

Further Thoughts on Competition for Essential Resources

DAVID TILMAN

*Department of Ecology and Behavioral Biology,
University of Minnesota, 318 Church St. SE, Minneapolis, Minnesota 55455*

Received October 30, 1986

Abrams (1987) notes several differences between his approach to resource competition and that of Tilman (1982). The theory presented by Abrams (1987) is more complex than that in Tilman (1982) because Abrams explicitly linked optimal foraging and resource competition (at least for a simple model), whereas I used optimal foraging to derive the qualitative form of consumption vectors and resource-dependent growth isoclines and then used these isoclines and consumption vectors to predict the outcome of competition. Despite these differences, the two approaches make qualitatively similar predictions. I used a simplified, graphical approach to resource competition because I wished to explore the broad implications of resource type and resource competition for the diversity, species composition, and successional dynamics of plant and animal communities. I have not been able to find any ways in which the more explicit theory developed by Abrams (1987) qualitatively changes any of the relationships between resource competition and community structure that were proposed in Tilman (1982). However, Abrams' paper raises several points that merit further discussion.

The most important point mentioned by Abrams is the occurrence of curved isoclines. Abrams and I seem to have independently discovered that it is unlikely for nutritionally perfectly essential resources to lead to resource-dependent growth isoclines with right-angle corners. The shape of a resource-dependent growth isocline is determined not just by the nutritional qualities of resources but also depends on the spatial and temporal pattern of resource availability in a habitat and its relation to the ways in which individuals obtain these resources (Tilman, 1982, pp. 20-21). Optimal foraging for nutritionally essential resources will lead to a resource-dependent growth isocline with a curved corner, not a right-angle corner, in all cases in which decreased effort foraging for one resource can lead to increased consumption of the other resource (Tilman, in preparation). I failed to realize this in Tilman (1982). I call nutritionally essential resources that lead to such curved isoclines "interactive-essential"

resources (Tilman, 1980) because the curvature indicates an interaction between the ability of a species to acquire and or use one nutritionally essential resource and the other. The cause of this curvature is easily explained. Imagine an individual whose reproductive rate is limited equally by two nutritionally essential resources, R_1 and R_2 , such as at point 1 in Fig. 1. It would have an isocline with a right-angle corner only if the addition of just R_1 or of just R_2 could lead to no increase in its growth rate (Fig. 1; Tilman, 1980). However, if it is limited equally by both resources, following the addition of R_1 it would be limited by R_2 . If it could expend less of its effort obtaining R_1 and thus increase its consumption rate of R_2 , it would acquire more of the resource that limited it and increase its growth rate. This necessarily means that it has a curved isocline (Fig. 1). The curvature can also be easily derived from consumption constraint curves and nutrition isoclines (Fig. 8 in Tilman, 1982).

Multicellular plants have an extremely plastic morphology (Harper, 1977). This morphological plasticity is directly related to the ability of an individual plant to acquire various limiting essential resources (Tilman, 1986, and in preparation). Plants require both light, an above-ground resource, and various nutrients, which are below-ground resources. To obtain more light, a plant must allocate more of its growth to stems and leaves, whereas to obtain more of a nutrient, it must allocate more of its growth to roots. The physical separation of nutritionally essential resources means that structures produced to obtain one of these cannot be used to

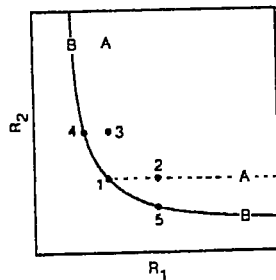


FIG. 1. The broken line labelled A shows the resource-dependent growth isocline of individuals with no phenotypic plasticity in their functional response to two nutritionally essential resources, R_1 and R_2 . At point 1 morph A is equally limited by R_1 and R_2 . The addition of just R_1 (i.e., going from point 1 to point 2) or of just R_2 (point 1 to point 3) does not increase its growth rate. In contrast, individuals of morph B are plastic, giving the curved isocline shown. Morph B can grow faster at points 2 or 3 than morph A because B can increase its consumption of the limiting resource by decreasing its effort in acquiring the non-limiting resource. The placement of these isoclines assumes, though, that there is no cost for plasticity. If plasticity had a cost, the isocline of morph A would cross that of morph B, and morph A would be the superior competitor through a range of intermediate resource availabilities, whereas morph B would dominate extreme habitats.

obtain the other (Tilman, 1986). However, it also means that a plant that can vary its morphology will be able to adjust the rate at which it acquires each resource. A morphologically plastic plant could thus be a superior competitor over a broad range of habitat conditions compared to a similar plant that was not morphologically plastic, if plasticity did not have a cost. This is easily seen by noting that the curved isocline of a morphologically plastic individual falls inside the right-angle isocline of an otherwise identical individual with a fixed morphology (Fig. 1; Tilman, in preparation). The morphologically plastic individual would outcompete the individual with the fixed morphology in all habitats except the habitats that lead to point 1 in Fig. 1. The simple relation illustrated in Fig. 1 may thus explain the prevalence of morphological plasticity in plants.

There are some important implications of morphological plasticity (or adaptive functional responses) for species competing for nutritionally essential resources. First, morphological plasticity can modify the size and shape of the regions of interspecific coexistence. This is analogous to the effect of phenotypic variability among individuals consuming perfectly essential resources (Tilman, 1982, pp. 244–247), which can cause a population to have, in total, a curved resource-dependent growth isocline and influence regions of coexistence. However, it is likely that there will be limits to the range of the morphological plasticity or functional response of a species. Such limits mean that each species may still be differentiated in its requirements for the limiting resources and thus that a variety of species can coexist across a spatially heterogeneous landscape (see Figs. 91 and 92 in Tilman, 1982). As discussed in Taylor and Williams (1975) and Tilman (1980, 1982, 1986), the same sort of interspecific differentiation that can lead to dominance and coexistence of various species in habitats that differ in their resource supply rates can occur whether the resources are perfectly essential or interactive-essential. This is not to imply that trade-offs in functional responses are unimportant. Such trade-offs, within a given individual, among individuals in the same species, and among species, are the ultimate underlying mechanism that can prevent one species from being a supercompetitor (Tilman, 1986). Abrams' (1987) paper is an important step in the development of theory of these trade-offs. However, contrary to what might seem to be implied by Abrams' paper, the work that I have already published does include such trade-offs qualitatively and is not qualitatively affected by this new work.

Abrams is correct that, in my analysis of MacArthur's (1972) model of competition for perfectly substitutable resources, which was peripheral to the main points of the book, I inadvertently treated resource consumption vectors as constant across a resource gradient, and that this error led to the constant values for the Lotka–Volterra competition coefficients shown in Figure 74 (Tilman, 1982). I discussed MacArthur's model (modified to

include a maximal per capita growth rate) and several other models of resource competition (Chapter 7 in Tilman, 1982) to demonstrate that the pattern of variation in Lotka-Volterra competition parameters along a resource gradient was highly dependent on the types of resources, the processes governing their supply, and the consumption characteristics of the species. Even after correcting for the error mentioned by Abrams, the conclusion I drew from those analyses still holds: "It is necessary to know the explicit, mechanistic model of resource competition in order to determine how the parameters of the Lotka-Volterra equations will change along a resource ratio gradient" (Tilman, 1982, p. 203). Abrams' (1987) analysis further demonstrates the dangers inherent in using "niche overlaps" on some unspecified "resource axis" as a basis for estimating competition coefficients. This and numerous other criticisms of the Lotka-Volterra approach to competition (e.g., Leon and Tumpson, 1975; Tilman, 1977, 1982; Schoener 1978; Abrams 1980, 1987) suggest that both theoreticians and field workers should study the mechanisms of competition rather than just the phenomenon of competition as summarized by the Lotka-Volterra or some other density-based model (Tilman, 1987).

Abrams (1987) is incorrect in stating that I generally treated functional responses as constant in Tilman (1982). As illustrated by Fig. 4 through 9 in Tilman (1982), a theory of optimal foraging predicts that functional responses should not be constant but can vary with the availability of all resources within the constraints of the foraging plasticity of a species and the structure of its habitat. I did treat functional responses (represented as consumption vectors) as variable along resource gradients throughout most of the book. However, I did this in a qualitative, graphical manner, not in the explicit manner in Abrams (1987). I did assume that consumption vectors were almost constant in the immediate vicinity of any given equilibrium point. Although this was probably an overly restrictive assumption for many cases, Tilman (1980, pp. 388-391) showed that the local stability of a two-species equilibrium point can depend on functional responses.

REFERENCES

- ABRAMS, P. A. 1980. Are competition coefficients constant? Inductive vs. deductive approaches. *Amer. Nat.* 116: 730-735.
- ABRAMS, P. A. 1987. The nonlinearity of competitive effects in models of competition for essential resources. *Theor. Popul. Biol.*, in press.
- HARPER, J. L. 1977. "Population Biology of Plants." Academic Press, London.
- LEON, J., AND TUMPSON, D. 1975. Competition between two species for two complementary or substitutable resources. *J. Theor. Biol.* 50: 185-201.
- MACARTHUR, R. H. 1972. "Geographical Ecology." Harper and Row, New York.

- SCHOENER, T. W. 1978. Effects of density-restricted encounter on some single-level competition models. *Theor. Popul. Biol.* 13, 365-381.
- TAYLOR, P., AND WILLIAMS, P. 1975. Theoretical studies on the coexistence of competing species under continuous flow conditions. *Canad. J. Microbiol.* 21, 90-98.
- TILMAN, D. 1977. Resource competition between planktonic algae: An experimental and theoretical approach. *Ecology* 58, 338-348.
- TILMAN, D. 1980. Resources: A graphical-mechanistic approach to competition and predation. *Amer. Nat.* 116, 362-393.
- TILMAN, D. 1982. "Resource Competition and Community Structure," Princeton Univ. Press, Princeton.
- TILMAN, D. 1986. Evolution and differentiation in terrestrial plant communities: The importance of the soil resource: light gradient, in *Community Ecology* (T. Case and J. Diamond, Eds.), pp. 359-380, Harper and Row, New York.
- TILMAN, D. 1987. The importance of interspecific competition. *Amer. Nat.* 129, 769-774.
- TILMAN, D. "Plant Strategies and the Dynamics and Structure of Plant Communities," Monographs in Population Biology, Princeton Press, in press.