

## Resource competition and plant traits: a response to Craine *et al.* 2005

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### Summary

**1** Resource competition theory incorporates the mechanisms that underlie consumer–resource interactions and the trade-offs that constrain these mechanisms. Contrary to assertions by Craine, the concept of  $R^*$  as the measure of resource reduction and the predictor of resource competition has not changed since it was proposed more than two decades ago.

**2** Resource reduction, as summarized in  $R^*$ , is readily observed. Soil concentrations of nitrate and water are decreased by plant uptake, and are lowered to different levels by different species. Tests have shown  $R^*$  theory to correctly predict competitive outcomes for a variety of organisms and ecosystems.

**3** Consumer–resource mechanisms are a building block for theories that incorporate other trade-offs faced by plants, such as those between competitive ability and dispersal.

**4** Numerous plant traits interactively determine  $R^*$  in a manner predictable from trait-based resource competition theory. The same traits shown by comparative research to be associated with plant dominance in low-nutrient habitats give lower  $R^*$  values, greater predicted competitive ability and greater predicted abundances in nutrient-limited habitats.

**5** Plant ecology needs closer links between analytical theory, observations and experiments. Simple verbal theories can generate novel ideas but the logical implications of such scenarios are best explored using the rigorous logic of mathematics. Predictions of theory can then be tested via experiments and comparative studies.

*Key-words:* analytical theory, coexistence, comparative studies, experimental tests,  $R^*$ , resource competition, resource isoclines, trade-offs

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### Introduction

In exploring the ideas that Phil Grime and I have developed on the forces structuring plant communities and determining patterns in plant traits, Craine (2005) raised some interesting points and provided some alternative perspectives. New ideas, and the discussion and research they can inspire, are essential to science. In that spirit, I offer several comments. Some clarify misunderstandings and others discuss insights in Craine (2005). These comments are presented within the context of the trajectories of resource competition

theory as it has been developed, tested and modified during the past 30 years.

In Tilman (1976, 1977, 1980) and especially in my first book (Tilman 1982), I discussed a simple but mechanistic theory of resource competition, which I later expanded to more explicitly consider how the mechanisms and outcome of resource competition were linked to plant traits (e.g. Tilman 1988, 1990, 1994, 2006; Fargione & Tilman 2002). My interest in plant traits developed because of the prediction of numerous theories that competitive coexistence, whatever its causes, required interspecific trade-offs in species traits (e.g. MacArthur 1972; Levin *et al.* 1977; Tilman 1977, 1980, 1982; Lubchenco 1978; Levins 1979; Armstrong & McGehee 1980; Hastings 1980;

Levin *et al.* 1984; Gaines & Roughgarden 1985; Chesson 1986). All trade-offs involve, as their most fundamental basis, the way in which an organism allocates resources or other factors that limit its fitness. My second book presented predictions of a model of competitive trade-offs that assumed that plants differed morphologically solely in terms of differences in biomass allocation to roots, stems and leaves (Tilman 1988). Though trade-offs may rarely be as simple or of as low a dimensionality as in this assumption, this model demonstrated that a simple theory could predict some of the major patterns in plant morphology seen along geographical-scale environmental gradients.

### Competition theory and plant traits

Like any theory that has undergone testing by a variety of scholars for the past 30 years (see reviews by Grover 1997 and Miller *et al.* 2005), the interpretation and application of resource competition theory has been modified in response to these tests. However, the basic mathematical theory of resource competition, including the concept of  $R^*$  and its use as a predictor of competition for a limiting resource, has not changed (i.e. compare Tilman 1977, 1980, 1982, with Tilman 1990, 1997, 2006, and with Fargione & Tilman 2002). Resource competition theory is a simple but mechanistic building block that encompasses the essence of consumer–resource interactions, and thus has been used to construct a wide variety of more complex models (e.g. Tilman 1990, 1994; Holt *et al.* 1994; Grover 1997; Chase & Leibold 2003). Contrary to Craine *et al.* (2005), resource competition theory never predicted that  $RGR_{max}$  determined the outcome of competition. Rather, 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), or, if there are two or more limiting resources/factors, on the positions of resource-dependent zero net growth isoclines, consumption vectors, and resource supply vectors (Tilman 1980, 1982). This prediction was mathematically correct when first made, it continues to hold mathematically even for much more complex models of resource competition, and thus, contrary to the assertion by Craine (2005), has never changed.

Let me elaborate on this point, for it is the basis of a fundamental misunderstanding of Craine (2005). Theory predicts that plant traits affect the outcome of interspecific resource competition via the effects of traits on resource reduction as measured by the  $R^*$  values (or isoclines, for two or more resources) of competing species; species influence each other solely because they shade each other, or have an impact upon the availability of water or nitrate or some other resource.  $R^*$  values and resource-dependent zero growth isoclines are the embodiment of the effects of species traits on resource reduction; these resource levels, in turn, are

the mechanism by which one species impacts upon another species.

This issue was explored in depth using five different differential equation models of increasing physiological and morphological detail to predict how plant traits determined the outcomes of resource competition. The simplest of these models (Model 1 of Tilman 1977, 1990, 2003) considered only the kinetics of resource-dependent growth of each species and its rate of loss. The most complex differential equation model of resource competition, Model 5, assumed that growth rate depended on tissue nutrient concentrations, that uptake followed Michaelis-Menten dynamics, that nutrients were withdrawn from older tissues and translocated to new tissues as the older tissues senesced, that tissue loss came from both senescence and consumption of tissues by herbivores and pathogens, and that nutrients were recycled via decomposition of litter. Analytical solution of Model 5 predicted that all of the physiological and morphological traits included in the model contributed to the determination of  $R^*$  of a species, and that the outcome of resource competition was determined by these  $R^*$  values. The resulting equation that related  $R^*$  to plant traits predicted that well-known physiological traits, such as greater tissue longevity and greater nutrient use efficiency, led to superior competitive ability (lower  $R^*$ ). This provided a mechanistic basis for patterns reported by Chapin (1980) and subsequently by numerous others. The traits known from comparative research to be associated with plant dominance in low-nutrient habitats were predicted by theory to lead to lower  $R^*$  values, and thus to greater competitive ability and abundance in nutrient-limited habitats (Fargione & Tilman 2002). It is precisely this sort of model that allows analytical exploration of the six scenarios presented by Craine (2005).

### Testing resource competition theory

The ability of resource competition theory to predict the dynamics and outcome of competition was readily demonstrated in studies of algae and bacteria (Tilman 1976, 1977; Hansen & Hubbell 1980; Tilman *et al.* 1982; Grover 1997; Miller *et al.* 2005). My initial efforts to apply it to terrestrial plants were more problematic. Although theory predicts that the outcome of competition for a limiting resource is determined solely by  $R^*$  values, I did not initially see a good way to directly measure  $R^*$ , and so tried an approximation (Tilman 1986). I grew seedlings of grassland species for 12 weeks on soils of differing N supply, and used short-term growth rate (RGR) as a proxy for  $R^*$ , suggesting that higher RGR on low N soil might be indicative of lower  $R^*$ .

Within a few years a series of field experiments on five perennial grasses had tested this simplifying assumption against predictions based on directly measured  $R^*$  values (Tilman & Cowan 1989; Tilman &

Wedin 1991a). The measured levels of extractable soil nitrate, the limiting resource, in equilibrium monocultures of each species (Tilman & Wedin 1991a) are, by definition, their  $R^*$  values. We found that slow-growing species tended to have lower  $R^*$  values, showing that our guess that high RGR on a low N soil would be associated with low  $R^*$  (Tilman 1986) had been wrong. The outcomes of three different kinds of competition experiments among various pairs of these five species on low N soils (Tilman & Wedin 1991a; Wedin & Tilman 1993) were, in all cases, correctly predicted by the observed  $R^*$  values of the species. Moreover, in competition plots, measured levels of soil nitrate were reduced down to the  $R^*$  value of the winner, and the losing species, which had a higher  $R^*$  value than this, was competitively displaced (Tilman & Wedin 1991b; Wedin & Tilman 1993). Also consistent with theory, competitive outcomes were identical whether species competed as seed vs. seed, via seed invasions into established monocultures of another species, or via vegetative invasion between adjacent monocultures.

The most interesting case was competition via vegetative invasion. When *Schizachyrium scoparium* or *Andropogon gerardi* (which had the lowest  $R^*$  values for nitrate) competed against *Agropyron repens* or *Agrostis scabra* (which had the highest  $R^*$  values) via vegetative invasion on low N soils, there was no above-ground vegetative invasion. Rather, *Schizachyrium* and *Andropogon* displaced higher  $R^*$  species via root growth into and resultant reductions of soil nitrate in the areas initially dominated by the higher  $R^*$  species (Tilman & Wedin 1991b; Wedin & Tilman 1993). Contrary to the assertion of Craine (2005) and Craine *et al.* (2005) that diffusion limitation of root nutrient uptake should prevent competitive displacement via resource reduction (the  $R^*$  mechanism), essentially complete competitive displacement occurred solely via root competition on these low nitrogen soils.

We have since performed similar long-term field competition experiments among other prairie perennials (Dybzinski & Tilman, in preparation). Our studies support the prediction of theory that species with lower  $R^*$  values are competitively dominant. As to plant traits, lower  $R^*$  for nitrate is strongly associated with higher root mass (Tilman & Wedin 1991a), which, itself, depends on root tissue density, root longevity and root tissue C:N (Craine *et al.* 2002), suggesting, as did Model 5 (Tilman 1990), that  $R^*$  summarizes and synthesizes the effects of numerous traits on competition.

Craine (2005) asserts that I have offered a 'shifting set of theories that have become reduced in mechanistic detail over time'; that  $R^*$  'can no longer be derived from any mechanistic model'; and that ' $R^*$  has been discredited and no viable model has been offered to replace it'. Quite to the contrary, in Tilman (1977) I tested the predictive abilities of both a simple theory (Model 1) and a more complex model that required measurement of more traits. Interestingly, the simpler

model was better presumably because, with fewer parameters, there was less accumulation of experimental error to cloud predictions. I next offered more complex elaborations of this theory to illustrate the unity between traditional ecophysiological perspectives and resource competition theory (Tilman 1990, 2003). Even our most recent papers derived  $R^*$  from both simple and complex mechanistic models precisely to illustrate the links between traits and  $R^*$  (e.g. Fargione & Tilman 2002; Tilman 2006). Finally, a recent review of tests of resource competition theory concluded that its predictions were generally well supported, but urged that more tests be performed (Miller *et al.* 2005). I fully concur with this recommendation.

### Final thoughts

Many challenges remain in the search for a more predictive and mechanistic understanding of plant communities. First, although resource competition theory has done a reasonably good job of predicting competitive outcomes in our field experiments, we have often observed competitive displacement in such experiments, whereas we observe the same species coexisting in nearby natural ecosystems. Such coexistence suggests that our theory and experiments are simplifications that miss important constraints and trade-offs that lead to coexistence in nature. Studies at Cedar Creek Natural History Area, Minnesota, have suggested that coexistence may result from competition-colonization trade-offs (Gleeson & Tilman 1990; Tilman 1994) or from interspecific differences in rooting depths or seasonality (Fargione & Tilman 2005). Such possibilities, and others, merit much further exploration in a variety of plant communities. Secondly, as articulated in the six scenarios of Craine (2005), neither current models nor field experiments have adequately addressed trait-based trade-offs related to plant foraging strategies for pulsed or spatially patchy nutrients and light. Indeed, light competition remains one of the central enigmas of plant ecology. Deeper exploration of Craine's six scenarios may well uncover important mechanisms of interspecific coexistence. Thirdly, plant ecology needs closer links between analytical theory, observations and experiments. Simple verbal theories based on patterns or perceived mechanisms are an important source of novel ideas. However, our discipline would advance more quickly if the logical implications of such scenarios were explored using the most rigorous language of logic yet invented – mathematics. Experimental and comparative tests of such predictions can then determine whether real organisms display the hypothesized suite of traits in the appropriate habitats, and whether species abundances change as predicted in response to competition and environmental manipulations. I hope that this interchange of ideas can help spur research that combines rigorous theory, experimentation and comparative studies.

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