On the Meaning of Competition and the Mechanisms of Competitive Superiority

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Introduction

Thompson (1987) evaluated my theory of plant competition, community structure and succession (Tilman, 1980, 1982, 1985, 1986a) by considering how five assumptions or predictions of my work compared with the ideas and data of Grime (1979). Thompson's predisposition toward believing the ideas in Grime (1979) is clearly indicated by his closing sentence, which stated that my work 'opens up arguments about the nature of competition (above and below ground and at low and high resource levels) and the evolution of life histories in response to stress, which I had hoped had been settled 10 years ago,' i.e. with the publication of Grime (1979). However, few issues in science are ever settled, once and for all time. Although Grime (1979) had a significant impact on the field, there is new observational, experimental and theoretical evidence that supports alternative conceptual approaches.

In this paper, I shall show the flaws in Thompson's evaluation of my work, suggest an alternative interpretation of Grime's work and present additional evidence that supports my theory. In doing this, I want to stress that it is not my purpose to try to dichotomize my work and that of Grime. Indeed, when viewed in a dispassionate manner, there are some broad, qualitative similarities between Grime's approach and mine. As Austin (1986) pointed out, both Grime and I agree that soil nutrient levels, light, disturbance and competition are important factors influencing plant community structure. However, Grime (1979) and I disagree about the ways in which these factors interact to structure plant communities. These differences are the subject of Thompson's paper and thus of this reply. In responding to Thompson, I shall first discuss the five points that he raised, and then consider some broader issues.

Thompson's five points

1 Thompson's first point concerns the differentiation among species that my theory requires if resource competition is to explain coexistence. The cause of the long-term persistence of numerous species within a region is one of the most fundamental ecological questions. In theory, there are many processes that can allow stable persistence of species. One of these is resource competition. However, resource competition theory (Tilman, 1980, 1982, 1988) predicts that numerous species can persist only if they are differentiated in their abilities to compete for the different limiting resources. If there are two limiting resources, this would require that the species be ranked in competitive ability for one resource in reverse order of their competitive ability for the second resource. Grime (1979) and Thompson (1987), though, asserted that plants are not differentiated but that a species that is a superior competitor for one resource is also a superior competitor for all other resources. This 'unified concept of competitive ability' is one of the critical assumptions that allowed Grime (1979) to develop his simple tripartite theory, for it allowed him to describe each species as falling at some point along a gradient from being a 'poor competitor' to being a 'superior competitor', without having to specify the factor for which a species was a superior or inferior competitor. There are two major lines of evidence that call Grime's unified concept of competitive ability into question.

First, numerous observational and experimental studies have shown that the relative abundances of plant species change in response to changes in the ratios of limiting resources. Such changes are consistent with the predictions of resource competition theory. However, they call into question Grime's unified concept of competitive ability because they demonstrate that the outcome of interspecific competition is different depending on which resource is limiting. For example, in the Park Grass Experiments, *Lathyrus pratensis* L. reached its peak abundance in plots that had low nitrogen:phosphorus (N:P) ratios, *Festuca rubra* L. reached its peak abundance in plots with intermediate N:P ratios and *Rumex acetosa* L. attained its peak abundance in plots with high N:P ratios (Tilman, 1982, pp. 162–184). Similar separations of species have been observed along many other experimentally imposed resource ratio gradients (e.g. Milton, 1947; Willis, 1963; Tilman, 1983, 1984, 1987a,b) and natural gradients (e.g. Snay-

don, 1962; Pigott & Taylor, 1964; Hanawalt & Whittaker, 1976, 1977a,b).

Moreover, pairwise competition experiments have shown that the relative abundances of species change in response to changes in the relative availabilities of limiting resources, just as resource competition theory predicts should occur. Stern & Donald (1962) showed that clover almost completely displaced a grass from a low nitrogen soil after 133 days but that the grass displaced the clover in high nitrogen plots. As emphasized by Harper (1977, p. 340), this experiment is best interpreted as one in which nitrogen addition shifts conditions from being competition for nitrogen to competition for light. Contrary to the generalization offered by Grime (1979), a different species is a superior competitor when nitrogen is limiting than when light is limiting. In reviewing plant competition experiments, Harper (1977, p. 369) noted that one of the most general features of such experiments is that the 'balance between a pair of species in mixture is changed by the addition of a particular nutrient, alteration of the pH, change in the level of the water table, application of water stress or shading'. Just such changes are predicted to occur by resource competition theory if species are differentiated in their competitive abilities for different resources but would not be predicted if Grime's 'unified concept of competitive ability' were correct. Even the data in Mahmoud & Grime (1976), which both Grime (1979) and Thompson (1987) cite as supporting their view, show such differentiation. Grime and Thompson say that these data support their case because, in pairwise competition experiments, *Arrhenatherum elatius* L. was more abundant than either *Agrostis tenuis* Sibth. or *Festuca ovina* L. in both the high nitrogen and the low nitrogen treatment. However, they failed to note that there were great changes in the *relative abundances* of the competitors between the two nitrogen levels. *Arrhenatherum* completely eliminated both *Festuca* and *Agrostis* from the high nitrogen, pairwise competition pots. At low nitrogen levels, *Arrhenatherum* was reduced to 63% of the total when it competed with *Agrostis* and to 60% of the total when it competed with *Festuca*. Thus, *Arrhenatherum* had a lower proportional abundance in the low N than in the high N treatment and *Agrostis* and *Festuca* had higher proportional abundances in the low N treatment. Such a pattern is consistent with the hypothesis that these species are differentiated in their abilities to compete for light versus nitrogen. The trends seen in these short-term experiments at two nitrogen levels reinforce the view that competition is an important process causing *Arrhenatherum* to dominate rich meadows and *Festuca* and *Agrostis* to dominate more nutrient poor habitats in nature. Grime (1979) also asserted that plants do not compete on nutrient poor soils. This assertion is inconsistent with numerous studies of both interspecific and intraspecific competition. If plants did not compete on poor soils, relative growth rates and average mass per plant would not decrease with increases in plant densities. However, numerous studies of plants growing in monocultures have shown that both of these decrease with increases in initial plant density on both poor and rich soils (e.g. Donald, 1951; Clatworthy, 1960, as quoted in Harper, 1977; Harper, 1961, 1977). Such a decrease in growth rate with increases in density is an essential feature of the 'law' of constant final yield (Kira, Ogawa & Shinozaki, 1953; Harper, 1977). Furthermore, the results reported in Mahmoud & Grime (1976) show that the presence of *Agrostis* led to a 30% decrease in the yield of *Arrhenatherum* and to a 43% decrease for *Festuca* and that the presence of *Arrhenatherum* led to a 60% decrease in the yield of *Agrostis* or *Festuca* during pairwise competition on a poor soil. Grime's (1979) assertion that plants do not compete on poor soils is also clearly refuted by Stern & Donald (1962).

The second problem with Grime's unified concept of competitive ability is conceptual. Thompson (1987) asserted that a species that is the 'better competitor above ground is also the better competitor below ground' and that 'this outcome is not just likely but inevitable.' In contrast, in a book that will appear in 1988, I present a detailed, mechanistic model of plant competition that predicts that interspecific differentiation is an inescapable outcome of the process of allocation and growth in multicellular plants (Tilman, 1988). The only mechanism of interaction included in this model is resource competition. The model, called 'ALLOCATE', assumes that plants start their life as seeds and that vegetative growth is determined by the process of allocation of photosynthate to the production of additional leaf, root and stem tissues. It is a model of competition among size-structured populations, with each individual plant undergoing continuous vegetative growth determined by its ability to acquire and use a soil resource and light. Plants impose the vertical light gradient through the amount of light each plant, with its own unique height, intercepts. Thus, the model captures some essential mechanisms of competition among size-structured plants.

The process of allocation imposes a major and inescapable constraint on plant form and function. Photosynthate allocated to produce more of one structure cannot be used to produce more of another structure. Because of the physical separation of above-ground and below-ground resources, a plant that allocates more of its photosynthate to the production of roots necessarily allocates a lower proportion to leaves or stems. This means that a plant that gains competitive ability for nitrogen by allocating a greater proportion of its production to roots necessarily decreases its competitive ability for light because it has lower allocation to leaves and/or stems, both of which are important in the acquisition of light. Details of the model, its predictions for numerous cases of competition and similarities and differences between the model and simpler isocline models of resource competition (Tilman, 1980, 1982) are presented in Tilman (1988).

All possible patterns of allocation to roots, leaves and stems, i.e. all possible morphologies, can be represented as points on the triangle of Fig. 1. Using the model ALLOCATE, numerous simulations of competition among plants that were identical in all respects except their morphology showed that, in a homogeneous habitat, a single species (i.e. a single allocation pattern) competitively displaced all others (Tilman, 1988). The winning morphology was determined by the nutrient supply rate of the soil and the disturbance rate of the habitat (Tilman, 1988), as summarized in Fig. 1. Each unique habitat, as defined by its nutrient supply rate and its disturbance rate, was found to have an associated plant morphology that is the superior competitor for that habitat. Thus, ALLOCATE predicts that the requirement of plants for both an above-ground resource, light, and for below-ground resources and the constraint on morphology caused by allocation, necessarily cause a plant to be a superior competitor in a small range of habitats. Plants that are superior competitors in nutrient poor habitats are necessarily inferior competitors in nutrient rich habitats. Those that are superior competitors at low disturbance rates are necessarily inferior at high disturbance rates and so on. This model assumed that all plants were physiologically identical and explored how morphology (as determined by allocation patterns) influenced competitive abilities in different habitats. A similar line of reasoning applies to allocation to various physiological processes. A plant that allocates more of its nitrogen to producing the pigments and proteins involved in photosynthesis necessarily has a lower proportion

to allocate to the production of the proteins involved in nutrient uptake. The allocation-based trade-offs that plants face in their morphology, physiology and life histories thus constrain each plant to being a superior competitor in a small portion of the total range of habitat conditions and necessarily mean that it will be an inferior competitor for other environmental conditions (Tilman, 1988).
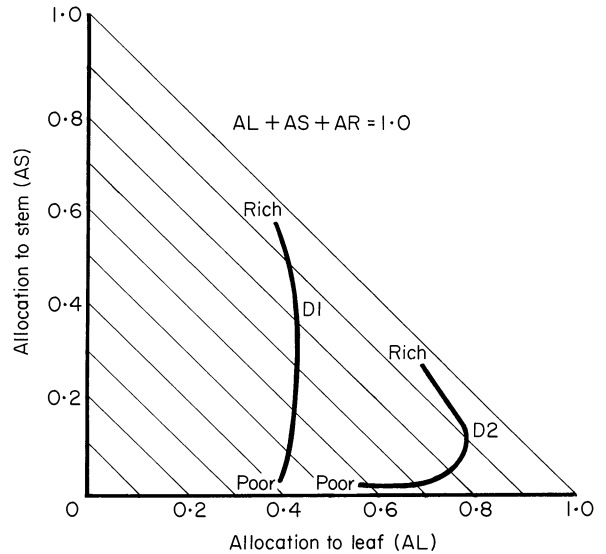

Fig. 1. The triangle illustrates all possible patterns of allocation of vegetative growth to leaf, stem and root for plants that differ only in their morphology, as determined by their allocation pattern. Note that allocation is expressed as a proportion of total production. Thus, where AL is proportional allocation to leaves, AS is proportional allocation to stems and AR is proportional allocation to roots: AL + AS + AR = 1·0. ALLOCATE, a model of competition, predicts that the superior competitor in a habitat will depend both on the nutrient supply rate of the soil and the disturbance rate (Tilman, 1988). The curve labelled D1 shows the different morphologies that are predicted to dominate different points along a gradient from habitats with poor soils to habitats with rich soils, where all habitats have the same low disturbance rate. The curve labelled D2 shows a similar gradient for habitats that have a high disturbance rate. Figure modified from Tilman (1988).

In total, there is neither empirical nor conceptual support for the contention of Grime (1979) and Thompson (1987) that all plants can be ranked from being poor competitors to good competitors, in general, independent of the resources for which they may be competing. Nor is there support for the assertion that plants should not compete on poor soils or in frequently disturbed habitats. Rather, the available evidence suggests that plant species are differentiated in their competitive abilities along major environmental gradients.

What would cause this major difference between Grime's unified concept of plant competitive ability and the predictions of resource competition theory? On the surface, it does not seem to be caused by Grime and I having different definitions of competition. Grime (1979, p. 8, his emphasis) stated 'Here competition is defined as *the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space* (Grime, 1973b). This choice of words allows competition to be defined in relation to its mechanism rather than its effects . . . ' ALLOCATE, the model that I developed in Tilman (1988), explicitly modelled competition in a manner essentially identical to that stated in Grime's definition of competition. The purpose of the model ALLOCATE was to determine the logical (i.e. mathematical) consequences of a mechanistic definition of plant competition. Contrary to the theoretically unfounded assertions made by Thompson, the model demonstrated that differentiation is an unavoidable outcome of the constraint plants face because of their requirement for both above- and below-ground resources and the trade-off they face because potential growth allocated to one function, such as nutrient uptake, cannot also be allocated to another function, such as light capture. The model ALLOCATE predicts that each species because of its particular morphology, physiology and life history, will be a superior competitor at a particular point along a productivity or disturbance gradient but will be an inferior competitor at other points. For the conditions for which a species is a superior competitor, it can acquire a continuously increasing share of both above- and below-ground resources. The demonstration that some species are superior competitors both above and below ground for a particular set of habitat conditions does not in any way contradict the predictions of resource competition theory. Thus, contrary to Thompson's interpretation, the work of Donald (1958) and Aspinall (1960) is consistent with the predictions of resource-based models of plant competition. The only possible objection that could be raised to resource-based models of competition using these studies is that one species outyielded the other on both low and high nitrogen soils. However, this would be a spurious objection since the relative yields of the species did change with nitrogen and since the experiments were of too short a duration (the longest being 72 days) to say much (if anything) about the actual outcome of competition. Indeed, as demonstrated in Tilman (1988), such short-term experiments are likely to have their immediate dynamics highly influenced by plant traits, such as maximal growth rates, that have little bearing on the long-term outcome of the competitive process. All else being equal, an inferior competitor that has a higher rate of vegetative growth will attain a period of transient dominance during the interval required for a more slowly growing superior competitor to reach a sufficient density to suppress the faster growing species.

2 The second point raised by Thompson concerns Grime's concept of 'stress'. Grime defined a stress as any factor, such as low availability of a nutrient, water or light, low temperature or low soil pH, that decreases the growth rate of a species below its maximum. He suggested that a given degree of stress, no matter what its source, would lead to the same plant traits. This was a useful broad-scale generalization for most factors other than light because it emphasized that many factors that cause low plant biomass may favour a somewhat similar suite of plant traits. However, on a finer level of resolution, especially when comparing below-ground and above-ground resources, I fail to see the utility of the concept of stress because different types of stress favour markedly different species. For instance, reviews of plant morphology and ecophysiology have shown that nutrient-poor soils favour plants with high allocation to roots and low allocation to stems whereas the low light availability at the soil surface associated with rich soils favours plants with low root allocation and high allocation to stems (Mooney, 1972, 1977; Chapin, 1980; Bloom, Chapin & Mooney, 1985). Root:shoot ratios vary by almost 50-fold between plants at the extreme ends of a soil-resource:light gradient (Whittaker, 1975; Barbour, Burk & Pitts, 1980; Webb *et al.*, 1983). However, the two ends of such a gradient are classified by Grime as being equally stressful, with the nutrient-poor end having the stress of low nutrient levels and the nutrient-rich end having the stress of low light. Is stress a useful concept when such great differences in plant morphology occur in habitats that would be classified as being equally stressful? Grime (1979) does not consider light to be a stress for the canopy species on a nutrient rich habitat but this view ignores the fact that all canopy individuals must begin their life as seedlings or shoots in the understory and that it is competition for light that explains the high allocation to stem of the canopy species. Moreover, the stress of low soil phosphorus leads to quite a different plant community than the stress of low nitrogen, low calcium or

waterlogging. In total, I feel that the concept of stress is too broad and too simplistic to be of much further use in plant ecology.

I agree with Thompson that, during secondary succession on a nutrient rich soil, both available soil nutrient levels and light availability are often lowest during the late stages of succession. Indeed, it was just this observation that led me to conclude that secondary succession on rich soils could be best explained as the transient dynamics of competitive displacement (Tilman, 1985). Transient dynamics, as I will discuss later, are greatly influenced by the morphologies, physiologies and life histories of plants.

Grime (1979) suggests that stress prevents competition from occurring. However, the models of community structure that I have developed suggest that competition is the primary mechanism of interaction among plants in low nutrient or low light habitats. Grime's assertion that competition becomes unimportant in stressful or disturbed habitats is logically flawed, as indicated by the work of Quinn & Dunham (1983). Different types and intensities of stress and different types and intensities of disturbance definitely do favour different plant traits, though this occurs not because increased stress or disturbance decreases the importance of competition but because the outcome of competition depends on the supply rates of limiting resources (stress) and on loss and mortality rates (disturbance). The underlying mechanism of interaction is always competition. I would like to echo Quinn & Dunham's plea for ecologists to stop trying to dichotomize and separate processes that are intimately linked in a multi-causal system. Nutrient, light and water availability, temperature, soil pH and various sources of plant mortality or loss of plant parts all influence the competitive interactions among plants. The question we should be asking is not whether it is competition, predation, disturbance or stress that is 'more important' in controlling the structure of particular plant community but how these forces interact to structure communities.

3 The third point raised by Thompson (1987) concerns the resource ratio hypothesis of succession (Tilman, 1985). His Fig. 1 suggests that he may have misunderstood an essential part of this theory. He asserted that his Fig. 1a illustrated a prediction of the resource ratio hypothesis of succession whereas it does not. His Fig. 1a shows an early successional species as having a higher nitrogen-dependent growth rate at low nitrogen levels but a lower growth rate at high nitrogen

levels than a late successional species. The resource ratio hypothesis does not assume that such nitrogen-dependent growth rate curves should cross. Rather, it assumes that a species that is a superior competitor for low nutrient levels is an inferior competitor for low light levels (Tilman, 1985). For cases of primary succession, I assumed that early successional species could grow more rapidly at low nitrogen levels than late successional species but that late successional species could grow more rapidly at low light levels than early successional species (Fig. 2a,b). Bazzaz (1979) and Tilman (1986a) reported data that support this assumption. Such differentiation among species leads to the resource-dependent growth isoclines of Fig. 2c. The isoclines show that the early successional species can maintain itself in a more nitrogen poor habitat than the late
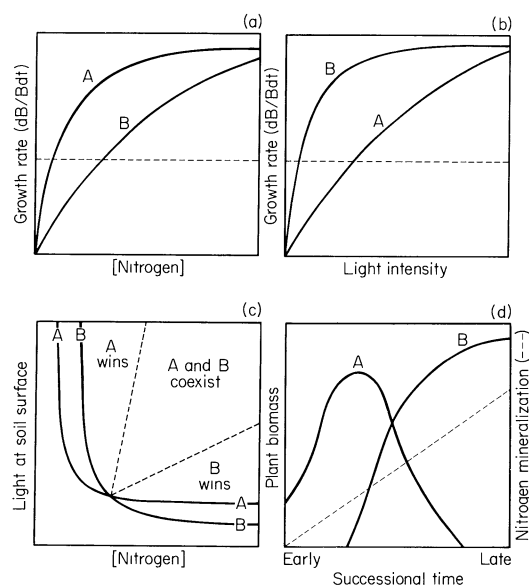

Fig. 2. (a) The dependence of the relative growth rate (dB/Bdt, where B is biomass per individual) of an early successional species, species A and a late successional species, species B, on the concentration of available nitrogen in a soil. The broken line shows the loss rate both species experience.

(b) The dependence of the relative growth rate of these two species on light is similarly illustrated.

(c) The solid curves labelled A and B are the resource-dependent growth isoclines for species A and B. The broken lines show the amounts of the two resources consumed by the two species. These define the habitat types in which A is competitively superior, both species coexist or B is competitively superior. See Tilman (1982) for further details.

(d) If the soil nitrogen mineralization rate (broken line) is low during early succession and slowly increases through time, as occurs during many primary succession, this would cause species A to be dominant during early succession and species B to be dominant during late succession.

successional species but that the late successional species can maintain itself in a lower light habitat than the early successional species. These differences would lead to a successional sequence (Fig. 2d) dominated first by the early successional species and then by the late species if soil nitrogen supply rates were to increase slowly through time, as in primary successions. As noted in Tilman (1985), such an increase must be sufficiently slow that competitive interactions could approach equilibrium at all times throughout the process. If nutrient levels changed rapidly, or if initial nutrient levels were high, there could also be a successional sequence but it would be determined by the *transient dynamics* (*sensu* Tilman, 1985) of the competitive interaction and would be strongly influenced by maximal growth rates.

Fig. 2 illustrated a theoretical case in which both species had similar maximal growth rates. Early successional species, especially those of secondary successions on richer soils, often have higher maximal growth rates than late successional species. Fig. 3, which illustrates a case presented in Tilman (1985, pp. 843, 848–849), shows that this need not change any of the predictions of the resource ratio hypothesis of succession. As for Fig. 2, the early successional species has a higher growth rate at low nutrient levels but a lower growth rate at low light levels than the late successional species. The traits shown in Fig. 3a and 3b lead to resource-dependent growth isoclines that are like those of Fig. 2c and to dynamics of secondary succession on a poor soil (with nutrient levels increasing slowly through time) that are like those of Fig. 2 (Tilman, 1985). The nitrogen-dependent growth curves of Fig. 3a are just like those that I observed in my study of successional plants (Tilman, 1986a,b). Thus, contrary to Thompson's assertion, they support the hypothesis that it is their ability to grow more rapidly at low nitrogen levels that makes certain species dominant on the nitrogen poor soils of early secondary succession at Cedar Creek Natural History Area.

Thompson suggested that the 300 mg kg^{-1} of total soil N that I used as indicative of a 'poor' soil was too high and re-analysed my results using a total soil nitrogen level of 50 mg kg^{-1}. I used a total soil N of 300 mg kg^{-1} because it is a lower bound on nitrogen levels in the most nitrogen poor fields of the secondary successional sequence at Cedar Creek Natural History Area (Tilman, 1986a, p. 555; Inouye *et al.*, 1987). There are no soils that are ever as poor as 50 mg kg^{-1} at Cedar Creek Natural History Area. Indeed, out of a total of 2262 soil
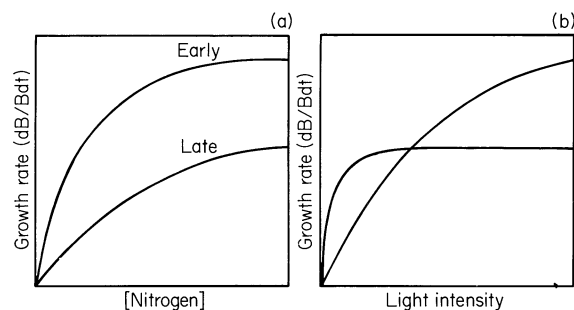

Fig. 3. (a) Nitrogen-dependent growth curves for an early and a late successional species.

(b) Light-dependent growth curves for an early successional and a late successional species. These curves lead to isoclines like those of Fig. 2c and to a pattern of primary succession like that of Fig. 2d. Moreover, these would lead to a period of transient dominance by species A during secondary succession on a poor soil.

samples analysed in a survey of the soils of successional fields at Cedar Creek, the most nitrogen poor sample had 148 mg kg^{-1} of N (Inouye *et al.*, 1987). Contrary to Thompson's suggestion, plant growth rates at 50 mg kg^{-1} are not all relevant to testing the resource ratio hypothesis at Cedar Creek and Thompson's re-analysis of my data is invalid.

As stated in Tilman (1986a), early successional plants at Cedar Creek have higher maximal growth rates on low nitrogen soils and extract more nitrogen from low nitrogen soils than do late successional species. This result is consistent with a prediction of the resource ratio hypothesis of succession. Contrary to Thompson's statement, I never interpreted this as *direct* evidence of competitive superiority. Rather, I said 'The greater ability of early successional species to acquire nitrogen and grow in nitrogen-poor soils suggests that they may be superior competitors for soil nitrogen compared to later successional species' (Tilman, 1986a, p. 561). The experiments reported in Tilman (1986a) were never planned to directly determine the differing abilities of these species to compete for nitrogen but were planned to determine their patterns of nitrogen-dependent growth. It is the latter information that is required for a direct test of the resource ratio hypothesis.

Thompson raised an important point when he noted that the nitrogen-dependent growth curves of the Cedar Creek species showed that the early successional species had higher maximal growth rates than the late successional species. Interspecific differences in maximal growth rates need not have any influence on the pattern of primary successions or of secondary successions that start

on extremely nutrient poor soils but can have a major impact on successional dynamics on more nutrient rich soils (Tilman, 1985). Their higher maximal growth rates could allow early successional species to attain a period of transient dominance during secondary succession at Cedar Creek, a possibility that I ignored when writing Tilman (1986a) because I had considered the soils too nitrogen poor to allow this. I have since concluded that transient dynamics are an important cause of successional dynamics at Cedar Creek (Tilman, 1987, 1988). A thorough analysis of secondary succession at Cedar Creek suggests that about half of the pattern is best explained as a result of the non-equilibrial transient dynamics of competitive displacement (caused by differences in maximal growth rates or colonization rates) and about half is best explained as resulting from slow accumulation of nitrogen favouring species that are superior competitors for light but inferior competitors for nitrogen (Tilman, 1988). The data reported in Tilman (1986a,b) are equally consistent with either or both hypotheses.

In Tilman (1985), I did not distinguish between the early successional species of nutrient poor soils and those of nutrient rich soils. I have since come to consider this to be an important distinction (Tilman, 1987, 1988). I agree with Thompson (1987) that the early successional species of nutrient rich soils are likely to have higher maximal growth rates than the early successional species of nutrient poor soils (Tilman, 1988). However, I disagree with Thompson's assertion that the species dominant during early primary succession on a nitrogen poor substrate are likely to be inferior competitors for nitrogen. Such species, as Chapin (1980) noted, have much higher root:shoot ratios than those dominant on richer soils. Although they may have lower rates of nutrient uptake per unit of root biomass, this is more than compensated for by their greater root biomass, which allows them to overcome the problem of diffusion-limited nutrient uptake and thus obtain more nutrient from a poor soil than species with lower root biomass but greater uptake rates (Chapin, 1980). Furthermore, according to Chapin (1980), 'When sampled under natural conditions, species from infertile sites generally have lower tissue concentrations than species from fertile sites' and 'can maintain metabolic effectiveness under conditions of nutrient stress.' Although careful studies of competition will be required to resolve this issue, Chapin's review supports the idea that the early successional species of nutrient poor soils can be superior

nutrient competitors than late successional species.

This view is reinforced by observations I have made at Cedar Creek. *Ambrosia artemisiifolia* L. is a common dominant of early successional fields in North America. During secondary succession on rich soils, it is often displaced within 2 or 3 yr, much as Thompson described for *Ipomoea hederacea* (L.) Jacq. However, during secondary succession on nitrogen poor soils, such as those of the sand plain at Cedar Creek Natural History Area, Minnesota, *Ambrosia* may persist as a local dominant for periods of 20 yr or more in *undisturbed* old fields (Tilman, 1988), despite the presence of many later successional species. The areas in which it persists are some of the most nitrogen poor regions of these old fields. It is rapidly displaced from such areas following nitrogen addition (Tilman, 1987a, 1988). *Hedeoma hispida* Pursh. and *Agrostis scabra* Willd. are other early successional species of nitrogen poor soils that show similar patterns at Cedar Creek (Tilman, 1987a, 1988). These patterns are suggestive of these early successional species being superior competitors for nitrogen compared to late successional species.

4 Thompson's fourth point is directed toward my generalizations about the dependence of plant morphology and life history on habitat productivity. I have extensively reviewed this literature in Tilman (1988) and will not repeat that review here. Suffice it to say that the review generally supports my earlier statements. The examples that Thompson mentions, when taken to their logical conclusion, also support me. Thompson (1987) states that *Dryas drummondii* Richards, an early successional species of Glacier Bay, may require 3 yr to flower. He cites this to suggest that early successional species of habitats with poor soils can be slow at reproducing. However, is 3 yr rapid or slow reproduction? This can only be told by comparison with the time required for earlier or later successional species to reproduce. The spruce and hemlock that are dominant during later stages of succession at Glacier Bay are much taller than *Dryas* and may require 50 yr or more to flower. The earliest dominants at Glacier Bay are the cyanobacteria of black crusts (Worley, 1973) and lichens, both of which can reproduce in a much shorter time than the 3 yr required by *Dryas*. They are also shorter than *Dryas* and may have higher maximal relative growth rates. Thus, when put in the context of the other species that are dominants along the productivity gradient of pri-

mary succession at Glacier Bay, the traits cited by Thompson for *Dryas* support my generalizations about the dependence of plant life histories on habitat productivity.

5 The fifth point raised by Thompson (1987) addresses the suggestion (Tilman, 1985) that the broad, qualitative similarities among primary successions, secondary successions on poor soils and secondary successions on rich soils could be explained by the life histories plants have evolved for different environmental conditions. I have elaborated greatly on this point in Tilman (1988). I fail to see how the views expressed by Thompson (1987) differ significantly from those in Tilman (1985). I said that the early dominants of secondary successions on rich soils were transients that attained their dominance because of their greater maximal growth rates but that the early dominants of primary successions were superior competitors for nutrients (Tilman, 1985, p. 843): 'For secondary succession on a rich soil, the population dynamics are not an equilibrium prediction of the model, but represent transient dynamics that are critically dependent on the maximal growth rates and resource requirements of the species. The simulations in figure 5 suggest that the transient dynamics of secondary succession will be similar to, but much faster than, the dynamics of primary succession if early successional species have a higher maximal rate of weight gain than the late successional species. In contrast, the assumption of higher growth rates for early successional species is of little importance during the much slower secondary succession on a nutrient-poor soil.'

On the meaning and mechanisms of competition

Thompson (1987) confuses the concept of competitive superiority with the processes that may explain why a species is competitively superior in a particular habitat. I define a species as being a superior competitor for a particular suite of environmental conditions if, given sufficient time for competitive interactions to go to completion, it displaces another species. This is the definition of competitive superiority that has been used in ecology since Gause's classical work. The difference between my work and that of Grime (1979) is not, I trust, in the definition of competitive superiority but in our differing views as to which traits might cause a plant to be competitively superior. Grime (1979) and Thompson

(1987) hypothesized that a superior competitor would be a species that is leafy, grows rapidly and can rapidly attain greater height than another species. In their view, inferior competitors are species that allocate less to leaf (and thus have lower relative growth rates; Tilman, 1988) but more to either stem or root. Thus, they emphasize processes that allow a plant to have immediate access to limiting resources, especially light. However, in doing this they ignore many other plant traits that may be more important determinants of the long-term outcome of competitive interactions among plants. As already mentioned, their view contradicts the logical outcome of a model that looks at the mechanisms of nutrient and light acquisition and utilization, for that model predicts that slow-growing plants with high root allocation are superior competitors in low nutrient, low disturbance habitats and that slow-growing plants with high allocation to stem are superior competitors in high nutrient, low disturbance habitats (Tilman, 1988). In my model, competition comes solely from the process of acquisition and utilization of limiting resources. Disturbance rates and nutrient supply rates do not change the intensity of the competitive interaction but rather influence the dynamics and outcome of the competitive process. This occurs because disturbance rates influence the resource requirements of the species (resource-dependent growth must balance disturbance-caused losses in order for a population to exist in a habitat) and both disturbance rates and nutrient supply rates determine the availabilities of soil resources and light (Tilman, 1982, 1988).

Although Grime and I have used 'competition' and 'competitive superiority' in quite different ways, I do not agree with Thompson's suggestion that this can explain our differences or that Grime's usage is correct. Competitive superiority is an experimentally observable reality. The only way to determine if a species is a superior competitor is to perform statistically sound experiments that are allowed to proceed for a long enough period of time that the outcome of the competitive interactions can be observed. The crux of our disagreement comes from the different traits that we believe allow plants to be competitively superior in particular habitats. Although mathematical theory supports my assertions over those of Grime (1979), experimentation is required to resolve our differences.

I believe that a major difference between Grime's view and mine comes from the different habitats in which we have done our work. I have worked

mostly in old fields and native prairie and savanna that are subject to natural disturbances and biotically-controlled levels of herbivory. In contrast, the pastures that Grime has worked in are subject to heavy sheep grazing. Before neolithic clearing and grazing began, Grime's richer pastures contained closed canopy forests and forests will still eventually return to these areas if grazers are excluded (Tansley, 1949). Thus, in the absence of unnaturally high densities of herbivores and thus unnaturally high rates of herbivore-caused disturbance, most areas in which Grime has worked would be forest. I find it interesting that the traits that Grime associated with superior competitive ability (leafy, high RGR, rapid increases in height) are the same traits that the model ALLOCATE predicts should maximize the ability of a plant to compete in a highly disturbed but nutrient rich habitat (Tilman, 1988). The traits that Grime associated with poor competitive ability are those that the model ALLOCATE predicts should maximize competitive ability in undisturbed habitats (Tilman, 1988). I believe that there are insights to be gained from Grime's work. However, these will require that the correlation between productivity and disturbance rates in pastures be taken into account and that it be realized that the pastures, when free of the unnaturally high grazing pressures maintained by predator control and artificial stocking, would return to forest (Tansley, 1949). Trees, with their inherently slow maximal rates of vegetative growth (Grime & Hunt, 1975) are the superior competitors for the pastures that Grime has studied if unnaturally high grazing is stopped. Thus, contrary to another of Grime's generalizations, rich soils, under more natural conditions, would favour species with low maximal growth rates. The high maximal growth rates Grime associated with plants dominant in rich pastures are best explained as resulting from the higher grazing rates that richer pastures receive (Tilman, 1988).

Equilibrium *vs* non-equilibrium approaches

Thompson introduced and concluded his paper by suggesting that there is a major conceptual difference between 'equilibrium' and 'non-equilibrium' models and that niche differentiation is assumed to be important for the former but not for the latter. One of the most fundamental questions ecologists address is 'What factors allow the long-term persistence of a species in a habitat?' Be they equilibrium or non-equilibrium models, all models that predict the long-term persistence of many species within a habitat necessarily assume

some unavoidable trade-off in the traits of the species (Tilman, 1986b). It is impossible to explain the persistence of many species, whatever the mechanism, without invoking 'niche differentiation'. The only alternative that could explain persistence of many species within a habitat would be to assume that all species were functionally identical. However, this assumption means that species would be subject to random walks to extinction and leads to the eventual dominance of a community by a single species (Hubbell, 1979; Hubbell & Foster, 1986). Any non-equilibrium model that explains persistence of many species can be changed, by the appropriate choice of scale or transformation of variables, into an equilibrium model that makes the same prediction. The critical aspect of these models is not whether they are equilibrium or non-equilibrium. The critical aspects are the environmental or biotic constraints that the models assume to be important and the mechanisms that could have led there to be unavoidable trade-offs in the ways that different species respond to these constraints. It is these trade-offs that cause differentiation and thus that allow coexistence. The theory of resource competition that I am developing is neither an equilibrium nor a non-equilibrium model. It is a theory of the mechanisms of plant competition. It can be solved mathematically to determine its 'equilibrium' predictions (e.g. Tilman, 1980, 1982) and it can be solved to determine its dynamics (Tilman, 1981, 1985, 1988), including transient dynamics.

It might be better to express the distinction that Thompson (1987) is drawing not as that between equilibrium and non-equilibrium theories but as between an approach that tries to understand broad-scale, long-term patterns in nature versus one that tries to understand short-term dynamic responses of communities to perturbations. The traits that Grime & Hodgson (1987) use to define competitive superiority are all traits that would allow a species to attain a temporary period of dominance after a perturbation. Thus, within a heavily grazed pasture, a plant species with a high relative growth rate, a high allocation to leaf and a high capacity for morphological flexibility would probably initially suppress other species when nutrients were added or when sheep or other sources of loss or disturbance were removed. This immediate dynamic response to a manipulation need not be related to the eventual, long-term effect of the manipulation (Tilman, 1985, 1988). Although rapidly growing species would initially dominate a rich pasture after sheep were removed,

the pasture would eventually become dominated by trees, which are some of the most slowly growing species (Grime & Hunt, 1975). It is the trees that are the true, long-term superior competitors for those conditions. Any other definition of competitive superiority is time dependent, for all perturbations can lead to a sequence of dominant species, much like a succession (Tilman, 1985, 1988). The definition of competitive ability that Thompson offers would force us to state that species A is a superior competitor for year 1, species B for year 2 and so on, through the entire successional sequence that resulted from a given manipulation. However, the species that attain periods of transient dominance are not superior competitors for the imposed conditions but attain temporary dominance because of the initial rarity of the eventual dominant or because they are better colonizers or have greater growth rates for the conditions that occur immediately after the perturbation.

If a model is a suitable description of nature, it should be able to predict both the long-term, equilibrial outcome of a particular set of conditions as well as the transient dynamics that a community would undergo following a wide variety of different types of perturbations. Both equilibrial predictions and predictions of short-term transient dynamics are critical aspects of ecological models and both should be used to test among models whenever possible. I can make sense of most of Grime (1979) and Thompson (1987) when I consider them to be discussing short-term transient dynamics. Indeed, many of their observations are consistent with the transient dynamics predicted by resource-based models of plant competition (Tilman, 1985, 1988).

Conclusions

I disagree with almost all of the major points raised by Thompson (1987). Observations, experiments and theory demonstrate that there is little justification for the assertion that species can be ranked, *in general*, as falling at some point along a gradient from inferior to superior competitors. Grime's 'unified concept of competitive ability' and his assertion that plants do not compete in either nutrient poor or disturbed habitats have little support. Rather, the available evidence shows that species are differentiated in their competitive abilities, with species that are superior competitors at one point along major environmental gradients, such as productivity or disturbance

gradients, being inferior competitors at other points on these gradients. This differentiation is an unavoidable outcome of the trade-offs that exist in the physiologies, morphologies and life histories of plants. Competition occurs at all points along such gradients. Because Thompson (1987) misinterpreted the resource ratio hypothesis of succession (Tilman, 1985), he incorrectly concluded that the data in Tilman (1986a), Rice, Penfound & Rohrbaugh (1960) and Parrish & Bazzaz (1982) did not support it. However, he was correct in suggesting that those results were also consistent with a model of succession as transient dynamics (Tilman, 1985, 1988). Further analyses of secondary succession at Cedar Creek, performed before I received Thompson's paper, suggest that both long-term nutrient accumulation and transient dynamics are important determinants of the successional pattern (Tilman, 1987a, 1988).

Grime has made major contributions to the field by sparking an interest in the dependence of plant life histories and morphologies on the disturbance regime and the productivity of habitats and by gathering detailed observational and experimental data. However, the inter-relations of variables and the multiple cause and effect relations of communities are too complex to allow them to be unambiguously explored with simple verbal models. Furthermore, Grime's triangular model is logically flawed, as pointed out by Loehle (1987). We need experiments and models that look explicitly at the underlying mechanisms whereby individual plants interact with each other and with the rest of their abiotic and biotic environment (Tilman, 1987b). Resource-based models of plant competition offer one such approach. They and other mechanistic approaches, may allow us to more fully understand the forces that determine the structure and dynamics of plant communities. All of these models should be tested using both short-term transient dynamic responses and long-term equilibrial patterns in communities subject to various experimental or natural manipulations.

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