ON THE RELATIONSHIP BETWEEN VEGETATION CLASSIFICATION AND ENVIRONMENTAL ASSOCIATION

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Abstract

Vegetation is organized at a number of integrated levels which can be abstracted into the individual, the population, the species and the community. Vegetation is normally classified at the community level and implicit in the recognition of a community is an assumed correlation between the community and its environment. The validity of this assumption is examined and the implications considered in relation to the classification of vegetation.

A means of recognizing a community in the field is proposed which depends on defining a community as a spatially delineated group of interacting individuals. Variables which relate directly to community function are then considered in relation to resource acquisition and utilisation by plants. These variables reduce to the amount (area and mass), distribution (height/life form/species), longevity, and annual efficiency of foliage. Application of the method is illustrated using field results.

It is concluded that interaction between individuals within communities (plant competition) limits the usefulness of current classificatory methods and that elucidation of community-environment interrelationships requires methods which allow separation of environmental and competitive effects. While this is not yet possible the method proposed should allow analysis of the competitive interactions within communities and provide a means of increasing the resolution of structurally based classifications.

Introduction

It has been suggested that the "basic purpose of classification is to organize information logically so that it can easily be comprehended and communicated" (Johnston and Lacey 1984). The ultimate classification could then be an equation where parameters characterizing the community indicate its position in a continuum covering all vegetation. However, given our current state of knowledge, the outcome is always less than this. The tendencies are to either compartment vegetation into a number of states (boxes) or to produce a statistical abstraction summarizing the observed variation over a limited range of conditions.

Where states are recognized they are usually organized hierarchically to show similarities, hence we have seral and climax states in vegetation successions. Statistical analysis can likewise result in a hierarchy of groupings. Alternatively, the vegetations may be ordered along vectors with the vectors summarizing the variance with regard to the measured variables. However, the validity of the classification or ordination cannot be tested as there is no standard or outcome with which to compare. The variables measured and used to characterize the community reflect prevailing perceptions. Acceptance usually depends on how well the final classification reflects those perceptions.

The absence of a correct answer or `absolute truth' means that the simplest (most easily comprehended and communicated) classification may result from the use of an arbitrary logic. The "factual key for the recognition of Australian" soils (Northcote 1971) represents such a system. It is logical, easily comprehended and communicated but does little to display the similarities in the performance of soils or elucidate their derivation. The classification of great soil groups (Stace et al. 1968) is based on soil derivation and hence related to performance but it is not as easily comprehended or communicated as that of Northcote (1971). This illustrates the main dichotomy in the `use' of classifications, that is, whether they are used to increase understanding or to communicate type.

The dilemma confronting classifiers of vegetation is therefore the reconciling of simplicity of application with an ability to increase understanding. Thus while Johnston and Lacey (1984) state the purpose (function) of their classification such that it could be achieved using an artificial classification this purpose is qualified by the suggestion that the classification could be used "for comparing vegetation patterns with patterns of environment and disturbance".

This suggestion that vegetation should correlate with environment is implicit or explicit in all vegetation classifications. Indeed, classical phytosociology is based on the assumption that vegetation reflects the physical environment (Mueller-Dombois and Ellenberg 1974). However, the nature of this association is uncertain.

The main concepts developed in plant ecology to characterize vegetation - environment associations are succession, the individualistic `hypothesis' and the continuum. The first views vegetation as an organism developing through a number of seral states into a climax which represents maximal community development under the prevailing conditions (Clements 1916). The individualistic concept (Gleason 1927) regards vegetation as reflecting interactions between individuals and their environment while the continuum concept (McIntosh 1967; Whittaker 1975) suggests that there should be an intergrade of vegetation along an environmental gradient; a continuum of vegetation in response to a continuum of environmental conditions.

The individualistic concept deals with mechanism while the successional and continuum concepts relate to states. Accepting the individualistic concept as a truism, the observable outcome could be distinct states and/or a continuum; a patchy environment can result in discontinuities or disjunct vegetation even where, theoretically, vegetation reflects a continuum. The perceived differences in concepts relate mainly to differences in emphasis.

The existence or otherwise of disjunct states is critical in the discussion of vegetation classification. Should vegetation be expressed as a continuum then any classification is artificial and serves only to provide a description of community type. Alternatively, if vegetation exists as a series of disjunct states, then natural classifications can be developed and used to analyse vegetation-environment associations. There is no a priori reason to assume that vegetation exists either as a series of definable states or as a continuum. However, there is likewise no a priori reason to expect the existence of plant species. It is true that species are an abstraction, and it can be argued that they are a figment of man's imagination but the species concept does provide a useful working hypothesis. It may likewise be useful to assume that plant communities exist as identifiable entities. The consideration then is, how might they be identified. This question is examined below by discussing the nature of the relationship between vegetation and environment. Vegetation characteristics considered useful in the description of communities are then considered in relation to function.

Background

This study was iniated to examine limitations to current methods of vegetation analysis and to explore the logical outcome of an approach to analyzing vegetation developed on a few simple assumptions. Given comment that the study lacked purpose it became evident that existing approaches were considered adequate and alternate proposals seen to be irrelevant. While the question of relevency is one for the future, the adequacy of assumptions embodied in current procedures can be examined.

Relationships between vegetation and environment are readily apparent at the broad scale. Differences between rain forest and desert in both vegetation and climate are clear. However, as the spatial scale decreases it becomes increasingly difficult to obtain environmental measurements that are independent of the vegetation. At the broad scale, effects of vegetation on environment are small compared with environmental differences but the magnitude of this difference decreases as the spatial scale and/or the environmental differences decrease.

This confounding between vegetation and environmental measurements caused by interaction affects studies on plant succession and environmental association in many ways. Nobel (1981) proposed the use of `dynamic attributes' in vegetation classification for successional studies where the attributes reflect, and are identified by, the interaction between plants and their environment. The environment is defined relative to plant response. Gillison (1981) also proposed the use of morphological characteristics for such studies. He later reduced a long list of attributes to a practical subset but the selection depended on an assessment of the characteristics that best explained `known' plant / environment associations. The logic used is, how does A relate to B when A has been defined in relation to B? The answer depends on the relationship defined between A and B.

Circularities are also commonly introduced by sampling methods. Sites are often selected because they are regarded as being indicative of particular states (associations). Statistical analysis then serves mainly to demonstrate the efficacy of site selection rather than indicate the true nature and distribution of vegetation. This situation is evidenced by the test applied ÁYto the Gradsect approach (Gillison and Brewer 1985). It is suggested that this approach is efficient in sampling for vegetation / environment associations, however, the test only demonstrated that the Gradsect procedure was more efficient in recreating a known pattern than the sampling procedure used to define that pattern. Logically it can never do more unless the sampling is structured so as to provide combinations of the pertinent environmental factors and the levels of the factors determined are unaffected by the vegetation.

Some of the above examples refer to procedures designed to investigate succession or disturbance. Beard (1944) suggested that correlations between vegetation and environment only occur when the vegetation is mature, stable and integrated. This begs the question as to how one recognizes such a condition. The usual procedure is to do so through environmental association; a mature, stable and integrated community exists where there is a common, identifable association between a vegetation type and a particular environment. The alternative is to refer to lists of the characteristics of these `climax' states. As the production of these lists depends on the prior recognition of the state, this does not avoid the problem of circularity.

The measurement of plant response to defined conditions is done routinely in plant physiological studies but even under controlled conditions care must be taken to ensure that plant response does not significantly alter the environment. In studies of leaf gas exchange efficient mixing of the air is required to ensure that the CO_2 uptake and H_2O loss by the leaf does not result in the leaf responding to conditions quite different to those being monitored in the chamber (Slatyer 1971).

Physiological measurements have been used to predict plant performance in the field. Parkhurst and Loucks (1972) evaluated the effect of leaf morphology on physiological performance in relation to environmental conditions but the optima obtained do not indicate optima for plants growing in mixtures. The optimum for a leaf in isolation need not be an optimum when leaves are clumped just as an optimum for a plant in isolation need not be an optimum when grown in either monocultures or mixtures.

Physiological measurements have been used in models to predict the performance of monocultures, more usually crops but also woody vegetation but even with monocultures it is difficult to adequately represent the interactions when a number of environmental factors affect performance. When modeling plant mixtures there is the additional difficulty of defining the interactions between the plants. Usually, the different plants are modelled as separate layers rather than individuals with assumptions made about the interrelationships between layers (McMurtrie and Wolfe 1983). Plants are assumed to exist; there is no differentiation between growth and recruitment. The results often indicate stable states but the answers obtained reflect the assumptions made concerning the nature of the interactions.

An alternative to modeling the vegetation as layers or biomass is to model communities as mixtures of individuals, keeping track of recruitment and mortality as well as growth (Shugart 1983). Successional patterns do emerge, the vegetation usually does tend to stabilize (reach a climax) and the patterns can change with change in the environment but these trends are only observed when the vegetation is averaged over large areas. Even when given a defined species complement and defined environmental conditions the results vary in both time and space.

The main characteristic of models is that the results obtained reflect the assumptions and constraints inherrent in the models. The validity of the results depends on these constraints and the purpose of the exercise. Deterministic models are usually valid where the structures can be defined but with analysis of vegetation change it is the structure that is being defined. This structure depends on the interaction between a fluctuating environment and the capabilities of a wide range of species in both growth and recruitment and, given our curent knowledge, can only be realistically simulated by incorporating a large probabilistic element.

The practical expression of vegetation description and environmental correlation is vegetation survey, the mapping of vegetation or environmental associations. Where this has been done over the same area by different people the results usually differ. These differences are invariably attributed to differences in purpose and scale but this is not always so. The boundaries of Land Systems surveyed on adjacent areas by different teams rarely coencide.

The Shoalwater Bay Training Area (SWBTA) on the Queensland coast just north of the Tropic of Capricorn has been surveyed using three methods, Land Systems, PUCE Terrain Analysis and numerical analysis of satellite imagery. The general purpose of all surveys was the documentation of the natural resource but with the emphasis of land use planning for the PUCE and Land Systems approaches and land management with the analysis of satellite imagery. Mapping of the 2,800 km^2 land area was at a scale of 1:100,000 for all surveys. Given that less than 7 % of the SWBTA has been cleared and the remainder is largely undisturbed, the vegetation should, theoretically at least, be mature, stable and integrated. This allows a comparison of techniques, particularly with regard to the elucidation of vegetation - environment associations.

The Land Systems approach is based on the precept that landscapes contain entities which are similar with regard to vegetation and soils (land units) and that these are arranged in the landscape in a definable manner. A land system is thus defined in terms of the occurrence and arrangement of land units. Arrangement is usually expressed in terms of position in a catena. This agglomerative approach is based on the concept that similar climates and geologies produce similar geomorphologies with the similarities being expressed in the patterns of vegetation and soils. It is assumed that vegetation and environment are correlated!

With the PUCE (Pattern-Unit-Component-Evaluation) method the geology map is regarded as absolute and this defines the provinces. These geological groups are then subdivided, firstly according to to local relief amplitude and drainage patterns to delineate terrain patterns and then on slope characteristics to delineate firstly units within patterns and then components within units. The method represents a hierarchical, divisive classification of the landscape.

The above description of the PUCE system relates to the method of application, and hence the form of output, rather than to the definitions given in the handbooks (Grant 1975 a, b). The delineation of terrain units theoretically depends on soil and vegetation characteristics; the numerical code used to label units indicates the slope, soil and vegetation. However, the slope categorization is the primary determinant and soil and vegetation only provide further subdivision where applicable. Such subdivision is rarely applied as soil and vegetation differences within terrain patterns are usually accommodated within the slope categorization.

The objective in land cover analysis of satellite imagery is usually to identify and map similar entities. The data are reflectance intensities for 4 or more spectral bands in a two dimensional spatial grid. The data can be assessed visually, in which case the approach is similar to the Land Systems. The delineation of spatial pattern is assisted by the enhancement of spectral of resolution relative to aerial photography and this helps to counter the absence of stereo capability. The terrain approach is inapplicable because of the lack of information for the third spatial dimension.

The rationale behind numerical analysis of satellite imagery varies with the objectives and interests of the researcher. There is an underlying theme that the spectral data contain information on land cover. There are, however, a number of dichotomies in analytical approach such as regarding the data as representing either a continuum or a non-random array of disjunct states and either basing the analysis on a field classification, which assists labelling, or making the analysis independent of field observation. The latter has theoretical advantages but makes labeling difficult. The objective is usually the production of map indicating the distribution of discrete entities rather than mixtures.

With the Land Systems study (Gunn 1972), vegetation was described using floristic and combined floristic / structural characteristics. The floristic classification served to describe the combinations of species recorded and little else. The structural classification was used in conjunction with photo patterns and lithology to map `mapping units'. The vegetation within the mapping units was defined in terms of the percentage occurrence of recognized vegetation types without any reference to spatial arrangement. Despite the Land Systems approach being based on an assumed correlation between vegetation and environment, the study did not identify the associations. This problem existed both within and accross lithologies for all except the obvious associations such as mangroves occurring on fine marine sediments.

In the terrain analysis (Grant et al. 1979), spatial arrangement was defined by catenary position with the catena being based on an analysis of slopes. The vegetation types occuring in the various catenary positions were given in the unit descriptions using the floristic / structural system employed in the Land Systems study. Distinctly different vegetation types were usually recorded for each position despite the fine partitioning of the landscape. A close relationship between vegetation and environment was not apparent where the environment was defined independently of the vegetation.

The analysis of satellite imagery provided an indication of the vegetation for every 80 x 60 m area of the SWBTA (Tunstall et al. 1987). This avoids errors associated with bias in sampling but there errors associated with incorrect labelling. The data have not yet been related to the environmental factors using analytical procedures because of problems in both constructing and analyzing such large data sets but analysis of the spatial belationships between the vegetation types demonstrates a nonrandom distribution of vegetation which can sometimes be interpreted in relation to catenas (Tunstall et al. 1984). There are general situations but there are also many exceptions.

A further study was conducted over part of the SWBTA within an area sufficiently small so as to effectively be uniform with regard to climate (Gunn 1978). Following a detailed soil survey he concluded that there was no observable relationship between soil and vegetation. No relationship between vegetation and environment was observed.

The conclusion from these studies is that while vegetation patterns can usually be defined and while these patterns can often be interpreted relative to environmental conditions, the association between vegetation and environment is not 1 to 1. Vegetation patterns are not just a consequence of environmental conditions. The question then is, what aspects of vegetation have most effect in limiting the degree of association between vegetation and environment.

Community definition

Vegetation is organized at a number of integrated levels which can be abstracted into the individual, population, species and community. A population is usually regarded as a group of reproductively interacting like individuals, a species a group of like individuals capable of interbreeding and, for the purposes of classifying vegetation on a functional basis, it is suggested that a community should be regarded as a group of interacting individuals (like and/or unlike). With these terms the level of abstraction increases with decreasing integration so while individuals can usually be recognized, community recognition can be difficult. Since vegetation is normally classified at the community level, the concept of a community warrants investigation.

The community concept recognizes that plants rarely exist as isolated individuals. Close proximity results in interaction (competition) between plants, and the environment experienced by an individual depends not only on the general environmental conditions but also on the modification of those conditions by its neighbours. This is exemplified by the distinction between physiological and ecological optima; the physiological optimum for a species being the environment in which it grows `best', the ecological optimum being where it grows `most', that is, where it competes most successfully with other components of the system. This distinction has long been recognized (Darwin 1859).

With interaction between individuals in a community the whole is not necessarily the sum of the component parts. Individuals only form a community where they interact and where they interact the community assumes characteristics which relate not only to the environment and the characteristics of the individuals but also to their interaction. In consequence, classifications of plant communities will provide a sound basis for the evaluation of the environment only when the interactions between components within communities are considered. This necessitates a community description which relates directly to a system function and an analytical method which allows separation of environmental and competitive effects. This suggestion may appear to characterize some current classificatory approaches but it does not. Current approaches seek to establish causal relationships using vegetation-environment correlations, but only the net product or end result of the interactions is analyzed and mechanisms are not explicitly considered. Such an approach is only successful when analysing simple systems, and with vegetation analysis it results in the use of arbitrary criteria in the collection and analysis of data. For example, a common method is to optimize sample size in relation to an information or variance coefficient statistic. This inevitably results in a sample size such that all the individuals within the sample do not compete. Competition between some individuals is prevented through spatial separation, while adjacent individuals interact strongly. Competitive interactions can rarely be evaluated with such variation in relationships between individuals within samples, hence vegetation-environment interrelationships can rarely be defined.

An alternative approach is to consider the proximity between individuals, as in `nearest neighbour' type analyses. This ensures interaction between individuals but does not define the unit of vegetation with which the environment is presumably correlated. A single plant interacts with several other plants, and while a consideration of all neighbours may theoretically be possible the additional problem of equivalence between individuals of differing size or life form has yet to be resolved. On statistical grounds, Grabau and Rushing (1968) proposed that the sample size should be based on the areas encompassed by 20 individuals. This recognizes the importance of interaction between individuals, but in both theory and practice their approach requires the existence of uniform vegetation.

In defining a plant community as a group of interacting individuals the question of community characterization is resolved into two main problems. Firstly, the recognition of a community in the field and secondly, the determination of characteristics which relate directly to the functioning of the community.

COMMUNITY RECOGNITION

The problem of community recognition is one of scale. Plants can vary in size and life form, consequently the size of a community can not be fixed but depends on both the size and distribution of individuals. In sampling for floristic associations the scale is usually determined by increasing the sample size until the species are regarded as being representatives of the site; with the approach proposed here the reverse is required. The sample size should be reduced to a level where the individuals under consideration form a strongly interacting unit. The description of the vegetation within the sample can be most readily obtained by assuming horizontal uniformity and recognizing vertical disjuncts. The vertical disjuncts will relate to age, life form and/or species. This does not require recognition of strata in the classical sense, but with sampling at this scale the vegetation will usually show discernible layering within each sample.

Sampling is most difficult where there is wide variation in life form within communities since the objective is to obtain a sample within which all individuals directly interact. An appropriate sample size may be 1 m^2 for grasses but may exceed 100 m^2 for trees. Also, grasses directly beneath a tree canopy would be expected to interact more with the tree than grasses away from the canopy. This problem can be resolved through characterization of boundary conditions. For example, the effect of trees can be evaluated in terms of the proximity of trees to the sample rather than through the presence of trees in the sample. In a shrub woodland Tunstall et al. (1981) used a 25 m^2 sample size which related to the distribution of shrubs. Within each sample grasses were regarded as being uniform while the effect of trees on the sample area was scaled according to the size and proximity of the adjacent trees. An alternative technique was used by Tunstall and Webb (1981) in which the distance from a single tree provided a measure of the effect of trees on the sample area.

Selection of variables

Plant characteristics which can be used to evaluate relative success or status are biomass, productivity (biomass increment/unit time) or production (nett photosynthesis). However, plant biomass is inappropriate for comparisons between life forms because of differences in longevities of different plant structures and measures of productivity are confounded by differences in the partitioning of photosynthate between growth and maintenance functions. Production is the most direct measure of gain, it is closely related to resource utilization (the amount of CO_2 energy, water, etc. acquired by plants) but it is difficult to measure.

Foliage is the main functional element of vegetation as energy from solar radiation is utilized by foliage to combine nutrients absorbed through the roots with atmospheric carbon dioxide to form organic compounds, thus to a first approximation the production/resource utilization of a community can be defined in terms of the amount and vertical distribution of foliage. This assumes that light is the major limiting factor or that there is a direct proportionality between the effect of light and other factors on plant production.

The simplest definition of the amount and distribution of foliage in a community, the height and projected foliage cover of the dominant stratum, has been used by Specht (1970) and others to classify Australian vegetation. In a more detailed analysis Tunstall et al. (1981) used estimates of the projected cover of each life form in communities to interpret the effects of disturbance on vegetation. Since none of these studies utilizes all the information contained in the description of the amount and distribution of foliage in the communities, the results do not indicate the full potential of the approach. The studies do however demonstrate that, for many purposes, simple estimates of foliage amount are adequate.

To obtain a more detailed description of a community it is suggested the following parameters should be considered:

a. light
  - foliage area
  - foliage distribution
  - foliage angle

b. nutrients
  - foliage mass
  - foliage longevity[1]

c. water
  - foliage area
  - foliage `efficiency'[2]

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[1] Leaf longevity can be seen to be a result of the balance between the energetic cost of the acquisition of new leaf (carbohydrate required for nutrient uptake as well as for structural development) and the most of maintaining old leaf under unfavourable conditions. High nutrient concentrations and high seasonality should lead to frequent leaf replacement, low nutrients and low seasonality to longer leaf life.

- stomatal pore length[3]

This reduces to the amount, distribution, longevity and annual `efficiency' of the foliage with foliage angle and stomatal pore length as secondary considerations. The rationale for the selection of some parameters is indicated below, and while relationships between resources and parameters are indicated they are only approximate.

Interpretation of community descriptions

It has been suggested above that the relative abundance of plants occurring in small, strongly interacting groups should be characterized, and that the stratification within groups be based on either height, life form, species or, if necessary, individuals. Data collected in this manner characterize the natural balance between plants growing in mixtures and so provide a basis for an evaluation of the competitive aspects of plant communities. An entire study area can be characterized or the range of variation in structure and composition of the vegetation within an area need only be considered. Techniques exist for the analysis of data from plant mixtures (van den Bergh 1968; de Wit 1960; Torssell and Nicholls 1976) but current competition theory relates primarily to annuals and requires that the plants occupy all the available space commensurate with the stage of development (full utilization of the available resource). Experimentally these constraints have been met by planting at high densities under favourable conditions which ensures well defined competitive relationships through uniform phasic development.

The results of a classical small plot experiment in which the relative yields of two species growing in mixtures were evaluated are shown in Fig. 1a (van den Bergh 1968). In such plots the axes do not characterize the dependence/independence of the variables. There is a strong correlation between the yields of the species and this relationship characterizes the competitive interrelationship between the two species for the given conditions. The correlation between tiller densities for two perennial grasses growing in mixtures in a field situation is not as strong (Fig. 1b), but there is still a general relationship between the relative yields of the two species. In a woodland situation there is no apparent relationship between grass biomass and the projected foliage cover of the taller components (Fig. 1c). These latter data illustrate the spatial variability in intact and regenerating native vegetation. They demonstrate that for a given overstory cover there is an upper limit to the amount of herbage that can exist but within this limit herbage biomass is apparently independent of the amount of trees and shrubs. The different life forms apparently function independently excepting where the total amount of vegetation is large.

The data in Fig. 1c do not fall into either the alleotrophic (plant distribution dependent on plant interaction) or autotrophic (plant distribution environmentally determined) categories of Tansley (1949). They are interpreted as demonstrating that within communities plants do not necessarily occupy all the available space, that there can be incomplete utilization of resource. While this could be due to a number of factors it is most likely a consequence of both irregular recruitment and the natural life cycles of plants (e.g. as with annuals vs perennials). Where plants co-exist the growth of different life forms need not be interrelated because of

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[2] There are difficulties in equating foliage between different life forms such as trees and grasses. The proportion of the year for which they are functional would provide a coarse rating but ideally this should be upgraded by considering the CO_2 fixed/unit of foliage/unit time. For perennials, the unit of time should be one year.

[3] Pore length is used as a simple measure of the capacity of a leaf to transpire water. At low stomatal densities stomatal conductance is directly proportional to stomatal density but depends on the 4th power of pore length (DeMichele and Sharpe 1974).

differences in phasic development, thus the amount of vegetation present at any time is not a direct measure of the available resource.

At present the inability to determine the level of resource utilization by different plant communities limits the application of competition theory. Successional theory (Cornell and Slatyer 1977), provides one means of evaluating the temporal variation in resource utilization by communities, but its application is limited through the long periods of observation required for characterization of perennial vegetation. This limitation could possibly be circumvented, for while succession is defined as change with time it can be expressed as variation in space. In an environmentally uniform system where changes in the composition of spatially separate plant communities occur independently, there will be a range of community composition and structure. In the absence of man made disturbances this range relates to the life cycle of the components and, if the area is sufficiently large, then all successional states will be seen at the one time. Variation in space becomes equivalent to variation in time. Such a concept was invoked in the classical description of succession from swamp to climax woodland or forest. Seral stages were viewed as positions in a catena rather than a single point being monitored over hundreds of years.

Time-space equivalence as defined above is virtually a truism. Such a concept is the basis of modern astronomy and is used in many disciplines. Gleason's (1927) rejection of the concept is based on his viewing succession as temporal change at a point with differences between points (spatial differences) being a consequence of differences in environment. Problems with this view are the organisms have a finite size and that change in an organism results in change in the environment (space).

The above approach does not necessarily solve the problem of using vegetation as an environmental indicator as the determination of successional characteristics by this means requires recognition of an environmentally uniform system. This can be straightforward with climate but with soils the interactions between plant and soil can produce differences related to plant distribution rather than the converse. Environmental uniformity is therefore not an absolute factor but varies depending on the time frame of interest. However, recognizing this constraint, characterization of the spatial variation in both the proportion and amounts of the plant components in communities illustrates a number of features of the communities. Taking as an example the two component system of trees and grasses such data define:

1. The upper limit to the magnitude of any component
2. The limits of one component relative to another (at a given level of trees the grass may be reduced below the maximum, and the limits define the maximum grass yield for any level of trees)
3. The distribution of points within such limits. With area based observations, this distribution illustrates the probability of observing any particular combination of the components.

The limits to the data define what is possible and the distribution of points within those limits define the probabilities. The limits relate directly to the environment and the capabilities of the plants; the distribution of points relates to their interaction.

Some of these aspects are illustrated in Fig. 2 which compares the responses of mosses and lichens to overstory cover for pine forests in central Sweden. For lichens (Fig. 2b) maximum yield occurs at around zero overstory cover and the yield decreases with increase in overstory cover. With mosses (Fig. 2a) maximum yield occurs at 40% overstory cover and the yield decreases with either an increase or decrease in cover. There is direct competitive interference between lichens and trees or shrubs whereas mosses exhibit a dependence on overstory cover.

The limits to the distribution of points in Figs 2a and b define the maximum yields of mosses and lichens in relation to overstory cover. They thus define the response of plants to a single factor but using field data which characterize a multifactorial situation. The use of boundary line analysis to determine single variable relationships from multifactorial data has been proposed by Webb (1972) and Jarvis (1976). This allows the characterization of limits but it is apparent that these limits are infrequently realized (Fig. 2). The laboratory determination of such relationship as suggested by Austin (1985) will therefore only be beneficial when all factors are known and all interactions understood. This situation does not currently exist and it appears most benefit will be gained through direct analysis of the processes operating in plant communities. Examples of such an approach are given by Cunningham et al. (1981) and Austin et al. (1984).

Discussion

A theoretical approach has been adopted mainly because of the lack of information on which a full analysis could be based. It is concluded that no current classificatory procedure allows elucidation of community-environment interrelationships but that classifications which relate directly to the functioning of the community (e.g. structural classifications based on the amount and distribution of foliage) provide a basis for an extension of knowledge. Such classifications currently function best at a broad scale but increased resolution could be obtained through incorporation of information on the balance between components within communities. A means of achieving this is suggested, but this requires changes in both the form of data collected as well as analytical methods.

Superficially, the proposed approach appears to be the antithesis of gradient analysis (Whittaker 1978). In reality the approaches are complementary and have many similarities. With gradient analysis a gradient is defined and vegetation distribution is determined relative to that pattern. Here it is suggested that the vegetation pattern be defined in an environmentally uniform system. However, the main dichotomy in practice relates to the entities that are defined. Gradient analysis is mainly applied to the analysis of the distribution of dominant species; dominant life forms are likely to be less subject to interplant competition than lower life forms. The approach suggested here is directed at analyzing the relationships between plants of different life forms rather than between plants of the same life form.

Simplifying assumptions are used with both approaches to avoid the confounding that arises through the interaction between plants and their environment. With rigorous gradient analysis it is assumed that species distribution depends solely on responses to environmental factors and that the level of these factors is unaltered by the presence of plants. The determination of the levels of environmental factors in a manner that incorporates plant effects in invalid because of the uncertainty as to cause and effect. Two consequences of this assumption are that species rather than vegetation patterns are usually predicted and there are usually significant differences between the predicted and observed. As stated by Austin (1983), species absence is readily apparent but often species are absent from sites within their absolute limits.

The assumption involved in the approach suggested here centres on the need to define an environmentally uniform area. Theoretically, like all assumptions, this assumption will rarely if ever be completely valid. In practice however, it can be usefully employed provided the magnitude of the differences arising from plant interaction is large compared with differences due to environmental factors. This demonstrates the complementary nature of this and the gradient analysis approach as gradient analysis is valid where environmental effects are large compared with those arising from plant interaction. One is technique is applicable where the environmental gradients are large, the other applies where environmental gradients are small.

The approach presented here allows definition of the maximum level of vegetation development, the maximum performance of plant species in a given environment and the likely outcome when the plants are grown in mixtures. Use of such a quantitative measures of plant and community performance should significantly improve the results obtained in gradient analysis and other methods designed to examine relationships between vegetation and environment.

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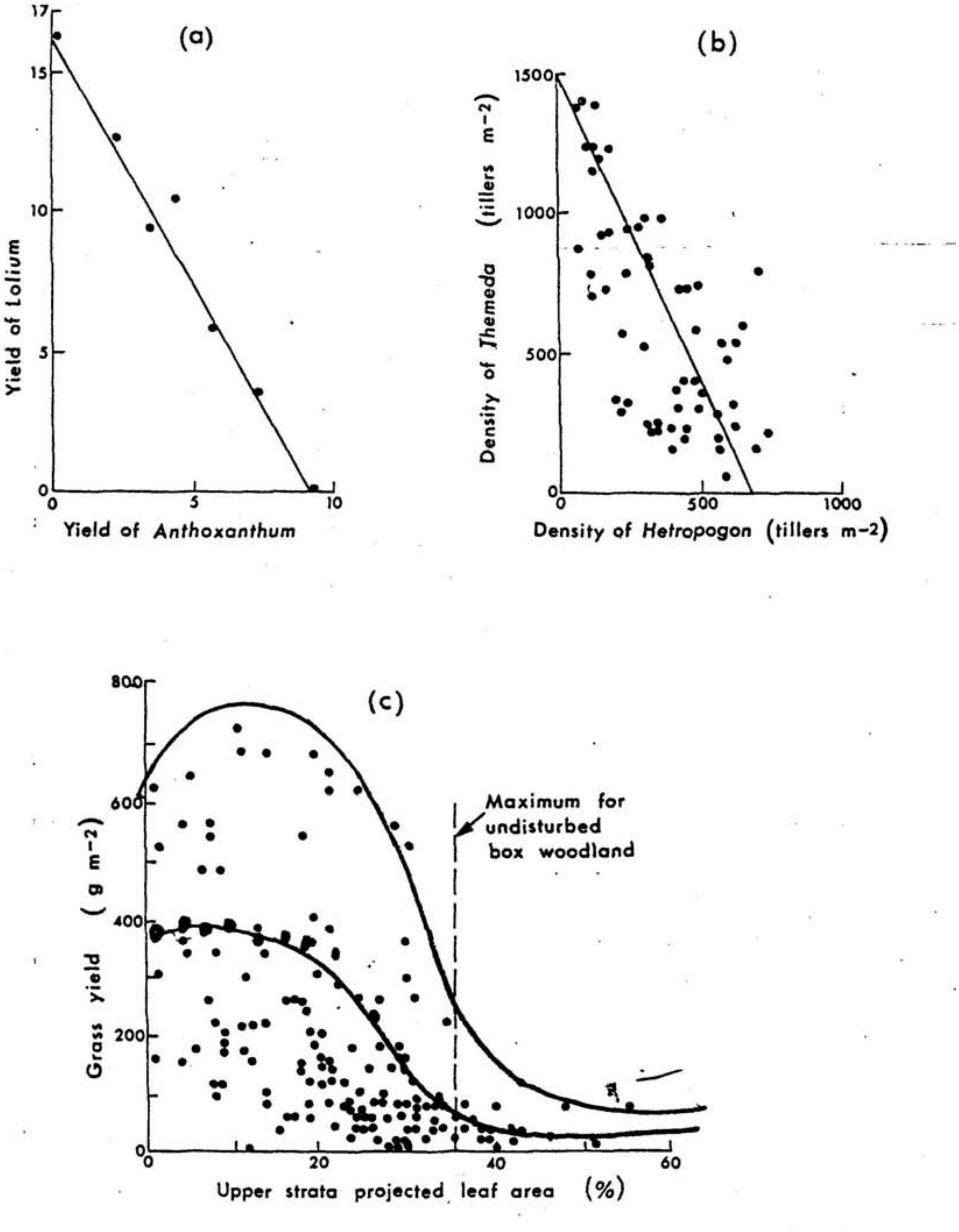

Fig. 1. Component replacement in two-component systems:

(a) *Lolium* versus *Anthoxanthum* in agronomic pot experiments (van den Bergh 1968).

(b) *Hetropogon* versus *Themeda* in agrostology field experiments (Torssell and Nicholls unpubl.).

(c) Herbage versus upper strata in woodland ecology field experiments (Tunstall and Torssell unpubl.).

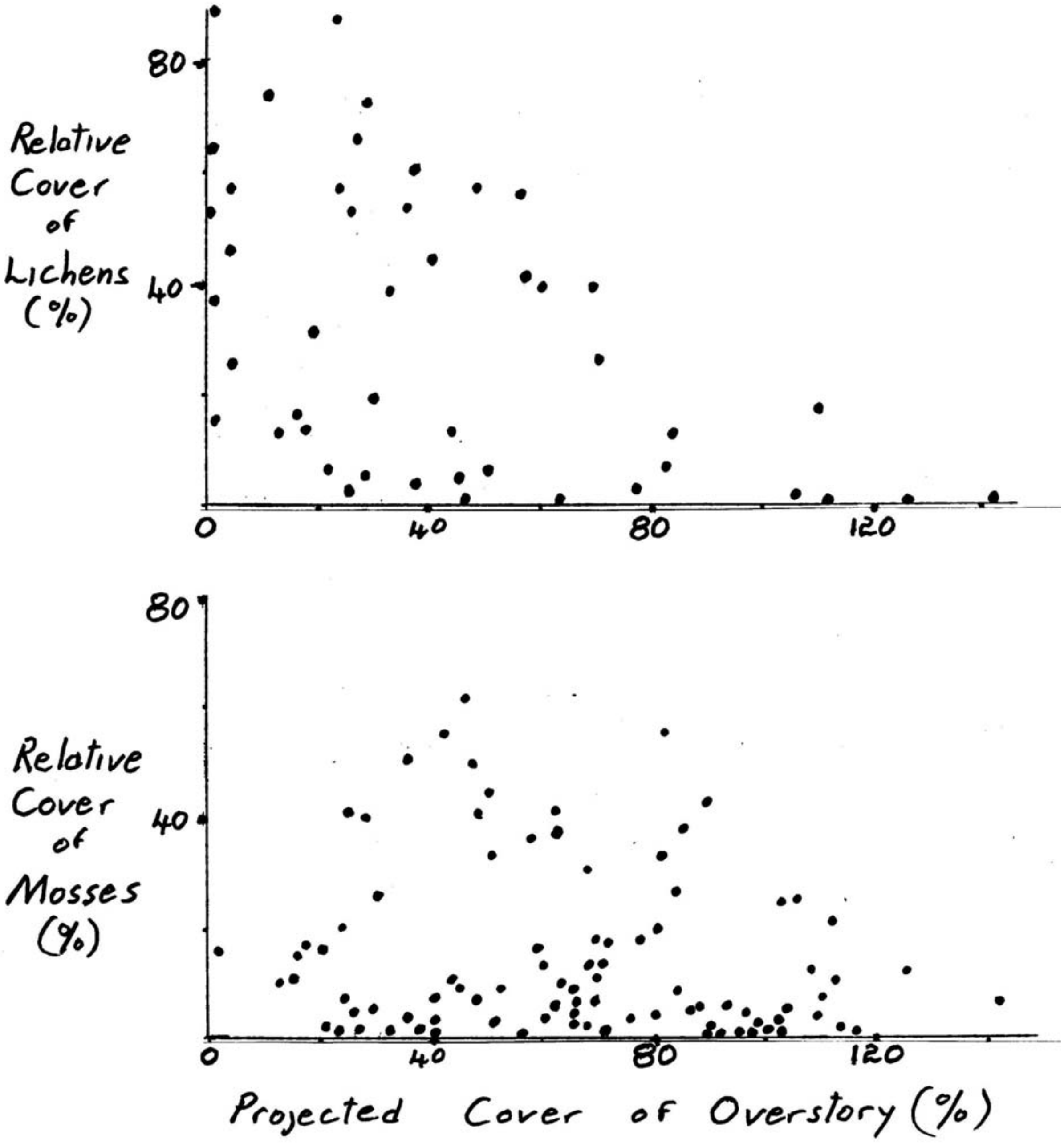

Fig. 2. Component replacement in pine forests of central Sweden:

(a) Relative foliage cover of mosses versus overstory projected foliage cover. (Tunstall and Torssell unpubl.).

(b) Relative foliage of lichens versus overstory projected foliage cover. (Tunstall and Torssell unpubl.).