

EDITORIAL

Introduction to the Special Feature on Mechanisms of Plant Competition

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This Special Feature brings together some of the latest ideas and evidence about how plants compete with one another. That there *are* new ideas about this enduring subject might come as a surprise to many ecologists. Indeed, when invited by the editors of *Functional Ecology* to guest-edit this Special Feature, our first reaction was to ask ourselves, ‘Surely all that stuff is so well known that there is nothing new to say.’ As is so often the case, more sober reflection revealed a contradictory reality. There is in fact a lot still to be said about plants’ competitive mechanisms, far more than can be covered in these few pages. And we hope you will be convinced that in exploring this topic, we are not just tinkering around the edges, but are addressing issues that should lie at the heart of current ecological thinking.

Most plant ecologists who have given serious thought to the subject will have asked questions similar to the following:

1. What is competition?
2. How does it happen?
3. Where is it happening?
4. When is it happening?
5. How can we quantify it?
6. How can we be sure we are really measuring it and not something that just looks like competition?
7. What is the influence (if any) of competition on a plant community and on the fitness of its members?
8. How does competition rate as an ecologically significant process compared with other things, such as environmental severity and habitat stability?

Regrettably, few of us have yet to find satisfying answers to most of these questions. Of course, basic processes of plant competition have been known for a long time, at least at a conceptual, macroscopic level. Plants that achieve greater root growth and faster uptake of water and nutrients or grow taller to produce extensive canopies to shade smaller neighbours, and which capitalize on that biophysical superiority by producing more offspring or durable vegetative structures, are likely to have an advantage over less well-endowed neighbours, other things being equal. But characterizing the *precise* cause-and-effect relationships that allow those and associated processes to

occur, quantifying their interactions with others and, crucially, revealing their impacts (if any) on population dynamics or community structure have proven to be fraught with practical difficulties. Theory is of little help: the notion that applying Lotka–Volterra models equates to truly understanding competition has been debunked repeatedly (Simberloff 1982; Peters 1991, pp. 56–8; Shipley 2010, pp. 22–25).

Nevertheless, it is impossible to imagine plant ecology without competition as one of its basic tenets, even plant ecology based on neutral models (Hubbell 2005). Few doubt that competition remains a useful and powerful idea, despite its reputation for fostering confusion, and the tendency of some ecologists to give it too much conceptual dominance, a stance lately criticized by Grime & Pierce (2012, p. 22) as ‘the product of some very muddled, non-Darwinian thinking’. In terms of understanding what competition is and what it does, it perhaps is not too fanciful to say that ecology is in a similar state to physics before Rutherford and Bohr characterized atomic structure or genetics until Watson and Crick discovered the double helix. Atoms and genes were useful, and powerful ideas long before their structures and modes of action were known, but only after those breakthroughs were made, could experiments be fully explained and, most importantly, experimental outcomes predicted. Competition has yet to yield to ecology’s equivalents of Rutherford *et al.*, whoever they may turn out to be, such that the idea of competition is transformed into a tangible, measurable process (or series of processes) that improves ecological understanding rather than confuses it. One (but not the only) prerequisite for achieving that goal is to understand much more about how, and under what circumstances, competitive processes operate. Which brings us nicely to competitive mechanisms.

Plants compete for resources: light; nutrients; water. Each resource has its own idiosyncrasies in terms of how its spatial and temporal availability is determined and responds to local depletion by competing plants (Craine & Dyzinski 2013). The scope of natural selection to produce structures better able to achieve resource capture in an environment comprising other individuals that are also potentially capturing those resources is limited by multiple biophysical constraints (Niklas & Hammond 2013). Such

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constraints allow the potential influences of defined traits on competitive outcomes to be predicted in general terms.

But ecologists are often concerned with the outcome of *specific* interactions between plants that occur in the field, usually in an ill-defined milieu comprising other plants, microbes, herbivores and microhabitats, with all the biological and environmental complexity that entails. In biology, 'mechanism' is now almost always prefaced with 'molecular'. Identifying the molecules with which plants sense their local environment and immediate neighbours, and the molecular receptors and effectors that then drive developmental and physiological responses that become manifested as changes in growth or fecundity, is one of the surest ways of opening the conceptual black-box of how plants compete (Pierik, Mommer & Voesenek 2013). It is a relatively short step from characterizing the molecular basis of competitive interactions to defining the sometimes profound influence that soil microbes, be they symbiotic, pathogenic or somewhere in between, can have on plants' competitive interactions (Hodge & Fitter 2013). Likewise, being able to determine the genetic relatedness of neighbouring individuals in a community, and the potential for self-/nonself-recognition mechanisms (Dudley, Murphy & File 2013), for which molecular tools are indispensable, should allow the influence of kinship on the extent of competitive interactions to be evaluated.

Competition between plants is often envisaged to be amenable to study largely by growing competitors together and harvesting them at an arbitrary but not-too-distant point in the future: the 'big plant-little plant' comparisons familiar from textbooks, undergraduate lectures and many influential papers. The limitations of that approach to the investigation of a dynamic phenomenon are clear, but rarely acknowledged (Trinder, Brooker & Robinson 2013). That, we argue, has restricted innovative thinking about how the competitive mechanisms expressed by an individual plant exert an influence on its neighbours. If short-term temporal dynamics are a fundamentally important aspect of plants' competitive interactions, it is then logical to consider competitive mechanisms that are influential over longer time periods and which can become manifested as differences in fecundity (Bonser 2013), with obvious links to population dynamics, community composition and, ultimately, evolution.

One of the major conceptual developments in this field over the past 40 years has been the general recognition that 'plant competition' is not necessarily the same everywhere and at all times, not least in terms of its magnitude (however that is measured) or its ecological impacts (ditto). Interactions between neighbours are modulated decisively by the environment in which those interactions occur. Benign, resource-rich and stable habitats tend to

encourage a predominance of competition. By contrast, plants growing at extremely harsh or resource-poor sites are more likely to exhibit facilitative, not competitive, interactions with their neighbours (Butterfield & Callaway 2013). Even so, harsh environments can select for plants that capture and use scarce resources in different ways, and which can shape local ecological diversity (Schwinning & Kelly 2013).

It is sometimes argued that competition is now such a familiar aspect of ecology that we can learn little more about it that is truly valuable or surprising. But if that were true, why do ecologists still spend so much time arguing about it? Our view is that we have barely begun to understand competition, either in terms of how it happens between particular individuals in specific locations or, most certainly, in terms of its long-term, large-scale significance. We hope that the contributions to this Special Feature will point towards better ways of answering questions such as those posed at the start.

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References

- Bonser, S.P. (2013) High reproductive efficiency as an adaptive strategy in competitive environments. *Functional Ecology*, **27**, 876–885.
- Butterfield, B.J. & Callaway, R.M. (2013) A functional comparative approach to facilitation and its context dependence. *Functional Ecology*, **27**, 907–917.
- Craine, J. & Dybzinski, R. (2013) Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, **27**, 833–840.
- Dudley, S.A., Murphy, G.P. & File, A.L. (2013) Kin recognition and competition in plants. *Functional Ecology*, **27**, 898–906.
- Grime, J.P. & Pierce, S. (2012) *The Evolutionary Strategies that Shape Ecosystems*. Wiley-Blackwell, Chichester, UK.
- Hodge, A. & Fitter, A.H. (2013) Microbial mediation of plant competition and community structure. *Functional Ecology*, **27**, 865–875.
- Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, **19**, 166–172.
- Niklas, K.J. & Hammond, S.T. (2013) Biophysical effects on plant competition and coexistence. *Functional Ecology*, **27**, 854–864.
- Peters, R.H. (1991) *A Critique for Ecology*. Cambridge University Press, Cambridge.
- Pierik, R., Mommer, L. & Voesenek, L.A.C.J. (2013) Molecular mechanisms of plant competition: neighbour detection and response strategies. *Functional Ecology*, **27**, 841–853.
- Schwinning, S. & Kelly, C.K. (2013) Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. *Functional Ecology*, **27**, 856–897.
- Shipley, B. (2010) *From Plant Traits to Vegetation Structure*. *Chance and Assembly of Ecological Communities*. Cambridge University Press, Cambridge, UK.
- Simberloff, D. (1982) The status of competition theory in ecology. *Acta Zoologica Fennica*, **19**, 241–253.
- Trinder, C.J., Brooker, R.W. & Robinson, D. (2013) Plant ecology's guilty little secret: understanding the dynamics of plant competition. *Functional Ecology*, **27**, 918–929.