Perspectives on Plant Competition: Some Introductory Remarks

James Grace David Tilman

Competition among plants was likely discovered by the first farmers during neolithic agriculture. Some of the first scientific treatments of the subject can be found in the works of de Crescentiis (1305) and DeCandolle (1820). Inspired by the logic of Malthus (1798), Darwin (1859) wrote extensively about competition as an important selective agent for all types of organisms. Early botanists and vegetation ecologists considered interspecific competition to be an integral part of nature. Agricultural and forestry practices have long attempted to minimize the effects of undesired plants. One of the first exclusive treatments of the subject was published in 1929 by Clements *et al.* This seminal work contains a detailed description of the early history of plant competition as well as a wealth of empirical information. As with most areas of science, the literature dealing with competition has grown dramatically in recent decades.

A wide range of meanings has been ascribed to the word "competition." Definitions range from the narrow to the general, from operational to philosophical, and from phenomenological to mechanistic. This range of definitions has caused confusion and continues to cloud discussions of the substance of competition. Several authors have attempted to define competition as a precise term (e.g., Harper, 1961; Milne, 1961) but it seems unlikely that a narrow definition is possible for a term that has been used so broadly. Rather, a more profitable approach may be to

define competition broadly, but to study specific kinds of competition, such as resource competition or interference competition (e.g., Tilman, 1982; Begon *et al.*, 1986). Because this is a book about contrasting perspectives, it is important to examine the definition used by each author, especially the operational definition of competition (i.e., how each measures competitive effect or competitive ability). In practice, far more confusion is generated through differences in operational definitions than through contrasting conceptual definitions because the latter are often quite general.

In reading this book, and in reading the plant competition literature in general, it is important to distinguish between two markedly different operational definitions of competition. The first stresses the total competitive effect of a species or of an entire community on another species. This definition, which has been used by Keddy, Grime, and others, is operationally based on the difference between the biomass that a target plant attains in the absence of some or all neighbors compared to its biomass in the presence of all neighbors. The additional biomass attained after the removal of competitors is the competitive effect of those plants on that species. This operational definition does not adjust for differences in the biomass of competitors removed, and thus does not measure the intensity of competition per unit neighbor biomass. Its use lies in its ability to demonstrate whether or not competition is occurring. If competition is occurring, it is expected, from first principles, that the magnitude of the total competitive effect would increase directly (though not necessarily linearly) with the amount of neighbor biomass removed. Thus, when all neighbors are removed, a target plant should be able to attain greater biomass in a productive community with an initial total biomass of 1000 g/m^2 than in an unproductive one with an initial biomass of 100 g/m^2. Because it depends on the amount of biomass removed, the total competitive effect, by itself, tells us little about the mechanism of competition, especially when comparing habitats that differ in productivity or standing crop.

A second operational definition of competition commonly used is the intensity of competition *per unit biomass*. Here the total competitive effect of all neighbors is divided by the amount of biomass removed to obtain a measure of the intensity or strength of competition. This measure can be used to make comparisons both within and among plant communities. Thus, it would be possible to ask if the intensity of competition per unit of neighbor biomass depended on the species of the neighbors, on the productivity of a habitat, or the disturbance rate of a habitat. This operational definition of the intensity of competition has been the standard for animal ecology, and is qualitatively consistent with the traditional definitions provided by the competition coefficient of the Lotka–Volterra

equations and by the relative yields used to analyze replacement experiments, and with the terminology in the work of Tilman, Goldberg, Pacala, Silander, and others. A portion of the controversy between Grime and Tilman may have resulted from their different operational definitions of competition. Grime, in asserting that the "strength of competition" was greater in more productive habitats, was most likely referring to what we have termed the "total competitive effect." In contrast, Tilman, in asserting that strength of competition should be approximately equal across a productivity gradient was referring to the "intensity of competition per unit neighbor biomass." The discussion above suggests that they may both be correct, once their definitions are understood. This illustrates the importance of understanding an author's operational definitions.

The contents of this volume are organized around three main subdivisions: (1) Perspectives on the Determinants of Competitive Success, (2) The Role of Competition in Community Structure, and (3) The Impact of Herbivores, Parasites, and Symbionts on Competition. The first section of the book deals with the question of "What determines competitive success?" In addressing this question, several of the papers deal, by necessity, with definitions of competition and competitive success. The paper by Connell distinguishes the traditional definition of competition in which members of a pair of species inhibit each other through effects on resources or on one another's abiotic environment, from "apparent" competition in which indirect negative effects are mediated through additional species, often on other trophic levels. Goldberg discusses some of the ways that plants interact via limiting resources by pointing out the distinction between the effects of plants on resources versus the response of plants to resource depletion. Grace deals further with definitions and with the determinants of competitive success in a chapter that discusses the similarities and differences between the theories of Grime and Tilman. Silander and Pacala present spatial models of neighborhood competition and use them to analyze experimental studies of competition among neighboring plants. Berendse and Elberse focus on the determinants of competitive success for nutrient-limited heathland and grassland species. Tilman discusses several different models of the mechanisms of nutrient competition to illustrate how each of them "abstracts" reality and how each incorporates both a plant's response to and its effect on resources. Finally, Williamson addresses some of the long-standing questions concerning the way to study allelochemic interactions among plants. He evaluates proposed methodologies by focusing on the degree to which apparent allelopathy might be adaptive.

The second section of this book provides a contrasting set of views about the consequences of competitive interactions for plant community

structure. It is a tacit assumption in all of these chapters that competition is one of, but by no means the only, force in natural communities. The section begins with Firbank and Watkinson, who address some of the methodological limitations associated with traditional additive and substitutive experiments and present a hybrid approach to studying the phenomenon of competition. Sommer analyzes the mechanisms of nutrient competition among phytoplanktonic algae and discusses how well such mechanisms can predict the patterns of species abundances in lakes. Both Austin and Keddy explore the role of competition in the distributions of species across habitats. Within-habitat effects of competition are examined by Bazzaz, who illustrates the complexity that exists in actual interactions among individuals as habitats change over time. The themes of complex explanations of pattern and even the lack of strong pattern within communities are addressed in the papers by Turkington and Mehrhoff and Fowler. Finally, Radosevich and Rousch examine the role of competition in agricultural systems.

The final section of the book places competition within the context of the interactions of plants with organisms on other trophic levels. These chapters demonstrate that the outcome of competition depends on the effects of herbivores, parasites, and symbionts. Allen and Allen discuss the role of mycorrhizae in altering competitive abilities, particularly during succession. Clay illustrates that nonmycorrhizal fungi can have strong effects on competitive interactions through both pathogenic and mutualistic mechanisms. The role of herbivores in both modifying competitive relations and in regulating populations are the themes addressed in the final two papers by Louda, Keller, and Holt and by Oksannen. All of the papers in this final section emphasize the need to integrate the mechanisms of competition into the framework of the entire foodweb. This was a major theme to come from our meetings, and is a fitting theme to end this book.

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