

Experimental evidence that interspecific competitive asymmetry increases with soil productivity

Paul Keddy, Lisa Twolan-Strutt and Bill Shipley

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This study tests the assertion that the degree of competitive asymmetry between pairs of plant species increases with increasing soil productivity. We measured the average degree of competitive asymmetry in an outdoor experiment involving 18 species of herbaceous wetland plants in each of three levels of soil productivity (1/10 NPK fertilizer + drained soil, full NPK fertilizer + drained soil and full NPK fertilizer + saturated soil). Plants, two per pot, were grown from seed over one growing season. The degree of competitive asymmetry increased 1.31 times in level 2 and 1.45 times in level three of the soil productivity treatment, relative to the least productive treatment.

P. A. Keddy and L. Twolan-Strutt, Dept of Biology, Univ. of Ottawa, Box 450, Stn. A, Ottawa, ON, Canada K1N 6N5. – B. Shipley (correspondence), Département de Biologie, Université de Sherbrooke, Sherbrooke, PQ, Canada J1K 2R1 (bshipley@courrier.usherb.ca).

There is an accumulating body of experimental evidence that shows pairwise competitive interactions amongst plants to be generally asymmetric; that is, if one measures the average decrease in plant performance of each plant due to the presence of the other, one plant suffers disproportionately more than the other. Most of this evidence has come from studies of intraspecific competition but this result has been found in interspecific experiments as well (reviewed in Shipley 1993, Shipley and Keddy 1994). That this result is often found does not mean that pairwise interactions are always asymmetric, nor does it follow that the degree of asymmetry is everywhere constant. Does the degree of interspecific asymmetry vary with environmental conditions? In particular, does the degree of asymmetry increase as the habitat becomes more productive? This is the question posed in this paper.

Silvertown et al. (1994) attributed an increased dominance of grasses over non-grasses with increasing rain-

fall in the Park Grass experiment to an increase in asymmetric competition between these two groups of plants and they explicitly hypothesized that the intensity of asymmetric competition would increase with increasing habitat productivity. Similarly, Harra and Yokozawa (1994) published a mathematical simulation of neighbourhood competition in which the degree of asymmetry increases as soil nutrient levels increase. These conjectures mirror the contentious hypothesis that the intensity of interspecific competition (irrespective of its symmetry) increases with increasing habitat productivity (Newman 1973, Grime 1979, Grubb 1985, Tilman 1988, Keddy 1990). The possibility that these two hypotheses are correct is exciting because it would point to a simple rule governing plant communities: as soil productivity increases, both the intensity and the degree of asymmetry of competitive interactions increase. There is experimental evidence that the intensity of interspecific competition often increases with soil

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productivity (Wilson and Keddy 1986, Bonser and Reader 1995, Kadmon 1995) although contrary evidence has also been published (Wilson and Tilman 1993, Reader et al. 1994). Despite a long-standing interest in plant ecology and agriculture in the effects of different fertilizer treatments on plant performance, few researchers have conducted a systematic search for changes in the degree of asymmetry between competing plant species as soil productivity increases. Mahmoud and Grime (1976) described an experiment involving three species of grasses grown in competition at two different levels of nitrogen in sand culture, and showed that the order of competitive dominance remained constant between the three species but the asymmetry of the competitive effects intensified in the more productive treatment. On the other hand, Harper's (1977) exhaustive review of plant competition experiments contains only scattered references to the degree to which the relative effects of competition by one species on another change with soil nutrient levels and/or soil water availability, and those studies that are cited (for example, Stern and Donald 1962) usually involve legume–nonlegume combinations. Thus, there is little published experimental evidence directly relevant to the question of changes in the degree of asymmetry of these interspecific interactions, and none that study the question using many species in a comparative manner.

In this paper we report upon the experimental measurement of competitive asymmetry in a set of 1080 pairwise interspecific interactions involving 18 herbaceous wetland species and three different soil conditions which represent different degrees of soil productivity.

The definition of soil "productivity" is, admittedly, poorly defined in the ecological literature. The intuitive meaning seems to refer to the amount of plant biomass that a given soil can produce. A quantitative equivalence of growth among species in an equivalent soil environment is clearly not expected since the amount of growth that a particular species will experience will depend both on the abiotic soil environment and on its inherent physiological potential. Furthermore, since productivity refers to "plant growth", soil productivity cannot be synonymous with soil nutrient levels; rather, it refers to the entire set of soil conditions that determine plant growth, including such attributes as water availability, nutrient levels, supply rates or pH. Thus, to say that one soil is more "productive" than another without reference to a particular species, one must refer to a qualitative property of the soil in which all (or a large majority) of the species increase their growth rate (but not necessarily to the same degree) in the more "productive" soil. It is therefore important to compare species that commonly occur in the same habitat type so all of the species in the experiment will respond qualitatively in the same way as the soil environment is manipulated.

Methods

The experiment involved 18 species of herbaceous wetland angiosperms; species names and details of the experimental design can be found in Keddy et al. (1994). The species were chosen to span a wide range of wetland habitats and included mud flat annuals (e.g. *Gnaphalium uliginosum* L.), long-lived clonal dominants (e.g. *Typha angustifolia* L.), dangerous invasive exotics (e.g. *Lythrum salicaria* L.) and nationally threatened species (e.g. *Sabatia kennedyana* Fern.).

The experiment was conducted in an outdoor compound, and involved 1080 pots (10 cm diameter with equal proportions of organic soil, sand and peat). The pots were arranged in randomized blocks. Each of the 5 blocks contained 216 pots with 72 pots in each of 3 soil treatments ("1/10 NPK + dry", "full NPK + dry" and "full NPK + wet"). The "full NPK + dry" treatment consisted of daily watering to maintain humid soil plus addition of 7 mg N, 11 mg P, 27 mg K and 17 mg calcium nitrate per pot every 12 d. Pots drained from the bottom and therefore soil was allowed to dry each day. The "1/10 NPK + dry" treatment was the same as that used in the first treatment except that the fertilizer addition was at 1/10 concentration. The "full NPK + wet" treatment was the same as the "full NPK + dry" treatment except that the drainage holes were at soil level so that the soil was continuously saturated with water. Since the species were wetland plants, we expected the soil productivity to increase in the order of "1/10 NPK + dry", "full NPK + dry" and "full NPK + wet". This result was indeed found, as reported in Keddy et al. (1994).

An additive competition design was used in which one of three "indicator" species was grown in all possible pairwise mixtures with each other and also with 15 other "neighbour" species in each block. The number of neighbour species differs slightly from that used in Keddy et al. (1994) because the patterns of mortality prevented some measures of asymmetry from being calculated. Each pot contained two plants: one from each species in the pair. Each block also contained a pot with a single plant of each of the 18 species grown alone. The indicator species were *Carex crinita* (a perennial tussock sedge), *Gnaphalium uliginosum* (an obligate mudflat annual) and *Lycopus americanus* (a perennial with a facultative annual life cycle). Plants were grown from seed from May to September and the final dry weights of aboveground tissues were measured at harvest.

The degree to which the growth of an average individual of the indicator species (i) was reduced when grown with one of the 17 other neighbour species (j) was measured by the ratio of its final dry weight in mixture (Y_{ij}) relative to its final dry weight in the absence of competing plants (Y_i). We transformed the dry weights to their natural logarithms to obtain nor-

Table 1. Summary of the three-way analysis of variance. The dependent variable is the square root of the degree of competitive asymmetry. Independent factors are the identity of the "target" species, the identity of the "neighbour" species and the level of soil productivity.

Source	df	Type III SS	F	prob(F)
Soil productivity (P)	2	0.49	8.39	0.01
Target species (T)	2	0.48	4.07	0.02
Neighbour species (N)	17	8.34	8.85	$<1 \times 10^{-7}$
P \times T	4	0.10	0.44	0.78
P \times N	33	3.82	1.96	0.01
T \times N	34	6.30	3.15	0
Residuals (P \times T \times N)	64	3.77		

mality. Thus, our average $\ln(\text{final dry weights})$, when back-transformed to an arithmetic scale, are the modal values which are the best estimates of central tendency. The competitive effect (C_{IN}) of each of the neighbour species (N) on one of the indicator species (I) was measured as: $C_{IN} = Y_{IN}/Y_I$. This is the amount by which the average growth of a lone individual of the indicator species was reduced by a single individual of the neighbour species. The asymmetry (A_{ij}) of a two-species interaction was measured by the ratio of the competitive effect of the stronger competitor to the competitive effect of the weaker competitor; thus, $A_{ij} = C_{ij}/C_{ji}$, where C_{ij} is greater than, or equal to, C_{ji} . A value of 1 indicates that the amount by which the growth of the indicator species was reduced by the neighbour species equalled the amount by which the growth of the neighbour species was reduced by the indicator species. Values greater than 1 indicate increasingly asymmetric interactions such that the weaker competitor has its growth reduced proportionately more than does the stronger competitor. Note that this definition of pairwise asymmetry differs from that given in Shipley (1993).

The degree of competitive asymmetry between any pair of species could potentially respond either to the identity of the indicator species, to the identity of the neighbour species, or to the three treatment levels of soil productivity. There were therefore three primary sources of random variation in the experiment. Since there was only one pot per block in which a single plant of a given species was grown alone, we could not calculate the competitive effects within each block without using the same value for the denominator, thus introducing a statistical dependence within each block. To avoid this, we used the means over the five blocks. This means that we did not have replication for the three-way interaction.

The analysis was a three-way ANOVA in which the three-way interaction served as the error term. Because the design was slightly unbalanced, we used Type III, or Sigma-restriction, sums of squares (Searle 1987). The asymmetry values were transformed to their square roots to produce normality.

Results

The mean value of the index of asymmetry was 1.68 showing that the pairwise interactions were generally asymmetric. The three-way analysis of variance is shown in Table 1. Asymmetry was lowest in the "1/10 NPK + dry" treatment at 1.52, which means that the dominant competitor had a competitive effect on the subordinate competitor that was 1.52 times larger than the competitive effect of the subordinate competitor on the dominant competitor. The average asymmetry increased to 1.73 in the "full NPK + dry" treatment level and increased again to 1.84 in the "full NPK + wet" treatment level.

Discussion

The patterns of asymmetry were affected by each of the three experimental variables. That our index of asymmetry depends quantitatively on the identity of the species involved in the interaction is to be expected. In fact, a study of the concordance of rankings of competitive effect and competitive response (*sensu* Goldberg and Fleetwood 1987) of this same data set (Keddy et al. 1994) showed that while the ranking of competitive effect was constant across environments, the ranking of competitive response was not. Thus, the significant effects of "neighbour" and "indicator" species were hardly surprising. The significant effect of soil productivity (*i.e.* fertilization and water availability) on the degree of asymmetry is probably the most interesting one for existing theory. It is well known that species richness declines in more productive habitats (summarized in Grace and Pugsek 1996), but it is unclear to what degree this can be attributed to the mechanism of competition. This study shows that one aspect of competition - asymmetry - increases with soil productivity in this set of wetland species. A previous analysis of these same data (Keddy et al. 1994) showed that both neighbour and indicator species grew poorest in the "1/10 NPK + dry" treatment and increased their growth significantly in the "full NPK + dry" and "full NPK + wet" treatments, the latter two treatments not

being significantly different given the statistical power available in that experiment. Thus our three treatments do represent a gradient of increasing productivity for these species although our three experimental treatments do not represent three equally spaced points along this gradient. It seems plausible that greater asymmetry would lead to more rapid rates of competitive exclusion, although the biological significance (as opposed to the statistical significance) of the average degree of asymmetry measured in the three treatments cannot be definitively determined from our experiments.

It is important to point out that our results refer to the average response of the entire set of species. The conclusions apply to the assemblage of species as a whole even though particular pairs of species, in particular environmental conditions, may have shown contrary results. Keddy et al. (1994) present a series of figures showing the responses of each species. The ability to observe such general trends is a strength of such multispecies studies. If we had limited our study to a few species, then the results would likely fluctuate depending on which pair we had chosen. Since the inferences about competition are usually (if often implicitly) applied to "species" in general rather than being limited to a particular pair, the degrees of freedom in testing our general hypotheses are based on the number of species studied. For this reason, we chose to increase the number of species studied.

Nonetheless, such a broad screening approach introduces several constraints which are important to bear in mind when transferring our results to the field. Our measures were based on growth over a single growing season. Longer experiments might be desirable, particularly for perennial species. We only used aboveground tissues since it was impossible to disentangle the roots of the competing plants. We do not know how the inclusion of belowground tissues might change the results. The plants were grown in pots; the intent was to force the species to interact but in nature there can be some spatial partitioning of the soil between the root systems that would reduce the intensity of competition. Finally, the experiment consisted of plants all sown as seedlings at the same time which tended to equalize the initial sizes of the competing plants. In the field, adults and seedlings often interact and this would presumably increase the asymmetry of the interactions. In spite of these limitations, our values are still the largest published data set that provides estimates of the degree of competitive asymmetry in an entire group of plant species.

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