

competition is itself a fundamental principle and should not be mistaken for scientific imprecision. Gaudet and Keddy themselves over generalize from their experiments. It is hardly surprising that 40 species tested individually against a single 'indicator' species under uniform conditions can be ranked in their competitive ability on the basis of a single character. It is even less surprising that this character should be biomass. Repeating the exercise for 10 species with another indicator species does not improve the generality of these results because so many parameters important to the outcome of competition were left unaltered. More sophisticated competition experiments conducted along a nutrient gradient have shown that the competitive rank of a species in a mixture may alter along the gradient¹². Furthermore, even when competitive ability is fixed, its importance in determining a plant's distribution depends upon many other environmental variables (see, for example, ref. 13).

I agree with Gaudet and Keddy on the need for generalization in ecology, on the potential fruitfulness of the comparative approach when correctly applied, and on the importance of biomass in competition when other things are equal. But, oversimplifying experimental systems does not provide a short-cut to ecological generality or transform community ecology into a predictive science.

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GAUDET AND KEDDY REPLY—We demonstrated an empirical relationship between plant traits and interspecific competitive ability¹. To maximize generality, the study used 44 wetland plant species of widely contrasting ecology from across eastern North America. We suggested that such empirical approaches would be one tool for developing general predictive models for plant communities. We are encouraged that this paper has produced some lively debate, but believe that the criticisms are without foundation.

Firbank and Watkinson observe that the predictor variables (plant traits) were not independent of the response variable (phytometer biomass), but missed our point that when the analysis was repeated with predictor variables from monocultures, the same answer was found. Further, the phytometers were seedlings and it is likely that they had minimal effect upon the adult test species. Bailey's suggestion of a multivariate extension is a good one; we were aware of the possibility, but chose to emphasize simplicity in our paper.

Firbank and Watkinson assume that our competitive ranking by size translates into a measure of relative growth rates, but

there is no basis for this^{14,15}. We acknowledged that other traits besides size are important. Our technique is a tool for measuring (as opposed to speculating about) the relative importance of different traits in determining competitive ability.

Silvertown emphasizes the inherently contingent nature of plant competition. We offer, as an alternative hypothesis, that contingency is largely an artefact resulting from the examination of similar pairs of species. That is, once the relationship between size and competitive ability is eliminated, only residual variance (contingency) remains.

We wish to emphasize our long-term goal — general testable predictions about real multispecies communities — all three critiques of our paper focus on this point. Our paper presented some results allowing such predictions. This long-term goal has two components: (1) the ability to predict plant competitive ability, and (2) an understanding of the implications of different competitive abilities for community organization. Our results are consistent with evidence from plant strategies⁷. We also have pervasive evidence of competitive hierarchies in multispecies communities of wild plants and that position in these hierarchies can be predicted from plant size^{16,17}. Plant size is correlated with species distributions along natural environmental gradients¹³ and relative abundance in turf⁸. Our technique has therefore quantified a broad general principle regarding plant competition and interpretation of our results does not appear to be limited to the experimental conditions of our study. With respect to implications for community organization, we are currently testing whether our measure of competitive ability will predict field distributions in a field data set collected from wetlands in eastern Canada. A general model of centrifugal organization of communities has been proposed^{18,19}; an essential element of this model is size-related competitive ability for light.

We reiterate our view that the status quo is not producing rapid progress in the

study of plant competition at the community level. On of the major drawbacks of current pairwise analyses is that they restrict the number of species that can be evaluated in any experiment. In arguing that existing methods suffice, Firbank and Watkinson seem to confuse the ability to predict competitive outcomes of pairs of annuals grown in pots with the development of predictive models for natural multispecies communities. Further, asserting that a phenomenon (for example, resources) has been 'investigated' does not provide evidence of progress.

Finally, Bailey accuses us of being reckless. Our paper simply proposed a research strategy, documented a significant empirical relationship, and invited further work. Whether any research path will yield scientific progress is ultimately not a matter of debate, but a matter of time and testing.

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- Gaudet, C.L. & Keddy, P.A. *Nature* **334**, 242–243 (1988).
- Cormack, R.M. in *Spatial and Temporal Analysis in Ecology* (eds Gormack, R.M. & Ord, J.K.) 151–252 (International Publishing House, Fairfield, 1979).
- Ford, E.D. & Diggle, P.J. *Ann Bot.* **48**, 481–500 (1981).
- Firbank, L.G. & Watkinson, A.R. *Oecologia* **71**, 308–317 (1987).
- Connolly, J.J. *appl. Ecol.* **22**, 503–517 (1985).
- Firbank, L.G. & Watkinson, A.R. *J. appl. Ecol.* **22**, 503–517 (1985).
- Grime, J.P. *Plant Strategies and Vegetation Processes* (Wiley, Chichester, 1979).
- Mitchley, J. & Grubb, P.J. *J. Ecol.* **74**, 1139–1166 (1986).
- Firbank, L.G. & Watkinson, A.R. in *Perspectives on Plant Competition* (eds Grace, J.B. & Tilman, D.) (Academic, New York, in the press).
- Tilman, D. in *Community Ecology* (eds Diamond, J. & Case, T.J.) 359–380 (Harper & Row, New York, 1986).
- Law, R. & Watkinson, A.R. *J. Ecol.* **75**, 871–886 (1987).
- Austin, M.P., Groves, R.H., Fresco, L.M.F. & Kaye, P.E. *J. Ecol.* **73**, 667–684 (1985).
- Wilson, S.D. & Keddy, P.A. *Ecology* **76**, 1236–1242 (1986).
- Grime, J.P. & Hunt, R.J. *J. Ecol.* **63**, 393–422 (1975).
- Shipley, B. & Keddy, P.A. *J. Ecol.* (in the press).
- Keddy, P.A. & Shipley, B. *Oikos* (in the press).
- Keddy, P.A. *Competition* (Chapman and Hall, London, in the press).
- Moore, D.J., Keddy, P.A., Gaudet, C.L. & Wisheu, I.C. *Biol. Conserv.* (in the press).
- Keddy, P.A. in *Perspectives on Plant Competition* (eds Grace, J.B. & Tilman, D.) (Academic, New York, in the press).

Another alternative to directed mutation

SIR—Cairns *et al.*¹ argue that bacteria can direct mutations, such that their rate of adaptation is enhanced. Their hypothesis rests on two types of observations. First, that the distribution of certain mutants obtained by selective plating from sister cultures is less variable than expected for spontaneous mutations. And second, following plating, certain mutants are observed after a delay that is inconsistent with their growth rate on the selective medium, implying that the mutations occur only (or more frequently) under selective conditions.

Alternative hypotheses have been

presented that could account for the unexpectedly low variance in numbers of mutants from sister cultures, most notably slower growth of mutants before selective plating^{2,5}. However, Cairns⁶ has challenged others to present alternatives to directed mutation that could explain why certain mutants appear only (or more frequently) under selective conditions.

We have such an alternative hypothesis. Consider the following haploid genotypes. *A* is used to found the sister cultures, and cannot grow at all after selective plating. *A* mutates to *A'*, which grows slowly after selective plating. *A'* mutates