

## Plant strategy theories: replies to Grime and Tilman

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### Summary

**1** In response to my essay review that attempted to reconcile the plant strategy theories of Grime and Tilman, Grime rejects five tenets that I had identified in his theories that were incomplete, inconsistent, or incorrect.

**2** Grime fails to adequately address three of these concerns. Regarding the other concerns, it is clear that the concept of relative importance needs to be developed further. For example, if both competition and the stress of low nutrient supplies can remove species from a given environment, then neither can be elevated over the other without being tautological.

**3** With regards to Tilman's response, it is clear that it will be important to be explicit about the relationship between data and models. At times, Tilman is neither evaluating individual models with a Popperian approach nor comparing contrasting models in a Bayesian fashion. As it stands, it is unclear what is required for Tilman to reject  $R^*$  as the mechanism of competition, or whether it passes some undetermined threshold of acceptability.

**4** Comparing concentration reduction to supply pre-emption as the mechanism of competition recommends supply pre-emption on many fronts. Supply pre-emption better represents the movement of nutrients in soil solution. Assuming well-mixed soil solutions can theoretically lead to improper prediction of competitive outcomes. Empirically, there are examples where  $R^*$  does not predict outcomes for competition for nutrients, and supply pre-emption appears to generate metrics (root length density) that are equivalent if not better than concentration reduction ( $R^*$ ) at explaining these outcomes.

**5** The next plant strategies paradigm will not be a result of choosing either Grime's or Tilman's theories, but represent a synthesis of the two sets of theories while also incorporating novel concepts and research. I agree with Tilman that more research is needed in understanding mechanisms of coexistence, but there still remains large gaps in our understanding of plant traits and growth that limit our understanding of competition for nutrients and will likely constrain our understanding of coexistence even more.

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Both Grime and Tilman had developed exemplary, broad-reaching theories regarding natural selection, the strategies of plants, and the functioning of ecosystems. Yet, as I reviewed their theories and worked to understand them, I identified inconsistencies between the two sets of theories as well as other assumptions that needed revision, as would be expected in any attempt to characterize such broad patterns. In response to my review of their theories (Craine 2005), and to their credit,

both Grime and Tilman took the time to respond in a manner that portends progress on a recalcitrant issue. Below, I address their comments separately to continue to further the discussion on the issues and hopefully encourage more empirical and theoretical research.

### Response to Grime

In my previous review (Craine 2005), I discussed five areas where Grime's theories could be improved. In his comment on that review (Grime 2007), Grime does not sufficiently address three of these points and for the

other two, his arguments appear untenable. Although, I believe that a new paradigm for understanding the roles of competition, stress, disturbance and the evolution of suites of traits in plant species is imminent, I prefer not to extend my comments at this time beyond my original five points. In my brief response to his comment, I will continue to focus on only nutrients and light as resources, and limit stresses to those of nutrient supply and shade.

With regards to my first point, Grime ignores the questions of what plant strategy would be associated with acquisition of nutrients that are supplied at a low rate that is uniform over space and time. Grime's hypotheses assume that nutrients are either supplied in patches of high availability, which his 'competitors' are best adapted to acquire, or as infrequent pulses, which his 'stress-tolerators' are best able to acquire after tolerating the intervening stress of low nutrient supplies. If nutrients are supplied at a low and uniform rate, then his characterization of stress-tolerators begins to unravel. It was my contention that species that he considers stress-tolerators have the suite of traits that best allow them to compete for nutrients when supplied at a low and uniform rate. In the absence of pulses, these species are best at reducing the availability of nutrients to neighbouring plants, making them the best competitors for nutrients (Craine *et al.* 2005).

Regarding my fourth point, Grime does not meaningfully address whether the growth of understory vegetation under shade-tolerant trees is controlled more by nutrient stress or by carbon stress. As Grime alludes, there is no doubt that understory vegetation can be co-limited by light and nutrients. Yet, the focus on the potential interaction between light and nutrient availability distracts one from the shift to greater limitation by light than nutrients as secondary succession proceeds and nutrient supply increase. For example, beneath the intact canopy of a stand of eastern hemlock (*Tsuga canadensis*), understory vegetation is generally absent. The light levels are so low that other species cannot maintain positive net photosynthesis, regardless of the nutrient supply. Although trenching (and the relief from nutrient competition from taller trees that accompanies it) can increase growth of understory vegetation under some situations, the cases cited by Coomes & Grubb (2000) suggest that when light levels are at their lowest, growth increases little in response to trenching, but increases greatly in response to addition of light to the understory.

For my fifth point, Grime does little to address whether his theories can accommodate plants that can tolerate the stress of shade and eventually overtop faster growing, less shade-tolerant species being better competitors for light. As stated in his comment, he had acknowledged that this scenario can occur, but he never incorporates this into CSR theory. For example, tree species such as eastern hemlock have traits that are associated with stress-tolerators, such as high leaf longevity and low maximal rates of photosynthesis. Yet, over long time-scales in the absence of disturbance, species such as

eastern hemlock are better able to pre-empt light from faster growing species that Grime considers the best competitors for light. Eastern hemlock accomplishes this not just by tolerating shade while in the understory waiting for a gap in the canopy, but by actively growing better in that shade due to their low whole-plant and leaf light compensation points (Craine & Reich 2005). In this case, some species that would be considered stress-tolerators are, in fact, the best competitors for light.

The other two tenets that I raised regarding Grime's theories both hinged on the concept of 'importance' in plant ecology. Grime had recently written, 'the importance of competition for resources as a determinant of the admission or exclusion of species from communities reaches a maximum under productive conditions and declines on highly infertile soils.' (Grime 2001, p. 40). With this in mind, I stated that Grime had ignored evidence that competition can be important in explaining the absence of species from communities when nutrient supplies are low. I also stated that Grime was inconsistent about the importance of disturbance at low nutrient supplies. On the one hand, he stated that disturbance is unimportant at low nutrient supply, but also stated that herbivory (something that Grime rightly considers a disturbance) was important for removing species at low nutrient supply. In his comment, Grime charged that my use of the term 'important', 'abandons completely the classical distinction of Welden and Slauson between ultimate and proximal determinants'. Grime also states that 'the ultimate selective mechanism responsible for the traits of the stress-tolerator, including its defensive characteristics, is the low availability of mineral nutrients.' With these and other statements, Grime fails to separate the many applications of importance. Welden & Slauson (1986) use 'importance' to mean the effect on a given process due to one factor relative to the total effect due to all processes. With regards to ultimate and proximal determinants, Welden and Slauson actually inveigh against invoking predominance of one cause over another *a priori*. The closest Welden and Slauson come to a separation between proximal and ultimate is in their separation of time scales of importance. For example, they recognize that a given factor could be important in reducing the immediate growth of a plant, but have little effect on its evolution.

In ecological time, competition can reduce the growth of plants in ecosystems with low nutrient supplies more than herbivory. Using herbivory as the comparative factor, Grime has stated that 'although competition, especially that for water and mineral nutrients, is not restricted to productive habitats, its importance in unproductive habitats is small relative to the ability to conserve the resources which have been captured and to resist the severe hazards to survival (e.g. herbivory, extreme climatic events) which characterize many infertile environments.' (Grime 2001, p. 39). From Wedin & Tilman (1993), it is clear that competition can be more important than herbivory in explaining the absence of fast-growing species from ecosystems with low nutrient

supply. In soils with low N content, *Agropyron repens* persisted, but was extirpated when grown in competition with *Schizachyrium scoparium*. Therefore, it would be incorrect to state that disturbance was more important than competition in reducing the growth of *Agropyron* in this example.

With regards to competition and nutrient stress, competition could be considered unimportant if the stress from low nutrient supply is considered to reduce the growth of species more than the reduction in nutrient availability due to competition. In his comment, Grime writes, 'Even if it could be established without doubt that competition was responsible for the last fatal step in the failure of *Agropyron* this does not diminish the importance of soil infertility as the dominant factor that has made the final extinction events possible.' Nutrient stress in the absence of competition only predominates over the nutrient stress caused by competition if the importance of nutrient stress in the absence of competition is tautologically elevated *a priori*. Imposing an order on the effects, such that low nutrient supply decreases growth first and then competition reduces it further, conceals the potential for an interaction or redundancy between competition and nutrient stress.

When the reductions in growth due to low nutrient supply are considered before competition, it is true that in the Wedin and Tilman *Agropyron-Schizachyrium* example, low nutrient supply would be calculated to be more important than competition. Yet, I had not mentioned that in the Wedin and Tilman experiment, at higher soil N content, *Schizachyrium* eliminated *Agropyron*. Just as it could be stated that the presence of competition had little impact on growth when compared with nutrient supply by assigning pre-eminence to low nutrient supplies arbitrarily, it could also be stated that reductions in nutrient supply are unimportant. At a given nutrient supply, competition is enough to remove the other species and further reductions in nutrient supply have little bearing on the outcome. It is impossible to separate the importance of competition and nutrient stress on growth in a situation where there is the equivalent of a statistical interaction between factors.

In support of the idea that stress-tolerators are poor competitors for nutrients, Grime cites numerous experiments that he has helped conduct. Yet, the results of these experiments are inappropriate for understanding nutrient competition in the absence of disturbance as they are a product of (i) short timeframes of experiments and (ii) nutrients being supplied in a manner that is not representative of ecosystems with low nutrient supplies. The six experiments that Grime cites in his comment (Grime & Curtis 1976; Mahmoud & Grime 1976; Grime *et al.* 1987; Campbell & Grime 1992; Fraser & Grime 1999; Buckland & Grime 2000) averaged only 16 months and none were longer than 24 months. Slow-growing species require multiple growing seasons to build their root systems (Craine *et al.* 2003) and become effective competitors for nutrients that are supplied at a low, uniform rate. The experiments he cited generally added

nutrients in short, high concentration pulses as opposed to slow, steady supply. By adding pulses of nutrients, there would be little time for depletion zones to develop around roots and concentrations at the root surface would be relatively high, favouring plants with roots with high uptake capacity.

Lastly, it is clear that competition has been important in low nutrient ecosystems during the evolution of Grime's stress-tolerators. Stress-tolerator plants such as the bunchgrass *Schizachyrium scoparium* are built to compete for nutrients. By producing thin roots with low nutrient concentrations that live a long time, these plants can amass root systems with high root length density. There is no advantage of dense root systems for nutrient acquisition in the absence of competition for relatively mobile nutrients such as nitrate (Craine 2006), and these large root systems would come at the expense of reproduction. High root length density allows plants to compete effectively for nutrients against other plants because the high root length density pre-empts low, uniform nutrient supplies from competing plants.

### Response to Tilman

There are few who have championed the use of analytical equations and rigorous experimentation in ecology more than Tilman. Upon examining the trajectory of Tilman's theories over time and his characterization of them in his response (Tilman 2007), I agree with Tilman that more attention is needed between empirical data and analytical models, hypotheses and theories.

#### ON THE RELATIONSHIP BETWEEN THEORY AND EMPIRICAL DATA

There are two approaches to the relationship between empirical data and models. The first approach is Popperian (Popper 1979; Hilborn & Mangel 1997). With the Popperian approach, theory is embodied in numerical or analytical models. Models are used to make predictions. If the predictions are not supported, the model, but not necessarily the theory, is rejected. When rejected, the model should be revised and tested anew. The second approach is Bayesian or one of likelihood, which I will refer to just as Bayesian (Hilborn & Mangel 1997). With the Bayesian approach, alternative models are tested and acceptance is probabilistic. Theories are still embodied in models. Models make their respective predictions. Whichever prediction is more likely to be true or whichever model best explains that data is the one accepted at that point as the best representation of the processes underlying the phenomena.

At times, Tilman's approach is Bayesian. In his response, he states that in 1977 (Tilman 1977) he tested the predictive abilities of two models and the simpler of the two was 'better'. Although he felt that the more complex model was worse because of accumulation of 'experimental error' that 'cloud[ed] predictions' as opposed to having made improper assumptions, at the

time he was comparing two models and accepting one based on its relative explanatory power. Although he is not comparing alternative models that differ in their basic assumptions, his approach to empirical tests of concentration reduction is similar. He states that the theory should be accepted because models that embodied concentration reduction predicted the outcomes of pairwise competition correctly.

At other times, Tilman's approach is Popperian. As I stated in my review, he had once written that a hypothesis 'can be rejected if any of [the hypothesis'] interrelated predictions is not supported by observational or experimental evidence' (Tilman 1985, p. 846). Yet, when data contradicted the predictions (or assumptions) of the ALLOCATE model (Shipley & Peters 1990), he did not reject the model, nor did he revise the model (Tilman 1991). He allowed a model to stand that would have been considered falsified with empirical data in a Popperian approach and offered no revision.

As a further example of the disconnect between empirical data and analytical theory, it is illustrative to examine Tilman's Model 5 (Tilman 1990) that he discusses in his response. Originating from the inverse function of the Monod model, Model 5 (like the previous four models in the paper) predicted that 'competitive ability is increased...by traits that increase [RGR<sub>max</sub>]' (Tilman 1990; p. 125). Tilman later states the logical opposite: 'plants that are superior nutrient competitors should have low maximal growth rates' (Tilman 1990; p. 128). This prediction does not come from any analytical theory, but comes from a conceptual link based loosely on empirical data between RGR<sub>max</sub> and parameters such as 'high root biomass, herbivory defenses, leaf and root longevity, efficient nutrient utilization' (Tilman 1990; p. 128).

In general, the role of RGR<sub>max</sub> in Tilman's theories is unclear. As I touched on in my original review (Craine 2005; p. 1047), separating mechanisms, proxies, predictions, assumptions and requirements of Tilman's analytical models is not an apparently straightforward process. For example, in Tilman's response to my article (Craine 2005), he states that in an earlier paper (Tilman 1986), he had 'used short-term growth rate (RGR) as a proxy for R\*, suggesting that higher RGR on low N soil might be indicative of lower R\*.' In the introduction to that paper, he had written that, 'greater relative growth rate [of early successional species], according to resource competition theory (Tilman 1982), should allow these species to acquire a larger proportion of soil nitrogen, and thus to inhibit the growth of later successional species.' Here, growth rates were not a 'proxy' for R\*, but appear to be the mechanism by which species obtain lower R\*.

Both the Bayesian and Popperian approaches to model testing have their benefits, but unfortunately the criteria that Tilman uses to reject (or accept) his model are unstated and appear confused. A Popperian approach would not allow a model to stand after empirical data falsified it. If, for Model 5, Tilman accepted that good

competitors for nutrients had a low RGR<sub>max</sub>, why was the model not considered falsified and rejected or revised? A Bayesian approach that was testing hypotheses regarding the mechanisms of competition would be testing competing models that had different assumptions (not just models that differed in their complexity). When I stated (Craine 2005) that Tilman's models were reduced in mechanism over time and that no viable model was left from which R\* could be derived, I was following Tilman's Popperian approach in rejecting models. It is true that Tilman did not reject any of these models, but from his earlier statements, it seems likely that he should have. Yet, Tilman is mute on the empirical results that would be required to reject any one of his models and offers no grounded explanation for why models are allowed to stand unrevised when their assumptions or predictions have been falsified.

#### FROM MODELS TO HYPOTHESES AND THEORIES

The lack of clarity regarding rejection (or acceptance) of individual models only increases when discussing the hypothesis of concentration reduction. Tilman states that 'from the inception of resource competition theory, the competitive outcomes have been predicted, via analytical theory, to depend on the levels to which each competitor can reduce a single limiting resource (their R\* values)'. Yet, quite simply, what theoretical argument or empirical result would be required for him to reject concentration reduction as the mechanism of competition?

Upon review, I cannot see how one can support concentration reduction over supply pre-emption as the mechanism behind competition for nutrients. From the vantage of first principles, the rate of uptake of nutrients by terrestrial plants is not determined by the average concentrations of nutrients in soil solution. Soil solutions are not well-mixed as they are in pelagic ecosystems as acquisition at the root surface exceeds the diffusion of nutrients to the root, creating diffusion gradients around roots. As such, average soil solution concentrations are not necessarily proportional to concentrations at the root surface. Assuming a well-mixed soil solution could be a simplification, but the focus on average rather than surface soil solution concentrations leads to improper predictions of competitive outcomes (Craine *et al.* 2005). For example, average soil solution nutrient concentrations are altered by soil moisture and plants that are superior competitors could theoretically have higher minimum soil solution nutrient concentrations than other plants if they reduce soil moisture to a lower level. Empirically, there are species that reduce soil solution nutrient concentrations to a lower level than species that are competitively superior to it. For example, in my review I discussed how *Solidago rigida* has lower R\* than competitively superior grasses. Fargione & Tilman (2006) concur with this assessment and show that across multiple experiments, *Solidago rigida* consistently has

the lowest  $R^*$  among species at Cedar Creek Natural History Area (Minnesota, USA), but does not have the highest relative yield when planted with other prairie species – it is consistently outcompeted by grasses.

What if one takes a Bayesian approach? Do  $R^*$  models predict competitive outcomes better than supply pre-emption? A main tenet with supply pre-emption is that root length dominance allows plants to pre-empt the supply of nutrients from reaching competitors. Although not formalized in analytical equations, it can be derived from numerical models of nutrient movement and uptake (Smethurst & Comerford 1993; Le Roux *et al.* 2003; Craine *et al.* 2005). These models show that plants that produce and maintain a higher root length density should best be able to pre-empt nutrient supplies, something that is not predicted by concentration reduction theory. Fargione & Tilman (2006) compare the relative explanatory power of soil nitrate concentrations of 12 species growing in monoculture vs. their root length density for predicting the relative yield of species growing in common. Root length density explained 44% of the variation in relative yield, a similar amount of variation as explained by soil nitrate.

I would never question whether the reduction of average soil solution nutrient concentrations is a useful predictor of competitive outcomes. I agree with many of Tilman's tenets on competition and broadly accept the looser statements he has made about the reduction of resource 'levels' or 'availability' leading to competitive exclusion. Here, I question whether concentration reduction is an appropriate abstraction of the mechanism of competitive superiority for nutrients. At this point, we know that conceptually the focus on average soil solution concentrations is a poor abstract, that this assumption leads to incorrect theoretical predictions of competitive outcomes, and there are empirical examples where  $R^*$  does not predict competitive superiority. From earlier discussion, we see that the models on which  $R^*$  are based produce incorrect assumptions regarding the relative relationships between competitive ability and traits such as  $RGR_{max}$ .

## Conclusions

The next paradigm will go beyond the narrow focus of my current comments and should be as broad as those originally proposed by Grime and Tilman. For example, it should encompass selective and non-selective disturbances as well as other stresses such as low water availability and harsh climates. Most importantly, the next paradigm will not be a result of choosing either Grime's or Tilman's theories, but represent a synthesis of the two sets of theories while also incorporating novel concepts and research. Both Grime and Tilman have done an excellent job of furthering the field and both of their ideas will serve as important components of a new synthesis.

More important than the categorical outcome of the debate on concentration reduction and supply, pre-

emption is the process by which hypotheses and models are evaluated. Although the balance of evidence should lead to supporting supply pre-emption over concentration reduction, it seems clear that changes in theories, whether verbal or mathematical, need to be expressed explicitly. Moreover, the criteria that we use to evaluate models and theories should be explicit and we need to think carefully about how individual models are evaluated, no less broader theories. Although I do not believe the goal posts should be moved entirely to coexistence before settling our understanding of resource competition, Tilman is correct in stating that our understanding of coexistence needs development. Too little research exists on the processes that generate diverse assemblages.

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