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THE USE OF VEGETATION IN ASSESSING THE PRODUCTIVITY OF FOREST LANDS

R. DAUBENMIRE

Department of Botany, Washington State University
Pullman, WA 99163[1]

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INTRODUCTION

Well over two centuries ago it became necessary in Europe to supplement the dwindling supply of timber from natural stands by the establishment of plantations. Recognition of the obvious variation in wood productivity and quality associated with habitat variance made it imperative to strive for means of evaluating environment potentialities as a guide in locating such plantations.

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[1] Present address: Route 1, Box 265A, Sorrento, Florida 32776.

Theoretically the best criterion of the productivity of a site for a given species is the growth rate of that species growing on that site (Spurr, 1964). At first wholly subjective appraisals were based on the appearance of the trees, as illustrated by G. L. Hartig's site quality classification of 1795 (see Cajander, 1949). A quarter of a century later these began to be replaced by the practice of measuring trees and arranging the data in tables or graphs showing the range in average tree height or volume at different times in the life history of the stands. This method has persisted to the present time, assuming that rate of height growth for the most part is an index of productivity, i.e., volume or dry weight of wood. Interpolated height at a standard age (e.g., 50 or 100 years) is referred to as *site index* and is used to compare site quality among stands of differing ages. The range of site index values for each species is commonly divided into five *site classes*, with Class I the best.

Limitations to this approach as reported in a voluminous literature are several, aside from difficulty in obtaining accurate height and age measurements (Mader, 1963). (1) A site cannot be evaluated unless it is supporting a sufficient number of trees (at least five) of the desired species, growing in a moderately dense stand (Alexander *et al.*, 1967; Holmes and Tackle, 1962; Lynch, 1958; Smithers, 1961) of at least 20 years age (Soc. Am. For., 1923). (2) During the life of a stand any unusual episode of damage from insect or fungus attack (Shea, 1964), surface fires, unusual wind breakage, amount of competitive stress during the early years, partial cutting, etc., once sustained, induces a negative error in subsequent productivity estimates, with such errors being cumulative (Frothingham, 1918; Hazard, 1937; Rowe, 1953; Soc. Am. For., 1923; Vincent, 1961). (3) Any precise measurement becomes an estimate of unknown accuracy when interpolated to a standard age, since an assumption has to be made as to the shape of the growth curve in that stand, and considerable variation in the shape of the height-growth curves for a species has been documented (Beck, 1962; Beck and Trousdell, 1973; Bull, 1931; Cajander, 1926; Carmean, 1956, 1972; Daubenmire, 1961; Graney and Burkhart, 1973; Grosenbaugh, 1960; Hodgkins, 1960; Illingsworth and Arlidge, 1960; Ilvessalo, 1937; Jameson, 1964, 1965; Jones, 1967; Lange, 1951; Leaf, 1956; Lorenz and Spaeth, 1947; Roe, 1967; Schönau, 1973; Spurr, 1956; Stage, 1963; Van Eck and Whiteside, 1963; Watt, 1953; Wiedmann, 1934; Zahner, 1962). Jones (1960), studying *Populus tremuloides*[2], concluded that height-age curves based on actual measurements of the course of growth by stem analysis are of limited value, since the curves differ from one clone to another in the same grove. (4) There are alternative methods used to develop site index curves, and these provide curves of differing character (Beck, 1971; Curtis, 1964; Hodgkins, 1960). (5) Without specific testing, site index for one species cannot be relied upon as an indicator of the performance of

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[2] Nomenclature in this paper follows Hitchcock, Cronquist, Ownbey & Thompson, 1955–69.

any other species on that site (Frothingham, 1918; Nelson and Beaufait, 1957) or the performance of trees grown from seed of the same species obtained elsewhere (Callaham and Liddicoet, 1961). A given spot of ground has potentially as many site quality classifications as species of trees and their ecotypes that can be grown there. (6) The same site index can characterize areas where combinations of environmental factors are so different that different silviculture is required. Therefore, site index has limited significance as a guide for timber management (Hodgkins, 1960). (7) Site index by itself is unreliable as an estimate of productivity, since stands with the same site index may support different numbers of trees per unit area when fully stocked. Therefore, some estimate of optimal tree density is needed to adjust site index and arrive at a productivity estimate, and a reliable way of doing this is not available (MacLean and Bolsinger, 1973).

In an effort to overcome some of the above limitations and evaluate environmental potentialities more directly, especially on sites lacking an adequate number of the desired tree species at the proper age, density, etc., attention was turned to soil properties more than a century ago (Della-Bianca and Olson, 1961). Chemical or physical properties of the soil were calibrated by their assessment in a series of stands exhibiting variation in timber productivity[3] , seeking to define those properties consistently related to good productivity and those associated with low productivity. This approach is still favored by some workers, but it, too, has serious limitations. (1) Man does not yet have the technology to make chemical and/or physical analyses of a soil profile enabling a quantitative expression of the degree of aeration or amount of resources (nutrients, water, heat) available to plants, integrating the annual variations in these, then balancing such information against possible detrimental soil properties such as excesses of certain solutes and depth of profile. Apparently identical profiles may be associated with marked differences in productivity, whereas different sets of soil conditions can add up to the same ecologic sum (Broadfoot, 1969; Covell and McClurkin, 1967; Damman, 1964; Kirsten, 1929; Lutz and Chandler, 1946; Phillips and Markley, 1963; Shetron, 1972; Sisam, 1938b, Wiedmann, 1934; Youngberg and Dahms, 1970; Zinke, 1959). (2) Such an evaluation requires that a pit be dug to the depth of rooting and then a guess be made as to the extent of area to which information derived from the pit applies. Mapping by this means is tedious, especially since forest lands are usually more heterogeneous than agricultural land, and errors in judgment are inevitable. In Europe a group of scientists collaborating on methods of site evaluation concluded: "Soil mapping was not separately evaluated, because today purely edaphic data are no longer generally considered sufficient for site characterization" (Ellenberg, 1967).

Another group of workers has placed heavy emphasis on topography, with convexity or concavity of slope, or with different positions on a slope (e.g., upper, middle, lower) being interpreted as indicative of moisture availabi-

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[3] The use of site index here induces error. See later discussion.

lity, and different aspects of slope indicating heat supply (Gaiser, 1951). Obviously differences in soil can add to or subtract from the apparent suitability of any one category of topography, and degree of slope is a significant variable, as is distance and height of the opposed slope. In the northern Rockies topography has little value as a criterion of site quality. For example, the *Pseudotsuga/Physocarpus* forest occurs on steep north-facing slopes at its lowest altitudinal limits, moves onto zonal soils at intermediate elevations, then onto the shallow soils of steep south-facing slopes at its highest limits (Daubenmire and Daubenmire, 1968). Despite these contrasts in topography, the height-age relations of seral trees (both *Pinus ponderosa* and *Larix occidentalis*) vary but little, within this habitat type yet differ markedly from their height-age relations in contiguous environments (Daubenmire, 1961; Roe, 1967).

Still another type of indirect approach to site evaluation is to combine a variety of physical factors such as macroclimate, topography, soil properties, etc., into equations (Czarnowski, 1964; Hills and Pierpont, 1960; Jones, 1971; Lemieux, 1961; Paterson, 1962). These must of necessity be based on a series of approximations since the basic data for forested areas are mostly sparse or difficult to obtain, and none of the equations has proven to have more than limited value or to have application in more than a restricted area.

The concept of using plant communities as criteria of site quality was expressed at least as early as 1892 (Magyar, 1933) and was then elaborated independently in Finland by A. K. Cajander and in Russia by G. F. Morosov at the end of that century (Köstler, 1956). This method involves first a classification of vegetation, with each type then calibrated against growth in existing stands of timber. The principles involved, their ecologic interpretation and their application to forest management, will form the remainder of this discourse.

A number of reviews of literature on the subject of site appraisal have been published (Burger, 1972; Carbonnier *et al.*, 1971; Doolittle, 1962; Jones, 1969; Ralston, 1964; Rennie, 1963; Wolak, 1967), but all of these have been prepared by workers whose experience has been centered on nonbiologic approaches. None has treated the principles of vegetative indicators, and none has pointed out the manifold applications of the biologic approach. The techniques mentioned above are aimed almost entirely at predicting or evaluating wood production. On the other hand, vegetative indicators are as useful for predicting optimal silviculture or forage production as for wood production (Mueller-Dombois, 1964; Pfister *et al.*, 1975).

This review will be concerned with vegetation of extratopical regions where nearly all the work has been done, but there is no reason to believe that the basic principles involved are restricted to this part of the globe.

PRINCIPLES

1. *Natural vegetation reflects the algebraic sum of all environmental factors important to plants.*

It does this better than man can judge from a consideration of all aspects of climate topography and soil which he considers relevant.

Appreciation of this principle has developed gradually since Alexander von Humboldt expounded his concept that the gross aspect of vegetation, irrespective of its taxonomic composition, is correlated with the character of the climate. A little over a century later Cajander (1926) was referring to vegetation reflecting soil differences within one climatic area when he wrote: "Vegetation with an abundance of species...takes from the very beginning to a considerable extent a different composition according to the differences in the quality of the different localities."

The practical value of the indicator significance of vegetation has been underscored by the negative results of thorough analyses of soils which showed that important discontinuities in stable vegetation are often determined by environmental differences either too subtle or too ephemeral to evaluate with present pedologic technology (Daubenmire, 1973; Gates *et al.*, 1956; Viro, 1961). On the other hand, communities which are closely similar in structure and floristic composition can occur on soils with very different profile characteristics (Daubenmire and Daubenmire, 1968).

The use of vegetative indicators (or of site index, or topography) does not necessarily provide any information on the physical factors responsible for growth differences from place to place, nor information on the degree to which genetics are involved. However, these phenomena are so exceedingly complex and interrelated that we may never achieve a high level of understanding of them.

2. *Species with the highest competitive powers are the best indicators (Anon, 1927; Long, 1953; Siren, 1955; Zon, 1906).*

As succession advances, the degree of similarity of vegetation among ecologically equivalent sites increases and is at maximum when competitive elimination has brought about a relatively stable condition. Seral[4] species are responding as much to the temporary increase in radiant energy at the ground level, or to the temporary reduction in root competition, or to strong herbivore activity, as to the intrinsic climatic and edaphic factors of a disturbed site. On the other hand, at climax seral species have been eliminated and all the remaining species are in equilibrium with competitive influences which are determined by relatively immutable physical factors of the habitat and the existing flora (University of British Columbia, 1959). There is only one type of such stable vegetation for a given spot, whereas a wide variety of per-

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[4] In the interest of precise expression it is desirable to define the use in this discourse of some terms relating to vegetation which are used widely but in different senses:

Climax: Any association which appears self-perpetuating in the absence of disturbance. There is no demonstrable evidence that it is susceptible to natural replacement by another mutations in seral vegetation is possible on that spot. As Cajander (1926) put it: "At first...a heterogeneous mixture grows on the cleared areas....Step by step with the growing intensity of the struggle between the plant individuals, those species which on that locality are biologically weaker are gradually exterminated, the result of which process is that the vegetation becomes more and more regular." "Climax forests provide the key to successful forest management" (Westveld, 1951).

In arriving at the preliminary classification of vegetation which this approach requires, emphasis must be directed to the composition of the oldest and most stable stands of forest available, for here the best indicators are found in the most nearly pure groupings. After a series of old stands have been analyzed, the critical species which are regularly present can be listed, and thereafter when a disturbed area is to be classified, these are the plants to be sought. Only confusion results if all species are considered of equal indicator value (Anderson, 1961), and this appears to lie at the root of some of the statements that the disturbed nature of most forest stands makes the vegetation-indicator method imprecise (Ritchie, 1961). Species highly successful in stressful environments (cold or dry) commonly play seral roles in less stressful environments, and this is not to be construed that the latter have become either temporarily or permanently more stressful.

Climax stands are indeed rare, but they are by no means necessary to ascertain the useful indicators, for once a closed forest canopy develops, seral shrubs and herbs soon disappear from shaded areas, and none but seedlings of the most shade-tolerant trees the habitat will support are successful. The character of the climax can be judged without reference to the canopy trees. Its nature can be predicted or its status defended by detailed population analyses in homogeneous tracts of tropical rainforest (Schulz, 1960) as well as in rigorous climates where habitats are often controlled by a single tree species after succession has run its course (Daubenmire and Daubenmire, 1968). Although little used in the twentieth century, the importance to

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community under the existing conditions of climate, soil and flora.

Habitat type: A collective term for all areas in which the integrated sum of all environmental conditions allows succession to proceed toward the same climax association.

Seral: Any community which through existing population structure, or observation through time, has demonstrated progressive (unidirectional) change in its composition or structure; any species unsuccessful in competing for habitat resources.

Sere: A particular sequence of stands which tend to follow in a definite order and culminate in a climax.

Stand: A continuous tract of vegetation which is homogeneous as to both composition and age.

Union: A single species of high abundance and distinctive ecology, or a rather well-defined list of species which are restricted to approximately the same narrow range of environmental variation in a vegetation mosaic. Commonly, unions have physiognomic as well as taxonomic distinctiveness, i.e., they may consist of tall shrubs, or of herbs, or of tree species, but this is not necessarily true; therefore, union is a more flexible term than layer, emphasizing ecology as judged by similar patterns of distribution rather than height. The unions in a landscape occur in different combinations.

be attached to population structure as an indicator of trend was clearly recognized by Morosov (Sukachev and Dylis, 1968). Zon (1906) wrote: "A forester who mistakes...temporary forest growth for the original natural types, thus failing to understand the natural evolution of the forest, will always have nature against him..."

"As is well known, both knowledge of any natural phenomena and rational practical utilization of them require systematic classification of these phenomena" (Sukachev and Dylis, 1968). Vegetation management is not practical without mapping, and mapping necessitates some type of classification. Continuum methodology, in which disturbed landscapes are sampled as static entities with no consideration given to the reproductive success of the species tallied, fails completely to reveal the existence of ecotones which can be defined on the basis of species with high competitive abilities. Such methods are purely descriptive, whereas the practice of defining habitat types on the basis of the superior competitors on each site is interpretive. As Stage (1974) has pointed out, "ordinations can be mapped, rather like contour maps. However, there *must* be as many maps as there are dimensions of the ordination space. The problem of interpreting the overlays of two or three layers of 'contours' would be difficult."

Although the best indicator species are those successful under the most intense competition, other plants too have distinctive ecologies, and some workers have studied them sufficiently that even the vegetation of recently plowed land has been shown to include useful indicators (Ellenberg, 1951; Gagnon and MacArthur, 1959; Guillebaud, 1930). However, this can be a treacherous endeavor, for as Bornebusch (1920, see Cajander, 1926) pointed out, a seral stand in one kind of environment may bear a close resemblance to the climax of another habitat type. For this reason computer analyses of a series of unstratified plot data can group stands from quite different environments into the same unit.

No matter what approach is followed in devising a vegetation classification, its ecologic significance must be considered as hypothetical until validated. A community type can be accepted as indicating an ecologically distinctive type of environment, i.e., a habitat type, only if it shows internal consistency, combined with distinctiveness from other communities, with respect to such features as topographic relations, soil type, hydrologic cycle, seral stages, susceptibility or resistance to disease, rate of tree growth, etc. The more of these characters shown to be distinctive, the more significant the vegetation unit.

3. *Forests are composed of unions which occur in different combinations.*

Each plant association may be looked upon as a combination of superimposed unions (usually layers), these commonly occurring in different combinations in different associations (Daubenmire and Daubenmire, 1968; McLean, 1970; Westveld, 1953).

The relative independence of overstory and understory was clearly recognized by Cajander (1926) when he wrote: "the influence on the ground vegetation of the different species of trees under the same conditions is comparatively insignificant." This conclusion has been well documented. For example, in eastern Washington and northern Idaho the undergrowth of *Pinus ponderosa/Festuca* stands is wholly different from that of *Pinus ponderosa/Physocarpus* stands, whereas no consistent differences have been found in the *Physocarpus* union as it occurs in many stands of *Pinus ponderosa/Physocarpus* as compared with many stands of *Pseudotsuga menziesii/Physocarpus* (Daubenmire and Daubenmire, 1968).

Forest undergrowth approximates climax status soon after the first seral trees form an essentially closed canopy, especially where the seral and climax overstories are of the same physiognomic type, e.g., evergreen conifers (Sisam, 1938a). For example, the undergrowth beneath seral *Pseudotsuga* stands along the west central coast of North America closely approximates that which will still be present after *Tsuga* replaced the dominant but nonreproducing *Pseudotsuga* overstory (Becking, 1956; Can. Soc. For. Eng., 1946; Spilsbury and Smith, 1947). This rapid approximation of stable structure in forest undergrowth has been recognized over a wide area (Heimburger, 1934; Linteau, 1955; Taylor, 1932).

In view of the above evidence it is interesting to note that Curtis and McIntosh (1951) wrote: It is "possible to predict with reasonable accuracy the important herb species to be found in stands in any given range of the continuum index" based on Wisconsin trees. Swan and Dix (1966), also using continuum methods, reached the same conclusions in Saskatchewan. This stands in sharp contrast with the results of typologic studies of Rocky Mountain forests. For example, the shrubs and herbs beneath self-reproducing pure populations of *Pinus ponderosa* are wholly different between *Pinus/Festuca idahoensis* and *Pinus Physocarpus* stands. The same contrast exists between *Abies lasiocarpa/Pachistima myrsinites* and *Abies lasiocarpa/Vaccinium scoparium* stands. Westveld (1953) reported the same phenomenon in east central North America.

4. *Each union is sensitive to different aspects of environment.*

On ascending the slopes of the Rocky Mountains one usually finds the first climax forests dominated by *Juniperus*, often in combination with *Pinus flexilis* or *P. cembroides* (S.L.). Successively farther into the mountains this belt typically gives way to forests of *P. ponderosa*, then *Pseudotsuga*, then *Abies lasiocarpa* with *Picea engelmannii*, and finally forest yields to alpine tundra. This regular sequence, observable from Alberta to the Mexican border, reflects a regular altitudinal gradient in macroclimate from warm-dry to cold-wet. No such regularity along the Rocky Mountain axis can be discerned in the undergrowth. On an area of just a few hectares within any one of the altitudinal belts, one finds differences in soil and topography reflected in distinctive undergrowth unions. As pointed out previously, one or more of the same undergrowth unions found in the *Pinus ponderosa* belt may extend into parts of the macroclimatic belt where *Pseudotsuga* comprises the climax overstory. Parkhurst and Loucks (1972) have also reached the conclusion that in Wisconsin the tree stratum is more coupled with macroclimate, whereas the forest undergrowth is more determined by microclimate and soil. A comprehensive classification of indicator vegetation for a large region, such as is being worked out for the Rocky Mountains (Layser, 1974), is ecologically more sound when the primary classes are based on the tree layer with these classes subdivided according to undergrowth unions (Long, 1953; Westveld, 1953).

This difference in the indicator significance of the different unions which are superimposed is most clearly demonstrated at ecotones where frequently only one union is replaced by another. In some places the tree stratum may be taxonomically insensitive to an environmental discontinuity which is clearly indicated by a change in the type of undergrowth, whereas elsewhere the same type of undergrowth may continue beyond a point where the overstory changes. Since there is substantial evidence that the rate of height growth may change significantly at limits where only one union differs between contiguous associations, it is clear that important environmental differences occur here (Daubenmire, 1961).

It is apparent from the above that forest undergrowth must be accorded as much importance as the overstory to maximize the indicator significance of vegetation, and a climax must be defined in terms of its component unions. Thus A/B/C would be a different type from A/B or A/B/D or E/B/D, with the environments of each being distinctive in some way.

As early as 1904 Morsov (see Heimburger, 1934) emphasized the reproductive capacity of trees as one of the chief distinguishing features of forest types, thus distinguishing between seral and climax types well before the concept of plant succession was generally recognized. Site quality was correlated with vegetation dynamics giving the tree stratum first consideration, with subdivisions then based on undergrowth. This concept is eminently sound, though long ignored. It appears to have wide application not only in Russia but in the Rocky Mountains and even in tropical rainforest, for Webb *et al.* (1967) concluded that "associations clearly have more reality when the different layers superimposed over one spot are considered as a unit." In east central North America Westveld (1953) observed that some climax forest types may differ only in their overstory, whereas other climaxes may differ only in their undergrowth (see also Robertson, 1945; Silker, 1966; and Daubenmire and Daubenmire, 1968). Others, while concentrating interest on types of forest undergrowth, have indicated the kinds of tree seedlings found in each undergrowth type, without grasping the significance of population structure for indicating successional trends and another order of environmental differentiation (Crandall, 1958; Heimburger, 1941).

Cajander (1926) based his classification upon only the undergrowth unions (shrubs, herbs, mosses and lichens), since through promiscuous logging the tree unions had been so thoroughly altered in Finland that he did not think it practical to determine the possible combinations of overstory and undergrowth in stable vegetation. Either he did not know of the importance the

Russians had attached to the dynamics of the tree stratum, or he underestimated its value. His classification proved highly useful largely because Finland is a small country with a relatively simple tree flora. But this point was lost on those who carried the vegetation indicator approach to North America, for most of them concentrated their attention on undergrowth without realizing that by using population structure to indicate successional trends, a new dimension can be added to the method. Too many North American workers sought homologs of Cajander's Finnish forest types, since they worked largely in subarctic forests which share many genera and some species with Europe. There has been too little appreciation of the well-documented fact that the same species in different geographic areas is usually represented by different ecotypes, which by their nature have different indicator significance.

Often bryophyte-lichen unions are also considered in searching for useful plant indicators, and there is little doubt but that these unions are sensitive to still different environmental conditions than are vascular unions. Hence, bringing them into consideration may refine the indicator approach still more. The degree to which this may be true, or practical in forestry, appears not to have been widely investigated or demonstrated (Brinkman, 1929, 1931, 1936; Hall, 1961, Klement, 1951).

As yet forest site quality has not been found related to microbial communities in the soil, despite their sensitivity to position in the horizon sequence (Shipman, 1955).

5. *Many aspects of vegetation are potentially significant as indicators.*

Concentrating attention on just the trees, or even just the dominants of the undergrowth cannot yield an ecologically refined classification of vegetation. *All* species must be studied quantitatively to learn which are useful indicators and whether or not their relative abundance is significant. Cajander (1926) concluded that in each community type "there exists a stock number of plant species, which are always or nearly always present and from this stock number there leads an uninterrupted series through those which are often present down to those which are only very seldom present."

Sukachev and Dylis (1968) describe an association uniform as to the dominants of all its unions, but in part of the range of the type the soil is a podzol and *Betula* and *Populus* are seral species, whereas elsewhere the soil is mull and these trees do not participate in the seral vegetation. This silviculturally significant variation in what would appear at first glance as one homogeneous unit is reflected in only minor members of the communities after the seral trees have been completely eliminated.

In the northern Rocky Mountains the total area in which the *Pseudotsuga menziesii/Physocarpus malvaceus* forest is climax can be readily split to indicate subtle but consistently different portions depending on whether or not the environment is moist enough for *Larix occidentalis* or *Pinus contorta* to participate in the seral stages (Daubenmire, 1973). There is no known character of the undergrowth or soil profile that can be used to make this distinction. Thus, drawing the character of seral relics into consideration can add to the indicator significance of vegetation, and this is highly practical since nearly all forest areas are normally logged or burned before seral trees from the preceding disturbance have been eliminated and stability achieved.

In places, simply the richness of the flora reveals important ecologic differences (Daubenmire and Daubenmire, 1968; Ilvessalo, 1924, Stanley, 1938). Even variations in the height of a ubiquitous species of herb such as *Pteridium* can have useful significance (Demounem, 1968; Stoeckeler, 1948; Stoeckeler and Limstrom, 1942; Ure, 1950).

Such findings as the above point up the importance of giving attention to a wide variety of community attributes, yet in the final analysis of the data only a few distinguishing features prove constant in their occurrence. These make is possible to construct a very simple key similar to those in taxonomic manuals, enabling others with minimal botanical training to identify the types. For example, anyone who understands how to use a key and can identify eight species of trees and 30 species of herbs and shrubs can classify forests at all altitudes in northern Idaho and eastern Washington (Daubenmire and Daubenmire, 1968; Deitschman, 1973; Roe, 1967). In Quebec one needs to recognize only 15 species of plants to distinguish 17 habitat types (Linteau, 1955).

Hodgkins (1960), Rowe (1956), Ure (1950), and Waring and Major (1964) have devised systems whereby numerical index ratings for environments are derived from quantitative analyses of vegetation plus values for weighting the contributions of different indicator species. This is a refined approach, but it involves infinitely more time to assess a site than is needed to simply inspect the stand while using a simple key. Furthermore, in units as complex as forest ecosystems there are limits to refinement which can be expected to have more than very local applicability (Vallee and Lowry, 1970).

6. *Habitat types are the basic ecologic units of landscapes.*

Each climax type indicates both the local and the geographic extent of land having essentially equivalent and permanent biologic potentialities. Such a category of land may support a series of vegetation types while recovering from disturbance or denudation. Therefore, it is the pattern of the *land units* having approximately the same capacity to produce vegetation (i.e., habitat types), rather than the pattern of vegetation existing at a particular time, that is the permanent feature of a landscape.

Cajander's adoption of the term "forest type" has long been recognized as an unfortunate linguistic choice (Sukachev and Dylis, 1968), for he specifically included all possible types of plant life which could grow in a given habitat type, e.g., the series of communities which appear following abandonment of a field, those that follow a forest fire, the kinds which develop when vegetation is modified by grazing, as well as the climax. The only feature which ties all these together is a specific range of climatic and edaphic factors whose extent is indicated by vegetation trends which progress toward the same type of stable condition.

In an effort to express the situation more accurately a number of workers have referred to Cajander's "forest types" as "forest site types." But since this is a basic ecologic concept which applies fully as well to steppe as to other nonforested landscapes, the term "habitat type" as used in the Rocky Mountains has more universal meaning.

There are some rare exceptions to the permanence of habitat types. Locally in subalpine parks in Utah excessive grazing has resulted in severe erosion which permanently reduced the capacity of the land to produce vegetation (Ellison, 1954). In limited areas in Finland (Cajander, 1926) and Alaska (Zack, 1950) *Sphagnum*, spreading from wet spots, may choke off reproduction in previously stable forest on the surrounding upland, replacing this forest of mineral soil with bog. Then in a time scale which is too gross to be taken into practical consideration, ridge tops in moist climates may slowly lose their stock of nutrients as leaching removes the weathered products of primary minerals, so the productive capacity of the land declines.

Exceptions such as the above are obviously few or relatively inconsequential in terms of current land use planning. For all practical purposes habitat types have fixed characters and boundaries.

PRACTICAL VALUE OF VEGETATIVE INDICATORS ON FOREST LANDS

The opinion has often been expressed that different classifications of vegetation are needed for differenet needs. This is patently true of superficial classifications, such as site index or of the classification based on the currently established trees of highest timber value, e.g., the "western white pine forest type." This is the "forest cover type" classification long used by U.S.A. foresters. But when a classification is based on sound ecologic principles, it at least approaches a "natural" system in that it serves a wide variety of needs (Univ. B. C., 1959) and eventually reveals a regularity in attributes other than those considered when arriving at the classification. This reduces the number of additional land classifications which are needed. Foresters have often expressed the opinion that such a system would be ideal, referring to it as a "total" or "absolute" classification (Silker, 1966; Sisam, 1938b).

Application of the ecologic principles discussed above leads to a habitat type classification which falls into this second category, since it has been found to be useful in predicting site values for a variety of alternative economic uses. For this reason mapping forest lands on the habitat type basis has been expanding rapidly (Daubenmire, 1973; Deitschman, 1973; Layser, 1974; Pfister, 1972; Wellner, 1972).

As Fenton (1947) pointed out, maps of existing vegetation are rendered obsolete by any harvesting or fire, or simply become obsolete with the passing of time owing to natural succession. On the other hand, the value of a habitat type map is as permanent as the landscape it represents (Westveld, 1951).

There is nothing inherent in a habitat type classification which reveals productivity, responses to various types of disturbance, disease hazard, etc. These have to be determined directly by field tests in each habitat type. The classification then becomes of paramount importance as a criterion of the additional area in which the same information is applicable. A high degree of accuracy cannot be claimed, but the applicability of the method to areas lacking trees suitable for direct evaluation of wood production and the utility of the method in other aspects of land management combine to make this approach highly valuable.

There follows a summary of the spectrum of practical applications of a habitat type classification, but there is no intent here of minimizing the need for an independent soil classification or for subdividing the area of each habitat type according to the current cover types, etc.

1. *Rate of tree growth.*

A thorough study made by Y. Ilvessalo in 1914 showed that "growth in all its aspects is different for the different forest types while for the same forest type it differs within comparatively narrow limits" (Cajander, 1926). From the yield tables coming out of that investigation, it became "possible to make comparative calculations as to the...profitableness of growing the different species of trees on the same area of ground" (Cajander, 1926). Many others have also found good correlations between rates of tree growth and types of forest undergrowth (Arnborg, 1950; Becking, 1956; Bornebusch, 1931; Glew, 1963; Heimburger, 1934; Hodgkins, 1961; Jameson, 1965; Leaf, 1956; Moir, 1972; Spilsbury and Smith, 1947. Others have found that differences in *either* overstory or understory may reflect environmental differences important for tree growth (Damman, 1964; Daubenmire, 1961; Linteau, 1955; Robertson, 1945; Roe, 1967; Westveld, 1952).

Crucial to the technique of using tree height growth as a criterion of productivity is an understanding that the shape of the growth curve for a species differs significantly among the habitat types in which the species may be found, with a high degree of uniformity within each one (Cajander, 1926; Daubenmire, 1961; Pagel, 1970; Roe, 1967). Cajander (1926) said the notion "that the normal curves of the different quality classes have an identical course," i.e., are harmonic, is "an assumption which is not only without any foundation, but, as the present writer showed before (1909)," as "in many cases even demonstrably erroneous." Half a century later Grosenbaugh (1960) reiterated: The "fact that height-on-age curves for a given species in different localities are not always parallel or proportionate...cannot be reconciled with the old site-index concept." No amount of complicated mathematical manipulation of data collected indiscriminately from a variety of habitat types can produce a single set of harmonic growth curves which reliably reflect a species' response over a wide area. Different ecotypes (The site index concept originated before the existence of ecotypes was demonstrated!), and perhaps different combinations of environmental factors within the range of one ecotype, may result in sigmoid growth curves of different shapes. In *Populus tremuloides* even different biotypes have consistently distinctive growth patterns (Jones, 1967). Failure to understand this ontogenetic factor may have accounted for much of the limited degree of success many have had in calibrating soil or topography in terms of growth potential (Della-Bianca and Olson, 1961), for such research has invariably used extrapolations from a "standard" set of harmonic site index curves or tables to compare with the physical data. All errors in such curves or tables are thus automatically added to the errors inherent in interpreting the soil or microclimatic data (Spurr, 1956)!

In eastern Washington and northern Idaho the highly significant differences in the growth curves among seven habitat types in which *Pinus ponderosa* grows, either as a climax or a seral tree, were established by grouping the raw data for height and age according to habitat types for analysis, rather than resorting to the "standard table" which was generally thought adequate for all ecotypes and all environments in the area (Daubenmire, 1961). There is indeed a considerable variation in growth rates within a habitat type, but a number of workers have concluded that the accuracy of prediction is improved by using vegetation indicators, especially as this reflects differences in the shapes of growth curves from place to place.

For a wide-ranging species there may be a dozen or more habitats in which it is well represented, with no two of these reflecting the same average productivity throughout the history of the stands. Although Hodgkins (1961) showed that by more meticulous analysis of the undergrowth it was possible to predict height growth with a standard error of only ±2.55 feet, so much work may not prove generally rewarding, for accidents of stand history can upset predictions by much more than this.

Another facet to the determination of rates of tree growth involves the well-recognized fact that those trees becoming established on a deforested site make faster growth than subsequent generations which get established under competition from the first. Thus, productivity tends to decline as climax is approached (Erdmann, 1924; Taylor, 1933; Williamson, 1963), so the capacity of a site to produce should be based on only the invading individuals. Usually this precaution is unnecessary, since fire, logging or insect devastation usually destroys a timber stand before climax equilibrium has been achieved.

2. *Appropriate silviculture.*

Harvest methods necessary to ensure good regeneration of trees, the amount and timing of thinning which is optimal, and other silvicultural measures required to meet demands for water, forage and recreation differ from place to place, and a number of workers have pointed out that vegetative indicators are useful as a guide to the extent of area in which each technique is appropriate (Anderson, 1961; Arnborg, 1945, 1950; Bornebusch, 1931; Boyd, 1969; Damman, 1964; Franklin *et al.*, 1970; Glew, 1963; Ilvessalo, 1954; Kabzems, 1951; Linteau, 1955; McLean *et al.*, 1971; Mueller-Dombois, 1964; Pfister, 1972; Ray, 1941; Waenink, 1974; Westveld, 1951, 1953). As Sukachev and Dylis (1968) say, the homogeneity within one habitat type "requires the application of identical forestry measures in identical economic conditions," reaffirming a principle that was discerned by G. F. Morosov nearly a century ago. Site index is no criterion of appropriate silvicultural treatment since different sets of environmental conditions which call for different types of management may result in the same site index (Hodgkins, 1960; Zon, 1913).

3. *Biologic hazards.*

It has been shown that for certain tree species, at least, susceptibility to disease (Daubenmire, 1961; Fenton, 1943; Kangas, 1952; Ray, 1941; Roe and Amman, 1970; Smith, 1972; Thomas, 1958; Van Arsdel, 1961; Van Groenewald, 1956, 1965) or to insect attack (Bess *et al.*, 1947; Johnson *et al.*, 1963; Mason and Tigner, 1972; Roe and Amman, 1970; Shepherd, 1959; Westveld, 1953) differ according to the kind of plant community the tree is growing in, so that vegetation can serve as an indicator of the area in which special preventative or compensative action is needed. By no means are all maladies sensitive to habitat type, but where there is a correlation, this is of considerable economic importance.

4. *Susceptibility to wind-throw.*

Susceptibility of trees to wind-throw may be indicated by associated vegetation which is sensitive to soil conditions which prevent deep rooting of trees (Day, 1950).

5. *Tree form and anatomy.*

Associated vegetation has been found correlated with the physical properties of wood (Kalninjs, 1949; Solncev, 1949; Vihrov, 1949) and with stem form or branchiness (Tikka, 1950).

6. *Reproductive habits.*

The capacity of broad-leaved trees to produce coppice shoots after harvest may differ distinctly among habitat types (Cajander, 1926).

7. *Game management.*

Big game populations are keyed mainly to the availability and quality of winter browse, which in turn varies with habitat type and topography. In the northern Rockies certain habitats produce a rich and varied stand of shrubs useful for wapiti and deer browse following logging or fire, with this supply of browse supporting game for several decades until it grows out of reach or a new coniferous canopy overtops it. Other habitat types in the same area are worthless for browse under climax conditions, with no improvement at any stage of the regeneration process following deforestation (Daubenmire and Daubenmire, 1968). Game managers in this region can ensure a continuing supply of browse in a multiple-use planning unit if they see that at least a few of the timber sales involve the clearing of portions of the browse-producing habitats at frequent intervals.

Wherever livestock or game show distinct preferences for certain vegetation types (Dealy, 1971; Mackie, 1970; Thelinius, 1972, Valleala, 1954; White, 1960), their ecology is best integrated into multiple-use planning when a habitat type map, with subdivisions showing current successional status has been made available.

8. *Ecotype distribution.*

The shrub *Ceanothus velutinus* has been found to have two ecotypes with their distributions correlated with differences in the tree layer (Wollum *et al.*, 1968). Racial variation in *Pseudotsuga menziesii* is correlated with vegetation (Silen, 1965). It is entirely possible that much, if not most, of the differences in tree growth associated with different habitat types may also have a genetic base where habitat types cover large and continuous areas. Preliminary measurements of two-year-old nursery-grown seedling of *Pseudotsuga menziesii* representing 24 locations in the northern Rockies showed that plants from two habitat types grew significantly slower than those from all other habitat types (Rehfeldt, 1974). Should this phenomenon prove to be commonplace, seed collection should be made by habitat type and the resulting nursery stock kept segregated so that appropriately adapted genotypes can be returned to their respective habitat types (Callaham, 1965). In fact, this precaution should be followed at present as a safeguard against making mistakes in planting which will endure for decades.

9. *Hydrologic cycles.*

The use and recharge of soil moisture through the hydrologic cycle bears a close relation to habitat types in the northern Rockies, with altitude, aspect and other physical features of the land bearing a far lower degree of correlation (Daubenmire, 1968).

Still other aspects of land use which differ among habitat types have been indicated by Cajander (1926), Linkola (1922) and Westveld (1951).

CRITICISMS AND CAUSES OF FAILURE

Several publications have ended with a conclusion that vegetation is not significantly useful in the evaluation of forest potentialities. The reasons for such failures are often obvious in the techniques. For example, Heringa and Cormack (1963) examined only six seral stands of *Pinus contorta* in Alberta and considered their data adequate for drawing the conclusion that plant life did not reflect soil differences. The number of permutations in ecosystems is so great that only masses of data drawn from a fairly wide area are adequate for drawing conclusions regarding indicator significance, especially when attention is restricted to unstable stands such as Heringa and Cormack used. In contrast, Pfister *et al.* (1975) have assembled complete floristic analyses, plus population structure of the trees and soil analyses for 1,478 stands of old timber as a basis for classifying habitats in western Montana.

Some writers have thought vegetative indicators are useful only where vegetation differences are wide. Again, Heringa and Cormack (1963) wrote that "the lack of any *striking* (italics mine) differences in composition and density of the ground vegetation makes it impossible to assign the name of any one ground cover plant or combination of plants to serve as indicators of a definite soil-forest type." Yet, four *minor* undergrowth species in their data show very good correlation with their soil data! Perhaps the most extreme view in this matter was that of Curtis and McIntosh (1951) who claimed that recognition of community types is valid only if their species lists are *wholly* different.

It is probably significant that the high variability reported within the same vegetation type, making the indicator concept unpopular in some quarters, was a consequence of either compromising raw height-age data by interpreting them through "standard site index curves," or defining vegetation types solely on the basis of undergrowth types. In eastern Washington and northern Idaho there are significant differences in the rate of height growth of *Pinus ponderosa* between the *Pinus ponderosa/Physocarpus* and the *Pseudotsuga/Physocarpus* habitat types, yet only the reproductive success of the two trees allows differentiation of the habitat types (Daubenmire, 1961).

Lutz and Chandler (1946) criticized the vegetation-indicator concept because "in the *Oxalis-Myrtillus* type the characteristic plant *Oxalis acetosella* may be lacking." However, in another place (loc. cit.) one reads "The characteristic features (of podzol profiles) as seen in the field are the layer of unincorporated organic matter, the gray A2 horizon and the brown to dark-brown B horizon. In less clear-cut profiles, however, *the identity of the soil may not be obvious,* (italics mine) and then the silica-aluminum ratio of the colloids becomes critical." Why must more exacting standards be required in synecology than in pedology?

As Linteau (1955) pointed out, there is a widespread lack of appreciation of the training in synecology necessary to work out an ecologically sound classification of vegetation. It is generally assumed that any attempt to calibrate soil profiles against rates of tree growth requires the special training obtained in at least two college-level courses in pedology, but those who have claimed no success with vegetation indicators have had far less training in synecology in preparation for their sally into this field. To work out a classification of habitat types requires as much special training and experience as is required to identify plant species in seedling and dormant stages (Branteseg, 1941; Cajander, 1949; Deitschman, 1973; Hilitzer, 1934; Westveld, 1951).

On the other hand, certain writers have overestimated the botanical acumen required to put into practical use the plant-indicator information obtained by a vegetation specialist. Once the classification has been worked out, a relatively simple key can be constructed which enables workmen to make correct classifications of sites after minimal coaching. The situation is analogous to species taxonomy, which to be sound must be based on a wide spectrum of information (morphology, anatomy, cytology, chemistry, geographic distribution, paleontology), yet a taxonomic manual enables the proper classification of individuals using only a few simple characters. Certainly the use of vegetation indicators does not require the services of a trained botanist as Donahue (1940) claimed.

In northern Idaho and eastern Washington site index showed only a low degree of correlation with soil profile characteristics, and a technically trained soils specialist would be needed to use such information (Base and Fosberg, 1971). In the same area vegetative indicators show a high degree of correlation with productivity and can be used by workmen with very different types of specialized training, if they can use a key and identify eight species of trees and 30 species of herbs and shrubs.

Kabzems (1951) wrote: "The rooting zone of the trees goes much deeper in the soil than the roots of the ground cover do." Therefore, he reasoned that forest undergrowth cannot reflect soil conditions which are most important for trees. The same opinion has appeared in the writings of others (Coile, 1938; Heiberg and White, 1956; Long, 1953; Sampson, 1939; Schmidt, 1954), but not one of these statements is backed by original data, nor is any source of data from literature cited. On the other hand, those who have actually investigated root stratification have come to a different conclusion, namely that the "feeding" roots of trees are usually near the soil surface where nutrients and oxygen are in better supply and, so, are intermingled with the roots of shrubs and herbs (Berndt and Gibbons, 1958; Cheney, 1932; Hopkins and Donohue, 1939; Kalela, 1950; Kivenheimo, 1947; Kochenderfer, 1973; Kujala, 1960; Pessin, 1939; Scully, 1942). In regions of low rainfall the shrubs and herbs which retain green leaves through the dry season have at least some deep roots which maintain contact with moist horizons as do the trees. The nutrients used by all these deeply rooted plants become concentrated in surface horizons through litter cast, creating a common nutritional dependence on these horizons by both deeply and shallowly rooted plants.

Another common assumption is that ground vegetation is destroyed by disturbances such as fire or clear-cutting (Kabzems, 1951; Sampson, 1939). Donahue (1940) and Korstian (1917) thought that the use of undergrowth indicators is limited to near-virgin conditions. This opinion is patently not true. Numerous studies have shown that in the first postfire season many undergrowth species, among which are valuable indicators, put up new shoots from surviving underground organs and continue to live until a new forest canopy has developed (McLean, 1969). MacLean and Bolsinger (1973) observed that "plants present before logging seem generally to have persisted in spite of heavy disturbance..." Even in early successional stages a satisfactory estimate of the climax for a site can be made by noting which tree seedlings and undergrowth species are surviving in spots of dense shade. Those opportunistic weeds which quickly invade many deforested habitats may indeed determine the superficial character of the vegetation, but valuable indicators are present from the start. One must know what to look for and be willing to part the weeds to find them (Linteau, 1955). Since habitat types in a given landscape are related in a catenary manner, the character of vegetation surrounding a deforested area greatly reduces the number of possibilities in classifying a recently burned site (Linteau, 1955).

As pointed out earlier, it is sometimes stated that forest undergrowth is conditioned as much by tree influence as by intrinsic habitat factors. It is certainly true that variations in the intensity of shade as the stand develops brings about drastic changes in the herbaceous and shrubby vegetation, with seral species most conspicuous at first and extreme shade commonly eliminating nearly all (even climax) plants during a midseral stagnation phase. Variations in shade from place to place in a mature stand also have strong influences on the *quantity* of undergrowth. However, variation in the species composition of the indicator group is relatively small, except that highly mycotrophic members rise in relative abundance at times and in places of heaviest shade.

Failure to understand that the classification of a community is based on a consideration of many attributes of the ecosystem, rather than simply a mechanical analysis of the flora with all species given equal consideration, is a common source of confusion even among plant ecologists. Each recurrent grouping of species such as might be established by a computer analysis of sample data cannot be assumed to represent a distinctive habitat type. Accidental inclusions and especially seral relics can create ecologically heterogeneous groups. Any community, whether suggested on the basis of mental abstraction or machine analysis, stands in need of validation as an ecologically distinctive type. It is valid in proportion to its distinctiveness in one or more ways such as (1) predictable relations with soil or topography in landscape mosaics, (2) a special type of seral vegetation, (3) distinctive susceptibility or resistance on the part of one or more species to attack by insects or fungi, (4) peculiar rates or patterns of tree growth or reproduction, etc.

Viro (1961) stated that outside Finland vegetation indicators have shown no useful degree of correlation with soil fertility. But he was referring to fertility as indicated by tests in a chemical laboratory, and in view of the extreme complexity of soil factors affecting availability, we cannot expect too much from the simple and conventional laboratory procedures available for these tests.

Arnborg (1950) found little use for undergrowth indicators in a section of Sweden and suspected this to be a consequence of a wider range in elevation than in nearby Finland where the technique has proven its merits for three quarters of a century. It is difficult to believe that differences in elevation which are sufficient to effect differences in tree growth are not reflected in ground vegetation if it is analyzed thoroughly. The correlations between habitat types and the growth of *Pinus ponderosa* (Daubenmire, 1961) and *Larix occidentalis* (Roe, 1967) in the Rockies were highly significant, yet both of these independent tests encompassed wide elevational ranges in mountains.

Donahue (1940) considered it a limitation of the plant indicator method that "each region may require a separate classification." This is patently true, but what method does not require separate testing in different regions? Furthermore, vegetation provides the best clue to the extent of land to which the classification developed in one area is applicable.

RESUMEN

Los principios básicos al empleo de tipos de vegetación en el evaluar de terreno forestál están enumerados y descutidos. (1) La vegetación refleja la suma de todos los elementos del medio ambiente que son importantes para las plantas. (2) Las especies con poderes en competencia más altos son las indicadores mejores. (3) Los bosques consisten en grupos ("unions") sobrepuestos que occuren en combinaciones distintas sobre el paisaje. (4) Cada "union" es sensitiva a unos aspectos especiales del medio ambiente. (5) Muchos carácteres de vegetación tienen significación potencial como indicadores ecológicos. (6) Los tipos de medio ambiente ("habitat types") son las unidades ecológicas más básicas del paisaje.

Los ejemplos del valor práctico de indicadores vegetales para la predicción de crecimiento de árboles, de silvicultura apropriada, de enfermedades de insectos y hongos, de variaciones raciales entre plantas, de facciones hidrológicas, y del valor de vegetación para el bienestar de animales están detallados.

Criticismos prévios del método de indicadores vegetales son reseñados y evaluados.

SUMMARY

The basic principles in the use of vegetation types as indicators on forest lands are enumerated and discussed. (1) Vegetation reflects the sum of all the elements of the environment which are important to plants. (2) The species with highest competitive powers are the best indicators. (3) Forests consist of superimposed groups ("unions") which occur in different combinations over the landscape. (4) Each union is sensitive to certain special aspects of environment. (5) Many characters of vegetation have potential significance as ecologic indicators. (6) Types of environment ("habitat types") are the most basic ecologic units of landscapes.

Examples of the practical value of vegetation indicators for predicting tree grown, appropriate silviculture, susceptibility to insect and fungus attacks, ecotypic variations among plants, hydrologic regimes, and the value of vegetation for wildlife are detailed.

Previous criticisms of the vegetation indicator method are reviewed and evaluated.

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