

Reconciling plant strategy theories of Grime and Tilman

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Summary

1 The theories of Grime and Tilman are ambitious attempts to unify disparate theories regarding the construction of plants, their interaction with the environment and the assembly of communities. After over two decades of parallel research, their ideas have not been reconciled, hindering progress in understanding the functioning of ecosystems.

2 Grime's theories do not adequately incorporate the importance of non-heterogeneous supplies of nutrients and how these supplies are partitioned over long time scales, are inconsistent regarding the importance of disturbance in nutrient-limited habitats and need to reconsider the carbon economy of shade-tolerant plants.

3 Failure to account for differences between aquatic and terrestrial systems in how resource supplies are partitioned led Tilman to develop a shifting set of theories that have become reduced in mechanistic detail over time. The most recent highlighted the reduction of nutrient concentrations in soil solution, although it can no longer be derived from any viable mechanistic model. The slow diffusion of nutrients in soils means that the reduction of average soil solution nutrient concentrations cannot explain competitive exclusion.

4 Although neither theory, nor a union of the two, adequately characterizes the dynamics of terrestrial plant assemblages, the complementarity in their assumptions serve as an important foundation for future theory and research.

5 Reconciling the approaches of Grime and Tilman leads to six scenarios for competition for nutrients and light, with the outcome of each depending on the ability of plants to preempt supplies. Under uniform supplies, pulses or patches, light competition requires leaf area dominance, while nutrient competition requires root length dominance. There are still important basic questions regarding the nature of nutrient supplies that will need to be answered, but recent research brings us closer to a unified set of theories on resource competition.

Key-words: competition, concentration reduction hypothesis, CSR hypothesis, disturbance, plant strategies, stress

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Introduction

Among the quarter of a million species of higher terrestrial plants, there is an incredible diversity of form and function. Likewise, there is great variation among habitats in resource availability and abiotic conditions. Plant traits do not vary randomly across ecological gradients and it has long been a central tenet of ecology that environmental conditions are largely responsible for the combinations of traits that have been selected in species and for the sorting of species into assemblages. The repeatable pattern of traits among evolutionarily

distinct taxa leads to the belief or, at least, the hope that there are just a few general strategies to cope with a diverse combination of conditions.

Understanding the distribution of plant species across environmental gradients requires bringing together theories regarding the construction of plants, as well as their interaction with the environment, and the assembly of communities. The debate that began with the publication of *Plant Strategies and Vegetation Processes* (Grime 1979, p. 34) and 'Resources: a graphical-mechanistic approach to competition and predation' (Tilman 1980) eventually ranged from the acquisition, allocation and loss of resources by plants via competition, facilitation, stress, disturbance and dispersal to dominance, diversity, distributions and succession. Both these two researchers

and many other researchers attempted to correct errors or to match up discrepancies between the two theories (Thompson 1987; Grace 1990, 1995; Shipley & Peters 1990; Berendse *et al.* 1992; Goldberg 1996). Of these, Grace (1990) most notably points out apparent differences between Grime and Tilman in operational definitions of competition and their consideration of population dynamics. Incorrectly though, Grace states that ‘once the differences in their definitions [of competition] are taken into account, the two theories can be seen to be largely compatible and the remaining differences are comparatively subtle’.

Both Grime and Tilman work in northern temperate grasslands and rely on a combination of natural history surveys, experiments and modelling to characterize theoretically important sets of plant traits across a broad suite of species and relate them to environmental conditions. Their definitions of resource (exploitative) competition, which they emphasize more than interference competition, are virtually indistinguishable. Grime defines resource competition as ‘the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space’ (Grime 1973) and Tilman’s approach is ‘essentially identical to that stated in Grime’s definition’ (Tilman 1987a, p. 307). Although both also highlight inevitable evolutionary tradeoffs in differentiating species and state that understanding plant traits, resource acquisition and loss by plants, and the effect of disturbance on individuals holds the key to understanding patterns of diversity (Grime 1977; Tilman 1982), their theories remain to be reconciled.

The genesis of both Grime’s and Tilman’s ideas can be found in a relatively few key sets of papers and the theories show relatively little, though not unimportant, change over time. In order to clarify and evaluate their positions, this review will focus on the mechanisms by which nutrient and light supplies are partitioned and the advantages of different sets of traits along nutrient gradients, but will also discuss the importance of competition at different nutrient/disturbance combinations. After focusing on various aspects of Grime’s and Tilman’s assumptions, my aim is to advance the debate by laying a basic framework for understanding competition under different light and nutrient supplies, based on how plants lower the availability of resources by preempting their supplies.

Grime

GENESIS OF A THEORY

A mixture of experimental research and gradient analyses published from 1963 to 1968 set the stage for Grime’s theories on the interaction among plant traits and between plants and their environment. Grime’s early work (Grime 1963) centred on why some grassland plant species (calcicole species) are more abundant on shallow calcareous soils and others on deeper, more acidic, productive soils (calcifuge species). In the absence

of competition, both types of species grew better on the more productive soils (Grime 1963). Species that grow in areas of low nutrient availability have roots with low maximum specific rates of acquisition (Clarkson 1965), reinforcing the idea that it was not a greater ability of the slow-growing species to acquire resources that led to their dominance. Nor is it differential uptake in the presence of competition that eliminates fast-growing species from low-nutrient environments, but rather the extreme water stress on shallow soils (Grime 1963) or differential herbivory (Grime *et al.* 1968).

Grime (1973) first quantified the relationships between species traits and their relative abundance. Grassland species were each assigned a score reflecting variables such as relative growth rate and maximum plant height, and sites from six different habitat types were characterized by the average score of the species within the assemblage, weighted by their relative abundance. This average score correlated positively with site fertility, leading Grime to suggest that the low incidence of fast-growing plants in some sites might be due to environmental stress, such as drought or mineral deficiency. Alternatively, disturbances, such as grazing or mowing, might prevent fast-growing species from dominating, leading to distinction between plants of fertile, disturbed areas from those of fertile, undisturbed areas (Grime 1977).

A triangle of species and habitats was described, in which slow-growing species that inhabited low-fertility, low-disturbance sites were called ‘stress-tolerators’, fast-growing species that inhabited high-fertility, low-disturbance sites were called ‘competitors’ and fast-growing species that inhabited high-fertility, high-disturbance sites were called ‘ruderals’. Tradeoffs differentiated stress-tolerators from faster growing competitors with inherently higher mineral nutrient concentrations, lower allocation to defence and lower investment in leaves and cell walls, as well as between ruderals and competitors (via allocation to reproduction).

Grime described the differences among the three strategies in response to stress as follows:

‘... a crucial genetic difference between competitive, stress-tolerant and ruderal plants concerns the form and extent of phenotypic response to stress ... such differences constitute one of the more fundamental criteria whereby the three strategies may be distinguished ... the stress-response of the ruderal ensures the production of seeds, those of the competitor maximise the capture of resources, whilst those of the stress-tolerator allow the conservation of captured resources.’ (Grime 1979, p. 46).

The plant traits that defined these strategies are tightly linked to environmental conditions in the habitats where they predominate. The importance of specific plant traits could not be separated from the importance of processes in different habitats. Grime’s hypotheses cover the roles of competition, nutrient stress and disturbance and their predominance, as well as the evolution of

species and the assembly of communities, but I focus on his concept of how nutrient supplies are partitioned among root systems, with an emphasis on the heterogeneity of supplies, on how the theories changed to account for the suite of traits that are found in shade-adapted plants and, finally, on his characterization of the relative importance of stress, competition and disturbance in the sorting of local assemblages.

PARTITIONING OF THE NUTRIENT SUPPLY

According to Grime, competition for nutrients is a race to produce roots in areas of high nutrient availability, but low root occupancy, thus allowing a plant to preempt nutrients from competitors. At the beginning of a growing season, plants race to acquire a general pulse of nutrients throughout the soil volume where roots have not yet explored. After this nutrient pulse is acquired, the race for resources can also involve producing roots in such patches (requiring accurate placement and proliferation of roots) or responding quickly to a large pulse (requiring rapid production, with scale and accuracy dependent on the nature of the pulse). Once widespread availability declines, competition is minimal until a new pulse initiates a new race.

In situations where nutrient availability is high for short periods, or in small patches, but nutrients still limit production, Grime's approach to competition seems reasonable. Spatial and temporal heterogeneity in supplies of nutrients are critical: the heterogeneous nature of nutrient supplies is embedded in the experiments that Grime cites as reflecting the nature of competition for nutrients (e.g. Mahmoud & Grime 1976), with no discussion of situations where nutrients are supplied uniformly in space and time. For example, there is currently little evidence that in humid, temperate, nitrogen-limited grasslands the majority of the nitrogen supply is necessarily delivered in pulses nor that a high fraction of the nitrogen that a plant acquires is from patches (Wedin & Tilman 1990, 1996). Grime does not discuss the mechanisms that underlie the resource dynamics when root systems are not re-established every year and/or there are no major pulses or patches of supply. It is then assumed that uptake is negligible between pulses or patches, and the emphasis is therefore on conservation rather than acquisition. Competition for nutrients can, however, occur with homogeneously low nutrient supplies (see below).

THE STRESS OF SHADE

Grime's mechanism of competition for light is the production of leaves above competitors. With a unidirectional light source, pre-empting the supply becomes a race to the top. Placing leaves rapidly above those of other species requires a fast growth rate and high acquisition potential of both light and below-ground resources.

Grime recognizes that shorter plants suffer from resource stress, but is unclear whether plants with shorter

canopies that can grow and overtop plants with taller canopies should be considered better competitors for light. The role of resources in the growth of plants in shade has always been central to Grime's view of plant strategies. For instance, shade-adapted tree species in North America have leaves with lower specific rates of respiration, as well as lower relative growth rates in full sun, than non-shade-adapted species (Grime 1965). Grime proposed that shade-adapted plants do not acquire light better when light levels are low, but conserve their carbon or energy better:

'... physiological studies suggest that natural selection in deeply shaded habitats has been associated with the evolution of mechanisms of conserving energy rather than with those which increase the quantity of energy captured. In particular, it seems likely that low respiratory rates may be important in maintaining the carbon balance of plants exposed simultaneously to low light intensity and high temperature...' (Grime 1979, p. 27).

By 2001, however, Grime no longer supported the idea that the suite of traits associated with shade-tolerance had been selected for their role in C dynamics, but hypothesized that it is a response to competition for nutrients, leading to low nutrient availability to understorey plants (Grime 2001, p. 34). Focusing on the low nutrient concentrations of the leaves of understorey vegetation, he reasons that mature canopy plants require a high quantity of nutrients to sustain their high productivity, leaving little for the understorey. In addition, as a consequence of the low C availability associated with shading, understorey plants have limited potential for root growth and roots cannot escape the depletion zones that develop around them, leaving the plant nutrient-starved. Consequently, understorey plants are adapted not to conserve energy but to conserve nutrients.

This line of reasoning depends on the availability of nutrients to understorey plants being low in shaded systems. Coomes & Grubb (2000) show that root competition between understorey and overstorey plants can occur in shaded habitats. But, it does not prove that the suite of traits that defines shade-tolerant plants is a result of the need to conserve nutrients in the face of nutrient stress. For example, there are studies that show that removing root competition has no effect on understorey woody plants, while increasing light levels greatly increases growth (Putz & Canham 1992). Certainly, supply rates can exceed uptake by vegetation and depletion zones of mobile nutrients would not be so strong that nutrients would limit the growth of plants.

THE IMPORTANCE OF COMPETITION, STRESS AND DISTURBANCE

The one idea of Grime's that has been most controversial is that, for the purposes of assembly of communities,

the importance of competition is greater at high than at low nutrient supply. Grime uses Welden & Slauson's (1986) definition of the relative importance of competition, i.e. the relative reduction of growth or a physiological process relative to the total sum of reduction due to that factor and others that are being contrasted. It is assumed that factors are additive in their effect on plant performance (Haag *et al.* 2004).

On soils that provide a low nutrient supply, fast-growing species are expected to dominate immediately after a disturbance, but differential susceptibility to stress agents or preferential consumption eliminates them in favour of slow-growing species that are better able to conserve their resources in the face of such factors. Grime therefore states that 'the capacity of slow-growing plant species to dominate vegetation on infertile soils is related more to the ability to protect nutrient capital than to capture nutrients at low external concentrations. If above-ground productivity is the metric by which the importance of competition and nutrient stress are compared, experiments at Cedar Creek by Wedin & Tilman (1993) support Grime's assertion that the importance of competition increases with nutrient supply. Using Welden and Slauson's additive approach to competition and stress, decreasing soil N content reduced above-ground biomass of *Agropyron repens* six times more than did 5 years of competition with *Schizachyrium scoparium*. However, although N stress reduced the biomass of *Agropyron*, only competition eliminated it. Therefore, at low nutrient supply, competition was more important than nutrient stress in explaining its absence from plots where *Schizachyrium* was also present.

Even when interpreting patterns from Cedar Creek, Grime considers herbivory to be a factor that excludes fast-growing species from low-nutrient systems (Buckland & Grime 2000; Grime 2001; Burt-Smith *et al.* 2003). If species such as *Schizachyrium* dominate on infertile soils because herbivores eliminate faster growing species and thus reduce competition, then disturbance is more, rather than less, important in low-nutrient systems. A central tenet of Grime's theories therefore needs to be revised. Although Grime may have meant that disturbance does not affect the dominant stress-tolerators, if it removes competitors, then it is important for the assemblage of the community.

Grime's approach to light competition also needs to be revised. Once a plant's canopy is superior to those in

the same vertical plane, the competition for light is essentially over. Plants in the understorey must tolerate the shade and wait for disturbance. Although alluring, this view of light competition masks the complexity of interactions among individuals in partitioning light supplies (Peterson & Pickett 1995).

The key to this argument is whether shorter plants compete with taller plants for light. The asymmetry of light competition (Schwinning & Weiner 1998) dictates that, once canopies are vertically separated, shorter plants cannot reduce the supply of light to taller plants, but does this mean that competition for light is then over? The answer to this question depends on the potential for mutually negative effects and possibly vertically overlapping canopies in the future, as well as the time scale of analysis. Although two canopies currently may be disjunct, their relative vertical placement may change – an herbaceous plant that holds its canopy above a young woody plant will likely find the situation reversed the following year. If taller trees slow or stop increasing in height, shorter trees have the potential to enter the upper canopy and reduce light levels for the once-taller trees. If there is the potential for vertical overlap of canopies, then competition for light can extend to plants with vertically disjunct canopies.

If the potential for competition is extended across generations and considered at the population level (Grace 1990), then the potential for mutually negative effects on fitness can be extended to all individuals in a vertical plane. Beneath the canopies of shade-adapted species, light levels can be reduced to such a low level that shorter individuals, if they can grow at all, cannot put on enough height to enter the upper canopy without a disturbance to the canopy. Yet, competition still should be considered important as understorey plants may have a negative effect on the next generation of seedlings of the taller species.

In summary, there are five tenets of Grime's work that are incomplete, inconsistent or incorrect (Table 1). First, there is no discussion of the dynamics of ecosystems where nutrients are supplied more or less homogeneously over space and time, but at a low level. As such, nutrient-limited ecosystems are assumed to be dominated by plants that can tolerate low nutrient supply, while waiting for an eventual pulse. Second, disturbance is assumed not to be important at low nutrient supply, yet at the same time Grime asserts that

Table 1 Five tenets of Grime's theories that require review and the evidence against them

	Grime's theory	Evidence against
1	Nutrient supply is heterogeneous in space and time	Nutrient supply can also be uniformly low
2	Disturbance not important at low nutrient supply	Grime also asserts that disturbance is a mechanism that eliminates species at low nutrient supply
3	Competition is not important at low nutrient supply	Competition can eliminate species at low N supply
4	Elimination of individuals in shade is due to nutrient stress	More parsimonious explanation is that carbon economics determines patterns
5	Competition is unimportant in shade	If competition occurs at the population level then competition for light would remain important in shaded environments

disturbance is important in removing species from these same habitats. Along the same lines, competition is assumed not to be important at low nutrient supply, but it is known that the presence of competitors can eliminate species associated with more fertile habitats when they grow at low nutrient supply. It has been countered that the low nutrient supply rate at which competition was assessed was not low enough (Thompson 1987), but minimum nutrient supplies required for positive growth have not been compared across species. Fourth, Grime now contends that the dynamics of plants in shade is driven by nutrient deficiencies. Yet, the hypothesis that the traits of species that dominate shaded habitats and the dynamics of assemblages there are driven by energy/carbon economies cannot be rejected, and may provide a more parsimonious explanation of patterns. Lastly, Grime also contends that competition is unimportant in shaded habitats. Although the stress of shade may eliminate many species, there is no discussion of how to accommodate the asymmetric nature of light competition and the potential for light competition in the future, which would maintain its importance in shaded habitats.

Tilman

THE GENESIS OF A THEORY

Like Grime, Tilman's theories can be better understood by examining his early research. Tilman (1977) sought to explain the patterns of two species of diatoms in Lake Michigan by understanding competition for two nutrients (Si and P). Nearshore and open-lake environments, which had, respectively, low and high Si : P ratios, were dominated by different diatoms. Using chemostats, Tilman manipulated the supplies of Si and P to cultures of the two diatoms growing in monoculture and together. He hypothesized that the species that had the higher relative growth rate in monoculture at a given resource supply ratio would be the better competitor at that ratio of supplies. As a consequence of different resource requirements, the diatom with the higher rate of growth at a given supply ratio should lower concentrations in solution below that necessary for sustained growth of other species, and therefore become dominant. Tilman found such patterns were observed when the supply of the nutrient was limiting to both species (Tilman 1976; Tilman 1977).

Based on this empirical evidence, and contemporary ideas regarding the roles of resources in production and competitive outcomes (Greeney *et al.* 1973), Tilman hypothesized that the key to competition for a given nutrient was reducing the concentration in solution below the level that was necessary for the populations of competitors to maintain themselves. Using the Monod model of growth as a framework (Monod 1950), this minimum concentration was called R^* .

Tilman (1990; p. 123) has described R^* in the following manner:

' R^* is the level to which the concentration of the available form of the limiting resource is reduced by a monoculture of a species once that monoculture has reached equilibrium i.e., once it has attained its carrying capacity ... Thus, R^* is the concentration of available resource that a species requires to survive in a habitat ... If all species are limited by the same nutrient, the species with the lowest R^* is predicted, at equilibrium, to displace all competitors.'

APPLYING THE THEORY TO TERRESTRIAL SYSTEMS

When Tilman began working in terrestrial systems, he sought to identify the ends of a successional series at Cedar Creek Natural History Area in Minnesota, where post-agricultural, low-productivity grasslands of different ages are interspersed in a matrix of oak savanna and closed-canopy oak forest. Instead of differing in soil depth and parent material, these sites were all derived from the same glacial outwash sand. The grassland species were primarily limited by N, which had been reduced by agriculture to approximately 50% of its original value (Tilman 1982). Over time, soil N content increased in the abandoned fields, leaving a successional gradient of young fields with low soil N content, older fields with higher soil N content, and native savannas and forests with the highest soil N content.

Tilman hypothesized that the successional sequence was driven by changes in soil nutrients and therefore the ratio of nutrient and light supplies (Tilman 1982, 1985). Plants that occupied low-N : light environments were postulated to be better competitors for N and those that occupied high-N : light environments were better competitors for light. Following the theory derived from the diatom research, competitive outcomes were predicted to depend on 'the requirements of the species for limiting resources and the availabilities of the resource' (Tilman 1985, p. 846). Tilman equated the successional sequence with N supply and assumed that competitive interactions determined their relative abundance. Early successional fields had the lowest soil N content, and were dominated by species such as *Ambrosia artemisiifolia-elatior* and *Agropyron repens*. It was assumed that these species required less N per unit light, had higher growth rates at low N and were able to extract more N from the low-N soils, thus leading to competitive superiority for N. Species, such as *Schizachyrium scoparium*, which appeared later in succession, were assumed to occupy habitats with high N availability and be better competitors for N. These species were hypothesized to require more N per unit light, have higher growth rates at high N and reduce light levels more than 'early' successional species.

When individual plants were grown for 12 weeks across a soil N gradient (Tilman 1986a), early successional species such as *Ambrosia* acquired more N than late successional species, consistent with the resource ratio hypothesis. Just as with diatoms, better competitors

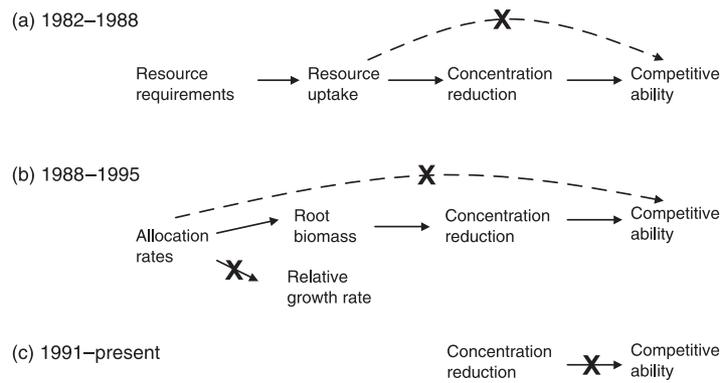


Fig. 1 The progression of the theories of Tilman regarding the relationships between plant traits, resource availability and competitive ability. An ‘X’ indicates that the pathway was falsified and would reject the causal set of mechanisms.

for nutrients grow faster at a given resource supply and, as a result, better lower the availability of nutrients. Yet late successional species, such as *Schizachyrium scoparium*, were not growing faster at high soil N content than early successional species: they were bigger across the entire soil N content gradient. Either the link between growth rates and competitive ability was wrong, the successional sequence was misunderstood and/or competition did not determine relative abundance at higher soil N contents. With this departure from theory, Tilman offered alternative hypotheses to explain the lower growth rates of the late successional species at high soil N content, including the late successional *Schizachyrium* being less susceptible to herbivory than early successional species in soils with high N content.

In analyses of 4 years of growth of plants in natural assemblages that had been fertilized at different rates with N (Tilman 1987b), it was still assumed that fast-growing, early successional species are better competitors for N than late successional species. However, although the short-term pot studies had supported the resource ratio hypothesis at just one end of the gradient, the N fertilization experiment did not support the hypothesis at either end. An early successional species (*Agropyron*), which had one of the highest relative growth rates in soils with low N content, dominated at high N supply. A late successional species (*Schizachyrium*), with one of the lowest growth rates on low-N soils, dominated plots with low N addition rates. The link between resource requirements, uptake rates and competition was beginning to look tenuous (Fig. 1a).

A SHIFT TO ALLOCATION AMONG ORGANS

Thompson (1987) suggested that ‘early colonists of most secondary successions owe their success firstly to good dispersal or a long-lived seed bank and secondly to rapid growth and reproduction under conditions of plentiful resources and low competition’. As an alternative to differences in competitive ability, Tilman & Cowan (1989) presented differences in colonization ability from the outset as an explanation for the lack of competitive success of early successional species. Plants

may be present early in succession either as a result of superior competitive ability when soil N is low or because the greater colonization ability of early successional species leads to ‘transient dynamics’ that maintain poorer competitors. As before (Tilman 1986a), eight herbaceous species were grown in pots in the field across a range of soil N content, but there was now intraspecific competition as plants were grown at two different densities for two growing season rather than just one. On the low-N soils, early successional species, such as *Agrostis scabra*, were found to have higher relative growth rate (RGR), lower root : shoot ratios, high yield and greater allocation to seed (Tilman & Cowan 1989). Although similar results were obtained, the interpretation was the opposite to that made previously, with early successional species being ‘inferior competitors for nitrogen’. How could traits, such as high RGR on low-N soils, that once implied competitive success for N, now be interpreted as traits of an inferior competitor for N?

Although not officially refuted, the ALLOCATE model (Tilman 1988) replaced both previous models, removing resource requirements as the centre of theory in favour of allocation among (rather than within) organs. Observations of biomass fractions of plants showed that mature C₄ grasses like *Schizachyrium*, which dominate many of the older successional grasslands, had a high fraction of biomass in roots and, as a result, were competitively superior for N in long-term experiments. Trees have a large fraction of their biomass in stems and leaves and, as a result, dominate relatively undisturbed environments with high N supply.

With ALLOCATE, the differences in species were not a result of differences in the ratio of demand, but of allocation, leading to differential ability to reduce the concentration of nutrients in soil solution and the availability of light at different heights. It did not focus on differences in resource growth, but on differences in resource availability reduction, thus increasing the level at which the mechanism behind the theory operates. Plants that allocate a large fraction of their biomass to roots are best able to reduce concentrations of nutrient in soil solution and are thus the best competitors when nutrients are limiting. Under ‘ideal’

conditions, these plants would grow slowly because they are allocating resources away from energy acquisition and towards heterotrophic roots. Plants that allocate a large fraction of their biomass to stems and leaves are best able to compete for light. They too would grow slowly under 'ideal' conditions because of their high allocation to heterotrophic stems. When competition is low, as when non-selective removal of biomass is high, plants that allocate the highest fraction to leaves would be favoured, and allocation predominantly to organs that acquire energy would lead to high RGR.

Gleeson & Tilman (1990) found support for the allocation-centric version of the resource ratio hypothesis in biomass ratios of plants along successional sequence of old fields at Cedar Creek. Rather than early successional plants growing faster and acquiring more N at low-N soils because they are superior competitors for N, their high RGR was taken to imply that they are transients. Sixty years after cessation of disturbance, the assemblage is dominated by slow-growing plants, such as *Schizachyrium*, that have a high fraction of biomass in roots and, presumably, allocate a large fraction of biomass to roots. The link is stated clearly: over the long-term, such species are 'superior nitrogen competitors because of higher root allocation' (Gleeson & Tilman 1990, p. 1144).

Shipley & Peters (1990) questioned this link between allocation and maximum RGR. Tilman (1991b) responded that the relationship between RGR and growth rate was a prediction of the ALLOCATE model, not an assumption. Yet, if a model produces a flawed prediction, then something must be flawed with the model (Shipley & Peters 1991). Tilman (1985) had himself asserted that his formulation of the resource ratio hypothesis 'can be rejected if any of these interrelated predictions is not supported by observational or experimental evidence'. Tilman then asserts that there is no need for allocation rates and RGR_{max} to be associated. Apparently, RGR_{max} now has little to do with competitive outcomes, and data from Poorter (1989) are cited to minimize further the importance of allocation between organs relative to within organs. The statement that 'leaf area ratio may thus be a better measure of allocation to photosynthesis than percentage leaf mass' (Tilman 1991a, p. 1270) is a marked reversal from earlier views, such as the assumption that 'species-to-species differences in morphology [i.e. allocation] are much greater than species-to-species differences in nutrient- or light-saturated rates of photosynthesis per unit biomass or respiration rates per unit biomass. This assumption is probably a valid first approximation.' (Tilman 1988, p. 60). In response to Shipley & Peters, Tilman (1991a, p. 1271) states that there are 'equally interesting and important trade-offs that plants face in allocating protein (i.e. nitrogen) to alternative physiological functions.' Apparently, not only does RGR_{max} have little to do with competition, but the morphology of leaves and roots has as much to do with competition as does allocation.

Tilman attempted to match RGR_{max} and relative allocation rates one more time (Gleeson & Tilman 1994) and, in the end, repudiates the central importance of allocation among organs. On seedlings in the greenhouse over a 2-month period under fertilized conditions, there was no relationship between relative allocation to root, leaf and stem and RGR_{max} . This is in contrast to the field studies in which slow-growing plants had a high fraction of biomass in roots, interpreted as high allocation to roots. Moreover, in the RGR experiment, late successional plants allocated less to roots rather than more. The stark contrast led Gleeson and Tilman to conclude that 'seedlings may have markedly different allocation than adults'. Although differences in longevity among roots of North American grassland species had long been known (Weaver & Zink 1945), and biomass fractions may be determined by differential longevity (Craine *et al.* 2002), the authors still asserted that allocation is important, but it exhibits high plasticity and therefore relative allocation rates are not 'fixed species attributes that determine growth rates' (Gleeson & Tilman 1994, p. 543). With relative allocation rates defining neither competitive ability nor differences in RGR (Fig. 1b), resource use efficiencies are offered as the key to understanding 'growth rate, optimal allocation, and potentially competition and succession' (Gleeson & Tilman 1994, p. 543).

THE DECLINE OF CONCENTRATION REDUCTION

Tilman's research can be considered an excellent example of using hypothesis testing to drive the development of scientific theory. However, if theories are to be considered mechanistic, they must remain mechanistic as they are revised. Research on diatoms led Tilman to propose that resource use requirements determined RGR and thus the ability of plants to lower resource concentrations, i.e. the concentrations of available resources in the environment determine competitive outcome at that supply rate. By 1994, Tilman had piece by piece reduced this theory, as applied to terrestrial plants, until all that was left was a metric derived from models that were based on linkages that were no longer valid.

Instead of reformulating the theories to incorporate differences in species in their construction and activity of organs, Tilman resets the standard, suggesting in 1991 that 'Recent work suggests that it may be unnecessary to measure all the morphological and physiological parameters in such models to predict the outcome of nutrient competition. Rather, a single number, R^* (the concentration of a limiting nutrient in a monoculture of a species at equilibrium), may integrate the effects of morphology and physiology on nutrient competitive ability' (Tilman 1991a, p. 1272). No viable model is left to suggest that concentration reduction is the mechanism of competitive outcomes, yet it is offered as the foundation of a theory of plant competition.

Although poorly tested, there is no doubt that R^* can predict some competitive outcomes (Tilman & Wedin 1991; Wedin & Tilman 1993), but its central role should be questioned. To begin, the theoretical mechanistic basis of R^* has been discredited and no viable model has been offered to replace it. Second, although R^* predicted competitive outcomes for six grasses, *Solidago rigida*, which is dominated by C_4 grasses in the absence of selective herbivory, both in experiments (Reich *et al.* 2001; Hille Ris Lambers *et al.* 2004) and in native assemblages (Weaver 1968; Inouye & Tilman 1995), has consistently lower R^* for NO_3^- than the C_4 grasses (Reich *et al.* 2001; Craine *et al.* 2002, 2003). Lastly, the theoretical dependence of uptake on average soil solution nutrient concentrations is unrealistic (Raynaud & Leadley 2004; Craine *et al.* 2005). Nutrient uptake by roots is determined by the concentrations of nutrients at the root surface, which may or may not correspond with the average soil solution concentrations.

With the final link between average soil solution concentrations and competitive outcomes severed (Fig. 1c), there is no unified theory relating plant traits, availability reduction and competitive outcomes. There might be remaining axiomatic notions that plant traits affect the availability of resources in the environment and it is the reduction of availability that determines competitive outcomes, but the robust, mechanistic set of theories that Tilman had developed has disintegrated. Even if reduction in concentrations was the mechanism behind competition for nutrients, it is not clear what the linkages are between plant traits, growth and supplies that allow plants to reduce concentrations below the level required for growth of competitors. Neither differences in uptake rates at a given supply ratio (Tilman 1986b) nor differences in allocation rates (Gleeson & Tilman 1994) are associated with long-term competitive success. At best, R^* is a useful correlate of factors that lead to long-term competitive success, but detailed studies of uptake suggest that reduction of average concentrations is not the mechanism of competitive dominance (Craine *et al.* 2005).

Reconciliation and synthesis

It is surprising how little research has addressed the mechanisms that underlie the theories of Grime and Tilman. For example, no research outside of Cedar Creek has tested the concentration reduction hypothesis in terrestrial ecosystems by measuring soil solution nutrient concentrations. This is not to discount the large body of work on related topics such as the phenomena of importance and intensity of competition among species in different habitats (Goldberg *et al.* 1999; Rajaniemi *et al.* 2003; Brooker *et al.* 2005). Also, tradeoffs have been observed in competitive ability for nutrients and light (Keddy *et al.* 2000; Groves *et al.* 2003; Fynn *et al.* 2005) and other mechanisms by which plants affect relative abundance, such as allelopathy (Callaway & Aschehoug 2000) and litter feedbacks to nutrient cycling (Aerts 1999; Suding *et al.* 2004), have been tested. Although this research does test hypotheses of Grime and Tilman, it is generally associated with derivative hypotheses, i.e. above the level of mechanism that represents their core theories, and therefore lies outside the purview of this discussion.

Although neither the theories of Grime or Tilman nor a union of the two are sufficient for explaining resource competition, their different assumptions complement each other and serve as an important point of departure for constructing new theories (Table 2). Tilman focused on uniform resource supplies while Grime emphasized patches and pulses of resources. Competition for light and nutrients was a race to the source for Grime, but a slow reduction of general availability for Tilman. For Grime, disturbance was selective while Tilman primarily focused on non-selective disturbances. By 1988, Tilman focused on tradeoffs in allocating resources among organs in explaining species differences while Grime had consistently focused on tradeoffs associated with the construction of individual organs. For Grime, stress or disturbance explained the absence of species from habitats, while for Tilman competition (and later colonization) explained absences with stress and disturbance affecting the nature of

Table 2 Key differences between Grime and Tilman as related to mechanisms of competition for light and nutrients

	Tilman	Grime
Characterization of N supply	Uniform in space and time	Pulses and patches
Mechanism of competition for N	Concentration reduction	Preemption of pulse/patch
Traits of species in low-N habitats	High allocation to roots	Low nutrient concentrations, high defensive allocation
Mechanism of competition for light	Reduction of availability	Race
Traits of species in shaded habitats	High allocation to stems and leaves	Low nutrient concentrations, high defense
Characterization of disturbance	Non-selective	Selective
Causes for difference among species in relative growth rates	Allocation among organs	Allocation within organs
Determinants of assemblages with low N supply	Competition for N	Selective disturbance and growth rate
Determinants of assemblages in shade	Competition for light	Selective disturbance

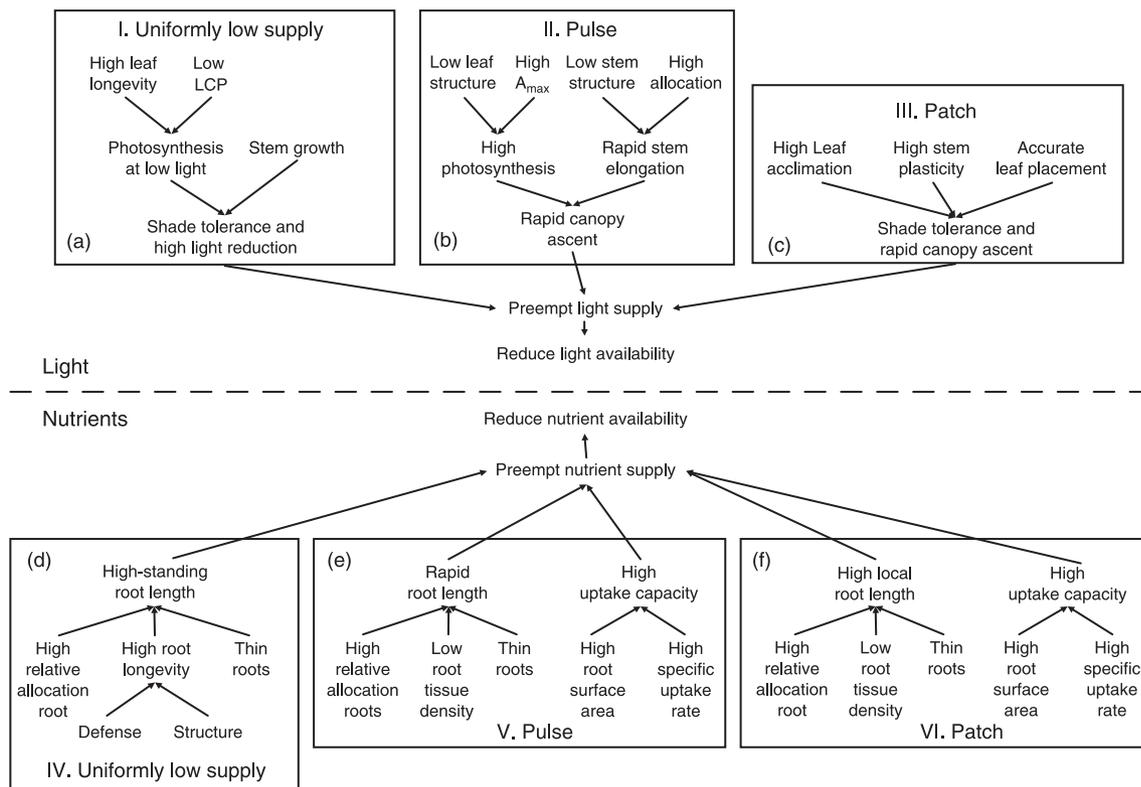


Fig. 2 Six scenarios for light (scenarios I–III; a–c) and nutrient (scenarios IV–VI; d–f) competition under uniform, pulsed and patchy supplies. Included are the proximal mechanism of supply pre-emption and distal processes or traits that determine supply pre-emption. Abbreviations: LCP, light compensation point; A_{max} , maximum photosynthetic rate.

competition. Much of the apparent debate that was generated between Grime and Tilman came as a failure adequately to reconcile these contrasting but compatible aspects of plant and ecosystem function.

To begin to reconcile and improve the theories of plant competition, it is important to begin by addressing the core principle of resource competition: the reduction of the availability of resources by one plant to another. Although plants successfully acquire the majority of their resource supplies by pre-empting supplies from competitors, the mechanism depends on the nature of the supply. With two resources (nutrients and light) being supplied uniformly in space and time, in patches or in pulses, six main scenarios for competition arise (Fig. 2).

COMPETITION FOR LIGHT

Pre-empting the light supply and reducing light availability to competitors requires leaf area dominance (Fahey *et al.* 1998), i.e. producing and maintaining high leaf area above competitors. When a stand experiences a pulse of light availability near the soil surface following a disturbance (scenario II), competition takes the form of a race centring on rapid ascension of the canopy (Fig. 2b). Pre-empting the light supply requires producing high leaf area quickly to avoid the lower light levels beneath the canopy. Because stems elongate rather than below the current canopy, new leaves must

continue to be produced rapidly as older leaves become shaded and no longer contribute to leaf area dominance. Low tissue density in leaves is favoured in order to maximize leaf area production rates – the high leaf longevity that accompanies high tissue density is of little advantage in a race for height. Stems must also elongate at a high rate, but the cost advantage of low tissue density must be balanced against the fact that it would limit the maximum height and increase susceptibility to disturbance. The race for light continues among neighbouring plants until ascension slows or stops due to endogenous factors and/or disturbance resets the race.

Once canopies are differentiated in height, plants under the upper canopy can experience uniformly low light levels (scenario I, Fig. 2a). Only plants able to grow at the low light levels can supercede the now stationary upper canopy (intragenerational competition), or be in a good position to respond when the canopy is disturbed (intergenerational competition). Grime advocated that shade plants rely on sunflecks and that shade-tolerant plants are better competitors for nutrients. A more parsimonious explanation is that shade-adapted plants are able to grow better at low light levels (or maintain themselves at very low light levels) as they have low whole-plant light compensation points (cf. Grime (1979) regarding conservation of energy). The leaves of shade-adapted plants have low nitrogen concentrations (Walters & Reich 1999), resulting in low

dark respiration rates and allowing plants to have net photosynthesis at a lower light level (Lusk 2002; Craine & Reich 2005). This low light compensation point extends to the whole plant as a consequence of low allocation to heterotrophic tissues (Reich *et al.* 2003). Shade-adapted plants do not just tolerate shade better, they actively grow better at low irradiance levels. The low light compensation point allows plants to maintain higher leaf area and cast deeper shade, which limits the ability of species with higher light compensation points (and seedlings of the same species) to establish beneath their canopies. The lower leaf light compensation point comes at a cost of high maximal rates of photosynthesis, which limits growth rates after a pulse of light availability.

Patches of high light supply (scenario III, Fig. 2c) are always temporary and, when gaps are large, the dynamics function effectively as with pulses (Fig. 2b). As Grime (2001) details, patches on the order of the size of the canopy of a plant require leaves to be projected accurately. As leaves fill the gap, they pre-empt the supply from shorter plants, assisting the race to reach the canopy before the gap is filled by taller neighbours. As plants in gaps experience variation in light supply with long periodicity, plasticity and acclimation in leaves and stems are emphasized (Bazzaz 1996).

COMPETITION FOR NUTRIENTS

Nutrients are supplied from all sides of a root and diffusion rates of nutrients in soil solution are low. Whether nutrient supplies are uniform, in patches or pulses, supply pre-emption requires root length dominance, having high root length of sufficient uptake capacity.

In a soil where a nutrient is supplied uniformly in space and time (scenario IV, Fig. 2d), but still remains the limiting resource, the focus on root length is generated from the low diffusion rates of nutrients in soils. As uptake capacity exceeds diffusion down the concentration gradient to the root surface (Tinker & Nye 2000), depletion zones extend outward from the root. When the depletion zones of two roots overlap, the roots are, by definition, competing for the same nutrients. Ensuring that its roots are closer to the points of supplies relies on a plant producing and maintaining high root or mycorrhizal length of sufficient uptake capacity. The greater the root length in a unit of soil volume, the greater the fraction of the nutrient supply that plant will acquire (Smethurst & Comerford 1993; Hodge *et al.* 1999; Raynaud & Leadley 2004). By maintaining a high fraction of the total root length in the soil, a plant can pre-empt the majority of the nutrient supply from competitors (Craine *et al.* 2005) and traits such as low root diameter, high allocation rates to roots and high root longevity, all of which increase the standing root length, become important. Plants might build up root length by having a low initial rate of biomass loss in the face of stresses or disturbances (stress tolerance, *sensu* Grime). Yet, a plant does not necessarily pre-

dominate habitats with low nutrient supplies simply because it tolerates the low supply while waiting for a pulse. It would actively grow at low nutrient supplies, allowing it to acquire increasingly greater fractions of the nutrient supply over time.

When nutrients are supplied heterogeneously in space (i.e. in patches, scenario VI, Fig. 2f), but uniformly over time, the reduction of availability still occurs through pre-emption of the supplies (Hodge *et al.* 1999). The greater the fraction of total root length in a patch a plant possesses, the greater the fraction of the nutrient supply it will acquire. High allocation to thin roots of high longevity should be favoured, as in the homogeneous scenario, although root length must now be deployed accurately. Whether specific uptake capacity becomes more important in patches than under uniform supplies will depend on whether soil solution nutrient concentrations at the root surface end up higher.

When nutrients are supplied in pulses that are uniform in space (scenario V, Fig. 2e), pre-emption of the supply takes the form of a race to take up nutrients that have already entered the soil solution. Although it is possible that the best way to pre-empt a pulse of nutrients is to have an extensive root system already in place, increased time between pulses will lead to maintenance costs exceeding both the costs of producing a new root system and the benefits of the nutrients acquired from the pulse. Competition for nutrients from a large, infrequent pulse therefore centres on the ability rapidly to produce root length of sufficient uptake capacity. Low root tissue density is one trait that would allow faster root length production with little performance cost, as there is little advantage to the greater root longevity that accompanies high tissue density.

THE WAY FORWARD

The six scenarios of light and nutrient competition help to bring together and contextualize important aspects of the theories of Grime and Tilman. How resources are supplied and the reduction of availability through pre-emption of supplies is critical for long-term productive understanding of resource competition. For example, it is uncertain whether competition for nutrients primarily occurs among plants or between plants and microbes (Hodge *et al.* 2000; Schimel & Bennett 2004). Under what conditions, after removal of the upper canopy, will established shade-tolerant plants dominate new seedlings with high photosynthetic rates?

Further development of theories of the dynamics of plant assemblages will entail incorporating specific stresses, non-selective and selective disturbances and regeneration dynamics, as well as broadening the integration of other plant traits such as defences and acquisition strategies for non-limiting resources. By drawing on the complementary ideas of Grime and Tilman, as well as others, and pursuing experimental, theoretical and conceptual advances, a more complete understanding of resource competition can be obtained.

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