SIMPLIFYING THE STUDY OF COMPETITION AT THE INDIVIDUAL PLANT LEVEL: CONSEQUENCES OF DISTINGUISHING BETWEEN COMPETITIVE EFFECT AND RESPONSE FOR FOREST VEGETATION MANAGEMENT

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(Received for publication 10 July 1995; revision 3 April 1996)

ABSTRACT

In a simple conceptual model of competition for resources the net interaction between plants is broken down into two distinct components: competitive effect on resources, or the rate at which resources are depleted by neighbouring plants, and competitive response to resources, or the degree to which a target plant is limited by resource availability. This mechanistic description of the process of competition suggests a number of ways in which predicting the impact of competition on individual plants could be simplified and made more general. All these possible simplifications have important assumptions that have rarely been tested. Therefore, they are currently best regarded as null hypotheses rather than firmly-established guides to forestry practice. Firstly, when the number of species is large, there are many fewer possible plant-resource interactions to be quantified than plant-plant interactions. This assumes that the net interaction between plants is indeed simply the composite of their competitive effects and responses. Secondly, not all possible plant-resource interactions must be studied at all stages. Specifically, the most important phase in forest vegetation management is seedling establishment of trees. In this situation, it should be necessary to quantify only the effect on resources of non-commercial vegetation and the response to resources of commercial tree seedlings to make predictions relevant to decisions about forest vegetation management. Thirdly, it should be possible to ignore species identity of competing vegetation around target tree seedlings if species of neighbours have equivalent effects on resources. This would greatly simplify the quantification of competitive interactions at any particular site. Equivalent competitive effects are most likely if sizes of species of competing plants are incorporated into measures of competitive effect. Finally, perhaps the most important factor currently complicating general predictions about the outcome of competition is variation among sites. If both effect and response curves for particular resources are known, along with the magnitude of change in abiotic resource supply, it should be possible to predict competitive effects across sites without repeating the detailed studies of effect and response.

Keywords: plant competition; mechanisms of competition; competitive effect; competitive response; productivity gradients; depletion ability; tolerance ability.

INTRODUCTION

One of the central concerns of research in forest vegetation management (FVM) is how to predict the impact of competition from existing vegetation on the establishment and development of stands of desirable species. Without reasonably accurate predictions of such impacts, balancing the various ecological and economic costs and benefits of vegetation manipulation to make sound management decisions about treatment will be impossible. While a large number of studies exist that quantify the impact of competition reduction on aspects of tree survival and growth (Stewart *et al.* 1984; Walstad & Kuch 1987), the vast majority of these are highly specific to particular situations. In hopes of broadening the interpretation of such studies, efforts have turned increasingly towards understanding the mechanisms of interactions (e.g. Stewart 1987; Nambiar & Sands 1993). Thus, the trend in FVM research on the process of competition has been towards more and more detailed measurements of aspects of the growth, ecology, physiology, and morphology of competing plants, as well as of the resources for which they compete and the environmental arena in which they compete. These measurements are often used, or at least viewed as useful, for complex simulation models of competition such as ecological field theory (Walker *et al.* 1989; Mou *et al.* 1993), and community dynamics models (e.g., Pacala *et al.* 1993). This kind of modelling approach incorporates many of the important details of the processes of acquisition and use of resources by plants and so is much more realistic than earlier, more simplistic models. Thus, detailed measurements are and will continue to be very useful for understanding the underlying mechanisms of interaction. However, they are rarely directly applicable in the field because their very complexity and realism makes them difficult to calibrate and the cumulative errors from all the input variables lead to large potential errors in quantitative predictions (Kimmins 1990; Doyle 1990).

In this paper, I argue, as a counterbalance to this trend of increasing complexity, that we also invest research time and effort into ways to simplify models—i.e., to reduce the number of critical variables. Such models will inevitably be less precise and realistic than the more specific, complex, simulation models but are potentially much more general. The question then becomes whether this loss of precision is too costly for the kinds of decisions that need to be made in FVM. Can a balance be struck where models are general enough that they are useful over a range of sites and species but specific enough that they are useful for making quantitative management recommendations? This question is, of course, unanswerable at the present time. The overall goal of this paper is to suggest research directions that would enable it eventually to be answered and potentially provide a more cost-effective basis for management.

GENERAL DESCRIPTION OF RESOURCE COMPETITION

As a number of authors have argued in recent years, understanding the mechanisms of interactions between plants is the key to being able to generalise and extend results from one study to other situations (Schoener 1986; Tilman 1987; Nambiar & Sands 1993). Thus, I start by describing the process of exploitative competition as an indirect interaction mediated through resources (Fig. 1). For one plant (A) to have a negative impact on another plant (B) through competition, plant A must have a negative effect on resource availability (i.e., deplete the resource) and plant B must have a positive response to availability of that resource (i.e., be limited by that resource). These two components of the process of competition are

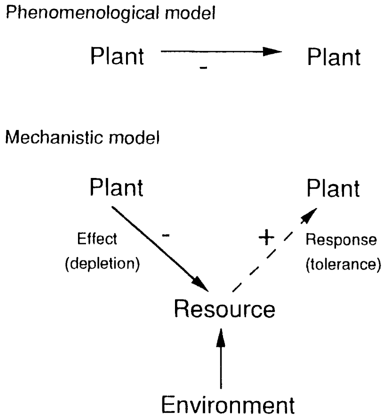

FIG. 1–Contrast between a phenomenological description of plant competition (plant-plant interactions) and a more mechanistic description that explicitly incorporates the resource for which the plants are competing. Only one direction of effects (Plant A on Plant B) is shown in the figure for clarity. The net interaction between two plants will be mutually negative if they **both** deplete the resource (have negative effects on resource availability) and are limited by the same resource (have positive responses to the resource).

called **competitive effect** and **competitive response**, respectively (Goldberg 1990). Effect competitive ability (=depletion ability) can be quantified as the change in resource availability as a function of abundance (e.g., density, biomass, total leaf area, etc.) of a "neighbour species" (Fig. 2A) and is similar to good competitors *sensu* Grime (1977). Stronger effect competitors for a particular resource cause larger decreases in availability of that resource per-unit amount (e.g., per-individual, per-gram, etc.). Response competitive ability (=tolerance ability) can be quantified as the amount of growth (or other measure of fitness) achieved by a target plant as a function of resource availability (Fig. 2B). Better response competitors for a particular resource can grow or reproduce more or survive longer at low levels of that resource and are similar to stress tolerators *sensu* Grime (1977) and good competitors *sensu* Tilman (1982). The shapes of the effect and response curves in Fig. 2 are those deemed to be most likely based on available evidence—these shapes are discussed in more detail in the section on "Comparisons across Environments". In the simplest example, the net effect of one plant on another is simply the composite of their effects and responses (Fig. 2C) although, in reality, because both components are dynamic, the situation will be much more complex. Nevertheless, recognition that

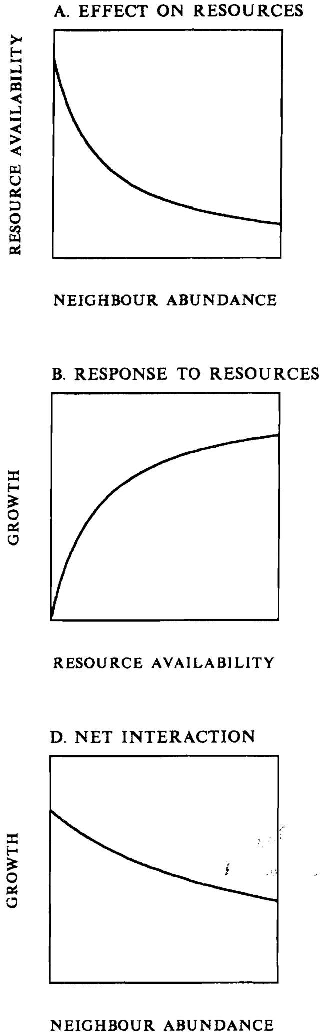

FIG. 2–Hypothetical examples of competitive effect of a neighbour on resource availability (Part A), competitive response of growth of a target species to resource availability (Part B), and the composition of the two functions to predict the net interaction between the target and neighbour species (Part C).

both components of competition must be significant and that they can be independently quantified has a number of important implications for both basic and applied ecology (Goldberg 1990).

The rest of this paper is organised around ways in which the mechanistic view of competition in Fig. 1 and 2 could simplify the study of competitive interactions in plant communities and aid in generalising across species and across environments. Before starting, it is important to emphasise that none of these simplifications will be strictly applicable in any circumstance—each rests on a set of assumptions that will, at best, hold rather roughly. However, each of these simplifications can be regarded as a null hypothesis—a starting point for investigating the competitive processes and outcomes in any particular system. The important question is then to what extent the underlying assumptions can be violated without changing the outcome. In fact, some of the simplifications I discuss are already standard practice in both applied and basic field ecology, even though the theoretical literature often regards them as unjustified. An important goal of this paper is to make the underlying assumptions of these simplifications explicit and discuss how they can be tested. Whenever possible, I have taken examples from the forestry literature or from my own work on herbaceous species. However, in most cases, relatively few data are available to test directly whether the simplifications suggested will be useful; thus, this paper is fairly speculative in tone. These speculations are offered in the hope of stimulating more direct tests.

Two caveats about the conceptual representation of competition in Fig. 1 are in order before elaborating on the simplifications and generalisations it implies. First, I restrict the following discussion of competitive interactions to competition for resources—light, water, or mineral nutrients—and ignore other forms of negative interactions between plants such as allelopathy or interactions mediated through herbivores or other natural enemies. Although allelopathic interactions can certainly occur and may be important in particular situations, their outcome will be a function of the chemistry of particular plant species. Thus, when allelopathy is an important mechanism of interaction, I doubt that any general model of interactions will be useful for predicting outcomes. Case-by-case analysis will probably remain the only viable approach. Interactions between plants mediated through natural enemies such as herbivores or pathogens can also be of major importance (Connell 1990; Holt & Lawton 1994) and, unlike allelopathy, these have many potentially generalisable aspects (e.g., Oksanen *et al.* 1990; Louda *et al.* 1990). Eventually, any model of competition for resources between plants will also have to include natural enemies of plants to be generally predictive of the outcome of interactions. However, strong interactions among plants clearly occur even in the absence of natural enemies and therefore it seems reasonable that a general model of plant-plant interactions should start with interactions involving resources.

The second caveat about the general description of interactions among plants depicted in Fig. 1 is that it assumes these interactions are exclusively negative, i.e., competitive. This is clearly not true; numerous examples of positive interactions among plants exist (reviews by Hunter & Aarssen 1988; Goldberg 1990; Bertness & Callaway 1994). Many of these examples involve resources and therefore simply change one of the signs in the bottom part of Fig. 1. Most commonly, the effects of plants on resources are positive, leading to a net positive effect of one plant on another (++ facilitation), although it is also theoretically possible that a plant could have a negative response to increasing "resources", also leading to a net positive effect (—facilitation). In most of the rest of this paper I focus on interactions where the effects of plants on resources are negative, leading to competitive interactions. In the final section, I discuss how previous conclusions might be modified or complicated by the existence of positive interactions involving resources.

IMPLICATIONS OF A MECHANISTIC APPROACH FOR SIMPLIFYING THE STUDY OF COMPETITION

Plant-resource *v.* Plant-plant Interactions

The most obvious opportunity for simplification by using a mechanistic approach is simply in the reduction of dimensionality possible by quantifying all possible plant-resource interactions instead of all possible plant-plant interactions. Because the number of plant-plant interactions increases exponentially as the number of species increases, while the number of plant-resource interactions increases only linearly, fewer relationships are involved in the latter once more than five species are involved (Fig. 3). The key assumption here is that knowledge of the two component plant-resource interactions adequately predicts the net plant-plant interaction (Fig. 2). This seems highly plausible based on available data. For example, in a factorial experiment, Mitchell *et al.* (1993) found that the combined densities of a hardwood and a grass were significantly correlated with both soil moisture and an index of pine water stress, which in turn was significantly correlated with pine volume growth. Similar results were found by Shainsky & Radosevich (1992) and Mitchell *et al.* (in prep.). In both reports (as well as in that by Goldberg 1990), however, the data on competitive effect and response came from the same plots as those quantifying the net interactions. The critical test of the assumptions embodied in Fig. 2 would be to measure independently competitive effect and response to predict the net effect and then to compare this predicted net effect with an observed net effect. This latter experiment has not been performed to my knowledge. Doing this properly, and indeed measuring plant-resource interactions in general, will require ways of integrating measures of both effect and response over time and space. Such measures already exist for some resources, such as the water stress integral of

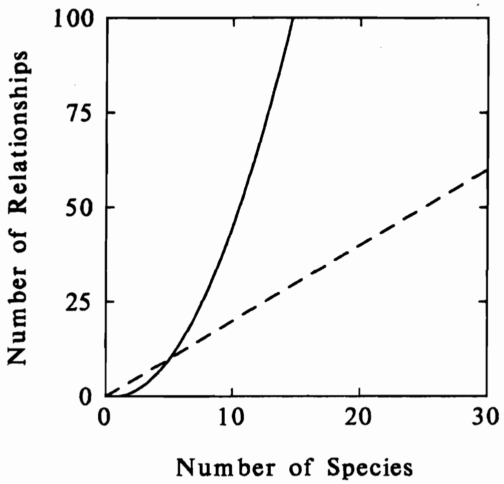

FIG. 3–The increase in number of pairwise relationships that must be measured as a function of the number of interacting species when studying plant-plant interactions (solid line) and plant-resource interactions (dashed line).

Myers (1988) for response of plants to water availability over a season, but a more general discussion of possible approaches to spatial and temporal integration of resource use is required.

Effect/response Usually Needed for Only a Subset of Species in Particular Situations

Depending on the situation, it may not always be necessary to know both effect on resources and response to resources for each of the interacting species in a community. For FVM, the tree establishment phase is particularly important. During this phase, the primary concern is with the effect of non-commercial vegetation on resources and the response of commercial tree seedlings to resources. This greatly reduces the number of plant-resource interactions that must be studied to make predictions about the short-term impact of competition. Similar interactions may be important in more natural settings—what determines whether a species can persist in a given environment is often whether its seedlings can establish under the prevailing competitive environment determined by mature vegetation. For agroforestry, the opposite set of interactions is important—typically, the interest is in the effect of the mature tree crop (often called shade trees) on resources and conditions and the response of the herbaceous crop to those resources/conditions (J. Vandermeer, pers. comm.).

This simplification assumes that effects of establishing trees on surrounding vegetation are minimal, which seems reasonable for young seedlings that are small relative to surrounding plants. For example, in mixtures involving a pine and two weedy species, Mitchell *et al.* (1993) found no significant effects of pine seedling density on soil moisture, although there were strong effects of both weedy species. However, the assumption clearly becomes less and less valid as the trees mature. In fact, the effect of growing trees on resources and the response of surrounding vegetation to this resource depletion often becomes an important component of vegetation management strategies as the stand matures. That is, the trees themselves can suppress their competitors by overtopping them or by reducing soil moisture or nutrients (e.g., Shainsky & Radosevich 1992). Thus, in later phases of stand development, the more important plant-resource interactions to measure may switch to effect of the commercially-desirable tree species and response of the non-commercial species.

Species-specificity of Interactions

A further simplification in quantifying competitive effect on or response to resources would be possible if species identities of the competing vegetation ("neighbours") and/or the responding individuals ("targets") could be ignored. Because the primary focus of FVM is on the response of particular species of commercial tree seedlings (the targets) to surrounding vegetation, no advantage would be gained by lumping target species, even if responses were similar among species. The key question, therefore, is whether it is possible to lump species of neighbours: do different neighbour species have similar enough effects on resources that a measure of total amount of vegetation accurately predicts the total resource depletion. The answer to this question depends at least partly on how "amount" is defined. Clearly, predictions based on total density of all plants will not be very accurate because the forestry and the ecological literature show that per-plant effects on resource availability typically differ strongly among species (e.g., Gordon & Rice 1993; Caldwell *et al.* 1985; Mitchell *et al.* 1993; Shainsky & Radosevich 1992; Canham *et al.* 1994; Mitchell *et al.* in prep.). However, it has been argued that a primary reason for such variation in per-plant effects is simply variation in plant size: the larger the plant, the more resources it can take up and therefore the more it can suppress growth or survival of other plants (Goldberg & Werner 1983). Thus, measures of resource depletion based on plant size (e.g., biomass, leaf surface area, root length) rather than plant number might be much more similar among species.

Arguing against this null hypothesis of equivalence of competitive effects on resources is a large body of literature demonstrating differences among species in per-unit size (e.g., per-unit leaf area or per-unit root length) uptake rates of resources under controlled conditions (Chapin 1980, 1988; Gordon & Rice 1993). These differences are real and can alter the outcome of competition in complex simulation models (e.g., Tilman 1988, 1990; Pacala *et al.* 1993). At issue, however, is whether these per-unit size differences among species are large enough to have significant impacts in the field, when other sources of variation are large. Chapin (1980, 1988) and Caldwell & Richards (1986) have argued that variation in size of plants (or of roots and shoots) will usually outweigh variation in per-unit size rates of nutrient uptake, implying that plant size is a sufficient predictor of per-plant effects. On the other hand, Pacala *et al.* (1993) showed that small changes in per-unit size characteristics of the species in their forest dynamics simulator can have large impacts on population dynamics.

Surprisingly few data are available to directly test the hypothesis that species are equivalent in competitive effects on a size, although not an individual, basis under field conditions. This paucity of data applies whether the goal is to quantify neighbour effects on resources or, more commonly, to quantify net effects of neighbours on target plant growth or survival. A rare exception for effects on resources is the report by Mitchell *et al.* (in prep.) who found equivalent per-gram effects on soil moisture and light among two woody species and one grass growing in monoculture field plots. Interestingly, this same study found non-equivalent per-gram net effects on target plant growth, although per-gram effects were much more similar among the neighbour species than were per-plant effects. Greenhouse studies also usually indicate that species have distinct per-unit size effects, although differences among species tend to be much smaller than in per-plant effects (Goldberg & Fleetwood 1987; Goldberg & Landa 1991; Gordon *et al.* 1989; Gordon & Rice 1993). In contrast, several other field studies comparing net effects on target plant growth have found equivalent per-gram competitive effects (Fig. 4; Goldberg 1987; Miller & Werner 1987), or very strong relationships between per-plant effects and plant size (Gaudet & Keddy 1988) or between total effects and abundance (Peart 1989). Results in this latter group are all based on comparing species within growth forms. It may be that grouping of species within but not between growth forms will be an acceptable simplification, although many more data comparing species, especially in the field, will be necessary to define such groupings within which effects are more or less equivalent (Goldberg 1996).

Given that there is a vast literature on competition in both forestry and ecology, it is worth discussing why data are so scarce for assessing whether it is possible to ignore neighbour species identity without losing power to predict target plant response to competition. One reason is that most field experiments that address this question for either effects on resources or on target plant growth compare neighbour species at their natural abundances (e.g., Allen

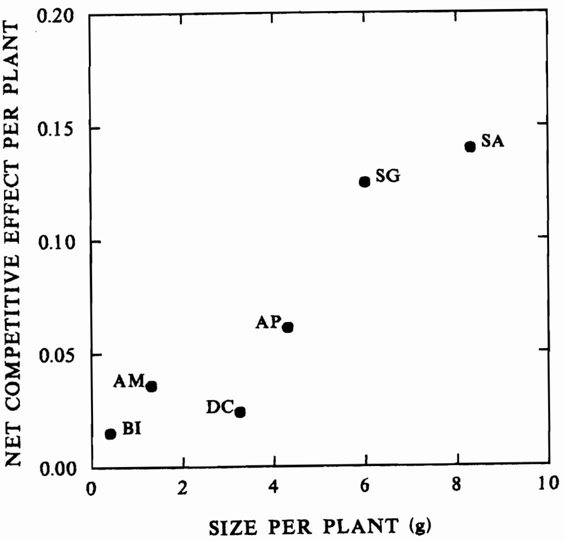

FIG. 4–The influence of size on per-plant net competitive effects of six herbaceous perennial species on growth of a target species, *Solidago altissima.* The neighbour species are BI=*Bromus inermis*, AM=*Achillea millefolium*, DC=*Daucus carota*, AP=*Aster pilosus*, SG=*Solidago graminifolia*, SA=*Solidago altissima*. Redrawn from Goldberg (1987), where *S. altissima* was listed as *S. canadensis*. Per-plant net competitive effect was quantified as "a" in a non-linear regression of the form: $T=T_{max}/(1 + aB)$, where T=target plant growth, B=neighbour density, and T_{max} and a are fitted parameters.

& Forman 1976; Fowler 1981; Silander & Antonovics 1982; Elliott & White 1987; Goldberg & Barton 1992). Comparisons at natural abundance confound differences in abundance between species with differences in their per-unit size effects and therefore cannot be extrapolated to other sites or times that may differ in abundances (Goldberg & Scheiner 1993). Studies comparing neighbour species on a per-individual basis (e.g., Mitchell *et al.* 1993) are somewhat more generalisable, but still cannot account for variation in size within and between neighbour species and sites.

Another, and perhaps more important limitation is that many field studies seem to already assume equivalence of competitive effects because they quantify only effects of total vegetation rather than effects of component species of the vegetation. For example, the predictive models of competitive effects on conifer growth reviewed by Stewart (1987) all use an index of total cover or height of all vegetation and ignore neighbour species. These models are reasonably successful in explaining variation in tree or stand growth (r^2 range from 0.48 to 0.97), suggesting that the lumping of all neighbour species is reasonable. A quantitative survey of field competition experiments in the ecological literature also demonstrates that most field-oriented plant ecologists simply quantify the effects of removing all vegetation (55 out of 87 experiments), or at most growth forms (28 out of 87 experiments), on fitness of some target plants (data from Appendix 2 of Goldberg & Barton 1992).

Thus, both the forestry and the ecological literature suggest that the intuition of field workers holds that quantification of total vegetation impacts is sufficient. Some recent theoretical models also assume that competitive effects, although not responses, are equivalent among species on a per-unit size basis (e.g., Kohyama 1992). This common intuition can be regarded as an indirect form of support for the hypothesis of equivalence of competitive effects on resources on a per-unit size basis. Unfortunately, the consequence of this intuition is that there are very few field examples where the hypothesis has been explicitly tested. Therefore, the adequacy of this assumption and the simplification it suggests (and which, in fact, is already common practice) is not really known.

Comparisons Across Environments

So far, I have discussed simplifications within a single environment. However, perhaps the most critical current problem in FVM is the lack of ability to generalise between environments with different soils or climates. Measurements of net competitive effects, thresholds, etc., are largely unique to a particular site. It has been argued that a more mechanistic approach that explicitly examines how plants use resources can provide a basis for generalising across sites that differ in resource availability (Tilman 1987; Stewart 1987; Nambiar & Sands 1993). The primary conceptual framework currently available for doing this is Tilman's (1982, 1988, 1990) R* framework. Although generating a rich array of predictions and explanations of commonly-observed patterns, this approach is difficult to apply in the field because the definition of competitive ability (R*) is based on population behavior at equilibrium, while most experimental work in terrestrial plant systems, especially woody plants, is restricted to short-term monitoring of individuals over segments of their life time. More generally, such a definition of competitive ability is usually irrelevant to the goals of FVM, which focus on response of individuals to competitors rather than on the establishment of equilibrium populations. Even systems under only moderate management intensity will not achieve true population equilibria because, management, by definition, disrupts internally-controlled dynamics.

The mechanistic framework in Fig. 1 and 2 offers a straightforward approach in principle to extending knowledge of interactions between individual plants and their resources to predict individual plant-plant interactions across environmental gradients and therefore reducing the need for highly detailed study in every system before making predictions about competitive impacts. However, there is currently neither a comprehensive theory for implementing this approach nor empirical data for testing it. In this section, I outline a conceptual framework based on the distinction between competitive effects and responses for predicting the outcome of individual-level competition across sites.

Sites can differ in numerous ways that can all influence the outcome of competition. However, a reasonable starting point for generalising about the outcome of competition for resources is to focus on environmental variation that is related to resources. Therefore, I restrict the discussion below to variation among sites due to differences in nutrient and/or water availability resulting from soil type and/or climate. Availabilities of different nutrients are usually positively correlated with each other, as are all mineral nutrients and water. However, gradients in supply rate of soil resources typically lead to gradients in productivity and standing crop and therefore to declines in light levels (Newman 1973; Tilman 1988). The discussion below assumes positively-correlated supply rates of different soil resources (different nutrients or nutrients and water) but negatively-correlated supply rates of soil resources and light across a productivity gradient.

Extending results from a set of plant-resource interactions as in Fig. 2 to another resource environment depends on if and how the effect and response curves in Fig. 2 change among environments. In the rest of this section, I speculate on some possible patterns in effect and response curves among environments. My main goal is to state explicitly the sorts of data needed to formulate a reasonable model of individual-level resource competition rather than to argue conclusively for a particular form of a model.

Competitive effect

The top row in Fig. 5 depicts competitive effects on a soil resource (Fig. 5A) and on light (Fig. 5B) for low and high productivity environments, where the productivity gradient is assumed to be due to a gradient in abiotic supply of a soil resource. Each of these "effect curves" can be characterised by three distinct aspects: (a) the y-intercept, (b) the shape and slope, and (c) the magnitude of resource depletion at natural neighbour abundance. In Fig. 5 abundance is considered to be a measure that incorporates plant size rather than just number of plants, such as biomass, cover, basal area, etc.

Intercepts: In an environment with a higher supply rate of a soil resource (e.g., higher mineralisation rate, higher rainfall) availability of that resource in the absence of plants (the y-intercept of the effect curve) should obviously be higher (Fig. 5A), while availability of light should not change (y-intercept of 100% of full sunlight; Fig. 5B).

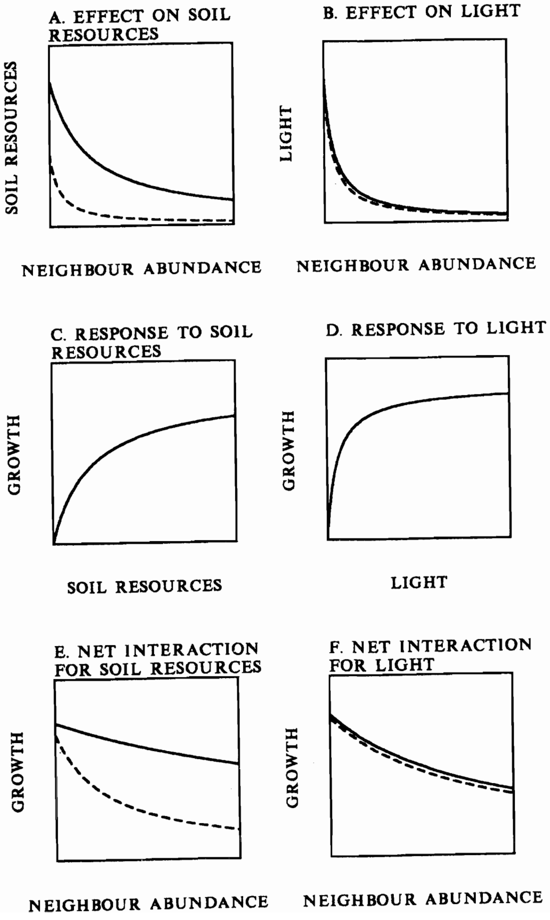

FIG. 5—Hypothetical competitive effects (Parts A, B), responses (Parts C, D), and their predicted net interaction (Parts E, F) for soil resources (left side) and light (right side) under high (solid line) and low (dashed line) productivity. For illustrative purposes, parts A and B show a gentler slope for soil resource depletion at higher productivity, constant slopes for light depletion regardless of productivity, and, for both light and soil resources, higher total effects at natural abundance at higher productivity. Responses to a given resource (parts C and D) are assumed to be similar in low and high productivity environments (*see* text). The net interactions in parts E and F are the composition of effect (A) and response (B) for nutrients and of effect (B) and response (C) for light, respectively.

Slopes: For slopes (per-unit size effects on resource availability), generalisations are more problematical and, in the absence of data, arguments can be made for increases, decreases, and constant values along productivity gradients. Because the slope of a curve is a fixed value only for a linear relationship, it is necessary to determine the typical shapes of the effect curves before making predictions about changes in slopes between environments. The most common observation is that soil resources and light decline linearly with measures of neighbour abundance other than density (e.g., Goldberg 1990; Elliot & Vose 1993; Gordon & Rice 1993), although non-linear, concave upward curves have been observed (Comeau *et al.* 1993). However, a linear relationship seems unlikely to be generally correct for at least three reasons. Firstly, a linear relationship implies that resources will decline to 0 at some value of neighbour abundance. Because plants are unlikely to be able to take up all of a resource, it is much more likely that resource availability will approach 0 asymptotically, i.e., the relationship will be concave upwards (Fig. 5A, B). Secondly, a linear relationship implies that resource uptake depends only on the amount of resource-acquiring tissue (e.g., root or shoot biomass, leaf surface area, total root length) and that the proportion of tissue used for acquiring a particular resource does not change with total abundance (e.g., proportion of biomass allocated to roots does not change with total neighbour biomass). Neither of these seems likely. For example, at higher neighbour biomass, it might take more tissue to extend a leaf or root to a position where resources are not yet depleted, causing an increase in the cost of acquiring a given unit of resource. This would mean a decrease in the per-unit size rate of depletion and therefore a concave upward effect curve would again be expected. Thirdly, linear effect curves combined with saturating response curves as described below generate a predicted shape for the net interaction curves that is strongly inconsistent with the available data—this problem is discussed in the section on Net Interactions. For all these reasons, I have depicted the competitive effect curves in Fig. 5A and B as concave upward rather than linear. The fact that relationships are most commonly (although not universally) presented as linear in the limited data sets available may simply be because of (a) failure to check statistically for non-linearity, (b) insufficient statistical power to detect departures from linearity, or (c) examination of only a limited range of neighbour abundance. Obviously, this is yet another area in which research is needed before a general model can be constructed.

Given non-linear competitive effects, it becomes important to define per-unit size competitive effects more precisely because slopes will differ depending on neighbour abundance. In fact, for effect curves with similar asymptotic values, slopes at low neighbour abundance will even be negatively correlated with slopes at high neighbour abundance. I focus on the slope of the steeper portion at low neighbour abundances because this is the most sensitive portion of the competitive effect curve.

For nutrients, the slope of the initial portion of the effect curve will most likely be less steep in more nutrient-rich environments (Fig. 5A) because the typical pattern is for plants to decrease their uptake capacity at higher nutrient supply (Chapin 1988). On the other hand, it is also possible that increased luxury consumption might cause steeper slopes in more productive environments. Similar arguments can be made for water. For light, a reasonable first approximation is that slopes will stay constant among environments (Fig. 5B), although changes in specific leaf mass or canopy architecture could cause changes in slope depending on how neighbour abundance is quantified. For example, the typical decrease in specific leaf mass at lower light levels could lead to a decrease in light depletion per-unit neighbour mass (although not per-unit neighbour leaf area).

Effects at natural abundance: Changes in the third aspect of competitive effect, the total amount of decrease in resource availability due to the presence of neighbours at their natural abundance, will depend quantitatively on changes in y-intercepts and slopes. Because biomass of neighbours typically increases at higher productivity, the total magnitude of effect at natural abundance for both light and soil resources will also typically increase at higher productivity, regardless of per-unit size effects, unless the slope is considerably gentler at higher productivity (Fig. 5A, B). Thus, it is of major importance that we distinguish between patterns in per-unit size competitive effects (slopes) and total effects at a particular neighbour abundance. The patterns in total effects can be seen more clearly in Fig. 6, where availabilities of a soil resource and of light in the presence (at natural abundance) *v.* absence of vegetation are compared across a productivity gradient instead of comparing only two productivity levels across a gradient in neighbour biomass as in Fig. 5A and B.

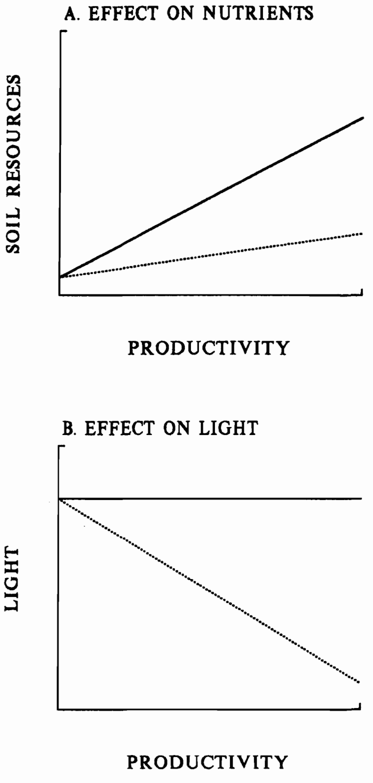

FIG. 6–Hypothetical relationships between soil resource availability (Part A) and light availability (Part B) along a productivity gradient in the absence of vegetation (solid line) and in the presence of vegetation at natural abundances (dotted line). (Redrawn from Goldberg 1990).

Empirical examples: I am not aware of any data sets that would allow assessment of all of the aspects of competitive effect on resources illustrated in Fig. 5A and B. As already noted, per-unit size competitive effects on resources are rarely measured in even a single environment, let alone compared among environments. However, I have compared total effects at natural abundance as in Fig. 6 in one system: a small-scale productivity gradient in herbaceous perennial old field vegetation in Michigan (Fig. 7). The productivity gradient (indicated by standing crop) was related to small-scale topographic variation, which influenced texture and drainage. The results for nitrogen are complex (Fig. 7A). If only the control (no removal) and complete removal of all vegetation and litter are compared, results are consistent with the predictions in Fig. 6A: both treatments showed significant increases in nitrogen with standing crop (used as an index of productivity) and the increase was much larger in the vegetation removal treatment than in the control with vegetation and litter present (significant differences in slope by ANCOVA, intercepts constant; Fig. 7A). Surprisingly, however, removal of only plants but leaving litter in place resulted in constant nitrogen availability along the productivity gradient (no significant slope with standing crop), at least within a single growing season, and no increase in nitrogen relative to controls (no significant difference in slope or intercept by ANCOVA; Fig. 7A). Thus, removal of established

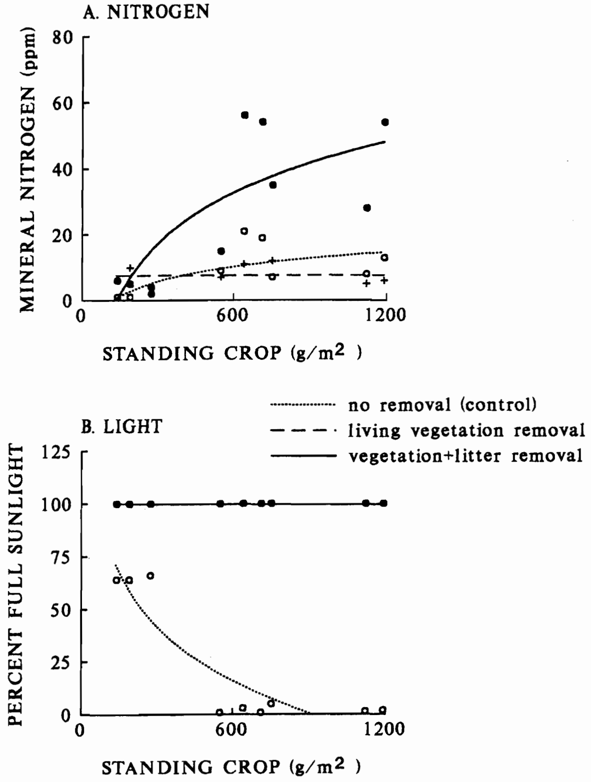

FIG. 7–Results of removal of vegetation on available nitrogen (Part A) and light (Part B) in a mid-successional old field at the Kellogg Biological Station, Michigan, United States. Vegetation was removed in spring 1988 by application of glyphosate (Roundup™) and subsequent clipping of dead and dying vegetation. Resource measurements were taken in August 1988. Light was measured just above the litter layer so did not differ between the complete removal and living vegetation removal treatments; only the complete removal treatment is shown. * indicates a significant linear or power regression of resources on standing crop (an index of productivity for this herbaceous perennial vegetation).

vegetation without also including litter would not necessarily have increased the nutrients available to other plants, which is not consistent with the processes assumed in generating Fig. 5A. One possible mechanism to explain this result is competition between microbes and plants for nitrogen. With litter left on the ground, microbes have a source of carbon and therefore can effectively take up any nitrogen unused by higher plants. Alternatively, with litter, soil moisture could be higher and stimulate microbial activity. Without litter, microbial activity is low and therefore mineral nitrogen can accumulate. Regardless of cause, this result suggests a level of complication in making predictions about competitive effects on soil resource availability that is discussed in the penultimate section. The results for light are much simpler and completely consistent with the predictions in Fig. 6B (Fig. 7B).

Competitive response

Modelling competitive response among environments would be greatly simplified by making two assumptions: (a) plant response to resources does not depend on the degree to which availabilities are determined by biotic (i.e., depletion by other plants) *v.* abiotic (e.g., soil type or climate) factors, and (b) responses to different resources do not interact. If both of these assumptions hold, response to a gradient of resource availability in one environment should predict response to that same resource in another environment with different abiotic levels of that resource. That is, response to a gradient in availability of a given resource should be constant between high and low productivity sites, although the actual resource availability will differ (Fig. 5C, D). Nambiar & Sands (1993) have argued that the first assumption is plausible, although little direct evidence exists. Ideally, testing this assumption will require experiments that create resource gradients through both abiotic and biotic means. The second assumption is known to be false in at least some instances (e.g., Kolb *et al.* 1990), although insufficient data exist to establish any general patterns in the relative importance and patterns of interactions among resources. Clearly, these are both critical areas of future research. In addition, research is needed on the nature of trade-offs in response to different resources. The usual assumption is that there are trade-offs in response to above-ground (light) *v.* below-ground (nutrients and water) resources (reviews by Tilman 1988; Smith & Huston 1989). However, relatively little direct evidence is available on the underlying causes of these trade-offs and almost nothing is known about trade-offs in response to different below-ground resources. For illustrative purposes, Fig. 5C and D show the simplest of constant response curves to a given resource, regardless of environment. In both examples, response curves are shown as non-linear, with a monotonically decreasing response up to an asymptote where the resource is no longer limiting to growth. This shape of response curve is well known for all plant resources (Larcher 1980; Chapin 1988).

Net interaction between plants

The main point of interest in practical terms is to predict the net interaction between plants in different environments, which is the minimum of the mathematical composition of the competitive effect and response for each resource (Fig. 5E, F). For example, in Fig. 5 a set of predictions can be made for growth as a function of competing plant biomass due to nutrient competition at low or high productivity and due to light competition at low or high productivity. In the hypothetical example depicted in Fig. 5, at high productivity the predicted growth for light competition is slightly lower and so determines the net interaction, while at low productivity the predicted growth for nutrient competition is lower and so determines the net interaction (Fig. 5E, F). This particular pattern for the identity of the limiting resource with respect to productivity seems likely in general but, for any particular case, will depend on the quantitative relationships in Fig. 5A–D.

The shapes of the net interaction curves in Fig. 5E and F are shown as close to linear or concave upwards, as predicted by effect/response curves with the shapes shown in Fig. 5A–D. This is consistent with empirically-derived net interaction curves based on neighbour abundance measures other than density, which are typically either linear (e.g., Goldberg & Landa 1991; Gordon & Rice 1993; Elliot & Vose 1993) or concave upwards (e.g., Goldberg & Fleetwood 1987; Goldberg 1987; Wagner & Radosevich 1991; Glover & Zutter 1993). If competitive effects on resources were actually linear as was discussed above, net interaction curves would be predicted to be concave downward—this has not been observed to my knowledge.

Unlike the component competitive effects and responses, a reasonable amount of data on at least some aspects of the net interactions between plants along productivity gradients is available (reviewed by Goldberg & Barton 1992; Kadmon 1995). Total competitive effects (absolute magnitude of net effect of plants on other plants at natural abundance) usually, although not always, increase with productivity. However, relative effects (reduction in target growth due to presence of neighbours expressed as a percentage of maximum target growth in that habitat) show much more variable results (*see* Goldberg & Scheiner 1993; Grace 1993). Data on per-unit size effects along a productivity gradient (slopes in Fig. 5E, F) are, in contrast, almost non-existent. In the only field study of which I am aware, Wilson & Tilman (1991) found that per-gram effects of neighbours (all species combined) on three different target species tended to decrease with increasing nitrogen levels (Fig. 8). More such information on per-unit size effects is essential for developing general models. If only information on total effects is available, it is impossible to separate whether sites or times or species differ in effect because of differences in total abundance or because of differences in per-unit size effects and therefore it is impossible to extrapolate results to any other system.

Clearly, much more data, as well as a more comprehensive theoretical framework, are needed to test whether and how knowledge of plant-resource interactions in a single environment can be used to predict how interactions among individual plants will change along abiotic resource gradients. The range of relationships depicted in Fig. 5 and 6 represents the beginning of such a theoretical framework as well as suggesting directions for empirical research.

COMPLICATIONS: NON-UPTAKE EFFECTS ON RESOURCES

I have suggested a variety of ways in which separating the process of competition into competitive effect (depletion) and competitive response (tolerance) could lead to greater ability to generalise and predict the outcome of competitive interactions among species and environments. However, distinguishing between these two components of the process of competition also raises a very important complicating factor: plants can have effects on nutrients and water (although not light) through mechanisms other than direct uptake of the resource and therefore potentially can have positive as well as negative effects on resource availability (Hunter & Aarssen 1988; Goldberg 1990; Bertness & Callaway 1994). Some of the possible mechanisms of non-uptake effects, as well as some plant traits that can influence

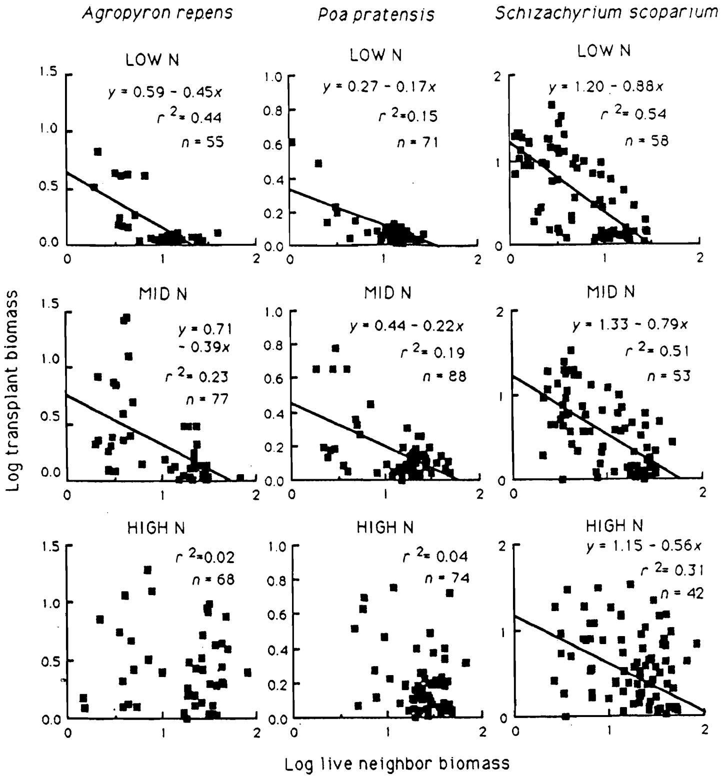

FIG. 8—Effect of neighbour biomass (all species combined) on growth of transplants of three grass species at three levels of nitrogen fertilisation in an old field in Minnesota (from Wilson & Tilman 1991).

the magnitude of such effects, are listed in Table 1. Many of these traits will be fairly specific to particular species and thus increase the variation among species even when individuals are compared on a per-unit size basis, as I have been urging. For example, Wedin & Tilman (1990) found that net annual rates of mineralisation diverged dramatically in initially identical soils among monocultures of five perennial grasses. The differences were apparently due to differences in below-ground litter quality—the species with lower net mineralisation rates in the soil had much higher C:N ratios and lignin concentrations (*see also* Wood *et al.* 1992 for a forestry example). Because it is likely that many of the traits listed in Table 1 are phenotypically plastic among environments, it is likely that non-uptake effects will complicate attempts to generalise across environments as well as among species.

Research on non-uptake effects and consequences for plant interactions has been relatively unfocused to date. Although numerous examples exist of mechanisms by which plants influence resources other than through uptake, only recently have there been attempts to generalise about patterns in their importance among species or environments. For example, Goldberg (1990) and Bertness & Callaway (1994) predicted that positive net effects due to non-uptake mechanisms would be greatest in more stressful (i.e., less productive) sites, leading to the curves for "with" and "without vegetation" in Fig. 6A

TABLE 1–Some mechanisms of non-uptake effects of plants on resources and relevant plant traits.

Process	Plant traits
Direct addition of available forms	
Nitrogen fixation	Nodule formation, root exudates
Leaching, throughfall, stemflow	Cuticle thickness, structural carbon concentration, stomatal density, bark roughness
Hydraulic lift	Rooting depth
Addition in organic compounds	
Decomposition	Tissue longevity, litter C:N, litter lignin and phenolic concentrations
Litter trapping	Above-ground architecture
Modification of physical environment	
Temperature amelioration	Above-ground architecture, leaf size
Soil modification	*see* Addition in organic compounds
Modification of microbial activity	Root exudates, *see* Modification of physical environment

crossing at low productivity levels. Results to date seem to be consistent with this prediction (*see* Bertness & Callaway 1994 for a review), although positive effects of plants on nutrients and water certainly can occur in relatively productive sites (e.g., Bradshaw & Goldberg 1989; Mitchell *et al.* 1993). Further elaboration and testing of this hypothesis are very important to FVM. If non-uptake effects are indeed relatively unimportant in the more productive environments where most commercial forestry is concentrated, the simplifications and approaches to generalisations I have been discussing throughout most of this paper are more likely to be useful.

CONCLUSIONS

The approach described in this paper can be viewed as a "minimalist" approach to predicting the effects of competition on plants. The major goal of this paper has been to state explicitly the assumptions underlying attempts to simplify the understanding and prediction of competitive interactions and to describe the sorts of data needed to test these assumptions. This is particularly important because many of the assumptions are already being made in FVM and ecological practice simply because they are convenient rather than because they have been empirically or even theoretically justified. Thus, by urging simplicity, I am not suggesting an approach to research on plant competition that is radically different from what already exists. I am, however, suggesting that researchers make the assumptions of their empirical work explicit and that these assumptions be tested in a variety of situations to evaluate when and where making these assumptions is likely to lead us astray.

The focus of this paper has largely been on the short-term effects of vegetation on resources and the response to these effects—the simplifications and attempts at generalisation are most likely to apply on relatively short time-scales. However, an increasingly important component of FVM research and management decisions will be on the impact of vegetation manipulation on long-term health of the ecosystem and sustained productivity. An understanding of how well these simplifying assumptions apply on different temporal scales will be critical to developing truly general models for forest vegetation management.

ACKNOWLEDGMENTS

Discussions with many people, including Robert Mitchell, Jacob Weiner, John Vandermeer, and Tim Howard, helped stimulate the development of the ideas in this paper. I am grateful to Ariel Novoplansky and Robert Mitchell for their valuable comments on earlier drafts, and to John Kasmer who helped collect the data for Fig. 7. Financial support was provided by grants from the National Science Foundation and The University of Michigan.

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