

Relative competitive performance of 63 species of terrestrial herbaceous plants

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Abstract. There is growing evidence that plant and animal species are arranged in hierarchies of relative competitive performance. More work is needed to determine which plant traits best predict relative competitive performance. We therefore measured relative competitive performance of 63 terrestrial herbaceous plant species using *Trichostema brachiatum* as a reference species (that is, phytometer or target species). The neighbour species came from a wide array of terrestrial vegetation types (e.g. rock barrens, alvars, old fields), and represented a wide array of growth forms (e.g. small rosette species such as *Saxifraga virginiana* and large clonal graminoids such as *Agropyron repens*). The experiment was repeated with two pot sizes: large (control) and small (stress treatment). Relative competitive performance in large pots (controls) was highly correlated with that in small pots (stress treatment) ($r = 0.90$, $p < 0.001$). The hierarchy of relative competitive performance in the large pots was also highly correlated with the hierarchy in the small (stressed) pots ($r_s = 0.91$, $p < 0.001$). Principal components analysis and multiple linear regression showed that plant size (measured by total biomass, above-ground biomass, below-ground biomass, canopy area, height and leaf area index) and leaf shape (measured as length to width ratio, length, width) were the two characteristics that best predicted relative competitive performance (large pots, $r^2 = 0.55$; small pots, $r^2 = 0.48$).

Keywords: Alvar; Barren; Competition; Competitive hierarchy; Old field; Phytometer; Rock barren; Trait.

Nomenclature: Gleason & Cronquist (1963); Morton & Venn (1990).

Introduction

Competition has been shown to be a major force organizing the assembly of plant communities (e.g. Weaver & Clements 1929; Harper 1977; Grime 1979; Keddy 1989; Grace & Tilman 1990), but the actual way in which the effects of competition create structure in these communities is still imperfectly understood. At least five current research paths in competition can be

identified, each associated with a different set of questions: (1) the issue of how competition influences the coexistence of similar species has long been of interest (e.g. Harper & Chancellor 1959; Fowler 1982; Aarssen 1983, 1989; Turkington & Mehrhoff 1989), as has (2) the role of competition in controlling plant distributions along gradients (e.g. Mueller-Dombois & Ellenberg 1974; Austin & Austin 1980; Austin et al. 1985; Gurevitch 1986; Keddy 1990; Burger & Louda 1995; Gaudet & Keddy 1995); (3) the relative importance of competitive response and effect is a relatively new area of activity (e.g. Goldberg & Fleetwood 1987; Goldberg 1990; Goldberg & Landa 1991) as is (4) testing for the existence of competitive hierarchies and exploring patterns in them (e.g. Mitchley & Grubb 1986; Keddy & Shipley 1989; Shipley 1993; Shipley & Keddy 1994; Goldberg 1996; Keddy et al. 1994, 2001). Both of the latter mesh with (5) the study of plant traits and their possible roles in determining competitive performance (e.g. Weaver & Clements 1929; Botkin 1977; Givnish 1982; Tilman 1982; Gaudet & Keddy 1988; Rösch et al. 1997; Weiher et al. 1999). The objective of this paper is to ask some basic questions within the domain of questions 4 and 5 using a comparative approach.

One important generalization about competition is the tendency of species mixtures to be sorted into hierarchies of relative competitive performance. In order to detect such hierarchies, species must be grown in all possible pairs and their performance tested against the null model devised by Shipley (1993). Such hierarchies seem to be typical of mixtures of plant species (Keddy & Shipley 1989; Shipley & Keddy 1994). The principal limitation of the experimental procedure is its requirement for growing species in all pairs, as the number of treatments increases as $n(n-1)/2$. Few experiments have therefore examined combinations of more than 10 species. A simplified procedure uses only a few columns of the entire matrix, in which case all species are compared against a few indicator or phytometer species. The mean competitive performance is then used as an

approximation of the hierarchy likely to have been found in the entire matrix of species pairs. While this simplification lacks the merit of first demonstrating a hierarchy in a full species matrix, and against a null model, it does allow examination of large numbers of species simultaneously. The use of the same word, hierarchy, in both cases, might be misleading, but in practice, all multispecies matrices which have been tested against null models show that hierarchies occur, so it seems reasonable to use the same word 'hierarchy' in both cases rather than invent a new term. Further, there is also evidence for similar hierarchies in corals, fungi, birds, mammals and insects (Keddy 2001), although none of the latter has been rigorously tested against the null model.

Gaudet & Keddy (1988) used this comparative approach to estimate the relative competitive performance of 44 herbaceous marsh plant species and to test whether competitive performance (that is, position in the competitive hierarchy) was correlated with plant traits. They found a strong relationship between the relative competitive performance and above-ground biomass, later showing that these same experimental estimates of competitive performance could predict the distribution of these species along natural gradients (Gaudet & Keddy 1995). Such comparative approaches have certain limitations. The two principal ones are (1) only one or a few reference species is used to rank the other species (as mentioned above with respect to the use of the term hierarchies) and (2) only one or a few standardized environments is examined. These limitations have to be balanced against the strengths: (1) the provision of quantitative estimates of relative competitive performance on large numbers of species simultaneously and (2) the fact that comparison is possible precisely because all species are measured against a common phytometer in a common environment.

How far can one generalize from studies of competition and plant traits in marshes? The only way to find out is to use the same approach in different habitats. We specifically chose old fields because there are many important published studies of competition among small groups of old-field species (e.g. Goldberg 1987; Gurevitch & Unnasch 1989; Aarssen 1989; Turkington & Mehroff 1989; Carson & Pickett 1990; Tilman & Wedin 1991a, b; Wilson & Tilman 1991; Campbell & Grime 1992; Turkington et al. 1993; Rajaniemi & Goldberg 2000), but a comparative approach has not yet been used in this vegetation type.

Recognizing the possibility that different rankings of relative competitive performance might arise in different environments, we also created two experimental treatments (large well-watered pots and small pots with frequent drought). Having first tested for any

effects of environment, we then explored the relationship between plant traits and relative competitive performance. Finally, we compare the traits that best predicted competitive performance in terrestrial plants to those in marsh plants.

Methods

Set up and maintenance of experiment

63 terrestrial herbaceous plant species (Table 1) were collected from a range of vegetation types in eastern Ontario. These were then grown with a target species (*sensu* Goldberg 1990) or phytometer (*sensu* Weaver & Clements 1929; Clements 1935), to provide an estimate of the relative competitive performance of each of these plant species. The vegetation from which the plants were collected included old fields with either deep clay or shallow sandy soils over Precambrian gneiss, old fields with shallow soils over limestone, rock barrens over Precambrian gneiss, and alvars (Nielsen 1993). The term alvar refers to vegetation growing in a thin layer of soil over flat limestone (Catling et al. 1975). The flora and vegetation of these sites is described further elsewhere: alvars (Belcher et al. 1992, 1995; Catling & Brownell 1999a), rock barrens (Catling & Brownell 1999b) and old fields (Keogh 2000). This array of habitats was included in the study principally to maximize variation in growth form and other ecological traits, but also because alvars and rock barrens support regionally rare plant species.

All species used in this experiment, except the phytometers, were collected as ramets between 25 April and 10 May 1990. A ramet is the functional unit of a plant; in this experiment, because all 63 species used were perennials, the functional unit was classified as the over-wintering portion of the plant usually consisting of a section of rhizome several cm long with one apical meristem (e.g. *Aster* spp. and *Solidago* spp.). Grass and sedge ramets usually consisted of a section of rhizome several cm long with several attached leaf blades. Since the plants were collected in early spring when leaves were barely emerged, it was not possible to identify them to species at the beginning of the experiment. Thus, some species were included a number of times, bringing the sample size to 77.

Trichostema brachiatum (*Lamiaceae*), the phytometer or target species chosen for inclusion in this experiment, is a small annual species that grows commonly in alvars. It was previously used in a study of competition (Belcher et al. 1995). Seedlings were collected at the four-leaf stage from the Burnt Lands alvar in Almonte, Ontario (45° 15' N, 76° 05' E) on 10 May

1990 (the site described in Belcher et al. 1992). Seedlings of approximately equal size were removed from the ground with the roots still surrounded by a layer of soil, to minimize transplant shock.

The experimental design required planting one phytometer in the middle of each pot (the target species *sensu* Goldberg 1990, phytometer *sensu* Clements 1935, or more generally, the reference species) with three ramets of a neighbour species. Hence, in this design, the phytometer is being used to measure the relative competitive performance of the neighbour species. The neighbour species were also grown alone in other pots to provide standard individuals upon which the plant traits could be measured. Both ramets (of neighbour species) and seedlings (of phytometers) were transported while moist to an outdoor compound at Carleton University (Ottawa, Ontario) in a cooler, and were transplanted within 24 h of their collection. Three ramets of each of the species were planted in a systematic design around the *Trichostema brachiatum* phytometer (five replicates pots for both pot sizes). As well, to assess growth in the two pot sizes, and to allow the measurement of traits on individuals that were crowded neither by neighbours nor phytometers, all species were planted singly in 1-l and 500-ml pots (10 replicates of the phytometers and five replicates of each neighbour species for both pot sizes)

Two different pot sizes (1 l, 500 ml) were used to create two treatment effects. The 1-l pots (control pots) were designed to allow the plants ample moisture, nutrients and space for maximal growth. The 500-ml pots (stress treatment), on the other hand, were designed to provide the plants with less than ample moisture, nutrients and space. To minimize other differences (beyond those of soil moisture, nutrients and space) each 500-ml container was placed inside a 1-l container. This controlled for any shading or microclimate effects that might differentially affect small pots. Similarly, each 1-l pot contained a 500-ml pot with its base removed to provide root access to the rest of the pot. Thus both treatments had two pots with two rims and two layers of plastic.

Once transplanting was completed, all the pots were randomly assigned to positions in a block so that shading by neighbouring plants was randomized. A 30-cm high cylindrical cage (window screening mesh), was placed over each pot to (1) simulate shading expected in summer grasslands and (2) to ensure that ramets did not fall over and unduly influence the growth of plants in other pots.

All plants were allowed ample water during the first two weeks after transplant. This gave them an opportunity to adjust after their initial transplant shock, reducing mortality. Then the plants in the stressed

treatment pots were allowed to dry to the point at which they began to wilt.

Post transplant seedling mortality was further reduced with a shade cloth (65% shade). The shade cloth was draped over a 2-m high frame, which surrounded the area where the plants were growing, and was left in place for two weeks. When removed, the shade cloth was replaced with bird netting which kept rodents, birds, and other potential herbivores from the experimental pots.

All pots were provided with two hydroponic fertilizers when leaf discoloration indicated the pots were not large enough to provide enough nutrients to sustain the plants over an entire growing season. On 20 June 1990 a syringe was used to inject each pot with a complete hydroponic fertilizer solution at the commercially recommended strength (B & B Hydroponics, Ottawa, Canada). The control pots received 10-ml of the hydroponic solution whereas the stressed treatment pots received 5 ml. The two hydroponic fertilizers were used in equal proportions. The first mixture (7-11-27) contained, by weight, Nitrogen (7.0%), Magnesium (3.75%), Phosphorus (11.0%), Potash (27.0%), Sulphur (4.8%), Iron (0.1%), Magnesium (0.085%), Zinc (0.03%), Boron (0.027%), Copper (0.0041%), and Molybdenum (0.009%). The second mixture (15-0-0) contained Calcium (19%), Nitrogen (15.0%) and Magnesium (3.98%).

Harvesting neighbour species and phytometers

Harvesting of the neighbour plants began on 1 August 1990 when several of the neighbour species began to senesce (indicated by yellowing of their photosynthetic tissue), and it continued for six weeks in order of the senescing sequence. Only those neighbour species that had been grown singly were harvested and used in the analysis – that is, all the traits were measured upon neighbour species that had been grown without interspecific competition, and without exposure to the phytometer. Hence the word ‘neighbour’ indicates only that these harvested plants represented one of the test species used as neighbours in the main experiment, not that the individuals themselves had served as neighbours. Harvesting consisted of removing the plant from its pot, washing all soil from the roots with water, and separating the shoots from the roots. Roots and shoots were dried to a constant weight at 60 °C and weighed to an accuracy of ± 0.005 g.

The *Trichostema brachiatum* phytometers began to senesce 14 August 1990; harvesting started on this date and continued over a two week period. All phytometers were collected, including those surrounded by the three neighbour species. Harvesting of the phytometers was done in the same manner as with the neighbour species.

Table 1. Relative competitive performance (Rcp) expressed as percent reduction in phytometer biomass for 63 terrestrial herbaceous plant species grown in control and stress treatment pots ($\pm 95\%$ confidence interval; $n = 5$).

Species	Rcp (control pots)	Rcp (stress treatment)	Species	Rcp (control pots)	Rcp (stress treatment)
<i>Lechea intermedia</i>	45.2 \pm 16.0	64.2 \pm 15.2	<i>Viola papilionacea</i>	96.7 \pm 2.8	96.2 \pm 2.0
<i>Sporobolus heterolepis</i>	51.2 \pm 26.1	64.9 \pm 7.8	<i>Muhlenbergia mexicana</i>	96.9 \pm 2.1	91.1 \pm 3.3
<i>Carex gracillima</i>	52.8 \pm 29.9	74.4 \pm 18.7	<i>Elymus trachycaulus</i> ²	97.0 \pm 1.6	94.4 \pm 2.5
<i>Carex rugosperma</i>	54.4 \pm 16.7	69.2 \pm 17.5	<i>Penstemon hirsutus</i>	97.0 \pm 1.1	96.2 \pm 1.6
<i>Danthonia spicata</i>	61.4 \pm 28.4	75.5 \pm 12.7	<i>Prunella vulgaris</i> ²	97.2 \pm 2.6	98.6 \pm 0.2
<i>Carex eburnea</i>	64.1 \pm 38.1	79.2 \pm 3.7	<i>Helianthus divaricatus</i>	97.2 \pm 0.9	98.6 \pm 0.2
<i>Danthonia spicata</i> ¹	64.8 \pm 32.7	68.4 \pm 10.8	<i>Plantago rugelii</i>	97.3 \pm 4.4	98.3 \pm 0.8
<i>Panicum depauperatum</i>	67.0 \pm 16.1	77.1 \pm 14.2	<i>Elymus repens</i> ²	97.4 \pm 1.2	95.4 \pm 3.8
<i>Carex crawei</i>	70.1 \pm 19.0	56.1 \pm 36.1	<i>Solidago hispida</i>	97.4 \pm 1.4	97.6 \pm 0.5
<i>Trichostema brachiatum</i>	71.8 \pm 8.4	79.2 \pm 15.2	<i>Hieracium piloselloides</i> ²	97.9 \pm 1.1	95.2 \pm 3.7
<i>Saxifraga virginiana</i>	72.9 \pm 16.2	75.6 \pm 8.8	<i>Linaria vulgaris</i> ²	97.9 \pm 1.2	94.9 \pm 2.6
<i>Carex pallescens</i>	74.9 \pm 6.4	70.0 \pm 25.8	<i>Aster ciliolatus</i>	98.0 \pm 0.8	98.3 \pm 0.6
<i>Carex pennsylvanica</i>	78.9 \pm 8.8	78.4 \pm 17.4	<i>Prunella vulgaris</i> ²	98.1 \pm 3.2	98.6 \pm 0.2
<i>Antennaria neglecta</i>	79.9 \pm 7.7	93.7 \pm 4.8	<i>Solidago gigantea</i>	98.1 \pm 2.7	98.6 \pm 1.9
<i>Mimaurtia michauxii</i>	80.7 \pm 16.0	75.4 \pm 22.5	<i>Aster ciliolatus</i>	98.1 \pm 1.3	96.2 \pm 2.1
<i>Panicum acuminatum</i>	81.6 \pm 5.0	88.8 \pm 5.3	<i>Poa pratensis</i>	98.2 \pm 1.1	96.6 \pm 1.3
<i>Anemone canadensis</i>	81.7 \pm 12.2	85.0 \pm 12.8	<i>Solidago ptarmicoides</i>	98.3 \pm 1.4	96.8 \pm 2.4
<i>Corydalis sempervirens</i>	83.1 \pm 15.9	78.8 \pm 18.6	<i>Potentilla recta</i> ²	98.5 \pm 0.7	98.3 \pm 1.1
<i>Equisetum arvense</i>	83.3 \pm 13.7	82.6 \pm 10.9	<i>Potentilla argentea</i> ²	98.6 \pm 2.5	96.3 \pm 3.3
<i>Carex richardsonii</i>	87.1 \pm 1.6	80.5 \pm 32.0	<i>Cirsium arvense</i> ²	98.7 \pm 0.5	98.4 \pm 0.4
<i>Solidago ptarmicoides</i>	88.1 \pm 17.3	90.0 \pm 16.7	<i>Ranunculus acris</i> ²	98.7 \pm 0.7	98.1 \pm 0.5
<i>Panicum acuminatum</i>	88.7 \pm 9.3	82.6 \pm 11.6	<i>Solidago rugosa</i>	98.8 \pm 0.6	97.4 \pm 2.1
<i>Agrostis gigantea</i> ²	90.0 \pm 7.4	90.5 \pm 3.9	<i>Phleum pratense</i> ²	98.9 \pm 0.8	92.1 \pm 10.6
<i>Sisyrinchium montanum</i>	90.1 \pm 12.6	93.5 \pm 3.3	<i>Senecio pauperculus</i>	98.9 \pm 0.7	96.2 \pm 1.7
<i>Antennaria howellii</i>	90.4 \pm 15.3	92.3 \pm 7.0	<i>Fragaria virginiana</i>	98.9 \pm 0.7	98.2 \pm 1.0
<i>Anaphalis margaritacea</i>	90.8 \pm 3.2	84.1 \pm 12.4	<i>Rumex acetosella</i> ²	98.9 \pm 0.4	97.8 \pm 1.4
<i>Bromus tectorum</i> ²	91.5 \pm 5.9	79.9 \pm 26.8	<i>Aster ciliolatus</i>	99.0 \pm 0.4	98.0 \pm 1.3
<i>Campanula rotundifolia</i>	91.8 \pm 5.7	84.1 \pm 17.6	<i>Echium vulgare</i> ²	99.0 \pm 0.5	97.8 \pm 1.1
<i>Bromus inermis</i> ²	92.3 \pm 9.7	92.8 \pm 3.4	<i>Solidago altissima</i>	99.0 \pm 0.5	98.3 \pm 0.5
<i>Solidago hispida</i>	93.1 \pm 10.8	89.1 \pm 16.9	<i>Solidago rugosa</i>	99.0 \pm 0.5	98.6 \pm 0.3
<i>Urtica dioica</i> ²	93.3 \pm 4.0	92.7 \pm 5.3	<i>Achillea millefolium</i> ²	99.0 \pm 0.6	98.4 \pm 1.4
<i>Glechoma hederacea</i> ²	93.8 \pm 3.6	89.8 \pm 7.4	<i>Chrysanthemum leucanthemum</i> ²	99.1 \pm 0.3	98.3 \pm 0.6
<i>Rumex acetosella</i> ²	94.4 \pm 2.9	93.6 \pm 5.1	<i>Taraxacum officinale</i> ²	99.1 \pm 0.4	98.0 \pm 1.8
<i>Berteroa incana</i> ²	94.5 \pm 4.1	88.0 \pm 5.5	<i>Plantago rugelii</i>	99.2 \pm 0.6	98.9 \pm 0.9
<i>Viola septentrionalis</i>	95.4 \pm 2.9	92.3 \pm 7.3	<i>Hieracium piloselloides</i> ²	99.3 \pm 1.4	98.1 \pm 1.0
<i>Scutellaria parvula</i>	95.5 \pm 3.1	95.6 \pm 2.16	<i>Trifolium pratense</i> ²	99.3 \pm 0.2	98.6 \pm 0.5
<i>Hypericum perforatum</i> ²	96.0 \pm 3.3	93.6 \pm 1.0	<i>Achillea millefolium</i> ²	99.4 \pm 0.3	98.7 \pm 0.5
<i>Hieracium pilosella</i> ²	96.2 \pm 2.2	92.7 \pm 2.8	<i>Plantago rugelii</i>	99.0 \pm 0.3	98.5 \pm 1.9
<i>Aster ciliolatus</i>	96.4 \pm 3.4	92.4 \pm 9.0			

¹Some species were collected from several different collection sites therefore there are replicates of the same species within the data set; in total there are 77 cases; ²Non-native species.

Measurement of plant traits

We measured various plant traits on the plants that were grown singly in order to determine whether they could be used to predict relative competitive performance. Just prior to harvesting, plant height, longest and shortest canopy diameter, leaf length, leaf width, leaf number and leaf area were measured. Canopy area and leaf shape, were derived from these. Plant height was measured from the base of the plant to the maximum height reached by the canopy. Canopy area was calculated using the standard equation for the area of an ellipse ($\text{Area} = xy/4p$, where x = the longest diameter of the ellipse and y = the shortest diameter of the ellipse). Average leaf length and width were assessed by measuring a representative sample of the various leaf sizes on

the plant and then calculating an average on the basis of the number of leaves in each of these representative size categories. Leaf area for each species was measured by tracing a representative selection of leaves on paper; area was measured using the image analyser computer package Optimas (Anon. 1990). Leaf area index (LAI) was calculated on the basis of the number of leaves in each of the representative size categories.

Soil measurements

During the growing season we measured soil depth at the field site of each plant species. We pushed a 4-mm diameter survey pin into the ground near the base of each plant and then took an average of 50 of these measurements. During the harvest, a soil sample was

taken from each of the pots containing a single neighbour species and analysed at the Agri-food laboratory in Guelph, Ontario for nitrate using KCl extraction.

Relative competitive performance

The relative competitive performance of each of the neighbour species was assessed in both the control and stress treatment pots. Relative competitive performance was estimated as the relative ability of each of the neighbour species to suppress the growth of the phytometer; we use the term relative competitive performance because we believe the term competition intensity is best reserved for multispecies associations (see Keddy 1989). It is probable that this design measures competitive effect (*sensu* Goldberg 1987, 1990, that is separate from competitive response), but we will use the less specific term 'relative competitive performance'. Due to the difficulty in removing phytometer roots from neighbour species roots, only above-ground biomass of phytometers was used. The relative competitive performance of each 'neighbour species' was calculated as: $RCP = (P_A - P_T)/P_A$ where P_A was above-ground biomass of the phytometer when grown alone, and P_T was above ground biomass of the phytometer when grown with neighbour species (Wilson & Keddy 1986a; Keddy 1989). P_A ($n = 10$) and P_T ($n = 5$) were expressed as the mean of the experimental replicates.

Statistical analysis

It was first necessary to determine whether the relative competitive performance differed among neighbour species. Because the distribution of phytometer biomass when grown with the neighbour species was non-normal in both control and treatment (Wilks Shapiro, $p < 0.0001$) (Zar 1984), a non-parametric test was used (Siegal 1956).

The relationship between relative competitive performance in the control and relative competitive performance in the stress treatment was examined next. The distribution of the data was markedly skewed (Wilks Shapiro $p < 0.0001$), so Spearman rank ordered correlation was used.

Principal Component Analysis (PCA) was used to reduce the many trait variables to a manageable number for a multiple regression of competitive performance upon plant traits. PCA extracts a linear combination of the original variables, producing a few composite axes or principal components that are orthogonal to one another (Manly 1986). This procedure is especially useful when the original variables measure a related trait, such as size or shape.

Results

Relative competitive performance

It was first necessary to assess whether the neighbour species caused a competitive effect on the phytometers. The biomass of phytometers when grown alone was significantly greater than the biomass of phytometers when grown with neighbour species in both the control (Mann-Whitney U Test, $n_1 = 20$, $n_2 = 380$, λ , $z = -7.39$, $p < 0.00001$) and the stress treatment (Mann-Whitney U Test, $n = 20$, 370 , λ , $z = -7.43$, $p < 0.00001$). Thus a competitive effect exists to be further explored.

It was next necessary to explore differences between control and experimental treatments. First, we examined the phytometers in each treatment. The biomass of phytometers grown alone in the control pots was significantly greater than the biomass of phytometers when grown alone in the stress treatment pots (Mann-Whitney U Test, $n_1 = 20$, $n_2 = 20$, $z = -3.80$, $p < 0.001$). Further, the biomass of phytometers when grown with neighbour species in the control pots was significantly greater than the biomass of phytometers when grown with neighbour species in the treatment pots (Mann-Whitney U Test; $n = 380$, 370 , $z = -2.54$, $p < 0.05$). Next we examined the neighbour species. The biomass of neighbour species when grown singly in the control pots was significantly greater than in the treatment pots (Mann-Whitney U tests: (1) total biomass; $n = 386$, 388 , $z = -7.42$, $p < 0.0001$, (2) above-ground biomass; $n = 386$, 388 , $z = -7.95$, $p < 0.0001$, and (3) below-ground biomass; $n = 385$, 388 , $z = -5.81$, $p < 0.0001$). Therefore the neighbour species were significantly affected by the two sets of conditions in the experiment.

The mean relative competitive performance of neighbour species in the control pots was not significantly different from the mean relative competitive performance of neighbour species in the treatment pots (Mann-Whitney U, $n = 77$, $z = 1.51$, $p = 0.13$). This indicates that competitive intensity did not vary between the two treatments.

Mean relative competitive performance (measured as percent reduction in phytometer biomass) of each species is shown in Table 1. The neighbour species caused dramatic reduction in growth of the phytometer. In 55/77 cases in the control pots and 51/77 cases in the stress treatment pots, the neighbour plants reduced growth of the phytometer by at least 90%. There were significant differences in relative competitive performance among species in the control pots (Kruskal-Wallis $K = 307.7$, $p < 0.0001$) and stress treatment pots (Kruskal-Wallis, $K = 286.2$, $p < 0.0001$) (Siegal 1956). Species can be ordered by relative competitive performance value, from the weakest competitor (*Lechea*

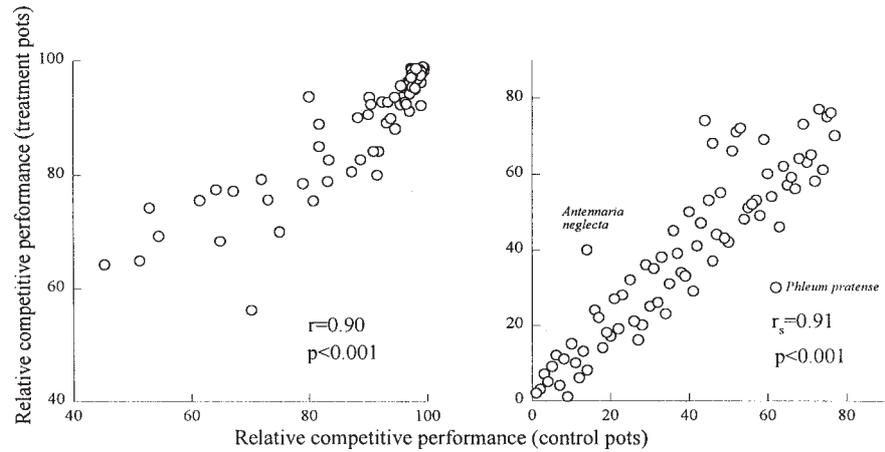


Fig. 1. Scatter plots of competitive performance in the stress treatment pots versus competitive performance in the control pots ($n = 77$). The left-hand figure shows competitive performance measured as percent reduction in phytometer and the right-hand figure shows only rank order (position in competitive hierarchy).

intermedia in the control pots and *Carex crawei* in the treatment pots) to the strongest competitor (*Plantago rugelii* in both pot sizes) (Table 1). Fig. 1 shows that relative competitive performance in the control pots was strongly correlated with relative competitive performance in the treatment pots.

Traits and relative competitive performance

Table 2 shows that relative competitive performance was correlated with many traits. Because of the complicated correlation structure in this data, we first analysed the plant traits to find uncorrelated principal components, and then asked which component (set of traits) best-predicted relative competitive performance. Soil data were omitted

Table 2. The correlation (r) between plant traits and their relative competitive performance ($n = 63$ species).

Plant traits	Control pots (r)	Stress treatment pots (r)
Biomass, total (g)	0.58 ****1	0.55 ****1
Biomass, below-ground (g)	0.55 ****1	0.59 ****1
Biomass, above-ground (g)	0.53 ****1	0.49 ***
Shoot to root ratio (g/g)	-0.15 ¹	-0.38 ***
Height (cm)	0.31 **	0.20
Leaf length (cm)	-0.29 *	-0.32
Leaf width (cm)	0.52 ****1	0.54 ****1
Leaf shape (length:width)	-0.51 ****1	-0.57 ****1
Leaf number	-0.05	-0.12
Leaf area index (cm ²)	0.45 ****1	0.33 ****1
Canopy area (cm ²)	0.26 * ¹	0.10
Average soil depth (cm) ²	0.34 *** ¹	0.36 *** ¹
Soil nitrate nitrogen (ppm) ³	-0.39 ****1	-0.28 * ¹

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.00001$.

Correlations are simple linear correlation with percent reduction in phytometer biomass; ¹data for these traits were log transformed and percent reduction in phytometer biomass was arcsine square root transformed; ²soil depth where plants occurred in the field; ³these are indirect measures of below-ground traits in that all pots received the same soil mixture and among species differences at the end of the experiment can be attributed to differences in below-ground activities.

from this procedure to concentrate on plant traits.

The remaining 11 variables yielded four principal components (PC) that could explain 89.6% of the variation in the variables for control pots and 89.1% for stress treatment pots (Table 3). Those variables, which carried the most weight for each principal component, were considered to be the most important. Using variables with component loadings of 0.5 or higher, PC1 may be interpreted as size (total biomass, above-ground biomass, below-ground biomass, canopy area, height, LAI), PC2 as the leaf shape measures (length:width, length, width), PC3 as the number of leaves and PC4 as the shoot:root ratio. The size measures, number of leaves and shoot:root ratio have positive coefficients for both control and treatment (Table 3). For control pots, length and length:width ratio have negative coefficients, while in stress treatment pots, length and length:width ratio is positive and width is negative.

Fig. 2 shows a forward stepwise multiple regression (α to enter = 0.05) of arcsine (relative competitive performance) against the four principal components for both treatments. For control pots, PC1 (size measures) and PC2 (leaf shape measures) were significant and explained 55.2% of the variation in relative competitive performance ($n = 71$, $p < 0.001$, Table 4). For stress treatment pots, PC1 and PC2 explained 48.4% of the variation ($n = 72$, $p < 0.001$, Table 5). For both regressions, the residuals were normal and homoscedastic.

To address the original question, regarding measurable traits that best predict relative competitive performance, it is necessary to consider the loadings of each variable of the principal components. For both control and treatment, *total biomass* explained the most variation for PC1 (component loading: control pots = 0.966, stress treatment pots = 0.953). *Length to width ratio* explained the most variation for PC2 (component loading; control pots = 0.980, stress treatment pots = 0.939).

Table 3. The results of a principal components analysis upon the correlation matrix of 11 plant traits. The coefficients in the columns indicate the importance of that plant trait in defining the principal component in that column. The columns are ordered by the percent of variance they explain (bottom row). Note that the coefficient for the length:width ratio on PC2 is negative for control pots (top), but positive for stress treatment pots (bottom). All variables have been log transformed.

Control	PC1	PC2	PC3	PC4
Total biomass	0.218	0.035	-0.045	-0.064
Above-ground biomass	0.208	0.032	0.088	0.185
Below-ground biomass	0.195	0.041	-0.176	-0.297
Canopy area	0.189	-0.137	0.047	0.149
Height	0.171	-0.136	-0.003	0.012
Leaf area index	0.160	0.106	0.090	0.182
Length:width	-0.009	-0.405	0.013	-0.050
Leaf width	0.031	0.321	-0.262	0.306
Leaf length	0.021	-0.303	-0.284	0.273
Leaf number	0.062	0.030	0.446	-0.376
Shoot:root	-0.028	-0.020	0.358	0.646
% variance explained	40.36	22.02	17.25	9.97
Stress treatment	PC1	PC2	PC3	PC4
Total biomass	0.221	-0.043	-0.016	-0.040
Above-ground biomass	0.205	0.013	0.130	0.250
Below-ground biomass	0.200	-0.094	-0.152	-0.293
Leaf area index	0.181	-0.072	0.039	0.295
Canopy area	0.172	0.188	0.043	0.052
Height	0.157	0.169	0.009	-0.098
Length:width	-0.016	0.357	-0.123	-0.083
Leaf width	0.058	-0.315	-0.157	0.343
Leaf length	0.039	0.232	-0.381	0.251
Leaf number	0.071	0.031	0.461	-0.351
Shoot:root	-0.058	0.136	0.331	0.636
% variance explained	39.24	23.91	16.50	9.42

Discussion

On the invariance of competitive hierarchies

The degree to which relative competitive performance changes with environment has been disputed for years. Some work suggests that a plant's competitive performance is highly dependent on the environment in which the plants are competing (Austin et al. 1985; Grubb 1985; Tilman 1988, 1990). Grubb (1985, p. 612) says "It is essential to appreciate that plants cannot be ordered in respect of their potential for interference without stipulating the conditions for growth; there are many experimental results published, showing that the outcome of interference between two species or two biotypes depends on temperature, water supply, pH and nutrient-regime". Other work, however, shows competitive ranking of species to be relatively independent from the environment (Fowler 1982; Grime 1979; Keddy 1989; Keddy et al. 2000). Our

experiment was explicitly designed to test between these views. We found that relative competitive performance under stressed conditions was strongly correlated with relative competitive performance under control conditions (Fig. 1). Other pot studies have found similar results (e.g. Gaudet 1994; Keddy et al. 1994, 2001). Moreover, although it is not mentioned in the conclusions of their published study, similar results were also found in a field experiment (Tilman & Wedin 1993; Keddy 2001).

In both the control and stress treatment, the weaker competitors tended to be small grasses and sedges (i.e. *Danthonia spicata*, *Carex rugosperma*) or small rosette species (*Saxifraga virginensis*, *Antennaria neglecta*). *Sporobolus heterolepis* was one of the weakest competitors in both treatments. *Sporobolus heterolepis* is a provincially rare species (Argus et al. 1987), and its regional distribution is largely limited to alvars (Catling et al. 1975). This finding is consistent with the view that

Table 4. Multiple regression between arcsine (relative competitive performance) and four principal components for control pots ($n = 71$, $r^2 = 0.55$, $F = 44.0$, $p < 0.001$).

Variable	Coefficient	t	p
Constant	1.204	63.19	0.000
PC1	0.146	7.648	0.000
PC2	0.100	5.191	0.000

Table 5. Multiple regression between arcsine (relative competitive performance) and four principal components for stress treatment pots ($n = 72$, $r^2 = 0.48$, $F = 34.3$, $p < 0.001$).

Variable	Coefficient	t	p
Constant	1.177	63.398	< 0.001
PC1	0.099	5.282	< 0.001
PC2	-0.117	-6.079	< 0.001

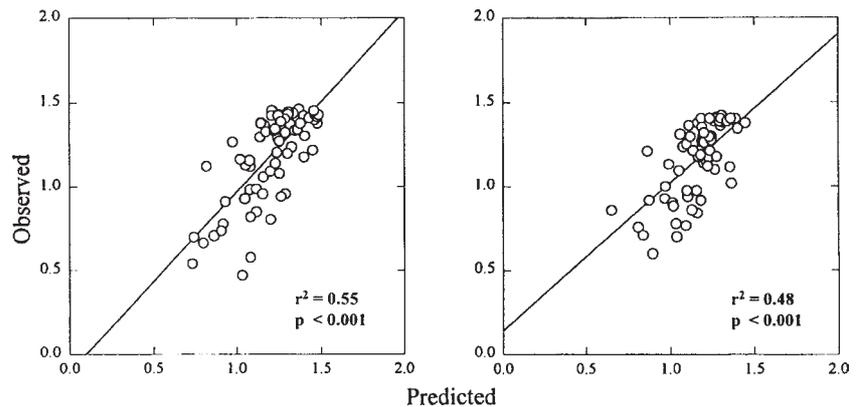


Fig. 2. Observed versus predicted values for relative competitive performance using data from control (left) and stressed pots (right).

some rare and endangered species are restricted to infertile or stressful habitats where they escape from competitors (e.g., Grime 1979; Moore et al. 1989). Many of the species near the high end of the competitive hierarchy were large or leafy species (i.e. *Plantago rugelii*, *Solidago* spp.). Furthermore, the majority of alien species tended to the strong end of the competitive hierarchy. This finding may be important for the control and management of alien plant species.

On one hand, these results refute the proposal that competitive hierarchies vary with environment and that all competitive interactions are contingent. However, it is important to remember that this is not a simple dichotomy. The presence of clear competitive hierarchies, and their constancy between treatments, does not exclude smaller scale contingencies. For example, in stress treatment pots, the narrow-leaved species fared relatively better, whereas in control pots broad-leaved plants did so. This relative advantage of narrow versus broad leaves is superimposed upon the positive effects of plant size and may explain some of the variance in Fig. 1. Individual responses of selected species also varied between treatments; for example, *Phleum pratense* showed a dramatic shift in relative competitive performance from the control to the stress treatment pots. In the control pots it was ranked 62/77 species in the competitive hierarchy, whereas its rank plummeted to 30/77 in the stress treatment pots. *Antennaria neglecta* also showed a dramatic shift in competitive ranking between treatments. In the control pots *Antennaria neglecta* was ranked 14/77 in the competitive hierarchy and in the stress treatment pots its rank escalated to 40/77. Such effects may in part be attributable to differences between relative competitive performance measured on a per gram basis and a per plant basis although a series of studies by Goldberg suggests that competitive effects measured on a per gram basis are the same for old field plants (e.g. Goldberg 1987; Goldberg & Landa 1991). They may direct us to peculiarities in the autecology or physiology of the species concerned. Similarly, our experiment measured only relative com-

petitive effect, and it may be that some of this variance can be accounted for by differences among species in competitive response (although it seems doubtful that the phytometer had much effect upon the surrounding neighbour species). Thus, while there was a significant correlation in relative competitive performance at the coarse scale, there remain autecological patterns to explore at the fine scale.

Such autecological patterns can be a significant problem when only a few species are used in a study. Note that the quotation from Grubb (1985) that opened the discussion refers to experiments using only two species or biotypes. The majority of studies concerning plant competition use only a few species interacting in pairwise situations (Williams 1962; Harper 1963; Goldsmith 1978; Mitchley & Grubb 1986; Wilson & Keddy 1986a; Tilman & Wedin 1993). When only a few species are used, one cannot distinguish between autecological peculiarities of the species concerned, and general scientific principles (Keddy 1993). Moreover, as Grubb's reference to biotypes suggest, very similar species are often used in competition experiments (e.g. Fowler 1982; Austin et al. 1985; Schoen et al. 1986). Changes in relative competitive performance may be much more pronounced when species of different competitive performance interact (Keddy & Shipley 1989; Keddy 1990; Shipley & Keddy 1994). Similar species also tend to have symmetric rather than asymmetric interactions (Wilson 1988; Johansson & Keddy 1991; Keddy 2001). In situations with similar species, hierarchies may be least important in determining the outcome of competitive interactions, and minor fluctuations in environment may then have a major influence on competitive rankings. The apparent importance of hierarchies of relative competitive ability may therefore depend upon the kind of experiment that is designed. The question is therefore not whether there is a right design or a wrong design, but rather which kind of design is most appropriate for which kinds of questions.

Traits and relative competitive performance

Size measures were the best predictor of relative competitive performance. Of those, total biomass explained the most variation. This finding is consistent with several past studies that have taken relative competitive performance and plant traits into consideration and have found size-related traits to be most important. As early as 1933, Clements summarized the results of many transplant and removal experiments in prairie vegetation and concluded that in general taller grasses have a competitive advantage over the shorter. Other more recent examples of these results have included Grime (1974), Goldsmith (1978), Goldberg & Fleetwood (1987), Wilson & Keddy (1986b), and Mitchley & Grubb (1986). Gaudet & Keddy (1988a) have used a similar design to measure relative competitive performance of 44 herbaceous marsh plant species; regression analysis revealed that average dry weight of the neighbour species when grown singly could explain 64% of the variation in relative competitive performance. When other size related variables were included in a multiple regression (height, canopy diameter, canopy area) they were able to explain 74% of the variation. These studies suggest that plant size may be a good predictor of relative competitive performance across a range of vegetation types.

The best leaf shape predictor, length to width ratio, has a different relationship with relative competitive performance for control and stress treatment pots. For control pots a plant with rounded leaves (forb species) were better competitors (as length:width decreased, relative competitive performance increased). For stress treatment pots, the opposite was true: plants with narrow leaves (a high length:width, such as grasses or sedges), were stronger competitors.

While this shift in relative competitive performance with changing leaf shape is interesting, the significance is unclear because so little is known about the factors affecting leaf form (Givnish 1987). Indeed, Givnish's comprehensive review makes no mention of competitive performance as a constraint on leaf shape, although he too notes the importance of plant size in controlling the height of leaves relative to neighbours (Givnish 1982). Leaf area is generally positively correlated with rapid growth (e.g. Reich et al. 1992; Reich 1993) which is thought to be one component of competitive ability (Grime 1973) but may also be related to factors such as resistance to herbivore damage (Southwood et al. 1986). The degree of dissection of leaves can vary with altitude, but the role in competition is apparently unknown (Gurevitch & Schuepp 1990; Gurevitch 1992). Experimental work has shown that both monocots and dicots, and linear leaved and broad-leaved plants, have

similar competitive effects on a per gram basis (Goldberg 1987; Goldberg & Landa 1991). Rosette plants may be a special case, where prostrate growth form makes the plant particularly sensitive to competition (e.g. Wilson & Keddy 1986; Reader & Best 1989) – but this is a function again of plant size rather than leaf shape.

On mechanistic interpretations

While our results show that measures of plant size and leaf shape are predominant traits associated with relative competitive performance (Fig. 2), they do not provide a mechanistic interpretation of resource competition, nor were they intended to. Large plants may simply have other traits which confer strong competitive performance, such as physiological activity rates (i.e. high rates of resource capture above- and below-ground, Chapin 1980). Screening for such traits, and testing for correlations between them and estimates of relative competitive performance, would be an obvious way to test this proposition. Biomass is associated with the ability to capture resources since it provides a large surface area for capturing resources (Grime 1979). This could simultaneously enhance growth and deny resources to neighbours (Keddy 1989; Goldberg 1990). It is also true that heavier plants also tend to be taller plants, at least in this vegetation type. We know that light availability and quality decrease exponentially with distance below the top of the canopy (Fitter & Hay 1983). Similarly, light penetration to the soil surface was a negative exponential function of above-ground biomass of five prairie grass monocultures (Tilman & Wedin 1991). As the larger plant gets taller, its shorter counterpart is more shaded. Thus the competitive interaction subsequently becomes more and more asymmetric (Wiener 1986; Keddy & Shipley 1989; Keddy 1989; Johanssen & Keddy 1991).

Since below-ground resources (soil nutrients and water) are also important for plant growth, an obvious question is whether biomass or height is less important in the stress treatment pots where below-ground resources were deliberately maintained at low levels. Height was no longer correlated with relative competitive performance (Table 2). This suggests that in the stress treatment pots, water or nutrients became a limiting resource. Shifts in allocation to roots versus shoots in response to light and soil resource availability are known to influence per-plant uptake rates of all resources (Chapin et al. 1987). Perhaps those plants that were able to allocate more energy to building a large and extensive root system were better able to monopolize the limiting resources in the stress treatment pots. Silvertown (1980) suggests that botanical equilibrium in the Park Grass experiments can be in part attributed to the limitation of grasses by soil nitrogen, and legumes by minerals, whereas the individual species representing

grasses and legumes may be determined by other factors.

To experimentally explore resources limiting performance of different species, Carson & Pickett (1990) applied four different treatments on old fields in New Jersey: (1) added macronutrients, (2) added water, (3) added light (achieved by tying back tall plants to remove their shade from a plot and (4) added disturbance (achieved by digging with a hand trowel early in the growing season). These fields are normally dominated by goldenrods and asters, with *Solidago canadensis* and *Aster pilosus* most common, and *S. graminifolia*, *S. juncea*, *S. rugosa* and *S. nemoralis* also found. Added nutrients increased the cover of these dominants, and added water also increased cover in the second year when rainfall was below normal. Disturbance significantly reduced canopy cover, but only for the first year. Subcanopy species (e.g. *Fragaria virginiana*, *Hieracium pratense* and *Rumex acetosella*) had the reverse response. These results make intuitive sense: since canopy-forming species are unlikely to be limited by the availability of light, soil resources remain the likely limiting factor. Further, since canopy plants remove light for subordinates, any factor that increases the growth of the canopy should further restrict the subordinate or subcanopy plants; hence the deleterious effects of added nutrients upon subcanopy species. Since canopy species are taller than subcanopy species, there is likely to be size dependence in relative ability to tolerate shortages of soil resources as opposed to shading.

Some caveats

Although the results of this experiment suggest invariant competitive rankings at the broad scale and contingent rankings at a finer scale, the experiment does not tell us how these results would have changed had the experiment been run over a longer period of time. Perhaps if this experiment had lasted several years, or even several plant generations, relative competitive performance would have changed. Current constraints in scientific funding seem to allow either the examination of a few species over many years or many species over one year. Neither is right or wrong, and each offers different windows into the same unknown region.

There may be a multitude of other factors that interact with positions in a competitive hierarchy. This experiment used only one treatment. Other environmental variables may also affect the hierarchy. Various forms of grazing have been found to control the composition of plant communities (e.g. Southwood et al. 1986; Louda et al. 1990; Campbell & Grime 1992; Turkington 1993; Burger & Louda 1995) and resistance to grazing may override competition as a factor controlling species composition in old fields. These questions, however, cannot

be answered until further studies using many species and multiple environmental treatments are carried out.

Phylogeny may also complicate interpretations (Hodgson 1986; Hodgson & Mackey 1986). Some closely related species such as *Carex* had similar competitive abilities (Table 1). Hodgson & Mackey (1986) report, not surprisingly, that plant families share similar life history traits. This, of course, does not obviate the merit of seeking broad correlations among plant traits, community properties, and environmental factors. It simply reminds us to consider evolutionary as well as proximate causes in interpreting such patterns.

Comparative approaches using reference species (phytometers) have certain advantages and disadvantages for studying competition. If this method is selected, the choice of a phytometer is still often subjective. *Trichostema brachiata* was chosen because it was abundant in the field, easy to collect, and had been found in past studies to be easily established as a seedling (Belcher et al. 1995). The results of this experiment, however, suggest that choosing a phytometer of greater competitive performance would have been preferable. *Trichostema brachiatum* was a fairly weak competitor and therefore most species at the high end of the competitive hierarchy were able to highly suppress it (Table 1). This obscured the range of competitive abilities of species at the upper end of the hierarchy. Using a phytometer with a more moderate competitive performance would probably have clarified the hierarchy of competitive abilities at the strong end of the continuum. A further limitation might have been our use of an annual reference species to assess the competitive performance of perennial species.

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