Ash on Alluvium											
0-10	1.21	11.6	4.7	6.9	1.21	6.2	.03	.26	7.4	3.3	10.9
10-30	1.23	10.8	5.0	5.8	1.43	6.5	.03	.16	8.2	3.5	10.4
30-70	1.09	12.6	5.1	7.5	3.26	6.4	.03	.19	8.9	4.0	11.7
70-100	1.31	8.9	4.4	4.5	1.78	6.5	.03	.15	7.4	3.5	9.8

rived. Finally, if these data are available for all depths down to one meter, bedrock permitting, the total storage capacity may be calculated, and the available moisture in the entire profile expressed as a percentage of the storage capacity, termed here simply "Available Moisture" or AM.

The formulae with an example are presented below:

Depth (cm)	B.D.	⅓ Atm. %	15 Atm. %	MRV (⅓-15 Atm. %)	Field Moisture Content % (corrected for rocks)
0-10	1.0	30.0	10.0	20.0	20.0

$$\text{Storage Capacity (cm)} = \frac{\text{B.D. X Depth (cm) X (MRV)}}{100}$$

Solving for the example: $\dfrac{1.0 \text{ X } 10 \text{ X } 20}{100} = 2.0 \text{ cm Storage Capacity}$

$$\text{Available Moisture \%} = \frac{\text{Field Moisture Content \%} - 15 \text{ Atm. \%}}{\text{MRV}} \cdot 100$$

Solving for the example: $\dfrac{20 - 10}{20} \cdot 100 = 50\%$ Available Moisture

$$\text{Available Moisture (AM)} = \frac{\text{Avail. Moist. \% X Storage Capacity of each horizon}}{\text{Total Storage Capacity}}$$

In a profile that is uniform throughout to a depth of 100 cm and is sampled at 10 cm intervals:

$$\frac{10 \ (50 \text{ X } 2.0)}{20} = 50\% \text{ of the Total Storage Capacity is Available; AM} = 50$$

AVAILABLE MOISTURE UNDER DIFFERENT VEGETATION TYPES

A summary of the variation in available moisture under different vegetation types is presented in Table 4. Samples were first taken April 1, 1961, but are not reported because 4 in. (100 mm) of precipitation had fallen recently in the form of rain and snow and all soils were well above field capacity.

In 1961 the last spring precipitation greater than .10 in. (2.5 mm) fell on May 30 (7.4 mm at Headquarters); the next precipitation did not come until September 17 (18 mm). In 1962 the last spring rain occurred on May 9 (18.5 mm) and essentially no more rain fell until August 7 when over 75 mm were recorded. The early fall precipitation during the second summer does not permit a direct comparison between the 1961 and 1962 data. Nevertheless, the agreement between the lowest AM values in 1961 and the 1962 figures is within 10% in all but one case. The precision of the method varied inversely with an increase in the rockiness and heterogeneity of the soil. A measure of the variation within a particular stand is not available. Even though values may be off by 10%, which is unlikely, a gradient can be established that is adequate for the use intended here.

Some points in Table 4 deserve emphasis:

1) Differences in the storage capacity are not correlated with differences in vegetation. The storage capacity under chaparral ranged from 1.5 to 13.3 cm; under redwood I stands it varied from 5.6 to 14.8 cm.

2) The productivity of redwood increased strikingly as the AM values for August increased up to about 70, beyond that a decrease in productivity was noted.

3) The grassland types in June had reduced the surface meter to around 20% of the storage capacity, whereas other vegetation types, not dominated by grass, were very near field capacity.

4) The increase in moisture under two of the grassland types during August is not a sampling error, but represents subsoil replenishment by seepage. The dry grass transpires no water, and the dry surface soil restricts evaporation. The surface 30 cm remained at PWP until fall precipitation occurred.

5) There appears to be no consistent relationship between elevation and AM, e.g., redwood and Douglas-fir III stands differing by 1600 ft elevation still had similar moisture regimes.

ESTABLISHMENT OF AN ENVIRONMENTAL MOISTURE GRADIENT

Of the 30 stands sampled, 27 demonstrated a meaningful distribution along a gradient based on the "Minimum Available Moisture" values (Minimum AM). This is the lowest value which the available soil moisture, expressed as a percentage of the storage capacity, reached during the year. The three remaining stands (2, 11, 22) were on the Eel River flood plain under the direct influence of a fluctuating water table. These stands emphasize the difficulty in obtaining a universal soil-moisture measure over a wide range of environments, and how sampling to a fixed depth can be misleading where a water table exists. The cottonwood stands, distributed parallel to the Eel River, are inundated and subject to the mechanical action of flood waters nearly

TABLE 4. Available moisture under different vegetation types. For other data on the sites see Table 2. Roman numerals indicate site productivity classes; see Table 20.

Vegetation Type	Storage Capacity (cms)	Available Moisture in Surface Meter as Percent of Storage Capacity (AM)			
		June 6, 1961	July 18, 1961	Aug. 16, 1961	Aug. 6, 1962
Cottonwood—Ash (2)*	7.7	172	80	36	36
Maple—Cottonwood (11)	19.2	115	43	36	33
Alder—Maple (22)		on rock outcrop in stream channel			
Alder (18)	10.4	215	92	78	68
Alder (17)	13.3	173	66	66	69
Bay—Maple—Redwood III (23)	9.2	339	86	71	76
Redwood Flat Ia (24)	11.4	168.	80	68	67
Redwood Flat Ia (20)	17.1	107	82	62	68
Redwood Flat Ia (1)	21.3	93	110	62	71
Redwood I—Douglas-fir II (21)	14.8	76	39	44	38
Redwood I—Douglas-fir II (19)	5.6	187	57	40	40
Redwood II—Douglas-fir III (16)	16.0	111	48	26	21
Redwood III—Douglas-fir III (26)	13.7	64	23	20	29
Redwood III—Douglas-fir III (25)	9.5	199	30	26	25
Redwood III—Douglas-fir III (8)	9.6	145	25	28	23
Redwood IV—Douglas-fir IV (30)	8.3	95	25	23	22
Douglas-fir IV (7)	19.0	89	38	11	17
Madrone—Tanoak—Douglas-fir IV (27)	18.9	76	41	19	28
Deciduous Oak—Douglas-fir III (28)	12.9	46	23	10	6
Deciduous Oak—Douglas-fir IV (15)	14.6	89	11	10	7
Deciduous Oak—Douglas-fir IV (10)	9.4	88	15	18	9
Grassland (12)	18.8	23	11	35	10
Grassland (9)	9.4	28	7	17	5
Grassland (3)	4.3	23	0	0	2
Chaparral—Douglas-fir V (5)	13.3	100	38	1	13
Chaparral (6)	2.6	166	0	0	0
Chaparral (4)	1.5	148	0	0	0
Incense-cedar—Douglas-fir IV (13)	17.4	95	33	17	15
Incense-cedar—Douglas-fir V (29)	2.6	82	1	0	0
Incense-cedar—Jeffrey pine (14)	2.1	54	0	0	0

*Figures in parentheses represent stand numbers.

every year. The water table fluctuates by as much as 20 ft (6 m), closely paralleling the rise and fall of the Eel River. Minimum AM values related to an estimate of the probability of annual flooding were assigned to these stands. The stand nearest the river (2) was assigned a value of 100%, while 11 received a 90% probability value. One other stand, dominated by alder and maple (22), was assigned a value of 85. In-this case, as with other alder stands, fluctuations in the water table were minor, and the mechanical action of water had far less significance than in the cottonwood type.

The distributional patterns for a number of species in relation to the derived moisture gradient are illustrated in Figures 3-5. For the trees, the ordinate represents the percentage of the total basal area accounted for by each species. A basal area comparison weights more heavily the occurrence of redwood and Douglas-fir. Nevertheless, the highest frequency and percent basal areal figures for a species usually were recorded at approximately the same position along the moisture gradient. The curves indicate the maximum basal area percentages or frequency values for particular Minimum AM values. All other frequency or basal area percentages fall in the area under the curves.

The point along the moisture gradient (or any other environmental gradient) at which the highest population density is observed (here expressed as basal area percentage or frequency) is defined as the "ecological optimum" for a given species. The greatest number of individuals does not necessarily occur where the most vigorous or largest specimens are to be found. For example, the largest tanoak (Lithocarpus densiflora) are located at around 40 on the moisture gradient, where individuals may reach heights of 125 ft; the ecological optimum is near 25 (Fig. 3).

A number of weedy species have bimodal distribution patterns similar to that illustrated by Galium aparine in Fig 4. The simultaneous study of population distributions along other gradients suggests light intensity may have a strong influence on this bimodal pattern. However, a number of other non-weedy species also exhibit bimodality; Rhus diversiloba and Umbellularia californica are examples. Whether this represents a simple response to another factor, results from ecotypic variation, or is forced exclusion by better-adapted species cannot be verified without more detailed investigation.

Dentaria californica shows differentiation into subspecies along both the moisture (Fig. 4) and the light gradient. Species such as Viola glabella and Hydrophyllum tenuipes, which are abundant where
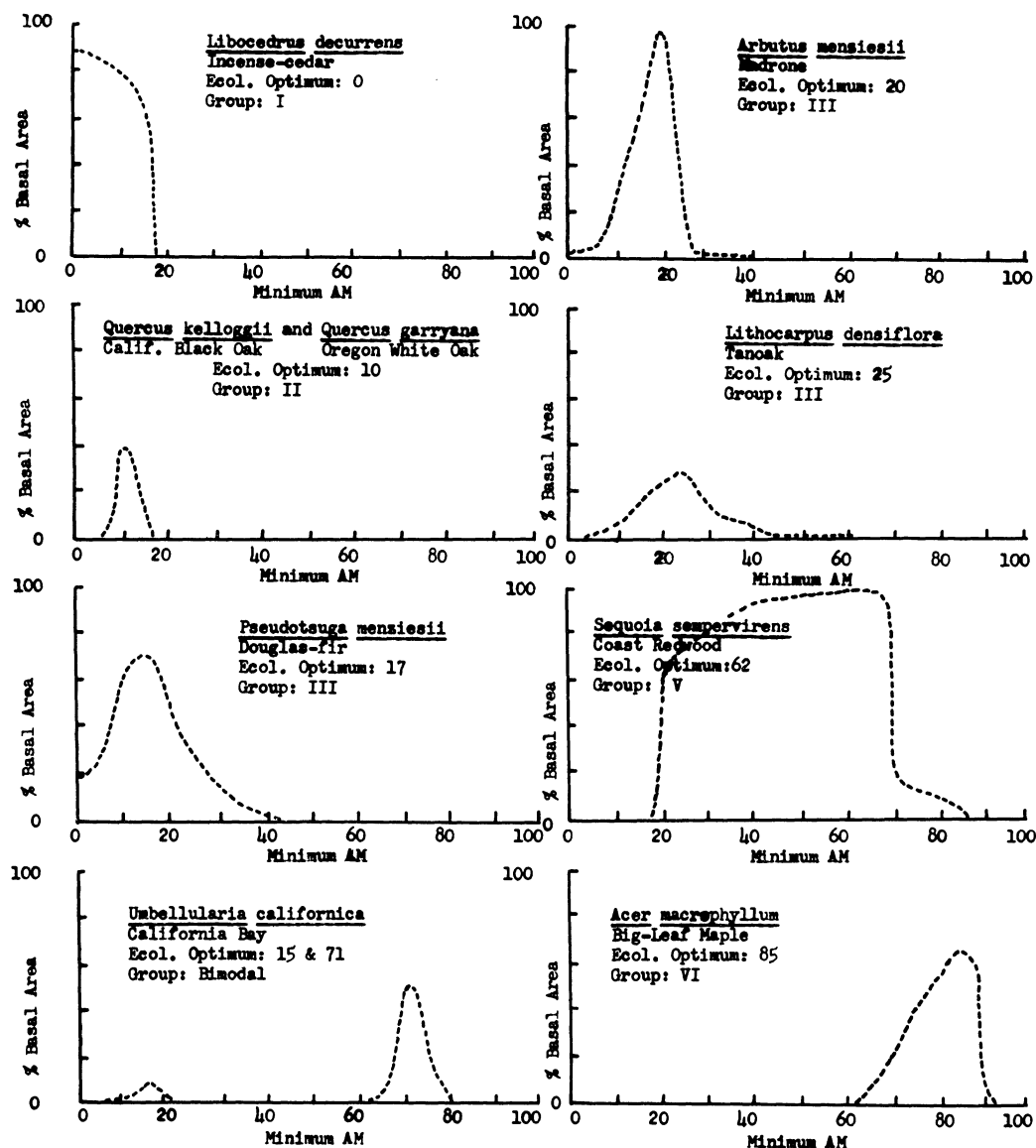
Fig. 3. Distribution of selected species in relation to the Minimum Available Moisture (Minimum AM).

found, but occur only over a narrow range of moisture conditions, are excellent "indicator species" for characterizing sites (Figs. 4, 5).

Derivation of a Vegetation Moisture Index

For simplification the species were grouped according to the position of their ecological optima along the moisture gradient. The limits of these groups reflect breaks where no ecological optima occurred. These groups do not necessarily occupy equal distances along the moisture gradient. Some of the limits are no doubt influenced by deficiencies in the initial sampling.

For each moisture group thus derived, an "Average Minimum Available Moisture" was calculated, based on the ecological optima of all species within the group (Table 5). The assignment of species to ecological groups is given in Table 6.

A number of possibilities exist in the choice of a moisture index based upon the vegetation. In this study it was decided to calculate a Vegetation Moisture Index based upon the number of species present in each moisture group, and then to use this to characterize each of the 30 stands investigated. This index is abbreviated (VMI)p; the "p" denotes that calculations are based only upon the presence of plants, not their abundance. Bimodal and insensitive species are excluded from the calculations. Basically, this is an overall Minimum AM average, weighted by the number of species in each group. A sample calculation is shown in Table 7.

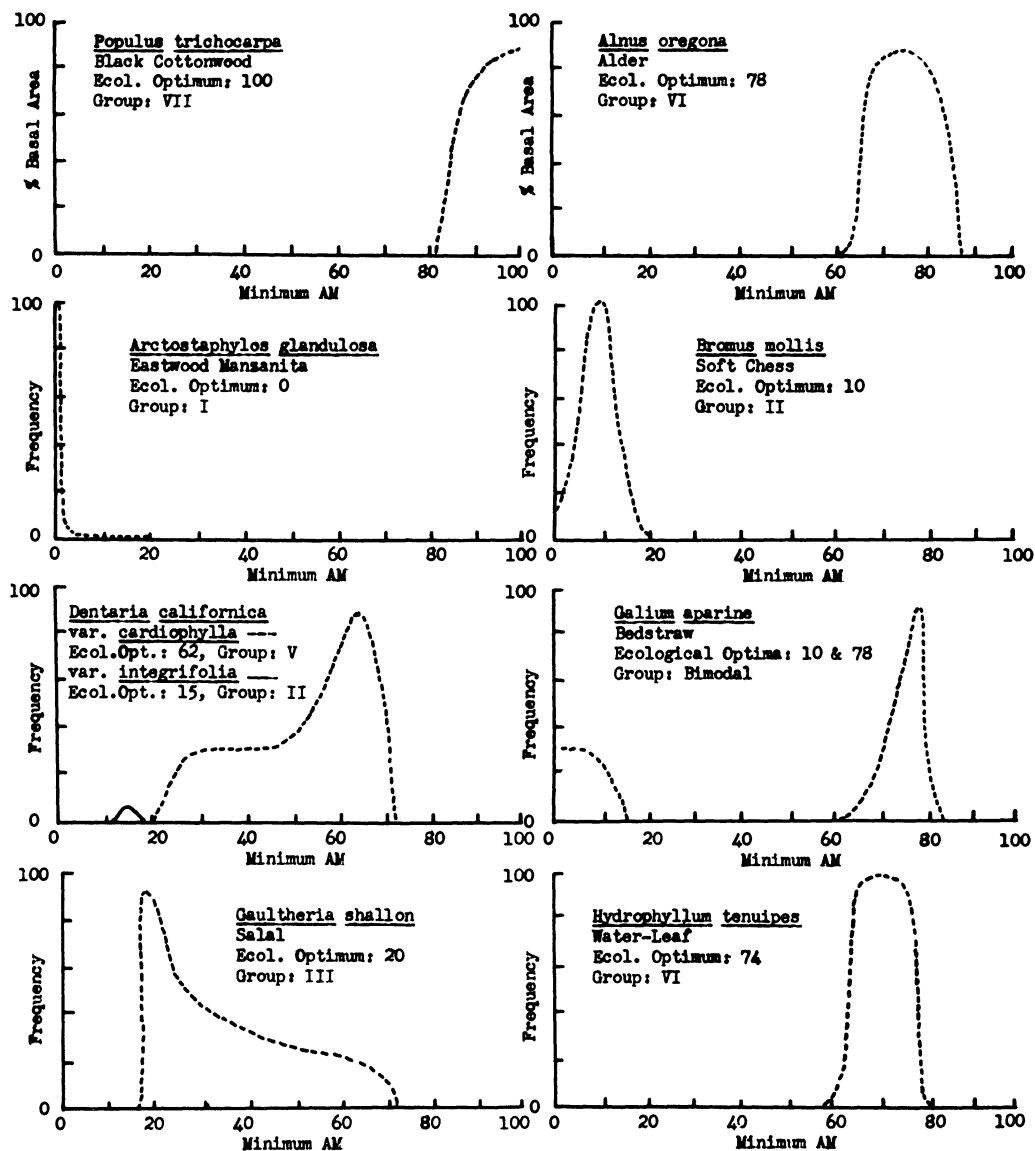Other indexes tested were weighted by the popu-

FIG. 4. Distribution of selected species in relation to the Minimum Available Moisture (Minimum AM).

TABLE 5. Characteristics of the moisture groups.

Moisture Group	Group Limits along Moisture Gradient (Min. AM)	Average Minimum AM for each Group	Number of Species in each Group
I	0	0.0	29
II	1–15	9.4	79
III	16–30	21.1	17
IV	31–55	44.9	14
V	56–65	63.0	11
VI	66–85	74.5	22
VII	86–100	95.0	7

lation densities of species within each group. However, because frequency and relative composition of the overstory are strongly influenced by factors not related to the moisture regime, the index based on species presence (VMI)p is recommended as having the most widespread utility. In addition to being better adapted to use on cutovers and other disturbed sites, it has the added advantage of simplicity.

A comparison of the (VMI)p derived from an analysis of the vegetation and the Minimum AM determined by sampling the available soil moisture was made by linear correlation analysis. Fig. 6 illustrates the distribution of the 30 stands in relation to the Minimum Available Moisture and the Vegetation Moisture Index. The correlation coefficient of .97 was significant at the 1% level.

Because of the nature of the (VMI)p, zero values are impossible unless all species belong to the first moisture group. For similar reasons values above 95
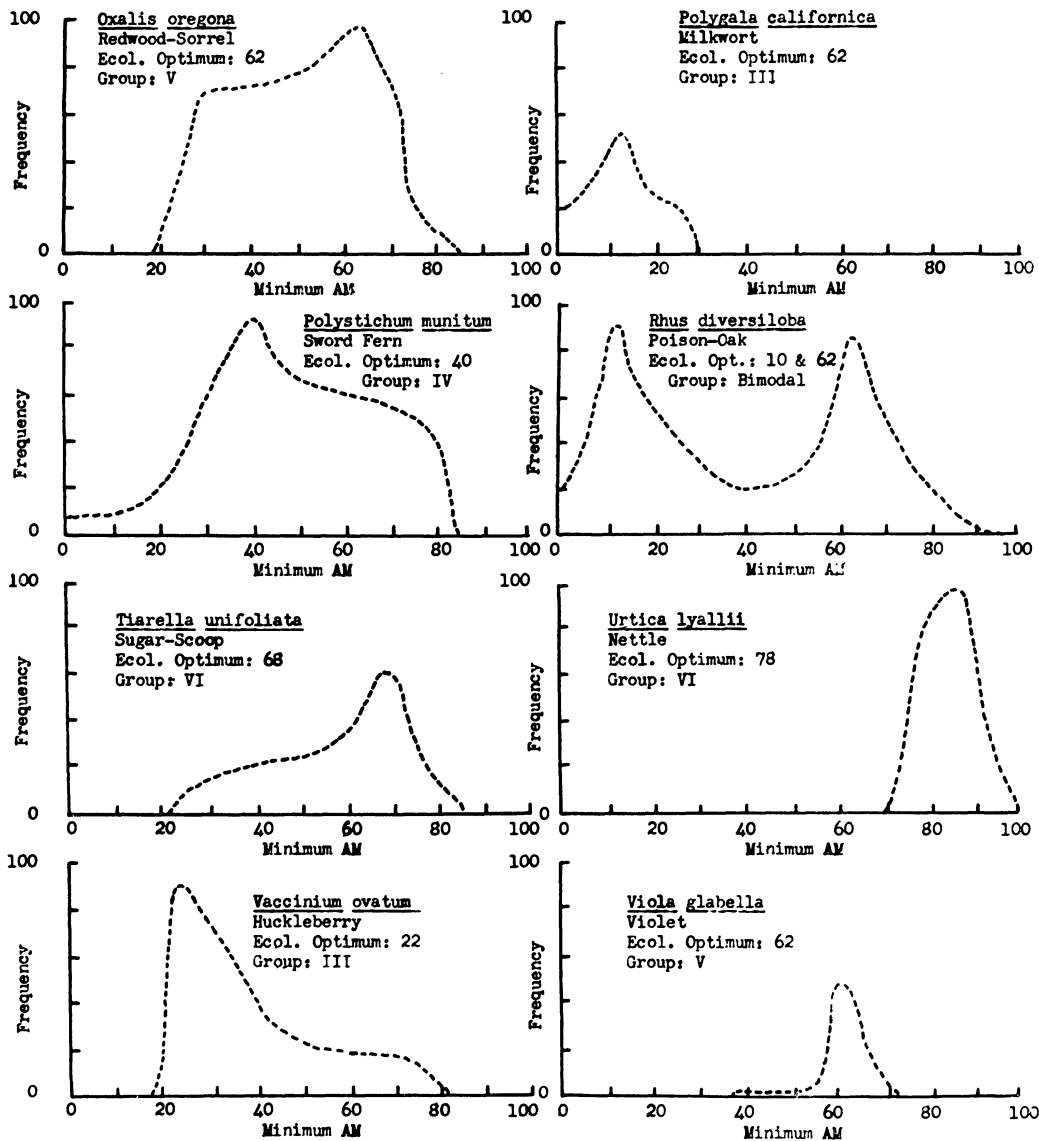
FIG. 5. Distribution of selected species in relation to the Minimum Available Moisture (Minimum AM).

are also impossible. That the correlation is not closer is due partly to errors in assessing species and to the paucity of species in some stands. Some precision is certainly lost by grouping species. For example, *Tiarella unifoliata* and *Urtica lyallii* were both placed in the same moisture group, although their ecological optima were separated by 10 units along the moisture gradient (Fig. 5).

Not only may the soil moisture values to be somewhat in error, but because they are point samples (taken from a single pit), disagreement is likely when compared with (VMI)p values that reflect conditions over a 100-ft-square area. Although all species used in the calculation of the (VMI)p appeared to be sensitive to the moisture gradient, other factors may be important in determining their distribution and contribute to some of the variation.

THE NUTRIENT GRADIENT

Although the essential elements for plant growth have been known for some time, the evaluation of soil fertility still remains a difficult and often perplexing problem. Too frequently "fertility" has been used interchangeably with "productivity." Site productivity reflects the net response of an organism or a community to all the environmental factors. Fertility, on the other hand, relates to the concentration of available plant nutrients, their relative balance, and rate of supply.

Even allowing for the difficulties of separating the effects of interactions of other environmental factors upon fertility, it is necessary to relate fertility to the response of a particular plant or plants. In studies of natural vegetation a selection of one of the most demanding indigenous species of trees,

TABLE 6. Distribution of species by ecological groups. M = moisture; N = nutrients; L = light; T = temperature; A = insensitive; B = bimodal; — = undetermined; ( ) = estimated, not used in calculations.

TABLE 6 cont.

Species	M	N	L	T
Acer circinatum	(V)	III	(I)	V
Acer macrophyllum	VI	II	I	III
Achillea borealis	I	I	—	—
Achlys triphylla	IV	III	I	IV
Actaea rubra	(V)	(III)	(I)	—
Adenocaulon bicolor	VI	II	I	—
Adiantum pedatum	V	III	(I)	IV
Aesculus californica	(II)	(II)	—	III
Agoseris grandiflora	II	I	(VI)	—
Aira caryophyllea	II	II	VI	—
Alnus oregona	VI	II	—	IV
Anagallis arvensis	(II)	(II)	VI	—
Anemone deltoidea	IV	III	I	V
Anemone quinquefolia	(VI)	—	—	—
Anthemis cotula	—	—	VI	—
Apocynum pumilum	II	I	V	—
Aralia californica	VI	III	I	—
Arbutus menziesii	III	II	—	IV
Arctostaphylos glandulosa	I	I	VI	III
Arenaria douglasii	II	II	IV	—
Artemisia douglasiana	VII	II	III	—
Asarum caudatum	IV	IV	I	IV
Aster radulinus	I	I	IV	III
Athyrium filix-femina	V	III	I	—
Avena barbata	II	III	VI	III
Baccharis pilularis	—	—	IV	IV
Blechnum spicant	VI	II	I	V
Briza minor	II	III	VI	III
Brodiaea ida-maia	II	II	—	IV
Brodiaea laxa	II	III	—	III
Brodiaea pulchella	II	I	—	—
Bromus carinatus	II	II	VI	—
Bromus mollis	II	II	VI	—
Bromus rigidus	II	II	VI	—
Bromus vulgaris	VI	IV	IV	—
Calochortus tolmiei	II	I	V	—
Carex hendersonii	VI	IV	—	IV
Ceanothus incanus	I	II	VI	IV
Ceanothus parryi	I	I	VI	IV
Cerastium vulgatum	II	III	IV	—
Chlorogalum pomeridianum	II	II	—	III
Chrysanthemum leucanthemum	—	—	VI	—
Cirsium arvense	VII	III	III	—
Cirsium pastoris	(II)	(II)	(VI)	—
Clarkia concinna	II	II	IV	IV
Clintonia andrewsiana	IV	IV	—	V
Collomia heterophylla	II	II	IV	—
Convolvulus arvensis	(II)	(II)	VI	—
Cornus nuttallii	VI	—	—	IV
Corylus cornuta	III	IV	III	IV
Cryptantha spp.	I	II	—	—
Cynoglossum grande	II	II	—	III
Cynosurus echinatus	II	III	VI	—
Cyperus eragrostis	VII	II	—	—
Danthonia californica	II	III	VI	V
Daucus pusillus	II	III	VI	—
Delphinium nudicaule	II	II	—	III
Dentaria californica var. cardiophylla	V	III	I	V
Dentaria californica var. integrifolia	II	II	IV	IV
Deschampsia elongata	B	—	VI	—
Dicentra formosa	(V)	(III)	(I)	—
Disporum hookeri	IV	III	I	V
Disporum smithii	V	IV	I	V
Dodecatheon hendersonii	II	II	IV	—
Dryopteris arguta	IV	A	II	—
Dryopteris dilatata	VI	IV	II	IV
Elymus glaucus	II	II	V	—
Elymus triticoides	I	II	—	—
Epilobium minutum	I	I	V	III
Equisetum arvense	VII	III	IV	—
Equisetum hyemale	VII	III	—	—
Equisetum telmateia	VI	III	III	—
Erechtites arguta	—	—	(IV)	V
Erechtites prenanthoides	A	II	IV	V
Eriodictyon californicum	(I)	(I)	IV	III
Eriogonum baileyi ssp. elegans	II	III	—	III
Eriogonum latifolium ssp. sulphureum	(II)	—	VI	V
Eriophyllum lanatum	II	I	V	—
Erodium botrys	(II)	—	VI	—
Erodium cicutarium	(II)	—	VI	—
Eschscholzia californica	I	I	VI	—
Euonymus occidentalis	VI	III	—	V
Festuca dertonensis	II	III	VI	—
Festuca megalura	II	II	VI	—
Festuca occidentalis	I	A	V	—
Festuca rubra	I	I	IV	—
Festuca subuliflora	III	III	III	V
Festuca subulata	VI	IV	II	—
Fragaria californica	II	A	V	IV
Fraxinus latifolia	VII	—	—	—
Galium aparine	B	II	IV	V
Galium californicum	III	II	IV	V
Galium divaricatum	I	I	VI	—
Galium parisiense	II	III	VI	—
Galium triflorum	VI	IV	II	—
Garrya fremontii	I	I	VI	III
Gastridium ventricosum	II	III	VI	—
Gaultheria shallon	III	III	II	V
Geranium dissectum	II	III	VI	—
Geranium molle	II	III	—	—
Glyceria elata	VI	III	—	—
Goodyera oblongifolia	III	—	—	II
Habenaria elegans	II	—	—	III
Habenaria unalascensis	III	—	—	III
Heteromeles arbutifolia	(II)	I	—	III
Hieracium albiflorum	II	II	IV	—
Hierochloe occidentalis	IV	IV	II	V
Holcus lanatus	—	—	VI	—
Holodiscus discolor	B	A	—	IV
Hordeum leporinum	II	III	VI	—
Hydrophyllum tenuipes	VI	III	I	IV
Hypericum perforatum	II	III	VI	—
Hypochoeris glabra	I	II	VI	—
Hypochoeris radicata	II	III	VI	—
Iris douglasiana	III	IV	II	V
Iris purdyi	II	B	IV	IV
Lactuca serriola	II	III	VI	—
Lathyrus vestitus	II	A	IV	IV
Libocedrus decurrens	I	I	—	II
Linanthus bicolor	II	II	—	III
Lithocarpus densiflora	III	A	—	IV
Lithophragma affinis	I	I	—	—
Lolium multiflorum	II	III	VI	—
Lolium perenne	II	III	VI	—
Lonicera hispidula	II	II	—	IV
Lotus humistratus	II	III	VI	—
Lotus micranthus	II	III	VI	—
Lotus purshianus	II	III	VI	—
Lupinus albifrons	I	II	VI	—
Lupinus bicolor	(I)	(II)	VI	V
Luzula subsesilis	II	II	IV	IV
Madia exigua	II	A	IV	—
Madia madioides	II	II	IV	IV
Medicago hispida	II	III	VI	—
Medicago lupulina	—	—	V	—
Melica californica	II	III	—	III
Melica geyeri	II	III	—	—
Melilotus albus	—	—	VI	—
Montia sibirica	V	III	I	—
Oenanthe sarmentosa	VI	III	—	—
Onychium densum	I	I	V	—
Osmorhiza chilensis	III	III	III	—
Oxalis oregana	V	III	I	V
Pedicularis densiflora	I	I	IV	III
Peridendia kelloggii	II	II	VI	III
Petasites palmatus	IV	IV	III	IV

TABLE 6 cont.

Species	M	N	L	T
Phacelia bolanderi	—	—	V	IV
Pinus jeffreyi	I	I	—	I
Pityrogramma triangularis	II	II	IV	—
Plagiobothrys ssp.	II	III	VI	—
Plantago lanceolata	II	III	VI	—
Plectritis congesta	II	I	—	II
Polygala californica	III	B	IV	V
Polypodium californicum	—	A	II	III
Polypogon monspeliensis	—	—	VI	—
Polystichum munitum	IV	II	I	IV
Populus trichocarpa	VII	III	—	—
Prunella vulgaris	—	—	IV	—
Pseudotsuga menziesii	III	B	—	IV
Pteridium aquilinum	A	III	III	—
Quercus chrysolepis	I	I	—	III
Quercus garryana	II	II	—	III
Quercus kelloggii	II	II	—	III
Ranunculus occidentalis	II	II	IV	III
Rhamnus californica	I	I	—	V
Rhamnus purshiana	(VI)	(III)	—	—
Rhus diversiloba	B	A	A	—
Rosa gymnocarpa	III	A	III	—
Rubus leucodermis	—	—	IV	—
Rubus parviflorus	VI	III	III	—
Rubus spectabilis	VI	III	—	IV
Rubus vitifolius	B	A	III	—
Rumex acetosella	II	A	VI	—
Sambucus caerulea	(I)	—	—	—
Sambucus callicarpa	VI	III	—	V
Sanicula crassicaulis	II	A	IV	—
Satureja douglasii	III	III	IV	V
Scoliopus bigelovii	IV	IV	I	V
Sequoia sempervirens	V	V	II	V
Sherardia arvensis	II	III	—	—
Silene californica	I	I	V	—
Silene gallica	I	II	VI	—
Sisyrinchium bellum	II	—	VI	—
Sitanion jubatum	—	—	VI	—
Smilacina racemosa	IV	III	—	—
Smilacina stellata	V	III	I	IV
Sonchus asper	II	III	—	—
Sonchus oleraceus	II	III	—	—
Stachys rigida	VI	III	II	—
Stachys rigida ssp. *quercetorum*	I	II	IV	—
Stellaria crispa	VI	II	—	—
Stellaria media	I	I	IV	—
Stipa pulchra	II	A	IV	III
Symphoricarpos mollis	II	A	IV	III
Tauschia kelloggii	II	II	—	III
Tiarella unifoliata	VI	IV	I	V
Torilis japonica	II	III	—	—
Torilis nodosa	II	III	IV	—
Trientalis latifolia	III	IV	I	IV
Trifolium bifidum	II	II	VI	IV
Trifolium dubium	II	—	IV	—
Trifolium microcephalum	I	II	VI	—
Trifolium microdon	II	III	—	IV
Trifolium oliganthum	II	II	VI	IV
Trifolium pratense	—	—	VI	—
Trifolium tridentatum	I	II	—	—
Trifolium variegatum	II	—	—	—
Trillium chloropetalum	IV	IV	I	V
Trillium ovatum	IV	IV	I	V
Trisetum cernuum	II	II	IV	IV
Umbellularia californica	B	II	(I)	IV
Urtica lyallii	VI	III	II	IV
Vaccinium ovatum	III	A	III	V
Vaccinium parvifolium	(IV)	(III)	—	—
Vancouveria planipetala	A	A	I	V
Viola glabella	V	III	I	—
Viola ocellata	II	III	IV	—
Viola sempervirens	IV	III	I	V
Whipplea modesta	III	A	III	V
Woodwardia fimbriata	V	III	I	—

TABLE 7. Vegetation of a splendid Redwood I—Douglas-fir II stand (19) showing the derivation of the Vegetation Moisture Index (VMI)p. Tree volume is 29,000 cu ft/acre; basal area is 350 sq ft/acre. The calculated (VMI)p compares favorably with a Minimum Available Moisture of 40 derived from direct soil-moisture measurement in both 1961 and 1962 (cf. Table 4).

Moisture Group II; Average Minimum AM: 9.4
    Lathyrus vestitus

Moisture Group III; Average Minimum AM: 21.1
    Lithocarpus densiflora   *Vaccinium ovatum*
    Pseudotsuga menziesii   *Trientalis latifolia*
    Corylus cornuta   *Iris douglasiana*

Moisture Group IV; Average Minimum AM: 44.9
    Polystichum munitum   *Dryopteris arguta*
    Trillium ovatum   *Viola sempervirens*
    Anemone deltoidea   *Achlys triphylla*
    Smilacina racemosa   *Disporum hookeri*
    Clintonia andrewsiana   *Hierochloe occidentalis*

Moisture Group V; Average Minimum AM: 63.0
    Sequoia sempervirens   *Adiantum pedatum*
    Oxalis oregona   *Dentaria californica* ssp.
                                        cardiophylla

Moisture Group VI; Average Minimum AM: 74.5
    Galium triflorum   *Rubus parviflorus*

Bimodal and Insensitive Species; not used in calculations
    Rhus diversiloba   *Vancouveria planipetala*

Sample calculation:
$$(VMI)p = (1 \times 9.4) + (6 \times 21.1) + (10 \times 44.9) + (4 \times 63.0) + (2 \times 74.5) = 986.0.$$
$$986.0/(1+6+10+4+2) = 43$$

shrubs, or herbaceous plants is desirable. It should be recognized, of course, that the differential response of various plant species to nutrient ions renders fallacious the use of one kind of plant to assess precisely the soil fertility for another. Experiments with crop plants alone should be discouraged if results are to be interpreted for other than agronomic purposes.

The most common methods of evaluating the fertility of soils are: 1) Pot studies which compare relative plant yields on various soils, and may be extended by fertilization trials to ascertain what nutrients, if any, are deficient; 2) correlation of soil chemical analyses with yields; 3) foliar analyses on a portion or all of selected test plants. The latter method can be of real value only with knowledge of the limiting and optimum concentrations of the various nutrients in addition to that one under specific test. In some cases all nutrients can be in nearly limiting quantities yet plants are produced which, while small, are still well supplied nutritionally. If more than one nutrient is deficient, this may become apparent only after the element most needed has been supplied. Mitscherlich's equation can be used to determine quantitatively the effects of various nutrients upon plant growth (Jenny 1941: 251).

In this study two approaches to the evaluation of soil fertility were attempted. First, a series of experiments was conducted growing different plants on

TABLE 8. Soil series characteristics.

Soil Series Name	Color of surface/subsoil	Reaction of surface/subsoil	Texture of surface/subsoil	Parent Material	Great Soil Group
Cahto	Very dark grayish brown/Brown	Slightly acid/ Moderately acid	Stony loam/ Stony loam	Hard sandstone	Lithosol
Dubakella	Reddish brown / Brown	Neutral/ Slightly basic	Stony loam/ Stony loam	Serpentine	Red Podzolic
Ferndale	Brownish gray/ Gray brown	Moderately acid/ Moderately acid	Silt loam/ Silt loam	Sedimentary alluvium	Podzolic alluvium
Hugo	Grayish brown/ Yellowish brown	Moderately acid/ Strongly acid	Loam/Clay loam	Hard sandstone and shale	Gray Brown Podzolic
Larabee	Grayish brown/ Pale brown	Moderately acid/ Strongly acid	Gravelly loam/ Clay loam	Weakly consol-idated conglomerate	Brown Podzolic
Laughlin	Grayish brown/ Yellowish brown	Moderately acid/ Moderately acid	Loam/Loam	Hard, noncalcareous sandstone and shale	Prairie, Non-Calcic Brown
McMahon	Pale brown/ Pale brown	Moderately acid / Slightly acid	Clay loam/ Clay	Sandstone with calcite seams	Prairie
Yorkville	Grayish brown/ Bluish gray	Moderately acid/ Basic	Clay loam/ Clay	Metasedimentary, glaucophane and sericite schists (may be partially serpentinized)	Prairie Planosol

a range of the surface soils. Then, by chemical analyses, relationships between the concentration of various nutrients in the soils and plant growth were investigated. Further chemical analyses were completed on all the soils studied in the field in hopes that a relative fertility ranking could be established.

SOIL SERIES CHARACTERISTICS

In California many forest soils have been classified and mapped as soil series. This Soil and Vegetation Survey is sponsored by the California Division

FIG. 6. Relationship between the calculated Vegetation Moisture Index (VMI)p and the measured Minimum Available Moisture in the surface meter of soil as a percent of the total storage capacity (Minimum AM). r = 0.97.

of Forestry, and the field work is being carried out under the direction of the Pacific Southwest Forest and Range Experiment Station of the U.S. Forest Service with the cooperation of the University of California. The soils have been classified mainly on the basis of color, soil reaction, parent material, and the type of vegetation generally associated with them. Depth, slope, and forest productivity classes are shown on the maps. Morphological descriptions of the series are on file and can be obtained from the Experiment Station in Berkeley. Some quantitative data have been published but, unfortunately, only a "typical profile" for each series is presented. The papers of Gardner (1958) and Storie & Wieslander (1952) deal with some of the soils in the redwood and Douglas-fir region of northwestern California. From these and the manual by Storie & Weir (1953) information was summarized on the series encountered in our study (Table 8). The color, soil reaction, and other characteristics within each of the different series are quite variable.

The best developed redwood stands occupy the alluvial flats growing on soils related to the Ferndale series. Other alluvial soils support stands of cottonwood, ash, bay, maple, and alder. Textures of these soils vary from gravelly loam to pure silt.

Nearly all the redwood growing on upland soils in the study area occur on the Hugo and Larabee series in the study area. The Hugo series, which covers over 80% of the area, is the most variable of those series studied. In the park it is developed upon arkose wacke, felsitic sandstone, and siltstone. Oak and Douglas-fir stands are found also on Hugo soils outside the Eel River valley.
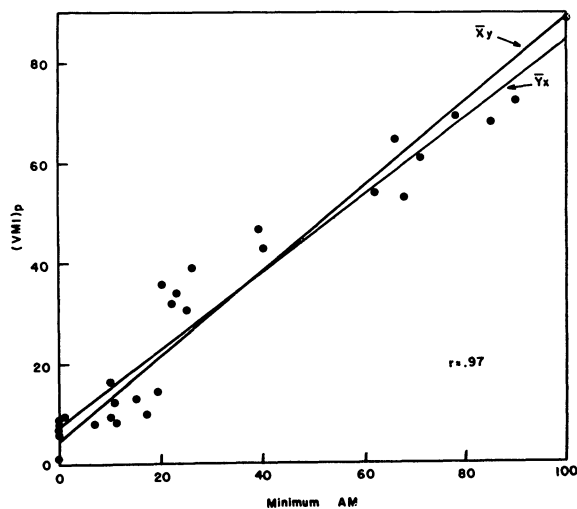
Some oak and Douglas-fir are present also on the predominantly grass-covered McMahon series along the boundary between the grasslands and soils supporting coniferous forest. The McMahon series is distinguished in the field by the occurrence of calcite seams in the parent material. The soils are unstable and have a strong tendency to slip. In this respect they are similar to the Yorkville soils, also a grassland series, which can be compared to a glacier with their almost predictable movement every winter (Gardner 1959). The Yorkville series may also have some free calcium carbonate in the subsoil in addition to some occasional serpentinized material. Chlorite, the dominant clay mineral, is a distinctive feature of this series. Laughlin was the last series investigated which supported grassland vegetation, and it differed from the McMahon and Yorkville series by having neither calcite seams nor a tendency to slip. In fact, the Laughlin soils appeared quite similar to the Hugo soils supporting oak and Douglas-fir.

The most unproductive forest soils in the region are represented by the Cahto and Dubakella series. The Cahto series contains shallow soils located on mountain ridge crests and is usually covered with chaparral, although some phases support stands of Douglas-fir, madrone, and tanoak. This series is very high in organic matter content and approaches what is known in Europe as a "Rankerboden" (Kubiena 1953:193). Such a soil has an A-C profile; the A horizon can almost be rolled up like a carpet; and the soil generally occurs on solid parent rock low in calcium.

The Dubakella, like the Cahto series, is generally shallow. Only on this series in the study area are stands of Jeffrey pine and incense-cedar to be found. The serpentine parent material produces a soil low in calcium with an excess of magnesium and often near-toxic amounts of chromium and nickel. Chrysotile, making up over 90% of the clay minerals, differentiates this series from all others in the study. As demonstrated by Barshad (1960), magnesium can be constantly replaced on the exchange complex though an interchange of hydrogen with magnesium in the octahedral layer of the clay mineral. This accounts for the occurrence of near neutral soils in regions where rainfall and climate lead to acid soil formation on other parent materials. Because of this constant re-supply of magnesium the imbalance of calcium and magnesium on serpentine-derived soils cannot be permanently corrected by applications of lime or gypsum.

Although near neutrality in reaction (Table 3) and in fact less acid than any other soils investigated in the area, these Dubakella soils support acidicole vegetation including *Calocedrus decurrens* (Torr.) Florin itself, *Calypso bulbosa*, and *Goodyera oblongifolia*. The effect is presumably due to the low percentage calcium saturation of the soil cation exchange complex.

SOIL CHEMICAL ANALYSES

Previous to analysis all soil samples were passed through a 2 mm sieve. Total nitrogen was determined by the macro-Kjeldahl method on duplicate 10 g samples. The maximum range between duplicates was .009% N, with an average range of .002. A Beckman Zeromatic pH meter was used to determine acidity on a saturation paste. Total phosphorus was determined according to procedures given by Johnson & Ulrich (1959). Nitric and perchloric acids were used for the digestion process; the molybdenum blue method with stannous chloride as a reducing agent was employed for color development. A Klett Summerson colorimeter with red filter was used for reading the degree of color development. Detection limits were .002% phosporus with subsample variation of ±.004.

Replaceable calcium, magnesium, and potassium were leached from 10 g samples of soil with neutral 1.0 N ammonium acetate. The extract was evaporated to dryness, the organic matter destroyed, the precipitate dissolved with concentrated hydrochloric acid and brought up to volume (50 cc) with water according to procedures given by Jackson (1958). The replaceable cations, including both soluble and exchangeable, were determined by flame photometry. Often results are expressed only as "exchangeable," disregarding the usually small soluble fraction. Replicates were run on 25 samples.

Calcium was read at 422.7 mu on a Model D.B. Beckman flame photometer above a saturated background of magnesium (Rich 1961). The detection limit was 0.1 me/liter. Determinations on duplicate samples with less than 10 me/100 g replaceable calcium agreed within ±0.1 me/100 g. Soils with up to 50 me/100 g of calcium varied by less than ±0.5 me/100 g on duplicate samples.

Sodium was not determined because it is nonessential for plant growth and occurs in concentrations far too low to have significant osmotic influence. On the alluvial flats the highest value of exchangeable Na^+ recorded by Zinke (1960b) was 0.45 me/100 g of soil with most values less than 0.1 me/100 g. A principal reason for determining Na^+ in the past has been to determine the sum of bases to subtract from CEC to get exchangeable H^+. It now appears that what was considered exchangeable H^+ is more often Al^{+++}, at least in acid soils. In basic soils often the sum of exchangeable bases may be greater than the total CEC.

For the determination of cation exchange capacity (CEC) the same soil sample earlier leached with ammonium acetate was leached with 1.0 N calcium chloride, replacing ammonium ions with calcium ions on essentially all of the exchange sites. All non-exchangeable calcium was then removed with rinses of water and methanol. A 2 g subsample was placed in a flask with 50 ml of 2.0 N magnesium acetate, shaken for 1 hr, an extract collected by filtering, and the CEC determined by reading the calcium

concentration in the extract on the flame photometer. Precision was similar to that achieved in the determination of replaceable calcium. With only slight modification this is the procedure given by Rich (1962).

Chemical analyses of the soils under all vegetation types are in Table 3.

INTERPRETATION OF SOIL CHEMICAL ANALYSES

Gessel (1962) noted that a nitrogen deficiency exists in most of the forest soils of the Pacific Northwest and that on most upland soils less than 0.1% total nitrogen could impair the growth of Douglas-fir. According to Wilde (1958) a total nitrogen content of 0.2% is adequate for most tree species. However, a high carbon to nitrogen ratio may indicate that microorganisms are utilizing most of the available nitrogen in the processes of decomposition, leaving little nitrogen for the use of higher plants.

Still, a high correlation between total nitrogen and tree growth is often noted (Viro 1961), particularly on soils where the total nitrogen content is generally low to start with and a small increase may have considerable importance to fertility. Tree species differ significantly from most agricultural plants in their demands for nitrogen as well as in their ability to utilize it. Having a well established root and shoot system, trees generally require nitrogen in smaller quantities than do rapidly growing annuals. Mycorrhizae also play an important part by increasing the surface area of tree root systems on many soils, which in turn favors increased nutrient uptake. Finally, most trees are able to utilize the ammonium (NH_4^+) and nitrate (NO_3^-) forms of nitrogen equally well. This is a real advantage because in most forest soils ammonium is in higher concentration than nitrate, partly through its ability to remain on exchange sites in this form.

Phosphorus is probably the most difficult macronutrient to evaluate in forest soils. On agricultural soils water-soluble phosphate has been used as a measure of the readily available phosphorus. On forest soils the phosphorus levels determined on water-soluble extracts are often exceedingly low, less than 0.05 ppm. On acid soils phosphorus is precipitated as aluminum and iron phosphates; on slightly basic soils it is usually precipitated as some form of calcium phosphate. Even though these compounds have very low solubilities, phosphorus may not be deficient to forest species. If the demands of a species are low the high ratio of insoluble to soluble phosphorus may not have any adverse effect at all because the rate of supply may be adequate. Additional phosphate may be available in forest soils in a chelated form or released through microbial action. These sources are strongly influenced by the type of forest humus and organic acids present (Viro 1961).

There is, at present, no universally acceptable method for determining the availability of phosphorus. Viro (1951), working on morainic and glacio-fluvial soils in Finland, found that of the four different methods tested the total phosphorus content of the clay fraction gave the highest correlation coefficient with the height growth of tree species in the field. All of his soils were quite acid, and under such conditions anion-exchange could permit phosphate to be absorbed in a form readily available to plants on clay minerals with broken bonds such as occur in kaolinite, on clay-sized oxides of iron and aluminum (Wiklander 1955), or on the amino groups of organic matter (Williams 1962).

When soils are leached with neutral 1.0 N ammonium acetate and the extract analyzed for calcium, magnesium, and potassium a good measure of the availability of these elements to many plants is obtained. The results are expressed as milliequivalents/100 gm of soil because the ions are taken up by plants from the soil solution on the basis of stoichiometry, not weight. For example, one H^+ ion may be given off by the plant root in exchange for one K^+ ion, or two H^+ ions for one Ca^{++} ion.

Vlamis (1949) demonstrated a relationship between the percent calcium saturation on the exchange complex of soils and the dry weight yield of barley and lettuce. A calcium saturation below 20% sharply reduced yields. On forest soils having calcium saturations of less than 20% the absolute amount of calcium probably can be more closely correlated with plant response. Less than 2 me/100 g of exchangeable calcium is limiting to most plants.

Magnesium is usally the element on the exchange complex most abundant after calcium. A ratio between the exchangeable forms of these two elements has been used to indicate the relative balance. Ratios as high as 30:1 calcium to magnesium do not prove unfavorable to most forest plants (Wilde 1958). However, when the ratio falls much below 1.0 calcium may be deficient. Exchangeable magnesium in concentrations less than 0.5 me/100 g is probably in critical supply.

Potassium is difficult to evaluate on some forest soils because much of it may become fixed in a form unavailable to most crop plants. Wilde (1958) has suggested that a much stronger extracting solution than ammonium acetate be used on forest soils to assess the true availability of potassium. He states that available potassium as low as 0.06 me/100 g is satisfactory for some pines, but more demanding species such as walnut, ash, basswood, Norway spruce, and bald cypress require about 0.30 me/100 g. Values below 0.10 me/100 g can therefore be considered as unfavorable for most plants.

Chemical analyses showing low nutrient status on soils influenced by ground water or lateral seepage may be completely misleading, for in such cases an adequate concentration of nutrients may be supplied continuously. The situation is analogous to sand cultures being maintained through additions of nutrient

TABLE 9. Top yields/container as percent of average maximum dry weight production.

Soil Series	Vegetation type and Stand No.	Barley		Fireweed		Redwood Greenhouse		Redwood Lathhouse		Douglas-fir	
		Average	Range	Average	Range	Average	Range	Average	Range	Average	Range
Alluvium	Alder (18)	100	91–109	100	82–134	14	6–29	34	30–42	20	17–24
Hugo	Redwood I (21) Douglas-fir I	97	87–112	95	86–111	10	7–13	30	21–38	22	18–24
Laughlin	Grassland (3)	92	85–98	53	38–71	100	81–112	96	94–98	33	19–44
Larabee	Redwood I (19) Douglas-fir II	86	80–96	38	29–48	7	6–8	—	—	—	—
Hugo	Redwood III (25) Douglas-fir III	50	42–57	53	40–69	18	8–27	18	12–24	100	73–130
Hugo	Deciduous Oak (15) Douglas-fir IV	—	—	—	—	—	—	51	30–72	64	56–79
Ferndale Alluvium (Recent)	Redwood Ia	43	39–46	42	38–50	37	32–46	—	—	—	—
Alluvium	Cottonwood (2) Ash	—	—	—	—	—	—	36	34–37	38	24–60
Ferndale Alluvium (Older)	Redwood Ia (1)	—	—	—	—	—	—	100	79–121	58	31–78
Yorkville	Grassland (12)	49	39–55	27	14–35	39	25–52	—	—	—	—
Cahto	Chaparral (5) Douglas-fir V	42	38–47	55	52–59	59	54–67	—	—	—	—
Cahto	Chaparral (6)	—	—	—	—	—	—	8	7–9	44	30–62
Dubakella	Incense-cedar (14) Jeffrey pine	36	31–42	4	3–6	7	5–10	1	0–2	7	5–9

solution. An excellent example is provided by the alder and maple stand (22) growing on rock outcrops in the center of a stream.

POT TESTS FOR THE EVALUATION OF RELATIVE FERTILITY

A series of pot tests was conducted with barley, Australian fireweed (*Erechtites arguta*, a vigorous weed of forest clearings introduced into the park), redwood, and Douglas-fir. The first three species were grown on surface soil collected to a depth of 10 in. (25 cm) and representing the range of conditions studied. All plants were germinated in cans and later thinned to 5 plants per container in the case of barley and redwood, and to 3 per container with the fireweed. They were grown under a greenhouse environment, and the soils were maintained near field capacity with de-ionized water until completion of the experiments: 1 month later for barley, 3 months later for fireweed, and 7 months later for redwood.

In a second study redwood and Douglas-fir were grown together from seed for 7 months in 8 in. clay pots. The study was conducted under a lathhouse environment similar to the microclimate associated with seedlings growing on the redwood-covered alluvial flats. Berkeley city water, which comes from a region of granitic parent material and therefore is low in mineral impurities, was used to maintain the soils slightly above field capacity. Earlier experience with redwood showed that where the soils could be kept above field capacity no detrimental effects to the

root systems were observed, and the damage otherwise encountered through the action of root fungi on grassland as well as redwood-supporting soils was avoided. In all studies plants were grown on three samples of each soil. Top yields expressed as a percent of the average maximum dry weight production are presented in Table 9.

The low yields of redwood and Douglas-fir on the alluvial soil supporting alder probably reflect the utilization by microorganisms of most of the nitrate-nitrogen during a 3 to 6 month storage period. When soil was used within a few weeks after collection, as was done in the barley and fireweed experiments, high yields resulted. The initial high concentration of nitrate-nitrogen in soils supporting alder is apparently the result of nitrogen fixation by *Streptomyces alni* (Bollen & Wright 1961) or other actinomycetes.

The recent alluvium deposited after floods is derived mostly from the erosion of Hugo soils and is predominantly from the subsoil. Such material contains less than 0.05 per cent total nitrogen. With time the nitrogen content in the alluvium under redwood increases to more than 0.1% through the incorporation of redwood litter. The alluvium under a cover of cottonwood does not increase in nitrogen but remains at approximately the same level as when deposited (0.03% in Stand 2). Low nitrogen content in the alluvium under cottonwood and the recent alluvium under redwood probably accounts for a similar, poor response of redwood seedlings on these soils. Accordingly, the higher nitrogen content in

the older alluvium is correlated with maximum red-wood dry weight production.

In the Larabee and Hugo surface soils from redwood-dominated stands, microorganisms appear to have a detrimental effect upon redwood and Douglas-fir seedling growth. Experiments carried out by Florence (1961) indicate that soil radiation treatment can improve the growth of redwood seed-lings, perhaps by reducing the microflora or altering its composition so that more nitrogen is made avail-able.

Bollen & Wright (1961) demonstrated that no nitrate-nitrogen was present in virgin redwood soils, and that none could be measured after 30 days in-cubation under laboratory conditions. It appears that on most of the redwood soils, available nitrogen might be the element in most critical supply. On the Yorkville and particularly the Dubakella soils a calci-um deficiency may account for the low yields.

Even if responses by all species were parallel, and they are not, it would be difficult to extrapolate the results of pot studies directly to the field. The importance of physical structure is not considered, nor are the effects of high rock content or the presence of a hardpan in the B horizon. Merely removing soils from the field and storing them under different environmental conditions can completely change the composition of the microflora and the availability of certain nutrients. A fertility estimate of hydro-morphic soils may be invalid by either pot tests or chemical analyses, particularly on coarse-textured soils where nutrients are continuously supplied to plants but no appreciable amounts are ever present at one time. In the lathhouse, temperature and light conditions may approximate field conditions, but the artificial moisture regime definitely does not. Certainly it is clear that the use of only one species for testing soil fertility, particularly a crop plant, is dangerous, regardless of the apparent advantages of growing genetically uniform, rapidly maturing plants.

CORRELATION BETWEEN PLANT YIELDS AND SOIL FERTILITY

Chemical analyses were run in duplicate on all soils used in the pot studies for determination of total nitrogen, total phosphorous, replaceable calcium, magnesium, potassium, and cation exchange capacity. The percent calcium saturation and calcium-mag-nesium ratios were calculated. A summary of these results follows:

1) Total nitrogen was above 0.1% on all but the alluvial soils recently deposited under redwood, the alluvium under cottonwood, and the Dubakella soils derived from serpentine.

2) Total phosphorus content ranged from 0.05% on the Dubakella series to 0.10% on one of the Cahto soils (from Stand 6). On the Yorkville soils and on the alluvium collected under cotton-wood values of 0.06 and 0.07% phosphorus were recorded. The older alluvium, which is apparently

quite fertile, had only 0.08% total phosphorus. All other soils used contained phosphorus at or above 0.08%.

3) Replaceable calcium was far above the minimum of 2 me/100 g except on the Dubakella series. The other soils investigated ranged from 8.0 to 28.3 me of calcium per 100 g of soil.

4) Replaceable magnesium varied from a low of 2.5 me/100 g on the Laughlin series to 15.3 on the Dubakella and 19.2 on the Yorkville series. Magnesium is probably not deficient on any of the soils used in the pot studies, but a value of 0.5 me/100 g was recorded in the subsoil (70-100 cm depth) of one of the Cahto soils under a chaparral stand (5).

5) A calcium saturation of 39% was recorded on the Yorkville soil; the Dubakella soil had only 13%. The other soils used had values above 50% calcium saturation. Calcium-magnesium ratios were above 1.0 on all but the Yorkville and Dubakella soils used in the pot studies.

6) Replaceable potassium did not appear to be de-ficient in any of the soils used in the pot studies. At a depth of 30-70 cm in a Dubakella soil a value of 0.03me/100 g was recorded. See Stand 29 in Table 3.

An attempt was made to derive equations pre-dicting the yields of barley and redwood on the basis of soil analyses. Relative units were used in ex-pressing the redwood yields to enable combining the data from the greenhouse and lathhouse experiments. A step-wise multiple regression program adapted to a 7090 computer was used for this purpose. The stepwise procedure investigates variables using an analysis of variance to select the order of variables, with that one being chosen at each step which reduces the variance of Y the most in a single iteration. Variables are continually evaluated and may be removed from the equation if no longer significant. Selection will stop when all variables have been in-cluded (and only those) which meet the significance test prescribed in the input data.

In the first run on this study the F level was set at 0 to allow all variables which did not have singularity with another to come in. This identified those variables that could not be forced into subse-quent runs.

In the second run all those variables which did not cause singularity were forced in. The F value was set at the 95% level. The program then selected the least significant variable of the total number forced in and rejected it. The program then re-calculated the regression coefficients on the matrix that remained. The process was repeated until only those variables which exceeded the F level remained. Since none of the variables which caused singularity in the first run were specifically eliminated (punched on the elimination card) they were still eligible for inclusion in the matrix if the variable which caused

singularity to occur had been eliminated in the step-wise process.

A third run was made selecting two and three variable equations which seemed logically important (e.g., Ca^{++} sat. % and % N). These were forced and held in the regression by not subjecting them to the step-wise elimination process at the specified F level. None of the selected equations had co-efficients of multiple determination above .40. For a detailed discussion of step-wise regression see Ralston & Wilf (1960: Chapter 17).

TABLE 10. Simple correlation coefficients of nutrient variables with barley and redwood yields. * significant at 5% level, ** significant at 1% level.

Variable	Barley	Redwood
%N	.63**	.29
Log %N	.62**	.48*
%P	.42*	.48*
Log %P	.42*	.44*
K^+	.04	.11
Log K^+	.16	.39*
Ca^{++}	.34	.25
Log Ca^{++}	.39	.46*
Mg^{++}	−.46*	−.34
Log Mg^{++}	−.45*	−.44*
CEC	.08	.05
Ca^{++} sat%	.51**	.53**
Ca/Mg	.61**	.37

The 13 variables tested appear in Table 10. By correlating each of these variables with barley and redwood yields the simple correlation coefficients presented in Table 10 were derived.

In most cases an improved correlation was obtained by expressing nutrient concentrations by their logarithms. Such a transformation would improve the linearity if plant response follows the "critical limits curve" concept. The Mitscherlich equation also assumes a logarithmic function between nutrient concentration and plant growth. Casida & Santoro (1961) showed an excellent correlation between the logarithm of manganese concentration and diameter growth of *Bacillus cereus* colonies. Leyton (1958) also cites evidence that nutrient concentration may affect plant growth logarithmically, at least in the range where one element is in deficient quantity.

The Log % N, Log Mg^{++}, Log % P, and Ca^{++} sat % were variables significantly correlated with the growth of both barley and redwood. Magnesium concentration was the only variable negatively corre-lated. This really indicates that the calcium satura-tion on the exchange sites decreases to a critical level as the replaceable magnesium increases.

The lesser response of redwood to some of the variables probably does not indicate so much a radically different nutrient requirement as it reflects the greater variation introduced by combining two quite different experiments. One had plants grown in a greenhouse without competition; the other was under a lathhouse environment with mixed species composition.

From the step-wise multiple regression results prediction equations for the yields of barley and redwood were selected which represented the fewest number of variables still providing a coefficient of multiple determination above .90. These equations are:

Dry Weight
of barley (g) = 1.99 + 3.695 (% N) − 0.931 (K^+) + 3.962 (Log Ca^{++}) − 0.096 (Mg^{++}) − 0.049 (CEC) − 0.066 (Ca^{++} sat %)
Average Yield = .500 g
Standard Error of Estimate = 0.063 g = 12.7%
Coefficient of Multiple Determination = 0.923

Relative Dry
Weight Yield
of Redwood (%) = 1031.68 − 1225.69 (% N) + 536.05 (Log % N) − 1271.69 (Log Ca^{++}) − 777.26 (Log Mg^{++}) + 48.84 (CEC) + 16.41 (Ca^{++} sat %) − 162.16 (Ca/Mg)
Average Yield = 47.92%
Standard Error of Estimate = 13.8%
Coefficient of Multiple Determination = 0.907

When the multiple regression equations were applied to soils not used in the pot studies, but to samples taken from the 10-30 cm horizons (Table 3), values beyond the original data were encountered and led to negative yield predictions in some cases. This meant that the equations could not be used to obtain a relative fertility ranking as had been planned.

The results also suggest care in using multiple regression techniques to arrive at biological con-clusions. As given, as the coefficients came out of the machine tested for significance, the equations were biologically meaningless. For example, one would not judge from the physiological literature that barley and redwood differed so radically in their responses to % N and Ca^{++} concentration as was indicated by the differences between the regression coefficients. They probably do not. In addition, many of the regression coefficients have negative signs, whereas only Mg^{++} concentration showed a negative correla-tion with barley and redwood yields when compared alone. Obviously, the equations are only of predic-tive value. They cannot be used with safety on data of a different nature than the original data from which they were derived, as was shown here, nor can biological conclusions be derived from either the mag-nitudes or signs of individual coefficients in the equa-tions.

These results should not be unexpected. Mathe-matical statistics can test a hypothesis. The origin of the hypothesis is a heuristic question with which mathematical statistics has nothing to do. It is clear from the results presented here that ecologists need some original ideas on plant nutrition.

SELECTION OF A NUTRIENT GRADIENT

The nitrogen content of the soil has long been regarded as an indirect measure of productivity (Jenny 1941). Zinke (1960c) showed a correlation coefficient of 0.71 between the log of soil nitrogen content (g/m^2. 122 cm) and the site index of *Pinus ponderosa* (height at 300 yrs). Since nitrogen is absent from all igneous and metamorphic rocks and low in sedimentary rocks, its concentration in soils represents not only the inherent fertility of the parent material but also the influence of moisture, temperature, and changes in the floristic composition and growth of the vegetation. The origin of nearly all the soil nitrogen is the vegetation and associated biota. Of course the nutritional aspects of the soil usually are not unfavorable if the nitrogen content is high. Conspicuous exceptions are raw humus podzols and stagnant peat bogs in which most of the nitrogen is in a form unavailable to plants.

As a single measure of fertility or nutrient status the soil reaction (pH) has been widely used, particularly where the dominant soils are infertile podzols and acid peats (Schlüter 1957, Ellenberg 1950, Schairer 1960, Schönhar 1954). Our pH data (Table 3) show a range from 4.8 in the subsoil under oak to 7.8 in the Yorkville parent material. The slightly basic reaction of some soils derived from serpentine certainly does not indicate a favorable nutrient balance. In the study area both high and low pH values may indicate infertile soils, but the high values (low hydrogen ion concentrations) common on serpentine soils cannot be interpreted as representing high fertility as such values might on podzolic soils in other parts of the world. The view that California serpentine soils are infertile because of high pH (Gordon & Lipman 1926) is also incorrect and makes no ecological sense.

In areas of relatively uniform climate and parent material, such as are found throughout much of the Lake States and Canada, the silt and clay percentage is closely related to the nutrient status of the soils. However, it is also correlated with the moisture holding capacity and thus, by itself, is better used as an indicator of productivity as Pawluk & Arneman (1961) have done. In New Brunswick, Loucks (1962) derived a synthetic nutrient regime gradient based on the silt and clay percentage expressed as a logarithm and integrated with soil depth, A horizon characteristics, and slope position. His gradient applied only to soils developed on argillaceous drift. Knowledge of the silt and clay percentage is of little value in the redwood region where a wide range of parent materials is encountered.

Other elements have been used as indexes of soil fertility. Schairer (1960) employed available potassium to align soils in order of increasing fertility. In Finland and Germany, Viro (1951) found that Scots pine productivity increased almost linearly with an increase of exchangeable calcium over a range from 5.4 to 26.8 equivalents/m^2 . 30 cms (150

TABLE 11. Total nutrient content of soils associated with various vegetation types. Total N is expressed as g/m^2 to a given depth; cations as equivalents/m^2 to a given depth.

Vegetation Type	Stand	Depth (cm)	Total N	Replaceable Cations		
				K$^+$	Ca^{++}	Mg^{++}
Incense-cedar—Jeffrey pine	14	30	127	0.33	4.6	20.6
		100	144	0.42	5.3	29.0
Incense-cedar—Douglas-fir V	29	30	92	0.15	3.5	7.8
		100	128	0.27	6.2	17.4
Incense-cedar—Douglas-fir IV	13	30	533	0.98	19.6	115.0
		100	1213	3.09	76.4	449.1
Chaparral	4	30	103	0.88	16.0	8.2
		100	110	1.24	24.1	12.5
Chaparral	6	30	419	2.33	31.6	11.1
		100	498	2.83	38.8	14.1
Chaparral—Douglas-fir V	5	30	1053	2.88	16.1	4.1
		100	2163	5.90	22.6	7.3
Grassland	3	30	358	1.32	20.4	7.5
		100	409	2.20	23.5	12.5
Grassland	12	30	341	1.61	50.0	87.6
		100	747	3.47	275.6	261.3
Grassland	9	30	522	1.94	42.6	13.6
		100	1025	4.31	148.4	47.1
Deciduous Oak—Douglas-fir IV	10	30	401	2.79	52.1	19.5
		100	773	5.65	154.9	69.4
Deciduous Oak—Douglas-fir IV	15	30	431	1.49	20.7	25.6
		100	831	4.40	68.9	153.6
Deciduous Oak—Douglas-fir III	28	30	503	3.64	58.5	22.1
		100	1036	7.67	155.5	75.4
Madrone—Tanoak—Douglas-fir IV	27	30	658	3.58	29.8	8.9
		100	1363	10.10	95.9	27.9
Douglas-fir IV	7	30	787	2.87	15.1	3.8
		100	1461	5.80	31.4	13.5
Redwood IV—Douglas-fir IV	30	30	156	1.00	6.5	3.2
		100	312	2.67	25.8	11.1
Redwood III—Douglas-fir III	8	30	195	1.76	22.2	7.0
		100	481	5.95	79.4	28.1
Redwood III—Douglas-fir III	25	30	451	1.67	63.8	28.7
		100	1018	4.63	204.8	97.3
Redwood III—Douglas-fir III	26	30	538	3.94	53.6	15.1
		100	1294	12.69	171.9	59.6
Redwood III—Douglas-fir III	16	30	530	2.92	72.2	17.3
		100	1358	9.06	211.0	69.5
Redwood I—Douglas-fir II	19	30	573	1.77	35.0	11.1
		100	1089	4.55	73.3	28.1
Redwood I—Douglas-fir II	21	30	849	1.89	76.4	27.7
		100	1666	4.83	212.8	103.0
Redwood Flat Ia	1	30	394	1.67	49.6	29.4
		100	836	4.66	125.4	88.6
Redwood Flat Ia	20	30	393	1.18	47.1	22.2
		100	1053	3.78	150.2	86.7
Redwood Flat Ia	24	30	715	2.08	76.6	15.5
		100	964	5.25	155.8	36.8
Bay—Maple—Redwood III	23	30	476	0.96	34.2	36.8
		100	931	2.86	85.4	41.9
Alder	17	30	392	1.04	44.4	18.7
		100	934	2.91	134.5	58.7
Alder	18	30	420	0.95	24.2	15.5
		100	987	2.80	81.1	65.2
Alder—Maple	22	No analyses, located on rock outcrop in stream channel				
Maple—Cottonwood	11	30	267	0.89	47.1	20.0
		100	750	2.34	136.7	61.8
Cottonwood—Ash	2	30	110	0.71	29.1	12.6
		100	347	2.14	97.1	43.8

— 750 Kg CaO/hectare) on diluvial and morainic soils. Paterson (1961) even used electrical conductivity of the soil solution as a rough measure of soil fertility in the Scandinavian countries. Electrical conductivity has been used in Scandinavian bog ecology for many years (Sjörs 1950).

ESTABLISHMENT OF AN ENVIRONMENTAL NUTRIENT GRADIENT

From studying 75 simple correlation coefficients obtained in deriving the multiple regression equations, it was found that the replaceable calcium as well as total nitrogen content were significantly and positively correlated with all of the variables presented in Table 10, except for the concentration of magnesium. Calcium was selected as the variable best related to soil fertility in the study area because it more ably separates the nutritional aspects of the soil from the other environmental effects. As measured, the replaceable calcium is also more closely related to the concept of nutrient availability than is the total nitrogen content.

Table 11 presents the nutrient data expresed on a square meter basis to depths of 30 and 100 cms. This quantitative measure represents more realistically the amount of the various elements available to the plant than would be the case if data were expressed in other units which do not account for high rock content, differences in bulk density, and variation in soil depth. A nutrient gradient based upon the equivalents of replaceable calcium present in a square meter to a depth of 30 cm was finally established. The surface 30 cm probably include most of the feeder root system of trees and nearly all the root systems of herbaceous plants.

Comparisons between shallow and deep soils are more valid at the 30 cm depth because the confounding introduced by differences in moisture storage capacity is lessened. In any case, the gradient would not be greatly changed if the calcium contents were expressed on a cubic meter basis. The rank-correlation coefficient (Dixon & Massey 1957) was 0.93 between the soils aligned by analyses calculated on a depth of 30 cms and the alignment based on the contents of a cubic meter.

Figure 7 illustrates the distributional patterns of a number of species along the nutrient gradient (Ca^{++} Eq/m^2 . 30 cms). In general, the species appeared much less sensitive to this gradient than to the moisture gradient. *Pinus jeffreyi*, *Onychium densum* and a few other plants restricted to soils derived from serpentine in the study area exhibited patterns similar to *Libocedrus* (= *Calocedrus*) *decurrens*. Chaparral species such as *Arctostaphylos glandulosa* occurred on slightly more fertile sites than the locally serpentine-restricted plants. Most of the grassland species were well-distributed over the 20 to 50 range on the gradient. *Danthonia californica* and a few other native perennials had more restricted distributional patterns.

Dryopteris arguta appeared to be insensitive to the nutrient gradient as defined here. In all, more than 20 species showed bimodal or insensitive patterns.
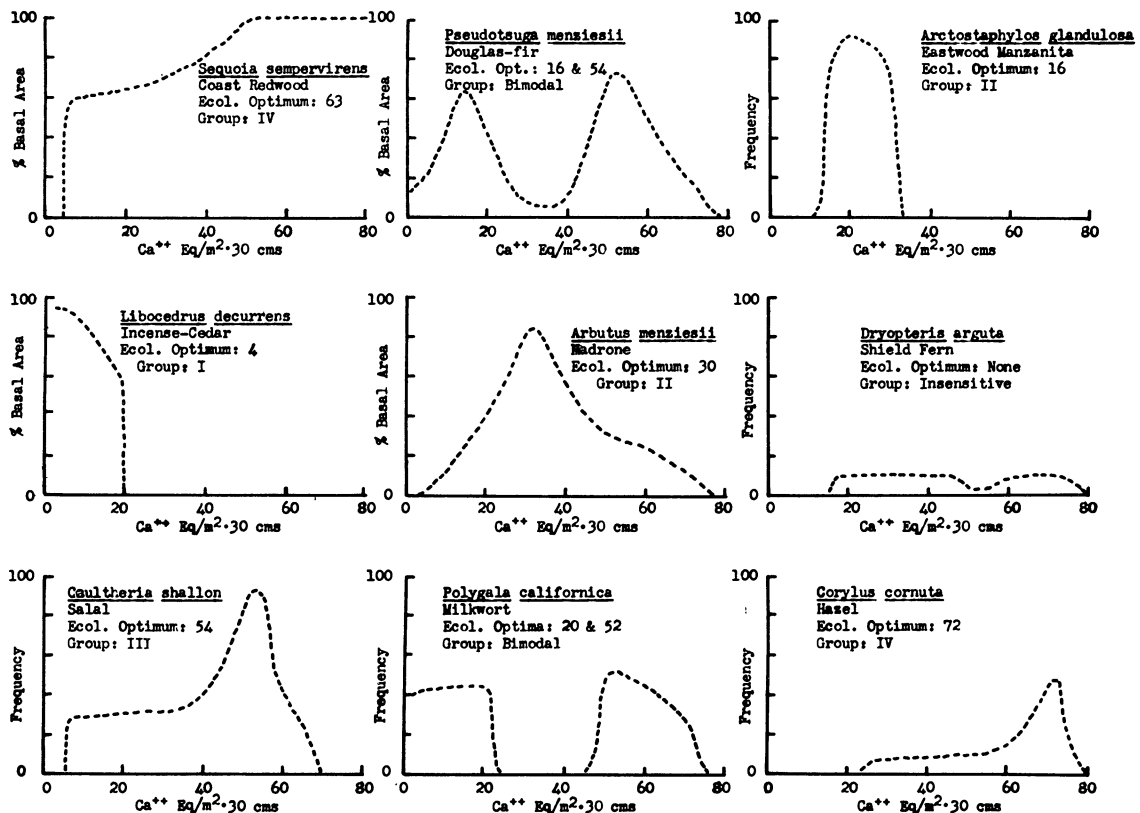

FIG. 7. Distribution of selected species in relation to a quantitative nutrient gradient of replaceable calcium (Eq/m^2 .30 cms).

The real significance of these two patterns may become apparent only with more intensive sampling and, eventually, a study of the genetic characteristics of the different populations. The bimodal pattern of *Polygala californica* suggests edaphic ecotypes as Whittaker has assumed in his paper on the vegetation of the Siskiyou Mountains (1960:311). However, experiments have yet to validate this assertion. Forced exclusion by better adapted species might just as well be the cause of a bimodal distribution (Knapp 1955, Ellenberg 1956, Walter 1960).

DERIVATION OF A VEGETATION NUTRIENT INDEX

Species were grouped according to the location of their ecological optima along the nutrient gradient. The gradient was divided into four equal sections because no apparent breaks in the distribution of ecological optima were observed. The characteristics of these groups are presented in Table 12. Table 6 assigns individual species to these groups.

TABLE 12. Characteristics of the nutrient groups.

Nutrient Group	Group Limits along Nutrient Gradient (Ca^{++} Eq/m².30 cms)	Average Ca^{++} Eq/m².30 cms for each Group	Number of Species in each Group
I	0–20	11.7	26
II	21–40	24.9	52
III	41–60	47.0	67
IV	61–80	73.0	16

A vegetation Nutrient Index (VNI)p was derived in a manner similar to that followed for the derivation of the Vegetation Moisture Index. A comparison of the (VNI)p values and the calcium concentration in the soils under the stands was made by linear correlation analyses (Fig. 8). The correlation coefficient was .784, still significant at the 1% level, but there was much greater variation between the observed and predicted values than was recorded with the moisture regime correlation. In addition to the reasons given for discrepancies between the Minimum-AM and (VMI)p values, two others should be mentioned. First, the nutrient gradient, as defined here, may not adequately represent the natural situation. Secondly, the gradient may describe a "potential" fertility which does not strongly influence the present distribution of species because other factors are relatively more important. The difficulties in evaluating the nutrient status of hydromorphic soils have already been discussed; low calcium concentrations in such soils can be offset by nutrient-rich seepage or ground water. Disregard of the other nutrients, and their relative abundance could account also for much of the observed variation. Finally, there is some evidence that another factor is relatively more important, or at least more closely correlated with the distribution of plants in the area. That factor is available soil moisture.

The sampling in this study could not be intensive enough to investigate soil nutrient status at several
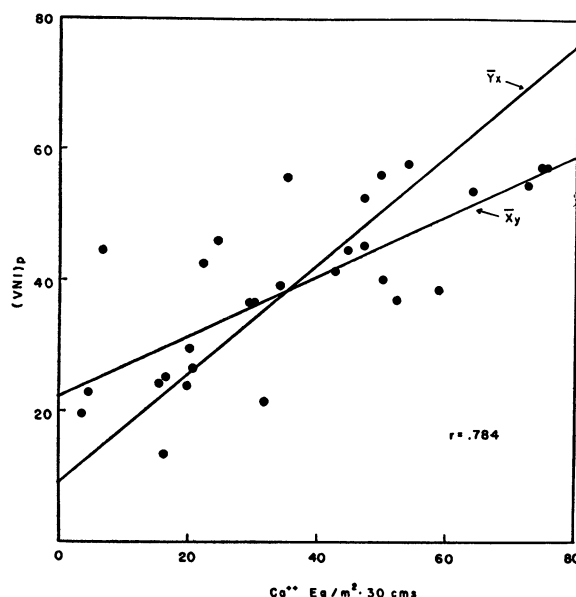

FIG. 8. Relationship between the Vegetation Nutrient Index (VNI)p and the replaceable calcium in the soil (Eq/m² .30 cm). r = 0.784.

different levels of soil moisture. Soil-moisture levels were unknown before this study was started. In the future, experiments could be designed to hold soil moisture constant by selecting plots on the basis of particular Minimum AM values.

THE LIGHT GRADIENT

Plants exhibit a number of physiological responses to solar radiation within the wave length range from 300 mu to 1000 mu. It is sometimes difficult to distinguish what part of this spectrum induces a particular response. Indeed, more than one response may be triggered by light within a narrow spectral band. Van der Veen & Meijer (1959) suggested the following spectral classification based upon dominant physiological responses.

1) All radiation greater than 1000 mu: no specific effect; wholly converted to heat if absorbed.
2) 700-1000 mu: specific elongation effect on plants.
3) 610-700 mu: spectral zone of maximum chlorophyll absorption and maximum photosynthetic activity; effect of "night-break" light also most marked.
4) 510-610 mu: zone of reduced photosynthesis for most plants and also reduced formative effect.
5) 400-510 mu: absorption by yellow pigments inducing phototropism, phototaxis, and protoplasmic streaming; second chlorophyll absorption peak.
6) 315-400 mu (ultra-violet A): formative effect on plants.
7) 280-315 mu (ultra-violet B): detrimental to most plants.
8) Less than 280 mu (ultra-violet C): rapidly kills plants.

The specific effects of light quality on seed germination, stomatal movement, phototropism, formation of anthocyanin, and other responses are discussed in detail by Van der Veen & Meijer. Wassink & Stolwijk (1956) concluded in their review article that photosynthesis, although possessing two peaks in its action spectrum, was related mainly to the total energy between 400 and 700 mu. Other parts of the spectrum affecting leaf development and pigment concentration influence photosynthesis indirectly, as do other physical factors (moisture, nutrients, and temperature). For optimum growth and development a wide range in the quality of radiation is necessary.

The relationships between plant growth and light intensity reflect, in part, the criterion chosen to assess "growth." Dry weight production was reported by Shirley (1929) to be almost directly proportional to light intensity up to about 20% of daylight; above this level the slope of the curve decreased. Shade tolerant plants showed decreases at lower light intensities than did intolerant species. In more recent papers Blackman and his associates found for a number of species that over the range from 100 to 10% of daylight net assimilation rate was directly proportional to the logarithm of the light intensity. Over the same range of light intensities the leaf-area ratio (leaf area/plant weight) exhibited an inverse linear relation to the logarithm of light intensity (Blackman & Rutter 1948; Blackman & Wilson 1951a, 1951b; Blackman & Black 1959). The relative growth rate, which was calculated as the product of the net assimilation rate and leaf-area ratio, showed a curvilinear relationship with the logarithm of light intensity (Blackman & Wilson 1951b).

In the experiments of Blackman & Wilson (1951b) the optimum light level for plant development was equivalent to full daylight or more and compensation points were similar for both "shade" and "sun" plants. This led to a redefining of "shade" and "sun" plants based on a differential ability to alter leaf-area ratios under shade, thus, a change from a physiological to a morphological definition of shade tolerance.

Blackman & Rutter (1946) explained one-third to three-fourths of the variation in density of *Scilla non-scripta* (L.) Hoffm. & Link (= *Endymion non-scriptus* (L.) Garcke) under different woodland communities by the linear regression of the square root of density against the logarithm of light intensity. In a study analyzing the distributional patterns of 47 species, Bray (1958) also justified the selection of a logarithmic light intensity scale. Bray tentatively explained the ecological distribution of plants in relation to light by a difference in compensation points or assimilation rates at a given light intensity. Along these lines, Shirley (1935) suggested the determining factor in plant distribution under forest cover was the ability to survive at light intensities too low for appreciable growth.

Decker (1955) criticized the use of unit leaf area

for expressing assimilation rates because the same leaf area may not have the same significance for "shade" as for "sun" plants. The light intensity where maximum photosynthesis occurs was also questioned as a valid measure of species tolerance to shade. In fact, Decker states that "there probably cannot be a universal denominator which will translate measurements of photosynthesis directly into reliable, broad ecological indexes, because the several aspects of ecological success are not necessarily closely and positively correlated." The explanation of differential ecological distribution in relation to light intensity may be contested, but evidence strongly supports the notion that a relationship exists between the logarithm of light intensity and plant growth or distribution.

Important in the consideration of light under a forest canopy is the possibility of change in light quality, as well as quantity. The differential absorption and transmission of light by vegetation is most apparent under a canopy of deciduous hardwoods (Knuchel 1914; Shirley 1929, 1935). In such forests, light intensity fluctuations with season are also more extreme. Knuchel concluded from study of more than a half-dozen species that under hardwoods the percentage of yellow and green light was increased significantly compared to the composition of sunlight in the open. Coombe (1957) compared a *Castanea* woodland with a *Picea* forest and stated that the deciduous cover was a very selective filter. All three authors concurred that light quality under most needle-leaved species changed very little as compared to skylight in the open.

Shirley (1935) went even farther, asserting that changes in spectral quality resulting from passage through a leafy canopy were of minor ecological significance. That herbaceous species do survive under dense shade but show none of the symptoms associated with plants grown under light of incomplete spectral quality supports his viewpoint. Still, as Coombe has emphasized, it is important to report the spectral sensitivity of the apparatus used for measuring light to facilitate the comparison of results and possible conversion to other energy units.

MEASUREMENT OF LIGHT INTENSITY

It is very difficult fully to evaluate diurnal and seasonal variations in light quality and quantity, even with modern instruments. Some of the difficulties were circumvented in this study by measuring light intensities only during the month of June after all deciduous hardwoods were in full leaf. The assumption was therefore implicitly made that light levels, and their effects, at other times of the year than June would correlate highly with the June measurements or would have no effects. Variations at many times of the year have no effect on plants at all—in the winter for example. The problem of evaluating diurnal fluctuations in light intensity was partially solved by selecting an integrating meter based on the chemical prop-

erties of anthracene. This choice also permitted a large number of simultaneous samples to be taken at a nominal expense (Dore 1958; Marquis & Yelenosky 1962). The sensitivity of anthracene lies largely in the ultra-violet, with absorption peaks at 360 mu and 379 mu. The glass containers utilized absorb much of the ultraviolet radiation and may partially offset any disadvantage associated with high ultraviolet sensitivity. Although not attempted, a measure of the variation in diurnal light intensity could be made if collections were taken at intervals throughout the day.

Anthracene ($C_{14}H_{10}$) in benzene solution polymerizes on exposure to sunlight into soluble dianthracene ($C_{14}H_{10})_2$. This photochemical reaction is independent of temperature under field conditions, but a pressure build-up with increasing temperature suggests care in the choice of containers. Analyses are made on the amount of unconverted anthracene remaining in solution after exposure.

A concentrated solution was prepared by dissolving 0.25 grams of anthracene in 125 ml of benzene, filtering, and then storing in an opaque, tightly capped bottle. For use the concentrated solution was diluted 1 : 100 with benzene in quantity sufficient to fill a selected number of 35 ml screw-top glass vials. If necessary, the concentration of the solution was adjusted so, when unexposed to light, a reading of approximately 1.00 optical density was obtained on a Beckman Model DU Spectrophotometer at 360 mu.

For both calibration tests and field use a similar procedure was followed. Glass vials were first filled with the prepared solution and sealed with a square of aluminum foil overlaid by a square of polyethylene before applying bakelite screw-caps. The vials were then stored, ten at a time, in light tight aluminum foil packs. Standard screens of green mosquito netting were constructed and calibrated with a Weston two-cell Illumination Meter (Model 603). Table 13 presents the average light intensities recorded with readings taken at 15 minute intervals from 10 :00-12 :00 A.M. on a cloudless day.

TABLE 13. Calibration of standard screens for light intensity measurements.

Layers of Netting	Percent of Daylight
0	100
1	44
2	18
3	8

On fresh anthracene solutions a linear relation between percent of full sunlight and the logarithm of optical density was found to exist. A standard curve is illustrated in Figure 9. The 100% level was replicated 5 times, the other levels 3 times. All points fell within the 95% confidence interval. Because data were available at both extremes, 0 and 100% light,
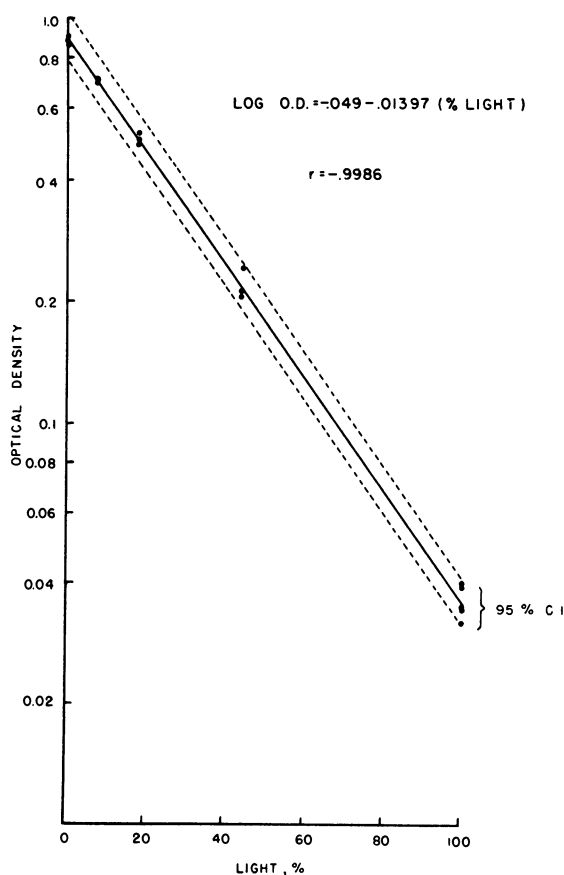

FIG. 9. Anthracene standard curve showing the regression of log of optical density on light intensity (%).

the 95% confidence interval appears between essentially parallel lines.

FIELD SAMPLING

An attempt to characterize the 30 stands by their average light intensities at ground level would have required an excessive number of samples. To attain a reliability within 10% of the mean at the 95% confidence interval Gatherum (1961) calculated that 136 to 1000 samples would be necessary in an oak forest, depending upon the uniformity of the overstory. For a study relating the distribution of 47 species in 17 stands, Bray felt 4000 intensity measurements still were insufficient (Bray 1958).

In this study it was desirable to sample, so far as possible, the range of light intensities over which each species grows. For such an approach, and with a limited number of samples, nonrandom sampling was adopted. Series of two square-meter circular plots were laid out in lines at irregular distances. At each plot two or three vials of anthracene solution were placed on uniform background (gray herbarium blotters), perpendicular to the contour. In cases where shrub cover dominated, some evaluation of light intensity was made at levels correspond-
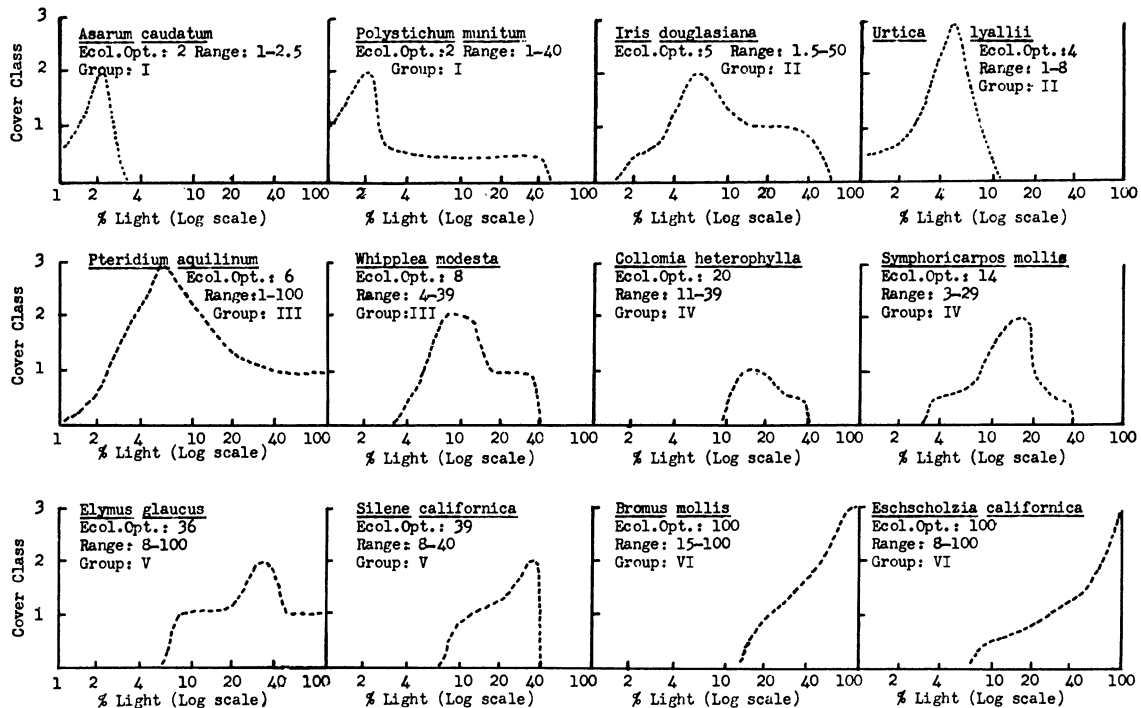
FIG. 10. Distribution of selected species in relation to a relative light intensity gradient.

ing to the average height of the shrubs. Other meas-urements were taken at ground level, after removing or compressing the herbaceous vegetation. Every species was assigned to one of the following cover-abundance classes (after Braun-Blanquet 1951):

5 covering 76-100% of ground
4 covering 51-75%
3 covering 25-50%
2 very numerous, or covering at least 5%
1 abundant, but with small coverage, or rather sparse with low coverage
+ sparse, with low coverage

To assure a valid comparison between plots the light-sensitive measuring units were placed out after sunset and collected the following evening (24-27 hours later). For every series standards were run in an open area (using calibrated mosquito netting). Each series of measurements was restricted to an area where differences in elevation and the duration of morning fog would not invalidate the results. All measurements were taken on nearly cloudless days with fog absent after 8:00 A.M.

ESTABLISHMENT OF AN ENVIRONMENTAL LIGHT GRADIENT

From a total of 136 sample plots the distri-butional patterns of more than 160 species were examined in relation to a logarithmic light intensity gradient. Figure 10 shows the distribution of 12 representative species along the light gradient. No tree species are shown because light measurements

were taken at not more than one meter above the ground, and sampling was restricted to undisturbed stands where few tree seedlings are to be found. Presented are the ecological optimum and the range of values over which each species was encountered. *Asarum caudatum*, wild ginger, was found restricted to sites with less than 3% of full daylight. Sword fern, *Polystichum munitum*, had its ecological opti-mum also at less than 3%, but extended up to 40%. At the other extreme occurred soft chess (*Bromus mollis*) and California poppy (*Eschscholzia cali-fornica*).

DERIVATION OF A VEGETATION LIGHT INDEX

For convenience in computing a Vegetation Light Index (VLI), the species were grouped according to the position of their ecological optima along the light gradient. The limits of these groups reflect apparent breaks in the distributional patterns of at least 10 species. Group VI may be unduly large, but a deficiency in measurements prevents more precise delineation at this time. For each light group an "Average Light Intensity Value" was calculated, based upon the ecological optima of all species with-in the group. The limits, number of species, and the average light intensity value for each group are given in Table 14. Assignment of species to the light groups has been given in Table 6.

Two Vegetation Light Indexes were calculated for each of the 30 stands. One was based upon the presence of species in each light group, and the other was weighted by the frequency value recorded for

TABLE 14. Characteristics of the light groups. Light was measured as percent of full sunlight.

Light Group	Group Limits along Light Gradient	Average Light Intensity Value for each Group	Number of Species in each Group
I	≤3	2.3	25
II	4–5	4.7	12
III	6–10	7.1	13
IV	11–25	16.4	35
V	26–50	34.0	12
VI	>51	100.0	61

each species in the field. Sample calculations are shown in Table 15. Tree species were excluded from most calculations because light measurements referred only to plants below 1 m in height, and by restricting sampling to only undisturbed stands few data on seedlings were gathered.

Statistically, there was no significant difference (at the 5% level) between the Vegetation Light Index based on presence (VLI)p, and that based on frequency (VLI)f, in all but 4 of the 30 stands. Since the relative abundance of species may be expected to change drastically when a stand is disturbed by cutting or fire, and because this change would not be reflected adequately if only the presence of species were considered, the (VLI)f was selected as the index most suitable for correlation with relative light intensity measurements under a wide variety of conditions. Correlation analyses between the

TABLE 15. Vegetation of a Maple—Bay stand (23) showing the derivation of the Vegetation Light Indexes (VLI)p and (VLI)f. Frequency data were obtained from randomly located plots (2 m² each) in an area 100 feet square. Plants found within this area but not occurring on any of the plots were assigned a 2% frequency value. The calculated (VLI)f of 2.5 corresponds with light intensity measurements averaging about 1% of full daylight.

(VLI)p	Light Group I; Average Light Intensity: 2.3		(VLI)f
(5×2.3)	*Acer macrophyllum* (seedlings)	70% frequency	(132×2.3)
	Polystichum munitum	20% frequency	
	Oxalis oregona	30% frequency	
	Viola glabella	10% frequency	
	Disporum hookeri	2% frequency	
	Light Group II; Average Light Intensity: 4.7		
(2×4.7)	*Dryopteris arguta*	2% frequency	(4×4.7)
	Stachys rigida	2% frequency	
	Light Group III; Average Light Intensity: 7.1		
(1×7.1)	*Rubus vitifolius*	2% frequency	(2×7.1)
	Bimodal, Insensitive, or Unevaluated Species		
	Rhus diversiloba	2% frequency	
	Umbellularia californica (seedling)	10% frequency	

(VLI)p=(5×2.3)+(2×4.7)+(1×7.1)=28.0/(5+2+1)=3.5
(VLI)f=(132×2.3)+(4×4.7)+(2×7.1)=336.6/(132+4+2)=2.5

(VLI)f and light intensity measurements were not attempted because of an insufficient number of samples under some of the more variable stands.

Figure 11 represents the distribution of 30 stands along a frequency weighted Vegetation Light Index (VLI)f. At one extreme on the gradient lies the maple—bay type where all light intensity measurements were less than 2%, and some were recorded
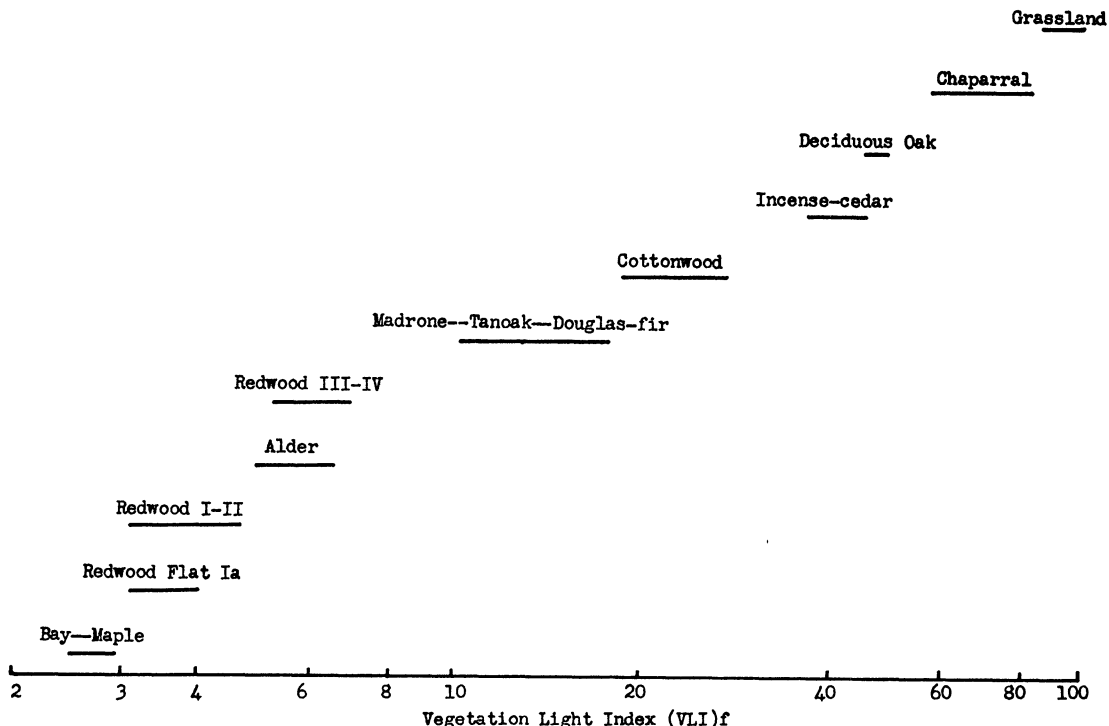

FIG. 11. Distribution of vegetation types in relation to a Vegetation Light Index (VLI)f based upon the frequency of non-arboreal species.

at less than 1%. Next occurs the redwood flat type with light intensity readings averaging near 2%. At the other extreme fall the grassland and chaparral types.

THE TEMPERATURE GRADIENT

Temperature influences the rate of chemical and biological processes. Plant growth, however, is not necessarily related to temperature during the growing season if other factors become critical. For many annuals, as well as other plants, day length rather than temperature triggers flowering. Initiation of growth in a number of trees similarly appears to be a photo-periodic response (Daubenmire & Deters 1947). For others there is a combined effect.

In the past Köppen, Mayr, Lang, De Martonne, Meyer, and others have developed empirical formulae and classifications relating temperature and other climatic features, particularly precipitation, to plant distribution. These and other climatic classifications are reviewed by Rubner (1938) and Daubenmire (1956). Most of these classifications are now of only historical interest. An exception is Thornthwaites' (1948) classification which includes an estimate of thermal effectiveness based on monthly mean temperatures and latitude. Using an annual sum of monthly heat indexes together with mean monthly temperature, an estimation of potential evapotranspiration is obtained from a nomogram and corrected for day length. The potential evapotranspiration is a measure of thermal effectiveness. This classification is widely used in plant geography and watershed management.

Paterson's CVP index (Climate, Vegetation, Productivity) has gained acceptance among foresters, at least in a modified form, throughout much of the world for estimating the potential productivity of large, inaccessible, or noninventoried areas. Paterson's index originally was derived from data on evapotranspiration, the average monthly temperature of the hottest month, the difference between the average temperature of the hottest and coldest month, the average precipitation, and the length of the growing season. The index was correlated with the measured yields of forests, mainly in Europe, and expressed the cubic meters of wood per hectare produced each year. The index has been tested in Germany by Weck and in Canada by Lemieux and found to be quite accurate (Lemieux 1961). In a recent publication Paterson modifies his definition of the growing season slightly and introduces a fertility factor based on the electrical conductivity of the soil solution (Paterson 1961).

With the advent of temperature controlled growth chambers, optimal day and night temperatures have been determined for numerous plants. Went (1957) discovered that the response of plants in controlled environments agreed closely with calculated "photo" and "nycto"—temperatures in the field. These values, more commonly referred to as "effective day"

and "effective night" temperatures, may be programmed into controlled laboratory experiments, with certain allowances for temperature extremes occurring during critical phases of plant development, to obtain results more closely related to field conditions and therefore more easily interpretable.

The effective day temperature is approximately half-way between the maximum and mean daily temperature; the effective night temperature is approximately half-way between the minimum and the mean daily temperature. Using just minimum and maximum temperatures furnished in meteorological data, the effective day and night temperatures may be approximated for any given period of time by the following formulae:

Effective Day Temperature = Temp. max. − ¼ (Temp. max. − Temp. min.)

Effective Night Temperature = Temp. min. + ¼ (Temp. max − Temp. min.)

Growth occurs predominantly during the night for many crop plants, but some respond more to the effective day temperature (Went 1953, 1957). With trees no simple relationship exists. Hellmers (1962) showed that, up to a certain point, the day and night temperature differential was important for the maximum dry weight production of Douglas-fir. Growth of redwood was found to respond to increasing day temperatures over a range of night temperatures. Only when day temperatures were held at 7°C did Hellmers find that night temperatures significantly affected growth. Hellmers' work was done with a 16-hr photoperiod and, unfortunately, at only low light intensities of around 600 fc (Hellmers & Sundahl 1959). Kienholz (1934) found no correlation between the rate of red pine terminal shoot elongation and daytime temperature, but there was a high correlation with minimum and mean night temperatures. Kramer (1957), working with loblolly pine, discovered growth increased with increasing day temperatures over a range from 17 to 30°C and decreased with increasing night temperatures from 11° to 23° C. Both he and Hellmers (1962) found growth, in the range investigated, was highly correlated with day-night temperature differential.

Predictions of the harvesting or flowering dates of various crops have been made by calculating "heat-sums," some type of summation of the total amount of heat received by plants during the growing season. Arnold (1960) illustrates the computation of heat-sums based on maximum and minimum temperatures above a given threshold of biological activity. Lindsey & Newman (1956) employed a slightly different approach, using daily maximum and minimum temperatures to calculate degree-hours above various statistically determined, meteorological threshold values. With Jeffrey pine, Hellmers (1962) showed that a 300° to 400° C degree-hour sequence in controlled environment chambers produced optimum dry weight yields. Theoretical objections to the heat-

sum concept are made because it usually assumes a linear growth curve and that plants may make direct use of heat energy. In addition, the concept completely disregards the importance of thermoperiodism and shifts in optimal temperature during plant development (Went 1953, 1957).

The paucity of weather stations in our study area makes direct extrapolation from the available records inadvisable. Nearly all the stations are restricted to valley bottoms and do not, under such circumstances, represent even the macroclimate of much of the area. Local climates are totally unmeasured. In this study minimum and maximum temperatures were measured under the various vegetation types for only a few days during July. From these measurements it can only be concluded that temperatures are less maritime over much of the area than would be suggested from published weather records.

Because of the known steep temperature gradient between fog-shrouded and fog-free areas, it was thought unwise to assume on theoretical grounds that one aspect might receive more or less radiation than another. Loucks (1962) made such assumptions but in New Brunswick, a climatically more uniform region. He made allowances, however, for the moderating effects of soil temperature upon air temperature, as well as the influence of relative slope position upon cold air drainage. Geiger (1961) has a detailed discussion of these problems. Work in Ontario by MacHattie & McCormack (1961) emphasized the necessity of recognizing modifying factors when they demonstrated with field measurements that a north slope could be warmer than a south slope.

ESTABLISHMENT OF AN ENVIRONMENTAL TEMPERATURE GRADIENT

In this study the plants alone were used to compare microclimatic variation among stands. Plants, particularly perennials, illustrate by their very presence that minimum temperatures have not fallen below the physiological tolerance of the species, with due consideration for the age of the plant and the stage of its development. An approach employing effective day-night temperatures seemed desirable. To this end, 20 of the 29 plant communities listed by Munz & Keck (1959) were selected, and the weather station records from areas where each community dominated were analyzed to obtain effective day and night temperatures.

The average monthly effective day-night temperatures for 29 California weather stations were calculated from U.S. Weather Bureau summaries (1925, 1934, 1958) or taken directly from the mimeographed paper by Kimball (1961). Copies of these data can be had on request from the authors. On plotting the effective day and night temperature data by months from each of the 29 stations, a separation into 5 groups, based on the non-overlapping of day and night temperature patterns and an effective night temperature range of less than 10°F during the

summer months, was suggested. On this basis the 5 patterns illustrated in Fig. 12 were constructed. The patterns reflect the temperature ranges of from 3 to 8 stations.

The arrangement of temperature patterns in relation to each other was determined by the presence of some communities in more than one temperature group (pattern). Yellow Pine Forests occur in both Group II and III. The North Coast Coniferous Forest exhibits its best development in Temperature Group IV, but is found also in Group V. Redwood achieves its best form under a temperature pattern similar to Group V, but also occurs in Group IV.

An arrangement based on heat-sums would have Group I patterns at one extreme and Group III patterns at the other. Such an arrangement would have breaks in the distribution of the plant communities defined by Munz & Keck (1959) which seem illogical.

An arrangement according to the length of the growing season was not used as a defining characteristic, although the growing season does increase proceeding from Group I through Group V. The growing season cannot be considered the number of days above a particular minimum temperature because growth thresholds vary between species. Similarly, it is meaningless to say that the growing season extends until the temperature drops below a certain minimum value when other factors such as the availability of soil moisture have earlier become limiting. As mentioned previously, photoperiod may influence growth initiation, and even high temperatures have been shown to induce dormancy in some plants long before the first autumn frost (Kramer 1957).

The dominant communities in the areas of each of the five temperature groups, characterized by the effective day-night temperature patterns shown in Fig. 12, are as follows: I. Subalpine temperature climate includes Munz & Keck's Subalpine, Red Fir, and Lodgepole Pine Forests. II. Cold desert and montane temperature climates include Northern Juniper Woodland, Sagebrush Scrub, and Mixed Coniferous Forest. We differentiate the *Pinus ponderosa* belt of the Sierra Nevada into an upper elevation, Mixed Conifer Forest community with *Pinus ponderosa, P. lambertiana, Pseudotsuga menziesii, Abies concolor, Calocedrus decurrens, Quercus kelloggii*, and occasionally *Sequoiadendron gigantea* from the lower elevation, pure Yellow Pine Forest community. III. Continental Central Valley and foothill temperature climates include Chaparral, Foothill Woodland, Northern and Southern Oak Woodlands, Valley Grassland, and pure, low altitude Yellow Pine Forest. IV. Cool, temperature climate includes Mixed Evergreen, Douglas Fir, and North Coast Coniferous Forests. V. Coastal, maritime temperature climate includes Redwood and Closed Cone Pine Forests, North Coast and Coastal Sage Scrubs, and Coastal Strand.

The ecological optimum for a particular plant species, with respect to temperature, is very difficult
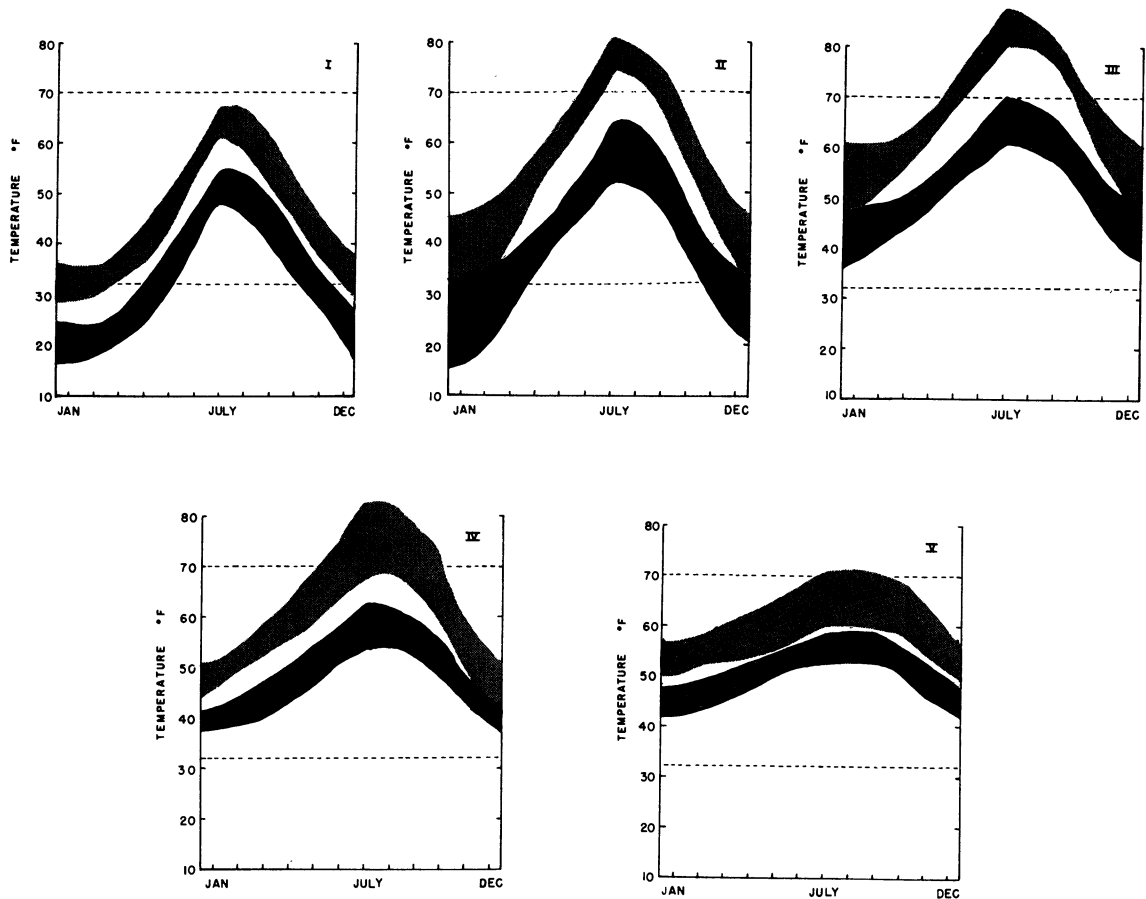
FIG. 12. Effective day and effective night temperature patterns. Reference lines are drawn at 70° and 32° F to aid in comparing one pattern with another.

to determine from Munz & Keck's descriptions because, as taxonomists, they are more interested in the range of a species than in where it dominates. When one must consider the entire genetic complex of a species, rather than relatively uniform local populations, problems of precise habitat description arise. Also, over a wide geographic range the continuous changing of associated species makes generalizing about the ecology of a single species very difficult.

In order to use Munz & Keck's flora (1959), the best readily available reference on the autecology of California plants, the following procedure was followed in assigning species to one of the five temperature groups.

1) A species listed under a community description in the introductory portion of the Munz & Keck flora was assigned to the same temperature group as that community.

2) A species listed in the manual in a number of different communities was assigned to the temperature group which contained the largest number of communities containing the species.

3) A species listed as equally represented over a range of not more than three groups was assigned to the centrally located, or "mean" temperature group of the three.

4) In those cases where a species was listed as having a range of occurrence in more than three adjacent groups, or was described by only vague generalities, no assignment was made.

DERIVATION OF A VEGETATION TEMPERATURE INDEX

All 30 stands were analyzed on the basis of their species composition. The distribution of species by temperature groups is given in Table 6. That few of the so-called weeds were assigned to any temperature group is probably due to their wide physiological potential, possibly to some ecotypic variation, and to the lack of attention paid to their ecology. No weed communities were recognized by Munz & Keck, although in European phytosociology they are the focus of much work.

In the calculation of a Vegetation Temperature Index (VTI)p a linear relationship between groups was assumed, although some other relationship may be equally justified. The actual calculations are precisely the same as those used by Ellenberg (1950,

1952), Bakuzis (1959) and Griffin (1962) in determining their vegetation-defined temperature indexes. Only the definition of temperature groups and the assignment of species to these groups varies. The calculation of Vegetation Light Indexes by both presence and frequency which is illustrated in Table 15 is analogous. The Vegetation Temperature Indexes calculated for stands in the study are summarized in Table 16.

TABLE 16. Summary of Vegetation Temperature Index (VTI)p values by vegetation types.

Vegetation Type	Number of Stands	(VTI)p Range	(VTI)p Average	Modal Temperature Group
Incense-cedar	3	3.2–3.3	3.26	III
Chaparral	3	3.5–3.6	3.58	III
Grassland	3	3.5–3.7	3.58	III
Deciduous Oak Douglas-fir IV	3	3.7–4.0	3.84	IV
Madrone, Tanoak	2	3.9–4.1	4.00	IV
Alder	3	4.0–4.3	4.13	IV
Cottonwood, Ash	2	4.3	4.30	IV
Redwood, Bay	11	4.4–4.7	4.55	V

All stands with redwood were grouped together in Table 16 because no microclimatic differences could be distinguished on the basis of (VTI)p values. The knowledge that redwood did not occur in stands with a (VTI)p below 4.4 can be useful only if it is recognized that ecologic, not physiologic, limits are implied. The (VTI)p values are correlated with the temperature group patterns, but have no one-to-one relationship. The modal temperature group for each of the vegetation types was the same for all stands included under each type. The modal temperature groups for each of the vegetation types was the same for all stands included under each type. The modal temperature groups are assumed to be directly related to the temperature group patterns presented in Fig. 12, but this relationship has been only approximately varified by comparison with data derived from the weather station at Scotia in the Eel River Valley and with records taken during the summer months on Grasshopper Peak by the California Division of Forestry.

By comparing the Vegetation Temperature Index values the study area can be subdivided into three statistically significantly different physiographic subunits: (1) the Eel River Valley which provides a pathway inland for summer fog off the Pacific Ocean; (2) the Grasshopper Peak area above 2,500 ft elevation; (3) the Salmon Creek drainage south of the park outside the effects of summer fog and therefore less maritime than the climate within the major drainage system. The Eel River Valley with 18 stands had an average (VTI)p equal to 4.35; the Grasshopper Peak stands, 6 in number, averaged 3.70; and the Salmon Creek drainage, also with 6 stands, had an average of 3.50. The mean (VTI)p of the Eel River Valley stands differed from the other areas at

the 1% level of significance. The mean indexes from the Salmon Creek and Grasshopper Peak areas were not significantly different at the 5% level.

The approach used here, while crude, seems to have some merits. The extent of its usefulness for genetic and ecological problems involved in comparing climates of different geographic areas is not known, but will be investigated in the future. Similar approaches by Ellenberg (1950) in Europe, and Bakuzis (1959) in Minnesota have already proven of value in their respective regions. Recently Griffin (1962) used the method to compare different seed source areas in a study of the intraspecific variation in *Pinus sabiniana*.

INTERRELATIONSHIPS BETWEEN MOISTURE, NUTRIENT, LIGHT, AND TEMPERATURE GRADIENTS AND THE VEGETATION

The value of presenting relationships in a multi-dimensional scheme has already been emphasized in the theoretical discussion. For mechanical convenience in drafting as well as for simplifying interpretation, only two coordinates have been presented at a time with a third dimension represented by isolines.

The distribution of major vegetation types within both environmentally and vegetationally defined moisture and nutrient coordinates is illustrated in Fig. 13. The Roman numerals indicate site index classes for redwood and Douglas-fir (Table 17), modified

TABLE 17. Ssite index classes based on the maximum height of old growth Redwood and Douglas-fir. See text for sources of data.

Site Class	Redwood	Douglas-fir
Ia	>300	—
I	251–300	>250
II	211–250	213–250
IJI	171–210	173–212
IV	131–170	133–172
V	≤130	≤132

slightly from those given by Barnes (1924) and McArdle et al. (1949). The greatest difference between the two patterns lies in the degree of compression in the vertical direction. The vegetation-derived pattern may more closely represent the true edaphic site complex because physical measurements of soil fertility did not take into account seepage and ground water supplied nutrients. Those situations where physiographic compensation was most apparent (Stands 22 and 30) did not correspond with the ecological optima of most species in the stands and therefore were not misrepresented when vegetation indexes were calculated.

In the redwood Ia type found on the alluvial flats, timber volumes from 35,000 to 80,000 cubic feet per acre were recorded. On the less fertile, dry
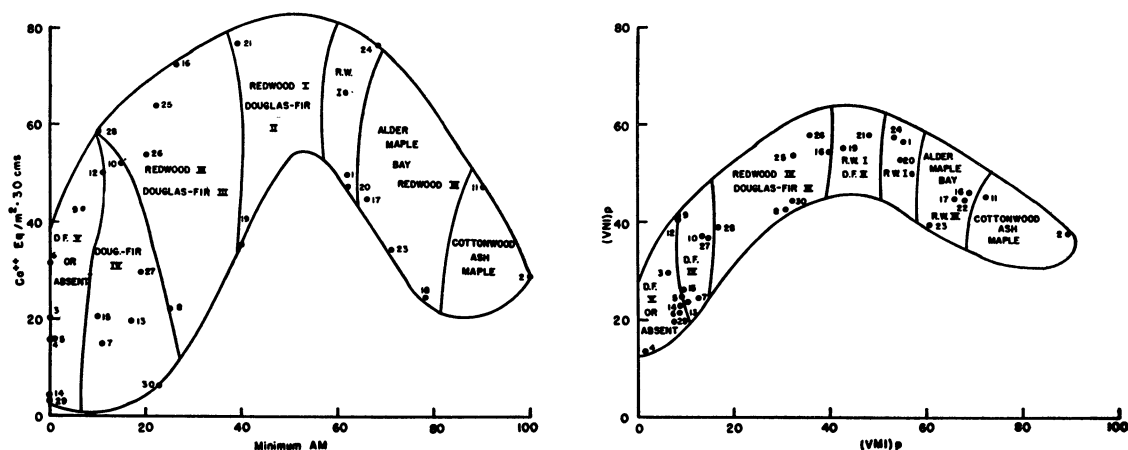
FIG. 13. Distribution of major vegetation types within environmental (left) and vegetational (right) coordinates of moisture and nutrients.

and wet sites, volume production dropped to less than 2,000 cubic feet per acre. Basal area and cubic foot volume data are summarized for each stand in Table 2. Cubic foot volumes for the conifers were calculated from basal area-total height correlations (Spurr 1952), and the hardwood volumes were determined from local volume tables.

Figure 14A illustrates the distribution of stand Vegetation Light Index values (VLI)f, within the moisture-nutrient coordinates (VMI)p and (VNI)p. The lowest indexes were recorded in nearly pure redwood and bay-maple stands. The light indexes increase progressively through the alder types to cottonwood-ash stands. In the other direction a very abrupt increase in (VLI)f values occurs as both moisture and nutrient indexes decrease. Grassland and chaparral types are situated in the dry and nutrient-poor region of the edaphic site complex.

Figure 14B presents the distribution of Vegetation Temperature Index values (VTI)p within edaphically related coordinates of (VMI)p and (VNI)p. The most maritime microclimates, it is shown, are

associated with the most fertile, mesic sites. As conditions become increasingly wetter the temperature indexes decrease slightly. The driest, least fertile sites have the most extreme, least maritime, microclimates.

A more complete picture of the relationships between all vegetation indexes is given in Fig. 15. In Diagram A an absence of mesic-infertile conditions is noted. Perhaps some unsampled rock-outcrops near the Eel River would represent such situations. Diagram B shows an abrupt decrease in the light indexes as the moisture indexes increase, reaching a low of 2.5 at a (VMI)p of 60.7. At higher moisture indexes the light values again increase. The third coordinate system using (VMI)p as one of the axes (Diagram C) shows (VTI)p increasing strikingly as the moisture indexes increase, reaching highest values, indicating the most maritime microclimates, between about 30 and 40 on the (VMI)p gradient.

In Diagram D an inverse relationship between the (VLI)f and (VNI)p is indicated. In other words, the stands with high nutrient indexes gen-
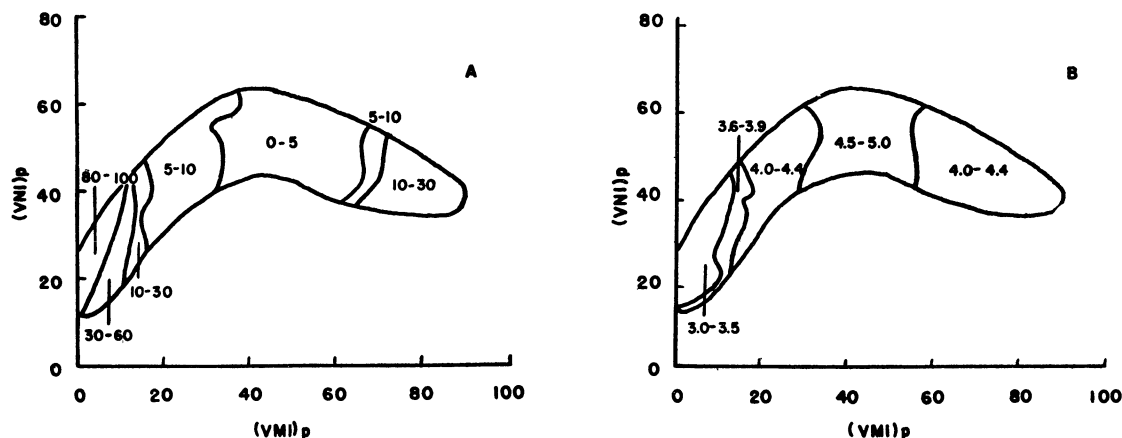

FIG. 14. Distribution of Vegetation Light Index (VLI)f values (Diagram A) and Vegetation Temperature Index (VTI)p values (Diagram B) within moisture (VMI)p—nutrient (VNI)p coordinates.
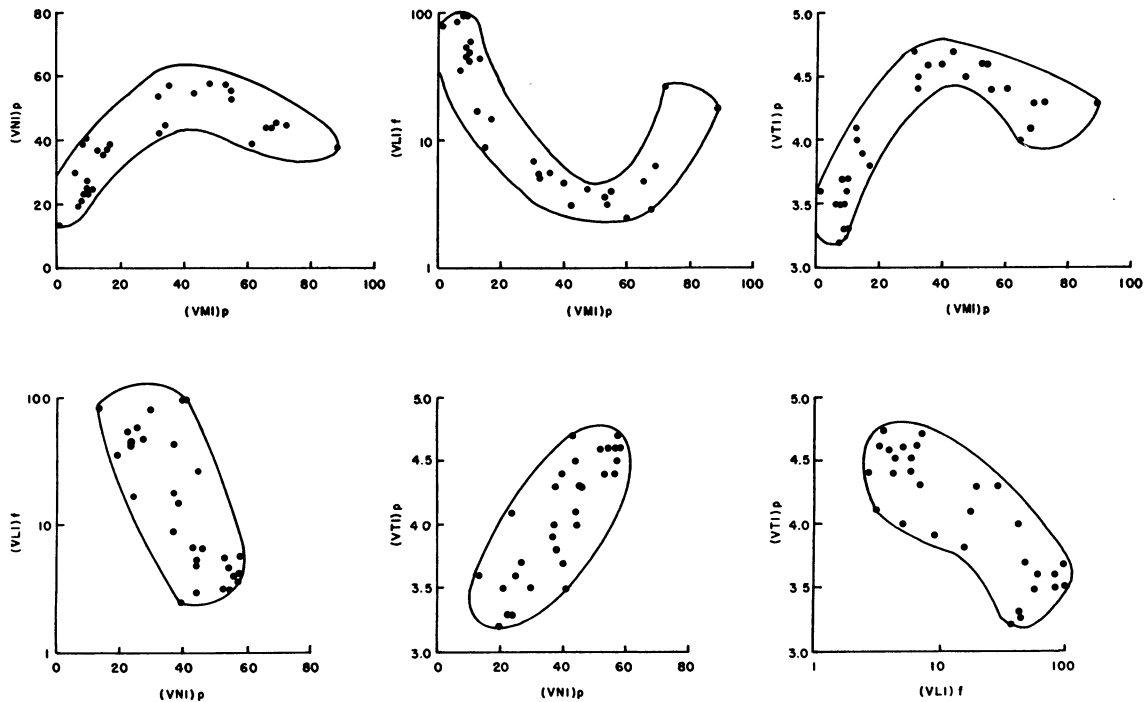
FIG. 15.   Bivarite relationships between vegetational indexes.

erally have lower light intensity index values than those with low nutrient indexes. A positive correlation between the (VTI)p and (VNI)p in Diagram E signifies that the most maritime microclimates are also associated with the most fertile sites. Finally, in Diagram F the pattern indicates that the most extreme sites are not those with the highest light indexes, but that a general trend from low (VTI)p associated with high (VLI)f to high (VTI)p associated with low (VLI)f does exist. The scale for (VLI)f, it should be noted, is logarithmic. A summary of all indexes used in constructing Fig. 15 is presented in Table 18.

Population distributions of selected species are illustrated in Figures 16 and 17 within coordinates of moisture-nutrients, and light-temperature. The (VLI)f values for all tree species relate to the light intensity beneath the tree canopies and are not indicative of tree seedling ecological requirements. The patterns are in agreement with generally recognized facts.

Redwood, the dominant, semi-permanent (climax) type in the region, occupies the fertile, moist sites associated with a moderate microclimate. The low (VLI)f values indicate that most of the light is absorbed by the tree canopy, permitting very little to reach the forest floor. In the study area incense-cedar and Jeffrey pine are both restricted to the least fertile sites with most extreme microclimates. In other parts of their geographic distribution they occupy quite different positions. Douglas-fir and particularly bay show indications of separate popula-

tions. The distribution patterns of *Polygala californica* show complete breaks within both coordinate systems. *Holodiscus discolor, Rhus diversiloba, Rubus vitifolius, Vancouveria planipetala, Dryopteris arguta* and other species which had bimodal or insensitive patterns to one or more of the gradients (See Table 6) warrant careful genetic investigation and also tests of competitive exclusion.

From the evidence of individual species distributions (Figs. 16, 17), boundaries between the vegetation units should not be sharp. There is no conflict here with the recognition of types of stands (associations) based on a characteristic species combination. Table 19, illustrating the occurrence of selected species within the 10 vegetation types, shows a number of species are exclusive. The species selected, for the most part, have relatively narrow distributions and their presence in a stand could be used to roughly define the vegetation type, and with the aid of figures presented in this section, the approximate position along the various gradients.

APPLICATIONS

A method which requires only the accurate recognition and listing of plant species (or at most, simple measures of abundance) and some simple calculations to compare different environments in regard to gradients has considerable practical significance. The vegetationally defined gradients can be used directly to help solve many problems without requiring expensive and time-consuming measurements of the environmental factors.
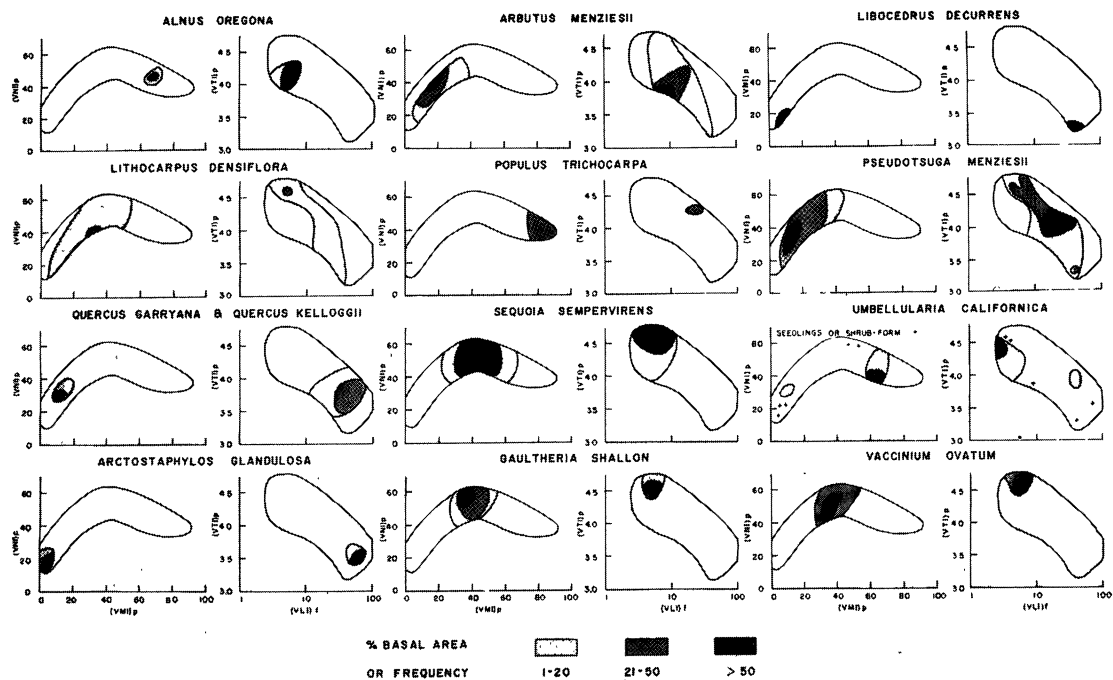
FIG. 16. Distribution of selected tree and shrub species within moisture (VMI)p—nutrient (VNI)p and light (VLI)f—temperature (VTI)p coordinates.
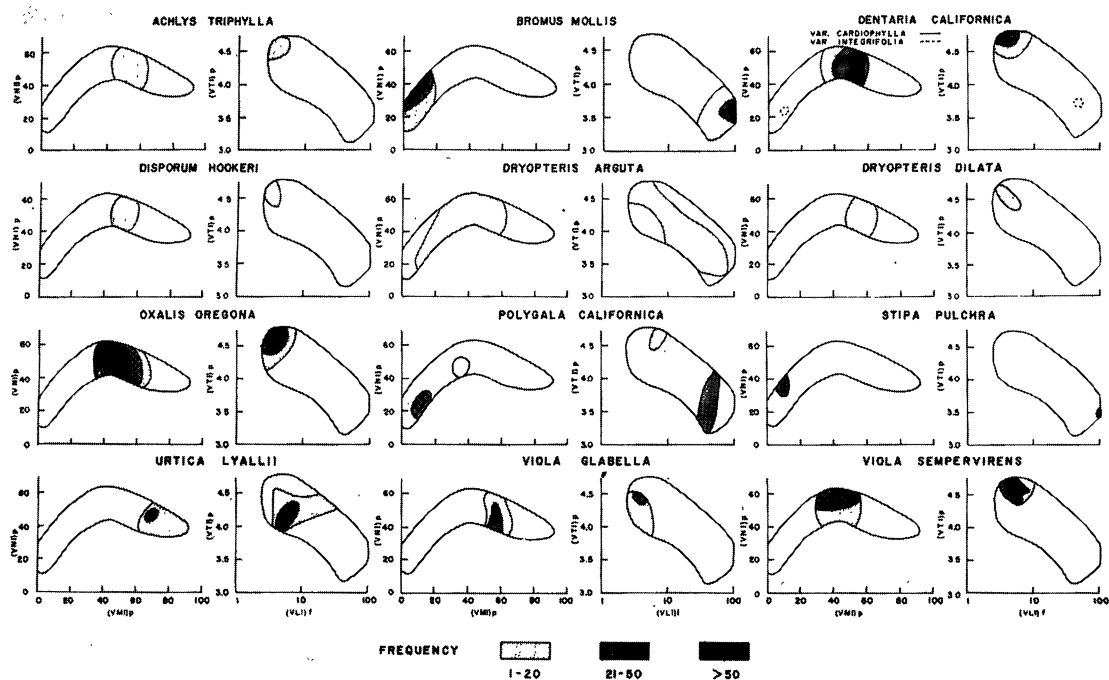

FIG. 17. Distribution of selected herbaceous species within moisture (VMI)p—nutrient (VNI)p and light (VLI)f—temperature (VTI)p coordinates (for D. dilata read D. dilatata).

TABLE 18. Summary of vegetation indexes for all stands.

Vegetation Type	Stand No.	(VMI)p	(VNI)p	(VLI)f	(VTI)
Incense-cedar Jeffrey pine	14	9.0	23.1	45.3	3.3
Incense-cedar	29	7.6	19.6	35.8	3.2
Incense-cedar Douglas-fir IV	13	10.1	23.8	43.1	3.3
Chaparral	4	1.3	13.6	82.4	3.6
Chaparral	6	8.4	21.5	55.7	3.5
Chaparral Douglas-fir V	5	9.7	25.2	59.5	3.6
Grassland	3	6.1	29.6	86.8	3.5
Grassland	12	8.4	40.5	98.2	3.7
Grassland	9	8.1	41.2	95.4	3.5
Deciduous Oak Douglas-fir IV	10	13.1	37.0	44.2	4.0
Deciduous Oak Douglas-fir IV	15	9.5	26.6	48.7	3.7
Deciduous Oak Douglas-fir III	28	16.8	38.7	15.5	3.8
Madrone Tanoak Douglas-fir IV	27	14.6	36.5	9.0	3.9
Douglas-fir IV	7	12.5	24.2	17.6	4.1
Redwood IV Douglas-fir IV	30	32.0	44.4	5.3	4.5
Redwood III Douglas-fir III	8	30.8	42.5	6.9	4.7
Redwood III Douglas-fir III	25	32.0	53.4	5.5	4.4
Redwood III Douglas-fir III	26	35.6	57.8	5.7	4.6
Redwood II Douglas-fir III	16	39.7	54.3	4.7	4.6
Redwood I Douglas-fir H	19	42.9	55.6	3.1	4.7
Redwood I Douglas-fir II	21	47.8	57.7	4.2	4.5
Redwood Ia	1	55.0	56.2	4.0	4.4
Redwood Ia	20	54.2	52.6	3.2	4.6
Redwood Ia	24	53.0	57.7	3.7	4.6
Bay Maple Redwood III	23	60.7	39.1	2.5	4.4
Alder	17	65.4	44.5	4.9	4.0
Alder	18	68.9	45.9	6.6	4.3
Alder Maple	22	67.7	44.5	3.0	4.1
Maple Cottonwood	11	72.0	45.3	27.2	4.3
Cottonwood Ash	2	89.1	37.5	18.2	4.3

For instance, park managers may use the Vegetation Light Index (VLI)f to determine where weed invasion may become a major problem. Below a (VLI)f value of 6 it is safe to say that only a few introduced weeds such as *Hedera helix* (German ivy) and *Vinca major* can survive, and these are only a threat in the study area under restricted edaphic and climatic conditions, i.e., Vegetation Moisture Indexes (VMI)p between 40 and 60, Vegetation Nutrient Indexes (VNI)p above 35, and Vegetation Temperature Indexes (VTI)p of 4.5 or above.

An area mapped in regard to the various vegetation indexes could be used by scientists in many fields to provide an initial framework for collecting and analyzing data. In other words, from a map of redwood area vegetation units floristically defined, one could read off environmental values for soil moisture, nutrients, light, and temperature regime. In biosystematic studies populations could then be selected which occupy the most different environments in the area. The differences could be quantitatively expressed. Seed source studies and future plantation areas could be easily evaluated and on a sounder basis than is now practiced where stratification by altitudinal zones and geographical location is employed.

In forestry different areas with similar environments could be selected by using the vegetation indexes, or maps derived from them, to conduct experiments on natural regeneration, brush control, growth response to silvicultural treatment, or prescribed burning. This would provide a welcome change from the present practice of sampling only by cover type, basal area, or site index classes.

The use of productivity alone as a foundation for any type of management should not be encouraged. Once virgin stands are removed the value of measurements on young-growth forests, even those fulfilling mensurational requirements for site index determinations, is in doubt. First, because such environmental factors as the mechanical effects of wind or a deep water table or hardpan may not be effective until trees near maturity; and secondly, because genetic variation is generally disregarded when comparisons are made between different areas.

Even when productivity is determined on old-growth stands, similar site classes may correspond to distinctly different environments. Site quality III redwood is found in two separate parts of the edaphic site complex (Fig. 13). On the drier aspects redwood and Douglas-fir occur together above a dense understory of huckleberry and salal. See distributions of *Vaccinium ovatum* and *Gaultheria shallon* in Fig. 16. But on the wetter situations bay and maple dominate with shrub cover nearly absent. Likewise, Douglas-fir III not only is produced in stands with redwood, but occurs with oak, characteristically with only a grass and forb understory.

Within each of the vegetation types a different successional potential may be expected. On the drier, more extreme microclimatic sites a fire during an

TABLE 19. Occurrence of selected species within the major vegetation types.

Species	1 Grass	2 Deciduous Oak Douglas-fir	3 Incense-cedar	4 Chaparral	5 Douglas-fir IV Madrone-Tanoak	6 Redwood III Douglas-fir III	7 Redwood I Douglas-fir II	8 Redwood Ia	9 Alder	10 Cottonwood Ash
Stipa pulchra	xx									
Sherardia arvensis	xx	x								
Danthonia californica	xx	x								
Cynosurus echinatus	xx	x								
Avena barbata	xx	x	x							
Lotus micranthus	xx	x	x							
Festuca megalura	xx	x	x							
Elymus glaucus	xx	x	x							
Eschscholzia californica	x		x							
Sanicula crassicaulis		x								
Dentaria californica var. integrifolia		x								
Melica geyeri		x								
Bromus mollis	xx	x	x	x						
Eriophyllum lanatum		x	xx							
Heteromeles arbutifolia			xx							
Plectritis congesta		x	xx							
Onychium densum			xx							
Silene californica		x	xx	x						
Tauschia kelloggii				x						
Chorogalum pomeridianum		xx		x						
Garrya fremontii				xx						
Pedicularis densiflora				x						
Ceanothus parryi				xx						
Ceanothus incanus				xx	x					
Aster radulinus				xx	x					
Arctostaphylos glandulosa				xx	x					
Apocynum pumilum				x	x					
Cynoglossum grande				x	x					
Viola ocellata		xx			x					
Gaultheria shallon						xx	x	x		
Vaccinium ovatum						xx	x	x	x	
Oxalis oregona						x	xx	xx	x	
Viola sempervirens						xx	x	x		
Trillium ovatum						x	x	xx		
Dentaria californica var. cardiophylla						x	x	xx		
Disporum smithii							x	xx		
Scoliopus bigelovii							x	x		
Clintonia andrewsiana							x	x		
Asarum caudatum							xx	x		
Achlys triphylla							x	x		
Anemone deltoidea							x	xx		
Tiarella unifoliata							x	xx	x	
Hierochloe occidentalis							x	xx	x	
Viola glabella							x	xx	x	
Rubus parviflorus							x	x	xx	
Adiantum pedatum							x	x	xx	
Blechnum spicant							x	x	xx	
Athyrium filix-femina								x	xx	
Hydrophyllum tenuipes								x	xx	
Urtica lyallii								x	xx	
Sambucus callicarpa								x	xx	
Dryopteris dilatata								x	x	
Rhamnus purshiana								x	xx	
Cornus nuttallii								x	x	
Aralia californica									x	
Glyceria elata									x	
Woodwardia fimbriata								x	x	
Acer circinatum									x	
Stellaria crispa									x	
Oenanthe sarmentosa									x	
Euonymus occidentalis									·x	
Artemisia douglasiana										xx
Cirsium arvense										xx
Salix lasiandra										x

unfavorable seed year may bring about the replacement of nearly pure stands of Douglas-fir with manzanita (*Arctostaphylos glandulosa*), other chaparral species (*Ceanothus incanus, C. parryi, Garrya fremontii*, etc.), or madrone. A fire, under the same conditions, on the more mesic, fertile sites (dominated by Redwood I—Douglas-fir II stands) often leads to brush fields dominated by *Ceanothus thyrsiflorus*.

In general, after disturbance of a stand by cutting or fire a number of light-demanding species assume dominance. Careful inspection, however, usually demonstrates that a majority of the species found in the original forest are still present, although in reduced numbers. Later, when young-growth forests take over, the successional species are greatly reduced, both in number and abundance. The successional species are not insensitive to the environment and may be assigned also to ecological groups according to their distribution along environmental gradients. So long as there is a complete plant cover and extensive erosion does not take place, the edaphic environment may not be drastically changed by fire or logging. Because the approach suggested here allows for the replaceability of one species for another and is not hampered by the dominance concept it has equal utility, regardless of the phase in succession.

Just outside the study area a comparison was made between an uncut Redwood I—Douglas-fir II stand with a basal area of 356 square feet per acre and an adjacent area, clearcut within the last 3-4 years, now dominated by *Erechtites arguta* and *E. prenanthoides*. The vegetation indexes were essentially the same on the two areas except for the (VLI)f, which was 34.0 on the cutover and 4.5 in the virgin stand. Other values in the uncut stand and cutover were respectively: (VMI)p: 43 and 47; (VNI)p: 55 and 53; (VTI)p: 4.7 and 4.5. This demonstrates how logged and burned areas may still be evaluated in relation to the semi-permanent types, a necessity in any detailed successional study.

Finally, the gradient analysis approach has application in plant sociology where the present system (Braun-Blanquet 1951) is limited in ecological interpretation and correlation from region to region by dissimilarities in regional floras. The method suggested here can be used gradually to bridge these gaps.

SUMMARY

For the ecological comparison of ecosystems a gradient analysis of floristically-defined vegetation stands is suggested which is applicable within the framework of presently accepted ecological theories and applies to both disturbed and undisturbed vegetation. An attempt was made to measure the environment in terms physiologically meaningful to plants, and at the same time, applicable to controlled environment studies. "Effective factors" which operate directly upon the plant were stressed rather than omnibus collections of several factors, e.g. elevation and parent material, or various forms in which the effective factors may be supplied to the plant.

Although few if any species respond identically to a given intensity of an environmental factor, plants may still be grouped in relation to the location of their ecological optima (highest population density, not size of individuals) along various effective environmental gradients. By analyzing the species composition of a stand in regard to these ecological groups, vegetation indexes were calculated which related directly to measured environmental gradients.

To demonstrate the approach, 30 stands, representing 10 relatively stable or persisting vegetation types, were examined in the vicinity of Humboldt Redwoods State Park located in the North Coast Ranges of California. Gradients of available soil moisture, soil nutrients, light, and temperature were employed in studying the distribution of the species in the vegetation.

The moisture gradient selected was defined as the minimum available moisture reached during the year in the surface meter of soil, expressed as percentage of the total storage capacity. This measure was found to be much more significant than total storage capacity on sites unaffected by a permanent water table. Where a permanent water table existed other parameters were required. The correlation between a Vegetation Moisture Index based on species presence (VMI)p and the Minimum Available Moisture had a correlation coefficient of .97 which was significant at the 1% level.

In an attempt to quantify a nutrient gradient, soil analyses and pot studies using redwood, Douglas-fir, barley, and Australian fireweed (*Erechtites arguta*) were conducted on soils collected from the study area. Multiple regression equations were useful in predicting dry weight yields of redwood and barley on the basis of soil chemical analyses, but the equations could not be applied widely and were biologically meaningless. Calcium and nitrogen were elements most highly correlated with the concentration of other nutrients. Because nitrogen is absent from the parent rock, its presence in the soil is related more closely to productivity than to fertility. Therefore, the replaceable (exchangeable + soluble) calcium concentration, expressed in equivalents per square meter to a depth of 30 cm, was selected for the establishment of a nutrient gradient. If certain limitations are recognized, plant yields may be a still better indicator of relative fertility. Microbiological problems encountered in this study invalidated their use here. The correlation between a Vegetation Nutrient Index based on species presence (VNI)p and the replaceable calcium in the soil yielded a coefficient of .784 which was significant at the 1% level.

To measure the light gradient a chemical light meter, consisting of anthracene in benzene solution, provided a means of measuring relative light in-

tensities at many different locations simultaneously, and integrating the energy received over an entire day. To make the Vegetation Light Index sensitive under both disturbed and undisturbed conditions a frequency estimate for each species was required. The Vegetation Light Index (VLI)f values varied from 98.2 on one of the grasslands to 2.5 in a bay-maple stand. The measured light intensities were, correspondingly, 100% and less than 1% of full sunlight for these two extremes.

The temperature gradient was not measured directly. Instead, effective day and effective night temperature patterns, related to constant day and night temperatures used in physiological, controlled environment studies, were analyzed for 29 weather stations where particular plant communities dominated. Five patterns representing a gradation from an extremely continental climate with short growing season to a maritime climate with nearly year-around growing season were presented. With the aid of the regional flora (Munz & Keck 1959) which lists the plant communities in which species occur, each species was assigned to a temperature pattern type that was assumed to be related to the species' ecological optimum. A Vegetation Temperature Index (VTI)p was derived, and the study area found to have three significantly different climatic subunits: (1) a main river valley providing a pathway inland for summer fog off the Pacific Ocean; (2) an area above 2,500 ft (760 m) elevation; (3) a drainage south of the park outside the effects of summer fog and therefore less maritime than the climate within the major drainage system.

Application of the gradient analysis approach is suggested for interpreting the significance of soil surveys, for many phases of forest research and management and in biosystematic studies.

The authors believe that only by employing physiologically oriented ecological measurements, such as were developed in this paper, can the present broad gap between laboratory plant physiology and "causal plant ecology" be bridged.

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