PREDICTING COMPETITIVE ABILITY FROM PLANT TRAITS: A COMPARATIVE STUDY OF 63 TERRESTRIAL HERBACEOUS PLANT SPECIES

by

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ABSTRACT

There is critical need for studies on interspecific competition which enable general principles to be deduced that apply beyond the species and conditions of a particular study or site. Studies on plant traits are a key part of this search for general principles. I measured relative competitive ability in 63 terrestrial herbaceous plant species using the phytometer *Trichostema brachiatum*, to test whether competitive ability can be predicted from simple measurable plant traits. The test species utilised in this experiment represented a wide array of terrestrial vegetation types (e.g. rock barrens, alvars, old fields), and an array of growth forms, from small rosette species (e.g. *Saxifraga virginiensis*) to large clonal graminoids (e.g. *Agropyron repens*). The experiment was carried out under both a "normal" and a "drought" treatment. Multiple linear regression showed that there was a strong relationship between plant traits and competitive ability (Normal treatment--r^2=0.54; Drought-- treatment r^2=0.55). Total plant biomass explained 34% of the variation in competitive ability in the normal treatment and below-ground biomass explained 35% of the variation in the drought treatment. Leaf shape explained most of the residual variation.

The competitive hierarchy for plants in the normal and drought treatment was compared. Rankings for individual species varied between treatments, however, when all species were compared simultaneously, competitive hierarchies in both treatments were highly correlated (r_s=0.91). This suggests that invariant and variant views of competitive

hierarchies are not mutually exclusive but instead depend on the scale at which competition is being addressed. On the broad scale, relative competitive abilities appear consistent across different environments.

Thus, both traits and hierarchies show general repeatable patterns that allow us to generalize from one set of circumstances to another.

RESUME

Il y a un besoin fondamental d'études sur la compétition interspécifique qui permettront de déduire certains principes généraux qui ne sont pas nécessairement liés à des conditions environnementales particulières ou aux espèces d'un site particulier. Les études qui utilisent les caractéristiques des plantes sont primordiales pour la définition de ces principes généraux. Hors de cette recherche, j'ai mesuré les tendances compétitives relatives de 63 espèces de plantes terrestres herbacées en me servant du phytomètre *Trichostema brachiatum*, afin de vérifier si les tendances compétitives de certaines plantes peuvent être prédites à partir de caractéristiques mesurables. Les espèces utilisées pour cette étude étaient typiques de plusieurs types de communautés végétales terrestres (ex. "rock barrens", "alvars", "old fields") et d'un grand nombre de morphologies, allant de petites espèces ayant la forme de rosettes (ex. *Saxifraga virginiensis*) à de grandes espèces de graminées (ex. *Agropyron repens*). L'expérience a été menée sous des conditions à la fois "humides" et sous des conditions de "sécheresse". Une régression linéaire d'ordre multiple a révélé qu'il y avait une relation importante entre les caractéristiques de plantes et leurs tendances compétitives (expérience sous conditions "humides"--r^2=0.54; expérience sous conditions de "sécheresse"--r^2=0.54). La biomasse totale de plantes explique 34% de la variation associée avec les tendances compétitives lorsque les conditions sont humides alors que la biomasse des parties souterraines de la plante explique 35% de la variation de ces mêmes tendances compétitives sous conditions de sécheresse. La forme des feuilles explique la variation résiduelle.

Les hiérarchies compétitives des plantes sous conditions normales et sous conditions de sécheresse furent comparées. On a découvert que le rang des espèces variait selon le traitement, bien que, lorsque toutes les espèces étaient incluses dans une analyse linéaire, les hiérarchies compétitives pour les deux types de traitements sont corrélées (r_s=0.91). Ceci suggère que des visions variante et invariante des hiérarchies compétitives ne sont pas mutuellement exclusives mais dépendent plutôt de l'échelle utilisée. En gros, les tendances compétitives relatives semblent persister d'un environnement à l'autre. Ainsi, les caractéristiques morphologiques et les hierarchies offrent des modèles qui se répètent et qui nous permettent d'établir certaines généralisations d'une série de circonstances à l'autre.

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INTRODUCTION

Competition is thought to be a major organizing influence in plant communities (Grime, 1979; Grace and Tilman, 1990; Tilman, 1988; Keddy, 1989) yet it is a process that is still poorly understood at the community level. There are few general predictive models (e.g. Tilman 1982, 1988; Givnish, 1982; Botkin, 1977) of interspecific competition in community ecology, probably in part because traditional studies of plant communities have tended to focus on only a few particular species. When such a small number of species is used in an experiment, we often cannot make broad generalizations (Connell, 1983; Schoener, 1983; Keddy, 1989, 1991; Goldberg & Barton, 1992). However, this problem can be solved in part by using a comparative approach, that is, by comparing the competitive abilities of many species simultaneously. This requires the systematic screening of a large number of species under standardized experimental conditions (eg. Grime & Hunt, 1975; Grime *et al.*, 1981; Gaudet & Keddy, 1988a; McCanny, *et. al.*, 1990; Keddy, *in press*). This method will let us look for quantitative relationships between plant traits and competitive ability.

This comparative approach was used by Gaudet and Keddy (1988a), to measure the relative competitive ability of 44 herbaceous wetland plant species and to test whether competitive ability was correlated with simple measurable plant traits. They found that there is a strong relationship between the competitive ability of herbaceous wetland plants and their above-ground biomass (Gaudet and Keddy, 1988a), and that nationally rare species have very low competitive ability (Gaudet and Keddy, 1988b).

But does this relationship occur in other plant communities? The results of numerous investigations suggest that height of canopy is of great importance in determining plant competitive ability (Clements, 1933; Grime, 1974; Goldsmith, 1978; Mitchley and Grubb, 1986; Goldberg & Fleetwood, 1987; Wilson and Keddy, 1986b; Mitchley, 1988; Keddy and Shipley, 1989). However most of these studies deal with only a few species, and do not explicitly test for quantitative relationships between plant traits and their competitive ability. The first objective of this study was therefore to test whether competitive ability of terrestrial herbaceous plant species could be predicted from simple measurable plant traits. I specifically chose dry old fields because there are so many published studies of competition among small groups of old field species (eg. Goldberg, 1987; Aarssen, 1989; Tilman, 1989; Tilman & Wedin, 1991a & b; Wilson & Tilman, 1991), but the comparative approach has not yet been used in this vegetation type.

A potential drawback to this comparative approach is that one might get different rankings of relative competitive ability in different experimental environments. Therefore, I also created two experimental treatments ("normal" and "drought") to determine (2) whether relative competitive ability varies between environmental conditions. Finally, since existing examples are from wetlands, I wanted to determine (3) whether or not those traits that best predict competitive ability in terrestrial vegetation differ from wetlands.

If differences do exist in traits predicting competitive ability, surely they can be found in comparing dry fields to wetlands.

METHODS

INITIAL SET-UP AND MAINTENANCE

Sixty-three terrestrial herbaceous plant species (**Table 1**) were collected from a range of vegetation types. These were then grown with a common indicator species, or phytometer ("phytometer" *sensu* Weaver & Clements, 1929; Clements, 1935), such that the relative competitive ability of each of these plant species (the test species) to suppress the phytometers could be assessed. Such an approach is referred to as a modified additive design (Welbank, 1963; Harper, 1977; Goldberg & Fleetwood, 1987; Gaudet & Keddy, 1988a; Keddy, 1989). The vegetation sites from which the plants were collected ranged from old fields, to rock barrens, to alvars (**Appendix 1**). An alvar is a Swedish term for a vegetation system growing in a thin layer of soil over an essentially flat limestone rock base (Catling *et al.*, 1975; Belcher, 1991a & b, Belcher *et al.*, 1992). Collecting from a range of vegetation types insured that the various plant species, chosen for inclusion in the experiment, possessed an array of growth forms and thus would likely have different competitive abilities. Alvars were included in this particular study, as they contain many rare species and some endemics, which may deserve listing with COSEWIC (Committee on the Status of Endangered Wildlife in Canada).

The test species used in this experiment were collected as ramets from the various vegetation sites. A ramet is the functional unit of a plant, and in this experiment, because all test species used were perennials, the functional unit was classified as the overwintering portion of the plant consisting (usually) of a section of rhizome several cm long with one apical meristem (e.g. *Aster* sp. and *Solidago* sp.). Grass and sedge ramets collected consisted (usually) of a clump of root or a section of rhizome several cm long with several blades already arising from the crown.

Trichostema brachiatum (family Lamiaceae), the phytometer chosen for inclusion in this experiment, is a small annual herbaceous plant species which grows commonly in alvars. These were collected at the four-leaf seedling stage from the Burnt Lands alvar in Almonte, Ontario (45°15'N, 76°05'E) on May 10 1990. Collection and transplant of ramets took place from April 25 1990 to May 10 1990. Phytometer seedlings of approximately equal size were removed from the ground with the roots still surrounded by a layer of soil to minimize transplant shock.

Both ramets of test species and seedlings of phytometers were transported to an outdoor compound at Carleton University (Ottawa, Ontario) in a damp cooler where they were transplanted within 24 hours of their collection. Single *Trichostema brachiatum* phytometers were planted in the middle of 1L and 500 mL plastic pots containing a 1:1:1 mixture of sand, soil and peat. Three individuals of each of the ramets were planted in a systematic design around the *Trichostema brachiatum* phytometer (5 replicates of each for both pot sizes). As well, all species were planted singly in the centre of the 1L and 500 mL pots (10 replicates of the phytometers and 5 replicates of each of the test species for both of the pot sizes) (Figure 1) to assess optimal growth under the experimental conditions.

Two different pot sizes (500 mL, 1L) were used in this experiment to create two treatment effects. The 1L pots ("normal treatment") were designed to allow the plants ample moisture, nutrients and space for maximal growth. This normal treatment was designed to duplicate mesic conditions and may not duplicate conditions found in the field. The 500 mL pots ("drought treatment"), on the other hand, were designed to provide the plants with less than ample moisture, nutrients and space for maximal growth. Thus, the normal treatment plants had a resting volume twice the drought treatment plants. To control for other conditions (beyond those of soil moisture, nutrients and space) each 500 mL container was placed inside a 1L container. This controlled for any shading or microclimate effects which 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. This allowed both treatments to have two pots with two rims and two layers of plastic.

Once transplanting was completed, all the pots were randomly assigned to blocks of 20. This insured random shading by neighbouring plants. A cylindrical cage 30 cm high, made out of window screening mesh, was subsequently placed around each pot to (1) duplicate shading expected in summer grasslands and (2) to insure that ramets did not fall over and unduly influence the growth of plants in other pots.

All plants were allowed ample moisture during the first two weeks after transplanting. This gave them an opportunity to adjust after their initial transplant shock, thus insuring reduced mortality. After this two week time period, the plants in the 500 mL pots were left to periodically dry to the point at which they looked water stressed (ie. withered), thereby enhancing the stressful environment being created in these smaller pots.

Post transplant seedling mortality was further reduced with a shade cloth (65% shade). This shade cloth was draped over a 2 meter 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 out of the experimental pots.

All pots were periodically provided with fertilizer as signs of leaf discoloration indicated the pots were not large enough to provide enough nutrients to sustain the plants over an entire growing season. On June 20, 1990 a syringe was used to inject each pot with a complete fertilizer solution at the commercially recommended strength (B & B Hydroponics, Ottawa, Canada). The fertilizer contained an equal mixture of 7-11-27 and 15-0-0 fertilizers. The 7-11-27 portion or the fertilizer 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 15-0-0 portion of the fertilizer contained Calcium (19%), Nitrogen (15.0%), and Magnesium (3.98%). The 1L pots received 10 mL of the hydroponics solution whereas the 500 mL pots received only 5 mL.

HARVESTING TEST SPECIES

Several of the test species began to senesce August 1 1990 (as made evident by yellowing of their photosynthetic tissue), thus harvesting of the single test plants was started and continued in order of their senescing sequence. Harvesting of the test species was carried over a six week period. Only those test species that had been grown singly were harvested. Harvesting consisted of removing the plant from its pot, washing all soil from the plants' roots with water, and separating the shoots of the plant from its roots. Roots and shoots were taken back to the lab and were dried to a constant weight in a 60°C drying oven and weighed to ±0.005 g.

MEASURING PLANT TRAITS

I measured some 20 traits over the course of the experiment to determine whether plant traits can be used to predict competitive ability. Traits measured included: biomass, morphological traits, soil depth, flowering, nutrient levels in soil at the end of the growing season, and the ability of plants to deplete water resources over a three hour time span (Appendix 4a & 4b).

Morphological traits

It has been suggested by past experiments that biomass indicates competitive ability (Gaudet & Keddy, 1988a), thus a measure of test species' biomass was included in this experiment. The dry biomass of test species shoots and roots was assessed by weighing them to a ±0.005 g accuracy. It has been suggested that plants can monopolise limiting resources will be competitive dominants (Tilman, 1982, 1988). Several resources for which plants compete include light, soil nutrients, and water. The morphological measurements chosen for inclusion in this experiment were those that would likely enhance a plant's ability to capture resources. The results of numerous investigations suggest that height of canopy is of great importance in determining a plant's competitive ability (Clements, 1933; Grime, 1974; Goldsmith, 1978; Mitchley and Grubb, 1986; Keddy and Shipley, 1989; Gaudet and Keddy, 1988a). Various aspects of leaf morphology (ie. leaf shape, leaf area, canopy area, leaf number) influence a plant's photosynthetic surface. Plants with large photosynthetic surfaces can monopolise light resources, which should give them a competitive advantage. Therefore, several traits concerning leaf morphology were assessed. Just prior to harvesting several other morphological measurements were made on each of the test plants: plant height, canopy diameter, leaf length, leaf width, leaf number and, leaf area (**Table 2**). Several other measures were derived from these measures. These included: canopy area and leaf shape. Plant height was measured from the base of the plant to the maximum height reached by the canopy. Canopy area was assessed by measuring the longest and shortest diameter reached by the canopy. Canopy area was then calculated using the standard equation for the area of an ellipse (Area=$xy/4\pi$, where x=the longest diameter of the ellipse and y= the shortest diameter of the ellipse). Average leaf length and width was assessed by measuring a representative sample of each 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 was measured by tracing a number of the plants' leaves on a piece of paper. The leaves traced were representative of the various leaf sizes on the plant. Their area was then measured using the image analyzer computer package Optimas (1990), and leaf area index (LAI) was calculated on the basis of the number of leaves in each of the representative size categories.

Flowering

The date that the various plant species began to flower was noted throughout the growing season. The day that the first species began to flower was marked as day one. This information was used to determine whether competitive ability can be predicted from knowledge of when plants flower.

Soil depth

I thought that some traits might be correlated with the soil depth at which plants occurred in the field. Therefore, during the growing season a measure of soil depth was taken at the field sites where each of the plant species had been collected. This was done by pushing a 4 mm diameter survey pin into the ground near the base of each plant and then taking an average of 50 of these measurements.

Nutrient removal

If the test species differed in their rates of nutrient removal, it was just possible that this could be detected by measuring the nutrients remaining in the soil at the end of the growing season. One central prediction is that species that can create the lowest level of the limiting resource (R^*) will exclude other species limited by that resource (Tilman 1976, 1982, 1990; Tilman and Wedin 1991a & b). Therefore, during harvest, a soil sample was taken from each of the pots containing a single test species and was sent to the Agri-food laboratory in Guelph, to be analyzed for five major macronutrients--nitrogen, potassium, magnesium, calcium, phosphorus--salts and pH.

Water uptake

Drought is known to be a factor with which many of these species must contend in the field (Catling et al, 1975). Therefore, I tried to measure their relative ability to exploit water from infrequent summer rainfalls. On July 26 and 27 1990, a time at which all plants had reached their peak height, plants grown singly in the drought treatment were compared for their relative ability to take up water. This consisted of randomly selecting plants growing in the 500 mL pots, saturating the soil with water, taking the pot's weight, and then three hours later measuring the weight again. This measurement was taken twice for all plants, once on July 26 and once on July 27.

COMPETITIVE ABILITY

The *Trichostema brachiatum* phytometers began to senesce August 14 1990, thus harvesting was started on this date and continued over a two week period. Harvesting of the phytometers was done in the same manner as with the test species. All phytometers were collected, including those surrounded by the three test species. The roots and shoots from all the test species and phytometers were later taken back to the lab and were dried to a constant weight in a 60°C drying oven, and weighed to a ±0.005 g accuracy.

The competitive ability of each of the test species was assessed in both the normal and drought treatments. Competitive ability was measured as the relative ability of each of the test species to suppress phytometer growth. Due to the difficulty in separating phytometer roots from experimental pots, only above ground biomass of phytometers was used. Competitive ability (CA) was calculated as:

$$\text{COMPETITIVE ABILITY (CA)} = \frac{(P_A - P_T)}{P_A}$$

where CA is a measure of the relative competitive ability of the test species, P_A is above ground biomass of the phytometer when grown alone, and P_T is above ground biomass of the phytometer when grown with test species. P_A (n=10) and P_T (n=77) were expressed as the mean of the experimental replicates. The difference between the biomass of the phytometers grown with and without test species is divided by the biomass of the phytometer grown without test species to account for environmental conditions (Wilson and Keddy, 1986a).

STATISTICAL ANALYSIS

In order to determine which trait(s) best predict competitive ability it is necessary to test whether the competitive abilities of the test species are significantly different. As the data for phytometer biomass when grown with test species in both treatments were non-normal (Wilks Shapiro, $p<0.0001$) (Zar, 1984) a non-parametric Kruskal-Wallis test was used to test for the significant differences between competitive abilities (Siegal, 1956).

Correlation analysis and univariate linear regression was used to determine which trait(s) best predicted competitive ability in each treatment. The residuals of the univariate regression analysis were then correlated with the various traits. Traits conferring significant correlation with these residuals were subsequently used in a stepwise forward multiple regression to determine which trait(s) best predict the residuals.

The relationship between competitive ability in the normal versus drought treatments was examined next. As data were markedly skewed (Wilks Shapiro, $p<0.0001$), Spearman rank ordered correlation was used to make this assessment.

Statistical analysis was done using the statistical packages STATGRAPHICS version 3.0 (1988) and SAS version 5 (1985).

Table 1 Plant species tested for their relative competitive abilities[1]

Species[2]	Family	Collection site[3]
**Achillea millefolium* L.	Asteraceae	c,d
**Agrostis gigantea* (Roth)	Poaceae	a
Anaphalis margaritacea (L.)Benth. & Hook	Asteraceae	b
Anemone canadensis L.	Ranunculaceae	b
Antennaria neglecta E. Greene	Asteraceae	c
Antennaria howellii E. Greene	Asteraceae	e
Aster ciliolatus Lindley	Asteraceae	a,b,d,e
**Berteroa incana* (L.) DC.	Brassicaceae	f
**Bromus inermis* Leysser	Poaceae	c
**Bromus tectorum* L.	Poaceae	a
Carex crawei Dewey	Cyperaceae	b
Carex eburnea Boott	Cyperaceae	e
Carex gracillima Schwein	Cyperaceae	a
Carex pallescens L.	Cyperaceae	d
Carex pensylvanica Lam.	Cyperaceae	e
Carex richardsonii R. Br.	Cyperaceae	e
Carex rugosperma Mackenzie	Cyperaceae	a
**Chrysanthemum leucanthemum* L.	Asteraceae	c
**Cirsium arvense* L. Scop.	Asteraceae	f
Campanula rotundifolia L.	Campanulaceae	e
Corydalis sempervirens (L.) Pers.	Fumariaceae	a
Danthonia spicata (L.) P. Beauv.	Poaceae	c,e
**Echium vulgare* L.	Boraginaceae	c
**Elymus repens* (L.) Gould	Poaceae	b
**Elymus trachycaulus* (Link.) Gould	Poaceae	e
Equisetum arvense L.	Equisetaceae	b
Fragaria virginiana Miller	Rosaceae	d
**Glechoma hederacea* L.	Lamiaceae	d
Helianthus divaricatus L.	Asteraceae	a
**Hieracium piloselloides* Villars	Asteraceae	b,c
**Hieracium pilosella* L.	Asteraceae	b
**Hypericum perforatum* L.	Hypericaceae	d
Lechea intermedea Legg.	Cistaceae	a
**Linaria vulgaris* Miller	Scrophulariaceae	c
Minuartia michauxii (Fenzl) Farw.	Caryophyllaceae	e
Muhlenbergia mexicana (L.) Trin.	Poaceae	b
Panicum acuminatum Sw.	Poaceae	c,e
Panicum depauperatum Muhlenb	Poaceae	a
Penstemon hirsutus (L.) Willd.	Scrophulariaceae	e
**Phleum pratense* L.	Poaceae	d
Plantago rugelii Decne.	Plantaginaceae	c,d,e
Poa pratensis L.	Poaceae	e
**Potentilla argentea* L.	Rosaceae	d
**Potentilla recta* L.	Rosaceae	c
**Prunella vulgaris* L.	Lamiaceae	c,e

Table 1 cont.

Species[2]	Family	Collection site[3]
Ranunculus acris L. [*]	Ranunculaceae	c
Rumex acetosella L. [*]	Polygonaceae	a,c
Saxifraga virginiensis Michxaux	Saxifragaceae	e
Scutellaria parvula Michxaux	Lamiaceae	e
Senecio pauperculus Michxaux	Asteraceae	e
Sisyrinchium montanum E. Greene	Iridaceae	a
Solidago altissima L.	Asteraceae	c
Solidago gigantea Aiton	Asteraceae	a,d
Solidago hispida Muhlaux	Asteraceae	b,d
Solidago ptarmicoides (Nees) B. Boivin	Asteraceae	a,e
Solidago rugosa Aiton	Asteraceae	b,c
Sporobolus heterolepis (A. Gray.) A. Gray	Poaceae	e
Taraxacum offinciale D. Weber. [*]	Asteraceae	d
Trichostema brachiatum L.	Lamiaceae	e
Trifolium pratense L. [*]	Caesalpiniaceae	d
Urtica dioica L. [*]	Urticaceae	b
Viola septentrionalis E. Greene	Violaceae	d
Viola papilionacea Pursh.	Violaceae	c

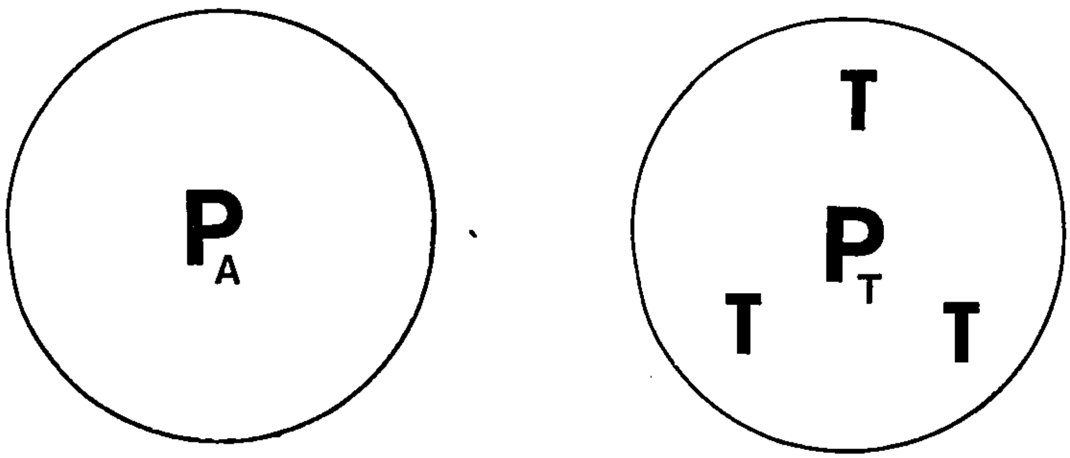
[*] Non-native species

[1] Competitive ability was measured as the test species' ability to suppress the growth of a common indicator species, or phytometer, *Trichostema brachiatum*

[2] nomenclature follows Morton and Venn (1990).

[3] Collection sites are as specified in **Appendix 1**

Figure 1 Experimental design for testing relative competitive ability (CA). Competitive ability is calculated as the percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.



$$CA=\frac{P^A-P^T}{P^A}$$

T=Test species

P_T=Phytometer grown with test species

P_A=Phytometer grown alone

Table 2 Measurements taken on each of the 63 test plant species.

Traits measured
Biomass, total (g)
Biomass, below-ground (g)
Biomass, above-ground (g)
Shoot-to-root ratio (g/g)
Height (cm)
Average leaf length (cm)
Average leaf width (cm)
Leaf shape (length:width)
Leaf number
Leaf area index (cm^2)
Canopy area (cm^2)
Date of flowering
Average soil depth (cm)[1]
Soil pH[2]
Soil nitrate nitrogen (ppm)[2]
Soil phosphorus (ppm)[2]
Soil potassium (ppm)[2]
Soil calcium (ppm)[2]
Soil magnesium (ppm)[2]
Soil salts (mmho/cm)[2]
Water uptake (g/s)

[1] soil depth where plants occurred in the field

[2] these 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

RESULTS

OVERVIEW

As one of the objectives of this experiment was to determine whether plant traits can be used to predict competitive ability, it was necessary to assess whether the test species caused a competitive effect on the phytometers. **Figure 2** depicts the mean biomass of the phytometers (*Trichostema brachiatum*) when grown with and without test species in both the normal and drought treatments. The biomass of phytometers when grown alone was significantly greater than the biomass of phytometers when grown with test species in both the normal (Mann-Whitney U Test, n=20,380 z=-7.39, p<0.00001) and the drought (Mann-Whitney U Test, n=20,370 z=-7.43, p<0.00001) treatments. Thus a competitive effect exists to be further explored.

Another one of the objectives of this experiment was to find out whether relative competitive ability varied among experimental treatments. Thus it was necessary to test whether the two treatments (normal and drought) created in this experiment (**Figure 2**) were significantly different. First, I examined the phytometers in each treatment. The biomass of phytometers grown alone in the normal treatment were significantly greater than the biomass of phytometers when grown alone in the drought treatment (Mann-Whitney U Test, n=20, z=-3.80, p<0.001). Further, the biomass of phytometers when grown with test species in the normal treatment were significantly greater than the biomass of phytometers when grown with test species in the drought treatment (Mann-Whitney U Test, n=380,370, z= -2.54, $p<0.05$). Next I examined the test species. The biomass of test species when grown singly in the normal treatment were significantly greater than in the drought treatment (**Figure 3**). Thus the two environmental treatments were different.

RELATIVE COMPETITIVE ABILITY

The mean competitive ability (measured as percent reduction in phytometer biomass *Trichostema brachiatum*) of each species is shown in **Tables 3a and 3b**. The test species caused dramatic reduction in growth of the phytometer. 55/77 plants in the normal treatment and 51/77 plants in the drought treatment reduced growth of the phytometer by at least 90% from the control size. There were significant differences in competitive ability among species in the normal treatment (Kruskal-Wallis, K=307.7, $p<0.00001$). Competitive abilities among species in the drought treatment were also significantly different (Kruskal-Wallis, K=286.2, $p<0.00001$) (Siegel 1956). Species can be arranged in a competitive hierarchy, ranging from the weakest competitor (*Lechea intermedea* in the normal treatment and *Carex crawei* in the drought treatment) to the strongest competitor (*Plantago rugelii* in both the normal and drought treatments).

INTENSITY OF COMPETITION

The mean relative competitive ability of test species in the normal treatment was not significantly different from the mean relative competitive ability of test species in the drought treatment (Mann-Whitney U, $n=77$, $z=1.51$, $p=0.13$). This indicates that competitive intensity does not vary between the two treatments.

UNIVARIATE ANALYSES

Competitive ability was correlated with many traits (**Table 4**). However, it was correlated most strongly with log total biomass in the normal treatment ($n=77$, $r=0.58$, $p<0.00001$) and log below-ground biomass in the drought treatment ($n=77$, $r=0.59$, $p<0.00001$). The mean morphological variables for each species are summarized in **Appendices 4a & 4b**. The correlation matrix between all measured traits is shown in **Appendix 3a & 3b**. **Tables 5a & 5b** describe the quantitative relationships between each of the measured traits and competitive ability. Water uptake rates were not included in this correlation analysis as I did not have a measure of water loss from a pot not housing a plant. Therefore it was not possible to normalise the data. However, correlation analysis was used to determine the relationship between water uptake rates and test species biomass ($n=68$, $r=0.49$, $p< 0.00001$). **Figure 8** depicts this relationship.

MULTIVARIATE ANALYSES

Figures 4 to **7** and **Appendix 2a & 2b** plot the relationship between percent reduction in phytometer biomass and each of the measured traits. These plots were assessed visually and those plots which did not appear linear were log transformed to create a more linear relationship. To determine whether other traits could explain residual variation from these plots, I calculated residuals and tested for correlation between them and the remaining traits. Several morphological measurements significantly correlated with these residuals. When these variables were included in a stepwise forward multiple regression, leaf shape was found to explain 20 percent of the residual variation in competitive ability in both the normal and drought treatments (Normal: $n=75$, $r^2=0.54$, $p<0.00001$; Drought: $n=75$, $r^2=0.55$, $p<0.00001$). Model fitting results are summarized in **Tables 6a & 6b** and predicted versus observed results are plotted in **Figures 9a & 9b.**

BETWEEN-HABITAT DIFFERENCES IN RELATIVE COMPETITIVE ABILITY

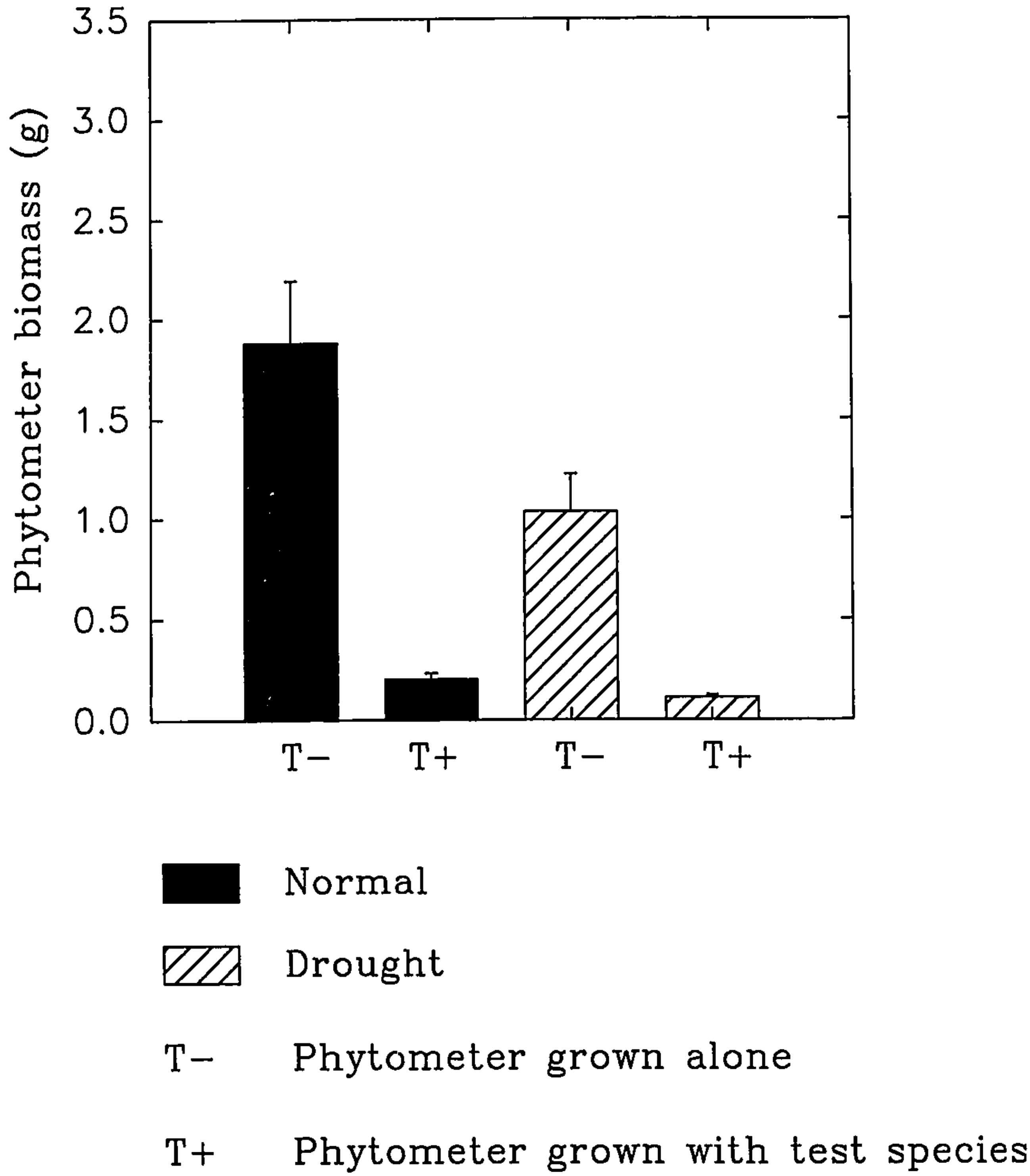
Competitive ability in the normal treatment was strongly correlated with competitive ability in the drought treatment ($n=77$, $r=0.90$, $p<0.00001$)(**Figure 10**). To look at order of competitive ability irrespective of magnitude, Spearman correlation analysis was also carried out ($n=77$, $r_s=0.91$, $p<0.00001$)(**Figure 11**).

PLANT TYPES AND COMPETITIVE ABILITY

Scatter plots of competitive ability versus log shoot biomass in the normal treatment and log root biomass in the drought treatment (**Figures 12a & 12b**) suggest that forbs, on a broad scale, are better competitors than graminoid and sedge species.

Comparing the residuals from a linear regression analysis of competitive ability versus log total biomass (normal treatment) and log below-ground biomass (drought treatment) shows that the competitive ability of the forbs was significantly greater than the competitive ability of grasses and sedges (Mann-Whitney U Test: Normal treatment--n=20,56, z=-4.95, $p<0.00001$;Drought treatment--n=20,56, z=-4.47, $p<0.00001$).

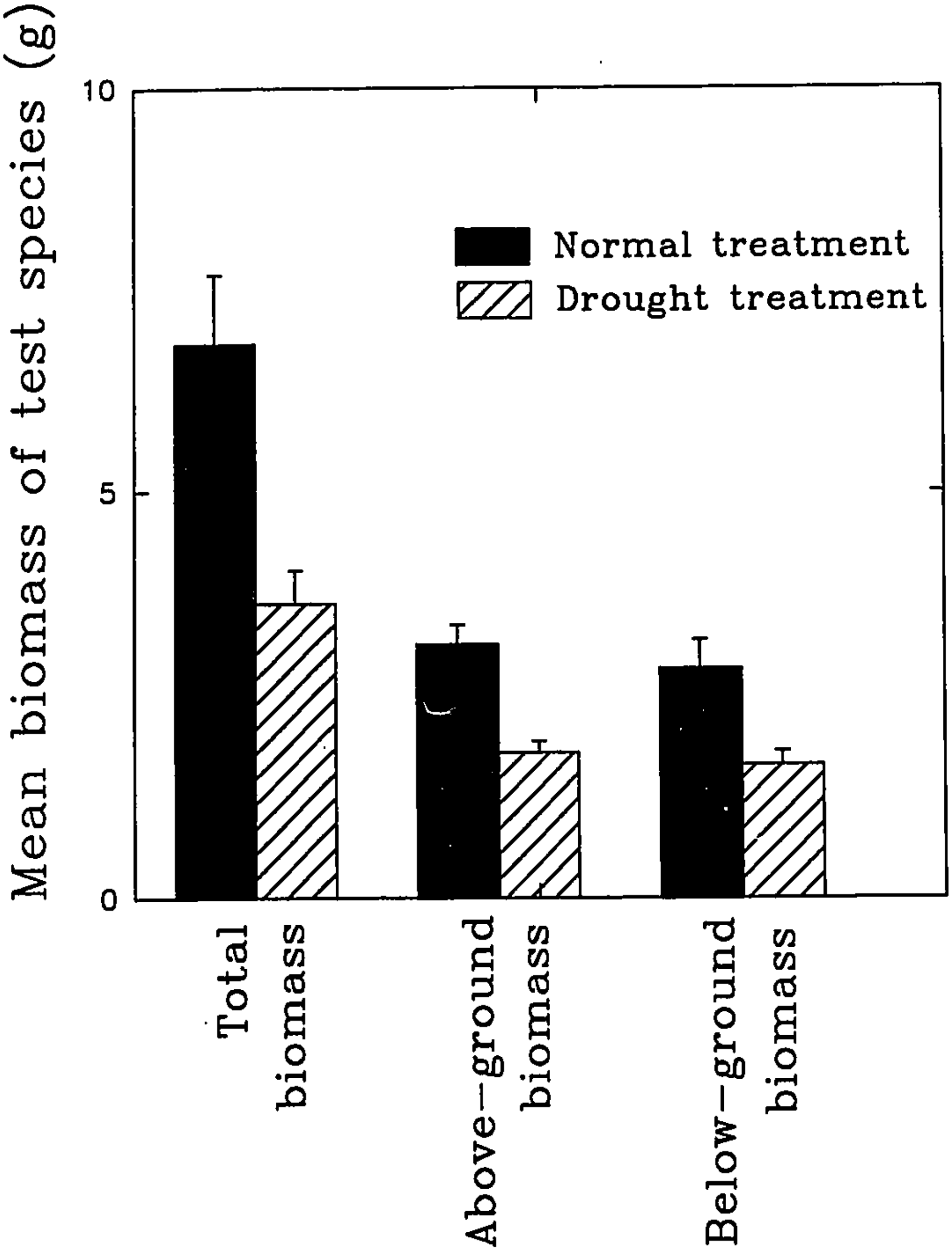
Figure 2 Comparison of mean above-ground biomass of the phytometer *Trichostema brachiatum* when grown alone and when grown with test species in both the normal and drought treatment. The histogram includes 95% confidence intervals.



3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Phytometer biomass (g)
T−
T+
T−
T+
Normal
Drought
T− Phytometer grown alone
T+ Phytometer grown with test species

Figure 3 Comparison of biomass for 63 terrestrial herbaceous plant species (test species) grown singly under normal and drought treatments. Histograms include 95 % confidence intervals.

The biomass of test species in the normal treatment was significantly greater than their biomass in the drought treatment (Mann-Whitney U Tests: (a) Total biomass--n=386,388, z=-7.42, p<0.00001, (b) Above-ground biomass--n=386,388, z=-7.95, p<0.00001, and (c) Below-ground biomass--n=385,388, z=-5.81, p<0.00001).



Mean biomass of test species (g)
10
5
0
Normal treatment
Drought treatment
Total biomass
Above-ground biomass
Below-ground biomass

Table 3a Relative competitive ability of test species in normal treatment (±95% c.i., n=5)

Test species	Competitive ability[1]	Collection site[2]
Lechea intermedea Legg.	45.2±16.0	a
Sporobolus heterolepis (A. Gray) A. Gray	51.2±26.1	e
Carex gracillima Schwein	52.8±29.9	a
Carex rugosperma Mackenzie	54.4±16.7	a
Danthonia spicata (L.) Beauv	61.4±28.5	c
Carex eburnea Boott.	64.1±38.1	e
Danthonia spicata (L.) P. Beauv.	64.8±32.7	e
Panicum depauperatum Muhlenb.	67.0±16.1	a
Carex crawei Dewey	70.1±19	b
Trichostema brachiatum L.	71.8±8.4	e
Saxifraga virginiensis Michxaux	72.9±16.2	e
Carex pallescens L.	74.9±6.4	d
Carex pensylvanica Lam.	78.9±8.8	e
Antennaria neglecta E. Greene	79.9±7.7	c
Minuartia michauxii (Fenzl) Farw.	80.7±16.0	e
Panicum acuminatum Sw.	81.6±5.0	e
Anemone canadensis L.	81.7±12.2	b
Corydalis sempervirens (L.) Pers.	83.1±15.9	a
Equisetum arvense L.	83.3±13.7	b
Carex richardsonii R. Br.	87.1±1.6	e
Solidago ptarmicoides (Nees) B. Boivin	88.1±17.3	a
Panicum acuminatum Sw.	88.7±9.3	c
**Agrostis gigantea* (Roth)	90.0±7.4	a
Sisyrinchium montanum E. Greene	90.1±12.6	b
Antennaria howellii E. Greene	90.4±15.3	e
Anaphalis margaritacea(L.) Benth & Hook	90.8±3.2	b
**Bromus tectorum* L.	91.5±5.9	a
Campanula rotundifolia L.	91.8±5.7	e
**Bromus inermis* Leysser	92.3±9.7	c
Solidago hispida Muhlenb.	93.1±10.8	b
**Urtica dioica* L.	93.3±4.0	b
**Glechoma hederacea* L.	93.8±3.6	d
**Rumex acetosella* L.	94.4±2.9	a
**Berteroa incana* (L.) DC.	94.5±4.1	f
Viola septentrionalis E. Greene	95.4±2.9	d
Scutellaria parvula Michxaux	95.5±3.1	e
**Hypericum perforatum* L.	96.0±3.3	d
**Hieracium pilosella* L.	96.2±2.2	b
Aster ciliolatus Lindley	96.4±3.4	a
Viola papilionacea Pursh.	96.7±2.8	c
Muhlenbergia mexicana (L.) Trin.	96.9±2.1	b
**Elymus trachycaulus* (Link.) Gould	97.0±1.6	e

Table 3a cont.

Test species	Competitive ability[1]	Collection site[2]
Penstemon hirsutus (L.) Willd.	97.0±1.1	e
**Prunella vulgaris* L.	97.2±2.6	c
Helianthus divaricatus L.	97.2±0.9	a
Plantago rugelii Decne.	97.3±4.4	e
**Elymus repens* (L.) Gould	97.4±1.2	b
Solidago hispida Muhlenb	97.4±1.4	b
**Hieracium piloselloides* Villars	97.9±1.1	b
**Linaria vulgaris* Miller	97.9±1.2	c
Aster ciliolatus Lindley	98.0±0.8	e
**Prunella vulgaris* L.	98.1±3.2	e
Solidago gigantea Aiton	98.1±2.7	d
Aster ciliolatus Lindley	98.1±1.3	d
Poa pratensis L.	98.2±1.1	e
Solidago ptarmicoides (Nees) B. Boivin	98.3±1.4	e
**Potentilla recta* L.	98.5±0.7	c
**Potentilla argentea* L.	98.6±2.5	d
**Cirsium arvense* L. Scop.	98.7±0.5	f
**Ranunculus acris* L.	98.7±0.7	c
Solidago rugosa Aiton	98.8±0.6	b
**Phleum pratense* L.	98.9±0.8	d
Senecio pauperculus Michxaux	98.9±0.7	e
Fragaria virginiana Miller	98.9±0.7	d
**Rumex acetosella* L.	98.9±0.4	c
Aster ciliolatus Lindley	99.0±0.4	b
**Echium vulgare* L.	99.0±0.5	e
Solidago altissima L.	99.0±0.5	c
Solidago rugosa Aiton	99.0±0.5	c
**Achillea millefolium* L.	99.0±0.6	d
**Chrysanthemum leucanthemum* L.	99.1±0.3	c
**Taraxacum offinciale* G. Weber.	99.1±0.4	d
Plantago rugelii Decne.	99.2±0.6	d
**Hieracium piloselloides* Villars	99.3±1.4	c
**Trifolium pratense* L.	99.3±0.2	d
**Achillea millefolium* L.	99.4±0.3	c
Plantago rugelii Decne.	99.4±0.3	c

Kruskal-Wallis: $K=286.2$, $p<0.00001$

* Non-native species

[1] Competitive ability was calculated as the percent reduction in phytometer biomass when grown with test species as compared to when grown alone

[2] Collection sites are as specified in **Appendix 1.** Some species were collected from several different collection sites therefore there are replicates of the same species within the data set

Table 3b Relative competitive ability of test species in drought treatment (±95% c.i.n=5)

Test species	Competitive ability[1]	Collection site[2]
Carex crawei Dewey	56.1±36.1	b
Lechea intermedea Legg.	64.2±15.2	a
Sporobolus heterolepis (A. Gray) A. Gray	64.9±7.8	e
Danthonia spicata (L.) P. Beauv.	68.4±10.8	e
Carex rugosperma Mackenzie	69.2±17.5	a
Carex pallescens L.	70.0±25.8	d
Carex gracillima Schwein.	74.2±18.7	a
Minuartia michauxii (Fenzl) Farw.	75.4±22.5	e
Danthonia spicata (L.) P. Beauv.	75.5±12.7	c
Saxifraga virginiensis Michxaux	75.6±8.8	e
Panicum depauperatum Muhlenb.	77.1±14.2	a
Carex eburnea Boott	77.4±3.7	e
Carex pensylvanica Lam.	78.4±17.4	e
Corydalis sempervirens (L.) Pers.	78.8±18.6	a
Trichostema brachiatum L.	79.2±15.2	e
[*]*Bromus tectorum* L.	79.9±5.9	a
Carex richardsonii R. Br.	80.5±32	e
Equisetum arvense L.	82.6±10.9	b
Panicum acuminatum Sw.	83.6±11.6	c
Campanula rotundifolia L.	84.1±17.6	e
Anaphalis margaritacea (L.) Benth & Hook	84.1±12.4	b
Anemone canadensis L.	85.0±12.8	b
[*]*Berteroa incana* (L.) DC.	88.0±5.5	f
Panicum acuminatum Sw.	88.8±5.3	e
Solidago hispida Muhlenb.	89.1±16.9	c
[*]*Glechoma hederacea* L.	89.8±7.4	d
Solidago ptarmicoides (Nees) B. Boivin	90.0±16.7	a
[*]*Agrostis gigantea* (Roth)	90.5±3.9	a
Muhlenbergia mexicana (L.) Trin.	91.1±3.3	b
[*]*Phleum pratense* L.	92.1±0.6	d
Viola septentrionalis E. Greene	92.3±7.3	e
Antennaria howellii E. Greene	92.3±7.0	e
Aster ciliolatus Lindley	92.4±9.0	a
[*]*Hieracium pilosella* L.	92.7±2.8	b
[*]*Urtica dioica* L.	92.7±5.3	b
[*]*Bromus inermis* Leysser	92.8±3.4	c
Sisyrinchium montanum E. Greene	93.5±3.3	b
[*]*Rumex acetosella* L.	93.6±5.1	a
[*]*Hypericum perforatum* L.	93.6±1.0	d
Antennaria neglecta E. Greene	93.7±4.8	c
[*]*Elymus trachycaulus* (Link.) Gould	94.2±2.5	e
[*]*Linaria vulgaris* Miller	94.9±2.6	c
[*]*Hieracium piloselloides* Villars	95.2±3.7	b

Table 3b cont.

Test species	Competitive ability[1]	Collection site[2]
**Elymus repens* (L.) Gould	95.4±3.8	b
Scutellaria parvula Michxaux	95.6±2.1	e
Senecio pauperculus Michxaux	96.2±1.7	e
Penstemon hirsutus (L.) Willd.	96.2±1.6	e
Aster ciliolatus Lindley	96.2±2.1	d
Viola papilionacea Willd.	96.2±2.0	c
**Potentilla argentea* L.	96.3±3.3	d
Poa pratensis L.	96.6±1.3	e
Solidago ptarmicoides (Nees) B. Boivin	96.8±2.4	e
Helianthus divaricatus L.	97.0±1.7	a
Solidago rugosa Aiton	97.4±2.1	b
Solidago hispida Muhlenb	97.6±0.5	b
**Echium vulgare* L.	97.8±1.1	e
**Rumex acetosella* L.	97.8±1.4	c
**Taraxacum offinciale* G. Weber.	98.0±1.8	d
Aster ciliolatus Lindley	98.0±1.3	b
**Ranunculus acris* L.	98.1±0.5	c
**Hieracium piloselloides* Villars	98.1±1.0	c
Fragaria virginiana Miller	98.2±1.0	d
Solidago altissima L.	98.3±1.1	c
**Chrysanthemum leucanthemum* L.	98.3±0.6	c
Aster ciliolatus Lindley	98.3±0.6	e
**Potentilla recta* L.	98.3±1.1	c
Plantago rugelii Decne.	98.3±0.8	e
**Cirsium arvense* L. Scop.	98.4±0.4	f
**Achillea millefolium* L.	98.4±1.4	d
Plantago rugelii Decne.	98.5±1.9	c
**Prunella vulgaris* L.	98.6±0.2	e
Solidago gigantea Aiton	98.6±1.9	d
Solidago rugosa Miller	98.6±0.3	c
**Prunella vulgaris* L.	98.6±0.2	c
**Achillea millefolium* L.	98.7±0.5	c
**Trifolium pratense* L.	98.8±0.5	d
Plantago rugelii Decne.	98.9±0.9	d

Kruskal-Wallis: K=307.7, p<<0.00001

* Non-native species

[1] Competitive ability was calculated as the percent reduction in phytometer biomass when grown with test species as compared to when grown alone.

[2] Collection sites are specified in **Appendix 1**. Some species were collected from several different collection sites therefore there are replicates of the same species within the data set.

Table 4 The correlation (r) among traits of 63 test species and their relative competitive ability, measured as percent reduction in phytometer biomass (*Trichostema brachiatum*)

Plant traits	Normal treatment (r)	Drought treatment (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^{***1}
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
Date of Flowering	0.33^{**1}	0.37^{**1}
Average soil depth (cm)[2]	0.34^{**1}	0.36^{**1}
Soil pH[3]	0.35^{**}	0.26^{*1}
Soil nitrate nitrogen (ppm)[3]	-0.39^{***1}	-0.28^{*1}
Soil phosphorus (ppm)[3]	undefined	undefined
Soil potassium (ppm)[3]	0.17	0.18^{1}
Soil calcium (ppm)[3]	-0.19	-0.01^{1}
Soil Magnesium (ppm)[3]	-0.14	0.06
Soil salts (mmho/cm)[3]	-0.09	-0.12^{1}

* p<0.05; ** p<0.01; *** p<0.001; **** p<<0.00001. Correlations are simple linear correlations with percent reduction in phytometer biomass.

[1] data for these traits were log transformed and percent reduction in phytometer biomass was arcsine square root transformed.

[2] soil depth where plants occurred in the field

[3] these 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

Table 5a The relationship between competitive ability (CA) and plant traits in the normal treatment.

Plant traits	**R^2**	**Linear Equation**	**F**
Biomass, total (g) [TB]	0.34^{****1}	CA=0.95+(0.21)Log(TB)	38.00
Biomass, below-ground (g) [BB]	0.31^{****1}	CA=1.04+(0.17)Log(BB)	33.26
Biomass, above-ground (g) [AB]	0.28^{****1}	CA=1.01+(0.19)Log(AB)	29.45
Shoot to root ratio (g)	0.02^{1} ns	---	---
Height (cm) [H]	0.09^{**}	CA=83.41+(0.21)(H)	7.72
Leaf length (cm) [LL]	0.08^{*}	CA=93.34+(-0.60)(LL)	6.76
Leaf width (cm) [LW]	0.27^{****1}	CA=1.11+(0.17)Log(LW)	27.23
Leaf shape (length:width) [LS]	0.26^{****1}	CA=1.17+(-0.11)Log(LS)	25.97
Leaf number	0.00 ns	---	---
Leaf area index (cm^2) [LAI]	0.21^{***1}	CA=0.67+(0.18)Log(LAI)	19.12
Canopy area (cm^2) [C]	0.07^{*1}	CA=0.89+(0.08)Log(C)	5.44
Date of flowering [F]	0.11^{**1}	CA=0.92+(0.10)Log(F)	8.68
Average soil depth (cm) [SD]	0.11^{**1}	CA=0.91+(0.14)Log(SD)	9.51
Soil pH (PH)	0.12^{**}	CA=-194.913+(37.00)(PH)	9.94
Soil nitrate nitrogen (ppm) [N]	0.15^{***1}	CA=1.20+(-0.21)Log(N)	12.84
Soil phosphorus (ppm)	undefined	undefined	---
Soil potassium (ppm)	0.03 ns	---	---
Soil calcium (ppm)	0.03 ns	---	---
Soil magnesium (ppm)	0.02 ns	---	---
Soil salts (mmho/cm)	0.01 ns	---	---

* $p<0.05$; $^{**}p<0.01$; *** $p<0.001$; $^{***}p<<0.00001$. R^2 values are based on simple linear regressions.

[1] data for these traits was log transformed and percent reduction in phytometer biomass was arcsine square root transformed.

Competitive ability (CA) was measured as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Table 5b The relationship between competitive ability (CA) and plant traits in the drought treatment.

Plant traits	**R^2**	**Linear Equation**	**F**
Biomass, total (g) [TB]	0.31^{****1}	CA=1.01+(0.17)Log(TB)	32.70
Biomass, below-ground (g) [BB]	0.35^{****1}	CA=1.07+(0.13)Log(BB)	39.77
Biomass, above-ground (g) [AB]	0.18^{***1}	CA=1.06+(0.13)Log(AB)	16.67
Shoot to root ratio (g) [ST]	0.14^{***}	CA=93.64+(-2.08)(SR)	12.36
Height (cm) [H]	0.04 ns	---	---
Leaf length (cm) [LL]	0.10^{**}	CA=92.87+(-0.48)(LL)	8.11
Leaf width (cm) [LW]	0.29^{****1}	CA=1.11+(0.14)Log(LW)	30.25
Leaf shape (length:width) [LS]	0.33^{****1}	CA=1.16+(-0.10)Log(LS)	35.39
Leaf number	0.01 ns	---	---
Leaf area index (cm^2) [LAI]	0.11^{**1}	CA=0.92+(0.10)Log(LAI)	8.68
Canopy area (cm^2) [C]	0.01 ns	---	---
Date of flowering [F]	0.13^{**1}	CA=0.94+(0.09)Log(F)	11.05
Average soil depth (cm) [SD]	0.13^{**1}	CA=0.94+(0.12)Log(SD)	11.21
Soil pH (PH)	0.07^{*1}	CA=-1.81+(3.27)Log(PH)	5.08
Soil nitrate nitrogen (ppm) [N]	0.08	CA=1.13+(-0.10)Log(N)	6.35
Soil phosphorus (ppm)	undefined	---	---
Soil potassium (ppm)	0.03^{1} ns	---	---
Soil calcium (ppm)	0.02^{1} ns	---	---
Soil magnesium (ppm)	0.00 ns	---	---
Soil salts (mmho/cm)	0.01^{1}	---	---

* $p<0.05$; $^{**}p<0.01$; *** $p<0.001$; $^{***}p<<0.00001$. R^2 values are based on simple linear regressions.

[1] data for these traits was log transformed and percent reduction in phytometer biomass was arcsine square root transformed.

Competitive ability (CA) was measured as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Table 6a Stepwise forward multiple regression for competitive ability as a function of plant traits when plants are grown in a normal treatment.

Stepwise selection for Competitive ability

F-to-enter: 4.00
F-to-remove: 4.00

Variables in Model	Coefficient	F-remove	Variables Not in Model	P Corr.	F-Enter
Log Total biomass	0.20	46.12	Soil depth	0.13	1.19
Log leaf shape	-0.10	32.57	Leaf length	0.018	0.023
			Log leaf width	0.10	0.72
			Log soil nitrates	0.19	2.76

R-squared = 0.55 Adjusted = 0.54 MSE = $8.51x10^{-3}$ D.F. = 72

Model fitting results for competitive ability

Independent variable	Coefficient	st. error	t-value	sig. level
CONSTANT	1.04	0.027	38.99	0.0000
Log total biomass	0.20	0.028	6.79	0.0000
Log leaf shape	-0.20	0.017	-5.71	0.0000

R-squared (ADJ.) = 0.54 SE = 0.092 MAE = 0.067 Durbin-Watson statistic = 1.63

Table 6b Stepwise forward multiple regression for competitive ability as a function of plant traits when plants are grown in a drought treatment.

Stepwise selection for Competitive ability

F-to-enter: 4.00
F-to-remove: 4.00

Variables in Model	Coefficient	F-remove	Variables Not in Model	P Corr.	F-Enter
Log Root biomass	0.11	39.13	Soil depth	0.14	1.46
Log leaf shape	-0.088	37.90	Log leaf length	0.087	0.54
			Log leaf width	0.087	0.54

R-squared = 0.56 Adjusted = 0.55 MSE = 5.12×10^{-3} D.F. = 72

Model fitting results for competitive ability

Independent variable	Coefficient	st. error	t-value	sig. level
CONSTANT	1.14	0.014	79.76	0.0000
Log root biomass	0.11	0.018	6.26	0.0000
Log leaf shape	-0.088	0.014	-6.16	0.0000

R-squared (ADJ.) = 0.55 SE = 0.072 MAE = 0.055 Durbin-Watson statistic = 1.86

Figure 4 Relationship between competitive ability (CA) and total biomass (TB) for 63 terrestrial herbaceous plant species grown singly in a normal treatment [CA (Arcsine square root transformed)=0.95+0.21Log(TB); n=77; r^2=0.34; F=38.00; p<0.00001].

R^2 and the equation of the line were calculated using an Arcsine square root transformation of competitive ability to account for the log transformation of total biomass. However, for simplicity on the figure, competitive ability was not transformed and the regression line is based on this non-transformed data. Competitive ability is expressed as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Normal treatment:

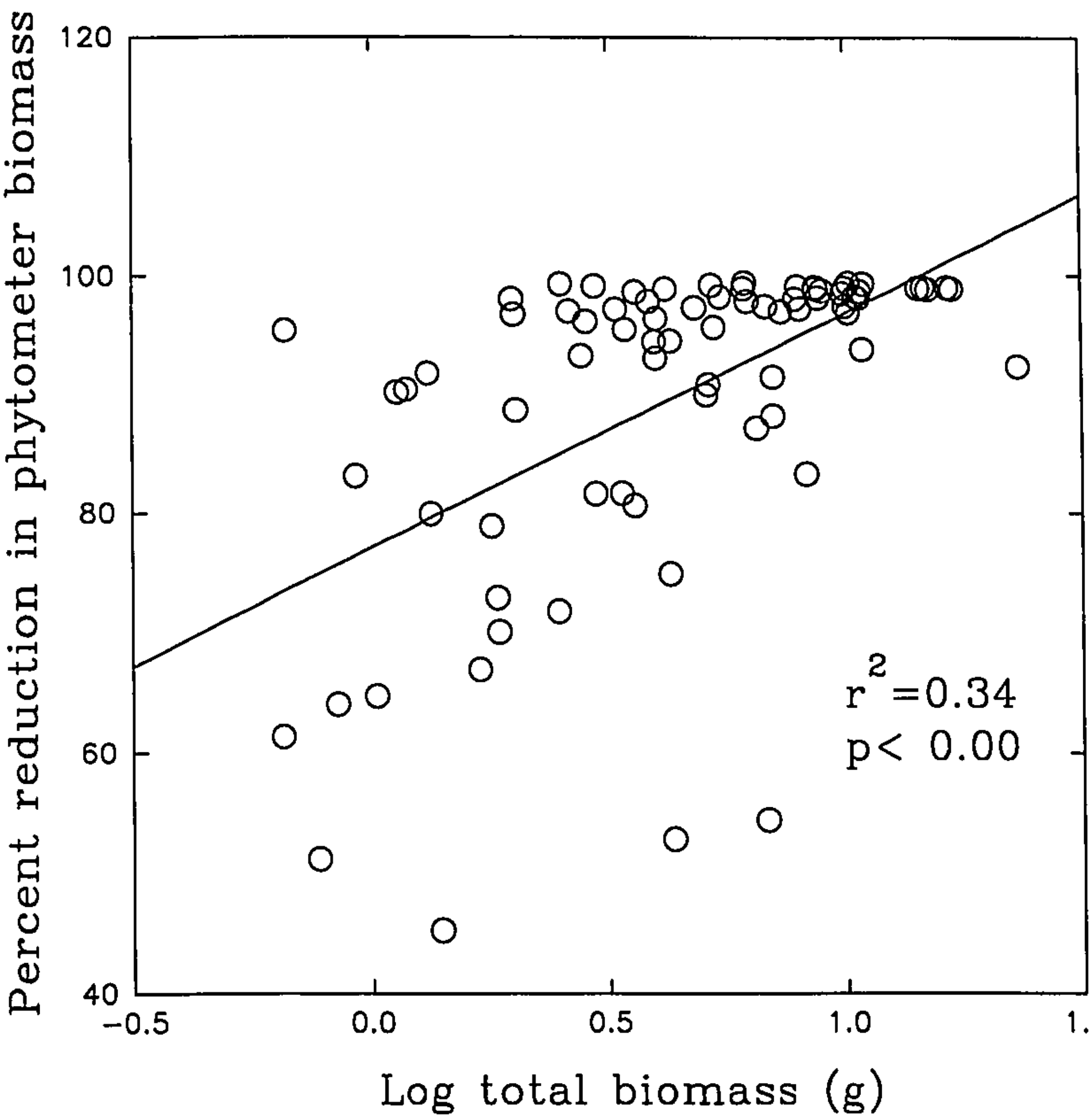


Figure 5 Relationship between competitive ability (CA) and (a) Below-ground biomass (BB) [CA (arcsine square root transformed) = 1.04 + (0.17)Log(BB); n=77; r^2=0.31; F=33.26; p< 0.00001], (b) Above-ground biomass (AB) [CA (arcsine square root transformed = 1.01 + (0.19)Log(AB); n=77; r^2=0.28; F=29.45; p<0.00001], (c) Average leaf width (LW) [CA (arcsine square root transformed) = 1.11 + (0.17)Log(LW); n=76; r^2=0.27; F=27.23; p< 0.00001], and (d) Leaf shape (LS) [CA (arcsine square root transformed = 1.17 + (-0.11)Log(LS); n=76; r^2=0.26; F=25.97; p<0.00001] for 63 terrestrial herbaceous plant species grown singly in a normal treatment.

R^2 and the equation of the line were calculated using an Arcsine square root transformation of competitive ability to account for the log transformation of the dependent variables. However, for simplicity on the figure, competitive ability was not transformed and the regression line is based on this non-transformed data. Competitive ability is expressed as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Normal treatment:

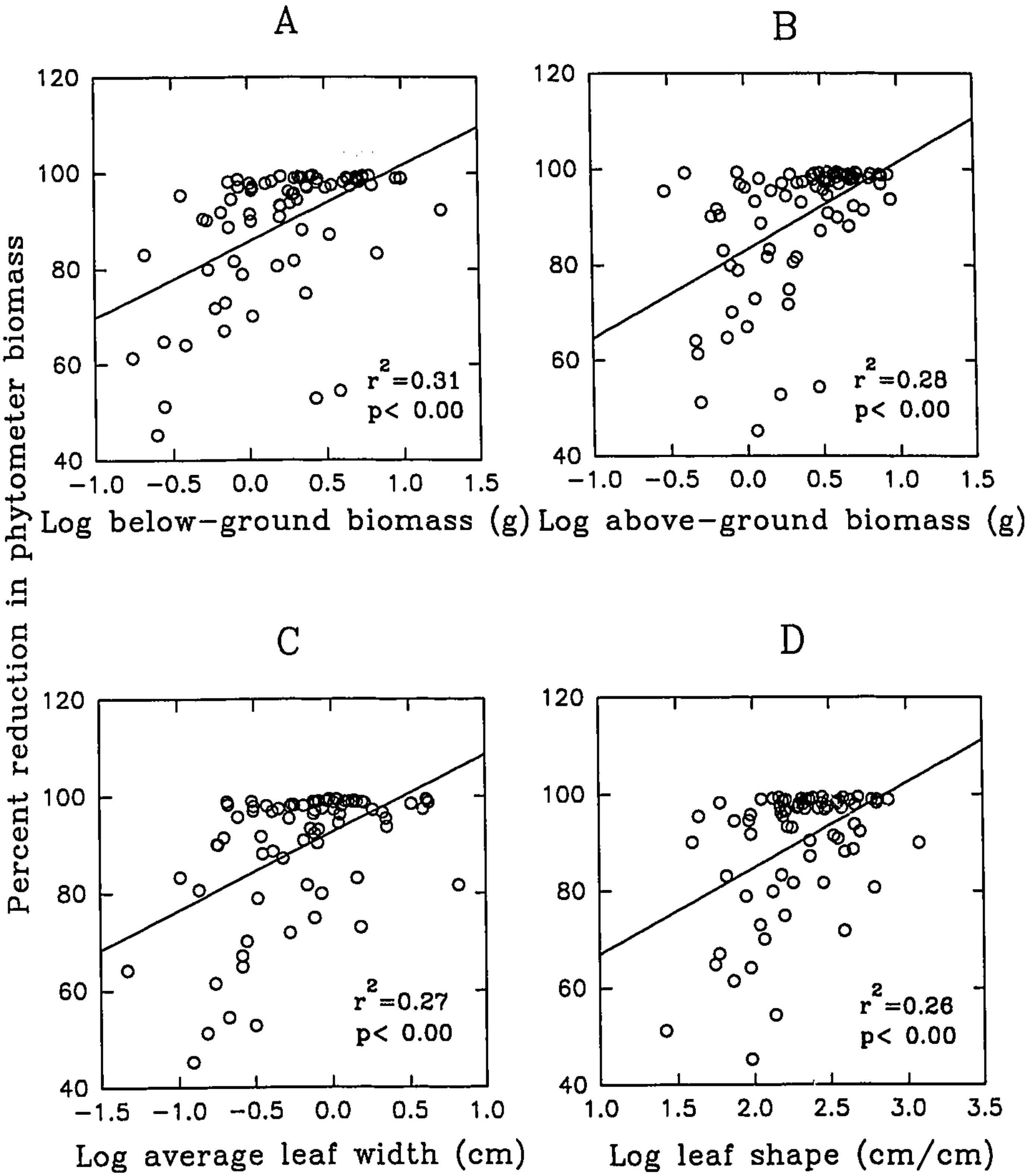


Figure 6 Relationship between competitive ability (CA) and below-ground biomass (BB) for 63 terrestrial herbaceous plant species grown singly in a drought treatment [CA (Arcsine square root transformed)=1.07+0.13Log(BB); n=77; r^2=0.35; F=39.77; p<0.00001.

R^2 and the equation of the line were calculated using an arcsine square root transformation of competitive ability, to account for the log transformation of below-ground biomass (BB). However, for simplicity on the figure, competitive ability was not transformed and the regression line is based on this non-transformed data. Competitive ability is expressed as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Drought treatment:

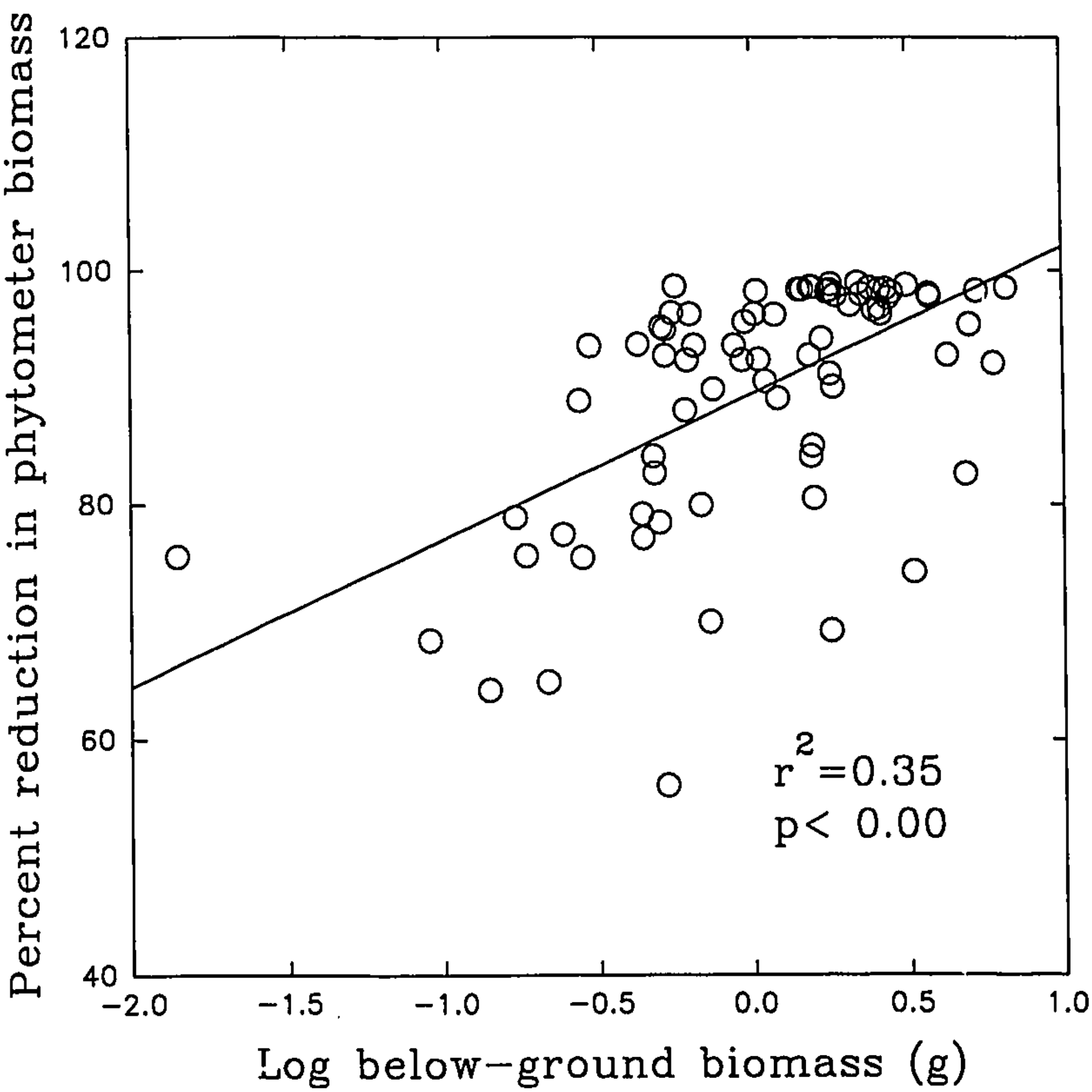


Figure 7 The relationship between competitive ability (CA) and (a) Total biomass (TB) [CA (Arcsine square root transformed) = 1.01 + (0.17)Log(TB); n=77; r^2=0.31; F=32.70; p< 0.00001], (b) Above-ground biomass (AB) [CA (Arcsine square root transformed) = 1.06 + (0.13)Log(AB); n=77; r^2=0.19; F=16.67; p<0.001], (c) Average leaf width (LW) [CA (Arcsine square root transformed) = 1.11 + (0.14)Log(LW); n=75; r^2=0.29; F=30.25; p< 0.00001], and (d) Leaf shape (LS) [CA (Arcsine square root transformed) = 1.16 + (-0.10)Log(LS); n=75; r^2=0.33; F=35.39; p<0.00001] for 63 terrestrial herbaceous test plant species grown singly in a drought treatment.

R^2 and the equation of the line were calculated using an Arcsine square root transformation of competitive ability to account for the log transformation of the dependent variable. However, for simplicity on the figure, competitive ability was not transformed and the regression line is based on this non-transformed data. Competitive ability is expressed as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Drought treatment:

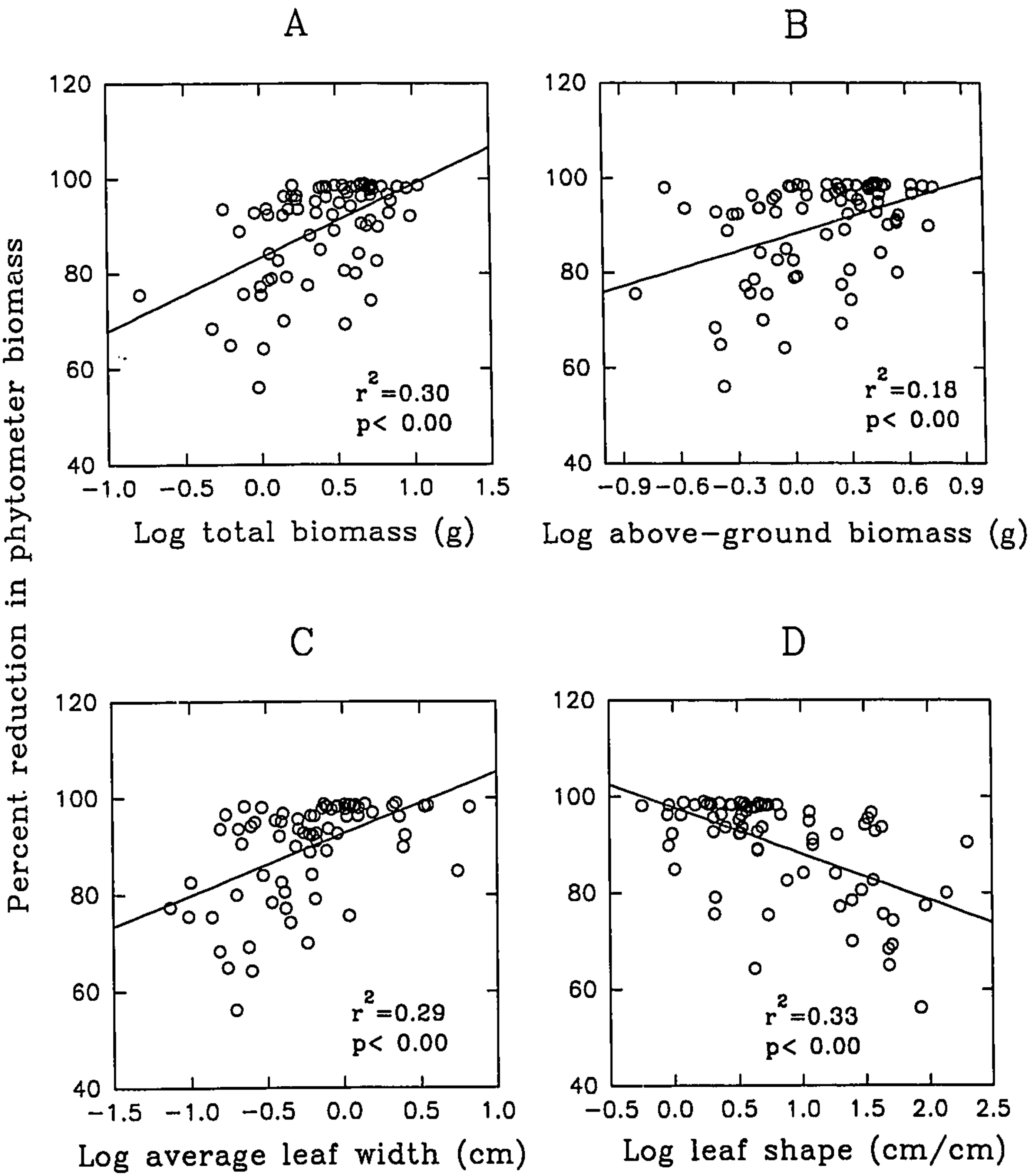
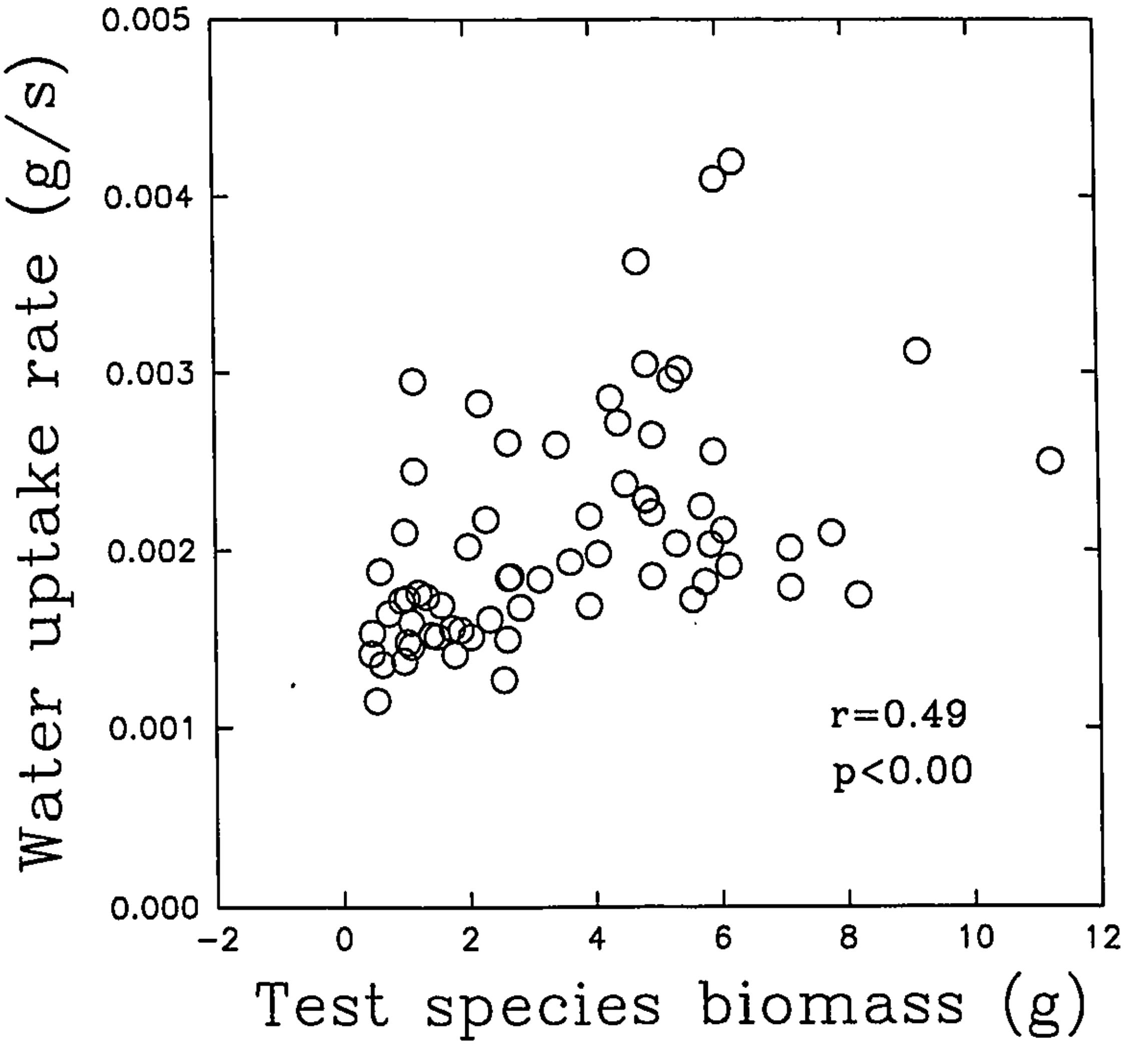


Figure 8 Scatter plot of the water uptake rates for 63 terrestrial herbaceous plant species versus their total biomass (g) ($n=68$, $r=0.49$, $p<0.00001$).



Water uptake rate (g/s)
0.000
0.001
0.002
0.003
0.004
0.005
-2
0
2
4
6
8
10
12
Test species biomass (g)
r=0.49
p<0.00

Figure 9a Observed versus predicted values for relative competitive ability as a function of plant traits in the normal treatment. Competitive ability is expressed as the percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Normal treatment:

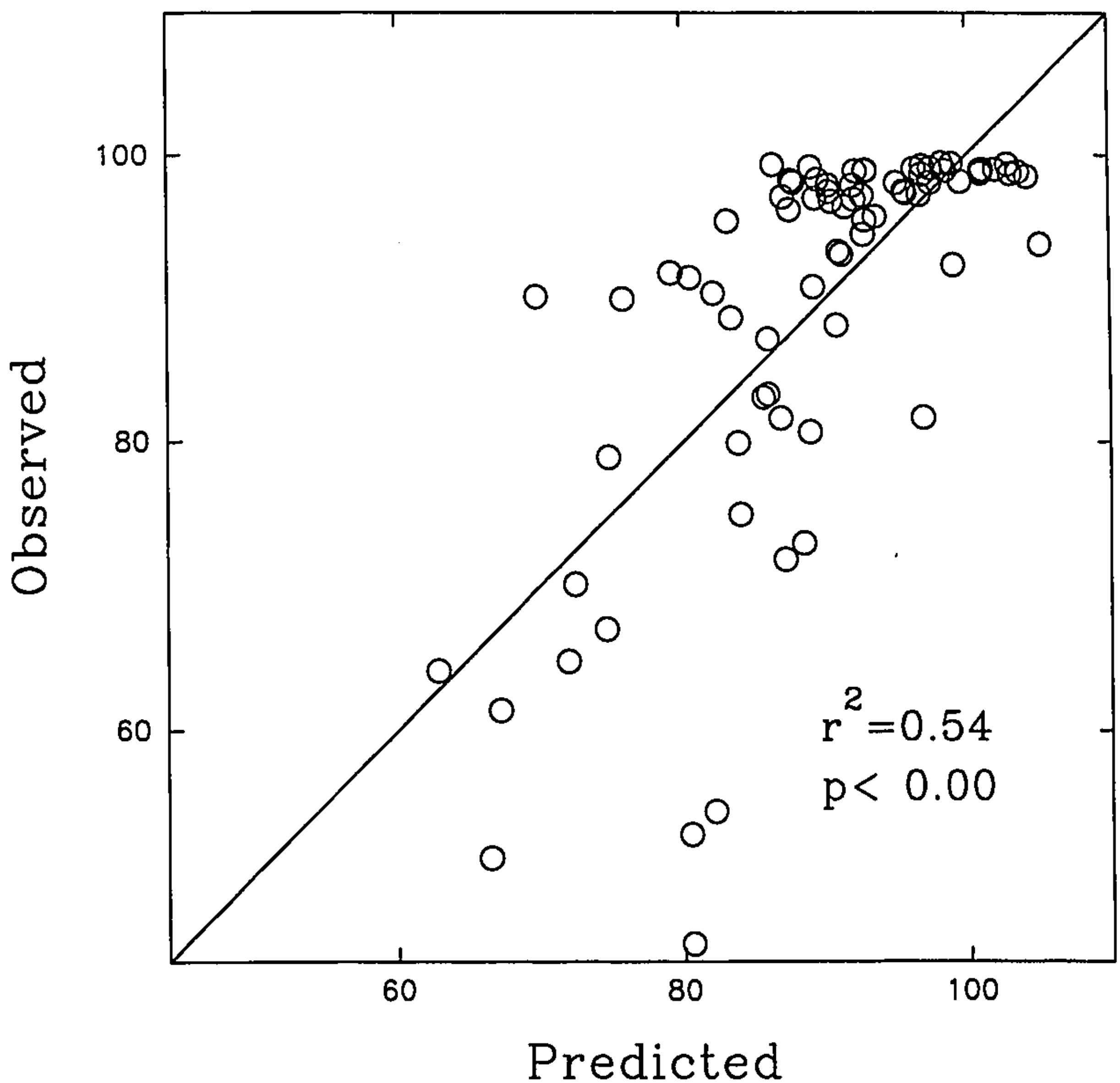


Figure 9b Observed versus predicted values for relative competitive ability as a function of plant traits in the drought treatment. Competitive ability is expressed as the percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Drought treatment:

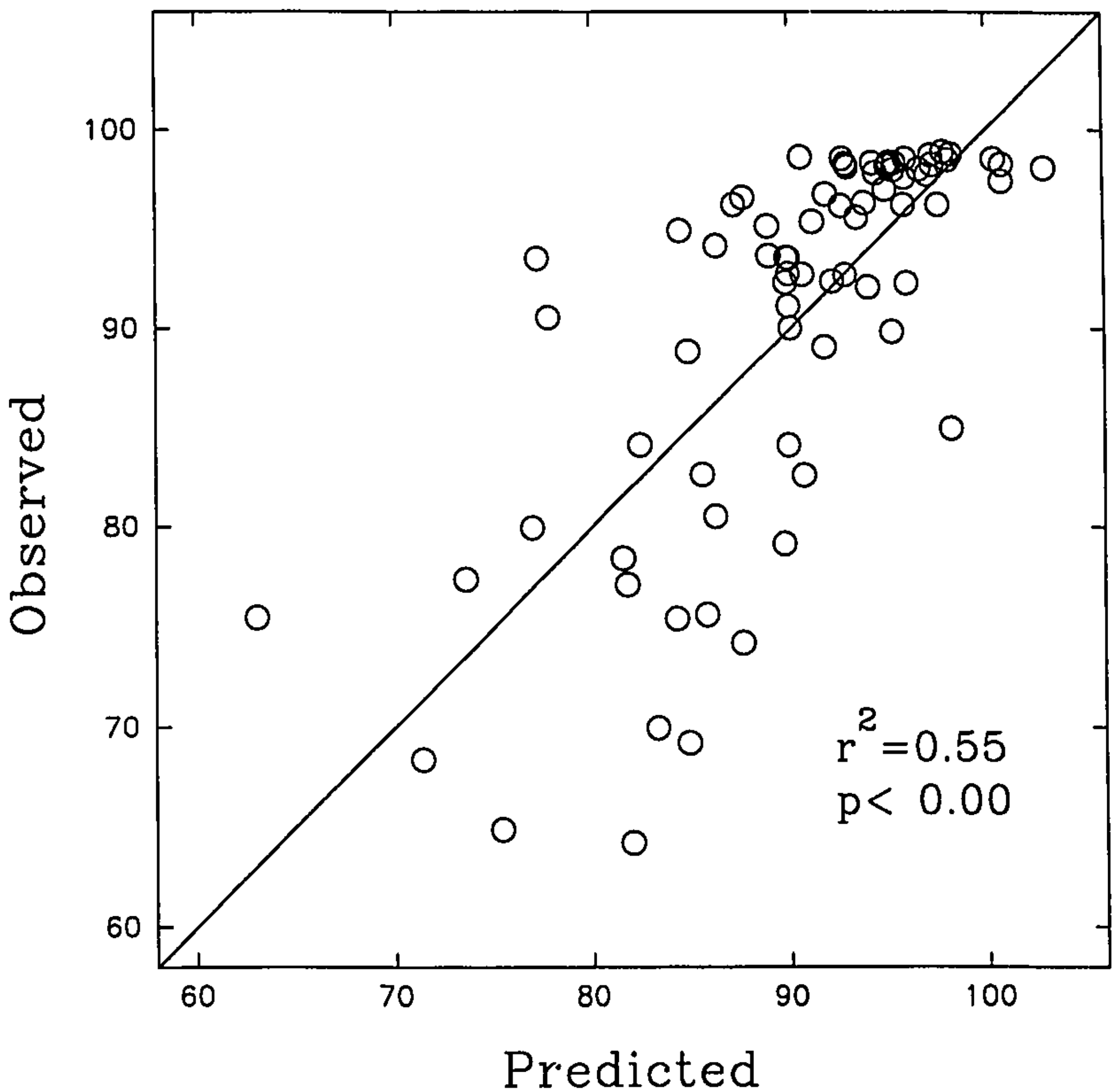
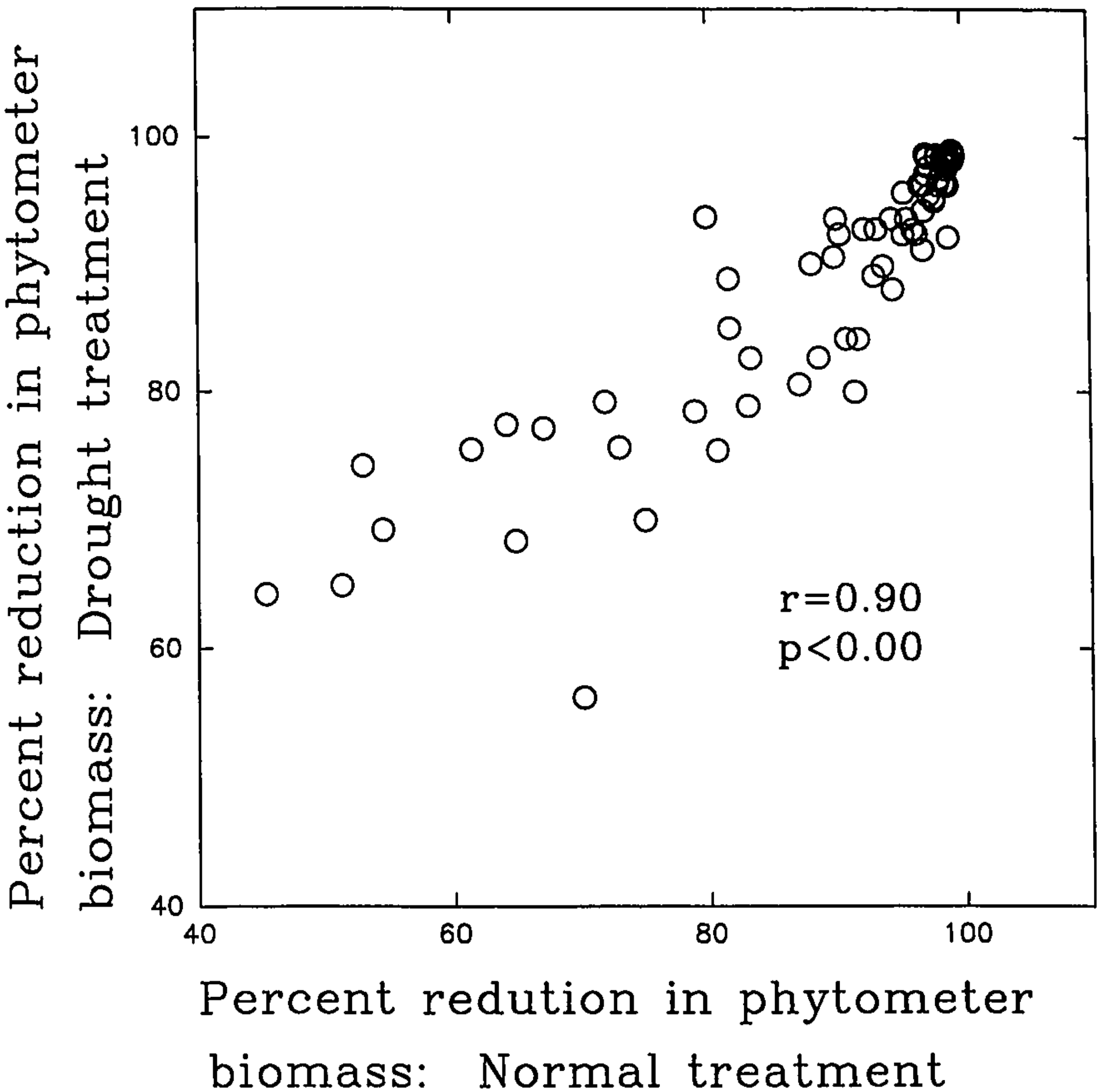
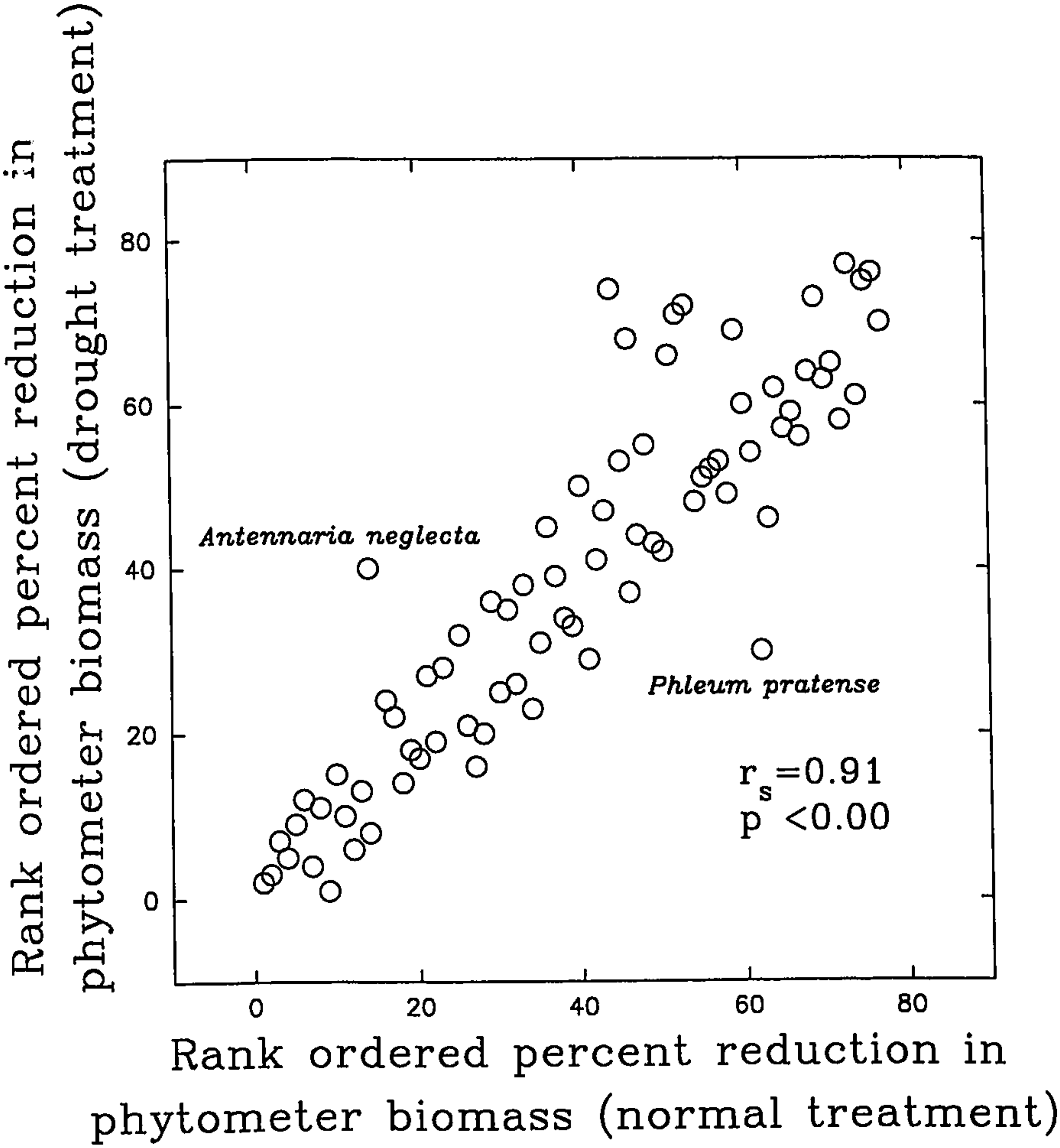


Figure 10 Relationship between competitive ability in the drought treatment and competitive ability in the normal treatment for 63 terrestrial plant species ($n=77$, $r=0.90$, $p<0.00001$). Competitive ability is expressed as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.



Percent reduction in phytometer
biomass: Drought treatment
100
80
60
40
r=0.90
p<0.00
40
60
80
100
Percent redution in phytometer
biomass: Normal treatment

Figure 11 Scatter plot of rank ordered competitive ability in the drought treatment versus rank ordered competitive ability in the normal treatment (n=77, r_s=0.91, p<0.00001). Competitive ability was calculated as the percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.



Rank ordered percent reduction in phytometer biomass (drought treatment)
Rank ordered percent reduction in phytometer biomass (normal treatment)
Antennaria neglecta
Phleum pratense
r_s=0.91
p <0.00
0
20
40
60
80

Figure 12a Scatter plot of competitive ability (CA) versus Log total biomass (TB) of 63 terrestrial herbaceous plant species when grown singly in the normal treatment. The plot indicates which species were forbs, grasses and sedges. Comparison of the residuals from linear regression analyses for competitive ability versus Log total biomass revealed significant differences between forbs versus grasses and sedges (Mann-Whitney U: $n=56,21$, $z=4.95$, $p<0.00001$).

Competitive ability is expresses as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Normal treatment:

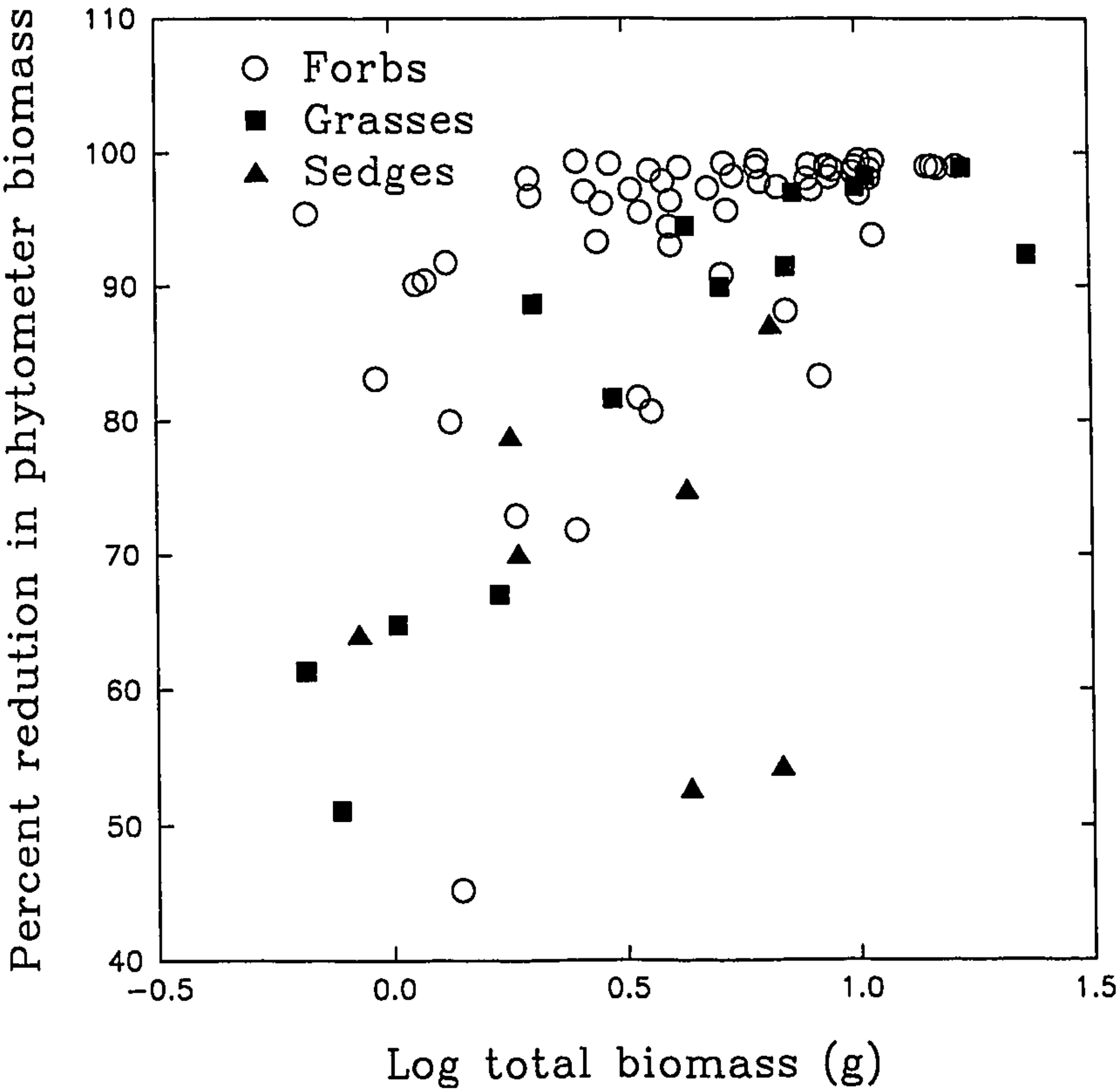
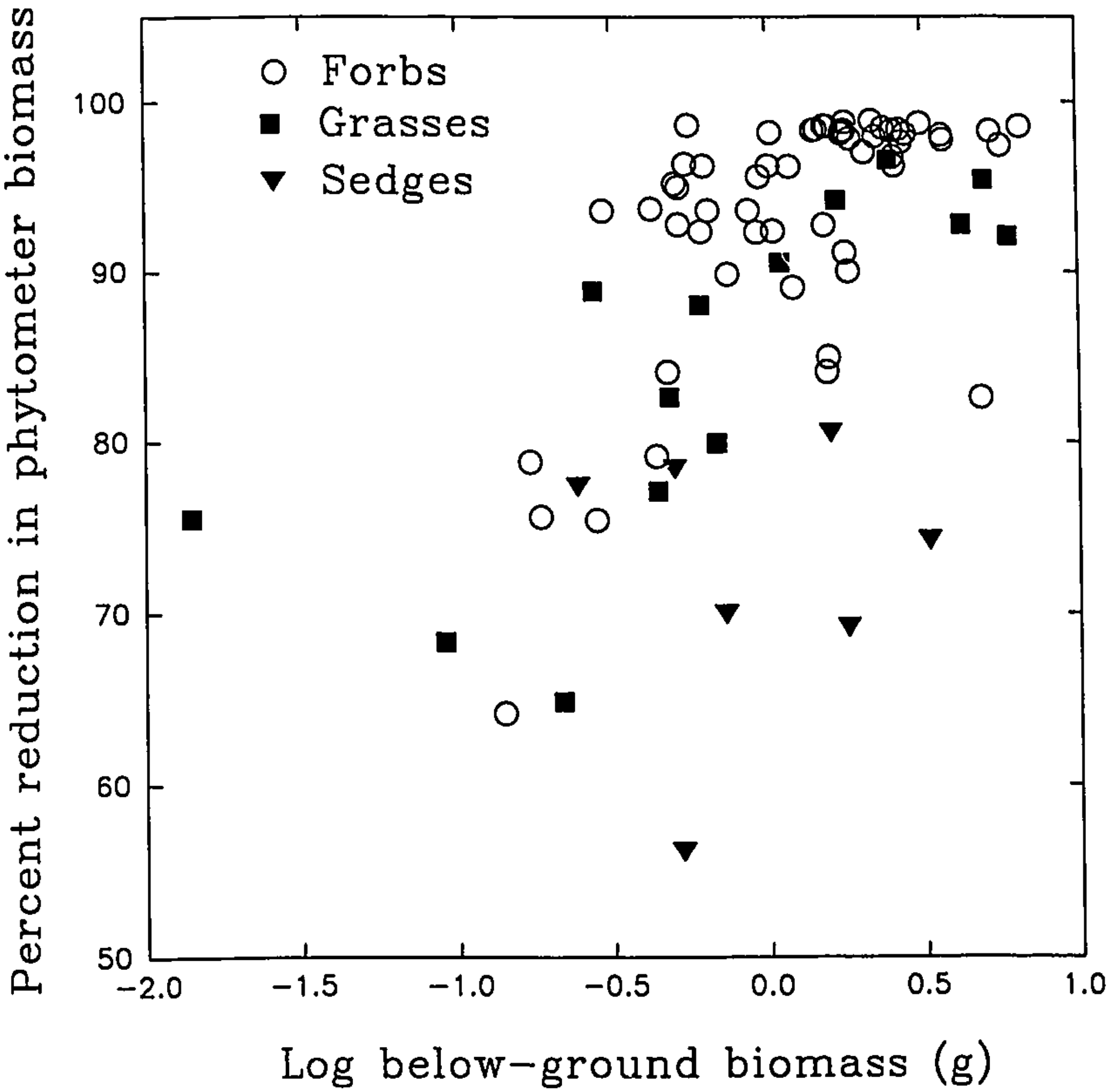


Figure 12b Scatter plot of competitive ability (CA) versus Log total biomass (TB) of 63 terrestrial herbaceous plant species when grown singly in the drought treatment. The plot indicates which species were forbs, grasses and sedges. Comparison of the residuals from linear regression analyses for competitive ability versus Log below-ground biomass revealed significant differences between forbs versus grasses and sedges (Mann-Whitney U: $n=56,21$, $z=4.47$, $p<0.00001$)

Competitive ability is expressed as percent reduction in phytometer biomass (*Trichostema brachiatum*) when grown with test species.

Drought treatment:



DISCUSSION

TRAITS AND RELATIVE COMPETITIVE ABILITY

Total biomass was the best predictor of competitive ability for the sixty-three terrestrial herbaceous plant species grown in the normal treatment. This finding is consistent with several past studies which have taken competitive ability and plant traits into consideration. As early as 1933, Clements summarized the results of hundreds of transplant and removal experiments in prairie vegetation and concluded that in general taller grasses have a competitive advantage over the shorter. Grime (1974) reviewed several investigations on competition and concluded that in a majority of competitive species height of canopy is of greatest importance. A study of sea-cliff plants by Goldsmith (1978) revealed that the larger plants tended to suppress the smaller ones. Goldberg and Fleetwood (1987) utilised neighbourhood experiments to look at competitive effect and response in four annual terrestrial herbaceous plant species. They found that species which attain larger sizes when grown with no competition generally have greater competitive effect (cause greater reductions in growth of target plant). Wilson and Keddy (1986b) experimentally derived a dominance hierarchy for seven shoreline species. The dominants in this hierarchy were tall, whereas the subordinate was a small rosette (Keddy 1989). Keddy and Shipley (1989) showed that 37% of the variation in competitive ability of these plants can be explained by difference in their heights. In a study of chalk grasslands, Mitchley and Grubb (1986) found a significant correlation between position of 6 plant species in a dominance hierarchy and mean turf height reached by these plants in monocultures. Gaudet and Keddy (1988a) screened for the competitive abilities of 44 herbaceous wetland plant species using a modified additive design. Competitive ability was measured as the relative ability of each of the test species to suppress the plant indicator (phytometer) *Lythrum salicaria*. Regression analysis revealed that average dry weight of the test species when grown singly could explain 64% of the variation in competitive ability. When other size related variables were included in a multiple regression (height, canopy diameter, leaf shape, canopy area) they were able to explain 74% of the variation.

Although these various past studies suggest that height, or some aspect of biomass is of great importance in determining plant competitive ability, only Gaudet and Keddy's study (1988a) and my study, was designed to explicitly test for a quantitative relationship between competitive ability and plant traits. Thus these two experiments are unique, as they allow for the generation of broad generalizations concerning plant competition. Both these experiments found that biomass is the best predictor of competitive ability. This suggests that biomass may be a good predictor of competitive ability across a range of vegetation types. However, it is interesting to note that while above-ground biomass was the best predictor of competitive ability in Gaudet and Keddy's study (1988a) of wetland plant species, this study found total biomass to be the best predictor of competitive ability across a range of terrestrial plant species. This finding suggests that the competitive interactions of wetland and terrestrial plants may be different. Although a mechanistic interpretation is not provided by either of these experiments, one might suggest that in wetlands, the ability to monopolise above-ground limiting resources (light) is of the greatest competitive advantage. Water and nutrients may only rarely limit plant growth in this habitat. Thus, having a large above-ground biomass allows a plant to monopolise light resources. However, in terrestrial vegetation, the ability to monopolise both above and below-ground limiting resources may be of similar importance for a competitive advantage. Thus having a large total biomass allows a plant to monopolise both above and below-ground resources.

It is interesting to note that in Gaudet and Keddy's study (1988a) biomass was found to predict 74% of the variation in the competitive ability of wetland plants, whereas in my study of terrestrial plants biomass was only able to predict 34% of the variation in competitive ability. This further suggests that the competitive interactions of wetland and terrestrial plants are different. It may well be that above-ground biomass is a strong predictor of competitive ability for wetland plants because it embodies several other traits which are collectively predictive of the competitive ability. However, in terrestrial systems, total biomass may not summarize the majority of traits that collectively predict competitive ability. Thus, perhaps knowledge of two or more traits is necessary to make accurate predictions of competitive ability in terrestrial plants, or there may exist another single trait, which was not measured, that is highly predictive of a terrestrial plant's competitive ability. It may also be that traits which confer resistance to other environmental factors such as grazing or fire override traits which confer competitive ability in terrestrial situations. That is to say, competition may be less important in old fields than in marshes.

ON MECHANISTIC INTERPRETATIONS

My results clearly suggest that size is the predominant trait associated with competitive ability, however, they do not provide a mechanistic interpretation of resource competition. Biomass may simply integrate other traits that confer strong competitive ability, such as physiological activity rates (i.e. high rates of resource capture above and below-ground) (Chapin, 1980). It should be noted, however, that biomass is a trait that is associated with the ability to capture resources (Grime, 1979) since it provides a high surface area for capturing resources and thereby simultaneously enhancing growth and denying them to neighbours (Keddy, 1989). Plants that strongly suppress other plants must be good at depleting resources and making them unavailable to neighbouring plants (Goldberg, 1990). Large plants can monopolise many resources (i.e. light, nutrients and water) that are crucial for growth and survival. For example, if two plants are grown in close proximity to one another, the taller plant is more easily able to intercept light photons, thus allowing further growth. Light availability and quality decrease exponentially with distance below the top of the canopy (Fitter and Hay, 1983). Furthermore, an experiment by Tilman and Wedin (1991b) utilising five grasses grown in monoculture revealed that light penetration to soil surface was a negative exponential function of above-ground biomass of these monocultures (r^2=0.79). Therefore, as the larger plant gets taller, its shorter counterpart becomes more shaded, thereby inhibiting its growth. Thus the larger the tall plant can grow, the more shading it incurs on smaller neighbouring plants and the competitive interaction subsequently becomes more and more asymmetric (Weiner, 1986; Keddy and Shipley, 1989; Keddy, 1989; Johanssen and Keddy, 1991).

Light is not the only resource for which plants compete. Soil nutrients and water are also important for plant growth. Access to light can control a plant's acquisition for these other resources. The fact that total biomass was a better predictor of competitive ability than either above or below-ground biomass on their own, and the fact that above and below-ground biomass are highly correlated across this range of species (**Appendix 3a & 3b**), suggests that the ability to capture resources both above and below-ground are important in determining competitive ability. Light is necessary both for constructing roots and for the physiological process of nutrient uptake. Thus larger plants with greater access to light are able to use that energy for greater root construction, which in turn enable the plant to monopolise water and nutrient uptake. Furthermore, smaller plants, which are shaded, not only are denied photons for growth of above-ground parts but growth of below-ground parts are also affected, which subsequently affects their ability to acquire nutrients and water (Keddy, 1989). Total plant biomass was significantly correlated with water uptake rate (**Figure 8**), which in turn would be an indicator of potential to exploit both light energy and below-ground resources.

The results of the drought treatment revealed that size was once again the predominant trait associated with competitive ability. However, below-ground biomass of test species appears to be a better predictor of competitive ability in the drought treatment as opposed to total biomass in the normal treatment. Although a mechanistic interpretation is once again not provided by these results, one might suggest that in a droughted environment, water becomes 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). I found that the drought treatment had significantly reduced species productivity (**Figure 3**). Therefore, it appears that those plants that could allocate more energy to building a large and extensive root system were better able to monopolise the limiting resources in the drought treatment, thus making them stronger competitors.

Beyond plant biomass, several other measured traits were found to correlate significantly with relative competitive ability (**Table 4**). Among these, it is noteworthy that leaf area index (LAI) had significant correlation values in both the normal and drought treatments. Once again, this is not surprising, if we look at plausible mechanistic interpretations. Large LAI allows for a greater photosynthetic surface, thus plants with a large LAI are able to monopolise light resources giving them a competitive advantage. It is interesting to note that LAI is significantly correlated with biomass in both the normal and drought treatments (**Appendix 3a & 3b**). To state the obvious, this suggests that LAI is one of the traits integrated or summarized by biomass, which we found to be strongly predictive of competitive ability.

The ability of plants to extract soil nitrogen was significantly correlated with relative competitive ability (**Tables 4a & 4b**). This result appears consistent with some recent work by Tilman and Wedin (1991a & b). Nitrogen is a principal limiting soil resource in old fields (Tilman, 1988). One central prediction is that the species that can create the lowest level of the limiting resource (R*) will exclude other species limited by that resource (e.g. Tilman 1976, 1982, 1990, Tilman and Wedin, 1991a & b). Tilman and Wedin (1991a) studied this prediction by preforming pairwise competition experiments using five old field grasses. They found that the outcome of competition on low nitrogen soils could be predicted by R^*. My experiment also showed significant correlation between the level of nitrogen that test species created when grown in monoculture and relative competitive ability (Normal treatment: $n=74$, $r=-0.39$, $p<0.001$; Drought treatment: $n=72$, $r=-0.28$, $p<0.05$). However, the interpretation of this depends upon whether these soil nitrogen levels are considered approximations of R^* or whether they simply reflect short term rates of nitrogen removal during this experiment.

When a multivariate regression analysis was carried out, leaf shape (length:width) was found to predict 20 percent of the residual variation in competitive ability in both the normal and the drought treatments. Upon reviewing the correlation between the various plant traits and competitive ability (**Tables 4a & 4b**) it becomes evident that leaf length is the component of leaf shape which causes the relationship to be negative. That is, the strong competitors in this experiment tend to be those plants with short leaf length and wide leaf width, whereas the weaker competitors tend to be those species with long narrow leaves. This finding suggests that on a very broad scale, graminoids and sedges may be weaker competitors than the forb species (**Figures 12a & 12b**). This finding was consistent in both the normal and the drought treatment.

Examination of the competitive hierarchy revealed some intraspecific differences in relative competitive ability (**Table 3a & b**). For example, the relative competitive ability of *Rumex acetosella* when collected from an old field was 94.4, whereas when it was collected from a rock barren its relative competitive ability escalated to 99.0 (**Table 3a**). One can only speculate as to the reasons behind these intraspecific differences. These differences could be explained by random variation, transplanting effects, or perhaps the site in which a plant grows does indeed affect competitive ability thus causing these intraspecific differences. However, these differences might be better explained through further experimentation which assesses the competitive ability of like species collected from a range of habitats.

COMPETITIVE HIERARCHIES AND EVOLUTION

Examination of the competitive hierarchy reveals that some closely related species have similar competitive abilities (**Tables 3a & b**). For example, the *Carex* species were consistently weak competitors in both the normal and the drought treatments. There is a growing awareness of the importance of evolutionary history in determining present day characteristics of species (Hodgson 1986; Hodgson and Mackey, 1986). Hodgson and Mackey (1986) have found that growth rate and seed size affect a plant's ability to exploit a habitat. They have further noted that plant families exhibit similar traits. They thus suggest that plant families have developed these traits evolutionarily. Thus, closely related species may have similar competitive abilities due to historical effects, just as there are historical effects of other plant traits.

ON THE INVARIANCE OF COMPETITIVE HIERARCHIES

The question of whether competitive hierarchies are variant or invariant has been disputed for years. Several works suggest that plants' competitive ability depends on the environment in which the plants are competing (Austin *et al.*, 1985; Tilman, 1988, 1990). Other works support the hypothesis that competitive rankings of species are relatively independent of the environment (Fowler, 1982; Grime, 1979; Keddy, 1989, 1990). My experiment revealed that on a broad scale, competitive hierarchies are invariant across treatment conditions (**Figures 10 & 11**). This trend becomes more evident through investigation of the various growth forms. In both the normal and the drought treatment the weaker competitors tended to include several low growing grasses and sedges (ie. *Danthonia spicata, Carex rugosperma*) and several small rosette species (*Saxifraga virginiensis* and *Antennaria neglecta*). It is interesting to note that *Sporobolus heterolepis* turned out to be one of the weakest competitors in both the normal and drought 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 lends support to the theory that rare and endangered species are limited by competition (Grime, 1979; Gaudet & Keddy, 1988b; Moore *et al.*, 1989). Many of the species at the high end of the competitive hierarchy were large leafy species (i.e. *Plantago rugelii*, *Solidago* spp.). Furthermore, the majority of non-native species (introduced species) tended to the strong end of the competitive hierarchy (**Tables & b**). This finding may be important for the control and management of invasive non-native plant species.

At first glance our results appear to refute the view that competitive hierarchies vary with environment. However, closer analysis reveals that there were apparent smaller scale shifts in the competitive ranking of species between the normal and drought treatment. For example, *Phleum pratense* showed a dramatic shift in competitive ability from the normal to the drought treatment. In the normal treatment it was ranked 62nd out of 77 species in the competitive hierarchy, whereas its rank plummeted to 30th in the drought treatment. *Antennaria neglecta* also showed a dramatic shift in competitive ranking from one treatment to the next. In the normal treatment *Antennaria neglecta* was ranked 14th in the competitive hierarchy and in the drought treatment its rank escalated to 40th. Thus, our work suggests that the variant and invariant views of competitive hierarchies in plants are not mutually exclusive, but instead address the question of competition at different scales.

The majority of studies concerning plant competition utilise only a few species interacting in pairwise situations (Williams, 1962; Harper, 1963; Goldsmith, 1978; Mitchley and Grubb, 1986; Wilson and Keddy, 1986a). Thus it is not surprising that the question of variant versus invariant plant competition has not been solved. Furthermore, it has been suggested that variance in competitive hierarchies becomes more pronounced when species of similar competitive ability are utilised (Keddy and Shipley, 1989; Keddy, 1990). When similar species compete, the interaction is fairly symmetric (*sensu* Wilson, 1988; Keddy, 1989; Johansson & Keddy, 1991). In these situations, hierarchies may be least important in determining the outcome of competitive interactions. Instead, minor fluctuations in environment may have a major influence on competitive rankings (Keddy, 1989). Many studies concerning plant competition utilise very similar plant species (e.g. Fowler, 1982; Austin *et al.*, 1985; Schoen *et al.*, 1986) Thus the variant view of competitive hierarchies is emphasized. However, according to my findings, the outcome of competitive interactions at the community level is relatively predictable, irrespective of environment. Thus, at a broad scale (a scale that incorporates many plant species with a range of competitive abilities) it may be possible to utilise plant traits to predict the outcome of competitive interactions across a range of environments.

COMPETITION INTENSITY

Intensity of competition in the normal and drought treatment did not vary. This suggests that competition is important in determining community structure in a variety of environments. This finding appears to contradict the hypothesis that competition becomes relatively less important in determining community structure under conditions of stress (Grime, 1973, 1988). However, my study utilised only two experimental treatments and species were limited to dry terrestrial systems. Therefore, future experiments need to be executed that compare species from several vegetation types across a variety of environmental treatments. Although intensity of competition did not vary, it may well be that competition shifted from being mainly above-ground in the normal treatment to being mainly below-ground in the drought treatment (e.g. Wilson, 1988; Tilman, 1988). This is suggested by the fact that below-ground biomass is a better predictor of competitive ability in the drought treatment. However, this interpretation is only speculative.

SOME CAVEATS

Although the results of this experiment suggest invariant competitive rankings at the broad scale and variant 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. Tilman and Wedin (1991a) suggest that short term experiments may not reveal the long-term outcome of competition. It may well be that if this experiment had been run over several years, position in the hierarchy would have changed. The competitive hierarchy I assembled may represent competitive rankings of species during the early stages of succession. The fact that *Plantago rugelii* and several other large leafy forbs (i.e. *Solidago* spp. and *Aster* spp.) were found to monopolise the top of the competitive hierarchy appears to support this hypothesis. These plant species are often found in abundance in disturbed sites (i.e. roadsides, the edges of walking paths etc.). These sites represent early successional sites. Of course, this is merely a suggestion and experiments will have to be run over longer periods of time to deduce conclusive answers concerning competitive hierarchies.

There may be a multitude of other factors that interact with positions in a competitive hierarchy. This experiment utilised only two treatments. Other environmental variables beyond the normal and drought treatment created in this experiment may effect the hierarchy. Various forms of grazing have been found to control the make-up of plant communities (eg. Louda *et al.*, 1990) 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.

The phytometer method is ideal for studying competition, especially if one wishes to examine large numbers of species under several environmental treatments. Traditional studies for measuring competitive ability tend to use pairwise combinations of all possible species interactions (Keddy, 1990). These diallele designs increase in size by the square of the number of species examined. Therefore, using pairwise combinations of all possible species interactions limits the number of species that may be logistically used in an experiment (Rigler, 1982; Keddy, 1988, 1990). But at present, the choice of a phytometer in an experiment is some what subjective. My phytometer was chosen on the basis that it was abundant, easy to collect and had been found in past studies to be easily established as a seedling (Belcher, 1991a). The results of this experiment, however, suggest that choosing a phytometer of moderate competitive ability would have been preferable. My results revealed that *Trichostema brachiatum* was a fairly weak competitor (**Tables 4a & 4b**). Therefore, the bulk of species at the high end of the competitive hierarchy were able to highly suppress the phytometer. This subsequently masked the range of competitive abilities of species at the high end of the hierarchy. Using a phytometer with a more moderate competitive ability, would probably have clarified the hierarchy of competitive abilities at the strong end of the continuum.

Competitive ability was calculated as the ability of the test species to suppress phytometer growth. It was not possible to remove the roots of the phytometer from the experimental pots as they had become intermeshed with the test species' roots. Therefore, only above-ground biomass was used to calculate competitive ability. Although above-ground biomass appears to provide a good estimate of competitive ability it should be noted that the results may have been slightly different had I been able to use total biomass to assess competitive ability.

CONCLUSIONS

In summary, on a broad scale, plant traits can be used to predict competitive ability in terrestrial herbaceous plant species. Therefore, within certain limits, one can predict the competitive ability of any target species in this study based on its morphology. My experiment revealed total biomass as the best predictor of competitive ability in a normal treatment and below-ground biomass as the best predictor in a drought treatment. This finding is similar to the results of competition studies in wetlands where plant biomass was also found to be the best predictor of relative competitive ability (Gaudet & Keddy, 1988a). This suggests that those traits which confer competitive ability may remain static across a range of plant systems. To test this hypothesis, it would be beneficial to study competitive hierarchies and plant traits in other plant systems.

There are differences between terrestrial and wetland systems. In terrestrial plants, total biomass was found to be the best predictor of competitive ability, whereas above-ground biomass was the best predictor of competitive ability in wetland plants. Furthermore, while biomass was able to predict 74% of the variation in competitive ability in wetland plants (Gaudet and Keddy, 1988a) it was only able to predict 34% of the variation in terrestrial plants. This suggests that competitive interactions of wetland and terrestrial plants are different.

My results revealed that on a broad scale, competitive ability was invariant across environmental treatments. This finding, and the relationship I found between competitive ability and plant traits suggests that traits may be used to predict competitive ability across a range of environmental conditions.

REFERENCES

Aarssen, L.W. 1989. Competitive ability and species coexistence: a "plant's eye" view. *Oikos* 56: 386-401.

Argus, G.M., K.M. Pryer, D.J. White, and C.J. Keddy. 1987. *Atlas of Rare and Vascular Plants of Ontario*. National Museum of Natural Sciences, Ottawa.

Austin, M.P., R.H. Groves, C.M.F. Fresco, and P.E. Kaye. 1985. Relative growth of six thistle species along a nutrient gradient with multispecies competition. *Journal of Ecology* 73: 667-684.

Belcher, J.W. 1991a. *The ecology of Alvar vegetation in Canada: description, competition and pattern*, M.Sc. Thesis, University of Ottawa, Ottawa.

Belcher, J.W. 1991. *The Ecology of Alvar Vegetation in Canada: Description, Competition and Pattern*. M.Sc. Thesis, University of Ottawa, Ottawa.

Belcher, J.W., P.A. Keddy, and P.M. Catling. 1992. Alvar vegetation in Canada: a multivariate description at two scales. *Canadian Journal of Botany* 70: 1279-1291.

Botkin, D.B. 1977. Life and death in a forest: the computer as an aid to understanding. Pages 213-233. *in* Hall and Day, eds. *Ecosystem modelling in theory and practice* Wiley, New York.

Catling, P.M., J.E. Cruise, K.C. McIntosh, and S.M. McKay. 1975. Alvar vegetation in southern Ontario. *The Ontario Field Biologist* 29: 1-25.

Chapin, F.S. III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11: 233-260.

Chapin, F.S., A.J. Bloom, C.G. Field, and, R.H. Waring. 1987. Plant response to multiple environmental factors. *Bioscience* 37: 49-57.

Clements, F.E. 1933. Competition in plant societies. *News Service Bulletin*, Carnigie Institution of Washington, April 2 1933.

Clements, F.E. 1935. Experimental ecology in the public service. *Ecology* 16: 342-363.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122: 661-696.

Fitter, A.H. and, R.K.M. Hay. 1983. *Environmental Physiology of Plants.* Academic Press, London.

Fowler, N. 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. *Journal of Ecology* 70: 77-92.

Gaudet, C.L. and, P.A. Keddy. 1988a. Predicting competitive ability from plant traits: a comparative approach. *Nature* 334: 242-243.

Gaudet, C.L. and P.A. Keddy. 1988b. The relationship between plant competitive ability, morphology and field distribution: implications for wetland management. Proceeding of a conference IN: *Wetlands Inertia or Momentum* Federation of Ontario Naturalists.

Givnish, T.J. 1982. On the adaptive significance of leaf height in forest herbs. *The American Naturalist* 120: 353-381.

Goldberg, D.E. 1987. Neighbourhood competition in an old field plant community. *Ecology* 68: 1211-1223.

Goldberg, D.E. 1990. Components of resource competition in plant communities. Pages 27-49 *in* J.B. Grace and JD. Tilman, eds. *Perspectives on plant* *competition* Academic Press, San Diego.

Goldberg, D.E. and, A.M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. *The American Naturalist* 122: 662-696.

Goldberg D.E. and, L. Fleetwood. 1987. Competitive effect and response in four annual plants. *Journal of Ecology* 75: 1131-1143.

Goldsmith, F.B. 1978. Interaction (competition) studies as a step towards the synthesis of seacliff vegetation. *Journal of Ecology* 66: 921-931.

Grace, J.B. and, D. Tilman. 1990. *Perspectives in plant competition.* Academic press, New York.

Grime J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.

Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* 250: 26-31.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley, London.

Grime, J.P. 1988. The C-S-R model of primary strategies-- origins, implications and tests. Pages 371-393 *in* L.D Gottlieb and S.K. Jain, eds. *Plant Evolutionary Biology*. Chapman and Hall, London.

Grime, J.P. and, R. Hunt. 1975. Relative growth-rate: its range and adaptive significance in local flora. *Journal of Ecology*. 63: 393-422.

Grime, J.P., G. Mason, A.V. Curtis, J. Rodman, S.R. Band, M.A.G. Mowforth, A.M., Neal and S. Shaw. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology*. 69: 1017-1059.

Harper, J.L. 1963. The nature and consequence of interference amongst plants. In: *Genetics Today Vol. 2* Pages 466-482.

Harper, J.L. 1977. *Population Biology of Plants*. Academic Press, London.

Hodgson J.G. 1986. Commonness and rarity in plants with special reference to the Sheffield flora part III: Taxonomic and evolutionary aspects. *Biological Conservation*. 36: 275-296.

Hodson J.G. and J.M.L. Mackey. The ecological specialization of dicotyledonous families within a local flora: some factors constraining optimization of seed size and their possible evolutionary significance. *New Phytol.* 104: 497-515.

Johansson, M.E., and P.A. Keddy. 1991. Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. *Oikos* 60: 27-34.

Keddy, P.A. 1989. *Competition.* Chapman and Hall, London.

Keddy, P.A. 1990. Competitive hierarchies and centrifugal organization in plant communities. Pages 265-290 *in* J.B. Grace and D. Tilman, eds. *Perspectives in Plant Competition.* Academic Press, San Diego.

Keddy, P.A. 1991. Plant competition and resources in old fields. *Trends in Ecology and Evolution.* 6: 235-237.

Keddy, P.A. 1992. A predictive approach to functional ecology. *Functional Ecology* in press.

Keddy, P.A. and, B. Shipley. 1989. Competitive hierarchies in plant communities. *Oikos* 54: 234-241.

Louda, S.M., K.H. Keeler and, R.D. Holt. 1990. Herbivore influence on plant performance and competitive interactions. Pages 413-444 *in* J.B. Grace and D. Tilman, eds. *Perspectives on plant competition*. Academic Press, San Diego.

McCanny, S.J., P.A. Keddy, R.J. Arnason, C.L. Gaudet, D.R.J. Moore and, B. Shipley. 1990. Fertility and the food quality of wetland plants: a test of the resource availability hypothesis. *Oikos* 59: 373-381.

Mitchley, J. 1988. Control of relative abundance of perennials in chalk grassland in Southern England. II. Vertical canopy structure. *Journal of Ecology*. 76:341-350.

Mitchley, J. and, P.J. Grubb. 1986. The control of relative abundance of perennials in chalk grasslands in southern England. I. Constancy of rank order and results of pot and field experiments on the role on inference. *Journal of Ecology* 74: 1139-1166.

Morton, J.K. and J.M. Venn. 1990. *A Checklist of the Flora of Ontario Vascular Plants*. University of Waterloo Press, Waterloo, Ontario.

Moore, D.R.J., P.A. Keddy, C.L. Gaudet and, I.C. Wisheu. 1989. Conservation of wetlands: Do infertile wetlands deserve a higher priority? *Biological Conservation* 47: 203-217.

Optimas 1990. Biosoft Version 3.0, Bioscan Inc., Washington USA.

Rigler, F.H. 1982. Recognition of the possible: an advantage of empiricism in ecology. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1323-1331.

SAS 1985 Version 5 Edition, SAS Institute Inc., Cary, NC, USA.

Schoen, D.J., S.C. Stewart, M.J., Lechowiez, and G. Bell. 1986. Partitioning the transplant site effect in reciprocal transplant experiments with *Impatiens capensis* and *Impatiens pallida*. *Oecologia (Berlin)* 70: 149-154.

Shoener, T.W. 1983. Field experiments on interspecific competition. *The American Naturalist* 122: 240-285.

Siegel, S. 1956. *Nonparametric Statistics for Behavioral Sciences*. Mcgraw-Hill, New York.

STATGRAPHICS 1989. Statgraphics Version 3.0, Statistical graphic

Corporation. STSC Inc., Rockville, Maryland, USA.

Tilman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*. 192: 463-465.

Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.

Tilman, D. 1988. *Plant Strategies and the Structure and Dynamics of Plant Communities*, Princeton University Press, Princeton, New Jersey.

Tilman, D. 1989. Competition, nutrient reduction and the competitive neighbourhood of a bunchgrass. *Functional Ecology* 3: 215-219.

Tilman, D. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117-140 *in* J.B. Grace and D. Tilman, eds. *Perspectives on plant competition.* Academic Press, San Diego.

Tilman, D. and, D. Wedin. 1991a. Dynamics of nitrogen competition between successional grasses. *Ecology* 72: 1038-1049.

Tilman, D. and D. Wedin. 1991b. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72: 685-700.

Weaver, J.E. and Clements, F.E. 1929. *Plant Ecology*, McGraw-Hill, New York.

Weiner, J. 1986. How competition for light and nutrients effects size variability in *Ipomoea tricolor* populations. *Ecology* 67: 1425-1427.

Welbank, P.J. 1963. A comparison of competitive effects of some common weed species. *Ann. App. Biol.* 51: 107-125.

Williams, E.J. 1962. The analysis of competition experiments. *Australian Journal of Biological Sciences* 15: 509-525.

Wilson, J.B. 1988. Shoot competition and root competition. *Journal of Applied Ecology* 25: 279-296.

Wilson, S.D. and, D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72: 1050-1065.

Wilson S.D. and, P.A. Keddy. 1986a. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *The*

American Naturalist 127: 862-869.

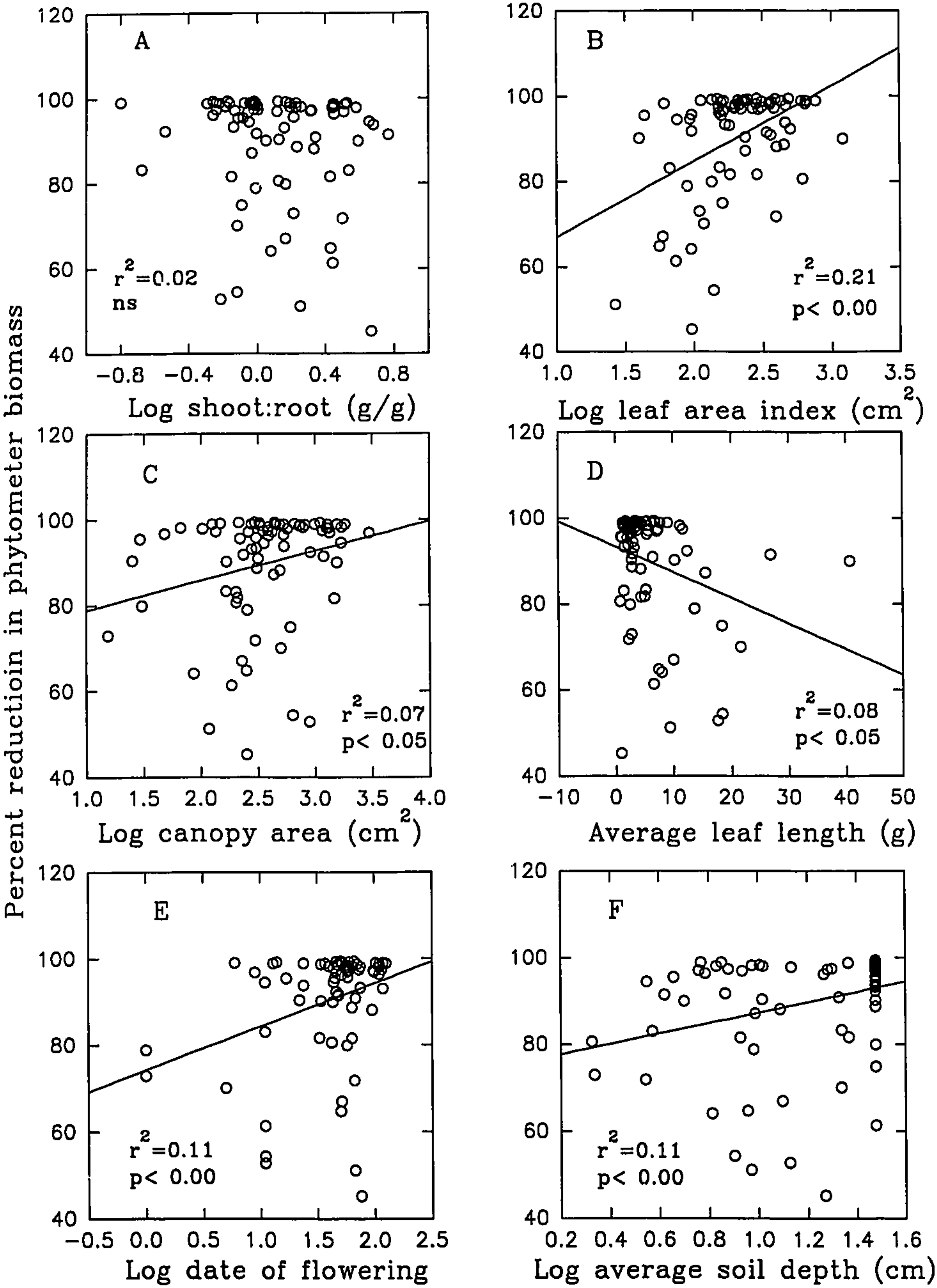
Wilson, S.D. and, Keddy, P.A. 1986b. Species competitive ability and position along a natural stress/disturbance gradient. *Journal of Ecology* 67: 1236-1242.

Zar, J.H. 1984. *Biostatistical Analysis* Prentice-Hall, Inc. New Jersey.

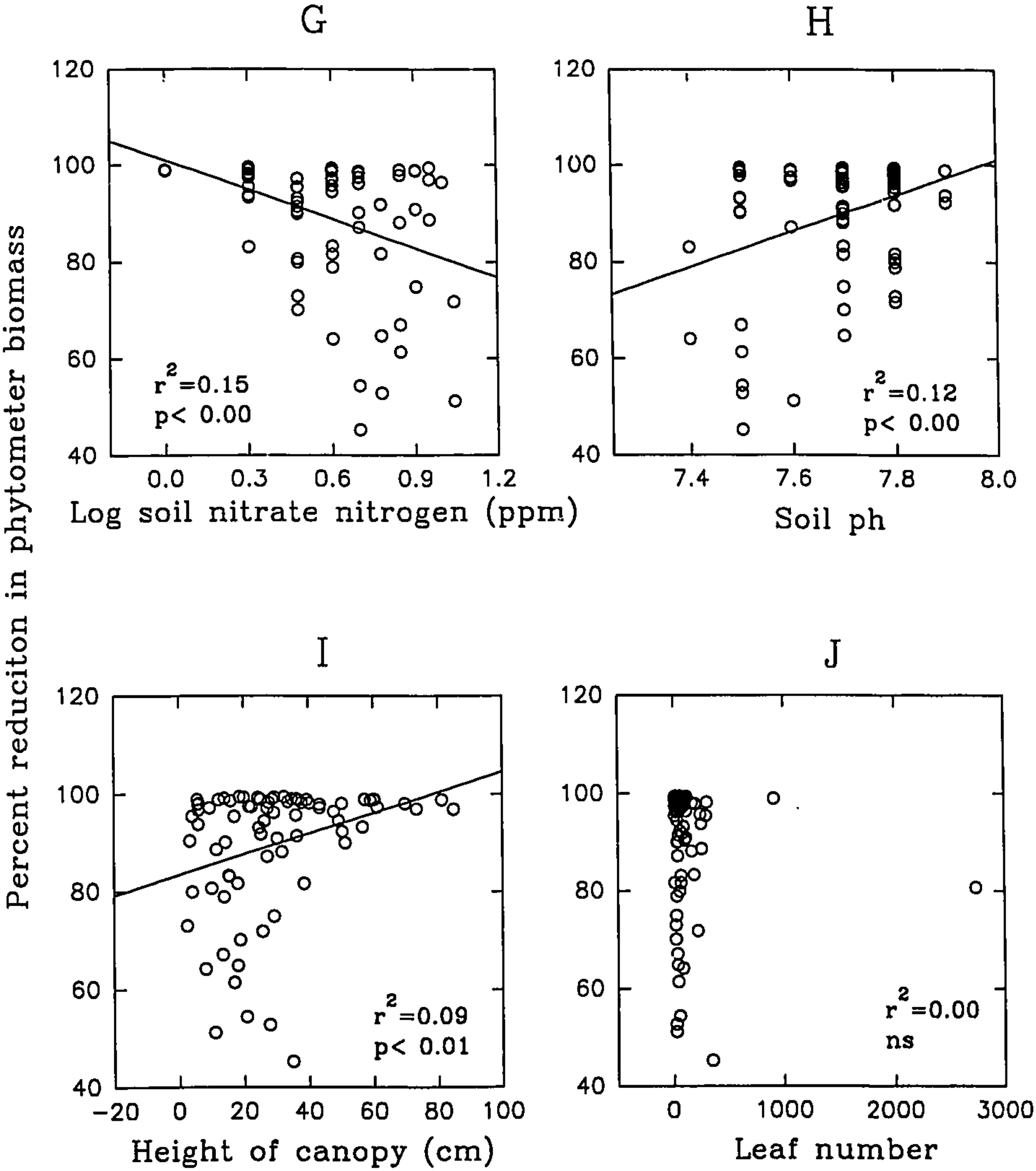
APPENDIX 1 Description and location of collection sites for 63 terrestrial herbaceous plant species tested for their relative competitive abilities.

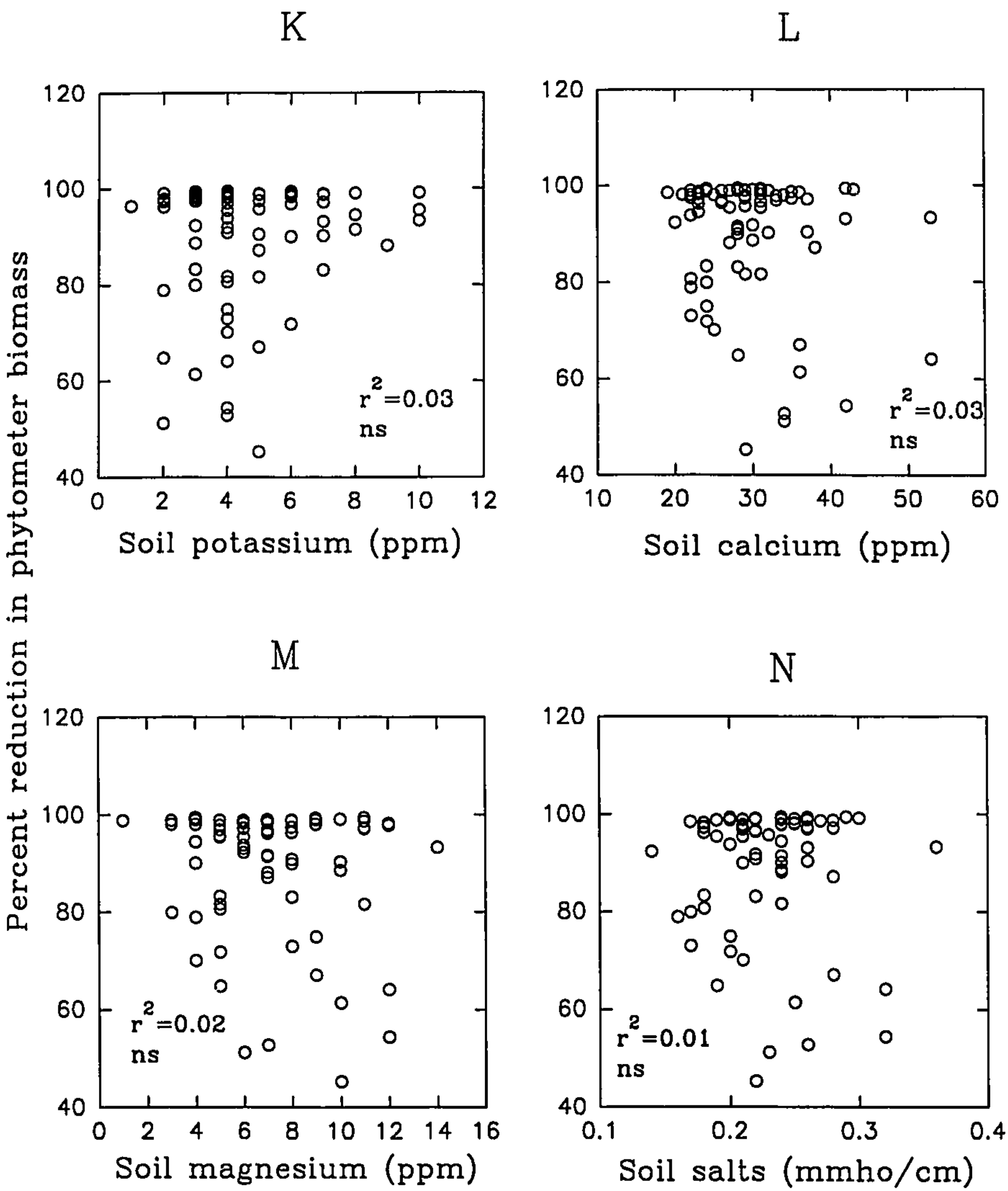
Code	Coordinates	Site Description
a	44°33N' 77°06'E	The site is located south of Kaladar, Ontario via highway 41 on the North west tip of Mellon Lake. The site consisted of a rock outcrop with several pockets of deep to shallow highly organic soil.
b	45°07'N 76°10'E	The site is located west of Carleton Place, Ontario along highway 7 on the private property of Dr. Paul Keddy, University of Ottawa. The site consisted of meadow openings in a deciduous forest and larger open fields. The soil in the area was highly organic in content and soil depth ranged from being very deep (>30cm) to a thin layer of soil over a protruding granite rock base.
c	45°30'N 75°20'E	The site is located in the township of Cumberland, Ontario at the Macskimming Outdoor Education Centre, Ottawa Board of Education. The Education Centre is located at the intersection of Highway 17 and Canaan Road. The site consisted of many open fields ranging from deep organic soil to deep sandy soil.
d	45°23'N 75°38'E	The site is located on several NCC greenbelt areas in Ottawa, Ontario. One site is at the intersection of Linda Lane and Billings Ave. The other site is located on Playfair Cres. The sites consisted of open fields with deep, highly organic soil.
e	45°15N 76°05E	The site is located at the Burnt Lands Alvar in Almonte, Ontario, just off of Highway 44. The Burnt Lands alvar is a large and relatively undisturbed alvar with extensive areas of open limestone rock flats and grassy meadows. The soil is highly organic in content.
f	45°23'N 75°41E	The site is located at Carleton University, Ottawa just behind the Carleton greenhouses on the Rideau River. The site consists of an open field with deep highly organic soil. Also on the site were sandy areas where sand had been artificially dumped.

Appendix 2a Relationship between relative competitive ability (CA) and (a) Shoot:root biomass (n=77), (b) Leaf area index (n=75), (c) Canopy area (n=77), (d) Average leaf length (n=76), (e) Date of flowering (n=72), (f) Average soil depth (n=77), (g) Soil nitrate nitrogen (n=74), (h) Soil pH (n=74), (i) Height of canopy (n=77), (j) Leaf number (n=76), (k) Soil potassium (n=74), (l) Soil calcium (n=74), (m) Soil magnesium (n=74) and (n) Soil salts (n=74) for 63 terrestrial herbaceous plant species grown in a normal treatment.



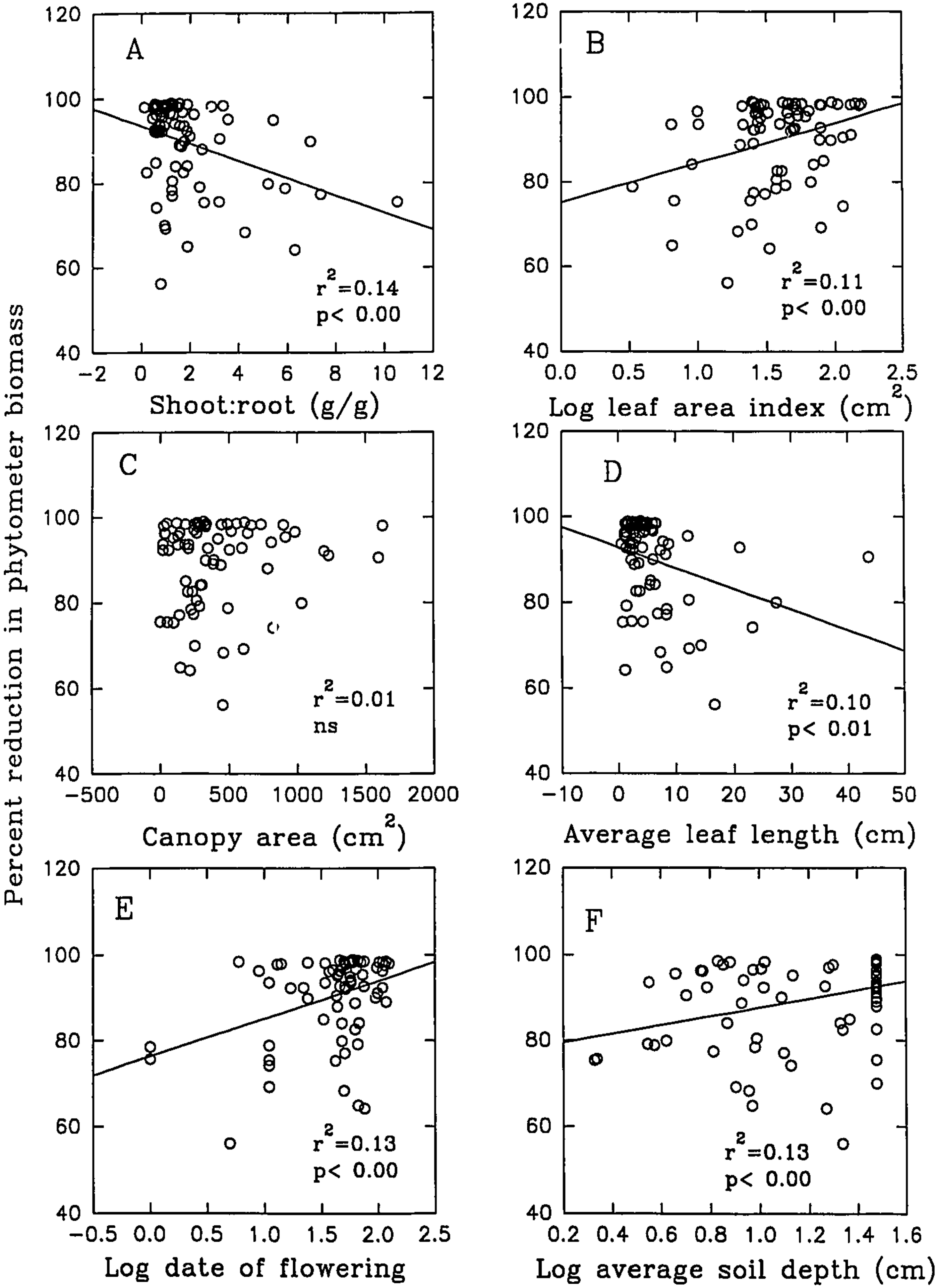
Percent reductioin in phytometer biomass
A
r² =0.02
ns
Log shoot:root (g/g)
B
r² =0.21
p< 0.00
Log leaf area index (cm²)
C
r² =0.07
p< 0.05
Log canopy area (cm²)
D
r² =0.08
p< 0.05
Average leaf length (g)
E
r² =0.11
p< 0.00
Log date of flowering
F
r² =0.11
p< 0.00
Log average soil depth (cm)

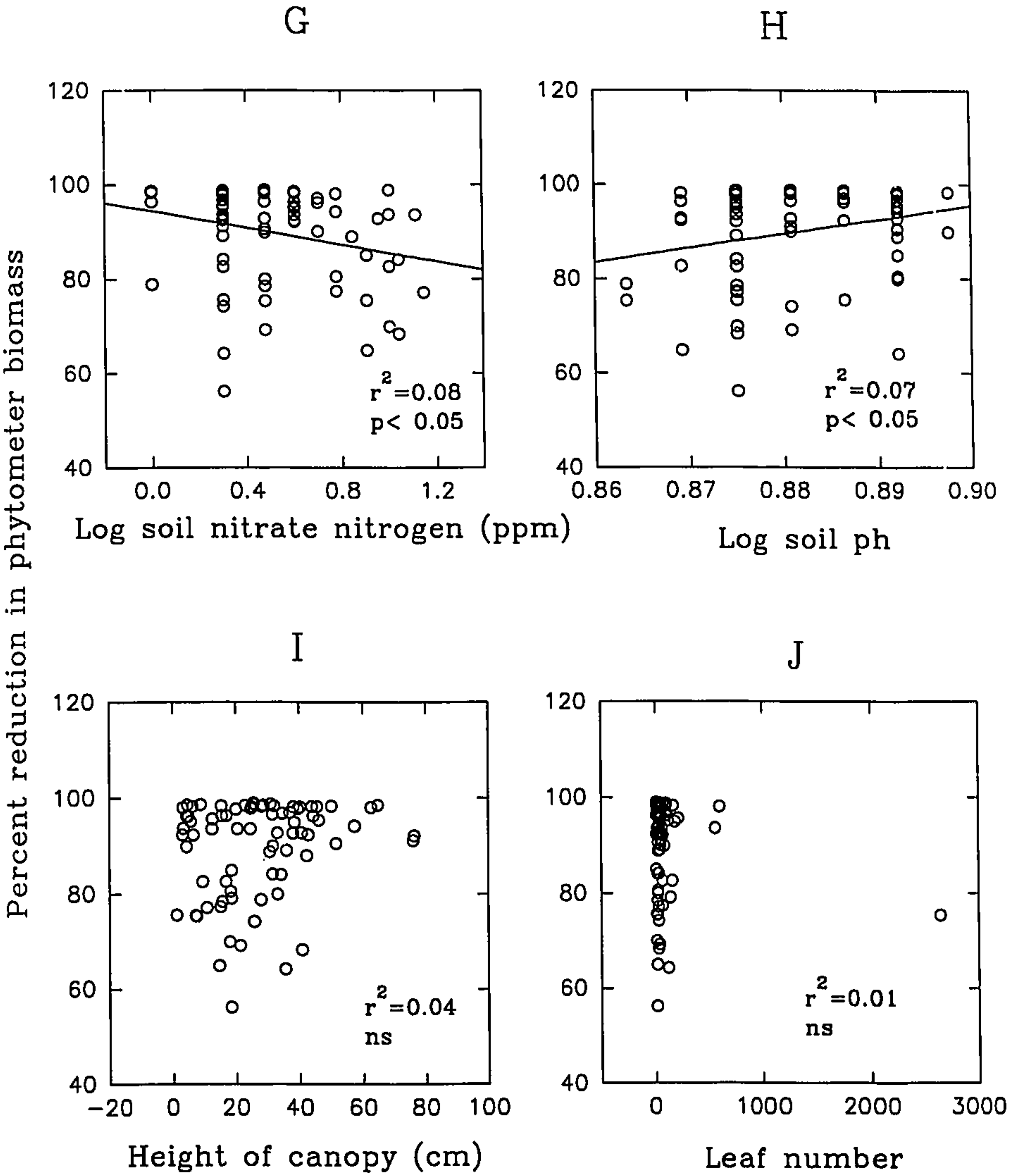

G
H
I
J
Percent reduciton in phytometer biomass
120
100
80
60
40
r²=0.15
p< 0.00
0.0
0.3
0.6
0.9
1.2
Log soil nitrate nitrogen (ppm)
r²=0.12
p< 0.00
7.4
7.6
7.8
8.0
Soil ph
r²=0.09
p< 0.01
-20
0
20
40
60
80
100
Height of canopy (cm)
r²=0.00
ns
0
1000
2000
3000
Leaf number



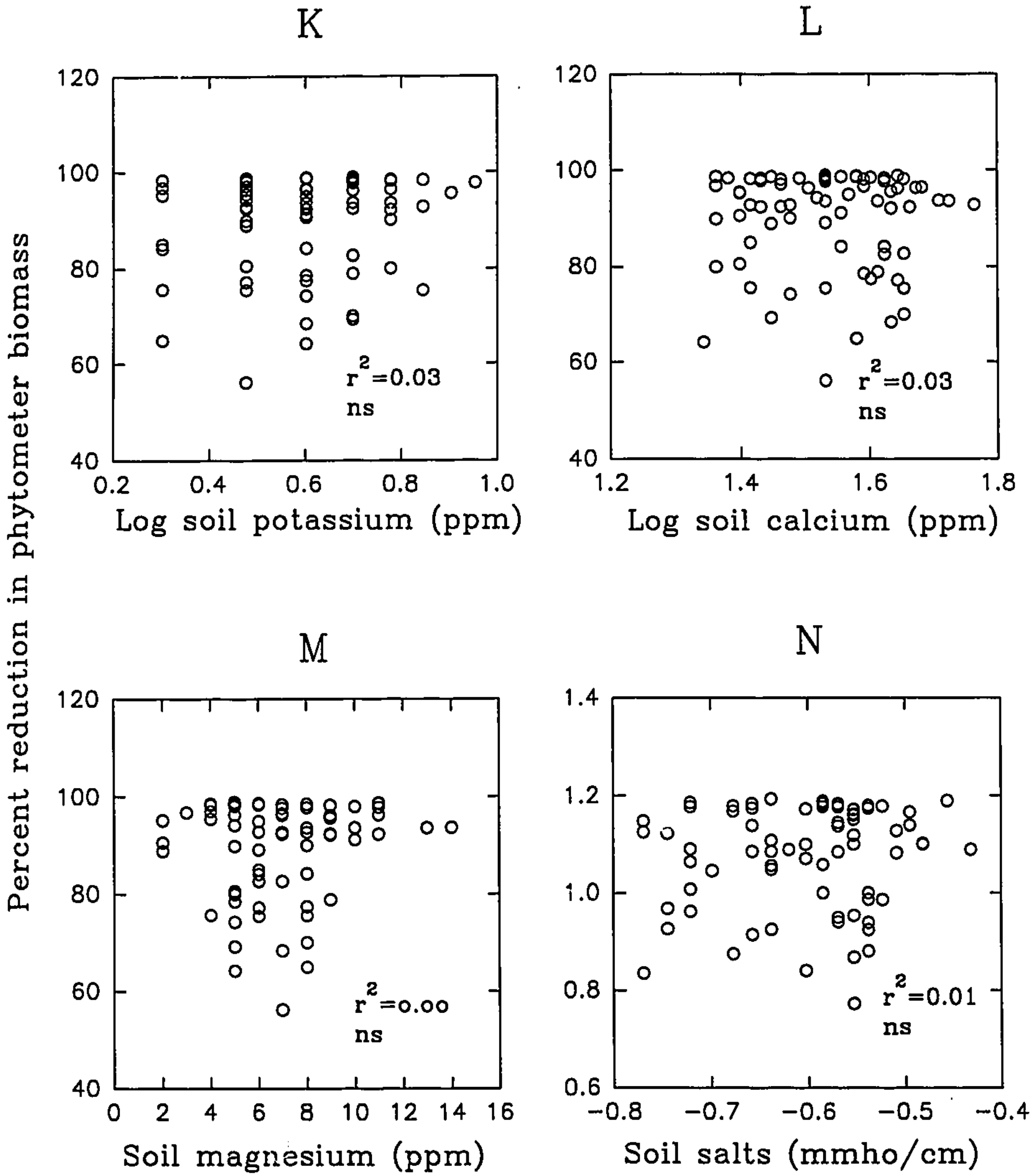
K
L
M
N
Percent reduction in phytometer biomass
Soil potassium (ppm)
Soil calcium (ppm)
Soil magnesium (ppm)
Soil salts (mmho/cm)
r^2=0.03
ns
r^2=0.03
ns
r^2=0.02
ns
r^2=0.01
ns

Appendix 2b Relationship between relative competitive ability (CA) and (a) Shoot:root biomass (n=77), (b) Leaf area index (n=75), (c) Canopy area (n=77), (d) Average leaf length (n=75), (e) Date of flowering (n=71), (f) Average soil depth (n=77), (g) Soil nitrate nitrogen (n=74), (h) Soil pH (n=72), (i) Height of canopy (n=77), (j) Leaf number (n=75), (k) Soil potassium (n=72), (l) Soil calcium (n=72), (m) Soil magnesium (n=72) and (n) Soil salts (n=72) for 63 terrestrial herbaceous plant species grown in a drought treatment.


Percent reduction in phytometer biomass
A
r^2=0.14
p< 0.00
Shoot:root (g/g)
B
r^2=0.11
p< 0.00
Log leaf area index (cm^2)
C
r^2=0.01
ns
Canopy area (cm^2)
D
r^2=0.10
p< 0.01
Average leaf length (cm)
E
r^2=0.13
p< 0.00
Log date of flowering
F
r^2=0.13
p< 0.00
Log average soil depth (cm)



G
H
I
J
Percent reduction in phytometer biomass
120
100
80
60
40
0.0
0.4
0.8
1.2
Log soil nitrate nitrogen (ppm)
$r^2=0.08$
$p< 0.05$
0.86
0.87
0.88
0.89
0.90
Log soil ph
$r^2=0.07$
$p< 0.05$
−20
0
20
40
60
80
100
Height of canopy (cm)
$r^2=0.04$
ns
0
1000
2000
3000
Leaf number
$r^2=0.01$
ns


K
L
M
N
Percent reduction in phytometer biomass
Log soil potassium (ppm)
Log soil calcium (ppm)
Soil magnesium (ppm)
Soil salts (mmho/cm)
r2=0.03
ns
r2=0.03
ns
r2=0.00
ns
r2=0.01
ns

Appendix 3a Correlation (r) between traits measured for 63 terrestrial herbaceous test plant species grown in a "normal treatment".

	Root biomass	**Shoot biomass**	**Shoot to root**	**Height**	**Leaf length**	**Leaf width**	**Leaf shape**	**Leaf number**	**Leaf area index**
Total biomass	n=77 0.91^{***}	n=77 0.83^{***}	n=77 -0.18	n=77 0.64^{***}	n=76 0.03	n=76 0.04	n=76 -0.10	n=76 0.02	n=75 0.48^{***}
Root biomass		n=77 0.52^{***}	n=77 -0.45^{***}	n=77 0.50^{***}	n=76 0.03	n=76 0.04	n=76 -0.11	n=76 -0.02	n=75 0.34^{**}
Shoot biomass			n=77 0.24^{*}	n=77 0.64^{***}	n=76 0.02	n=76 0.03	n=76 -0.06	n=76 0.07	n=75 0.53^{***}
Shoot to Root				n=77 0.03	n=76 0.11	n=76 -0.15	n=76 0.20	n=76 0.04	n=75 0.20
Height					n=76 0.14	n=76 -0.17	n=76 0.03	n=76 -0.05	n=75 0.33^{**}
Leaf length						n=76 -0.18	n=76 0.82	n=76 -0.20	n=75 0.25^{*}
Leaf width							n=76 -0.33^{**}	n=76 -0.18	n=75 0.07
Leaf shape								n=76 -0.10	n=75 0.17
Leaf number									n=75 0.27^{*}

Appendix 3a cont.

	Canopy area	Date of Flower	Soil Depth	Soil pH	Soil N	Soil K	Soil C	Soil Mg	Soil salts
Total biomass	n=77 0.56^{***}	n=72 0.37^{**}	n=77 0.39^{**}	n=74 0.42^{**}	n=74 -0.26^{*}	n=74 -0.06	n=74 -0.25^{*}	n=74 -0.06	n=74 -0.11
Root biomass	n=77 0.33^{**}	n=72 0.28^{*}	n=77 0.35^{**}	n=74 0.36^{**}	n=74 -0.27^{*}	n=74 -0.11	n=74 -0.26^{*}	n=74 -0.01	n=74 -0.19
Shoot biomass	n=77 0.70^{***}	n=72 0.38^{**}	n=77 0.32^{**}	n=74 0.39^{**}	n=74 -0.17	n=74 0.02	n=74 -0.18	n=74 -0.11	n=74 0.02
Shoot to root	n=77 0.23^{*}	n=72 0.02	n=77 -0.16	n=74 -0.10	n=74 0.15	n=74 0.07	n=74 0.00	n=74 0.02	n=74 0.05
Height	n=77 0.76^{***}	n=72 0.52^{***}	n=77 0.24^{*}	n=74 0.24^{*}	n=74 -0.04	n=74 0.02	n=74 -0.04	n=74 0.09	n=74 0.10
Leaf length	n=76 0.28^{*}	n=72 -0.22	n=76 -0.22	n=74 -0.07	n=74 0.01	n=74 0.00	n=74 0.03	n=74 0.08	n=74 0.02
Leaf width	n=76 -0.17	n=72 -0.12	n=76 0.24^{*}	n=74 -0.01	n=74 -0.13	n=74 -0.05	n=74 0.01	n=74 0.04	n=74 0.02
Leaf shape	n=76 0.20	n=72 -0.18	76 -0.31^{**}	n=74 -0.20	n=74 0.02	n=74 0.03	n=74 0.21	n=74 0.11	n=74 0.13
Leaf number	n=76 0.00	n=72 0.11	n=76 -0.14	n=74 0.15	n=74 -0.08	n=74 -0.04	n=74 -0.13	n=74 -0.10	n=74 -0.13
Leaf area index	n=75 0.35^{**}	n=72 0.35^{**}	n=75 0.07	n=74 0.26^{*}	n=74 -0.16	n=74 -0.10	n=74 -0.14	n=74 0.09	n=74 -0.05
Canopy area		n=72 0.32^{**}	n=76 0.14	n=74 0.32^{**}	n=74 -0.09	n=74 -0.04	n=75 -0.14	n=74 -0.02	n=74 0.00
Flower			n=72 0.12	n=72 0.16	n=72 -0.09	n=72 -0.14	n=72 0.05	n=72 0.17	n=72 0.07
Soil Depth				n=74 0.02	n=74 -0.11	n=74 -0.05	n=74 0.01	n=74 -0.05	n=74 0.05
Soil pH					n=74 -0.07	n=74 -0.23^{*}	n=74 -0.71^{***}	n=74 -0.50^{***}	n=74 -0.63^{***}
Soil N						n=74 -0.18	n=74 0.09	n=74 0.00	n=74 0.11
Soil K							n=74 0.23^{*}	n=74 -0.06	n=74 0.31^{**}
Soil C								n=74 0.48^{***}	n=74 0.91^{***}
Soil Mg									n=74 $.45^{**}$

*=p<0.05, **=p<0.01, ***=p<0.00001

Appendix 3b Correlation (r) between traits measured on 63 terrestrial herbaceous test plant species grown in a "drought treatment".

	Root biomass	Shoot biomass	Shoot to root	Height	Leaf length	Leaf width	Leaf shape	Leaf number	Leaf area index
Total biomass	n=77 0.89***	n=77 0.84***	n=77 -0.24***	n=77 0.63***	n=75 0.13	n=75 0.13	n=75 -0.02	n=75 -0.05	n=74 0.69***
Root biomass		n=77 0.51***	n=77 -0.46***	n=77 0.53***	n=75 0.06	n=75 0.11	n=75 -0.10	n=75 -0.07	n=74 0.51***
Shoot biomass			n=77 0.08	n=77 0.56***	n=75 0.18	n=75 0.12	n=75 0.09	n=75 -0.01	n=74 0.72***
Shoot to Root				n=77 -0.12	n=75 0.05	n=75 -0.17	n=75 0.30**	n=75 0.07	n=74 -0.07
Height					n=75 0.07	n=75 -0.09	n=75 0.12	n=75 -0.07	n=74 0.46***
Leaf length						n=75 -0.16	n=75 0.87***	n=75 -0.16	n=74 0.25*
Leaf width							n=75 -0.31**	n=75 -0.16	n=74 0.28*
Leaf shape								n=75 -0.09	n=74 0.05
Leaf number									n=74 0.21

Appendix 3b cont.

	Canopy area	Date of Flower	Soil Depth	Soil pH	Soil N	Soil K	Soil C	Soil Mg	Soil salts
Total biomass	n=77 0.58***	n=71 0.45**	n=77 0.30**	n=72 0.31**	n=72 -0.47***	n=72 0.09	n=72 -0.26*	n=72 -0.15	n=72 -0.07
Root biomass	n=77 0.38***	n=71 0.38**	n=77 0.31**	n=72 0.14	n=72 -0.39**	n=72 0.16	n=72 -0.12	n=72 -0.04	n=72 0.02
Shoot biomass	n=77 0.66***	n=71 0.41**	n=77 0.21	n=72 0.42**	n=72 -0.42**	n=72 -0.01	n=72 -0.35**	n=72 -0.24*	n=72 -0.16
Shoot to root	n=77 0.01	n=71 -0.10	n=77 -0.13	n=72 0.10	n=72 0.11	n=72 -0.18	n=72 -0.18	n=72 -0.12	n=72 -0.22
Height	n=77 0.74***	n=71 0.57***	n=77 0.17	n=72 0.15	n=72 -0.24*	n=72 0.00	n=72 -0.12	n=72 -0.13	n=72 -0.04
Leaf length	n=74 0.49***	n=71 -0.21	n=74 -0.22	n=72 0.16	n=72 0.04	n=72 -0.05	n=72 -0.21	n=72 -0.24*	n=72 -0.27*
Leaf width	n=74 -0.12	n=71 -0.11	n=74 0.27*	n=72 0.17	n=72 0.05	n-72 0.13	n=72 -0.06	n=72 -0.04	n=72 -0.01
Leaf shape	n=74 0.44**	n=71 -0.20	n=74 -0.32**	n=72 0.06	n=72 0.09	n=72 -0.07	n=72 -0.14	n=72 -0.18	n=72 -0.20
Leaf number	n=74 0.26*	n=71 0.33**	n=74 0.12	n=72 0.09	n=72 -0.17	n=72 0.04	n=72 -0.03	n=72 0.05	n=72 0.09
Leaf area index	n=74 0.55***	n=71 0.31**	n=74 0.24*	n=72 0.33**	n=72 -0.28*	n=72 0.10	n=72 -0.22	n=72 -0.12	n=72 -0.04
Canopy area		n=71 0.29**	n=77 0.06	n=72 0.38**	n=72 -0.24*	n=72 -0.09	n=72 -0.30**	n=72 -0.27*	n=72 -0.20
Date of Flower			n=69 0.10	n=69 0.14	n=69 -0.19	n=69 -0.09	n=69 -0.14	n=69 -0.10	n=69 -0.02
Soil Depth				72 n=-0.16	n=72 0.04	n=72 0.11	n=72 0.25*	n=72 0.29*	n=72 0.29*
Soil pH					n=72 -0.30**	n=72 -0.36**	n=72 -0.82***	n=72 -0.48***	n=72 -0.72***
Soil N						n=72 -0.09	n=72 0.50***	n=72 0.26*	n=72 0.38**
Soil K							n=72 0.39**	n=72 0.34**	n=72 0.47***
Soil C								n=72 0.60***	n=72 0.89***
Soil Mg									n=72 0.57***

*=p<0.05, **p<0.01, ***=p<0.00001

Appendix 4a Mean for height (cm), canopy area(cm^2), shoot biomass (g), root biomass (g), total biomass (g), shoot:root biomass, soil depth (cm), date of flowering, leaf length (cm), leaf width (cm), leaf shape, leaf number, leaf area index (cm^2) for 63 terrestrial herbaceous plant species (5 replicates per species) grown in a normal treatment. Table also includes mean above-ground biomass of phytometer (*Trichostema brachiatum*) when grown with each of the test species.

Appendix 4a

Species	Height	Canopy area	Shoot biomass	Root biomass	Total biomass	Shoot: roots	Soil depth
Achillea millefolium	36.30	459.01	4.25	4.40	8.65	0.97	30.00
Achillea millefolium	32.50	444.14	4.05	6.10	10.15	0.66	30.00
Agrostis gigantea	51.22	1542.35	4.03	1.04	5.07	3.87	5.03
Anaphalis margaritacea	30.20	317.83	3.51	1.60	5.12	2.19	21.29
Anemone canadensis	18.10	210.39	1.39	1.98	3.37	0.70	23.28
Antennaria howellii	3.50	25.29	0.68	0.51	1.18	1.34	10.38
Antennaria neglecta	4.10	30.59	0.79	0.54	1.34	1.46	30.00
Aster ciliolatus	50.20	1316.86	5.03	2.81	7.84	1.79	10.46
Aster ciliolatus	47.80	533.10	2.94	1.05	3.99	2.80	6.13
Aster ciliolatus	40.20	783.01	3.43	5.31	8.75	0.65	30.00
Aster ciliolatus	60.20	1815.59	8.61	5.56	14.18	1.55	30.00
Berteroa incana	49.20	1680.91	3.49	0.78	4.27	4.50	30.00
Bromus inermis	50.44	913.53	5.17	17.91	23.08	0.29	30.00
Bromus tectorum	36.40	1195.00	5.99	1.03	7.01	5.82	4.19
Campanula rotundifolia	25.30	236.46	0.65	0.66	1.32	0.98	7.37
Carex crawei	18.80	502.03	0.80	1.06	1.86	0.76	21.71
Carex eburnea	8.20	86.94	0.46	0.39	0.85	1.20	6.48
Carex gracillima	27.80	890.83	1.64	2.69	4.33	0.61	13.34
Carex pallescens	29.25	611.65	1.91	2.36	4.27	0.81	30.00
Carex pensylvanica	13.90	254.37	0.88	0.91	1.79	0.97	9.57
Carex richardsonii	27.10	436.33	3.11	3.37	6.48	0.92	9.72
Carex rugosperma	20.80	637.11	2.94	3.88	6.82	0.76	7.97
Chrysanthemum leucanthemum	34.80	437.31	2.87	5.06	7.94	0.57	30.00
Cirsium arvense	59.10	816.94	7.87	2.82	10.69	2.79	30.00
Corydalis sempervirens	15.50	203.30	0.72	0.21	0.93	3.40	3.74
Danthonia spicata	18.10	250.20	0.75	0.28	1.02	2.68	9.02
Danthonia spicata	17.00	184.25	0.48	0.17	0.65	2.75	30.00

Appendix 4a cont.

Species	Height	canopy area	Shoot biomass	Root biomass	Total biomass	Shoot: root	Soil depth
Echium vulgare	25.10	277.96	3.82	2.28	6.10	1.67	7.11
Elymus repens	61.20	1163.21	3.61	6.34	9.95	0.57	30.00
Elymus trachycaulus	73.30	1335.62	4.14	3.18	7.32	1.30	8.60
Equisetum arvense	15.30	165.83	1.44	6.81	8.25	0.21	21.77
Fragaria virginiana	5.80	1282.78	6.66	2.01	8.67	3.31	30.00
Glechoma hederacea	6.00	536.27	8.94	1.88	10.81	4.76	30.00
Helianthus divaricatus	43.32	420.53	3.39	4.62	8.02	0.73	19.16
Hieracium pilosella	29.20	389.87	1.00	1.83	2.83	0.55	18.47
Hieracium piloselloides	20.00	215.20	0.89	1.62	2.51	0.55	30.00
Hieracium piloselloides	5.90	103.33	2.81	1.03	3.84	2.73	13.61
Hypericum perforatum	36.13	305.00	3.26	2.01	5.27	1.62	30.00
Lechea intermedea	34.85	249.76	1.15	0.25	1.40	4.64	18.61
Linaria vulgaris	43.40	572.65	4.91	1.30	6.21	3.77	30.00
Minuartia michauxii	10.10	204.66	2.05	1.54	3.59	1.33	2.12
Muhlenbergia mexicana	84.80	2983.76	7.71	2.42	10.13	3.19	30.00
Panicum acuminatum	38.60	1467.31	2.15	0.81	2.96	2.67	8.45
Panicum acuminatum	11.60	308.85	1.27	0.74	2.01	1.70	30.00
Panicum depauperatum	13.50	229.02	1.00	0.69	1.69	1.46	12.46
Penstemon hirsutus	27.25	262.18	1.76	0.86	2.62	2.04	5.78
Phleum pratense	81.20	1556.09	7.63	9.12	16.75	0.84	30.00
Plantago rugelii	22.30	350.29	2.41	2.40	4.81	1.00	7.58
Plantago rugelii	18.66	296.04	3.49	2.65	6.14	1.32	30.00
Plantago rugelii	24.38	325.52	3.10	2.12	5.21	1.46	30.00
Poa pratensis	37.80	1701.13	5.21	5.25	10.46	0.99	9.41
Potentilla argentea	15.90	328.43	2.75	0.85	3.60	3.23	30.00
Potentilla recta	33.60	725.71	4.75	5.10	9.85	0.93	30.00
Prunella vulgaris	6.25	66.88	1.24	0.74	1.98	1.68	6.77

Appendix 4a cont.

Species	Height	Canopy area	Shoot biomass	Root biomass	Total biomass	Shoot: root	Soil depth
Prunella vulgaris	9.50	134.30	2.21	1.07	3.28	2.07	30.00
Ranunculus acris	36.90	747.71	4.41	4.52	8.93	0.98	30.00
Rumex acetosella	28.60	534.60	4.76	5.19	9.94	0.92	30.00
Rumex acetosella	26.30	355.28	1.86	2.09	3.95	0.89	3.55
Saxifraga virginiensis	2.56	15.48	1.14	0.70	1.84	1.62	2.17
Scutellaria parvula	17.08	220.27	1.49	1.93	3.42	0.77	4.57
Senecio pauperculus	12.30	125.59	1.98	2.20	4.18	0.90	5.89
Sisyrinchium montanum	14.40	167.38	0.60	0.53	1.13	1.12	30.00
Solidago altissima	60.00	989.60	6.66	9.72	16.38	0.68	30.00
Solidago gigantea	69.64	1263.46	6.47	4.18	10.65	1.55	30.00
Solidago hispida	21.60	383.40	3.31	3.48	6.79	0.95	19.91
Solidago hispida	24.70	279.35	2.34	1.63	3.97	1.44	30.00
Solidago ptarmicoides	31.66	492.34	4.78	2.24	7.01	2.14	12.26
Solidago ptarmicoides	27.60	392.35	4.01	1.43	5.44	2.80	10.16
Solidago rugosa	39.50	493.27	5.00	9.89	14.89	0.51	23.24
Solidago rugosa	57.40	662.70	5.42	9.14	14.56	0.59	30.00
Sporobolus heterolepis	11.00	116.63	0.49	0.28	0.77	1.78	9.32
Taraxacum offinciale	14.00	147.34	0.40	2.55	2.95	0.16	30.00
Trichostema brachiatum	25.73	299.53	1.88	0.60	2.48	3.13	3.50
Trifolium pratense	29.40	1117.59	5.31	5.57	10.88	0.95	30.00
Urtica dioica	56.60	306.73	1.16	1.61	2.77	0.72	30.00
Viola papilionacea	6.02	48.23	0.93	1.07	2.00	0.87	30.00
Viola septentrionalis	4.20	29.36	0.30	0.36	0.66	0.82	30.00

Appendix 4a cont.

Species	Date of flower	Leaf length	Leaf width	Leaf shape	Leaf number	Leaf area index	Phyto-meter shoot biomass
Achillea millefolium	6.00	4.01	0.83	4.85	45.00	230.44	0.02
Achillea millefolium	66.00	3.39	0.96	3.52	56.67	284.23	0.01
Agrostis gigantea	43.00	40.65	0.18	221.73	31.33	1201.00	0.19
Anaphalis margaritacea	68.00	6.50	0.66	9.85	110.67	358.52	0.17
Anemone canadensis	33.00	5.06	6.62	0.76	7.50	181.36	0.34
Antennaria howellii	22.00	2.76	0.81	3.41	98.67	233.74	0.18
Antennaria neglecta	57.00	2.46	0.86	2.88	50.33	133.58	0.38
Aster ciliolatus	109.00	2.07	0.38	5.45	166.33	198.64	0.04
Aster ciliolatus	109.00	2.79	0.77	3.63	113.33	161.41	0.07
Aster ciliolatus	109.00	1.34	0.57	2.34	303.33	282.54	0.03
Aster ciliolatus	125.00	1.23	0.30	4.04	912.33	596.94	0.02
Berteroa incana	44.00					93.82	0.10
Bromus inermis	46.00	12.43	0.78	16.00	58.00	497.38	0.14
Bromus tectorum	48.00	26.90	0.20	134.50	43.67	336.55	0.16
Campanula rotundifolia	48.00	2.92	0.35	8.34	75.50	96.31	0.15
Carex crawei	5.00	21.58	0.28	77.06	16.67	116.93	0.56
Carex eburnea		7.91	0.05	169.57	82.67	94.95	0.67
Carex gracillima	11.00	17.63	0.32	55.66	20.33		0.89
Carex pallescens	0.00	18.38	0.77	23.77	21.00	159.80	0.47
Carex pensylvanica	1.00	13.68	0.33	41.45	24.50	89.43	0.40
Carex richardsonii		15.61	0.48	32.30	33.00	234.43	0.24
Carex rugosperma	11.00	18.32	0.21	85.89	51.67	137.39	0.86
Chrysanthemum leucanthemum	51.00	2.96	0.93	3.17	67.00	208.10	0.02
Cirsium arvense	70.00	2.50	1.04	2.41	70.33	365.17	0.02
Corydalis sempervirens	11.00	1.40	1.46	0.96	65.00	66.52	0.32
Danthonia spicata	50.00	7.42	0.26	28.55	35.00	55.86	0.66

Appendix 4a cont.

Species	Date or flower	Leaf length	Leaf width	Leaf shape	Leaf number	Leaf area index	Phyto-meter shoot biomass
Danthonia spicata	11.00	6.59	0.17	38.00	37.67	73.28	0.73
Echium vulgare	52.00	7.75	1.36	5.71	18.67	221.72	0.02
Elymus repens	73.00	11.67	0.45	25.74	54.33	150.45	0.05
Elymus trachycaulus	58.00	5.67	0.31	18.29	44.67	218.26	0.06
Equisetum arvense		5.23	0.10	50.61	185.00	152.60	0.31
Fragaria virginiana	24.00	2.53	1.57	1.61	102.67	428.73	0.02
Glechoma hederacea	24.00	2.15	2.27	0.95	250.00	457.52	0.12
Helianthus divaricatus	97.00	7.18	1.84	3.91	22.67	379.35	0.05
Hieracium pilosella	51.00	5.44	1.13	4.82	23.00	151.94	0.07
Hieracium piloselloides	51.00	5.36	1.07	5.03	37.00	147.48	0.01
Hieracium piloselloides	44.00	1.60	0.54	2.99	193.33	210.62	0.04
Hypericum perforatum	58.00	0.93	0.25	3.76	243.67	96.22	0.08
Lechea intermedea	76.00	0.83	0.12	6.70	350.67	95.61	1.03
Linaria vulgaris	57.00	3.40	0.31	10.84	202.33	461.85	0.04
Minuartia michauxii	42.00	0.75	0.14	5.46	2733.33	611.59	0.36
Muhlenbergia mexicana	99.00	7.24	0.41	17.52	67.00	294.22	0.06
Panicum acuminatum	63.00	4.32	0.70	6.20	63.00	285.45	0.35
Panicum acuminatum	63.00	2.82	0.42	6.78	253.33	449.65	0.21
Panicum depauperatum	51.00	10.01	0.26	38.50	31.00	59.27	0.62
Penstemon hirsutus	46.00	3.62	0.78	4.62	42.67	265.68	0.06
Phleum pratense	52.00	9.05	0.21	43.10	64.00	163.48	0.02
Plantago rugelii	60.00	7.40	3.88	1.91	9.33	308.01	0.05
Plantago rugelii	50.00	6.71	4.07	1.65	17.67	485.04	0.01
Plantago rugelii	60.00	6.92	4.13	1.67	9.00	244.95	0.01
Poa pratensis	40.00	11.21	0.21	52.53	55.00	60.88	0.03
Potentilla argentea	47.00	1.39	1.63	0.85	64.33	156.13	0.03

Appendix 4a cont.

Species	Date of flower	Leaf length	Leaf width	Leaf shape	Leaf number	Leaf area index	Phyto-meter shoot biomass
Potentilla recta	56.00	3.18	3.26	0.98	36.67	352.17	0.03
Prunella vulgaris	57.00	2.71	1.16	2.33	49.33	214.01	0.04
Prunella vulgaris	60.00	1.98	1.03	1.92	64.33	195.19	0.05
Ranunculus acris	34.00	4.49	4.21	1.07	10.50	309.25	0.02
Rumex acetosella	13.00	2.89	0.77	3.77	94.67	112.72	0.02
Rumex acetosella	11.00	2.97	1.11	2.67	32.33	75.26	0.10
Saxifraga virginiensis	1.00	2.71	1.53	1.77	18.33	109.75	0.51
Scutellaria parvula	45.00	1.05	0.53	1.99	294.67	157.12	0.09
Senecio pauperculus	37.00	2.25	0.79	2.84	76.00	234.75	0.02
Sisyrinchium montanum	34.00	10.29	0.18	57.17	38.50	39.92	0.19
Solidago altissima	102.00	6.34	1.23	5.17	103.67	642.81	0.02
Solidago gigantea	75.00	3.65	0.66	5.53	79.00	353.20	0.04
Solidago hispida	115.00	3.21	0.87	3.70	93.67	198.52	0.05
Solidago hispida	118.00	3.18	0.82	3.86	92.00	179.05	0.13
Solidago ptarmicoides	95.00	4.32	0.36	12.10	162.67	394.63	0.22
Solidago ptarmicoides	64.00	5.51	0.55	10.02	93.33	640.33	0.03
Solidago rugosa	109.00	3.51	1.46	2.41	106.33	654.83	0.02
Solidago rugosa	118.00	4.33	1.30	3.34	98.50	763.09	0.02
Sporobolus heterolepis	67.00	9.34	0.15	60.93	21.67	26.57	0.92
Taraxacum offinciale	14.00	5.13	1.40	3.66	14.33	134.89	0.02
Trichostema brachiatum	66.00	2.20	0.53	4.13	216.33	390.25	0.53
Trifolium pratense	46.00	1.76	1.09	1.61	115.67	387.87	0.01
Urtica dioica	75.00	1.53	0.73	2.09	86.00	167.14	0.13
Viola papilionacea	9.00	2.70	2.12	1.27	19.00	164.49	0.06
Viola septentrionalis	17.00	2.04	2.24	0.91	7.00	43.92	0.09

Appendix 4a cont.

Species	pH	Soil nitrates	Soil P	Soil K	Soil Ca	Soil Mg	Soil salts
Achillea millefolium	7.70	1.00	1.00	8.00	31.00	4.00	0.25
Achillea millefolium	7.70	2.00	1.00	6.00	28.00	4.00	0.24
Agrostis gigantea	7.70	3.00	1.00	6.00	28.00	8.00	0.21
Anaphalis margaritacea	7.70	8.00	1.00	4.00	28.00	8.00	0.22
Anemone canadensis	7.80	6.00	1.00	4.00	31.00	5.00	0.24
Antennaria howellii	7.50	3.00	1.00	5.00	37.00	10.00	0.26
Antennaria neglecta	7.80	3.00	1.00	3.00	24.00	3.00	0.17
Aster ciliolatus	7.80	2.00	1.00	4.00	34.00	9.00	0.25
Aster ciliolatus	7.70	10.00	1.00	1.00	26.00	8.00	0.22
Aster ciliolatus	7.80	2.00	1.00	3.00	21.00	9.00	0.18
Aster ciliolatus	7.80	2.00	1.00	4.00	32.00	5.00	0.24
Berteroa incana							
Bromus inermis	7.90	3.00	1.00	3.00	20.00	6.00	0.14
Bromus tectorum	7.70	3.00	1.00	8.00	28.00	7.00	0.24
Campanula rotundifolia	7.80	6.00	1.00	4.00	30.00	7.00	0.22
Carex crawei	7.70	3.00	1.00	4.00	25.00	4.00	0.21
Carex eburnea	7.40	4.00	1.00	4.00	53.00	12.00	0.32
Carex gracillima	7.50	6.00	1.00	4.00	34.00	7.00	0.26
Carex pallescens	7.70	8.00	1.00	4.00	24.00	9.00	0.20
Carex pensylvanica	7.80	4.00	1.00	2.00	22.00	4.00	0.16
Carex richardsonii	7.60	5.00	1.00	5.00	38.00	7.00	0.28
Carex rugosperma	7.50	5.00	1.00	4.00	42.00	12.00	0.32
Chrysanthemum leucanthemum	7.70	2.00	1.00	10.00	29.00	7.00	0.25
Cirsium arvense	7.60	8.00	1.00	7.00	35.00	6.00	0.28
Corydalis sempervirens	7.40	2.00	1.00	7.00	28.00	8.00	0.22
Danthonia spicata	7.70	6.00	1.00	2.00	28.00	5.00	0.19
Danthonia spicata	7.50	7.00	1.00	3.00	36.00	10.00	0.25

Appendix 4a cont.

Species	Soil pH	Soil nitrates	Soil P	Soil K	Soil Ca	Soil Mg	Soil salts
Echium vulgare	7.60	2.00	1.00	8.00	27.00	7.00	0.22
Elymus repens	7.60	5.00	1.00	5.00	35.00	11.00	0.26
Elymus trachycaulus	7.70	9.00	1.00	4.00	33.00	5.00	0.26
Equisetum arvense	7.70	4.00	1.00	3.00	24.00	5.00	0.18
Fragaria virginiana	7.70	4.00	1.00	4.00	31.00	1.00	0.26
Glechoma hederacea	7.90	2.00	1.00	4.00	22.00	6.00	0.20
Helianthus divaricatus	7.70	4.00	1.00	2.00	37.00	11.00	0.28
Hieracium pilosella	7.80	5.00	1.00	2.00	23.00	7.00	0.18
Hieracium piloselloides	7.70	4.00	1.00	3.00	24.00	4.00	0.20
Hieracium piloselloides	7.50	2.00	1.00	2.00	33.00	12.00	0.24
Hypericum perforatum	7.70	4.00	1.00	5.00	29.00	5.00	0.23
Lechea intermedea	7.50	5.00	1.00	5.00	29.00	10.00	0.22
Linaria vulgaris	7.80	7.00	1.00	3.00	29.00	5.00	0.21
Minuartia michauxii	7.80	3.00	1.00	4.00	22.00	5.00	0.18
Muhlenbergia mexicana	7.80	4.00	1.00	4.00	26.00	7.00	0.21
Panicum acuminatum	7.70	4.00	1.00	5.00	29.00	11.00	0.24
Panicum acuminatum	7.70	9.00	1.00	3.00	30.00	10.00	0.24
Panicum depauperatum	7.50	7.00	1.00	5.00	36.00	9.00	0.28
Penstemon hirsutus							
Phleum pratense	7.90	2.00	1.00	5.00	22.00	6.00	0.19
Plantago rugelii	7.80	2.00	1.00	3.00	29.00	6.00	0.21
Plantago rugelii	7.50	2.00	1.00	4.00	42.00	11.00	0.29
Plantago rugelii	7.50	4.00	1.00	6.00	43.00	9.00	0.30
Poa pratensis	7.80	2.00	1.00	6.00	23.00	6.00	0.18
Potentilla argentea	7.50	4.00	1.00	6.00	36.00	7.00	0.27
Potentilla recta	7.70	5.00	1.00	3.00	19.00	7.00	0.17
Prunella vulgaris	7.80	2.00	1.00	4.00	22.00	4.00	0.18

Appendix 4a cont.

Species	Soil pH	Soil nitrates	Soil P	Soil K	Soil Ca	Soil Mg	Soil salts
Prunella vulgaris	7.80	3.00	1.00	7.00	23.00	6.00	0.18
Ranunculus acris	7.60	5.00	1.00	5.00	23.00	11.00	0.19
Rumex acetosella	7.80	8.00	1.00	7.00	29.00	4.00	0.24
Rumex acetosella	7.80	4.00	1.00	8.00	23.00	4.00	0.24
Saxifraga virginiensis	7.80	3.00	1.00	4.00	22.00	8.00	0.17
Scutellaria parvula	7.70	2.00	1.00	10.00	31.00	6.00	0.21
Senecio pauperculus	7.80	7.00	1.00	6.00	28.00	3.00	0.20
Sisyrinchium montanum	7.50	5.00	1.00	7.00	32.00	4.00	0.24
Solidago altissima	7.80	2.00	1.00	2.00	26.00	9.00	0.22
Solidago gigantea	7.80	2.00	1.00	3.00	25.00	3.00	0.24
Solidago hispida	7.80	2.00	1.00	3.00	22.00	8.00	0.18
Solidago hispida	7.50	3.00	1.00	7.00	42.00	6.00	0.26
Solidago ptarmicoides	7.70	7.00	1.00	9.00	27.00	7.00	0.24
Solidago ptarmicoides	7.70	5.00	1.00	4.00	31.00	12.00	0.25
Solidago rugosa	7.80	1.00	1.00	4.00	24.00	8.00	0.21
Solidago rugosa	7.70	1.00	1.00	3.00	24.00	8.00	0.21
Sporobolus heterolepis	7.60	11.00	1.00	2.00	34.00	6.00	0.23
Taraxacum offinciale	7.50	4.00	1.00	4.00	30.00	10.00	0.22
Trichostema brachiatum	7.80	11.00	1.00	6.00	24.00	5.00	0.20
Trifolium pratense	7.80	9.00	1.00	3.00	31.00	9.00	0.26
Urtica dioica	7.50	2.00	1.00	10.00	53.00	14.00	0.36
Viola papilionacea	7.60	4.00	1.00	6.00	31.00	7.00	0.22
Viola septentrionalis	7.80	3.00	1.00	4.00	27.00	5.00	0.19

Appendix 4b Mean for height (cm), canopy area (cm^2), shoot biomass (g), root biomass (g), total biomass (g), shoot:root biomass, soil depth (cm), date of flower, leaf length (cm), leaf width (cm), leaf shape(cm), leaf number, leaf area index (cm^2) for 63 terrestrial herbaceous plant species (5 replicates per species) grown in a drought treatment. Table also includes mean above-ground biomass of phytometer (*Trichostema brachiatum*) when grown with each of the test species.

Appendix 4b

Species	Height	Canopy area	Shoot biomass	Root biomass	Total biomass	Shoot: root	Soil depth
Achillea millefolium	32.00	284.00	2.17	2.67	4.84	0.81	30.00
Achillea millefolium	30.90	271.81	1.71	3.12	4.83	0.55	30.00
Agrostis gigantea	51.62	1596.55	3.49	1.09	4.58	3.19	5.03
Anaphalis margaritacea	31.40	305.80	2.87	1.53	4.40	1.87	21.29
Anemone canadensis	18.60	188.45	0.91	1.55	2.46	0.59	23.28
Antennaria howellii	3.10	21.18	0.51	0.61	1.12	0.83	10.38
Antennaria neglecta	3.40	21.90	0.67	0.43	1.09	1.56	30.00
Aster ciliolatus	45.40	734.54	2.51	1.78	4.29	1.41	10.46
Aster ciliolatus	42.68	506.16	1.94	1.04	2.99	1.86	6.13
Aster ciliolatus	44.30	640.19	2.04	2.57	4.62	0.79	30.00
Aster ciliolatus	62.40	1627.09	5.42	3.66	9.07	1.48	30.00
Berteroa incana	42.20	785.51	1.50	0.60	2.10	2.49	30.00
Bromus inermis	40.54	599.23	2.74	4.20	6.94	0.65	30.00
Bromus tectorum	33.00	1034.13	3.51	0.68	4.19	5.19	4.19
Campanula rotundifolia	34.20	295.47	0.67	0.47	1.14	1.41	7.37
Carex crawei	18.50	456.24	0.42	0.52	0.95	0.81	21.71
Carex eburnea	15.10	246.68	1.78	0.24	2.02	7.35	6.48
Carex gracillima	25.70	823.54	1.99	3.25	5.24	0.61	13.34
Carex pallescens	18.00	254.47	0.68	0.72	1.40	0.94	30.00
Carex pensylvanica	15.70	226.89	0.62	0.50	1.11	1.24	9.57
Carex richardsonii	18.30	268.77	1.97	1.56	3.53	1.26	9.72
Carex rugosperma	21.28	611.04	1.76	1.77	3.53	0.99	7.97
Chrysanthemum leucanthemum	25.00	186.53	0.95	1.76	2.71	0.54	30.00
Cirsium arvense	50.00	494.80	4.81	1.44	6.25	3.34	30.00
Corydalis sempervirens	27.75	495.83	1.00	0.17	1.17	5.88	3.74
Danthonia spicata	40.75	460.07	0.38	0.09	0.47	4.25	9.02
Danthonia spicata	7.30	55.61	0.15	0.01	0.16	10.54	30.00

Appendix 4b cont.

Species	Height	Canopy area	Shoot biomass	Root biomass	Total biomass	Shoot: root	Soil depth
Echium vulgare	39.50	331.95	1.79	3.69	5.49	0.49	7.11
Elymus repens	45.98	913.65	2.20	4.97	7.16	0.44	30.00
Elymus trachycaulus	57.40	811.47	2.27	1.66	3.93	1.37	8.60
Equisetum arvense	16.80	236.18	1.00	4.78	5.77	0.21	21.77
Fragaria virginiana	6.30	899.55	2.95	1.03	3.98	2.86	30.00
Glechoma hederacea	4.46	334.87	5.13	0.74	5.87	6.92	30.00
Helianthus divaricatus	36.92	247.63	1.68	2.05	3.73	0.82	19.16
Hieracium pilosella	38.00	349.19	0.81	1.52	2.32	0.53	18.47
Hieracium piloselloides	40.20	325.20	0.98	1.74	2.72	0.57	30.00
Hieracium piloselloides	5.70	97.59	1.79	0.51	2.30	3.53	13.61
Hypericum perforatum	24.54	209.31	1.12	0.65	1.77	1.73	30.00
Lechea intermedea	35.50	217.48	0.88	0.14	1.02	6.30	18.61
Linaria vulgaris	38.40	422.23	2.81	0.52	3.33	5.40	30.00
Minuartia michauxii	7.60	100.28	0.72	0.28	0.99	2.58	2.12
Muhlenbergia mexicana	76.00	1229.62	3.48	1.77	5.25	1.97	30.00
Panicum acuminatum	30.50	443.16	0.45	0.27	0.72	1.64	8.45
Panicum acuminatum	9.50	202.20	0.82	0.48	1.30	1.72	30.00
Panicum depauperatum	10.80	144.20	0.55	0.44	0.99	1.26	12.46
Penstemon hirsutus	17.00	141.53	0.81	0.63	1.44	1.29	5.78
Phleum pratense	76.30	1198.52	3.59	5.93	9.52	0.61	30.00
Plantago rugelii	15.30	248.74	1.15	1.41	2.55	0.81	7.58
Plantago rugelii	23.00	335.99	3.04	2.38	5.42	1.28	30.00
Plantago rugelii	25.60	319.69	2.65	2.17	4.82	1.22	30.00
Poa pratensis	31.50	984.65	2.83	2.44	5.28	1.16	9.41
Potentilla argentea	15.46	268.10	1.18	0.55	1.73	2.15	30.00
Potentilla recta	28.14	448.65	2.60	2.54	5.14	1.03	30.00
Prunella vulgaris	4.75	49.43	1.53	1.56	3.09	0.98	6.77

Appendix 4b cont.

Species	Height	Canopy area	Shoot biomass	Root biomass	Total biomass	Shoot: root	Soil depth
Prunella vulgaris	8.90	123.02	1.06	0.56	1.62	1.88	30.00
Ranunculus acris	38.20	666.05	2.50	2.80	5.29	0.89	30.00
Rumex acetosella	24.76	299.48	1.74	1.85	3.59	0.94	30.00
Rumex acetosella	20.46	181.58	0.66	0.87	1.53	0.75	3.55
Saxifraga virginiensis	1.22	4.08	0.59	0.18	0.77	3.19	2.17
Scutellaria parvula	12.58	129.23	0.78	0.94	1.73	0.83	4.57
Senecio pauperculus	5.04	40.38	1.53	1.18	2.70	1.30	5.89
Sisyrinchium montanum	12.40	129.53	0.27	0.30	0.57	0.91	30.00
Solidago altissima	43.80	447.21	2.70	5.25	7.95	0.51	30.00
Solidago gigantea	28.50	489.65	1.95	1.53	3.48	1.27	30.00
Solidago hispida	20.00	278.03	2.52	2.71	5.23	0.93	19.91
Solidago hispida	36.00	390.19	1.86	1.20	3.06	1.55	30.00
Solidago ptarmicoides	31.60	392.13	3.15	1.80	4.95	1.75	12.26
Solidago ptarmicoides	34.70	517.81	4.24	2.55	6.79	1.66	10.16
Solidago rugosa	39.40	423.94	2.76	5.66	8.41	0.49	23.24
Solidago rugosa	64.60	558.10	4.20	6.55	10.75	0.64	30.00
Sporobolus heterolepis	14.70	148.94	0.41	0.22	0.62	1.89	9.32
Taraxacum offinciale	3.30	26.95	0.21	2.23	2.45	0.09	30.00
Trichostema brachiatum	18.53	287.80	1.04	0.43	1.47	2.39	3.50
Trifolium pratense	25.38	617.81	2.76	1.79	4.55	1.55	30.00
Urtica dioica	33.00	207.35	0.39	0.52	0.91	0.76	30.00
Viola papilionacea	4.44	32.22	0.61	1.01	1.62	0.60	30.00
Viola septentrionalis	6.60	63.24	0.48	0.92	1.41	0.52	30.00

Appendix 4b cont.

Species	Date of flower	Leaf length	Leaf width	Leaf shape	Leaf number	Leaf area index	Phyto-meter shoot biomass
Achillea millefolium	6.00	4.53	0.92	4.92	38.67	57.28	0.02
Achillea millefolium	66.00	2.48	0.75	3.31	50.33	41.58	0.01
Agrostis gigantea	43.00	43.67	0.22	201.54	24.33	115.58	0.10
Anaphalis margaritacea	68.00	6.39	0.62	10.31	35.33	69.78	0.16
Anemone canadensis	33.00	5.63	5.50	1.02	9.67	82.35	0.16
Antennaria howellii	22.00	2.05	0.63	3.25	51.67	25.50	0.08
Antennaria neglecta	57.00	2.04	0.80	2.55	65.33	39.60	0.07
Aster ciliolatus	109.00	1.24	0.23	5.46	171.67	28.98	0.02
Aster ciliolatus	109.00	2.01	0.60	3.33	64.67	49.42	0.08
Aster ciliolatus	109.00	1.45	0.61	2.36	111.33	45.03	0.04
Aster ciliolatus	125.00	1.42	0.29	4.83	604.00	152.19	0.02
Berteroa incana	44.00						0.12
Bromus inermis	46.00	21.13	0.55	38.18	38.00	78.74	0.07
Bromus tectorum	48.00	27.40	0.20	137.00	25.00	66.31	0.21
Campanula rotundifolia	48.00	5.46	0.30	18.40	22.50	9.07	0.16
Carex crawei	5.00	16.71	0.20	84.98	13.67	16.36	0.45
Carex eburnea		6.83	0.07	93.09	69.00	25.43	0.23
Carex gracillima	11.00	23.33	0.45	51.84	32.67	114.92	0.27
Carex pallescens	0.00	14.37	0.58	24.78	13.67	24.54	0.31
Carex pensylvanica	1.00	8.43	0.34	24.79	19.67	36.87	0.22
Carex richardsonii		12.26	0.41	29.66	26.67	37.27	0.20
Carex rugosperma	11.00	12.27	0.24	51.11	37.33	78.52	0.32
Chrysanthemum leucanthemum	51.00	2.22	0.77	2.87	53.67	45.17	0.02
Cirsium arvense	70.00	5.94	2.12	2.81	21.33	105.09	0.02
Corydalis sempervirens	11.00					3.33	0.22
Danthonia spicata	50.00	7.28	0.15	47.50	30.00	19.35	0.33

Appendix 4b cont.

Species	Date of flower	Leaf length	Leaf width	Leaf shape	Leaf number	Leaf area index	Phyto-meter shoot biomass
Danthonia spicata	11.00	4.20	0.10	43.48	23.67	6.76	0.25
Echium vulgare	52.00	4.54	1.04	4.38	25.67	49.75	0.02
Elymus repens	73.00	12.07	0.36	33.53	35.00	60.90	0.05
Elymus trachycaulus	58.00	7.90	0.25	31.59	36.00	27.61	0.06
Equisetum arvense		3.64	0.10	36.37	164.00	37.65	0.18
Fragaria virginiana	24.00	1.72	1.17	1.47	104.00	77.51	0.02
Glechoma hederacea	24.00	2.24	2.45	0.91	84.67	93.68	0.11
Helianthus divaricatus	97.00	5.78	1.55	3.72	16.67	52.70	0.03
Hieracium pilosella	51.00	4.16	0.92	4.52	21.33	28.55	0.08
Hieracium piloselloides	51.00	4.70	0.91	5.15	22.00	30.47	0.02
Hieracium piloselloides	44.00	1.29	0.39	3.27	125.00	28.76	0.05
Hypericum perforatum	58.00	0.54	0.16	3.41	560.50	21.45	0.07
Lechea intermedea	76.00	1.06	0.25	4.23	123.33	33.11	0.37
Linaria vulgaris	57.00	3.04	0.26	11.56	188.00	46.47	0.05
Minuartia michauxii	42.00	0.74	0.14	5.44	2643.33		0.25
Muhlenbergia mexicana	99.00	8.27	0.67	12.41	52.00	132.16	0.09
Panicum acuminatum	63.00	2.74	0.60	4.54	25.67	20.37	0.12
Panicum acuminatum	63.00	3.02	0.39	7.68	67.33	40.72	0.18
Panicum depauperatum	51.00	8.37	0.42	19.92	28.67	30.72	0.24
Penstemon hirsutus	46.00	4.44	0.65	6.86	25.33	32.41	0.04
Phleum pratense	52.00	7.35	0.38	19.17	72.33	47.57	0.08
Plantago rugelii	60.00	6.66	3.35	1.99	9.00	51.49	0.02
Plantago rugelii	50.00	6.48	3.54	1.83	15.00	156.67	0.02
Plantago rugelii	60.00	3.83	2.21	1.73	10.67	24.94	0.01
Poa pratensis	40.00	6.02	0.17	35.43	42.00	9.97	0.04
Potentilla argentea	47.00	1.13	1.25	0.90	54.00	27.67	0.04

Appendix 4b cont.

Species	Date of flower	Leaf length	Leaf width	Leaf shape	Leaf number	Leaf area index	Phyto-meter shoot biomass
Potentilla recta	56.00	3.13	3.40	0.92	17.67	57.04	0.02
Prunella vulgaris	57.00	2.32	1.20	1.94	34.00	45.87	0.01
Prunella vulgaris	60.00	2.36	1.03	2.30	23.33	25.86	0.01
Ranunculus acris	34.00	3.76	6.61	0.57	18.67	79.90	0.02
Rumex acetosella	13.00	2.71	0.73	3.71	50.67	27.78	0.02
Rumex acetosella	11.00	2.50	0.51	4.90	24.00	10.16	0.07
Saxifraga virginiensis	1.00	2.26	1.09	2.07	12.00	24.13	0.25
Scutellaria parvula	45.00	1.04	0.51	2.05	216.67	53.48	0.05
Senecio pauperculus	37.00	3.60	1.06	3.41	104.00	26.57	0.04
Sisyrinchium montanum	34.00	8.85	0.21	42.81	19.33	6.49	0.07
Solidago altissima	102.00	5.06	0.79	6.44	96.00	130.84	0.02
Solidago gigantea	75.00	5.03	1.08	4.64	38.00	51.18	0.01
Solidago hispida	115.00	3.40	0.84	4.04	53.67	26.65	0.02
Solidago hispida	118.00	3.50	0.78	4.50	44.67	25.52	0.11
Solidago ptarmicoides	95.00	6.05	0.49	12.35	52.67	77.67	0.10
Solidago ptarmicoides	64.00	4.74	0.41	11.65	97.33	64.47	0.03
Solidago rugosa	109.00	2.98	1.13	2.64	95.67	85.33	0.03
Solidago rugosa	118.00	3.96	1.11	3.56	107.67	141.41	0.01
Sporobolus heterolepis	67.00	8.37	0.17	48.31	19.33	6.54	0.36
Taraxacum offinciale	14.00	4.63	1.26	3.69	11.67	21.16	0.02
Trichostema brachiatum	66.00	1.38	0.65	2.11	143.67	43.28	0.22
Trifolium pratense	46.00	1.67	1.39	1.20	101.00	94.82	0.01
Urtica dioica	75.00	1.37	0.67	2.05	41.00	50.77	0.08
Viola papilionacea	9.00	2.63	2.30	1.14	10.00	26.45	0.04
Viola septentrionalis	17.00	2.45	2.51	0.98	7.33	26.10	0.08

Appendix 4b cont.

Species	Soil pH	Soil nitrates	Soil P	Soil K	Soil Ca	Soil Mg	Soil salts
Achillea millefolium	7.60	2.00	1.00	6.00	40.00	7.00	0.29
Achillea millefolium	7.50	2.00	1.00	3.00	38.00	5.00	0.26
Agrostis gigantea	7.80	3.00	1.00	4.00	25.00	2.00	0.19
Anaphalis margaritacea	7.50	2.00	1.00	4.00	36.00	8.00	0.26
Anemone canadensis	7.80	8.00	1.00	2.00	26.00	6.00	0.19
Antennaria howellii	7.70	2.00	1.00	5.00	27.00	7.00	0.23
Antennaria neglecta	7.50	10.00	1.00	5.00	51.00	14.00	0.33
Aster ciliolatus	7.90	1.00	1.00	2.00	24.00	5.00	0.19
Aster ciliolatus	7.70	2.00	1.00	3.00	29.00	9.00	0.22
Aster ciliolatus	7.70	1.00	1.00	3.00	32.00	5.00	0.22
Aster ciliolatus	7.80	2.00	1.00	3.00	29.00	5.00	0.28
Berteroa incana							
Bromus inermis	7.80	3.00	1.00	3.00	26.00	6.00	0.19
Bromus tectorum	7.80	3.00	1.00	6.00	23.00	5.00	0.19
Campanula rotundifolia	7.50	11.00	1.00	2.00	42.00	6.00	0.29
Carex crawei	7.50	2.00	1.00	3.00	34.00	7.00	0.28
Carex eburnea	7.50	6.00	1.00	4.00	40.00	8.00	0.27
Carex gracillima	7.60	2.00	1.00	4.00	30.00	5.00	0.22
Carex pallescens	7.50	10.00	1.00	5.00	45.00	8.00	0.29
Carex pensylvanica	7.50	3.00	1.00	4.00	39.00	5.00	0.27
Carex richardsonii	7.80	6.00	1.00	3.00	25.00	5.00	0.18
Carex rugosperma	7.60	3.00	1.00	5.00	28.00	5.00	0.21
Chrysanthemum leucanthemum	7.50	4.00	1.00	6.00	34.00	9.00	0.26
Cirsium arvense	7.50	2.00	1.00	5.00	42.00	5.00	0.30
Corydalis sempervirens	7.30	1.00	1.00	5.00	41.00	9.00	0.28
Danthonia spicata	7.50	11.00	1.00	4.00	43.00	7.00	0.28
Danthonia spicata	7.50	8.00	1.00	3.00	34.00	8.00	0.23

Appendix 4b cont.

Species	Soil pH	Soil nitrates	Soil K	Soil P	Soil Ca	Soil Mg	Soil salts
Echium vulgare	7.50	2.00	1.00	9.00	42.00	8.00	0.32
Elymus repens	7.80	4.00	1.00	3.00	25.00	4.00	0.17
Elymus trachycaulus	7.80	6.00	1.00	3.00	33.00	5.00	0.23
Equisetum arvense	7.50	2.00	1.00	5.00	42.00	7.00	0.29
Fragaria virginiana	7.80	3.00	1.00	3.00	26.00	5.00	0.22
Glechoma hederacea	7.90	3.00	1.00	3.00	23.00	5.00	0.23
Helianthus divaricatus	7.70	5.00	1.00	3.00	29.00	4.00	0.28
Hieracium pilosella	7.60	2.00	1.00	3.00	30.00	8.00	0.24
Hieracium piloselloides	7.40	3.00	1.00	3.00	45.00	5.00	0.29
Hieracium piloselloides	7.80	2.00	0.90	2.00	25.00	2.00	0.18
Hypericum perforatum	7.50	4.00	1.00	6.00	41.00	10.00	0.28
Lechea intermedea	7.80	2.00	1.00	4.00	22.00	5.00	0.17
Linaria vulgaris	7.50	4.00	1.00	4.00	37.00	6.00	0.28
Minuartia michauxii	7.30	3.00	1.00	7.00	45.00	6.00	0.29
Muhlenbergia mexicana	7.60	2.00	1.00	4.00	36.00	10.00	0.25
Panicum acuminatum	7.80	7.00	1.00	3.00	28.00	2.00	0.20
Panicum acuminatum	7.40	10.00	1.00	5.00	45.00	6.00	0.30
Panicum depauperatum	7.50	14.00	1.00	3.00	44.00	6.00	0.29
Penstemon hirsutus							
Phleum pratense	7.50	4.00	1.00	6.00	43.00	9.00	0.31
Plantago rugelii	7.80	1.00	1.00	5.00	27.00	6.00	0.21
Plantago rugelii	7.70	4.00	1.00	5.00	38.00	8.00	0.27
Plantago rugelii	7.60	3.00	1.00	5.00	34.00	5.00	0.23
Poa pratensis	7.60	2.00	1.00	4.00	39.00	7.00	0.27
Potentilla argentea	7.40	3.00	1.00	6.00	48.00	11.00	0.32
Potentilla recta	7.60	4.00	1.00	7.00	31.00	4.00	0.26
Prunella vulgaris	7.70	2.00	1.00	4.00	34.00	5.00	0.27

Appendix 4b cont.

Species	soil pH	Soil Nitrates	Soil K	Soil P	Soil Ca	Soil Mg	Soil salts
Prunella vulgaris	7.70	2.00	1.00	5.00	28.00	6.00	0.19
Ranunculus acris	7.70	4.00	1.00	6.00	34.00	5.00	0.25
Rumex acetosella	7.80	2.00	1.00	5.00	27.00	11.00	0.21
Rumex acetosella	7.50	2.00	1.00	5.00	34.00	8.00	0.25
Saxifraga virginiensis	7.70	2.00	1.00	2.00	26.00	4.00	0.18
Scutellaria parvula	7.50	2.00	1.00	8.00	43.00	9.00	0.31
Senecio pauperculus	7.50	5.00	1.00	5.00	44.00	7.00	0.27
Sisyrinchium montanum	7.50	13.00	1.00	4.00	53.00	13.00	0.33
Solidago altissima	7.60	1.00	1.00	6.00	34.00	5.00	0.27
Solidago gigantea	7.80	3.00	1.00	3.00	23.00	4.00	0.22
Solidago hispida	7.50	2.00	1.00	5.00	34.00	7.00	0.28
Solidago hispida	7.50	2.00	1.00	3.00	34.00	6.00	0.23
Solidago ptarmicoides	7.60	5.00	1.00	6.00	30.00	8.00	0.26
Solidago ptarmicoides	7.80	2.00	1.00	2.00	23.00	3.00	0.17
Solidago rugosa	7.70	2.00	1.00	4.00	30.00	6.00	0.28
Solidago rugosa	7.60	1.00	1.00	4.00	36.00	11.00	0.26
Sporobolus heterolepis	7.40	8.00	1.00	2.00	38.00	8.00	0.25
Taraxacum offinciale	7.60	6.00	1.00	5.00	39.00	10.00	0.28
Trichostema brachiatum							
Trifolium pratense	7.70	10.00	1.00	4.00	44.00	11.00	0.35
Urtica dioica	7.40	9.00	1.00	7.00	58.00	7.00	0.37
Viola papilionacea	7.50	4.00	1.00	4.00	47.00	9.00	0.32
Viola septentrionalis	7.40	4.00	1.00	4.00	46.00	11.00	0.27