

A new model for the continuum concept

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Accepted 12.04.89

Keywords: Environmental gradient, Fundamental niche, Niche theory, Realized niche, Species response curve

Abstract

A reformulation of the continuum concept is presented after considering the implications of the community/continuum controversy and current niche theory. Community is a spatial concept dependent on landscape pattern while the continuum is an environmental concept referring to an abstract space. When applying niche theory to plants, the mechanisms of competition are ill-defined and the assumption of bell-shaped response curves for species unrealistic.

Eight testable propositions on the pattern of response of vegetation to environmental gradients are presented 1. Environmental gradients are of two types. a) resource gradients or b) direct physiological gradients. 2. The fundamental niche response of species to resource gradients is a series of similar nested response curves. 3. The fundamental niche response of species to direct gradients is a series of separate, independent, overlapping response curves. 4. Species fundamental response curves are such that they have a relative performance advantage in some part of the environmental space. 5. The shape of the realized niche is variable even bimodal but predictable from the fundamental response given the other species present. Propositions 6–8 describe the response shapes of emergent community properties to environmental gradient; species richness is bimodal, dominance trimodal and standing crop unimodal. Detailed comparisons of these propositions are made with the alternative theories of Ellenberg, Gauch and Whittaker, Grime, and Tilman. These theories are incomplete lacking several generally accepted properties of plants and vegetation.

Introduction

Vegetation science can be defined as *the study of those processes which determine the patterns of composition and emergent properties (e.g. species richness) observed in vegetation*. Theory can be defined as 'a coherent group of general propositions used as principles of explanation for a class of phenomena' (Macquarie Dictionary). There is

relatively little theory associated with vegetation science given this definition, nor have vegetation scientists actively sought to develop theory. The Uppsala symposium on 'Theory and Models of Vegetation Science' (Prentice & van der Maarel 1987) marked a major shift and recognition of this deficiency. At that meeting, one of us (Austin 1987) tested a series of propositions arising from the continuum theory put forward by Gauch &

Whittaker (1972). These propositions were rejected for canopy species in eucalypt forest in south-eastern New South Wales, Australia. The more positive aspect of scientific research is postulating new hypotheses or new, more robust theoretical frameworks. In this paper, we attempt to re-express the continuum theory of vegetation in a more robust form, which a) allows for the patterns detected in the eucalypt forests, b) provides mechanistic processes rather than phenomenological descriptions to account for the patterns and, c) presents testable hypotheses which can be deduced from the theoretical propositions advanced.

A re-formulation of continuum theory should resolve

- a) lingering problems from the continuum/community controversy, for example, the sharp boundaries between vegetation types often observed in the field (Austin 1985, 1986),
- b) problems apparent in current continuum and niche concepts applicable to vegetation, e.g. the skewed as opposed to symmetric response curves of species (Austin 1986, 1987, and in press),
- c) differences between continuum theory and other theories of vegetation organization (Austin 1986), for example those of Tilman (1988) and Grime (1979).

We treat each of these issues in the following sections:

Continuum/Community controversy

Although no major debates are now conducted in the ecological literature regarding whether vegetation can be described in terms of continua or communities (Austin 1985), other ecologists (experimentalists, modellers and theoreticians) still persist in designing experiments, models etc. on the assumption that communities exist and can be recognised (Austin in press), while phytosociologists still define associations (Westhoff & van der Maarel 1978). The vast majority of applied ecologists concerned with management of nature reserves continue to use the term community.

The evidence for the continuum presented by Cottam & McIntosh (1966) is less than convincing as was pointed out by Daubenmire (1966). The controversy can be resolved without repeating old arguments if the two ideas of a continuum and a community are based on different incompatible frames of reference. Fig. 1 shows a transect up a mountain in an area with 4 species present. Species associations which might be recognised due to their frequency along the transect are A, AB, B, C, D with the combinations BC and CD being regarded as ecotones. These 'communities' composed of co-existing species are a consequence of the spatial pattern of the landscape. If we examine the altitudinal gradient however we find a continuum of species regularly replacing each other in the sequence A, B, C, D with increasing altitude. If the transect were taken through an adjacent area where the first bench were 30 m lower, then the combination AB would immediately become rare. At 170 m only species A would be present. Similarly if the second bench or tableland were 30 m higher the combination BC would become common. On such a transect the 'communities' recognised would be A, B, BC, C and D with ecotones AB and CD. *Communities or associations are a function of the landscape examined.* Abrupt changes or gradual transitions may occur depending on the landscape pattern. Co-occurring groups of species can be recognised for any particular region with a recurrent pattern of landscape. Many phytosociologists would recognise such associations as *noda* within a continuum (Ellenberg 1988). Labelling these communities is useful for communication and research, but extrapolation of these communities to other regions will *be accurate only* if the regions have similar landscape patterns of environment and climate.

The continuum in relation to altitude will continue to exist and be applicable in another region *provided* the correlations between growth-influencing variables (e.g. rainfall and temperature), and altitude do not change (Austin 1980).

We conclude from this that:

1. The continuum concept applies to the abstract environmental space, not necessarily to any

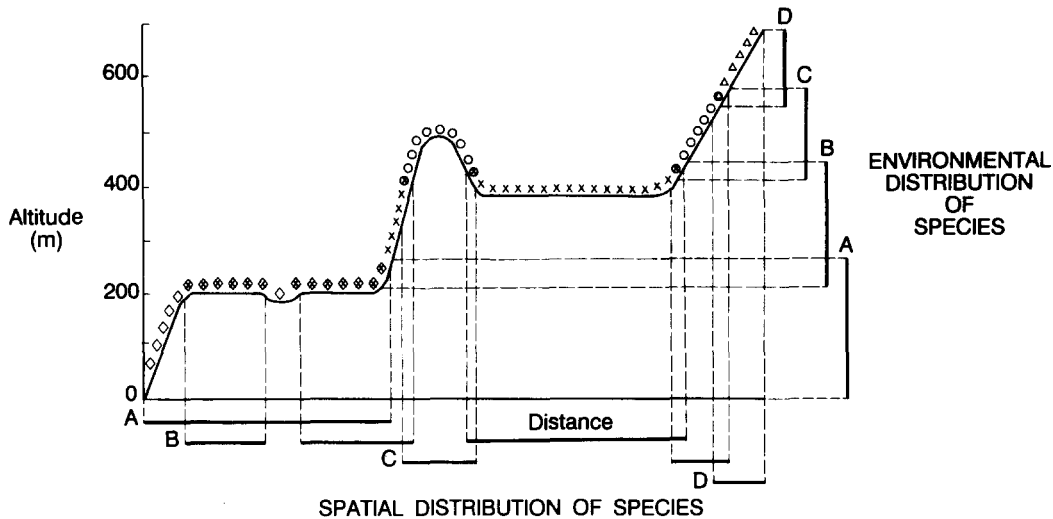


Fig. 1. Patterns of co-occurrence of four species on a landscape along an indirect environmental gradient altitude, note continuous variation of composition along altitude gradient. A plant community is a landscape concept and recognition of communities depends on the frequency of environmental combinations in a particular landscape.

geographical distance on the ground or to any indirect environmental gradient.

2. The concept of a community of co-occurring species can only be relevant to a particular landscape and its pattern of combinations of environmental variables; community is a landscape property.

For a theory of vegetation to be generally applicable it must be expressed in terms of an environmental space defined by causal environmental variables whose values are independent of location. The continuum concept, of which three variants can now be recognised (Austin in press) fulfils this criterion but one of the major deficiencies of this theory has been the failure to adequately define an environmental gradient.

Current Continuum theory

Two recent reviews of continuum theory (Austin 1985 in press) make the point that there are three possible variants of the basic concept: a) Gleason's original individualist continuum with species abundance optima and their limits independently distributed along an environmental gradient (Gleason 1926), b) Gauch & Whittaker's

version (1972) where 'major' species are regularly distributed along the gradient with optima evenly spaced while 'minor' species are independently distributed. c) stratal continuum (Austin 1985) in which each stratum e.g. trees, shrubs and herbs has a continuum of composition with either regular or irregular species distributions and with the relationships between strata either independent or correlated. Currently, there is insufficient evidence to distinguish between these possibilities, although Austin (1987) has demonstrated for one vegetation type that canopy species optima are not regularly distributed along a temperature gradient.

There is a close correspondence between these views of the vegetation continuum and how animal ecologists consider species in relation to niche theory. To quote from Giller (1984) 'Individuals of one species using marginal resources *presumably* cannot exploit them as efficiently as individuals of other species for which these resources are nearly optimal' (our italics). This model is summarised in Fig. 2a, and can be re-expressed as the realized niche of species *b* being restricted to the optimal region of its fundamental niche by competition from species *a* and *c*. This concept is probably the reason for Gauch &

Whittaker (1972) suggesting that canopy species have regular modes (optima) along environmental gradients. In contrast Ellenberg (Mueller-Dombois & Ellenberg 1974) proposed that the realized niche (ecological response in his terms) could take any one of a number of shapes (e.g. Fig. 2b and c) including the niche theory's proposed response (Fig. 2a). His explanation for the occurrence of skewed and bimodal responses was that the competitive effect of better adapted species could restrict a species to those environments *at the extremes of its tolerance* provided it had an advantage in that environment.

Most species responses (Austin 1987 in press) appear to be skewed, contrary to the bell-shaped

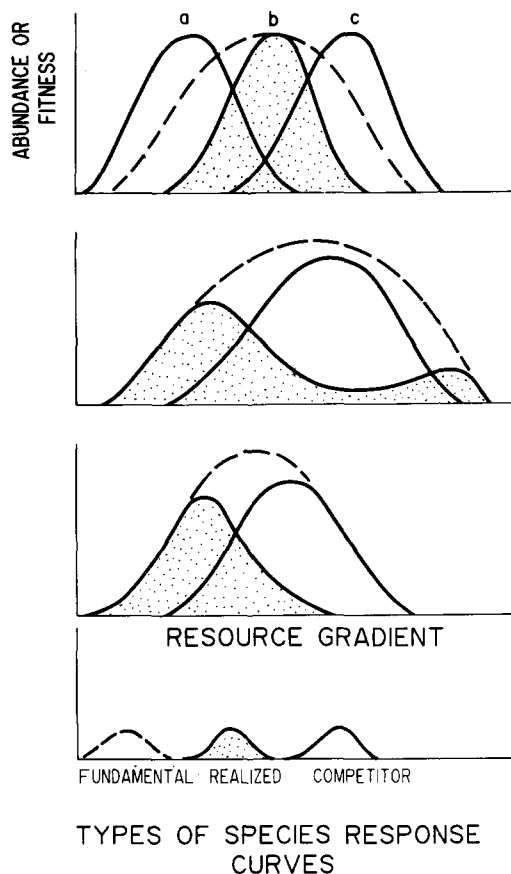


Fig. 2. Types of species response curve along an environmental gradient (a) classic niche concept with realized niche under optimum conditions, (b) and (c) Ellenberg's concept of realized niche under extreme conditions of fundamental niche (b) with bimodal variable shape (c) restriction to one extreme only.

pseudo-gaussian curves common in theoretical treatments of niche and continuum theories. There are three major weaknesses to current niche and continuum theories: 1) they are non-mechanistic and the mechanisms of competition are undefined; 2) the bell-shaped pseudo-gaussian response curves for both fundamental and realized niche responses are unrealistic for plants; 3) the environmental and/or resource gradients are ill-defined and the response to all gradients is assumed identical in shape.

We propose a new model of the continuum concept of vegetation composition which explicitly takes account of these problems.

New model for a Continuum

Environmental gradients

Three types of environmental gradient can be recognised (Austin 1980):

1. *Indirect* environmental gradients are the factor-complex gradients of Whittaker (1978) such as altitude. The influence of an altitudinal gradient is through variables like temperature and rainfall which have a direct effect on plant growth and have complex location-specific correlations with altitude. Relationships based on such gradients cannot be extrapolated beyond the environment where they were measured and are not considered further.
2. *Resource* gradients for plants are those where the varying resource is consumed by plants in order to grow. There are only a limited number of such resources for autotrophic organisms: light, water, carbon dioxide, oxygen and essential mineral nutrients. These differ from resource gradients for animals such as food size in that plants show only more or less inclusive niche responses to these resources. The response of plants is generally taken to be of a limiting response type with an eventual decline due to toxicity at levels beyond that normally experienced under natural conditions (Fig. 3a).
3. *Direct* gradients for plants are those that have

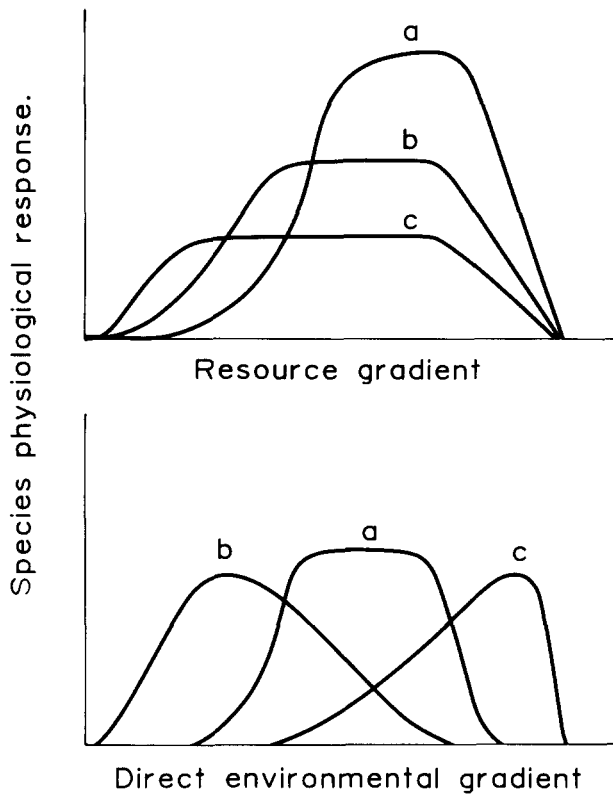


Fig. 3. Proposed differences in species fundamental response to (a) resource and (b) direct gradients.

a direct physiological impact on plant growth but are not consumed. The two clearest examples are air temperature and soil pH which govern growth rates and the maintenance of plant physiological integrity. The fundamental response may show differential adaptation to different temperature regimes with species optima being spaced along the gradient (Fig. 3b).

The first proposition of our re-expression of continuum theory is therefore:

Proposition (1) Environmental gradients to which a continuum theory can be applied are of two types a) resource gradients, b) direct physiological gradients.

Plant physiological response

There has been little discussion in the continuum literature about the fundamental response of

plants in the absence of competition, herbivory and disease (Gauch & Whittaker 1972; Whittaker 1978). Ellenberg suggested that plant species have similar optima and physiological response curves on the basis of his early experiments (Ellenberg 1953, 1954; Mueller-Dombois & Ellenberg 1974). Species fundamental niches will often tend to be nested (or inclusive), with highly-productive species (a in Fig. 3a) having response curves which include or at least have the same range as those of less productive species (b, c in Fig. 3a). However we also conclude that species fundamental responses to direct environmental gradients are neither inclusive or nested, species showing distinct separate optima and different individualist ranges of response (Fig. 3b).

This evidence leads us to put forward two further propositions:

Proposition (2) The fundamental niche response of species to resource gradients will take the form of a series of nested response curves.

Proposition (3) The fundamental niche response of species to direct environmental gradients will take the form of a series of separate, independent, overlapping response curves.

The evidence for these propositions is generally based on biomass response curves, i.e. based on vegetative growth rather than some integrated fitness measure. The propositions *may not* therefore apply to fitness measures involving germination and reproductive success (Bazzaz pers. comm.).

Smith & Huston (1989) have developed a model of plant dynamics which examines patterns of plant functional response to environmental factors (and associated life-history characteristics) at the level of the individual plant. They define a simple 2-dimensional (light*water) environmental space and examine patterns of growth response to the availability of these two resources. The approach is based on cost-benefit analysis and focuses on two specific trade-offs: (1) the trade-off between maximum growth rate under high resource conditions (either water or light) and the ability to continue photosynthesis and growth (i. e., survive) under conditions of low resource availability (Parsons 1968; Grime 1977; Chapin 1980; Orians & Solbrig 1977; Bazzaz

1979; Huston & Smith 1987; Tilman 1988), and (2) the limit to the combined tolerance a plant can exhibit to low availability of both light (above-ground resource) and water (below-ground resource), see Fig. 4. These patterns of trade-off are a function of an array of constraints ranging from biochemical to carbon allocation at the level of the whole plant (also see Tilman 1988 for similar discussion for light * nitrogen). The implication of these patterns is that a series of physiological/morphological adaptations define relative performance optima in different positions in the resource space. This leads to a fourth proposition:

Proposition (4) Species fundamental response curves will be such that in a particular portion of the resource space a species will have a relative performance advantage over other species.

The exact possibilities for trade-offs need to be examined carefully. Some species of plants appear able to adapt simultaneously to low moisture and low nutrient conditions. Grime (1979) has drawn attention to these 'stress-tolerators' which combine slow growth rates with a variety of distinctive morphological, life-history and physiological properties. The combination of physiological and morphological properties of plants are not

unlimited and we need knowledge of the functional combinations of viable properties (cf. Tilman 1988).

Plant realized niche (Ecological response)

Austin (1987), in testing a series of propositions regarding the species response curves put forward by Gauch & Whittaker (1972), showed that the response curves were predominantly skewed with the tails towards more mesic conditions for eucalypt species on a temperature gradient in south-eastern Australia. A review of studies with oldfield species (Tilman 1987) and aquatic species (Wilson & Keddy 1985) shows a similar predominance of skewed curves (Austin in press).

It is necessary to provide mechanisms whereby the fundamental response curve is modified to become the realized response curve observed under conditions of competition, herbivory and disease. Experiments (Austin 1982; Austin & Austin 1980; Austin *et al.* 1985) have demonstrated that performance in polyculture. (multi-species mixture) can be predicted from monoculture performance (Fig. 5). In a trade-off situation similar to Fig. 4 the progressive decrease in physiological advantage for an extreme-adapted species until it is outperformed by the more productive species would give rise to a skewed response curve for the realized niche. The response would be steep towards the extreme and have a long tail towards the more productive conditions. Measures of relative physiological and ecological performance are necessary to make the prediction and the results are totally dependent on the suite of species studied (Austin 1982). Subsequent tests of these relationships have shown that both morphological and physiological properties of the species are needed to predict the outcome of multispecies competition (Austin *et al.* 1985; see also Gaudet & Keddy 1988). A further proposition can be developed from these observations and experiments:

Proposition (5) The realized (ecological) response of a species in multispecies mixtures can be determined from its fundamental (physiologi-

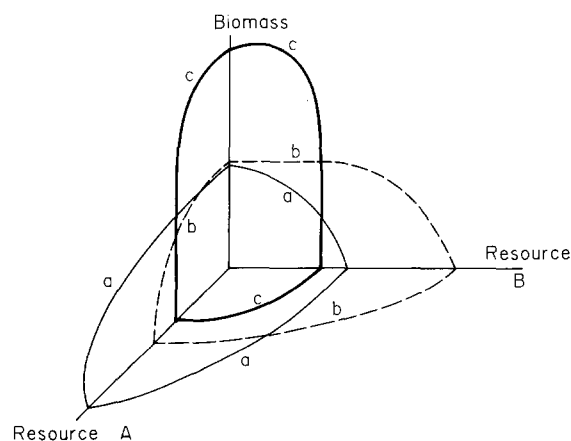


Fig. 4. Three probable types of species trade-offs in fundamental physiological response. Species (a) Growth and survival under low levels of resource A, but not B. (b) Growth and survival under low levels of resource B, but not A. (c) Maximum growth under high levels of resources but inability to survive under low resource level A or B.

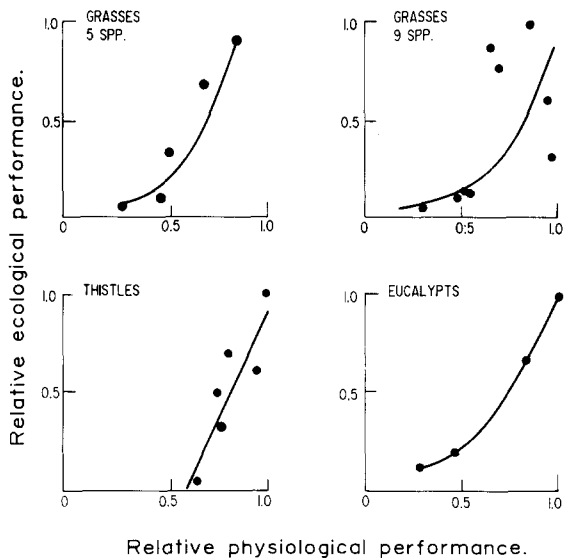


Fig. 5. Examples of the prediction of species realized (ecological) response in multispecies mixture from the species fundamental (physiological) response in monoculture.

cal) response (i.e. an integrated measure of whole plant growth in monoculture) *provided* such information is available for *all* species in the community.

The corollary of this proposition is that the shape of the realized response curve is a function of the other species present and may easily show very complex forms.

The mechanisms associated with this prediction are presumably competitive exploitation of the resource at low levels, the interaction between competitive resource exploitation and light competition with canopy closure at intermediate levels and at high, toxic levels interaction between competition for light and physiological tolerance of toxic conditions (Austin 1982; Tilman 1988). Direct gradients will show greater partitioning of responses along the gradient due to differential physiological adaptations with the relative performance being determined by plant relative growth rates and ability to form a closed canopy. Grace (1988) has recently shown that relative physiological performance in monoculture (Austin 1982) at an early stage of growth is a better predictor of the realized ecological performance in mixture at a later stage than physiological performance at that time. This suggests

that relative growth rate is the predictor of relative physiological performance not biomass.

Emergent (community) properties

Several emergent properties can be observed in vegetation comprising a number of species: the number of species co-existing (species richness), the degree of dominance exerted by an individual species, and the total biomass (standing crop) produced by the vegetation. There is an expanding literature on the causes of species diversity (e.g. Grime 1973; Huston 1979; Brown 1981), but precise mechanisms of general application remain elusive. A recent empirical study (Margules *et al.* 1987) has shown that complex patterns of species richness in relation to environmental gradients emerge when several different environmental variables are considered simultaneously. Austin (1980) drew attention to a number of patterns that these community properties show along environmental gradients e.g. in total biomass and dominance. Gauch & Whittaker (1972) were unable to recognise any pattern of species richness along environmental gradients, contrary to Grime (1973) who demonstrated a strong relationship between species richness and pH. Grime (1979) presents a unimodal relationship between species richness and standing biomass plus litter. In view of these conflicting results, any propositions about these community properties are necessarily speculative without further research.

Proposition (6) Species richness will show two maxima at intermediate positions on both resource and direct gradients, these will be at intermediate positions between extreme values (e.g. of either deficiency or toxicity on a resource gradient) and the most equitable value.

This is equivalent to the bimodal curve of species richness in Fig. 6a. It is probable that species richness curves for functional groups (e.g. ephemerals, annuals, epiphytes or trees) or for taxonomic groups (e.g. *Eucalyptus*, dipterocarps, conifers or mosses) will show the clearest patterns. Grubb (1987) provides additional information and discussion suggesting that different life-

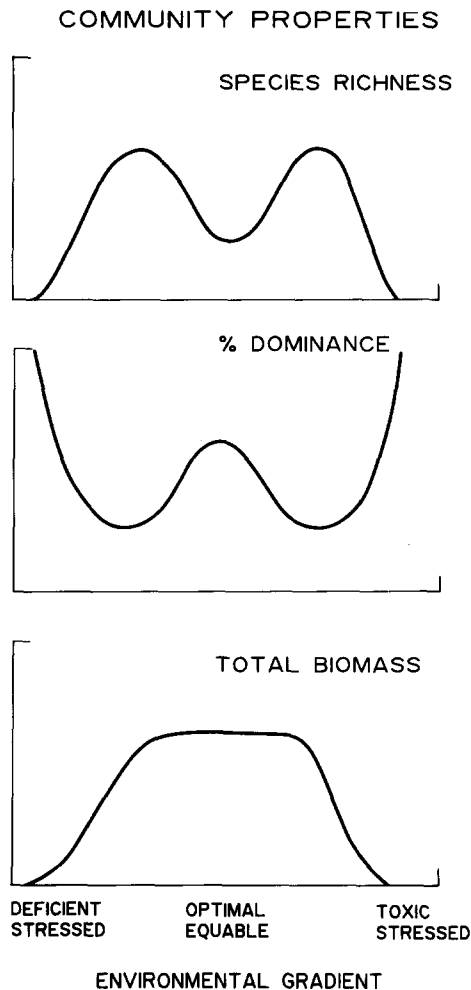


Fig. 6. Postulated patterns for community properties along an environmental gradient.

forms will show different patterns of species richness along environmental gradients.

Proposition (7) Dominance, the maximum proportion of total biomass represented by a single species will show three maxima, under extreme conditions where only one (or very few) species may exist and under optimal conditions where competitive processes determine species composition (Fig. 6b).

These propositions follow suggestions of Grime (1973, 1979; see also Tilman 1982) with recognition that any gradient, resource or direct, has two extremes of stress which can not be collapsed into a single stress value as the processes determining 'stress' are fundamentally different at

the opposing extremes of deficiency and toxicity. Proposition (8) Vegetation standing crop (total biomass) shows a bell-shaped response curve to environmental gradients (Fig. 6c).

This may appear self-evident but the implications need to be explored. If total productivity is highly constrained, then it appears unlikely that a low productivity environment can support numerous different growth forms or survival strategies. The maintenance cost and absolute amount of resource required to support large life-forms e.g. trees may preclude their occurrence in low resource environments.

These propositions concern plant-environment relationships and they are essentially static concepts. The roles of herbivores, disease and disturbance are not addressed, neither is plant reproduction, persistence or senescence, and yet the levels of these factors and plant variables can themselves be influenced or even determined by environmental gradients. It has been hypothesized that the evolution of plant response to herbivory has been directly influenced by nutrient availability. Grime (1977) and Chapin (1980) have suggested that low maximum growth rate is advantageous in low nutrient environments. However, low growth rate also reduces the ability of plants to regrow following herbivory. Thus, plants with inherently slow growth rates have evolved chemical defenses that reduce herbivory (Bryant *et al.* 1983) suggesting a gradient of herbivory paralleling that of nutrient availability.

Alternative community theories

There has been little active development of continuum theory since the 1960's (Goodall 1963; Whittaker 1967; McIntosh 1967) with the exception of the statement by Gauch & Whittaker (1972). Independent developments have however occurred which actively concern the behaviour of vegetation along gradients. We consider here four specific sets of theoretical concepts, those of Ellenberg (1953, 1954; Mueller-Dombois & Ellenberg 1974) regarding species response curves, of Grime (1979) concerning species pri-

mary strategies for survival in vegetation, of Tilman regarding nutrient-ratios (Tilman 1982) and light/nitrogen gradients (Tilman 1988) and of Bazzaz (pers. comm.). We examine their theories/hypotheses in relation to the eight propositions put forward here.

The earlier workers (Ellenberg, Gauch and Whittaker) make no special distinction between environmental gradients, though Whittaker (1978) clearly recognised the indirect nature of his factor-complex gradients (Table 1). Grime and Tilman both concentrate on two types of gradients, disturbance and productivity. They effectively collapse the resource and direct gradient spaces into a single dimension. Grime (1979) equates low production with stress and hence with stress tolerator species. Tilman considers that nutrient (resource) availability will determine a productivity gradient and that light (at ground level) as a resource will be negatively correlated with the productivity gradient.

There does not appear to be any reason to assume all resources, e.g. light, water, oxygen, carbon dioxide and mineral nutrients, have the same type of productivity gradient. This needs research. The failure to distinguish direct physiological gradients as having fundamentally different properties e.g. they are not consumed, must lead to limited generality of any predictions based on a purely production-gradient concept. The possibilities are numerous when a 2-dimensional environmental space is considered (Fig. 7). The combination of a resource gradient in phosphorus

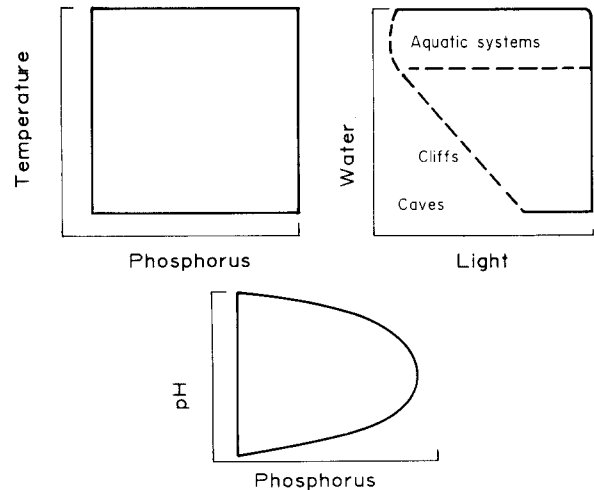


Fig. 7. The different possible combinations of resource and direct environmental gradients will determine the differently shaped environmental spaces within which species are evolved.

with a direct temperature gradient will give a more-or-less rectangular space as the two gradients will be largely independent and all possible combinations would be viewed as likely to occur (Fig. 7a). The combination of the two resource gradients such as water and light presents a more complex picture (Fig. 7b). If there is a supra-abundance of water, then terrestrial vegetation can not survive; fundamentally different physiological and morphological adaptations are necessary. The combination of low light and low moisture is extremely rare and imposes difficulties for terrestrial plants. Adaptive trade-offs have not been achieved.

The possible combinations of a direct gradient such as pH with a resource such as phosphorus is governed by chemical laws. Available soil phosphorus is controlled by the soil pH and is increasingly less available at low and high pH (Russell 1973). The range of feasible combinations of other resources needs to be carefully examined, because there are biological constraints of plants' response to many variables. Plant response to herbivores appears related to nutrient availability. Plants in low nutrient, hence low productivity environments may have adaptations to avoid grazing, while in productive, high nutrient environments plant response to herbivory may include high

Table 1. Nature of environmental gradients.

Ellenberg	No distinction as to type
Gauch & Whittaker	No distinction as to type
Grime	a) Stress/Productivity b) Disturbance
Tilman	a) Productivity b) Disturbance
Bazzaz	a) Resource b) Disturbance
Austin & Smith	a) Resource b) Direct

regrowth rates. Fire frequency is a function of both environmental conditions and vegetation productivity. There are therefore limited combinations of fire and other environmental variables but in addition there is a feedback relationship with the dependent variable plant biomass.

The fundamental response of species has not been considered very extensively by theoreticians (Table 2). Tilman is very explicit but restricts his consideration to non-toxic resource levels. This may be reasonable for many natural situations but the frequent occurrence of water-logging in many high moisture habitats would need to be taken into account, as would photo-inhibition in high light environments. Declines in growth in experiments at less than excessive nutrient levels also occur (Bradshaw *et al.* 1964). The implication of such declines should be incorporated into theoretical models. The volume of the resource/direct gradient space that a species' physiology allows it to function in is usually unknown for vegetative growth, yet what is required for

theoretical models is a measure of fitness. Current propositions (Table 2) are speculative. Response to direct gradients as distinct from resource gradients has barely been considered (Table 2). The size of the volume or range of fundamental response within a resource space has similarly been ignored (Table 2) though this will affect the range of applicability of Tilman's models (1988).

Ecological responses are only now being described adequately for species (Austin 1987) and there is an urgent need for further confirmatory studies. Few if any studies have adequate data to rigorously test alternative hypotheses (Table 3). Tilman (1987) provides one clear example from his survey of old fields, where a great variety of skewed response curves are apparent, contrary to his theoretical assumptions.

There is no common agreement on patterns of species richness along gradients (Table 3). Grubb (1987) summarises many of the alternative possible causes of species richness including age, area, isolation, glaciation and disturbance, factors

Table 2. Patterns of fundamental response: alternative propositions.

	Species fundamental response to a resource gradient	Species fundamental response to a direct environment gradient	Ranges of fundamental response in resource space
Ellenberg	Similar optima Variable shape Inclusive?	As for resource gradient	?
Gauch & Whittaker	Not considered	Not considered	Not considered
Grime	Not considered	Not considered	Not considered
Tilman	Law of diminishing returns, Nested	Not considered	Not specified beyond threshold level for growth
Bazzaz	Variable shape, Nested	Various	Limited range
Austin & Smith	Similar Optima, Law of Diminishing returns with Decline at high levels, Nested	Dissimilar optima, Variable shape, Independent	Limited range Certain combinations of responses non-viable

Table 3. Patterns of response along an environmental gradient.

	Species realized ecological response to an environment gradient	Patterns of species richness along environmental gradient	Patterns of single species dominance along environmental gradient	Pattern of standing crop (total biomass) along environmental gradient
Ellenberg	Variable including Bimodal	High in stable and unstable environments Low in intermediate conditions	Extreme environments	Not considered?
Gauch & Whittaker	Pseudo-Gaussian	No consistent patterns	Extreme environments	Not considered
Grime	Not specified	High under intermediate stress/productivity conditions	Bimodal Extreme and productive environments	Linear increase along stress/productivity gradient
Tilman	Bell-shaped?	High with spatial heterogeneity of resources and at low resource levels	Bimodal, as for Grime	Law of diminishing returns
Bazzaz	Variable	Not considered	Unimodal (for nutrient-gradient)	Bell-shaped
Austin & Smith	Variable, Context-sensitive	Bimodal, high at levels intermediate between optimal conditions and both extremes.	Trimodal, both extremes and the productive environments	Bell-shaped

which are independent of gradients. He draws attention to observations of species richness of certain life forms (climbers and forest herbs) which appear to have maximum richness in the most productive environments. Life forms and particular physiological categories of plants (e.g. C_4 plants) can be expected to show complex response patterns particularly when more than one gradient is considered (Margules *et al.* 1987; Minchin 1989). There is substantial agreement about the occurrence of high dominance in extreme environments, more recent authors also suggest a dominance maximum in productive environments. This needs further examination, can this suggestion be maintained when tropical rainforest is so species rich? Similar differences apply to single species dominance and total biomass (Table 3).

The concept of vegetation as a continuum with continuously varying composition and structure will only form the basis for a predictive theory if there is an explicit link with environment. Our reformulation requires that the continuum response is a consequence of two distinct types of environmental gradient. The fundamental and realized responses of plants to these gradients differ. As a consequence, vegetation patterns and the physiological mechanisms and types of competitive processes (exploitative or interference) will vary with position in the environmental space defined by these gradients.

Our set of propositions and the differences of opinion (Tables 1, 2, 3) provide a set of multiple hypotheses regarding these patterns. These need to be tested in a variety of habitats and a much fuller knowledge is needed of where in the environmental space the results are obtained. Individual studies restricted to a single habitat in a poorly specified part of the environmental space will continue to produce contradictory results. Many authors (Table 1) consider disturbance gradients but ignore direct environmental gradients such as temperature. Comparison of their results and specification of an adequate theoretical model will require comparative information on the position in the environmental space defined by resources, disturbance and direct

variables. Species response in an experimental situation can be predicted from physiological response (Fig. 5; Austin 1982; Grace 1988), but given the context-sensitivity of the prediction, further simplifying concepts need to be found before prediction of the composition of natural vegetation will be possible. Although we distinguish the fundamental response to two types of gradients, we cannot yet distinguish differences in the ecological response to the two types of gradients.

The challenge for vegetation scientists is to devise observational tests and experiments which will discriminate between the various theoretical propositions of different authors. The set of propositions outlined here replace those of Gauch & Whittaker (1972); they are a mixture of mechanistic statements, descriptive plant physiological responses, and speculative possibilities for ecological responses. Their positive feature is that they are operational and can be tested. Alternative theories also have this feature but lack several currently accepted features of plants and vegetation which need to be incorporated.

References

- Austin, M. P. 1980. Searching for a model for use in vegetation analysis. *Vegetatio* 42: 11–21.
- Austin, M. P. 1982. Use of a relative physiological performance value in the prediction of performance in multispecies mixtures from monoculture performance. *J. Ecol.* 70: 559–570.
- Austin, M. P. 1985. Continuum concept, ordination methods, and niche theory. *Ann. Rev. Ecol. Syst.* 16: 39–61.
- Austin, M. P. 1986. The theoretical basis of vegetation science. *TREE* 1: 161–164.
- Austin, M. P. 1987. Models for analysis of species' response to environmental gradients. *Vegetatio* 69: 35–45.
- Austin, M. P. in press. Community theory and competition in vegetation. In: Tilman, D. & Grace, J. B. (eds), *Perspectives in plant competition*, Academic Press, London.
- Austin, M. P. & Austin, B. O. 1980. Behaviour of experimental plant communities along a nutrient gradient. *J. Ecol.* 68: 891–918.
- Austin, M. P., Groves, R. H., Fresco, L. M. F. & Kaye, P. E. 1985. Relative growth of six thistle species along a nutrient gradient with multispecies competition. *J. Ecol.* 73: 667–684.

- Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Ann. Rev. Ecol. Syst.* 10: 351–371.
- Bradshaw, A. D., Chadwick, M. J., Jowett, D. & Snaydon, R. W. 1964. Experimental investigations into the mineral nutrition of several grass species IV Nitrogen level. *J. Ecol.* 52: 665–676.
- Brown, J. M. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Amer. Zool.* 21: 877–888.
- Bryant, J. P., Chapin III, F. S. & Klein, D. R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357–368.
- Chapin, F. S. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11: 233–260.
- Cottam, G. & McIntosh, R. P. 1966. Vegetation continuum. *Science* 152: 546–547.
- Daubenmire, R., 1966. Vegetation: identification of typical communities. *Science* 151: 291–298.
- Ellenberg, H., 1953. Physiologisches und ökologisches Verhalten derselben Pflanzenarten. *Ber. Deutsch. Bot. Ges.* 65: 351–62.
- Ellenberg, H. 1954. Über einige Fortschritte der kausalen Vegetationskunde. *Vegetatio* 5/6: 199–211.
- Ellenberg, H. 1988. *Vegetation ecology of central Europe*. 4th ed; Cambridge University Press. Cambridge.
- Gauch, H. G. & Whittaker, R. H. 1972. Coenocline simulation. *Ecology* 53: 446–51.
- Gaudet, C. L. & Keddy, P. A. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* 334: 242–243.
- Giller, P. S. 1984. *Community structure and the niche*. Chapman & Hall, London.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 1–20.
- Goodall, D. W. 1963. The continuum and the individualistic association. *Vegetatio* 11: 297–316.
- Grace, J. B. 1988. The effects of plant age on the ability to predict mixture performance from monoculture growth. *J. Ecol.* 76: 152–156.
- Grime, J. P. 1973. Control of species density in herbaceous vegetation. *J. Envir. Manage.* 1: 151–167.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer. Nat.* 111: 1169–1194.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. J. Wiley & Sons, Chichester.
- Grubb, P. J. 1987. Global trends in species richness in terrestrial vegetation: a view from the northern hemisphere. In: Gee, J. M. R. & Giller, P. S. (eds), *Organisation of communities past and present*. Blackwell, Oxford.
- Huston, M. 1979. A general hypothesis of species diversity. *Amer. Nat.* 113: 81–101.
- Huston, M. & Smith, T. M. 1987. Plant succession: Life history and competition. *Amer. Nat.* 130: 160–198.
- MacIntosh, R. P. 1967. The continuum concept of vegetation. *Bot. Rev.* 33: 130–187.
- Margules, C. R., Nicholls, A. O. & Austin, M. P. 1987. Diversity of *Eucalyptus* species predicted by a multi-variable environmental gradient. *Oecologia* 71: 229–232.
- Minchin, P. 1989. Montane vegetation of the Mt. Field Massif, Tasmania: a test of some hypotheses about properties of community patterns. *Vegetatio* 83: 97–110.
- Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. J. Wiley & Sons, New York.
- Orians, G. H. & Solbrig, O. T. 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *Amer. Nat.* 111: 677–690.
- Parsons, R. F. 1968. The significance of growth-rate comparisons for plant ecology. *Amer. Nat.* 102: 295–297.
- Prentice, I. C. & van der Maarel, E. (eds), 1987. *Theory and models in vegetation science*. *Vegetation* 69. Junk, Dordrecht.
- Russell, E. W. 1973. *Soil conditions and plant growth*. Longmans, London.
- Smith, T. M. & Huston, M. 1989. A functional classification of plant types: linking spatial and temporal pattern in plant communities. *Vegetatio* 83: 49–69.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton Univ. Press, Princeton.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* 57: 189–214.
- Tilman, D. 1988. *Plant strategies and the structure and dynamics of plant communities*. Princeton Univ. press, Princeton.
- Westhoff, V. & van der Maarel, E. 1978. The Braun-Blanquet approach. In: Whittaker, R. H. (ed.), 'Classification of plant communities', Junk, The Hague.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biol. Rev.* 42: 207–264.
- Whittaker, R. H. (ed.) 1978. *Ordination of plant communities*. Junk, The Hague.
- Wilson, S. D. & Keddy, P. A. 1985. Plant zonation on a shoreline gradient: physiological response curves of component species. *J. Ecol.* 73: 851–860.