

Plant Competition and Resources in Old Fields

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THERE IS A LONG HISTORY of experimental studies of competition, one classic work having been published by Clements *et al.*¹ in the 1920s. Although the occurrence of competition seems to have been an ongoing controversy among zoologists, botanists have tended to accept it as a working hypothesis—largely because of the sheer abundance of plants (99.9% of the world's biomass) and the obvious impact of plant neighbours upon each other.

But whether one studies plants or the remaining 0.1% of the world's biomass, it is obvious that we have many special cases and few general theories (e.g. Refs 2–4) – except for the obvious one that competition occurs in some places and at some times with some species. This is hardly an inspiring improvement, given that more than 50 years have passed since Clements *et al.* wrote their book. If the Wright brothers had been trained as ecologists, we would probably still be sailing across the Atlantic to deliver scholarly papers on the many shapes and sizes of wings in birds and butterflies.

One of the fresh approaches offered in the last decade has been Tilman's work^{5,6}. Tilman's strategic view is that generality will arise only through studies of mechanism. If we focus on mechanism, then we must ask about the resources for which plants compete. Nitrogen is the principal limiting soil resource in terrestrial plant communities. Similarly, light is the principal above-ground resource. These are often negatively correlated in nature. Therefore, light:nitrogen ratios are a key feature that describes the resource state of a particular community. One central prediction is that the species that can create the lowest level of the limiting resource (R^*) will exclude other species. A second is that species differ in the ratio of their above- to below-ground competitive abilities, and this determines which species will eliminate others in a particular habitat.

Testing Tilman's work

These ideas have stimulated considerable attention, but there have been surprisingly few tests to date. There may be several reasons for this. One appears to be simple laziness. Many authors cite Tilman's books, but only as a prelude to describing patterns and ideas that are decades old. It thus appears that while Tilman is widely cited, he is

seldom read, rarely given serious thought, and almost never challenged experimentally. (Tilman at least is cited, which is more than one can usually say for Clements.)

The discrepancy between Tilman's citation rate and the lack of novel experiments to test his ideas is noteworthy. Perhaps one explanation is that his work is not easily falsifiable. It is often far easier to find results that are consistent with a model than to refute it. Tilman himself writes in his first book 'To test this theory thoroughly, it will be necessary to know the resource requirements and competitive interactions of the dominant species under controlled conditions, the correlations between the distributions of these species in the field and the distribution of limiting resources, and the effects of various enrichments on the species composition of natural communities'. Given the reluctance among plant ecologists to use large experiments critically to test theory, perhaps it is not surprising that so few have risen to Tilman's challenges.

Another problem may be the difficulty in deciding what to test. For example, we already know that intermediate levels of biomass and/or disturbance lead to increased diversity, so clearly another description of this will not tell us anything of value about Tilman's models. Similarly, we already know that woody plants replace herbaceous plants through successional time, so demonstrating this outcome (again) has no merit either. What is it exactly that needs to be tested? The difficulty in deciding this is illustrated by a recent paper⁷ that challenges Tilman's model by trying to test assumptions about patterns in root versus shoot allocation in plants.

New experimental results from Tilman and Wedin

Tilman and his student David Wedin have been pressing ahead themselves to test the model using almost exactly the protocol quoted above. In several forthcoming papers they report on a series of studies examining competition among old field grasses for soil nitrogen. These papers will be of interest not only because of their size and complexity, and the duration of the experiments they report, but because they ought to provide a powerful test of the

Tilman model (since they use his model system rather than someone else's).

We might begin our examination of this work by asking whether we can measure R^* for nitrogen, and, if so, whether it varies among species. In order to measure R^* , Tilman and Wedin⁸ established a soil-fertility gradient ranging from sand to black soil. They then established monocultures of five different perennial grass species on these soils, and measured the concentration of available soil nitrogen (estimated as extractable soil NH_4 and NO_3) under different species. Under low-nitrogen conditions, they found significant differences among species in the estimate of R^* for nitrogen. For example, values of soil nitrate ranged from 0.24 mg N/kg (*Agrostis*) to 0.02 mg N/kg (*Andropogon*). There were, however, no significant differences in R^* among species when they were grown at the highest nitrogen level. These results suggest that plants might compete by lowering soil nitrogen levels, at least in infertile soils. This nicely mirrors what we know about above-ground competition, where plants shade one another and reduce the light available for neighbours.

This leads naturally to a second question: which traits are the best predictors of R^* ? Using five species, and measuring both plant traits and the soil nitrogen levels they create, Tilman and Wedin¹⁰ found that root biomass alone explained 73% of the variance in R^* among species. Total biomass has been shown elsewhere to be the best overall predictor of plant competitive ability across 44 species⁹, and now Tilman and Wedin have nicely illustrated one possible component of this, namely, the effects of below-ground biomass on soil resources (Fig. 1).

Of course, the foregoing work addresses R^* and plant traits, but not necessarily competition. So let us turn to the results of competition experiments¹⁰ and to two questions central to Tilman's work and to the issues of competition and prediction. (1) If one can measure the reduction of soil nitrogen to different equilibrium levels (R^*), can one use this to predict competitive outcomes among pairs of species? And, (2) do different competitive abilities for light:nitrogen ratios predict

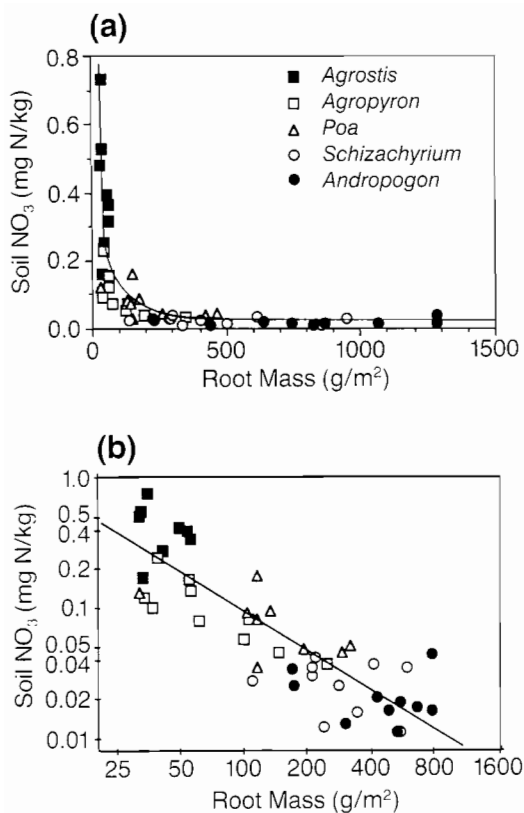


Fig. 1. The level of available soil nitrogen plotted against root biomass (a) on a linear scale. (b) on a log scale, in five old field grass species grown at ten different nutrient levels for three years. Adapted from Ref. 8 with permission

successional change in old fields? The prediction is that early successional species have greater competitive ability for nitrogen, whereas late successional species have greater competitive ability for light. Let us consider these predictions in turn.

Using pairwise competition experiments, Tilman and Wedin examined competition among four species of perennial old field grasses – the early successional *Agrostis scabra* and *Agropyron repens* and the later successional *Schizachyrium scoparium* and *Andropogon gerardi*. The experiments included soil types ranging from infertile (no topsoil) to fertile (90% topsoil), and the results for competition are presented in three nitrogen categories: low, medium and high. In one series of results, *Agrostis* (highest R^*) is strongly suppressed by both *Schizachyrium* and *Andropogon* (lower R^*), irrespective of soil nutrient status. The results are less clear for species with R^* values that are more similar. However, in a note added in proof, the authors state that competitive displacement was simply slower for species with similar R^* values, and that their results after five years further support resource-competition theory.

Now to the question of resource ratios. A surprise was that among the

four species in the competition experiment, the early successional dominants, *Agrostis* and *Andropogon* 'were inferior N competitors relative to later successional species'. *Agrostis* in particular often had R^* values for nitrogen an order of magnitude above other species. If we are indeed willing to make the assumption that R^* measures competitive ability, then indeed this falsifies the resource-ratio hypothesis, which proposes that early successional species are better competitors for soil nitrogen. Tilman and Wedin suggest that the alternative paradigms emphasizing trade-offs between competitive ability and colonization ability may be better able to account for changes in species composition through successional time.

Some consequences for the study of competition

The immense research potential of looking for simple empirical relationships in the study of plant competition is illustrated by the relationship between R^* for nitrogen and root biomass. Although limnology has benefited from this approach¹¹, its potential in many areas of plant community ecology has been overlooked^{4,9}. Such quantitative relationships among plant traits and competitive ability are particularly important if we are to develop general theories based upon traits rather than species nomenclature.

Grime and his co-workers pioneered the idea of screening for plant traits – that is, growing large numbers of species under standardized conditions and measuring the plants' responses to these conditions. Grime and Hunt¹² used relative growth rates as a trait, whereas others have tried screening directly for competitive ability itself⁹. There could be merit in screening for R^* , particularly if simpler methods were developed. One could then ask, as Tilman and Wedin did, which plant traits are correlated with R^* , and perhaps use R^* as one possible indicator of competitive ability. However, since the ultimate objective of predictive ecology is to predict difficult things (e.g. the outcome of competitive interactions) from easily measured ones (e.g. height, biomass), R^* may have two disadvantages as a predictive trait. First, it appears to be difficult to measure, and second, even if we developed a simple bioassay for it, there is no evidence that it offers better predictive ability than simply measured traits such as size or biomass. Perhaps we will find some day that size and biomass work well on a coarse scale, with screening for R^*

being helpful where fine-scale prediction is needed.

We often talk about competition between two species as if it were generally a finely balanced interaction. Studies on very similar species in pots have suggested that rather small changes in the environment can shift the competitive advantage from one species to another. This may be largely an artifact of examining very similar species; in most cases it appears that competitive abilities are in fact asymmetric, with the consequence that we can explore hierarchies of competitive ability in plant communities¹³. A critical test of this is to run competition experiments in very different environments to test whether the outcome is dependent upon environment. The competition experiments described above, where *Andropogon* and *Schizachyrium* displaced *Agrostis* irrespective of soil nitrogen regime, are strong experimental evidence in support of the invariance of competitive hierarchies.

Conclusion

The Tilman and Wedin studies have interesting results in areas such as plant traits and resource depletion, resource ratios and the predicted invariance of competitive hierarchies. Where does this leave the study of plant competition? Although we now have results from a subset of species in one vegetation type, any important general theory needs to be able to predict at a broader scale – across many species and habitats. It will therefore be useful to have other examples using different species and habitats. But such studies will need to be carefully focused, because another front for debate is now opening – the interpretation of this series of experimental papers, including the many associated ones not yet published.

Such discussions about interpretation may arise precisely because of the sheer complexity of this work. Five species (or four), ten soil treatments combined into four levels (or eight soil treatments combined into three levels), different sowing ratios, a cluster of related papers with other results – at some points it felt like the work attempted to overwhelm by sheer volume. I dearly wished to see a single figure plotting competitive ability against R^* , which surely is a critical test for resource-competition theory. Perhaps this desire for clarity was my own fault for accepting a *TREE* commission while on sick leave, but I suspect other readers will have the same reaction in trying to cut through the details to reach the heart of the matter.

If such simplicity were there, another important point would be obvious – that fundamentally the work is based upon five species at most. If the critical test of resource-competition theory is whether R^* predicts competitive ability, then in spite of the amount of work done and reported, we really have a plot with only four points on it (estimates of R^* for five species, but estimates of relative competitive ability for only four; this could be pushed to six if every pairwise outcome were evaluated independently, but not plotted in the same way). The design of experiments to maximize the generality of conclusions is an interesting general problem, and one with some possible solutions⁴. Certainly, for testing an important theory, I would have preferred to see a test using many more

species with less detail presented for each. Given the cost of large competition experiments, and their importance for testing theory, perhaps there is a methodological question we need to examine more closely: are important theories best tested using very detailed experiments on a few species, or very general experiments on a large number of species? Graduate discussion groups may want to examine a set of papers from each approach, and wrestle with the problem over a semester.

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