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COMPETITION IN SHORELINE PLANT COMMUNITIES:

A COMPARATIVE APPROACH

by

Connie Lee Gaudet

Thesis submitted to
The School of Graduate Studies and Research
University of Ottawa

in partial fulfillment of the requirements for the degree of Doctor of Philosophy
in the Ottawa-Carleton Institute of Biology

Ottawa, Ontario
Canada

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ABSTRACT

I tested the general hypothesis that competitive ability is an important determinant of pattern in shoreline plant communities. Specifically I tested four predictions generated from this general hypothesis: 1) the competitive performance of plant species is related to their distribution along natural gradients of fertility and standing crop; 2) the competitive performance of plant species is related to measurable plant traits; 3) the competitive performance of plant species is not significantly affected by changing nutrient supply; and 4) there is an "evolutionary trade-off" between nutrient stress tolerance of species and competitive performance that underlies the distribution of species along natural gradients of fertility and standing crop. These questions were posed at a broad, multi-species scale using comparative measures of competitive performance, stress tolerance, and morphology from over 40 shoreline plant species, and field distribution data from several natural shoreline communities in Ontario, Nova Scotia and Quebec. Results showed that the experimentally determined measure of the relative competitive performance of a species was significantly correlated with its position along natural gradients of fertility and standing crop; and with simple measurable plant traits, in particular above-ground biomass (r_s=0.92; $p<.0001$). Results also showed that the competitive performance of species under high and low nutrient conditions was significantly correlated after two growing seasons ($r_s = 0.76$; $P<.001$); and that stress tolerance, measured as the relative biomass production of species under low nutrient conditions, was inversely correlated with competitive performance ($r = -0.62$, $p<.005$).

ABSTRAIT

Une approche comparative, i.e. l'analyse systématique d'une grande quantité d'espèce d'écologie contrastante, a été employée pour explorer le rôle de la compétition le long des gradients naturels de stress dans des communautés végétales riveraines. Spécifiquement, j'ai testé quatre hypothèses apparentées qui soulèvent des questions au sujet du rôle que joue la compétition dans la structuration des communautés naturelles: 1) la performance compétitive des espèces végétales est reliée à leur distribution le long des gradients naturels de fertilité et de récolte sur pied; 2) la perfomance compétitive relative des espèces végétales est reliée à des traits végétaux simples et mesurables; 3) la performance compétitive relative des espèces végétales n'est pas affectée de façon significative par des changements de régime nutritif; et 4) il existe un "échange évolutionnaire" entre la tolérance que possèdent les espèces envers le stress, et la performance compétitive relative qui est à la base de la distribution des espèces le long du gradient du milieu. Ces questions ont été posées sur une large échelle comprenant de nombreuses espèces. Les résultats ont montré que la mesure de la performance compétitive relative d'une espèce, déterminée expérimentalement, manifestait une corrélation significative avec la position le long des gradients naturels de fertilité et de récolte sur pied; et avec des trait végétaux simples et mesurables, en particulier, la biomasse au dessus du sol ($r_s = 0.92$; $p < .0001$). Les résultats ont également montré que la performance compétitive relative en présence de régimes nutritifs fort et faible manifestait une corrélation significative après deux saisons de croissance ($r_s = 0.76$; $p < .001$); et que la production relative de biomasse des espèces en présence d'un régime nutritif faible manifestait une corrélation inverse avec la performance compétitive à cette échelle grossière qui comprend de nombreuses espèces.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the support of a great many colleagues, friends and family. In particular, I would like to thank my supervisor Paul Keddy who demonstrated great patience with me in finalizing this thesis and was the inspiration and guiding light throughout this work. I thank him especially for sharing with me his broad and challenging perspective on community ecology. I also like to thank the members of my Committee for their constructive review of this work throughout its development .

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Finally, I wish to thank all of my family members that suffered with me, and learned to live with my hectic schedule throughout the many years of hard work on this thesis.

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TABLE OF CONTENTS

List of Tables

List of Figures

List of Appendices

We have inherited from our forefathers the keen longing for unified, all-embracing knowledge. The very name given to the highest institution of learning reminds us that from antiquity, and throughout many centuries, the universal aspect has been the only one to be given full credit. But the spread, both in width and depth, of the multifarious branches of knowledge during the last hundred odd years has confronted us with a queer dilemma. We feel clearly that we are only now beginning to acquire reliable material for welding together the sum total of all that is known into a whole: but on the other hand, it has become next to impossible for a single mind to fully command more than a small specialized portion of it all.

I can see no other escape from this dilemma (lest our true aim be lost for ever) than that some of us should venture to embark on a synthesis of facts and theories, albeit with second-hand and incomplete knowledge of some of them - and at the risk of making fools of ourselves.

So much for my apology...

E. Schrodinger (1967)
from "*What is Life and Mind and Matter*"
Cambridge University Press, Great Britain, 1967

GENERAL INTRODUCTION

The search for theories and models in vegetation science seems most likely to succeed if clear questions about community level phenomenon are posed using measurable variables. What is less clear is which questions, and which variables, will produce the rapid progress, rigorous predictions and broad generalizations we require...

(Keddy 1987)

Community ecology has evolved largely as a descriptive science with emphasis on quantitative techniques for describing vegetation pattern. The difficulty in making the transition from description of pattern to an understanding of the underlying mechanisms and the development of general predictive models of community pattern and process has been emphasized by several authors (e.g., Keddy 1987; Tilman 1990). As a consequence there has been a strong movement towards experimental analysis of mechanism in plant communities. However, though description of pattern and the supporting quantitative techniques have been developed specifically to address the broad community level of organization, experimental techniques at the community scale are still evolving and their application and interpretation has often been controversial. Nowhere is this controversy more pronounced than in understanding the importance and role of competition in plant community structure (e.g., Grace and Tilman 1990). Decades of emphasis on interspecific competition has yielded an overwhelming body of special cases but few general principles (Keddy 1989; Grime 1974). This is in part due to a reductionist approach, with techniques borrowed largely from population biology, with emphasis on the intensive exploration of pair-wise interactions or the performance of individual species. Though yielding a large body of scientific data, the complexity of these results seems so overwhelming that it has in fact been assumed that there are no general principles that apply to competition. Posing clear questions at this coarse level of organization has in itself proved challenging. As Peters (1980) stresses, too often we are testing "untestable" concepts rather than testable hypotheses. If scientific progress is to be made, we need to pose clear questions about competition, identify measurable variables, and develop methodologies appropriate at the community level of organization.

In this thesis, I test several predictions generated from the general hypothesis that competitive ability is an important determinant of community pattern. Specifically I test the following predictions: 1) the competitive performance of plant species is correlated with their distribution along natural gradients of fertility and standing crop; 2) the relative competitive performance of plant species is correlated with measurable plant traits; 3) the relative competitive ability of plant species is not significantly affected by changing environmental conditions - specifically nutrient supply; and 4) there is an "evolutionary trade-off" between stress tolerance of species and relative competitive performance that underlies the distribution of species along natural fertility gradients.

To maximize the number of species that can be evaluated, and therefore the generality of the results, a comparative approach as described by Grime (1979) is used to test these predictions. This approach involves the systematic comparison of a large number of species with regard to quantifiable differences in ecological or physiological performance under standardized experimental conditions, and allows plants to be described and compared in functional rather than taxonomic terms. The variables derived from such a comparative screening represent inherent species differences presumed to be of ecological significance, which can then be evaluated with regard to their importance in explaining community pattern.

The relationship between competitive ability and general pattern in the field is examined in the context of natural environmental gradients along which vegetation characteristics, plant traits, species composition, and presumably underlying processes, co-vary. The analysis of pattern and process along natural gradients that transcend many different plant communities enables broad generalization beyond not only the species, but the environmental conditions of a particular study.

CHAPTER 1

COMPETITIVE PERFORMANCE AS A GENERAL DETERMINANT OF PATTERN IN NATURAL PLANT COMMUNITIES

" the test for ecology is not logical consistency, aesthetic appeal or mathematical precision, but the accuracy and utility of its predictions. Experimental ecologists have often neglected the latter, conceptual ecologists have frequently ignored both."

Peters (1982)

Abstract

The assumption that the competitive ability of plant species varies along natural gradients of resource availability and disturbance is implicit in many models of plant community structure but has rarely been tested empirically at a scale that enables broad generalization. I tested the hypothesis that relative competitive performance of plant species is correlated with distribution along natural gradients of fertility and standing crop at a community scale. The distribution of 40 species of herbaceous plants from lake and river shorelines in Nova Scotia, Quebec, and Ontario was quantified in relation to mean standing crop, and the phosphorus, nitrate, magnesium, potassium, pH and percent organic content of soil (n = 217 quadrats). The mean position of species along the standing crop and macronutrient gradients was weighted to account for the frequency of a species in each quadrat. Competitive performance was measured in an outdoor experiment using a "phytometer" method in which each species was grown with *Lythrum salicaria* (n = 5 replicates per species). The relative ability of each species to suppress the growth of *L. salicaria* was used as a measure of relative competitive performance. This measure of competitive performance was significantly correlated with the mean position of species on the standing crop (r = 0.81; p<.00001), percent organic content (r = 0.71; p<.00001); phosphorous (r = 0.70; p <.00001), nitrate (r = 0.67; p<.00001), magnesium (r = 0.66; p <.00001), and potassium gradients (r = 0.61; p <.00001).

INTRODUCTION

Despite the fact that interspecific competition is considered to be a major determinant of pattern in natural communities, decades of research have yielded few general principles (Price 1984; Connell 1983; Schoener 1983; Keddy 1989). This is in part due to traditional approaches to plant community ecology which have emphasized the description of general pattern rather than experimental determination of underlying mechanisms. Though such descriptive studies provide strong inferential evidence that competition is a major determinant of pattern (e.g., Menges and Waller 1983; Day *et al.* 1988), it is usually impossible to discern deterministic mechanism from passive observation (Strong 1983). A more recent emphasis on reductionist approaches has lead to the intensive exploration of pair-wise interactions under a number of experimental conditions in the belief that complex natural systems can be understood through a detailed exploration of its "parts" (Harper 1977; Harper 1982; Grubb, 198; Solbrig *et al.* 1979). However, there is an emerging realization that models of community structure are scale dependent (Moore 1990; Allen 1987; O'Neill *et al.* 1986) and that properties at a community or ecosystem level cannot be fully understood or predicted by intensive study of lower order or finer scale interactions at the population level (Keddy 1990)..

Both the traditional descriptive approaches and the more recent approaches emphasizing population interactions have failed to deliver general predictive models of plant competition (Tilman 1987; Austin 1986; Keddy 1987). An alternative approach forges a link between descriptive ecology - traditionally concerned with pattern - and experimental ecology - traditionally concerned with process (Mertz and McCauley 1982). In the current research, I use such a "combined" approach, incorporating analysis of distribution patterns in the field with an experimental determination of competitive performance, to directly assess the relationship between competitive performance and pattern.

The assumption that competitive ability varies along natural environmental gradients of stress/resource availability and disturbance is implicit in many general models of plant community structure (Austin 1986; Ellenberg 1988; Grime 1977, 1979; Tilman 1982, 1985, 1988; Southwood 1988; Keddy and MacLellan 1991; Keddy 1990) such that the interaction between competitive ability, resource availability and disturbance determine vegetation composition (Austin 1986). Despite its central importance to plant community theory, this basic relationship between competitive ability and distribution along natural gradients of stress and disturbance has not been tested empirically at a scale that enables generalization beyond the particular study conditions or species.

I therefore tested the hypothesis that species distribution along environmental gradients of stress and disturbance in shoreline plant communities is related to their competitive performance. To test this relationship at a scale enabling maximum generality, the current study was designed to meet the following objectives: 1) to provide a quantitative measure of the relative competitive performance of a diverse range of herbaceous plant species from a naturally occurring community; 2) to provide a measure of the environmental distribution of species on natural environmental gradients of fertility and standing crop using data from a diverse range of sites; 3) to test whether there is a relationship between the experimental measure of competitive performance and mean position on the environmental gradient.

Shoreline plant communities are highly suited to a test of this relationship. Species composition has been shown to vary along natural environmental gradients of stress and disturbance related to wave exposure in shoreline communities (Keddy 1983; 1985). Grace and Wetzel (1981) and Snow and Vince (1984) present evidence that competition produces zonation patterns in marshes, and Wilson and Keddy (1986a) have shown that, for specific sites, competition intensity increases along a gradient of soil organic content and that the mean position of species along this gradient is related to relative competitive ability (Wilson and Keddy 1986b). This last experiment had only seven species and a single environmental measure (percent soil organic content). I test the generality of this relationship across a range of sites, species and environmental conditions (standing crop, soil phosphorous, magnesium, potassium, nitrate, pH, and percent soil organic content). These environmental measures are considered important indicators of nutrient stress and, in the case of percent organic content and standing crop, of disturbance and exposure (Grime 1979, Wilson and Keddy 1986b). The interrelationship between each of these variables and plant distribution has not previously been addressed at this scale.

The usual approach to measuring competitive performance is to assess the performance (relative yield) of species in all possible pair-wise combinations (e.g., Harper 1977; de Wit 1960). This approach is logistically demanding and limits the number of species that can be tested. To increase the number of species that could be examined, I used a "phytometer" or indicator (Clements 1933) approach based on a modified additive design (Harper 1977) in which the relative competitive performance of a species is evaluated by measuring the relative ability to suppress the growth of a common indicator or background species (phytometer). A bioassay or indicator approach is a common approach for examining a large number of species with diverse morphologies (e.g., McCanny *et al.* 1990; Reader and Southwood 1981). Though relatively novel in exploring mechanism in natural communities, the advantage of the phytometer approach is that it provides values of competitive performance on an arbitrary scale for a large number of species. Though this method has received little experimental attention in studies of plant competition (except see Mitchley and Grubb 1986; Welbank 1963), it is ideally suited to the current research with emphasis on a comparative screening of a large number of species.

METHODS

Study locations

To maximize generality, sampling areas were selected from a broad geographic region, including both lake and river shorelines and inland marsh. Sites represented a broad range in standing crop and species composition (**Table 1.1**).

One group of wetlands occurred in the Tusket River Valley in Yarmouth Co., Nova Scotia. Wilsons Lake and Ellenwood Lake (43°55’N,65°53’W) in the Tusket River system have sandy, gravel and boulder shorelines characterized by exceptional species richness and the presence of many rare and endangered species (Keddy 1985, Wisheu 1987, Wisheu and Keddy 1989). A second wetland represented the Georgian Bay area of Ontario. Axe Lake (45°23’N, 79°30’W), a remnant of the shoreline of glacial Lake Algonquin, is a small, sandy lake that supports a rich Atlantic coastal plain flora (Keddy 1981, 1983, 1985). The third group of wetlands were located in the Ottawa River watershed. A general description of these wetland types can be found in Day *et al.* (1988), Shipley (1987), Shipley *et al.* (1991), and Moore (1990). The Westmeath study location (45°47’N, 76°50’W) is a riverine shoreline located on the Ottawa River 22 km southwest of the city of Pembroke. At this location, two open beach sites with low standing crop as well as three moderate to high standing crop sites in a sheltered bay were surveyed.

Table 1.1 The three most abundant species[1] in descending order found in each of the wetland sites sampled in this study. Mean standing crop and number of quadrats (n) for each site are also shown.

Standing Crop (g/m^2)	**Location and Site Number[2]**	**Species**
16 (n=15)	Westmeath I	*Scirpus americanus* *Carex lenticularis* *Salix lucida*
25 (n=16)	Axe Lake	*Rhyncospora fusca* *Eriocaulon septangulare*[3] *Xyris difformis*[3] *Cladium mariscoides*
29 (n=3)	Ellenwood Lake	*Juncus militaris* *Eriocaulon septangulare* *Isoetes sp.*
33 (n=10)	Wilsons Lake I	*Gratiola aurea* *Juncus pelocarpus* *Ranunculus reptans*
131 (n=15)	Luskville I	*Leersia oryzoides* *Lindernia dubia* *Eleocharis erythropoda*[3] *Salix interior*[3]
160 (n=15)	Luskville II	*Eleocharis erythropoda* *Leersia oryzoides* *Lythrum salicaria*
218 (n=15)	Westmeath II	*Scirpus americanus* *Hypericum boreale* *Fimbristylis autumnalis*
256 (n=11)	Wilsons Lake II	*Euthamia galetorum* *Cladium mariscoides* *Sabattia Kennedyana*
340 (n=8)	Stony Swamp	*Bidens cernua* *Leersia oryzoides* *Galium palustre*

Table 1.1 (continued)

Standing Crop (g/m^2)	**Location and Site Number**[2]	**Species**
338 (n=9)	Breckenridge	*Spartina pectinata* *Carex crinita* *Scirpus americanus*
369 (n=15)	Luskville III	*Scirpus americanus* *Calamagrostis canadensis* *Cladium mariscoides*
421 (n=5)	Ottawa Beach	*Eupatorium maculatum* *Lythrum salicaria* *Phalaris arundinaceae*
498 (n=15)	Luskville IV	*Agrostis stolonifera* *Scirpus fluviatilis* *Sparganium eurycarpum*
528 (n=15)	Westmeath IV	*Carex vesicaria* *Lemna minor2* *Hydrochoris morsus-ranae*
628 (n=5)	Lucerne Blvd.	*Phalaris arundinacea* *Hypericum ellipticum* *Lythrum salicaria*
652 (n=15)	Westmeath III	*Scirpus acutus* *Potentilla palustris* *Polygonum amphibium*
1110 (n=15)	Luskville V	*Typha xglauca* *Rumex verticillatus* *Galium sp.*
1263 (n=15)	Westmeath V	*Typha xglauca* *Lemna minor* *Sium suave*

[1] nomenclature as in Gleason and Cronquist (1963) except *C. lanuginosa* Michx., D. acuminatum (Swartz) Gould and Clark, *T. xglauca* Godron and *Euthamia galetorum* (Greene)

[2] because of a broad range in standing crop and species composition, Westmeath, Luskville and, to a lesser extent, Wilsons Lake, have been divided into distinct sampling units based on standing crop increments. This division has been made for descriptive purposes only.

[3] these species had the same abundance

A very high standing crop *Typha* marsh located 15 km south of Westmeath was also surveyed. The Luskville study location (45°31'N, 76°6'W) is also a riverine shoreline located 5 km west of Luskville, Quebec on the Ottawa River. The survey included two low standing crop shoreline sites, moderate and high standing crop sheltered marshes and a very high standing crop *Typha* marsh (see Moore 1990). Several smaller sites were also sampled along the Ottawa River. Breckenridge and Lucerne Boulevard are moderate standing crop sites on the Ottawa River about 5 km and 30 km east of the Luskville site respectively. The Ottawa Beach site is also located on the Ottawa River, about 1 km west of Ottawa, Ontario. Stony Swamp is a large wetland complex comprised of several beaver ponds and is located about 10 km inland from the Ottawa Beach site in Nepean, Ontario.

Collectively, these sites encompassed a broad range in plant life form. Plant life history types included evergreen rosette species (e.g.,*Lobelia dortmanna, Eriocaulon septangulare*), insectivorous species (e.g., *Drosera intermedia)*, reeds (e.g., *Scirpus validus, Eleocharis palustris*), annuals (e.g., *Bidens cernua*), facultative annuals (e.g., *Lythrum salicaria*) and large clonal perennials (e.g., *Typha latifolia, Phalaris arundinaceae*). In general, low standing crop sites such as Axe and Wilsons Lake are characterized by species of varying life form (e.g., annuals, evergreen and slow-growing perennials) while high standing crop areas are dominated by fast-growing perennials capable of clonal spread.

Field Survey

The study locations (Table 1.1) were surveyed as follows: Westmeath (August 25-26, 1987); Luskville (August 18-19, 1987); Wilsons Lake and Ellenwood Lake (October 7-8, 1988); all other sites between August 26 and September 6, 1988). At each site or standing crop increment, 5 to 15 quadrats (0.5 m x 0.5 m) were placed according to a restricted randomization procedure over an area of approximately 100 m^2 as follows. A random number table was used to determine the number of paces and compass direction for placement of each quadrat. Randomization was restricted such that areas that were obviously disturbed or transition zones between wetland and upland areas were not sampled. After the quadrat was placed on the ground, each quadrat was subdivided into 9 equivalent sections using thin metal rods. The frequency of each species within the quadrat was then measured as the number of subsections (0-9) in which it occurred. Given the scope of the current study, this frequency approach was considered a reasonable compromise between sampling methods such as point cover and biomass determination which provide detailed information on distribution but are labour intensive, and simple presence/absence approaches (Goldsmith and Harrison 1976). After the species occurrence and frequency was recorded for each quadrat, the vegetation within the quadrat was clipped at ground level, dried to constant biomass at 60^{0}C and weighed to determine standing crop. All voucher specimens were deposited at the Agriculture Canada herbarium (DOA) or University of Ottawa herbarium (OTT). A total of 217 quadrats were examined. Nomenclature is as described in

Gleason and Cronquist (1963) except *C. lanuginosa* Michx., D. acuminatum (Swartz) Gould and Clark, *T. xglauca* Godron and *Euthamia galetorum* (Greene).

Soil analysis

Five soil cores (10 cm depth, 3 cm diameter) were taken from each quadrat sampled as part of the field survey. One core was taken from the centre and one from each corner and samples were pooled for each quadrat and frozen within eight hours. Soil samples were then analyzed for four major macronutrients; nitrate, phosphorus, potassium, and magnesium; pH and percent organic content. Chemical analyses were performed by Agri-Food Laboratories in Guelph, Ontario. Nitrates were extracted in deionized water and assayed with an ion selective electrode; total phosphorous was measured by the sodium bicarbonate extractable method and potassium and magnesium were assayed by ammonium acetate extraction method (McKeague 1978). Percent organic content was calculated from weight loss on ignition at 500^0 C (Dean 1974).

Because data were not normally distributed, relationships between these soil variables were calculated using the non-parametric Spearman rank correlation coefficient (Zar 1984).

Species Position Along the Environmental Gradients

The frequency of species in each quadrat in which it was present, was used to calculate the weighted mean position of species along each measured gradient. Only species present in at least five quadrats were examined. The mean position of each species along a specified environmental gradient was calculated as follows:

$$e_i = \frac{\Sigma a_{ij} b_j}{\Sigma a_{ij}}$$

where e_i represents the mean position of the ith species on the specified environmental gradient; a_{ij} represents the frequency of the ith species in the jth quadrat and b_j represents the environmental measure for that quadrat. The environmental measures used were above-ground standing crop (g/0.25 m^2), soil nitrate content (ppm), soil phosphorous content (ppm), soil magnesium content (ppm), soil potassium content (ppm), soil percent organic content, pH and standing crop. This equation provides a weighted estimate of mean position of a species along the specified gradient.

Competitive Performance

Relative competitive performance was experimentally determined for forty-four herbaceous wetland species representing a broad range in life history types from small evergreen rosette species (e.g., *Eriocaulon septangulare*) to large clonal perennials (e.g., *Typha xglauca*). A modified additive design was used to assess competitive performance as the relative performance of each species (test species) to suppress the growth of a common indicator species or phytometer (Gaudet and Keddy 1988).

All 44 species were tested against the phytometer *Lythrum salicaria*. This species was selected because it is a ubiquitous wetland species of moderate size that is easily established as a seedling and grows vigorously to adult size. To test the robustness of the phytometer method, a subset of ten species were additionally tested against the phytometer *Penthorum sedoides*. To ensure standardization of experimental conditions (i.e. uniformity of phytometers at onset of the experiment), selection of phytometers was based on certain consistent traits such as availability of seed, ease of establishment, germination rate, and uniformity in size and development of seedlings. The two different phytometer species used did however, show substantial variation in life form. For example, *Lythrum salicaria* is a large, erect branching species with many small leaves, and *Penthorum sedoides* is relatively small, erect to decumbent, usually un-branched species with fewer, and larger leaves. To ensure uniformity in size and developmental stage, all phytometers were grown from seed collected at the Luskville study site in September 1985, cleaned and stored at 4° C in sterile, wet sand until March 1986. Seeds were germinated on filter paper, transplanted to a sterile planting medium and grown in a glasshouse at 70" . On April 15, 1986, seedlings, selected for uniformity in size, were transplanted to the centre of 1-litre pots filled with a sterile, organic potting mix (ProMix^R), left to adjust for 1 week, and misted daily.

In April 1986, test species were collected as ramets (vegetative units comprised of a single viable shoot) from the study locations described above. Four individuals of each test species were planted in a systematic design around a single phytometer. Test species were also planted singly to assess growth under the experimental conditions. Pots were placed in a randomized block design (five replicates per species) in an outdoor compound and watered daily. A cylinder of fibreglass window screen 30 cm high was installed around each pot on 30 May to ensure that ramets did not influence the growth of plants in other pots. The experiment was harvested during September 1986 just as plants began to senesce as evidenced by yellowing of photosynthetic tissue. Plants were dried to constant weight and the total biomass of the test species and biomass of the phytometer in each pot was measured. Below ground portions were separated and washed prior to drying.

Results from the competition experiment were used to determine relative competitive performance. Competitive performance was expressed as the percent reduction in phytometer biomass as follows (Figure 1.1):

$$CP_i = \left(\frac{P_1 - P_{2i}}{P_1} \right) 100$$

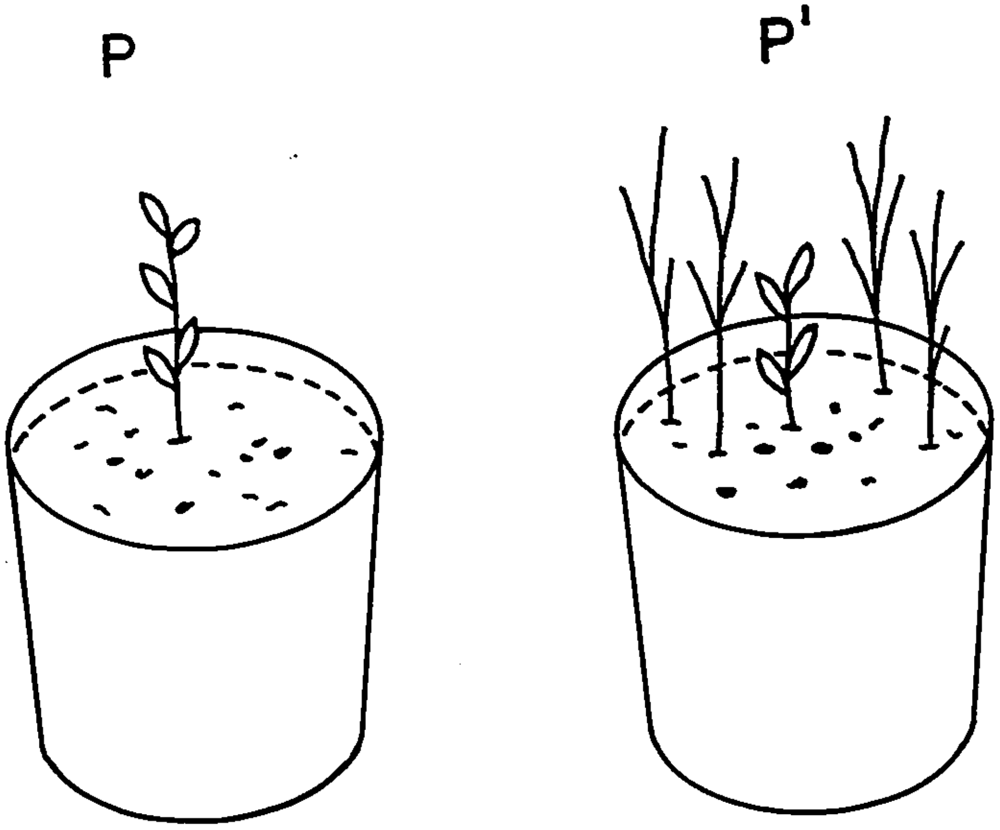
where CP_i is the relative competitive performance of the ith species; P_1 is the biomass of the phytometer grown alone (control) and P_{2i} is the weight of the phytometer when grown with the ith species. Results were based on the average value of five replicates per species. Because data were not normally distributed, and assumptions of homogeneity of variances were violated, a non-parametric Kruskal-Wallis single factor analysis of variance by ranks was used with to test for a significant species effect on percent reduction in phytometer biomass (Zar 1984).

Competitive Performance and Field Distribution

Correlations were calculated between mean position on the nitrate, phosphorous, magnesium, potassium, percent organic content, pH, and standing crop gradients using Pearson's r. Parametric tests are considered to be more powerful than non-parametric tests (Zar 1984), where assumptions of the normal distribution are not violated. In this case, transformed data approximated a normal distribution, and a parametric test was used. Phosphorous, nitrate, standing crop, magnesium and potassium were log transformed and percent organic content was arcsine square-root transformed. Only 40 species were used in this analysis due to a lack of adequate field distribution for four of the species.

Statsgrahics^R (Version 4.0, STSC, 1989) and **Tablecurve**^{R} (Version 3.0, Jandel Scientific, 1991) statistical software packages were used for all statistical analysis.

Figure 1.1 Experimental design for determination of relative competitive performance using the phytometer approach. P = phytometer; P^1 = phytometer grown with the test species.



RESULTS

The Environmental Gradient

The sampling results for each quadrat (n=217) are shown in Appendix 1.1. When all quadrats were considered, there were significant correlations between almost all of the measured environmental variables (Table 1.2) although no correlation coefficient was greater than $r_s = 0.77$. Among the nutrients, the strongest correlations were between soil nitrate concentration and soil phosphorous concentration ($r_s = 0.72$); between soil potassium concentration and soil magnesium concentration ($r_s = 0.70$); and between soil phosphorous concentration and soil magnesium concentration ($r_s = 0.66$). Phosphorous was also highly correlated with percent organic content of the soil ($r_s = 0.77$). All of the soil fertility measures (N, P, K, Mg, % organic content) were significantly correlated with above-ground productivity (standing crop) with the strongest correlations being between standing crop and percent organic content of the soil and ($r_s = 0.77$) and between standing crop and soil phosphorous concentration ($r_s = 0.76$). The relationship between standing crop, macronutrient levels and percent organic content of the soil is shown graphically in Figure 1.2.

The pooled data set was collected over a broad geographic range incorporating variation in years, climate, bedrock types, watershed hydrology and sampling teams. To reduce such large scale variation, I examined the local (within site) variation for the Westmeath and Luskville study sites. These sites represented a broad range in standing crop and species composition as indicated in Table 1.1. In general, there were strong correlations among nutrients and between nutrients and standing crop at this scale (Tables 1.3 and 1.4). However, there were some noteworthy differences. At the Luskville site (n = 75 quadrats) standing crop was most strongly correlated with percent organic content of the soil ($r_s = 0.89$). At the Westmeath site (n = 75 quadrats), soil phosphorous concentration was highly correlated with standing crop ($r_s = 0.80$) as was percent organic content of the soil ($r_s = 0.74$). In comparing the Westmeath and Luskville sites, it appears that percent organic content is the single most consistently reliable indicator of productivity across this range of sites and conditions.

Species Position on the Environmental Gradient

The first quantitative variable needed for testing the hypothesized relationship - the mean position of each species on the seven measured environmental gradients - was calculated according to the equation outlined in the Methodology. The mean position of each species on each environmental gradient is summarized in Table 1.5. When all 40 species are considered, the mean position on the standing crop, nitrate, phosphorous, magnesium, potassium and percent organic content gradients is significantly correlated (Table 1.6), suggesting that species are not uniquely distributed along each of the different environmental gradients.

Table 1.2 Spearman rank correlation (r_s) between all measured environmental variables from all study sites (n=217 quadrats). SC = above-ground standing crop ($g/0.25m^2$); % org = soil percent organic content; P = soil phosphorous content (ppm); K = soil potassium content (ppm); N = soil nitrate content (ppm); Mg = soil magnesium content (ppm).

	% org	P	N	K	Mg	pH
SC	0.77 p<.00001	0.76 p<.00001	0.66 p<.00001	0.58 p<.00001	0.67 p<.00001	-0.28 p<.00001
% org		0.77 p<.00001	0.57 p<.00001	0.50 p<.00001	0.51 p<.00001	-0.47 p<.00001
P			0.72 p<.00001	0.56 p<.00001	0.66 p<.00001	-.13 p=.0662
N				0.53 p<.00001	0.63 p<.00001	-0.02 p=.8137
K					0.70 p<.00001	-0.28 p<.00001
Mg						-0.14 p=.0291

Figure 1.2 Relationship between standing crop ($g/0.25m^2$) and **a)** soil phosphorous (ppm); **b)** percent organic content of the soil; **c)** soil magnesium (ppm); **d)** soil potassium (ppm); and **e)** soil nitrate (ppm). Each point represents an individual quadrat.

Figure 1.2

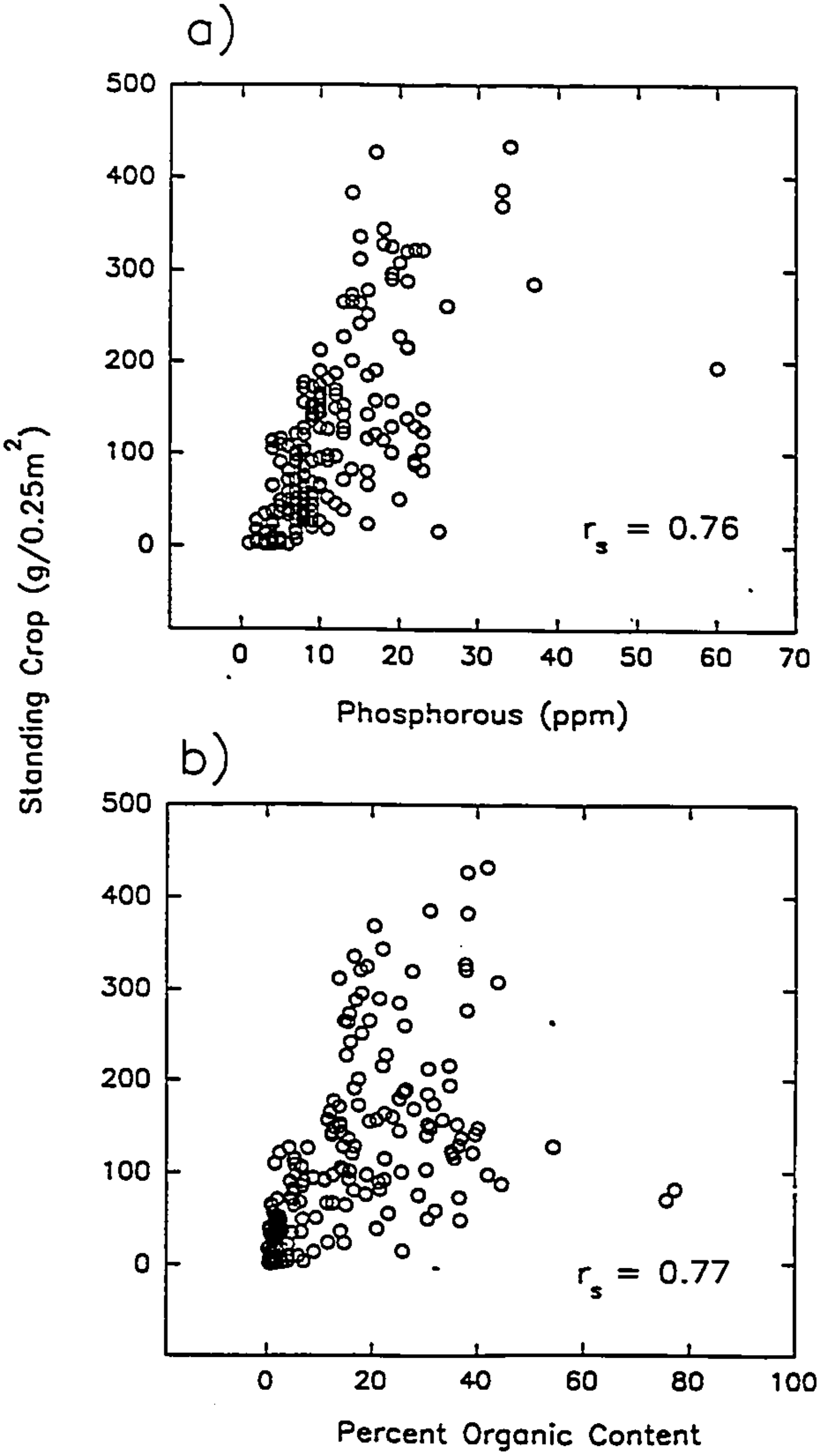

a)
Standing Crop (g/0.25m^2)
500
400
300
200
100
0
0
10
20
30
40
50
60
70
Phosphorous (ppm)
r_s = 0.76
b)
500
400
300
200
100
0
0
20
40
60
80
100
Percent Organic Content
r_s = 0.77

Figure 1.2

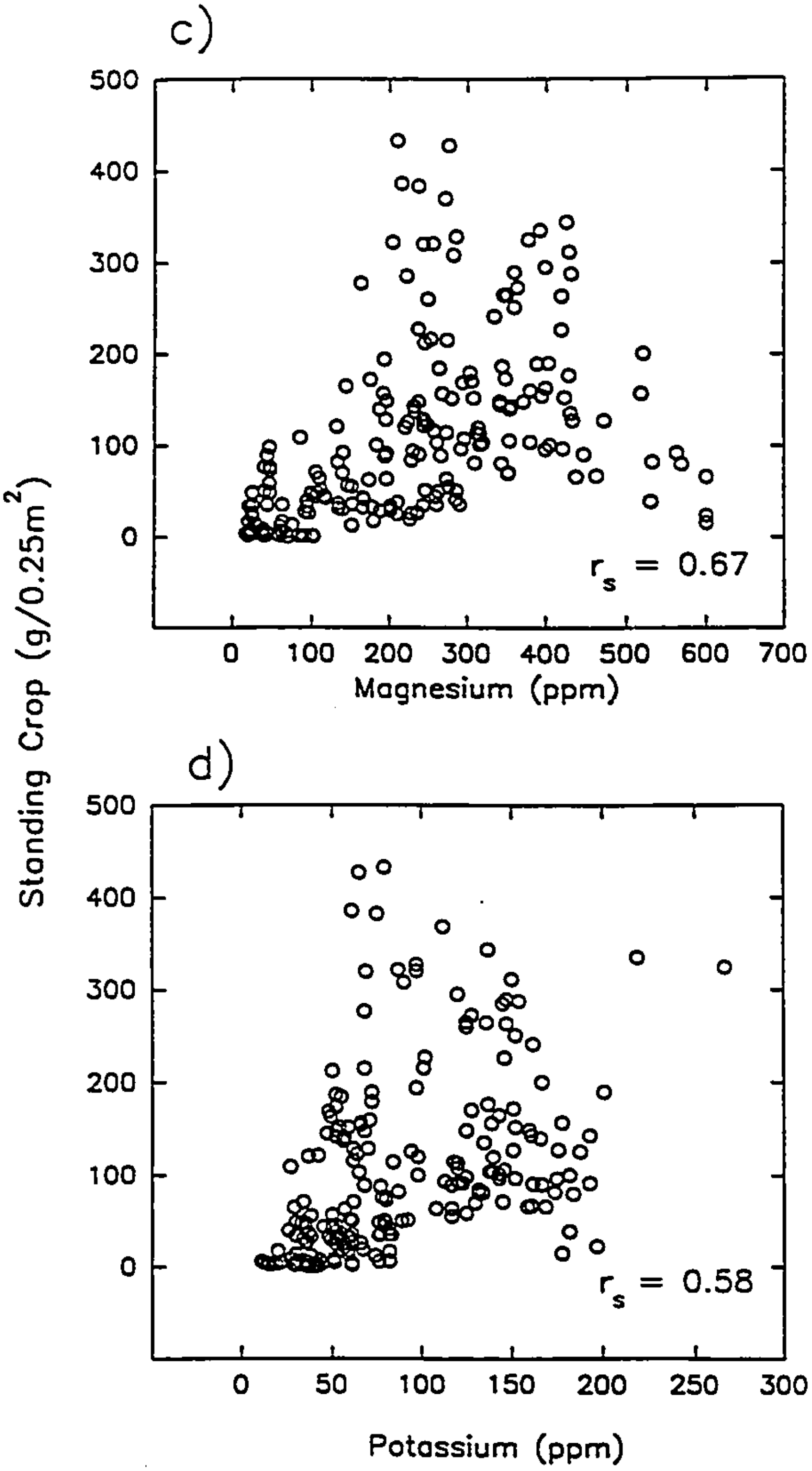

c)
Standing Crop (g/0.25m^2)
500
400
300
200
100
0
0
100
200
300
400
500
600
700
Magnesium (ppm)
r_s = 0.67
d)
500
400
300
200
100
0
0
50
100
150
200
250
300
Potassium (ppm)
r_s = 0.58

Figure 1.2

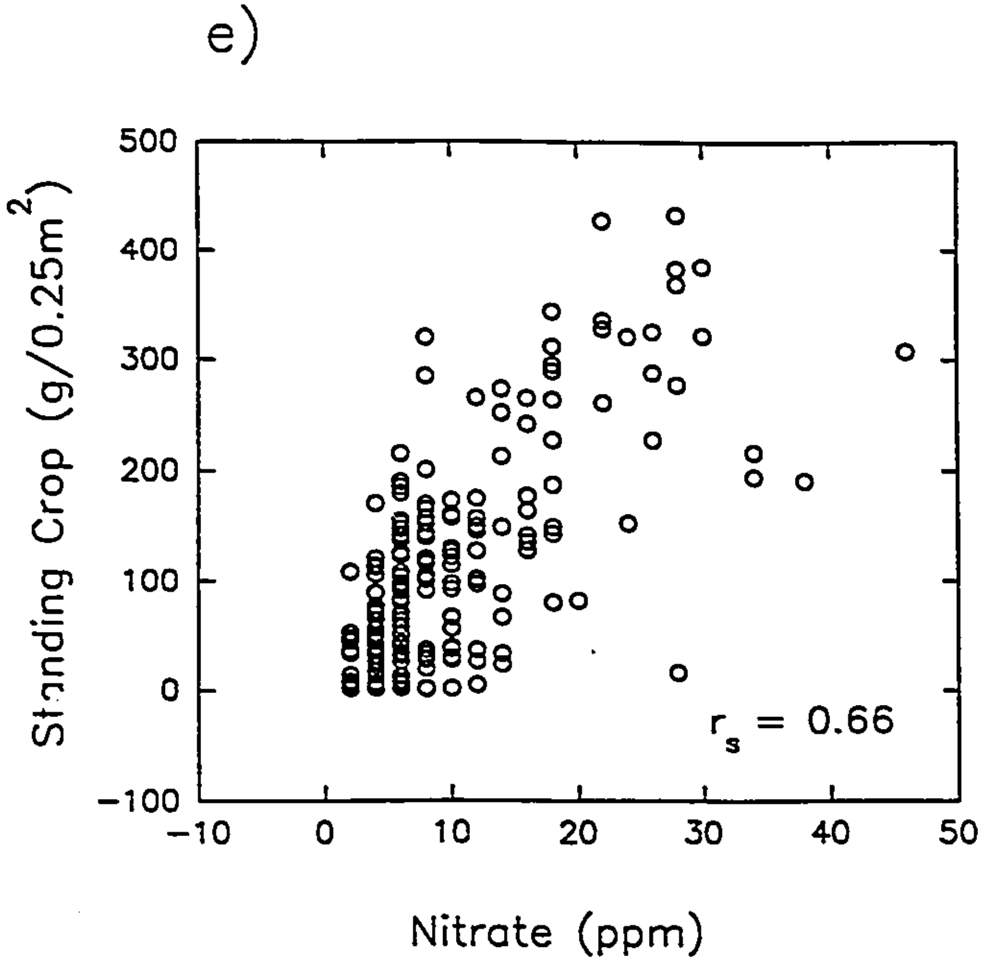

e)
Standing Crop (g/0.25m^2)
500
400
300
200
100
0
−100
−10
0
10
20
30
40
50
Nitrate (ppm)
r_s = 0.66

Table 1.3 Spearman rank correlation (r_s) between environmental variables for Luskville study site (n = 75 quadrats). SC = above-ground standing crop ($g/0.25m^2$); % org = soil percent organic content; P = soil phosphorous content (ppm); K = soil potassium content (ppm); N = soil nitrate content (ppm); Mg = soil magnesium content (ppm).

	% org	**P**	**N**	**K**	**Mg**	**pH**
SC	0.89 p<.00001	0.67 p<.00001	0.57 p<.00001	0.75 p<.00001	0.75 p<.00001	-0.81 p<.00001
% org		0.65 p<.00001	0.61 p<.00001	0.85 p<.00001	0.85 p<.00001	-0.81 p<.00001
P			0.65 p<.00001	0.43 p=.0002	0.45 p<.0001	-0.33 p=.0042
N				0.53 p<.00001	0.61 p<.00001	-0.45 p=.0001
K					0.90 p<.00001	-0.78 p<.00001
Mg						-0.72 p<.00001

Table 1.4 Spearman rank correlation (r_s) between environmental variables for Westmeath study site (n = 75 quadrats). SC = above-ground standing crop (g/0.25m^2); % org = soil percent organic content; P = soil phosphorous (ppm); K = soil potassium (ppm); N = soil nitrate (ppm); Mg = soil magnesium (ppm).

	% org	**P**	**N**	**K**	**Mg**	**pH**
SC	0.74 p<.00001	0.80 p<.00001	0.69 p<.00001	0.76 p<.00001	0.69 p<.00001	-0.45 p=.0001
% org		0.80 p<.00001	0.61 p<.00001	0.66 p<.00001	0.62 p<.00001	-0.61 p<.00001
P			0.62 p<.00001	0.82 p<.00001	0.59 p<.0009	-0.46 p=.0001
N				0.68 p<.00001	0.53 p<.00001	-0.18 p=.1303
K					0.64 p<.00001	-0.35 p=.0028
Mg						-0.72 p<.00001

Table 1.5 Mean position and standard error (in brackets) of forty wetland species along the following environmental gradients: standing crop (SC), soil percent organic content (Org), soil phosphorus content (P), soil nitrate content (N), soil pH (pH), soil magnesium content (Mg) and soil potassium content (K). Species position was weighted by frequency of occurrence within each quadrat. The number of quadrat subdivisions in which a species occurred is indicated (n). Unless indicated by an *, species occurred in at least five $0.25m^2$ quadrats.

SPECIES	n	SC $(g\ 0.25m^{-2})$	Org (%)	P (ppm)	N (ppm)	K (ppm)	pH	Mg (ppm)
Acorus calamus	15	158.23 (8.11)	23.06 (2.69)	12.93 (1.68)	8.13 (0.57)	117.27 (15.35)	5.93 (0.14)	399.00 (34.59)
Bidens cernua	93	83.6 (4.92)	22.58 (2.60)	9.43 (0.42)	6.34 (0.26)	93.42 ((3.73)	6.64 (0.14)	220.67 (9.67)
Carex crinita	24	68.91 (6.26)	18.55 (0.85)	17.29 (0.74)	14.33 (0.68)	183.58 (2.08)	6.4 (0.02)	565.10 (5.93)
Carex rostrata	13	109.63 (19.96)	23.99 (2.15)	13.46 (0.92)	10.92 (3.30)	97.92 (6.2)	6.62 (0.14)	178.54 (16.78)
Drosera intermedia	60	18.22 (1.66)	4.14 (0.61)	4.13 (0.28)	3.53 (0.11)	47.97 (3.44)	5.62 (0.05)	34.08 (2.37)
Dulichium arundinaceum	17	11.67 (1.39)	7.57 (0.92)	6.29 (0.47)	3.71 (0.28)	52.29 (4.71)	5.27 (0.05)	29.29 (1.76)
Eleocharis erythropoda	247	48.89 (1.71)	2.63 (0.12)	8.25 (0.11)	5.51 (0.13)	73.28 (1.94)	7.45 (0.05)	212.47 4.56)
Eleocharis palustris	219	87.09 (2.37)	5.88 (0.26)	6.65 (0.14)	6.48 (0.25)	111.28 (3.18)	6.38 (0.04)	286.66 (7.99)
Eriocaulon septangulare	72	44.91 (4.02)	2.03 (0.09)	4.67 (0.22)	4.53 (0.65)	32.68 (1.06)	6.73 (0.09)	85.96 (5.57)
Eupatorium maculatum	19	88.36 (10.33)	5.74 (0.90)	9.58 (0.39)	6.42 (0.66)	120.32 (15.13)	7.06 (0.13)	188.32 (11.73)
Galium palustre	15	74.16 (5.23)	17.29 (1.96)	8.87 (0.62)	7.47 (0.49)	114.87 (2.07)	6.67 (0.09)	217.47 (13.31)
Hypericum ellipticum	28	42.25 (7.3)	3.23 (0.55)	5.14 (0.37)	4.00 (0.18)	38.82 (2.08)	6.34 (0.21)	75.39 10.20)
Iris versicolor	21	92.6 (9.8)	19.38 (3.4)	7.95 (1.5)	9.29 (1.73)	96.57 (12.06)	6.9 (0.17)	207.76 (39.41)
Juncus filiformis	16	5.67 (1.13)	1.46 (0.29)	5.25 (0.17)	4.00 (0.12)	61.5 (2.46)	6.47 (0.15)	44.87 (1.82)
Juncus militaris	15	8.35 (0.38)	3.95 (0.69)	4.00 (0)	5.73 (0.18)	51.14 (1.47)	5.4 (0.0)	38.27 (4.62)
Juncus pelocarpus	70	7.24 (1.04)	2.26 0.18)	3.86 (0.23)	3.8 (0.07)	46.86 (2.93)	5.98 (0.06)	39.73 (1.74)
Leersia oryzoides	308	53.37 (2.25)	2.99 (0.20)	7.9 (0.12)	5.99 (0.15)	71.28 (1.80)	7.4 (0.05)	213.12 (4.62)
Lobelia dortmanna	27	5.42 (0.75)	1.06 (0.12)	2.52 (0.20)	3.41 (0.18)	33.89 (2.52)	5.8 (0.03)	29.19 (2.13)
Lysimachia Nummularia	18	19.77 (0.95)	20.25 (1.32)	20.5 (1.09)	21.00 (1.69)	187.5 (2.3)	6.4 (0.04)	600.00 (0.01)
Lysimachia terrestris	24	13.31 (2.64)	5.34 (1.02)	6.42 (1.15)	3.8 (0.11)	62.79 (3.71)	5.67 (0.15)	38.58 (3.08)

Table 1.6 (continued)

SPECIES	n	SC (g 0.25m^{-2})	Org (%)	P (ppm)	N (ppm)	K (ppm)	pH	Mg (ppm)
Lysimachia thyrsiflora	84	113.22 (4.95)	13.11 (0.46)	10.25 (0.45)	10.05 (0.48)	150.66 (2.18)	7.73 (0.03)	399.86 (7.58)
Lythrum salicaria	245	114.86 (6.08)	8.08 (0.36)	8.55 (0.25)	7.34 (0.25)	119.67 (2.79)	6.5 (0.08)	310.16 (12.71)
Mentha arvensis	9	95.34 (5.85)	7.89 (0.61)	8.88 (0.42)	7.33 (0.58)	151.11 (8.15)	6.88 (0.16)	229.11 (1.82)
Onoclea sensibilis	28	59.31 (6.17)	15.18 (2.57)	10.61 (0.98)	9.07 (0.65)	165.79 (5.5)	6.44 (.03)	456.68 (25.12)
Panicum longifolium	17	35.25 (2.98)	5.54 (0.51)	5.0 (0.0)	4.0 (0.0)	74.24 (1.21)	5.03 (0.16)	27.12 (1.45)
Phalaris arundinaceae	69	145.18 (6.00)	13.41 (0.41)	26.8 (4.95)	10.87 (0.48)	145.87 (5.32)	6.1 (0.09)	324.39 (12.19)
*Polygonum hydropiperoides**	6	131.80 (18.9)	21.01 (0.76)	19.00 (1.41)	9.67 (0.33)	183.67 (4.48)	6.28 (0.03)	540.50 (9.62)
Potentilla Anserina	130	67.29 (1.62)	11.5 (0.39)	7.55 (0.21)	9.22 (0.38)	35.4 (0.87)	7.78 (0.01)	72.81 (1.90)
Ranunculus reptans	50	3.55 (0.25)	1.71 (0.11)	4.48 (0.19)	4.0 (0.0)	56.3 (1.9)	6.26 (0.08)	43.88 (1.04)
Rhyncospora fusca	72	22.21 (1.75)	4.3 (0.43)	3.64 (0.18)	3.70 (.08)	47.93 (2.89)	5.44 (0.06)	25.59 (1.25)
Rumex verticillatus	68	261.76 (5.89)	16.1 (0.23)	15.06 (0.24)	14.00 (1.16)	162.69 4.39)	5.6 (0.03)	384.9 (3.91)
Sabatia Kennedyana	42	27.4 (2.65)	5.6 (0.75)	5.4 (0.24)	4.0 (0.0)	69.14 (2.46)	5.6 (0.09)	49 (1.93)
Scirpus fluviatilis	103	126.22 (2.98)	14.44 (0.18)	9.99 (0.26)	11.45 (0.40)	149.26 (1.67)	5.5 (0.02)	377.29 (5.33)
Scirpus validus	484	64.07 (1.77)	7.81 (0.47)	4.8 (0.14)	8.58 (0.33)	68.60 (2.17)	7.32 (0.04)	168.38 (5.61)
Spartina pectinata	48	100.77 (8.65)	13.92 (1.18)	13.9 (0.85)	11.71 (0.80)	137.13 (8.98)	6.6 (0.08)	422.08 (26.72)
*Stachys palustris**	7	90.9 (4.34)	11.02 (0.96)	9.00 (0.04)	8.00 (0.00)	162.11 (3.41)	7.7 (0.09)	237.95 (22.90)
Triadenum Fraseri	90	75.46 (4.64)	15.33 (1.4)	3.4 (0.29)	6.90 (0.44)	75.46 (5.03)	6.9 (0.09)	152.06 (13.35)
Typha xglauca	222	285.29 (5.90)	25.29 (0.70)	21.76 (0.69)	22.23 (0.69)	121.85 (3.13)	6.8 (0.07)	301.00 (5.44)
Viola lanceolata	44	22.39 (2.25)	5.22 (0.52)	5.11 (0.13)	4.0 (0.0)	62.43 (1.76)	5.42 (0.11)	31.00 (1.14)
Xyris difformis	32	9.65 (1.4)	1.69 (0.49)	2.34 (0.19)	3.5 (0.16)	27.47 (2.81)	5.88 (0.07)	22.84 (1.29)

Table 1.6 Spearman rank correlation (r_s) between mean position on all measured environmental gradients for forty wetland plant species. Mean species position on each environmental gradient was calculated according to the equation described in the Methodology. SC = standing crop (g/0.25m^2); % org = soil percent organic content; P = soil phosphorous (ppm); K = soil potassium (ppm); N = soil nitrate (ppm); Mg = soil magnesium (ppm).

	% org	**P**	**N**	**K**	**Mg**	**pH**
SC	0.76 $p<.00001$	0.77 $p<.00001$	0.78 $p<.00001$	0.72 $p<.00001$	0.74 $p<.00001$	0.37 $p<.0206$
% org		0.79 $p<.00001$	0.86 $p<.00001$	0.74 $p<.00001$	0.71 $p<.00001$	0.23 $p<.1941$
P			0.86 $p<.00001$	0.87 $p<.00001$	0.88 $p<.00001$	0.30 $p=.0649$
N				0.80 $p<.00001$	0.86 $p<.00001$	0.41 $p=.0100$
K					0.88 $p<.00001$	0.24 $p=.1321$
Mg						0.40 $p<.0127$

Competitive Performance

The second variable needed to test the proposed relationship is relative competitive performance. The relative competitive performance of each species (expressed as percent reduction in the biomass of the phytometer *Lythrum salicaria*), is shown in Table 1.7. A Kruskal-Wallis single factor analysis of variance by ranks (Zar 1974) showed that there is a significant species effect on percent reduction in phytometer biomass ($H = 171.766$; $k = 44$; $p<.0001$). It is therefore reasonable to assume that species differ in relative competitive performance under the conditions of this experiment. When species are ranked in terms of their relative competitive performance in a competitive hierarchy, they range from the strongest competitor (*Lythrum salicaria;* competitive performance = 96%), to the weakest competitor (*Ranunculus reptans;* competitive performance = 1%). Though the term hierarchy is used here for simplicity of expression in discussing results, it does not imply transitivity (i.e. constancy in relative competitive performance such that if species A>B and B>C, then A>C). There is however, evidence to support the assumption that hierarchies are highly transitive (Keddy and Shipley 1989).

Table 1.7 Relative competitive performance expressed as percent reduction in phytometer biomass for 44 herbaceous shoreline plant species (five replicates per species). All species were grown with the phytometer *L. salicaria* in a sterile, high-nutrient organic mix (Promix^{R}).

Species	**Relative Competitive Performance (%)**	**Standard Deviation**
Lythrum salicaria	96	1.58
Bidens cernua	91	5.54
Phalaris arundinacea	89	7.02
Stachys palustris	87	3.91
Typha xglauca	86	6.80
Scirpus fluviatilis	82	7.09
Pilea pumila	80	2.49
Carex rostrata	79	3.97
Lysimachia thyrsiflora	77	3.83
Lysimachia ciliata	76	5.03
Potentilla anserina	72	4.82
Rumex verticillatus	69	3.39
Eupatorium maculatum	69	5.43
Mentha arvensis	67	15.17
Acorus calamus	67	4.39
Iris versicolor	63	9.03
Hypericum ellipticum	62	3.11
Scirpus validus	59	8.93
Polygonum hydropiperoides	59	19.20
Spartina pectinata	59	6.99
Lysimachia Nummularia	58	7.79
Carex crinita	58	7.89
Galium palustre	56	8.63
Triadenum Fraseri	52	8.26
Viola lanceolata	51	8.38
Impatiens capensis	49	12.18
Leersia oryzoides	48	5.03
Lysimachia terrestris	44	4.32
Onoclea sensibilis	40	7.50
Dulichium arundinaceum	37	6.80
Eleocharis erythropoda	29	11.40
Panicum longifolium	26	9.3

Table 1.7 continued

Species	Relative Competitive Performance (%)	Standard Deviation
Eriocaulon septangulare	25	5.40
Rhyncospora fusca	25	13.44
Anenome canadensis	23	12.66
Sabattia Kennedyana	23	17.93
Juncus pelocarpus	23	2. 51
Drosera intermedia	14	9.91
Juncus filiformis	14	16.68
Eleocharis palustris	13	17.35
Juncus militaris	11	7.81
Xyris difformis	10	4.95
Lobelia dortmanna	4	9.31
Ranunculus reptans	1	4.09

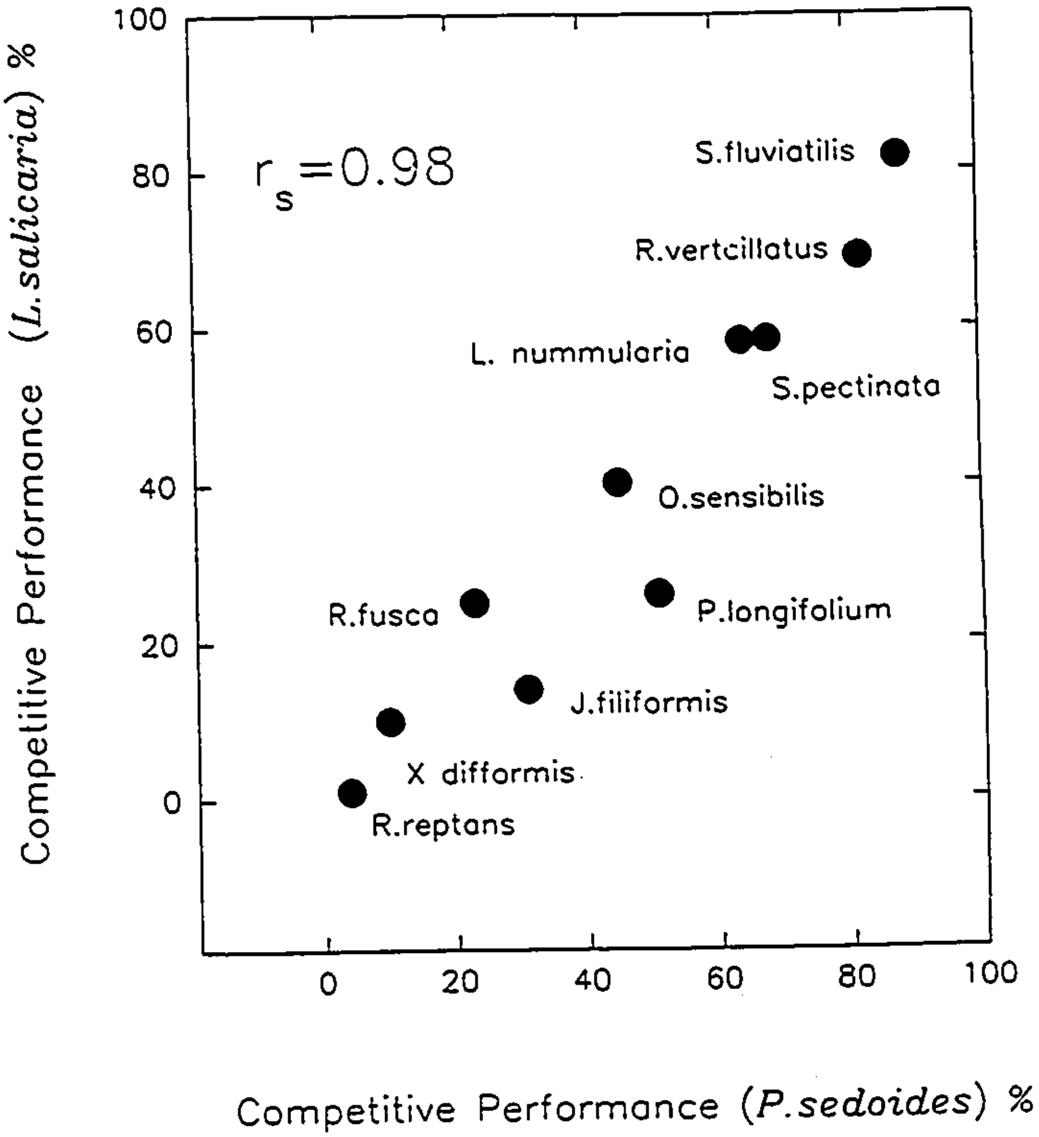
Results using *Penthorum sedoides* as a phytometer were similar. The relative competitive performance of each species is summarized in Table 1.8. A Kruskal-Wallis analysis of variance by ranks indicated a significant variation among species' competitive performance ($H = 43.27$; $k = 10$; $p < .00001$). Spearman rank correlation showed that competitive performance using *L. salicaria* as a phytometer was highly correlated with competitive performance using *P. sedoides* as a phytometer ($r_s = 0.98$; $p < .0001$; Figure 1.3). This suggests that the phytometer method provides a robust measure of relative competitive effect and that the hierarchy established using this method is a reasonable approximation of a more global measure of competitive performance that would have been obtained if all possible pair-wise interactions were considered.

Table 1.8 Relative competitive performance expressed as percent reduction in phytometer biomass for 10 herbaceous shoreline plant species (five replicates per species) grown with the phytometer *Penthorum sedoides*. All species were grown in a sterile, high-nutrient organic mix (Promix^R).

Species	**Percent Reduction in Phytometer Biomass**	**Standard Deviation**
Scirpus fluviatilis	88	5.74
Rumex verticillatus	82	4.39
Spartina pectinata	68	6.13
Lysimachia Nummularia	64	8.46
Panicum longifolium	51	8.98
Onoclea sensibilis	45	6.74
Juncus filiformis	31	9.83
Rhyncospora fusca	23	11.27
Xyris difformis	10	5.17
Ranunculus reptans	4	6.32

Figure 1.3 The relationship between relative competitive performance evaluated using two different phytometers: *Penthorum sedoides* and *Lythrum salicaria*. Competitive performance is based on percent reduction in phytometer biomass when grown with test species (n = 10 species; 5 replicates per species).

Figure 1.3


r_s=0.98
S.fluviatilis
R.vertcillatus
L. nummularia
S.pectinata
O.sensibilis
R.fusca
P.longifolium
J.filiformis
X difformis
R.reptans
100
80
60
40
20
0
0
20
40
60
80
100
Competitive Performance (L.salicaria) %
Competitive Performance (P.sedoides) %

Competitive Performance and Species Distribution

Now that the two key variables - species competitive performance and position on the environmental gradients - have been quantified, the key hypothesis can be tested. Data was log transformed (standing crop, phosphorous, nitrate, potassium, magnesium, pH) or arcsine square-root transformed (percent organic content) for further analysis.

Species competitive performance was significantly correlated with position on each environmental gradient except the pH gradient (Table 1.9). The relationship between competitive performance and species position on the standing crop, percent organic content, phosphorus, nitrate, potassium and magnesium gradients is shown in Figure 1.4. When all six environmental variables were included, multiple linear regression showed that there was a strong predictive relationship between species competitive performance and mean position on the environmental gradient ($R^2 = 0.67$; $p<0.00001$; Appendix 1.2). However, a single variable, standing crop, could explain most of this variation ($R^2 = 0.64$; $p<.00001$).

The shoreline plants used in this study included an equal number of monocotyledons and dicotyledons from along the environmental gradient. When these two major taxonomic groups were treated as separate data subsets, the relationship between position on the environmental gradient and competitive performance was much stronger for monocotyledons than for dicotyledons (Table 1.10). Though both monocotyledons and dicotyledons showed a strong relationship between competitive performance and position on the standing crop gradient (monocotyledons: $r = 0.84$, $p < .00001$; dicotyledons: $r = 0.82$, $p < .00001$). monocotyledons showed a strong relationship between competitive performance and position on the percent organic content, phosphorous, nitrate, potassium and magnesium gradients. Dicotyledons, in contrast, were much more weakly correlated with position on the of the macronutrient gradients (Figures 1.5 and 1.6). These results suggest that the effect of macronutrient levels on species distributions may differ for these two taxonomic groups.

Table 1.9 Correlation (r) between relative competitive performance and mean position on each environmental gradient for 40 species of wetland plants. Competitive performance (expressed in terms of percent reduction in phytometer biomass) was arcsine square-root transformed for analysis. All measures of mean position on the environmental gradient were log transformed except for percent organic content which was arcsine square-root transformed.

Mean Position on Environmental Gradient	Correlation (r) with Competitive Performance	p
Standing crop (g $0.25m^2$)	.81	$<.00001$
Soil nitrate content (ppm)	.67	$<.00001$
Soil phosphorous content (ppm)	.70	$<.00001$
Soil magnesium content (ppm)	.66	$<.00001$
Soil potassium content (ppm)	.61	$<.00001$
Soil pH	.40	.0108
Percent organic content	.71	$<.00001$

Figure 1.4 Relationship between relative competitive performance (percent reduction in phytometer biomass) and position of species (n = 40) on the a) standing crop (g/0.25m^2); b) percent organic content; c) soil phosphorous (ppm); d) soil nitrate (ppm); e) soil magnesium (ppm); and f) soil potassium (ppm) gradients. Competitive performance is expressed as percent reduction in the biomass of the phytometer *Lythrum salicaria*. The relationship between pH and standing crop is not shown due to the non-significance of the relationship.

Figure 1.4

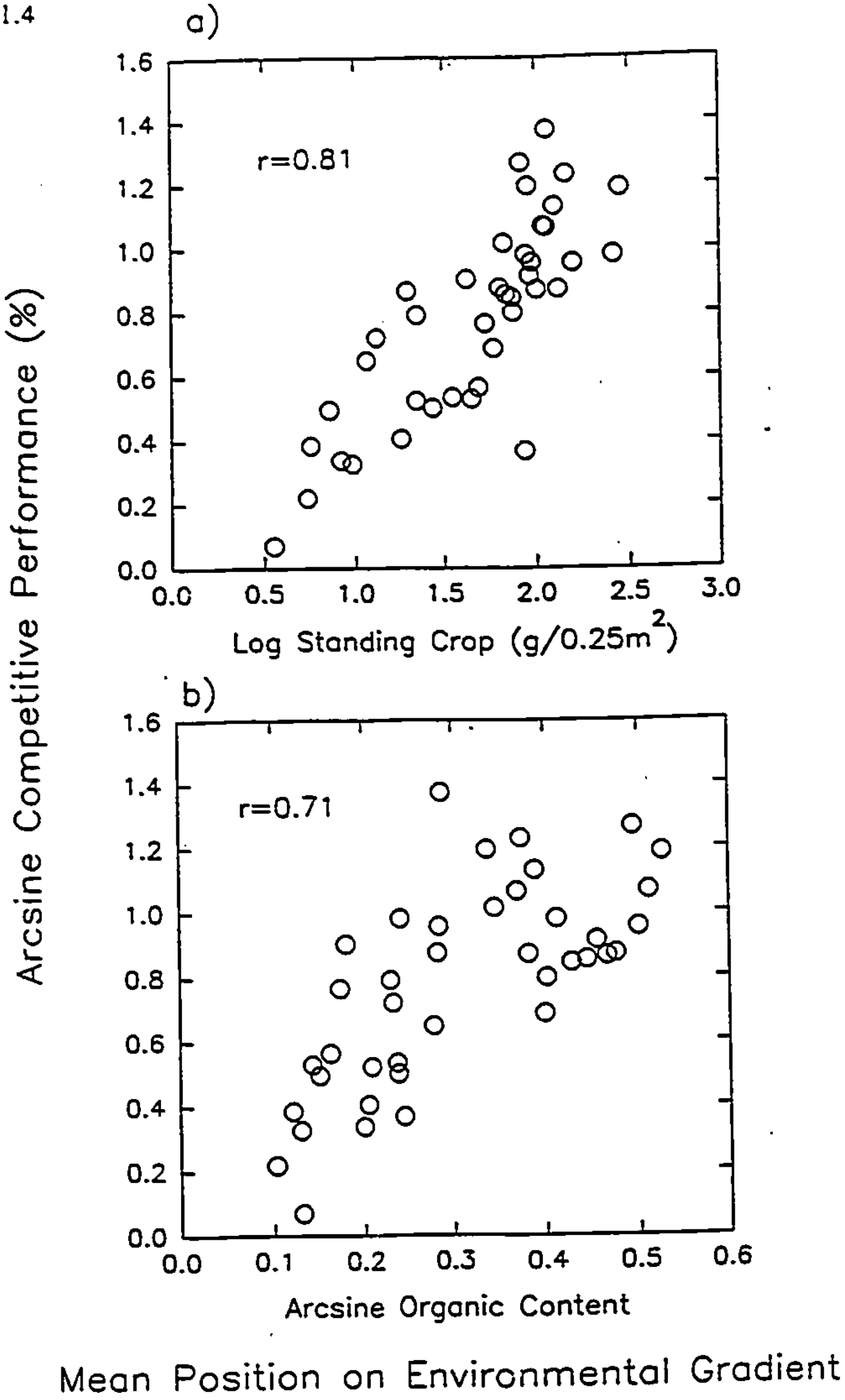

a)
r=0.81
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Log Standing Crop (g/0.25m²)
b)
r=0.71
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Arcsine Organic Content
Arcsine Competitive Performance (%)
Mean Position on Environmental Gradient

Figure 1.4

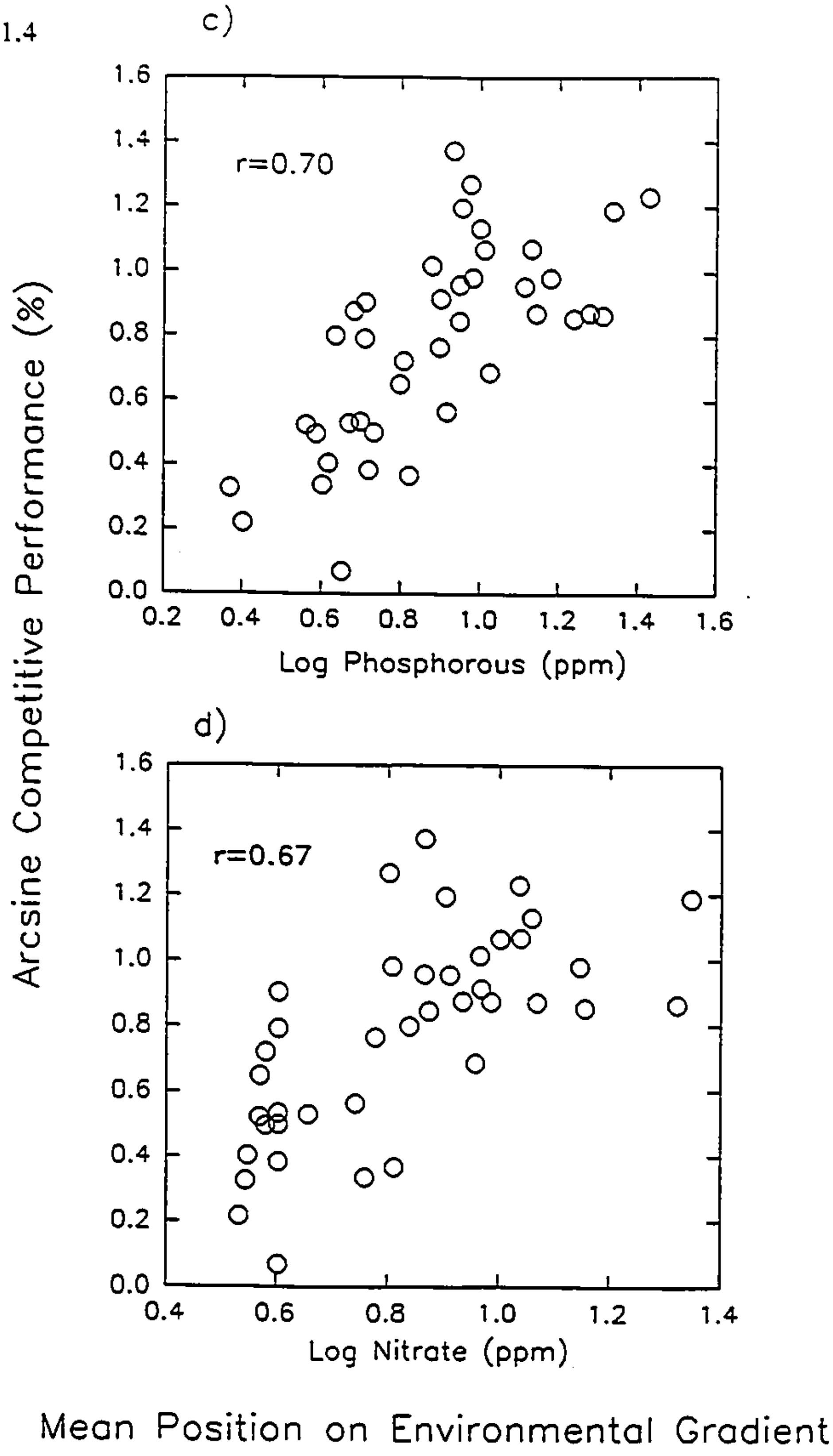

c)
r=0.70
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Log Phosphorous (ppm)
d)
r=0.67
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.4
0.6
0.8
1.0
1.2
1.4
Log Nitrate (ppm)
Arcsine Competitive Performance (%)
Mean Position on Environmental Gradient

Figure 1.4

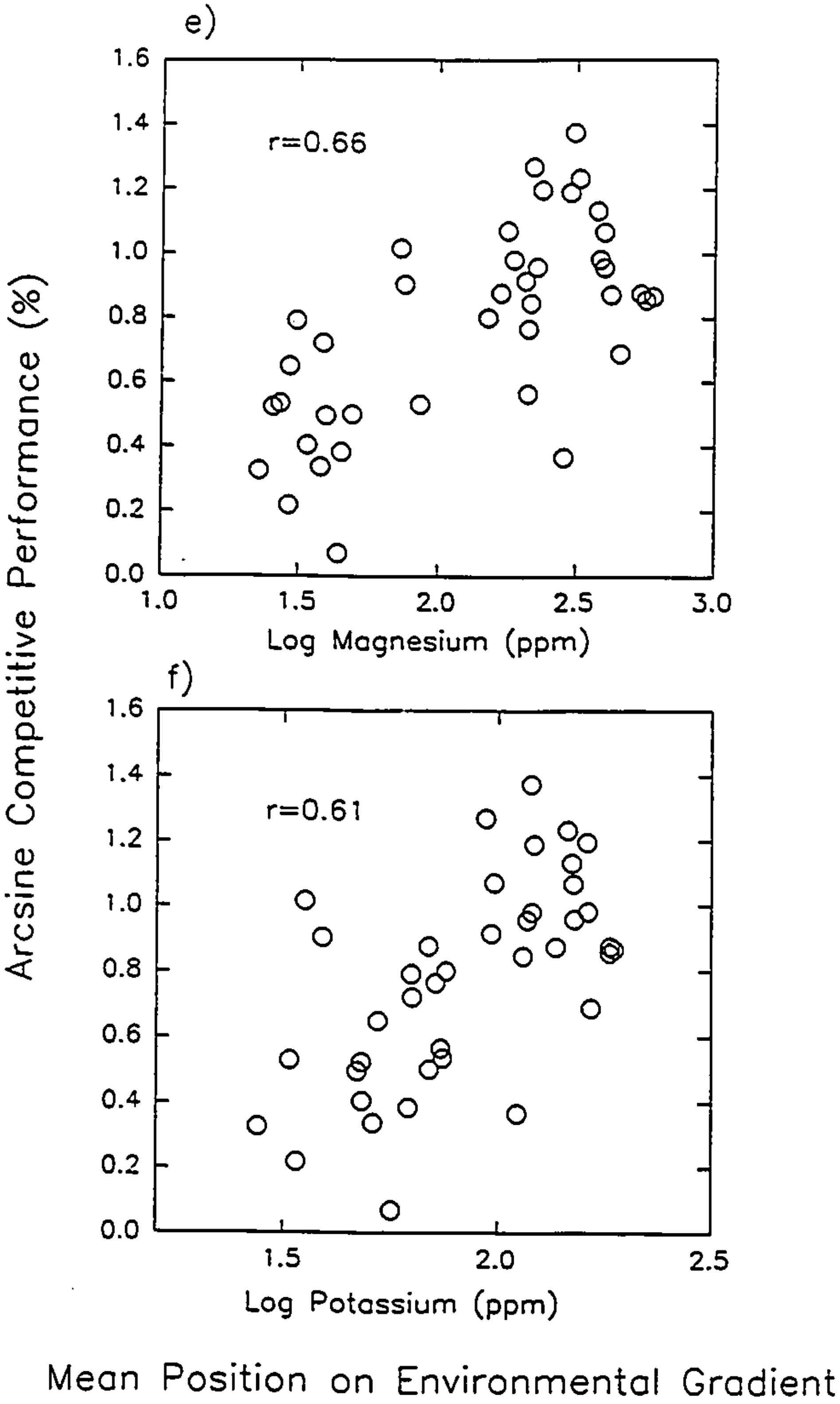

e)
r=0.66
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1.0
1.5
2.0
2.5
3.0
Log Magnesium (ppm)
f)
r=0.61
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1.5
2.0
2.5
Log Potassium (ppm)
Arcsine Competitive Performance (%)
Mean Position on Environmental Gradient

Table 1.10 Correlation (r) between relative competitive performance and mean position on each environmental gradient for monocotyledon species only (n=20) and dicotyledon species only (n=20). Competitive performance (expressed in terms of percent reduction in phytometer biomass) was arcsine transformed for analysis. All measures of mean position on the environmental gradient were log transformed except for percent organic content which was arcsine transformed.

Mean Position on Environmental Gradient	**Correlation (r) with Competitive Performance**	
	Monocot	**Dicot**
standing crop (g/0.25m^2)	.84 $p<.00001$	.82 $p<.00001$
soil phosphorous content (ppm)	.86 $p<.00001$	.41 $p=.07$
soil nitrate content (ppm)	.85 $p<.00001$	.54 $p=.01$
pH	.27 $p=.24$	.53 $p=.02$
soil potassium content (ppm)	.76 $p<.00001$	.50 $p=.02$
soil magnesium content (ppm)	.74 $p<.00001$	.63 $p=.003$
percent organic content	.85 $p<.00001$	.60 $p=.006$

Figure 1.5 Relationship between relative competitive performance and position on the **a)** standing crop; **b)** percent organic content; **c)** phosphorous; and **d)** nitrate gradients for monocotyledons (n=20). Relative competitive performance is expressed as percent reduction in the biomass of the phytometer *Lythrum salicaria*.

Figure 1.5

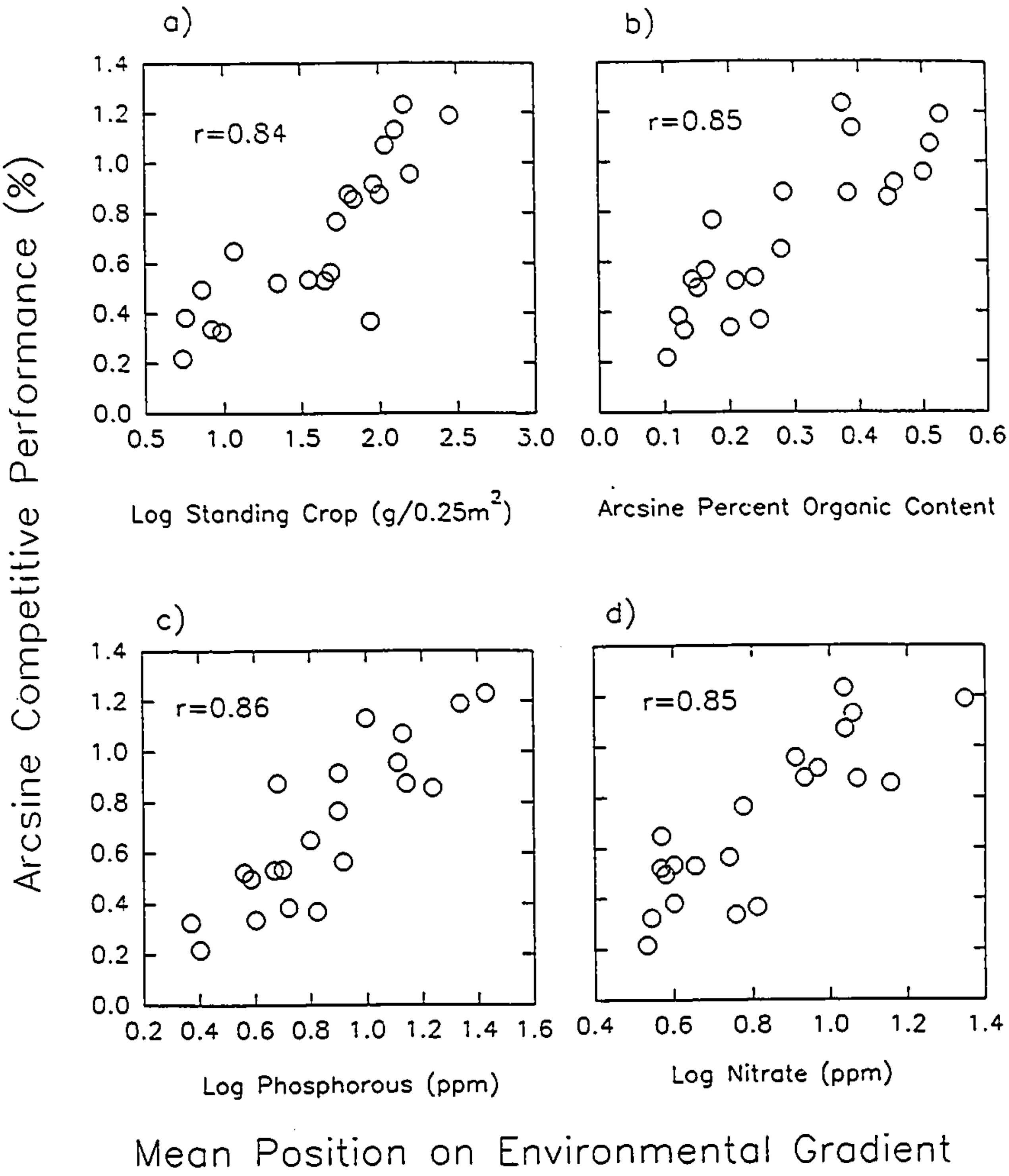
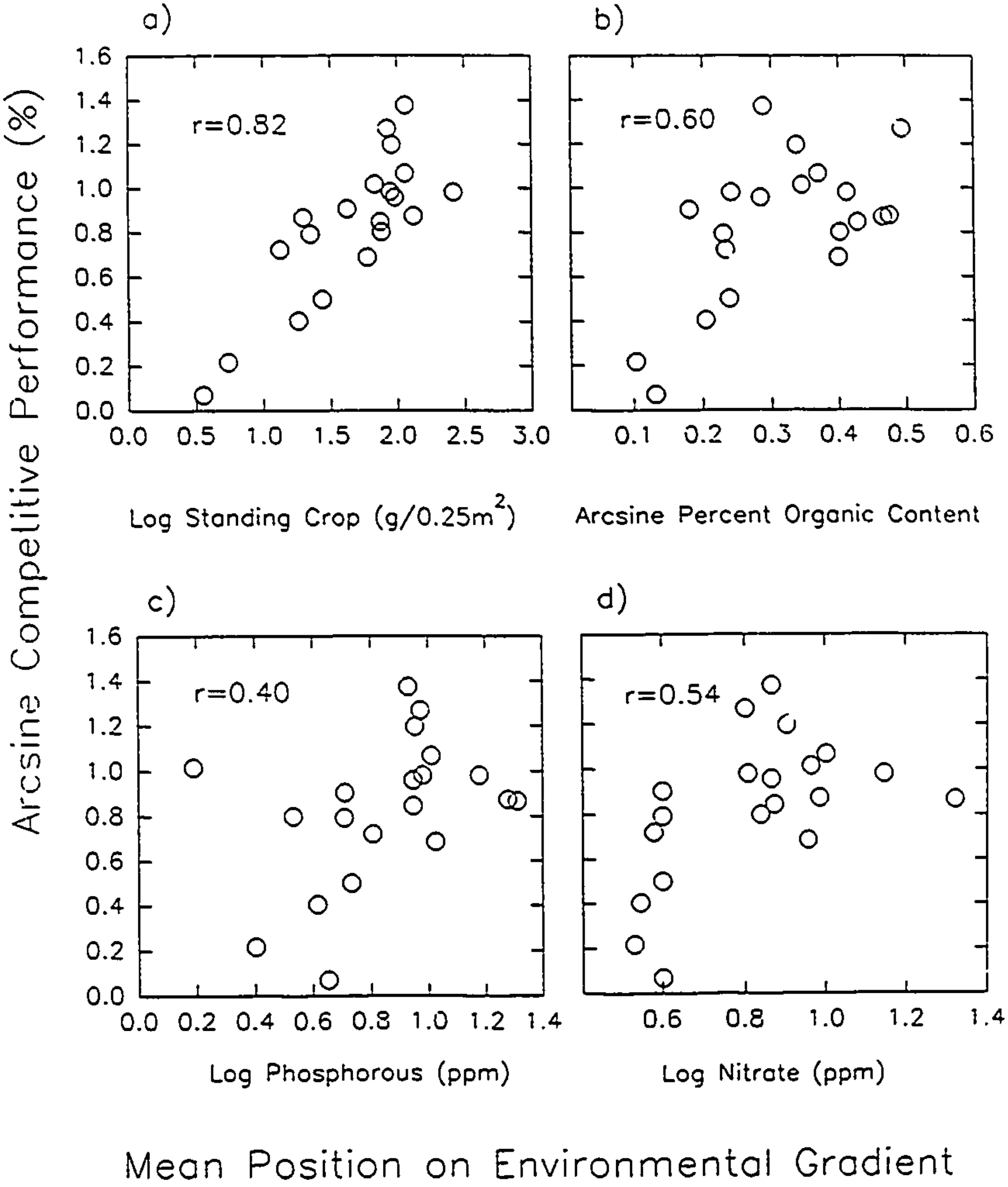

a)
r=0.84
Log Standing Crop (g/0.25m^2)
b)
r=0.85
Arcsine Percent Organic Content
c)
r=0.86
Log Phosphorous (ppm)
d)
r=0.85
Log Nitrate (ppm)
Arcsine Competitive Performance (%)
Mean Position on Environmental Gradient
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0.5
1.0
1.5
2.0
2.5
3.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0.4
0.6
0.8
1.0
1.2
1.4

Figure 1.6 Relationship between relative competitive performance and position on the **a)** standing crop; **b)** percent organic content; **c)** phosphorous; and **d)** nitrate gradients for dicotyledons (n=20). Relative competitive performance is expressed as percent reduction in the biomass of the phytometer *Lythrum salicaria*.

Figure 1.6


a)
b)
c)
d)
r=0.82
r=0.60
r=0.40
r=0.54
Arcsine Competitive Performance (%)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0 0.5 1.0 1.5 2.0 2.5 3.0
Log Standing Crop (g/0.25m²)
0.1 0.2 0.3 0.4 0.5 0.6
Arcsine Percent Organic Content
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
Log Phosphorous (ppm)
0.6 0.8 1.0 1.2 1.4
Log Nitrate (ppm)
Mean Position on Environmental Gradient

DISCUSSION

The Environmental Gradient

Standing crop is an important variable underlying community pattern, and is implicit in many general models of community organization (Grime 1973, 1979; Wheeler and Giller 1982; Day *et al.* 1988; Wilson and Keddy 1986a; Moore *et al.* 1989). It is therefore important to understand the environmental conditions underlying the standing crop gradient. The results of the current research show that in the shoreline plant communities studied each of the measures of soil fertility (macronutrient levels and percent organic content) are significantly correlated with standing crop. However at the local scale, when the Westmeath and Luskville study sites were considered individually, percent organic content of the soil was the only variable that showed a consistently strong relationship to standing crop. Differences between the Luskville and Westmeath sites and the pooled data set may be due to inherent variability in nutrient data collected over a range of site conditions, geographic regions, and years. The standing crop gradient is proposed to be a combined gradient of stress (measured here as nutrient concentration) and disturbance (Grime 1979). This in turn could influence the relative contribution of measures of fertility to above-ground productivity (standing crop). Percent organic content is a fertility measure that incorporates the effects of disturbance in lakeshore wetlands (Keddy 1983; Wilson and Keddy 1985; Day *et al.* 1988) and this may be why it shows a more consistent relationship with standing crop than direct measures of macronutrient levels. These results do however, confirm that in shoreline plant communities, fertility is significantly correlated with standing crop. The relative importance of disturbance, or other variables, in explaining the remaining variation is an important question that remains to be explained at this level of general community organization.

Competitive Performance

This experiment has measured only one aspect of what might be generally referred to as competitive ability. I have therefore used the word competitive performance to describe the direct measure of species effect on a common phytometer. When I refer to competitive performance, I mean competitive success within the limitations of the methodology. Results of the comparative screening of species shows that the 44 wetland species in this study vary significantly in their relative competitive performance, forming a competitive hierarchy with large, leafy species (e.g., *Typha xglauca, Scirpus fluviatilis*) at the top of the hierarchy and small isoetid species (e.g., *Eriocaulon septangulare, Lobelia dortamanna*) at the bottom of the hierarchy. It appears that many plant and animal communities have competitive hierarchies (Gilpin *et al.* 1986; Goldsmith 1978; Wilson and Keddy 1986b; Mitchley and Grubb 1986). Keddy and Shipley (1989) found highly significant hierarchies in published competition matrices from seven different plant communities including lakeshores, sea-cliffs and chalk grassland. However, the small number of species involved makes it difficult to draw generalizations about pattern or mechanism in natural communities. The experimentally derived hierarchy in this study provides a systematic measure of competitive performance for a large number of species and a general tool for exploring the relationship between competitive ability and coarse-scale community pattern.

The ranking of species in the competitive hierarchy is noteworthy. The species with the highest performance to suppress the growth of a neighbour are all tall, leafy species capable of fast growth (e.g., *Bidens cernua*) or extensive lateral spread (e.g., *Typha xglauca*) and conform to Grime's (1977; 1979) proposed characteristics of competitive dominants. These characteristics are considered generally indicative of an ability to capture resources, especially to pre-empt light and space, and are examined in detail in Chapter 2.

Many factors may influence a species' ranking within a competitive hierarchy (Gilpin *et al.* 1986; Harper 1977; Fowler 1982). This experiment was conducted under conditions considered to be most representative of the highly productive conditions of wetlands and those in which competition is presumably most important (Grime 1979; Wilson and Keddy 1986a). Our results do not exclude the possibility that the hierarchy varies with varying environmental conditions (Tilman 1985). This hypothesis is partially tested in Chapter 3. Further work is needed to empirically test the relationship between the competitive performance of species under different conditions.

There are some limitations to the approach used to measure competitive performance in this study. Recently, Grace *et al.* (1992) experimentally explored Connolly's suggestion (Connolly 1986) of size bias in competition experiments, concluding that measures based on Relative Yield were correlated with initial size of plants over at least two years. The importance of initial plant size cannot be clearly separated in the current experiment which was run over only one year and it may be that results would have varied if the experiment had been run over a longer period of time. However, results of Chapter 3 show that competitive performance was still highly correlated after two growing seasons. Though this study provides a direct measure of competitive performance across a range of species, a single starting density was used that may not reflect the actual density at which species interact in the field. Starting density was held constant to enable a systematic screening of relative competitive performance for a large number of species and this method necessarily requires some loss of detail in the pursuit of generality. How different densities would have effected the results is not known. The experimental conditions may also have limited the contribution of such factors as lateral spread to relative competitive performance. Under the experimental conditions of this study, annual species such as *Bidens cernua* exhibited a high relative degree of competitive performance. In field situations, the capacity for extensive lateral spread and pre-exemption of space by long-lived perennial species such as *Typha* sp. may strongly influence dominance (e.g., Grace and Wetzel 1981; Day *et al.* 1988).

There remains a great deal of controversy surrounding the measure and interpretation of competitive ability for plant species. Use of a comparative approach as described here is relatively novel but is amenable to addressing questions at the broad, multi-species scale. While subject to recognized limitations, this experiment does allow, as so traditional pair-wise experiments, among-species comparisons of competitive performance while controlling for density, abiotic factors and neighbours (McGilchrist 1965; Harper 1977; Fowler 1982). The phytometer approach, though sacrificing the detailed results of experiments based on pair-wise interactions, enables a systematic exploration of the competitive performance of a large number of species. Whether other approaches provide a more useful estimate of competitive ability, with broad predictive power at this general scale of community organization, remains to be examined.

Competitive Performance and Field Distribution

Previous work has described the role of competition in producing zonation patterns (e.g., Connell 1961; Lubchenco 1980; Austin and Austin 1980). More recently, Wilson and Keddy (1986b) have shown that competitive ability varies predictably along a fertility gradient. However, these studies examined only a few species under a limited range of conditions. Inferences about the relationship between competitive ability and field distribution have also been drawn from studies that have measured species characteristics possibly related to competitive success such as maximum potential growth rate (Grime and Hunt 1975; Boorman 1982) or height

(Menges and Waller 1983). However, there is no conclusive evidence that these traits actually confer improved competitive performance at the general scale at which they were examined in the field. Growth rate, for example, may relate to both ruderal (*sensu* Grime 1979) and competitive strategies. Experimentally derived measures of competitive performance for a large number of species allow a direct test of the predicted relationship between competitive ability and distribution. My results clearly show that a species position along a natural gradient of fertility is related to its relative competitive performance such that the strongest competitors tend to be found at the high end of the fertility gradient whereas poor competitors tend to be found at the low end.

The relationship between competitive performance and position on the environmental gradient is significant even given the expected sampling variability in results from such a broad range of sites and the coarse screening technique used to measure relative competitive performance. This suggests that the relationship between competition and pattern in the field is an important and pervasive feature of natural shoreline plant communities. These results also suggest that competitive hierarchies may be an important basis for understanding process and pattern in natural plant communities. More emphasis is needed on the systematic exploration of competitive hierarchies as fundamental predictors of community pattern.

My results leave an important unanswered question. If inability to compete for resources limits the distribution of competitive subordinates in high standing crop, fertile areas, then what limits the occurrence of competitive dominants in low standing crop, infertile areas? Is there a trade-off between competitive performance and the ability to withstand low nutrient availability? It has been proposed (Grime 1979) that species of high competitive performance are limited by their inability to tolerate stress or disturbance and that species found at low biomass sites will either be disturbance tolerant or stress tolerant (Givnish 1988; Grime 1979). Wilson and Keddy (1986b) suggest that disturbance eliminates competitive dominants in shoreline communities, thereby allowing competitive subordinates to occupy more stressed or disturbed sites.

The attributes that confer competitive dominance such as tall leafy shoots may make these species susceptible to disturbance such as wave damage (Menges and Waller 1983) or high water levels (Grace and Wetzel 1981). In this study, the species of low competitive performance which occur at the nutrient poor end of the gradient, have traits of species that have been considered to be stress tolerators by Grime (1977; 1979). For example, *Eriocaulon septangulare* and *Lobelia dortmanna*, are small isoetid evergreen species with characteristic "stress tolerant" morphologies and life-histories as described by several authors (e.g., Boston and Adams 1987; Wisheu and Keddy 1989; Day *et al.* 1988) - though in many cases, the relationship between stress tolerance and morphology/life-history has been inferred from distribution patterns. Shipley and Keddy (1988) show that shoreline species demonstrate a trade-off between maximum relative growth rate and sensitivity to nutrient stress. Grace and Wetzel (1981) show a similar trade-off between two species of *Typha* though water level is the relevant stress/disturbance. Whether such a trade-off exists between competitive performance and stress tolerance will be examined in Chapter 3.

Considerable variability remains in the relationship between competitive performance and field distribution. This may be due to problems with the measurement of competitive performance, in the measure of relative species position along the environmental gradient, or simply to the fact that things other than competition influence field distributions. The frequency measure used may have yielded different results than a more detailed examination of the distribution pattern of species along the gradients (Goldsmith and Harrison 1976). However, species relative competitive performance is very unlikely to be the only determinant of pattern along the shoreline gradients examined here and it is clearly not expected that all, or even most, of the variation can be explained by a single measure of competitive performance. Explaining the residual variation along the gradient is an important goal for future research.

As discussed above, the different results for monocotyledons and dicotyledons are noteworthy. My results show that much of the variability in distribution of monocotyledons along the standing crop gradient can be explained by the relationship between competitive performance and fertility as measured by macronutrient levels. On the other hand, dicotyledons showed a much weaker relationship between competitive performance and distribution along macronutrient gradients.

Monocotyledons may have evolved more mechanical and physiological resistance to wave exposure and flooding, common types of disturbance in shoreline communities (Menges and Waller 1983; Grace and Wetzel 1982). For example, monocotyledons have meristems buried even during peak growth, whereas dicotyledons expose them at the top of the stem. Therefore, though both groups of species vary predictably along a combined gradient of stress and disturbance (i.e. the standing crop gradient); the variation in monocotyledon distribution may be explained more clearly by fertility gradients. The distribution of dicotyledons on the other hand, may be more affected by the disturbance component of the gradient. Given that major studies on shoreline plant communities have concluded that disturbance is a major determinant of pattern (e.g., Day *et al.* 1988; Moore 1990), an examination of this general conclusion with reference to these two taxonomically distinct groups may be warranted.

CHAPTER 2

THE RELATIONSHIP BETWEEN COMPETITIVE PERFORMANCE AND PLANT TRAITS

A COMPARATIVE APPROACH

" Dating back to Darwin, a ...goal of ecologists has been to be able to predict the outcome of competition from an analysis of the characteristics of species in isolation"

J. B. Grace (1990)

Abstract

I tested the hypothesis that the relative competitive performance of plant species is correlated with easily measured plant traits. The competitive performance of 44 herbaceous shoreline plant species was determined as the relative ability of a species to suppress the growth of a common phytometer (*Lythrum salicaria*). The experiment was conducted over one growing season in a sterile, high nutrient, organic medium. Several morphological and biomass measures were made on each of the 44 species at the time of harvest (above and below-ground biomass, root:shoot ratio, height, leaf number, leaf length, leaf width, leaf area, canopy diameter and canopy area). Competitive performance was significantly correlated with several measures - above and below-ground biomass, height, leaf width, leaf area, canopy diameter and canopy area, but most strongly with the above-ground biomass of the test species ($r_s = 0.92$, $p<.00001$).

INTRODUCTION

Predicting the outcome of competitive interactions is a fundamental challenge in plant community ecology. The analysis of the quantitative relationship between simple, measurable plant traits and competitive performance provides a potentially powerful tool in unravelling the complexity of competition at the multi-species, community scale. This approach has two fundamental strengths in developing general theory. Firstly, establishing a link between plant traits and competitive performance provides a basis for predicting complex, difficult to measure parameters from easily measured ones - an important aim of predictive ecology (Peters 1982). Secondly, theory built on measurable attributes of functional rather than taxonomic significance is not limited by species nomenclature, enabling generalization beyond the species of a particular study.

Several authors have advocated the use of physiological, morphological or behavioral traits to predict the outcome of competition (e.g., Grime 1974, 1977; Tilman 1987; Givnish 1982; Grace 1988; Goldberg 1990; Tilman and Wedin 1991). Though this relationship has received some experimental attention (e.g., Grace 1988; Goldberg 1990; Berendse and Elberse 1990; Weiner 1984) there has been no systematic analysis of the relationship between plant traits and experimental measures of competitive performance for a diverse, multi-species community at a scale that would enable generalization beyond the particular species and conditions.

An analysis of the relationship between plant traits and competitive ability has important implications for understanding mechanisms underlying observed pattern in the field. Several authors have described plant traits along environmental gradients and have inferred competition as an important underlying mechanism (e.g., Givnish 1982; Menges and Waller 1983; Day *et al.* 1988). Other studies have shown that species competitive ability varies predictably along natural gradients in the field (Wilson and Keddy 1986b) and that this is a generalized trend across shoreline plant communities (Chapter 1 results). Establishing a link between plant traits and competitive performance would provide a powerful unifying framework for development of general theory, tying together observed distribution patterns, measurable traits, and competitive ability.

The relationship between plant traits and competitive ability was tested using plant species from shoreline plant communities representing a broad range in life-history and morphology. This community is well suited to a test of the proposed relationship: there is strong inferential evidence that competition is an important determinant of pattern in shoreline communities (Wilson and Keddy 1986a,b) and that this pattern is underlain by predictable variation in simple measurable plant traits (e.g., Menges and Waller 1983; Day *et al.* 1988).

To test the proposed relationship, relative competitive performance was experimentally determined for 44 species of shoreline plants as the ability of each species to suppress the growth of a common phytometer, *Lythrum salicaria*. Plant traits selected for analysis were measurable traits that vary broadly across species of shoreline plant communities (Gaudet and Keddy 1988), and that are presumably important predictors of competitive ability (e.g., Grime 1977).

METHODS

Competitive Performance

Relative competitive performance was experimentally determined for forty-four herbaceous wetland species as described in Chapter 1 and in Gaudet and Keddy (1988). Species used in this study represented a broad range in life history types from small evergreen rosette species (e.g., *Eriocaulon septangulare*) to large clonal perennials (e.g., *Typha* x*glauca*). Most studies on competitive interference within plant communities are based on considerations of population density, but this obscures variation due to other factors such as plant size (Weiner 1984; Penridge and Walker 1986). Therefore, this study was conducted at a single density with the effects of distance kept constant so that the effects of other parameters could be clearly interpreted.

All 44 species were tested against the phytometer *Lythrum salicaria*. To assess the effect of different phytometers on results, a subset of 10 species were tested against the phytometer *Penthorum sedoides*. Phytometers and handling are described in Chapter 1.

Plant Traits

All 44 species were grown with phytometers and in isolation over one growing season and harvested immediately prior to senescence in the fall. Just prior to harvest, several morphological measurements were made on plants grown in isolation and on plants grown with the phytometer.The following measurements were made: maximum height, maximum canopy diameter, leaf width, length, and number of leaves. Several other measures were derived from these measures. Leaf area was estimated as leaf width multiplied by leaf length. Canopy area was estimated as the number of leaves multiplied by leaf area. For the purposes of comparison, species that were essentially leafless (e.g., reeds such as *Scirpus validus*) were considered to be comprised of a single leaf or photosynthetic "shoot".

Plants (phytometer and test species) were harvested and dried to constant weight for biomass determination. Below-ground parts were separated and washed prior to drying. The shoot to root ratios were estimated as the ratio of above-ground biomass to below-ground biomass.

Spearman rank correlation coefficients were used to describe the relationship between plant traits and competitive performance due to significant departures from normal distributions for several of the data sets. Because non-parametric tests were used, data was not transformed prior to analysis. All statistical analysis was performed using **Statsgraphics**^{R} statistical software package by Statistical Graphics System Corporation

(Version 4.0; Copyright© 1989 STSC Inc.).

RESULTS

The mean competitive performance for each species is summarized in Table 1.7 (Chapter 1) and morphological variables for each species are summarized in Appendices 2.1 and 2.2. Several of the measured traits are significantly correlated with each other. Plant above-ground biomass is strongly correlated with height (r_s = 0.80; $p < .00001$) and canopy area (r_s = 0.74; $p < .00001$), and to a lesser extent with canopy diameter (r_s = 0.64; $p < .00001$) and leaf area (r_s = 0.65; $p < .00001$). These variables can all be considered measures of plant size or, in the case of canopy area and leaf area, as relative estimates of available photosynthetic area. The Spearman rank correlation (r_s) between all measured traits is shown in Appendix 2.3.

Competitive performance was significantly correlated with eight of the traits measured, but most strongly with the above-ground biomass of the test species (r_s = 0.92; $p < .00001$). Total biomass, below-ground biomass, height, leaf width, leaf area, canopy diameter and canopy area were also significantly correlated with competitive performance ($p < .001$), though relationships were much weaker than between biomass and competitive performance (Table 2.1 and Figure 2.1 a-f). The strong relationship between above-ground biomass and competitive performance may be due to the fact that this variable integrates several of the other variables related to size and photosynthetic area as discussed above.

A major objective of this study was to identify general relationships between plant traits and competitive performance. Therefore, several other analyses were performed to determine whether the relationships described above were robust. The morphological traits discussed above were measured on plants interacting with the phytometer. It is possible that traits measured under competitive conditions are a unique response to that particular competitive interaction, and would have no general relevance or predictive power outside of this specific set of conditions. To test wether this relationship between competitive performance and plant traits was based on inherent species differences and was not simply a unique consequence of the competitive interaction, the relationship between competitive performance and plant traits was also tested using morphological measurements taken from test species grown singly i.e. without competition, under otherwise identical conditions. Results showed that above-ground biomass of species grown singly was highly correlated with competitive performance ($r_s = 0.91$; $p<.00001$; Figure 2.2). Mean biomass measurements for species grown in isolation are included in Appendix 2.1.

Table 2.1 Spearman rank correlation (r_s) between traits of 44 test species and relative competitive performance expressed as percent reduction in phytometer biomass (*Lythrum salicaria*).

Plant Traits	**Correlation (r_s) with Relative Competitive Performance**	**p**
Biomass, total (g)	0.89	$p < .00001$
Biomass, above-ground (g)	0.92	$p < .00001$
Biomass, below-ground (g)	0.84	$p < .00001$
Height (cm)	0.61	$p = .0001$
Leaf length (cm)	0.18	$p = .2339$
Leaf width (cm)	0.59	$p = .0001$
Leaf area (cm^2)	0.57	$p = .0002$
Leaf number	0.41	$p = .0076$
Canopy diameter (cm)	0.69	$p < .00001$
Canopy area (cm^2)	0.73	$p < .00001$

Figure 2.1 Relationship between relative competitive performance and a) above-ground biomass; b) height; c) leaf width; d) leaf area; e) canopy diameter; and f) canopy area for 44 herbaceous plant species. Relative competitive performance is expressed as the percent reduction in the biomass of the phytometer *Lythrum salicaria* when grown with each of the test species (5 replicates per species).

Figure 2.1.

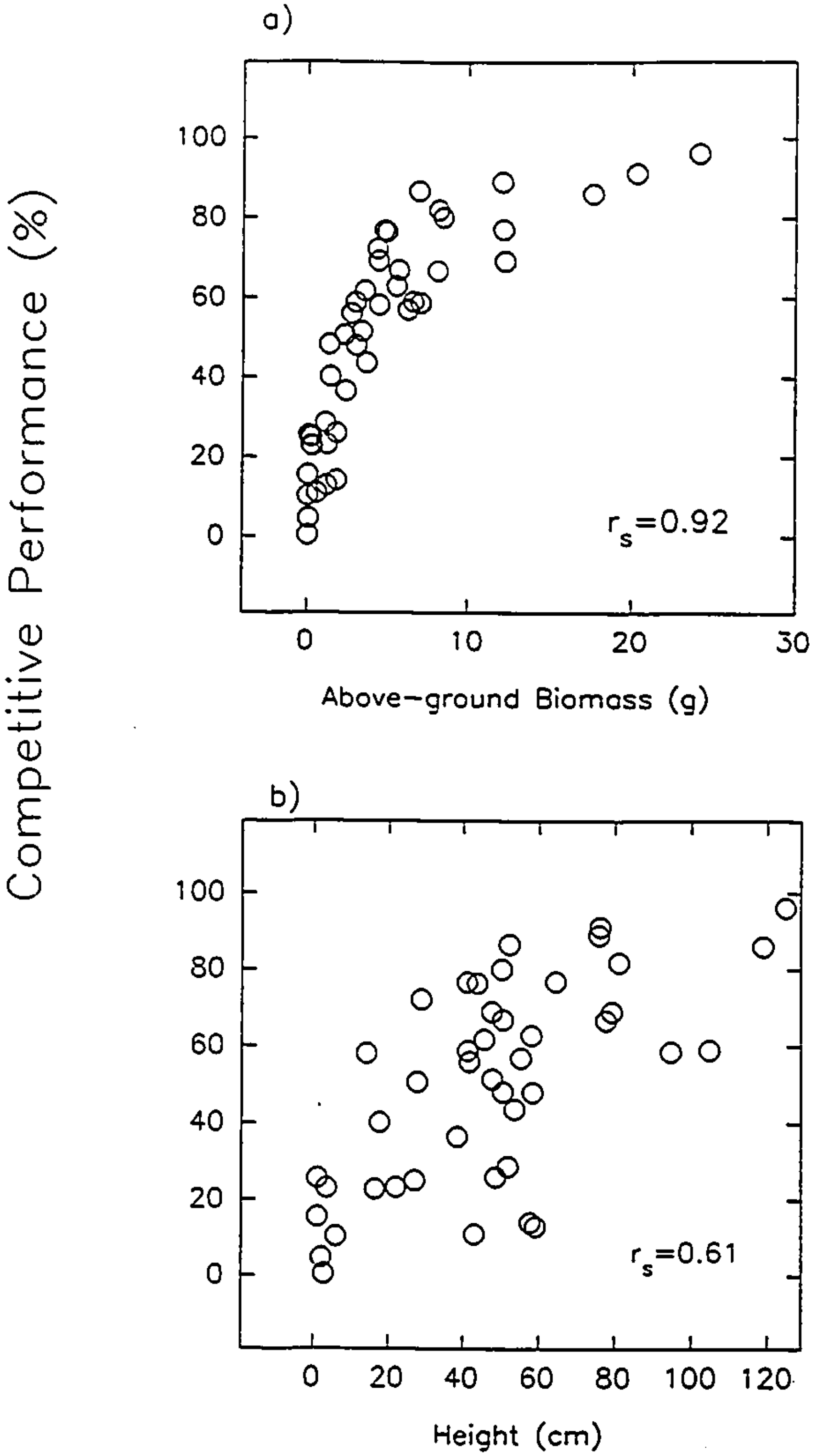

a)
Competitive Performance (%)
100
80
60
40
20
0
0
10
20
30
Above-ground Biomass (g)
r_s=0.92
b)
100
80
60
40
20
0
0
20
40
60
80
100
120
Height (cm)
r_s=0.61

Figure 2.1

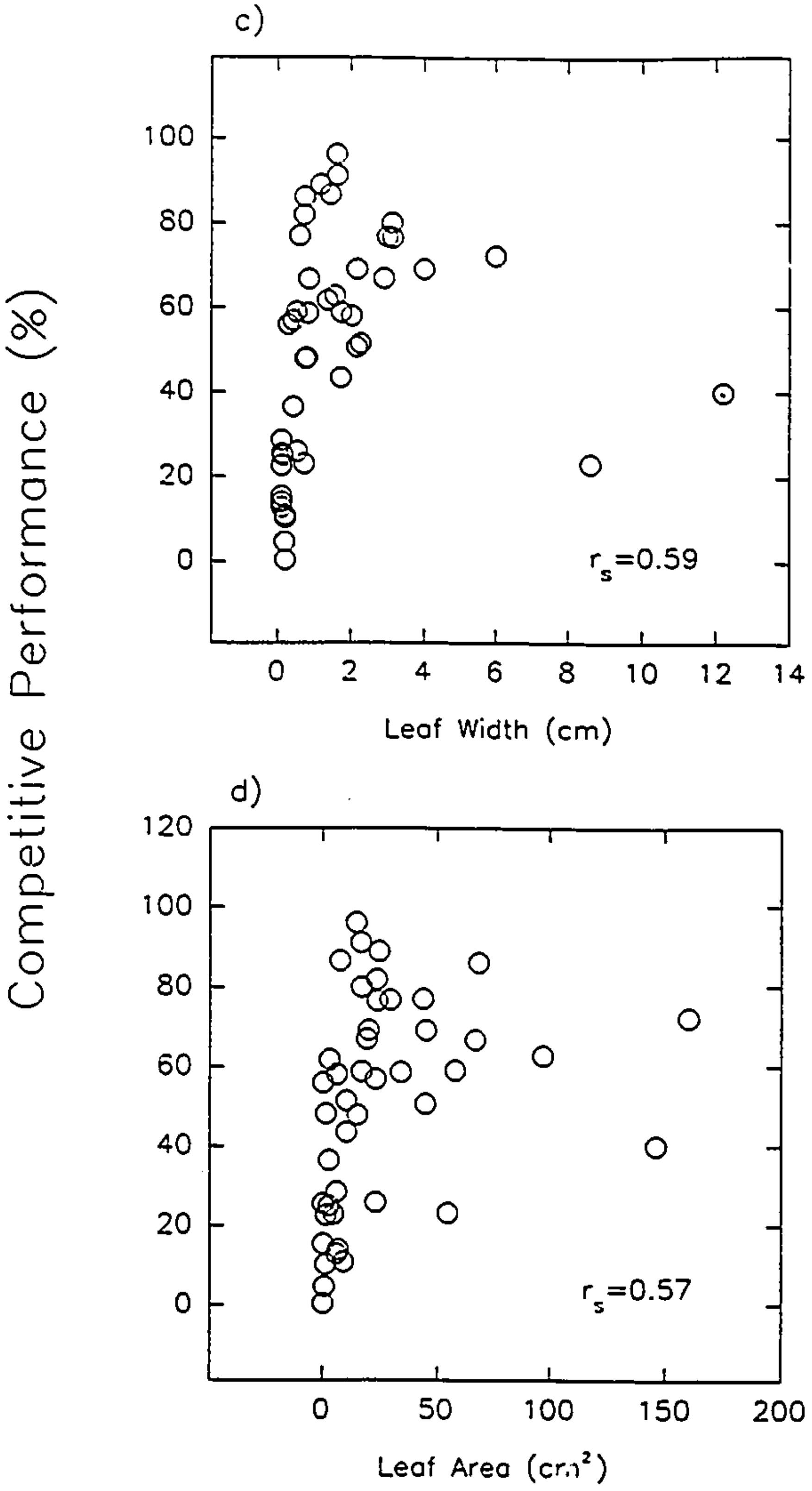

c)
Competitive Performance (%)
100
80
60
40
20
0
0
2
4
6
8
10
12
14
Leaf Width (cm)
r_s=0.59
d)
120
100
80
60
40
20
0
0
50
100
150
200
Leaf Area (cm²)
r_s=0.57

Figure 2.1

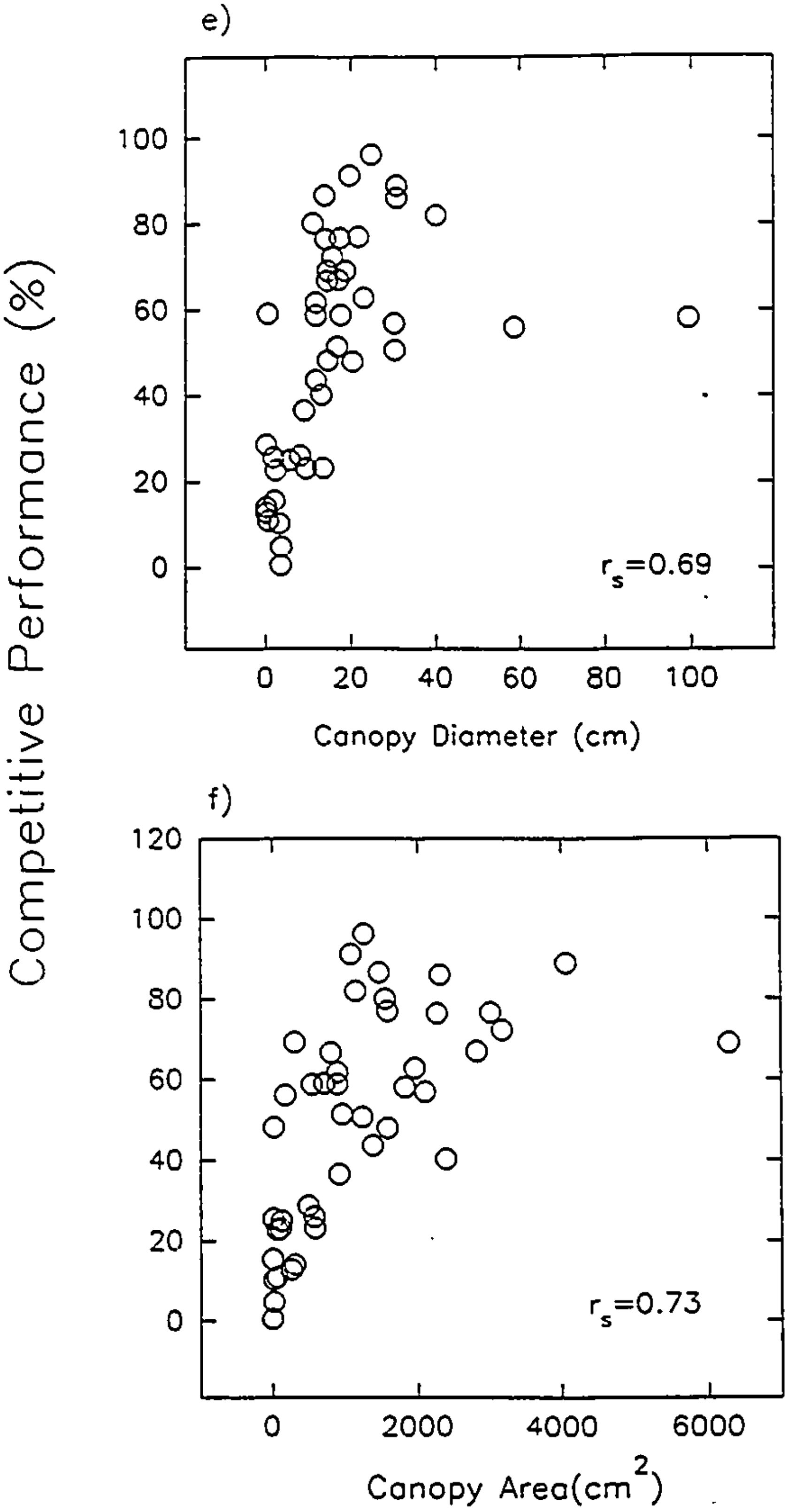
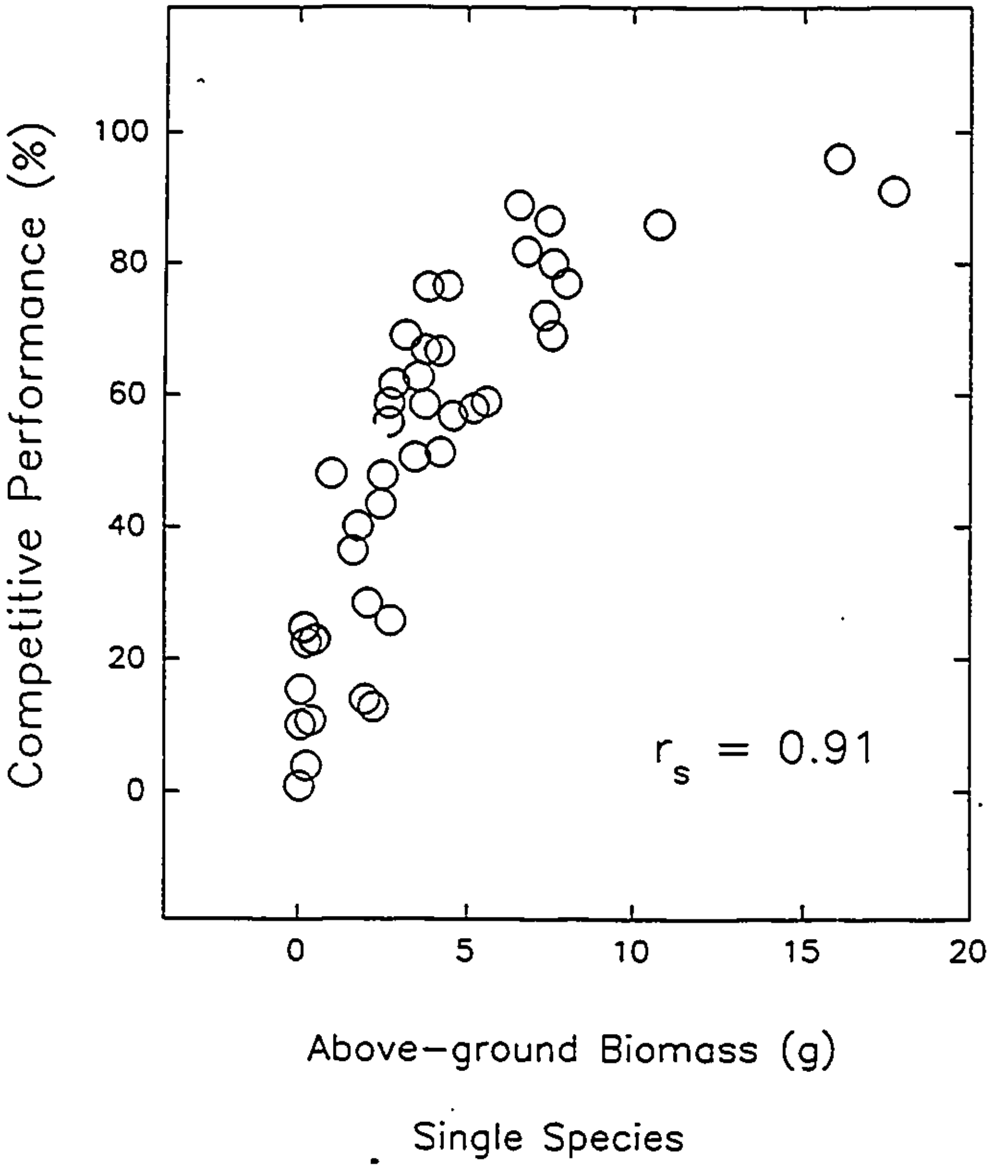

e)
Competitive Performance (%)
100
80
60
40
20
0
0
20
40
60
80
100
Canopy Diameter (cm)
r_s=0.69
f)
120
100
80
60
40
20
0
0
2000
4000
6000
Canopy Area(cm^2)
r_s=0.73

Figure 2.2 Relationship between above-ground biomass of species grown singly and their relative competitive performance for 44 herbaceous plant species. Relative competitive performance is expressed as the percent reduction in the biomass of the phytometer *Lythrum salicaria* when grown with each of the test species (5 replicates per species).

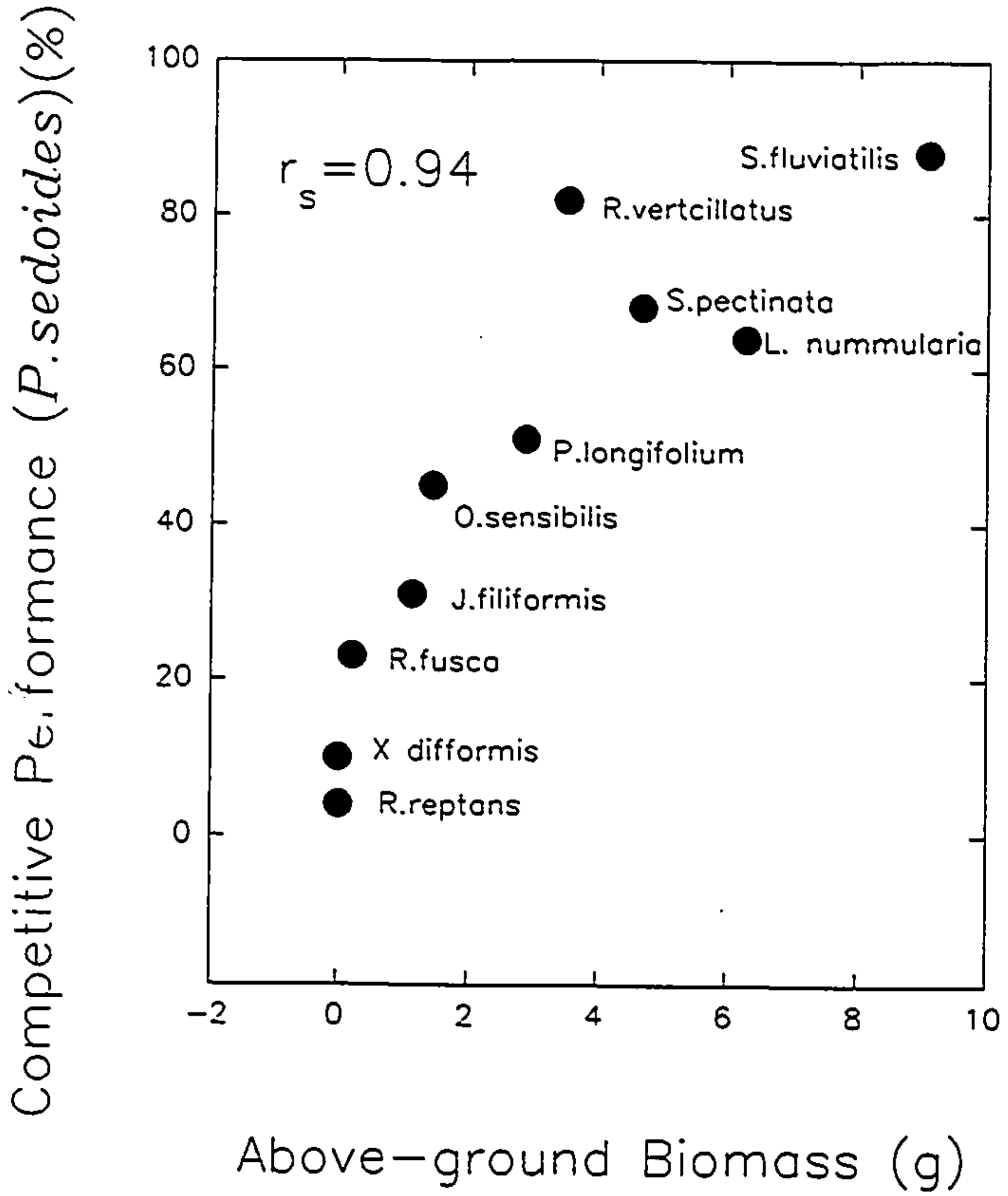
Figure 2.2


Competitive Performance (%)
100
80
60
40
20
0
0
5
10
15
20
Above−ground Biomass (g)
Single Species
$r_s = 0.91$

The relationship between above-ground biomass and competitive performance was also tested for the subset of ten species that were grown with the phytometer *P. sedoides* to assess the effect of different phytometers on results. Changing the phytometer had no obvious effect on results. Above-ground biomass was highly correlated with competitive performance ($r_s = 0.94$; $p < .005$; Figure 2.3). The relative competitive performance of the ten species grown with *P. sedoides* is shown in Table 1.8. (Chapter 1)

Figure 2.3 Relationship between relative competitive performance and the above-ground biomass of test species using *Penthorum sedoides* as the phytometer. Relative competitive performance is expressed as percent reduction in phytometer biomass when grown with the test species. The biomass of test species when grown with *P. sedoides* is summarized in Appendix 2.3.

Figure 2.3



$r_s=0.94$
S.fluviatilis
R.vertcillatus
S.pectinata
L. nummularia
P.longifolium
O.sensibilis
J.filiformis
R.fusca
X difformis
R.reptans
100
80
60
40
20
0
−2
0
2
4
6
8
10
Competitive Performance (P.sedoides)(%)
Above−ground Biomass (g)

DISCUSSION

The results of this study show that this experimental measure of competitive performance is correlated with simple measurable plant traits, particularly the above-ground biomass of species. Results show that this relationship is significant irrespective of wether traits are measured from species grown in the presence of competition or grown singly, or wether a different phytometer is used to assess competitive performance. This suggests that the relationship is robust in predicting competitive performance beyond the particular conditions of this experiment. Further work is needed to test the generality of this relationship.

These results show that, at least under these conditions, species of similar biomass will have similar competitive abilities. This does not preclude the possibility that where biomass is similar, other factors may become more important in determining the outcome of competitive interactions. Though our results show that biomass has the best predictive value across this broad range of species morphologies and environmental conditions, in a study that considers a small number of species with a small biomass range, height or other life-history or morphological variables could be the critical determinant of dominance. Replacement series experiments (Harper 1977) often use a small number of species that can be of similar biomass (e.g., Wilson and Keddy 1986b; Goldsmith 1978; Mitchley and Grubb 1986) making it difficult to discern general patterns that apply beyond the species in the experiment.

If species are very close in biomass, results may actually be a measure of "per unit" effect. This may explain why such studies have failed to yield general relationships.

The current experiment examines a large number of species across a broad biomass range and addresses absolute or total effect. An appreciation of the differences between "total competitive effect" and "per unit competitive effect" may resolve much of the controversy surrounding interpretation of competitive interactions and their role in shaping natural communities (Grace and Tilman 1990; Grace 1991). Also, an explicit understanding of the scale at which results are relevant is critical in resolving conflicting results about the importance of plant traits as determinants of competitive ability. Whether per unit or absolute effects are important may ultimately depend on whether coarse or fine scale pattern is being addressed by the study.

The results of this experiment are based on competitive performance under fertile or optimal conditions. How these results would have varied with other conditions is unknown. However, results of Chapter 3, showing that competitive ability under high and low nutrient conditions is correlated, suggest that this relationship is generalized across nutrient levels at this broad multi-species scale.

My results do not provide a mechanistic interpretation of resource competition (*sensu* Tilman 1990). Biomass may simply integrate or summarize other traits such as high rates of resource capture above and below ground (Donald 1958; Chapin

1980). It has been suggested that at high nutrient levels, light becomes the critical limiting resource (Tilman 1986; Schmitt *et al.* 1986) and traits I have identified may be primarily associated with competition for light. It is noteworthy that the traits that were correlated most strongly with relative competitive performance i.e. above and below ground biomass, height, and canopy area, are traits presumably associated with high rates of resource capture (Grime 1979).

The fact that above and below-ground biomass are highly correlated across this range of species also suggests that resource capture above and below ground may be equally important in predicting competitive performance, at least in this group of herbaceous plant species. Shipley and Peters (1990) similarly found that root to shoot ratios did not vary significantly with growth rate across a similar range of herbaceous plant species.

It is also interesting to note that biomass is a better predictor of competitive performance than height alone, despite the fact that height would be closely associated with ability to compete for light (e.g., Givnish 1982; Grime 1979). However, these results are not surprising if one considers that height alone does not ensure high rates of resource capture above ground (i.e. light interception). Tall reedy species with "leafless" shoots such as *Scirpus validus*, were intermediate in competitive performance in this study while tall "leafy" species such as *Lythrum salicaria* and *Typha xglauca* were superior competitors. Clearly, the leafless species have a lower capacity for interception of light. As stated previously, biomass may be the best predictor of relative competitive performance simply because it integrates several of the factors which are presumably related to high rates of resource capture/preemption (Grime 1979).

It is also noteworthy that species that occur at the top of the competitive hierarchy are characteristic of species from fertile habitats while species at the lower end of the hierarchy are typical of species from low nutrient stressed habitats (Chapter 1). These results conform well to the model of centrifugal organization (Rosenzweig and Abramsky 1986) proposed for wetlands (Keddy 1990). In this model, competitive dominants are represented by a few very large, leafy species which form high biomass monocultures under high nutrient, undisturbed conditions. The species of high relative competitive performance in this study are large, leafy species such as *Typha* x*glauca* which as would be predicted by the model of centrifugal organization.

What are the general implications of these results in understanding the organization of natural communities? Published research suggests that size-related variables are pervasive indicators of competitive dominance in a variety of herbaceous plant communities (Mack and Harper 1977; Goldsmith 1978; Snaydon and Howe 1986; Mitchley and Grubb 1986), and within forest monocultures (Weiner 1984). It has been shown that plant biomass or height varies predictably along natural gradients of stress and disturbance (Wilson and Keddy 1986b; Menges and Waller 1983).

Successional and even evolutionary patterns are represented by increases in plant biomass (Tilman 1986). The occurrence of natural gradients of plant biomass in the field and the relationship between plant traits and competitive performance suggest that competition is an important determinant of community pattern.

CHAPTER 3

THE EFFECT OF NUTRIENT STRESS ON COMPETITIVE PERFORMANCE:

CONTINGENCY OR GENERALITY?

... ecological patterns, about which we construct theories, are only interesting if they are repeated. They may be repeated in space or in time and they may be repeated from species to species. A pattern which has all of these kinds of repetition is of special interest because of its generality, and yet these very general events are only seen by ecologists with rather blurred vision. The very sharp-sighted always find discrepancies and are able to say that there is no generality, only a spectrum of special cases. This diversity in outlook has proved useful in every science, but it is nowhere more marked than in ecology.

MacArthur (1968)

Abstract

I tested the hypothesis that the competitive performance of plant species is correlated under high and low nutrient conditions. The competitive performance of 26 shoreline plant species was experimentally determined as the relative ability to suppress the growth of the phytometer *Penthorum sedoides* under high and low nutrient extremes. Plants were grown in sterile sand in Hoagland's nutrient solution full-strength (high nutrient) or diluted 10 times (low nutrient) over two growing seasons. Although shifts in relative competitive performance were apparent between nutrient levels, results showed that when all species were considered, competitive performance under high and low nutrient conditions was significantly correlated in both year 1 ($r_s = 0.66$) and year 2 ($r_s = 0.74$). There does however, remain a great deal of variation that cannot be explained by the experimental data. Results of this study also show that the intensity of competition is significantly reduced under low nutrient conditions and it may be that under these conditions i.e. when competition is "relaxed", factors other than competition have a relatively greater influence on plant biomass.

INTRODUCTION

There is increasing evidence that competitive hierarchies exist in both plant and animal communities (Gilpin *et al.* 1986; Goldsmith 1978; Keddy and Shipley 1989; Keddy 1989). However, an important question remains. Are these hierarchies invariant such that a species relative competitive ability (and therefore ranking in the hierarchy), is not significantly influenced by changing environmental conditions, or are they contingent such that competitive ranking cannot be predicted in the absence of precise knowledge of environmental conditions such as resource levels. Some work suggests that competitive performance is highly contingent on precise combinations of resource levels and that this contingency underlies observed pattern in the field (Tilman 1988; Tilman 1990; Silvertown 1989). Other work suggests that competitive ability is an inherent species trait which is relatively independent of precise environmental conditions (Grime, 1979; Keddy 1989; Gaudet and Keddy 1988; Keddy 1990). Resolving these two different hypotheses about the nature of competitive ability is an important step in developing predictive theory for plant competition. Here, I offer a critical test between these views by comparing the competitive performance of plant species in two contrasting environments.

Traditional experimental methods for the assessment of relative competitive performance are logistically limited to a relatively small number of species and may overemphasize contingency by creating exactly those circumstances where general predictive relationships are most elusive (Keddy 1989). In Chapter 1, an indicator or phytometer method is presented to measure relative competitive performance in a large number of species simultaneously. A major unanswered question in that study was whether the results would vary among environmental conditions, particularly different fertility levels. I therefore carried out another study using this design at two fertility levels. In this study, I test the hypothesis that competitive performance is correlated under high and low nutrient conditions.

METHODS

Experimental Procedure

The phytometer or indicator method described in Chapter 1 was used to assess the relative competitive performance of 26 wetland plant species (test species) by measuring suppression in the growth of *Penthorum sedoides* (phytometer species) . Phytometers were grown from seed in compartmentalized flats in a sterile organic medium in a glasshouse maintained at approximately 25^0 C. Test species ramets were collected in late April 1987, prior to emergence, from the shoreline areas described in Chapter 1 and were taken immediately to the experimental compound for planting. Ten seedlings of the phytometer, *P. sedoides* were selected for initial biomass determination. The initial biomass of *P. sedoides* was 0.14 grams dry weight (standard error ±0.035). Phytometers were selected for uniformity in size and planted in the centre of 1 litre pots filled with wet, sterile sand. Three individual ramets of each of the 26 test species were planted in a symmetrical pattern around the phytometer (n = 10 replicate pots per species). Species were also planted singly in pots (i.e. in the absence of competition) under otherwise identical experimental conditions (n = 10 replicates per species). The plants were placed in an outdoor compound at Carleton University, Ottawa, Ontario on May 1, 1987, a period coinciding with the natural growing season of these species. Each pot was encircled with mesh screening 15 cm. in height (to prevent plants from avoiding competitive interactions within the pot and from interfering with other pots), and then placed in individual 2 litre plastic tubs. Replicates were arranged in a randomized block design (five blocks).

A gradient of nutrient concentration was established using a modified Hoagland's solution at full-strength and one-tenth of this concentration (Appendix 3.1). This degree of variation in nutrient supply was known to have significant effects on plant growth (Shipley and Keddy 1988) and therefore created very different environments. Within each block, replicates of each species were randomly assigned to either a fertile (high nutrient) treatment or infertile (low nutrient treatment), giving five replicates per species/per treatment overall. One litre of nutrient solution was added to the two-litre tub under each pot, and was completely replaced two times per week. Plants were exposed to normal seasonal precipitation. During peak July and August temperatures, plants were also misted daily to avoid desiccation.

The experiment was conducted over two growing seasons, April 1987 to September 1988. Above-ground biomass was harvested and dried to constant weight after plant senescence in 1987. The dormant below-ground portions of the perennial plant species were stored in a cold room at 4° C over winter (November to March). Both above and below-ground biomass of phytometers and test species were harvested, washed (in the case of below-ground biomass), dried to constant biomass and weighed at the end of the 1988 season.

Competitive Performance

Relative competitive performance was calculated as described in Chapter 1, for each species, year, and treatment. Because below-ground biomass was not harvested in the first year (to avoid killing the plants), competitive performance was based on relative suppression of above-ground biomass of the phytometer to enable comparison between years.

The relationship between relative competitive performance under low and high nutrient conditions was assessed using Spearman rank correlation analysis. Kruskal-Wallis analysis of variance by ranks (Zar 1984) was used to test for a significant effect of species and nutrient treatment on the phytometer biomass. The Mann-Whitney test for paired samples was used to evaluate the direct effects of treatment on the test species above and below ground biomass (Zar 1974). Non-parametric tests were used because data violated assumptions of normality and homogeneity of variances required for parametric analysis. All analysis was performed using **StatsGraph**^{R} Version 3.0 (1988).

RESULTS

Effect of the Experimental Nutrient Regime on Species Biomass

Before examining competitive hierarchies directly, it is important to ascertain that the fertility regimes used in the experiment represented significantly different environmental conditions for the species in this study. Examination of the effect of fertility on plant productivity (biomass) provides a direct test of this. When data for all species were pooled, there was a significant effect of the nutrient treatment on plant above-ground biomass (Mann-Whitney; $n = 23,23$; $z = 3.14$; $p < .0005$). Under low nutrient conditions above-ground biomass converged within a very narrow range (Figure 3.1) with a median biomass of less than 1 gram (mean = 1g; standard error ±0.23 g). The median above-ground biomass of test species under high nutrient conditions was 21 grams (mean = 20g; standard error ±3.62g). The different nutrient regimes also had a significant effect on test species below-ground biomass (Mann-Whitney; $n = 23,23$; $z = 2.45$; $p < 0.05$). Below-ground biomass under high and low nutrient conditions is shown graphically in Figure 3.1. When data for all species were pooled, the median below-ground biomass of test species grown under high nutrient conditions was 59 grams (mean = 60g; standard error ±12.56g), while under low nutrient conditions, it was 6 grams (mean = 11g;

standard error ±3.26g).

These results were not a consequence of competitive interactions under high and low nutrient conditions, as similar effects were noted in the same species grown singly (Figure 3.1). The nutrient treatment had a significant effect on both above-ground biomass (Mann-Whitney; $n = 23,23$; $z = 4.91$; $p<.0001$); and below-ground biomass (Mann-Whitney; $n = 23,23$; $z = 3.60$; $p<.0001$).

When data for all 23 species were pooled, there was also a significant increase in the ratio of below to above-ground biomass allocation under low nutrient conditions (Mann-Whitney; $n = 23,23$; $z = 4.02$; $p< 0.0001$). The median below to above ground ratio was 5.54 (mean = 8.2g; standard error = ±1.43g) under low nutrient conditions and 2.2 (mean = 2.51g; standard error = ±0.27g) under high nutrient conditions. The increased apportionment to below-ground biomass under low nutrient conditions is shown graphically in Figure 3.2.

Intensity of Competition

When the biomass of phytometers grown singly ($n = 10$) was compared with the biomass of phytometers grown with neighbours under high nutrient ($n = 114$) and low nutrient ($n = 107$) conditions, a Kruskal-Wallis one-way analysis of variance by ranks showed that competition had a significant effect on phytometer biomass under both high nutrient conditions ($k = 2$; $H = 19.16$; $p<.0001$) and low nutrient conditions ($k = 2$; $H = 8.76$; $p<.0005$). Though there was therefore a significant competitive effect under each nutrient regime, the intensity of the effect varied between the conditions. Under high nutrient conditions, the phytometer was suppressed by an average 58% as compared to 34% under low nutrient conditions, indicating that competition was less intense under low nutrient conditions (Figure 3.3). When percent reduction in phytometer biomass under high nutrient conditions was compared with percent reduction in phytometer biomass under low nutrient conditions, a Kruskal-Wallis analysis of variance by ranks showed that the treatment effect was significant ($n = 114,107$; $k = 2$; $H = 20.78$; $p<.0001$).

Figure 3.1. Box and whisker plots of the above and below ground biomass for 23 shoreline plant species grown under high and low nutrient regimes. Test species refers to species grown with a phytometer (i.e. with competition). Single species refers to species grown without neighbours (i.e. in the absence of competition) under otherwise identical experimental conditions. The "box" represents data between the upper and lower quartiles (median value indicated as line intersecting box) and the whiskers extend to the upper and lower 95th percentile. Minimum and maximum values are indicated with circles. When data for all 23 species were pooled, biomass under high and low nutrient conditions was significantly different for each of the above conditions as follows: **a)** Mann-Whitney $z = 3.14$; $p < 0.0005$); **b)** Mann-Whitney $z = 2.45$; $p < 0.05$; **c)** Mann-Whitney $z = 4.91$; $p < 0.0001$; and **d)** Mann-Whitney $z = 3.60$; $p < 0.0001$.

Figure 3.1

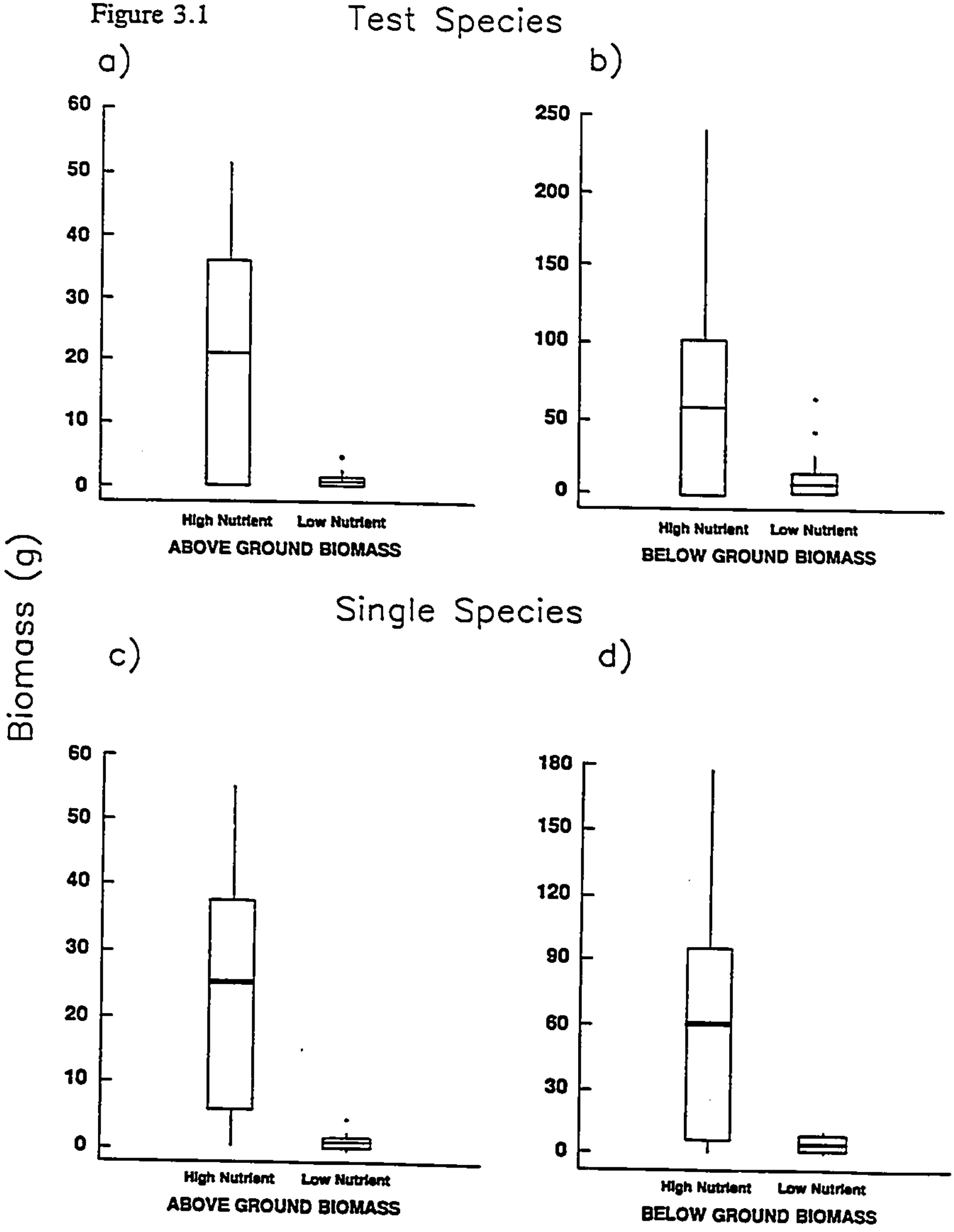

Test Species
a)
60
50
40
30
20
10
0
High Nutrient
Low Nutrient
ABOVE GROUND BIOMASS
b)
250
200
150
100
50
0
High Nutrient
Low Nutrient
BELOW GROUND BIOMASS
Biomass (g)
Single Species
c)
60
50
40
30
20
10
0
High Nutrient
Low Nutrient
ABOVE GROUND BIOMASS
d)
180
150
120
90
60
30
0
High Nutrient
Low Nutrient
BELOW GROUND BIOMASS

Figure 3.2 Box and whisker plots of the ratio of below-ground to above-ground biomass (g/g) for 23 shoreline plant species grown under high and low nutrient regimes. The "box" represents data between the upper and lower quartiles (median value indicated as line intersecting box), and the "whiskers" extend to the upper and lower 95th percentiles. Circles indicate maximum and minimum values. When data for all 23 species were pooled, the ratio of below to above-ground biomass was significantly different between high and low nutrient conditions (Mann-Whitney $z = 4.02$; $p < 0.0001$).

Figure 3.2

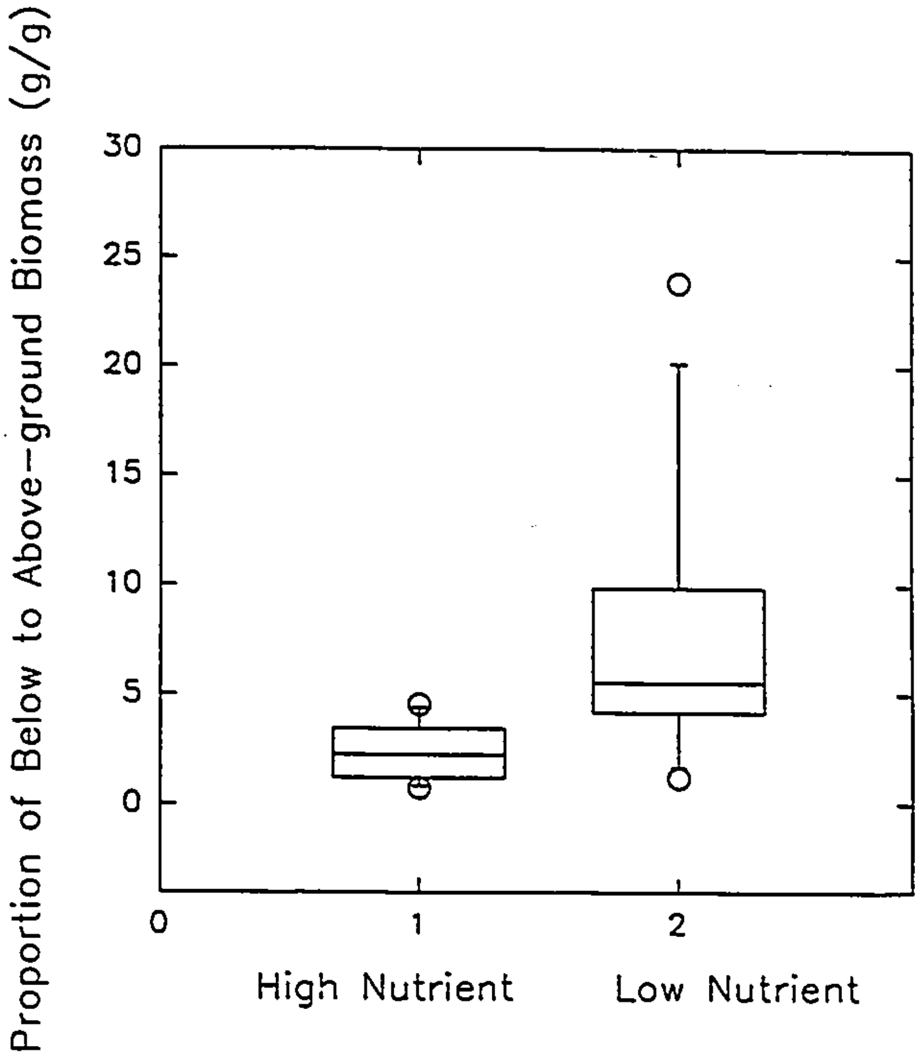
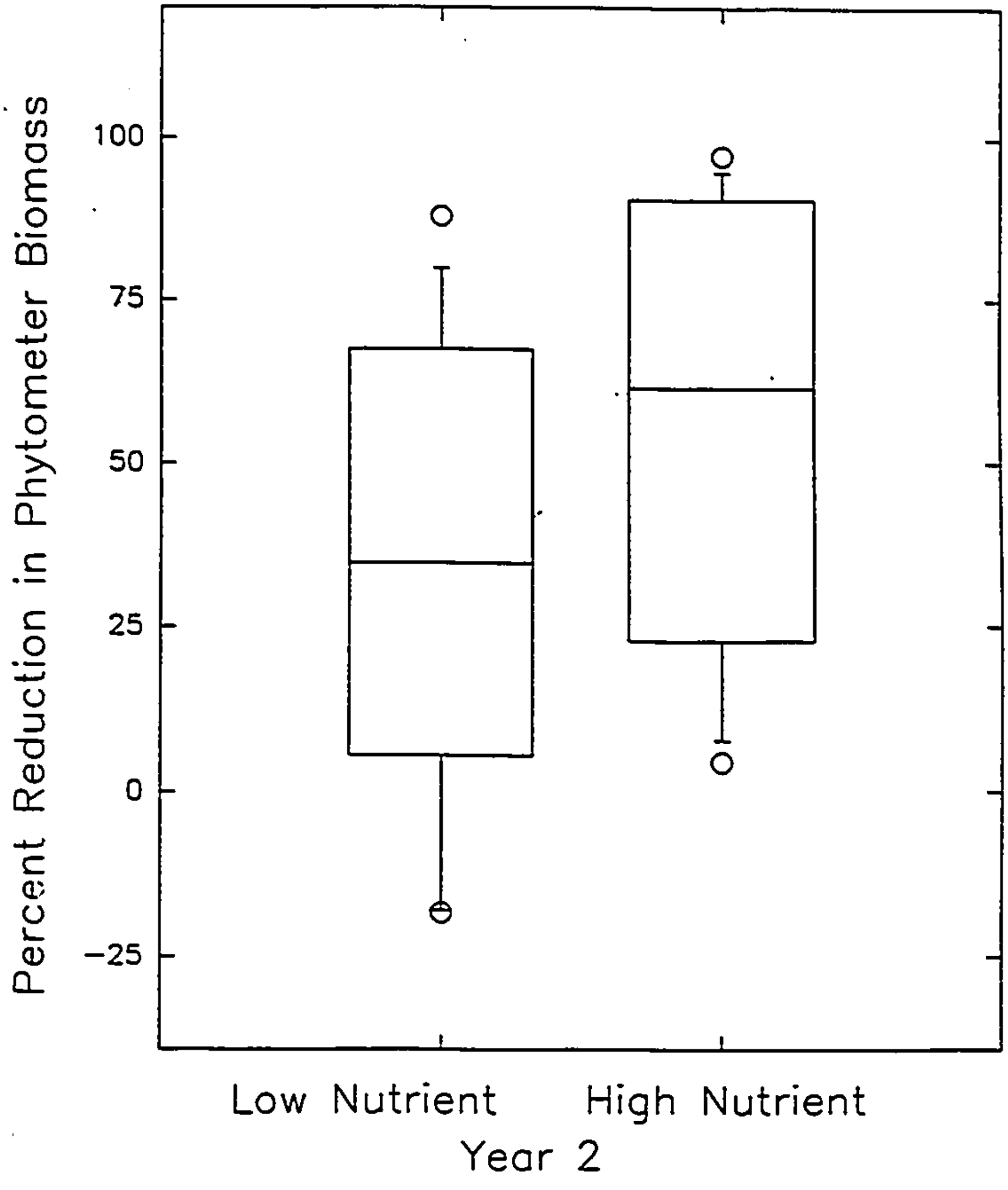

Proportion of Below to Above-ground Biomass (g/g)
30
25
20
15
10
5
0
0
1
2
High Nutrient
Low Nutrient

Figure 3.3 Box and whisker plots of the percent reduction in phytometer biomass when data for all 23 species are pooled under high and low nutrient conditions. The "box" represents data between the upper and lower quartiles (median value indicated as line intersecting box), and the "whiskers" extend to the upper and lower 95th percentile. Circles indicate maximum and minimum values. There is a significant effect of nutrient treatment on percent reduction in phytometer biomass (Kruskal-Wallis analysis of variance by ranks: $n = 114,107$; $k = 2$; $H = 20.78$; $p<.0001$).

Figure 3.3


Percent Reduction in Phytometer Biomass
100
75
50
25
0
−25
Low Nutrient
High Nutrient
Year 2

Competitive Performance

Relative competitive performance in rank order is shown for year 1 and year 2 in Tables 3.1 and 3.2 and graphically in Figure 3.4. In each case, a Kruskal-Wallis analysis of variance by ranks showed that there was a significant species effect on reduction in phytometer biomass (Year 1 low nutrient: $k = 26$; H = 88.99; $p<.0001$; Year 1 high nutrient: $k = 26$, H = 119.23; $p<.0001$; Year 2 low nutrient: $k = 23$; H = 97.44, $P<.0001$; Year 2 high nutrient: $k = 23$; H = 104.13; $p<.0001$). It is therefore reasonable to rank species in terms of relative competitive performance for each year and treatment level.

Competitive performance under high and low nutrient conditions was significantly correlated in both year 1 ($r_s = 0.65$ $p<.005$; n = 26) and year 2 ($r_s = 0.76$; $p<.0005$; n = 23). The relationship between species competitive performance under high and low nutrient levels is shown graphically in Figure 3.5 for each year. When a single outlier (*Rumex verticillatus*) was removed in the analysis for the second year, the r_s increased to 0.84 ($p < 0.001$). This genus is known to be a concentrator of phosphorous and is also anomalous in work done by McJannet, Pick and Keddy (Keddy, *pers. comm.*). *Rumex* sp. was also found to be a significant outlier to the general relationship in a study of competition in mown fields (Fowler 1982).

The relative competitive performance of species was highly correlated between years under high nutrient conditions ($r_s = 0.87$; $p<.001$; n=23; Figure

3.6), suggesting that the hierarchy formed under high nutrient conditions is relatively invariant over time. In contrast, the competitive performance of species under low nutrient conditions shows no significant relationship between years. It may be that under low nutrient conditions, a longer period of time is required to establish a hierarchy and this may explain why the correlation between competitive ability under high and low nutrient conditions is stronger in the second year.

Above versus Below-Ground Performance

The relationships described above were based on above-ground biomass of the phytometer to enable comparison between years. It is possible that the below-ground hierarchy is important, especially under low nutrient conditions. However, phytometer biomass (a direct measure of competitive performance) is highly correlated above and below-ground both under high nutrient conditions ($r_s = 0.94$; $p < .00001$; $n = 23$) and low nutrient conditions ($r_s = 0.71$; $p < .001$; $n = 23$).,

It is also possible that test species traits contribute differently to competitive performance above and below-ground (see Chapter 2). The experiment was not designed to test this directly. However, biomass measures made on the test species at the time of harvest were available for analysis. Table 3.3 summarizes the relationship between test species biomass and competitive performance above and below-ground. Under high nutrient conditions, the above-ground biomass of the test species is highly correlated with phytometer biomass both above and below ground. In contrast, no single measured trait is highly correlated with below-ground competitive performance under low nutrient conditions. This may suggest that below-ground biomass of the phytometer biomass varies independently of competitive performance under low nutrient conditions and is consistent with earlier results showing that species generally allocate a higher proportion of biomass below-ground under low nutrient conditions.

Table 3.1. Relative competitive performance and standard deviation (in brackets) for 26 shoreline plant species (in rank order) under high and low nutrient conditions after one growing season. Relative competitive performance was estimated as the percent reduction in above-ground biomass of a common phytometer *Penthorum sedoides* (5 replicates per species).

Year 1			
High nutrient		Low nutrient	
Species	**% Reduction in phytometer biomass**	**Species**	**% Reduction in phytometer biomass**
Lythrum salicaria	96 (1.40)	*Sparganium eurycarpum*	57 (5.16)
Bidens cernua	94 (2.31)	*Typha xglauca*	56 (5.36)
Sparganium eurycarpum	94 (2.68)	*Spartina pectinata*	55 (11.82)
Typha xglauca	93 (4.26)	*Bidens cernua*	52 (13.48)
Mentha arvensis	88 (8.15)	*Eleocharis calva*	52 (15.82)
Scirpus fluviatilis	86 (6.63)	*Eleocharis acicularis*	48 (13.86)
Rumex verticillatus	86 (5.16)	*Eleocharis palustris*	46 (14.49)
Phragmites communis	82 (6.40)	*Scirpus fluviatilis*	45 (10.38)
Phalaris arundinaceae	78 (7.64)	*Acorus calamus*	44 (8.84)
Spartina pectinata	77 (4.44)	*Phragmites communis*	40 (13.16)
Acorus calamus	73 (2.31)	*Rumex verticillatus*	37 (18.24)
Eleocharis palustris	50 (8.78)	*Juncus filiformis*	35 (7.76)
Euthamia galetorum	48 (4.63)	*Carex crinita*	34 (8.00)
Eleocharis calva	45 (18.28)	*Phalaris arundinaceae*	31 (20.76)
Carex crinita	43 (7.72)	*Mentha arvensis*	29 (11.63)
Dulichium arundinacea	30 (13.44)	*Lythrum salicaria*	29 (12.90)
Eleocharis acicularis	22 (8.84)	*Ranunculus reptans*	24 (12.75)
Triadenum fraseri	19 (4.70)	*Triadenum fraseri*	19 (10.66)
Lysimachia terrestris	19 (5.48)	*Viola lanceolata*	19 (11.37)
Ranunculus reptans	19 (3.78)	*Hypericum ellipticum*	15 (16.30)
Juncus pelocarpus	15 (11.70)	*Lysimachia terrestris*	14 (17.13)
Juncus filiformis	11 (11.24)	*Scirpus torryei*	1 (16.10)
Viola lanceolata	6 (16.42)	*Juncus pelocarpus*	-1 (10.64)
Hypericum ellipticum	4 (10.4)	*Dulichium arundinaceaw*	-1 (15.23)
Lobelia dortmanna	1 (5.70)	*Lobelia dortmanna*	-5 (15.30)
Scirpus torreyi	-4 (2.56)	*Euthamia galetorum*	-5 (9.82)

Table 3.2. Relative competitive performance and standard deviation (in brackets) for 23 shoreline plant species (in rank order) under high and low nutrient conditions after two growing seasons. Relative competitive performance was estimated as the percent reduction in above-ground biomass of a common phytometer *Penthorum sedoides*. Numbers of species vary between years due to overwinter mortality (*R. reptans*, *L. dortmanna*) or because the species was an annual (*B. cernua*).

Year 2			
High nutrient		Low nutrient	
Species	**Reduction in phytometer biomass (%)**	**Species**	**Reduction in phytometer biomass (%)**
Typha xglauca	99 (0.8)	*Lythrum salicaria**	95 (4.68)
Spartina pectinata	97 (1.16)	*Phalaris arundinaceae*	84 (4.70)
Phalaris arundinaceae	94 (3.06)	*Spartina pectinata*	79 (16.90)
*Phragmites communis**	92 (7.63)	*Typha xglauca*	78 (5.47)
Scirpus fluviatilis	92 (2.48)	*Euthamia galetorum**	69 (5.50)
Sparganium eurycarpum	91 (2.31)	*Mentha arvensis*	69 (12.56)
Mentha arvensis	90 (5.77)	*Acorus calamus*	63 (5.40)
Lythrum salicaria	89 (4.75)	*Phragmites communis*	58 (7.39)
Euthamia galetorum	88 (4.87)	*Juncus filiformis*	56 (8.24)
Rumex verticillatus	83 (6.46)	*Eleocharis palustris**	39 (10.20)
Acorus calamus	74 (12.22)	*Sparganium eurycarpum*	39 (13.50)
Eleocharis calva	62 (14.66)	*Eleocharis calva**	35 (10.24)
Eleocharis palustris	61 (17.76)	*Lysimachia terrestris*	32 (16.00)
Lysimachia terrestris	53 (11.32)	*Dulichium arundinaceum*	24 (10.93)
Carex crinita	46 (12.64)	*Scirpus fluviatilis*	23 (6.48)
Juncus filiformis	34 (5.87)	*Triadenum fraseri*	17 (15.05)
Dulichium arundinaceum	25 (5.52)	*Carex crinita*	7 (13.00)
Hypericum ellipticum	22 (12.60)	*Viola lanceolata**	5 (14.53)
Eleocharis acicularis	17 (10.99)	*Juncus pelocarpus*	-15 (12.84)
Juncus pelocarpus	10 (8.07)	*Hypericum ellipticum*	-16 (9.17)
Triadenum fraseri	8 (2.96)	*Eleocharis acicularis**	-18 (9.20)
Viola lanceolata	6 (4.40)	*Rumex verticillatus*	-18 (17.81)
Scirpus torryei	1 (21.02)	*Scirpus torreyi**	-19 (16.79)

* 4 replicate (all others have five replicates)

Figure 3.4 Box and whisker plot of the relative competitive performance of shoreline plant species grown under **A)** low nutrient conditions: year 1; **B)** high nutrient conditions: year 1; **C)** low nutrient conditions: year 2; and **D)** high nutrient conditions: year 2. The central "box" covers the middle 50% of the data values, between the upper and lower quartiles, the "whiskers" extend to minimum and maximum values. Rank order corresponds to the order of species for each year and condition as indicated in Tables 3.1 and 3.2, such that the species to the extreme left on each graph is the highest ranked species for the corresponding year and treatment in the tables.

Figure 3.4

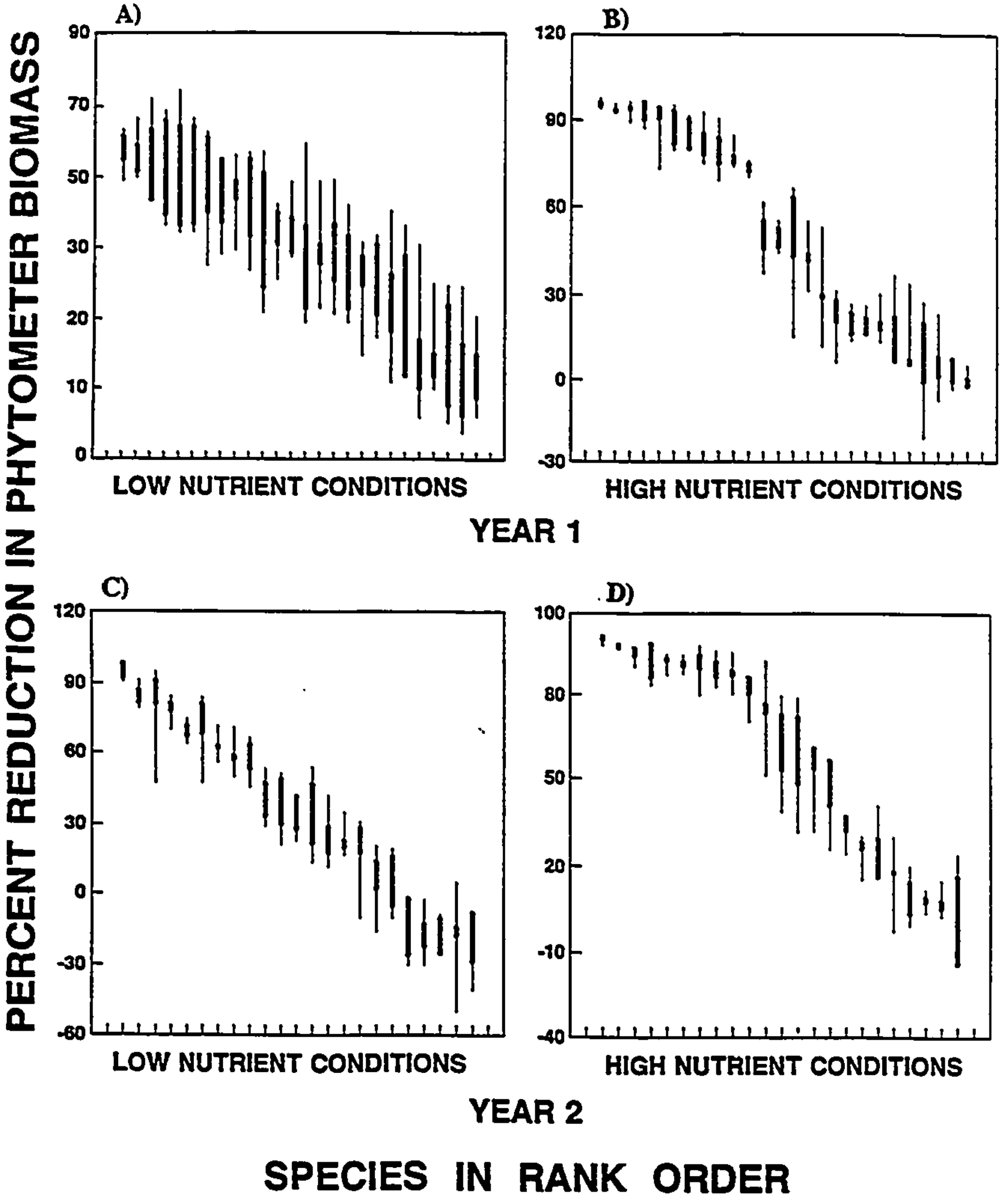

A)
B)
C)
D)
PERCENT REDUCTION IN PHYTOMETER BIOMASS
90
70
50
30
20
10
0
120
90
60
30
0
-30
LOW NUTRIENT CONDITIONS
HIGH NUTRIENT CONDITIONS
YEAR 1
120
90
60
30
0
-30
-60
100
80
50
20
-10
-40
LOW NUTRIENT CONDITIONS
HIGH NUTRIENT CONDITIONS
YEAR 2
SPECIES IN RANK ORDER

Figure 3.5. Relationship between competitive performance under low nutrient conditions and competitive performance under high nutrient conditions **a)** Year 1 results ; **b)** Year 2 results. Species names are indicated for year 2 results only as follows:1 - *Lythrum salicaria*; 2 - *Phalaris arundinacea*; 3 - *Phragmites communis*; 4 - *Typha xglauca*; 5 - *Euthamia galetorum*; 6 - *Mentha arvensis*; 7 - *Acorus calamus*; 8 - *Spartina pectinata*; 9 - *Juncus filiformis;* 10 - *Lysimachia terrestris*; 11 - *Eleocharis palustris*; 12 - *Eleocharis calva*; 13 - *Sparganium eurycarpum*; 14 - *Scirpus fluviatilis*; 15 - *Triadenum Fraseri*; 16 - *Dulichium arundinaceum*; 17 - *Carex crinita*; 18 - *Viola lanceolata*; 19 - *Scirpus Torreyi*; 20 - *Juncus pelocarpus*; 21 - *Eleocharis acicularis*; 22 - *Hypericum ellipticum*; 23 - *Rumex verticillatus.*

Figure 3.5

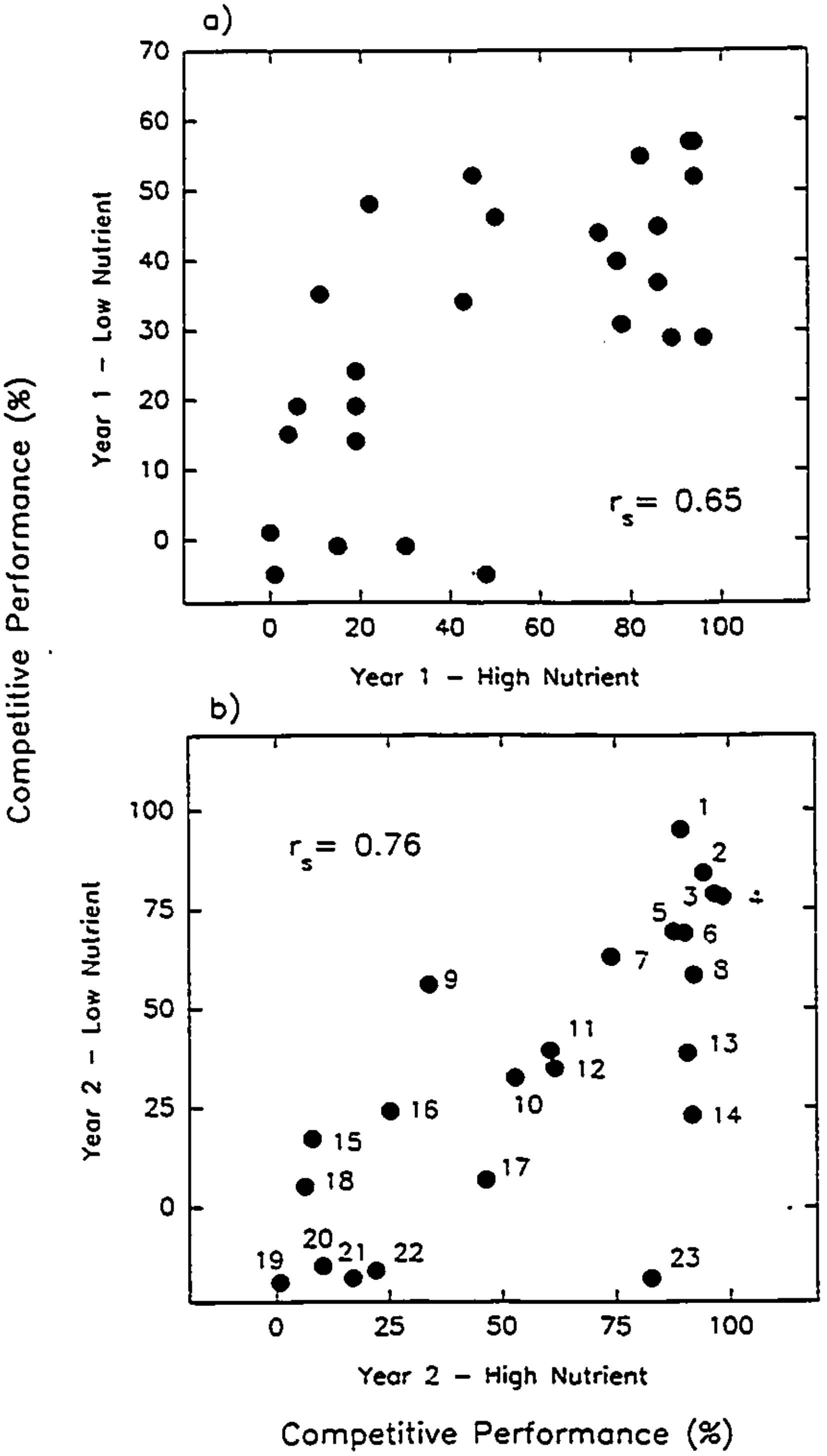

a)
70
60
50
40
30
20
10
0
Year 1 - Low Nutrient
0
20
40
60
80
100
Year 1 - High Nutrient
r_s= 0.65
b)
100
75
50
25
0
Year 2 - Low Nutrient
0
25
50
75
100
Year 2 - High Nutrient
r_s= 0.76
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
Competitive Performance (%)
Competitive Performance (%)

Figure 3.6 Relationship between mean competitive performance of species (n = 23 species) over two growing seasons under **a)** high nutrient conditions; and **b)** low nutrient conditions.

Figure 3.6

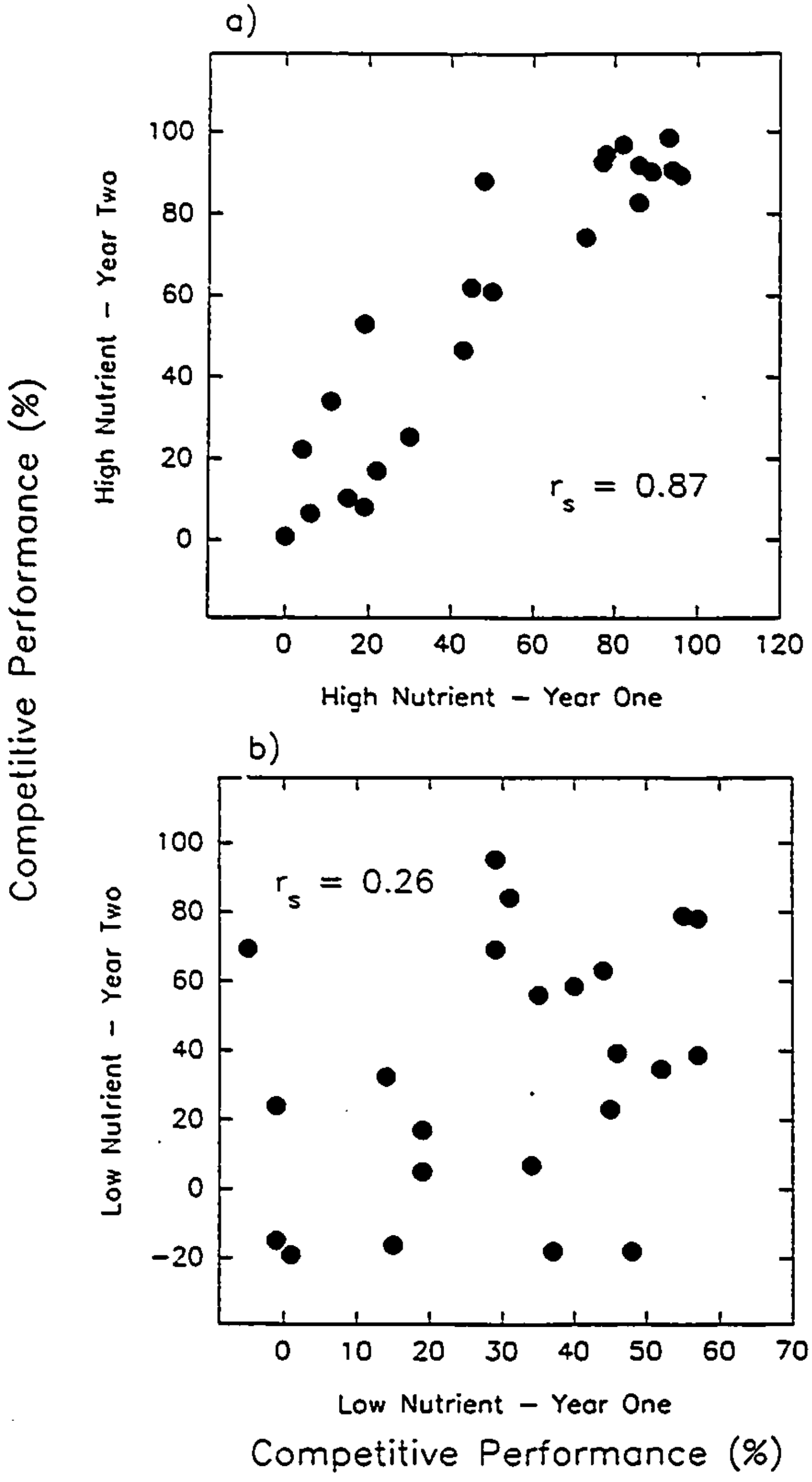

a)
High Nutrient – Year Two
100
80
60
40
20
0
0
20
40
60
80
100
120
High Nutrient – Year One
r_s = 0.87
b)
Low Nutrient – Year Two
100
80
60
40
20
0
−20
0
10
20
30
40
50
60
70
Low Nutrient – Year One
r_s = 0.26
Competitive Performance (%)
Competitive Performance (%)

Table 3.3 Spearman rank correlation (r_s) between above and below-ground biomass of the phytometer (*Penthorum sedoides*) and above and below-ground biomass of test species (n=23) under high and low nutrient conditions. Phytometer biomass is a direct measure of the competitive effect of a species.

		Phytometer Biomass (g)			
		High Nutrient		Low Nutrient	
		above	below	above	below
Test Species Biomass (g)					
High Nutrient	**above**	-.91 p<.00001	-.85 p=.0001	-.72 p=.0007	-.47 p=.0279
	below	-.88 p<.00001	-.84 p=.0001	-.53 p=.0123	-.40 p=.0585
Low Nutrient	**above**	-.88 p<.00001	-.83 p=.0001	-.69 p=.0012	-.56 p=.0082
	below	-.80 p=.0002	-.80 p=.0002	-.56 p=.0086	-.53 p=.0133

DISCUSSION

Competitive Performance

Although shifts in ranking of species were apparent between high and low nutrient conditions, there were repeated, predictable patterns at the multi-species scale and statistical comparison between treatments indicated that there was a significant positive relationship between species' competitive performance at high and low fertility. In general, irrespective of nutrient level, large, leafy species typical of fertile habitats (e.g., *Lythrum salicaria*, *Sparganium eurycarpum*, *Typha xglauca*) emerged near the top of the hierarchy as would be predicted from other studies (Day *et al.* 1988; Keddy 1983). Small rosette species (*Lobelia dortmanna*, *Viola lanceolata*) and partially evergreen species typical of infertile habitats (*Juncus pelocarpus*, *Eleocharis acicularis*, *Ranunculus reptans*) are near the bottom of the hierarchy, which is consistent with other studies (Givnish 1988; Wilson and Keddy 1986b; Goldsmith 1978). Therefore, the main axis appears to represent growth form, which in turn varies with habitat.

My study was not set up to explore mechanisms underlying competitive performance. However, these patterns in size suggest a mechanistic interpretation. Large plants have larger surface areas for extracting resources from the environment, and therefore also have a greater ability to create nutrient depletion zones irrespective of resource levels. In the case of light, large plants, being generally taller, can intercept light, thereby denying it to smaller neighbours (Keddy and Shipley 1988). Superimposed on this may be differences in nutrient uptake rates per unit surface area, or differences in efficiency of use or conservation, which contribute to the residual variation.

It is also noteworthy that there are obvious shifts in species competitive performance between years 1 and 2 under low nutrient conditions. One possible interpretation is that under low fertility conditions, position in the competitive hierarchy is more variable. This would be consistent with suggestions that under fertile conditions, competitive hierarchies tend to result from strong asymmetric competition for light (Keddy 1989). Asymmetrical competition is characterized by a strong dominance and suppression interaction with a clear winner and loser. In contrast, under infertile conditions, root competition may predominate, in which case competition may be more symmetric (Weiner 1986). Where competition is symmetric, there is no pronounced dominance/suppression. Under these conditions, shifts in competitive rankings may result from the fact that there is no asymmetric advantage that is maintained and enhanced over time.

The reduced intensity of competition under low nutrient conditions may be also be important in accounting for shifts in ranking, As competition intensity decreases, other factors unrelated to competition may become increasingly important as determinants of plant biomass. However, an alternative explanation is that under conditions of low fertility, plants may simply take longer to establish a hierarchy. In this case it may be significant that the correlation between high and low fertility increased from over the course of the experiment.

Results of this experiment do not support the view that root and shoot competition vary independently as suggested by Wilson (1988), at least for shoreline plant species. However, root and shoot competition were not studied independently in this study. It may be, that if species were prevented from competing above-ground, results of below-ground competition alone would have resulted in a different hierarchy. Whether competitive ability varies below and above -ground under varying conditions remains to be tested for shoreline communities.

Contingency and Scale

The simple dichotomy between contingency and invariance of competitive ability I posed in the introduction is misleading. Rather than diametrically opposed world views, the contrasting views about competitive ability and contingency appear to represent research at two different scales. In understanding the implications of results, it is important to distinguish between coarse and fine scale relationships. The current study was designed to explore general, coarse scale pattern across a large number of species and habitats. Fine scale work on small numbers of species can emphasize contingency and miss general predictive relationships. In fact, one could argue that the past emphasis upon contingency arises because experiments using a few pairs of species in varied environments were only capable of detecting contingency; the nature and scale of the experiment may have predetermined the outcome. Contingency at the level of pair-wise interactions may explain fine scale pattern in the field. It has been suggested that equivalence in competitive performance is likely to foster coexistence of species (Aarson 1983; 1985). It is at this scale, where competitive interactions may be increasingly symmetrical (*sensu* Wilson 1988; Keddy 1989) that contingency may be most pronounced, and minor fluctuations in the environment may have a major influence on dominance in the field.

Though coarse scale work can provide general predictive relationships, it may overlook the details of species interactions that contribute to understanding of fine scale pattern and mechanism in the field. Therefore though the current results show that at the broad community scale, the outcome of competitive interactions may be relatively predictable independent of the environment, these results cannot address questions related to the outcome of competitive interactions between similar species or fine scale pattern. Further empirical work is needed to sort out the factors that may be operating at different scales of organization.

Intensity of Competition

My results also indicate that the intensity of competition is reduced by approximately 25% relative to fertile conditions. Similar results have been noted for shoreline plant communities by Wilson and Keddy (1986a) in a study of diffuse competition in the field. This supports the general hypothesis (Grime 1979; Huston, 1979) that under infertile conditions, factors other than competition may become increasingly important in structuring natural communities. The supposition that competition becomes more intense or important as resources are increasingly limited (Fowler 1986) is not supported by these results.

The results were based on a comparison of only two nutrient levels, and it is not known how results would have varied with different nutrient regimes. However, the experimental conditions clearly had a significant effect on species productivity and biomass allocation. It is therefore reasonable to assume that the two nutrient levels created very different environments. We do not know how these results would have changed over a longer period of time. Tilman (1988) and Berendse and Elberse (1990) show that time-span may be an important consideration when evaluating competitive ability.

It may be that other environmental variables unrelated to nutrients will exert influences on plant hierarchies. There can be no clear answer to this question until more studies are carried out at the community scale. There are so few studies using large numbers of species in contrasting environments that generalization about the invariance of competitive hierarchies is not yet possible. The phytometer approach makes such studies more feasible than past pair-wise designs which increased the size of experiments by the square of the number of species examined. It may be that different patterns will emerge if different floras are examined. If wetlands are generally light limited, then it may be that hierarchies are produced by different competitive abilities for light based on above-ground traits. Perhaps other habitats such as prairies and deserts are different. Hierarchies there may be associated with below-ground traits. Such ideas remain speculative until the comparative studies are carried out.

CHAPTER 4

STRESS TOLERANCE AND COMMUNITY PATTERN

... it is better to deal incompletely with the whole than wholly with the incomplete...

Herman Daly, World Bank (undated)

Abstract

I tested the general hypothesis that stress tolerance is an important determinant of pattern in natural shoreline plant communities. This study addressed three specific predictions related to this general question 1) stress tolerance of species varies predictably along natural gradients of nutrient stress and productivity; 2) there is an "evolutionary trade-off" (i.e. an inverse relationship), between the stress tolerance of species and competitive performance under optimal conditions; and 3) the relative below to above-ground biomass allocation of species is predictably related to nutrient stress tolerance and the distribution of species along nutrient gradients. The study was designed to address these questions at a scale that enables broad generalization. The stress tolerance of 21 shoreline plant species was experimentally determined as the relative biomass accumulation of species grown under high and low nutrient conditions over two growing seasons. Two measures of stress tolerance or sensitivity were calculated for each species: 1) the relative decrease in biomass under low nutrient (stressed) conditions as compared to performance under high nutrient (optimal) conditions; and 2) the relative biomass accumulation of species under low nutrient conditions. Relative biomass production under high nutrient conditions, and the below to above-ground biomass ratio, was also calculated for each species. These measures of stress tolerance were then compared with experimentally determined measures of the relative competitive performance for the 21 species, and the mean position of each species along standing crop, percent soil organic content,

nitrate, and phosphorous gradients, using field distribution data from lake and river shoreline plant communities in Ontario, Nova Scotia, and Quebec (Canada). Measures of stress tolerance based on relative differences in performance under high and low nutrient conditions, or on direct measures of growth under high nutrient conditions were not significantly correlated with either field distribution or competitive performance. Only the measure of stress tolerance based on relative biomass production under low nutrient conditions was significantly correlated with measures of field distribution or relative competitive performance. This may in part be explained by the fact that most species showed a shared response to increased fertility. This response may be generally adaptive in disturbed, shoreline plant communities.

INTRODUCTION

The relative competitive performance of shoreline plant species has been shown to be correlated with their mean position on nutrient gradients in the field (Chapter 1). Further, the relative competitive performance of these species has been found to be relatively invariant with respect to changing nutrient supplies (Chapter 3). Therefore, it seems unlikely that shifts in competitive dominance under conditions of different nutrient availability provide an adequate explanation of why some species dominate in nutrient stressed habitats. A basic premise of competition theory as proposed by Grime (1979) is that there are evolutionary trade-offs between competitive ability under high nutrient conditions and stress tolerance such that in unproductive habitats, species of high competitive ability will be replaced by plants which are capable of tolerating the prevailing stress. There is some support for this theory (e.g., Grace and Wetzel 1981; Colwell and Fuentes 1975). Other authors (Tilman 1990) suggest that stress tolerance is an important determinant of dominance in nutrient poor environments, though environmental stresses are seen largely as external constraints that determine which species are most "competitive" in a given environment (Oksanen 1990; Ellenberg and Meuller-Dombois 1974). Notwithstanding differences in presumed underlying mechanisms, tolerance to low resource levels, or traits associated with efficiency of resource capture under nutrient stress, should be important determinants of community pattern.

Despite the presumed importance in community theory, few studies have tried to measure stress tolerance or determine its relationship with either natural distribution patterns or measures of relative competitive ability. There is only indirect evidence of the suggested trade-off for a sufficiently large number of species to enable generalization (Shipley and Keddy 1988) and this study examined only seedling traits. Studies linking pattern in the field to measures presumably related to stress tolerance have typically dealt with only a few species or provide only inferential evidence based on traits presumed to be linked with stress tolerance (e.g., Tilman and Wedin 1991; Oksanen 1990).

Progress in understanding the importance of stress tolerance at the community scale requires an approach which enables the simultaneous examination of a large number of species (Keddy 1992). In this study, a comparative approach based on the systematic screening for plant traits, is used to examine the relationship between species' response to nutrient stress, competitive performance and distribution in the field (Gaudet and Keddy 1988).

Specifically, I tested the following predictions: 1) nutrient stress tolerance/sensitivity (*sensu* Shipley and Keddy 1989) in adult plants is related to their distribution along natural fertility gradients; 2) nutrient stress tolerance/sensitivity is inversely related to relative competitive performance; and 3) Below:above ground biomass allocation is related to stress tolerance, and/or distribution of species along natural environmental gradients in the field.

METHODS

The measurement of relative competitive performance and field distribution is described in Chapter 1. To evaluate the relationship of these variables to stress tolerance, a "bioassay" (*sensu* McCanney *et al.* 1990) of stress tolerance was also needed. Grime (1979) defines stress as "the external constraints which limit the rate of dry matter production of all or part of the vegetation". A bioassay based on the effect of nutrient stress on relative biomass production was used as a simple measure of stress tolerance. A gradient of nutrient concentration was established using a modified Hoagland's solution. Two concentrations were used - a full-strength solution (high nutrient) and one-tenth of this concentration (low nutrient).

Experimental Procedure

Twenty-one species of emergent macrophytes typical of lake and riverine shorelines in north-eastern North America, were used in the experiment. Ramets of each species were collected in April 1987, just prior to emergence, from the shoreline areas described in Chapter 1. Individual ramets, selected for uniformity in size were planted centrally in 1 litre pots filled with sand (n = 10 replicates per species). Ten ramets of each species were also selected and dried to constant weight for determination of initial biomass. All other experimental procedures are as described in the Methods section of Chapter 3.

Measures of Stress Tolerance/Sensitivity

Four measures of stress tolerance/sensitivity were explored in this study:

1) **Stress Sensitivity** - Stress can be measured as the decrease in concentration of resource levels from the optimal level (▲C). Sensitivity to stress can be measured as the decrease in relative growth (biomass production) from its optimum (▲B) such that a value of zero indicates that growth is not affected by a decrease in resource levels and the species is not sensitive to the stress (Shipley and Keddy 1988). Because species were grown for the same time period and under identical nutrient levels (▲C), sensitivity was simply expressed as biomass production under low nutrient conditions relative to high nutrient conditions as follows:

$$S = \frac{(B_{it2}-B_{it1})^{H} - (B_{it2}-B_{it1})^{L}}{(B_{it2}-B_{it1})^{H}}$$

where S = sensitivity to nutrient stress; B_{it} = biomass (g) of species **i** at time **t** under high **(H)** or low **(L)** nutrient conditions, **t1** = starting biomass (g), and **t2** = biomass (g) at end of the second growing season. Using this equation, values of S = 0 would represent species that grew equally well under high and low nutrient conditions, and values of S greater than zero would indicate species that are increasingly sensitive to reduced nutrient levels. Starting biomass of species is included in Appendix 4.1.

2) Stress Tolerance - The above measure of sensitivity is based on a comparison of performance under optimal versus stressed conditions. Stress tolerance was also measured directly as relative biomass production (RBP) under low nutrient (stressed) conditions. This provides a measure of intrinsic differences in species' performance under infertile conditions. Typically, maximum relative growth rate (R*max*) is used as a comparative measure of the relative rate of biomass accumulation across species (e.g., Shipley and Keddy 1988; Shipley and Peters 1990). Here, relative biomass production was determined as the relative or proportional increase/decrease in biomass over the second growing season as follows:

$$\mathbf{RBP} = \frac{\mathbf{B}_{it2} - \mathbf{B}_{it1}}{\mathbf{B}_{it2}}$$

Where **RBP** = relative biomass production; $\mathbf{B}_{it2}$ = biomass of species **i** at time **t**; and **t1** = biomass at the end of the first growing season and **t2** = biomass at the end of the second growing season. Calculations were performed for above-ground biomass to enable comparison between years.

3) Relative Growth Under Optimal Conditions - Stress tolerant species are also assumed to exhibit low maximal growth rates (R*max*) under optimal conditions (e.g., Tilman 1990; Grime 1979), and therefore, similar measurements were made on the same species grown under high nutrient conditions. Both of these measures were then used to explore possible relationships between mean position on the environmental gradient and relative competitive performance.

4) **Below:Above Ratios** - It has been suggested that the allocation of photosynthetic to non-photosynthetic tissue is important under conditions of nutrient stress (Oksanen 1990; Tilman 1988, 1987; Chapin and Shaver 1985). The ratio of below to above-ground biomass could therefore serve as a simple, measurable surrogate of stress tolerance. Because all species were herbaceous perennials without woody tissue, root:shoot ratios (photosynthetic to non-photosynthetic tissue), were calculated simply as the ratio of below to above-ground biomass for each species. To enable comparison across species, the relative change in biomass was also calculated as the below:above ratio under low nutrient conditions divided by the below:above ratio under high nutrient conditions. This provides a simple measure of the relative increase in the below-to above ground ratio for a species such that values greater than 1 represent increasingly greater apportionment below-ground under low nutrient conditions.

Relative Competitive Performance

Relative competitive performance, expressed as percent reduction in phytometer biomass, was calculated for each species and nutrient level as described in Chapter 3.

Field Distribution

The mean position of each species along natural environmental gradients (standing crop; nitrate, phosphorous, percent soil organic content) was calculated from 217 quadrats as described in Chapter 1.

Data were transformed as indicated in the results and Pearson's r was used to test for a correlation between stress tolerance and position on the standing crop gradient and relative competitive performance. All analysis was performed using **StatsGraph**^{R} statistical software package (Version 4.1).

RESULTS

Stress Sensitivity

In general, all species showed a marked response to decreasing nutrient levels both above and below-ground (Tables 4.1 and 4.2). Values could be expected to range between 0 and +1 with scores of 0 representing no sensitivity to nutrient stress and +1 representing species that were extremely sensitive to nutrient stress (values less than zero are also theoretically possible and would represent species that grew better under nutrient stressed conditions). Results showed that of the 21 species, only *Eleocharis acicularis*, a small (approximately 3 cm in height), partly evergreen species was unaffected by the decreased nutrient supply. Of the remaining 20 species, 19 species had values between 0.80 and 0.98 and one (*T. xglauca*) had a value of 0.70, indicating that most species are sensitive to nutrient stress.

Stress Tolerance (RBP)

Relative biomass production (RBP) under both high and low nutrient conditions is shown in Table 4.3. Species showed a broad range in response to low nutrient conditions. Several species (i.e. *T. xglauca*, *S. eurycarpum*, *L. salicaria*, *M. arvensis*, *P. arundinacea*, *R. verticillatus*, *S. fluviatilis*, *S. pectinata*) actually showed a negative growth response in that they had values of less than zero. These species can be considered intolerant of nutrient stress over the two year period of this experiment in that they did not replace tissue lost to senescence after the first growing season.

Ratio of Below to Above-ground Biomass

In general, species exhibited an increased allocation of biomass below-ground in response to nutrient stress (Table 4.4). When data for all 21 species were pooled, the difference in the proportion of below to above-ground biomass is significantly higher under low nutrient conditions (Mann-Whitney test; $n = 21$; $z = -2.77$; $p<.001$). The relative change in below:above-ground biomass under high and low nutrient conditions is shown in Table 4.4. Only 4 of the species showed little or no response to decreased nutrient supply (*E. acicularis*, *H. ellipticum*, *T. fraseri*, *E. galetorum*). Three of these species spread vegetatively by above-ground stolons) and are typically found in nutrient stressed habitats (Wisheu and Keddy 1988).

Table 4.1 Above-ground biomass (standard deviation), of twenty-one herbaceous shoreline plant species grown under high and low nutrient conditions produced by Hoagland's solution full-strength or diluted X 10. Unless indicated by an *, the biomass under the two different nutrient regimes is significantly different for each species ($n=5$; $p < 0.05$). Relative decrease = the biomass reduction under low nutrient conditions as a proportion of the biomass under high nutrient conditions

SPECIES	**BIOMASS (g)**		**RELATIVE DECREASE**
	High Nutrient	**Low Nutrient**	
Acorus calamus	35.64 (12.44)	1.58 (0.31)	0.96
Carex crinita	38.11 (10.88)	0.90 (0.30)	0.98
Dulichium arundinaceum	12.00 (1.56)	0.37 (0.08)	0.97
Eleocharis acicularis	0.60 (0.40)	0.57 (0.33)	0.05*
Eleocharis calva	24.00 (7.18)	1.07 (0.13)	0.96
Hypericum ellipticum	3.40 (2.61)	0.15 (0.04)	0.96
Juncus filiformis	15.23 (8.35)	0.60 (0.15)	0.96
Juncus pelocarpus	4.46 (1.97)	0.11 (0.08)	0.98
Lythrum salicaria	39.68 (8.92)	1.47 (0.27)	0.96
Lysimachia terrestris	21.99 (8.82)	1.10 (0.25)	0.95
Mentha arvensis	29.05 (8.91)	0.76 (0.65)	0.97
Phalaris arundinacea	54.35 (12.43)	1.60 (0.87)	0.97
Rumex verticillatus	32.40 (10.41)	1.34 (0.47)	0.96
Scirpus fluviatilis	37.60 (2.28)	1.26 (0.61)	0.97
Scirpus torreyi	5.97 (2.47)	0.09 (0.05)	0.98
Euthamia galetorum	37.98 (10.93)	0.86 (0.28)	0.98
Sparganium eurycarpum	25.62 (8.26)	0.57 (0.24)	0.98
Spartina pectinata	35.44 (4.19)	0.86 (0.22)	0.97
Triadenum fraseri	5.26 (2.50)	0.20 (0.02)	0.96
Typha xglauca	54.76 (16.02)	4.49 (1.03)	0.92
Viola lanceolata	0.79 (0.62)	0.07 (0.02)	0.91

Table 4.2 Below-ground biomass (standard deviation) of twenty-one herbaceous shoreline plant species grown under high and low nutrient conditions (Hoagland's solution full-strength or diluted X 10). Unless indicated by an *, the biomass under the two different nutrient regimes is significantly different for each species ($n=5$; $p < 0.05$). Relative decrease = the biomass reduction under low nutrient conditions as a proportion of the biomass under high nutrient conditions

SPECIES	BIOMASS (g)		RELATIVE DECREASE
	High Nutrient	Low Nutrient	
Acorus calamus	59.30 (10.47)	8.40 (0.40)	0.86
Carex crinita	138.93 (69.68)	3.40 (1.51)	0.98
Dulichium arundinaceum	19.04 (1.40)	0.94 (0.44)	0.96
Eleocharis acicularis	0.62 (0.20)	0.80 (0.41)	-0.30*
Eleocharis calva	72.46 (16.58)	7.98 (4.83)	0.89
Hypericum ellipticum	6.59 (2.73)	0.12 (0.05)	0.98
Juncus filiformis	75.60 (21.60)	5.67 (2.22)	0.93
Juncus pelocarpus	3.32 (1.05)	0.33 (0.20)	0.90
Lythrum salicaria	40.57 (13.12)	7.21 (4.37)	0.82
Lysimachia terrestris	36.81 (9.60)	1.30 (0.63)	0.96
Mentha arvensis	25.68 (14.75)	0.12 (0.07)	0.99
Phalaris arundinaceae	120.15 (40.91)	9.15 (4.06)	0.93
Rumex verticillatus	94.45 (16.29)	8.47 (1.64)	0.91
Scirpus fluviatilis	173.10 (41.20)	6.49 (2.64)	0.96
Scirpus torreyi	6.05 (1.76)	1.16 (1.45)	0.80
Euthamia galetorum	94.57 (25.76)	1.45 (0.49)	0.98
Sparganium eurycarpum	72.17 (22.74)	8.13 (6.39)	0.89
Spartina pectinata	75.07 (23.74)	5.36 (1.23)	0.93
Triadenum fraseri	5.94 (2.93)	0.29 (0.09)	0.95
Typha xglauca	176.03 (28.74)	49.78 (12.37)	0.71
Viola lanceolata	0.41 (0.17)	0.01 (0.01)	0.98

Table 4.3 Relative biomass production of plant species (n = 21 species) under high and low nutrient conditions. Results are from the second growing season. Relative biomass production = the proportional increase or decrease in biomass (g. dry weight) over the second growing season. Under low nutrient conditions, this is considered as a measure of relative stress tolerance.

Species	**Relative Biomass Production**	
	Low Nutrient	**High Nutrient**
Acorus calamus	0.33	0.99
Carex crinita	0.17	1.76
Dulichium arundinaceum	0.19	-0.70
Eleocharis acicularis	0.98	0.18
Eleocharis calva	1.39	0.95
Euthamia galetorum	0.58	1.27
Hypericum ellipticum	0.56	1.00
Juncus filiformis	1.63	2.25
Juncus pelocarpus	0.45	2.16
Lythrum salicaria	-0.84	0.10
Lysimachia terrestris	0.51	4.01
Mentha arvensis	-0.60	0.90
Phalaris arundinaceae	-0.40	1.18
Rumex verticillatus	-0.16	1.58
Scirpus fluviatilis	-0.05	0.85
Scirpus torreyi	0.72	1.55
Sparganium eurycarpum	-0.78	0.70
Spartina pectinata	-0.63	0.33
Triadenum fraseri	0.61	1.24
Typha xglauca	-0.33	0.67
Viola lanceolata	0.13	4.27

Table 4.4 Ratio of below to above ground biomass for twenty-one herbaceous shoreline plant species grown under high and low nutrient conditions (Hoagland's solution full-strength or diluted X 10). Relative Change = the relative increase or decrease in below/above-ground such that values of 1 indicate no difference in allocation between treatments and values greater than 1 indicate a relatively greater apportionment below-ground under low nutrient conditions.

SPECIES	**BELOW/ABOVE RATIO**		
	High Nutrient	**Low Nutrient**	**Relative Change**
Acorus calamus	1.68	5.92	3.52
Carex crinita	3.66	4.24	1.16
Dulichium arundinaceum	1.61	3.25	2.01
Eleocharis acicularis	1.47	1.48	1.00
Eleocharis calva	3.03	7.59	2.50
Hypericum ellipticum	1.94	1.30	0.67
Juncus filiformis	4.97	9.55	1.92
Juncus pelocarpus	0.75	4.45	5.93
Lythrum salicaria	1.11	7.19	6.47
Lysimachia terrestris	1.68	4.21	2.50
Mentha arvensis	0.95	2.11	2.22
Phalaris arundinaceae	2.22	6.00	2.70
Rumex verticillatus	2.92	6.36	2.18
Scirpus fluviatilis	4.67	7.06	1.51
Scirpus torreyi	1.01	8.57	8.48
Euthamia galetorum	2.49	1.83	0.73
Sparganium eurycarpum	2.85	15.87	5.57
Spartina pectinata	2.14	7.14	3.34
Triadenum frasen	1.13	1.50	1.33
Typha xglauca	3.24	11.60	3.58
Viola lanceolata	0.67	1.50	2.24

Stress Tolerance/Sensitivity and Relative Competitive Performance

Measures of relative competitive performance for the species used in this experiment are included in Chapter 3; Table 3.2.

Of all the estimates of stress tolerance or sensitivity, including the proportion of below to above-ground biomass, only relative biomass production (RBP) under low nutrient conditions had a significant relationship with species competitive performance (Table 4.5). The relationship is shown in Figure 4.1. As shown in this figure, several species have stress tolerance values below 0, i.e. they did not fully replace tissue lost to senescence the previous season. These species are all large, highly competitive species characteristic of undisturbed, fertile shorelines (Chapter 1 results, Day *et al.* 1987).

Stress Tolerance/Sensitivity and Position on the Standing Crop Gradient

The mean position of the species on the standing crop gradient is shown in Chapter 1; Table 1.5. Again, only relative biomass production (RBP) under low nutrient conditions showed a consistent relationship to position of species on environmental gradients of fertility/productivity (Table 4.6). The relationship between this measure of stress tolerance and standing crop (log transformed data) is shown in Figure 4.2. However, previous results show that stress tolerance is also correlated with competitive performance and results of Chapter 1 demonstrate that there is a significant relationship between competitive performance and environmental distribution of species. When the interaction with competitive performance is considered, the partial correlation coefficient for stress tolerance is only -0.41, while for competitive performance it is 0.55. Multiple regression analysis shows that competitive performance and stress tolerance together explain 58% of the variation in position on the standing crop gradient ($R^2 = 0.58$; $F = 14.80$; $p = 0.0002$) with competitive performance alone explaining 52% of this variation ($F = 22.83$; $p = 0.0001$).

Table 4.5 Correlation (r) between measures of species stress tolerance/sensitivity and their relative competitive performance under high nutrient conditions (n = 21 species). Values in bold are significant at the 0.01 level[2].

	Correlation (r) with Competitive Performance[1]
Below to above-ground biomass (g/g)[1]	
low nutrient	0.53 p=0.0128
high nutrient	0.47 p=0.0333
Stress Tolerance (relative biomass production (RBP) under low nutrient conditions)	**-0.62** p=0.0025
Stress Sensitivity[2] (relative decrease in biomass between high and low nutrient conditions)	0.12 p=0.5893
Maximum growth rate (relative biomass production (RBP) under high nutrient conditions)	0.33 p=0.1493

1 - arcsine transformed

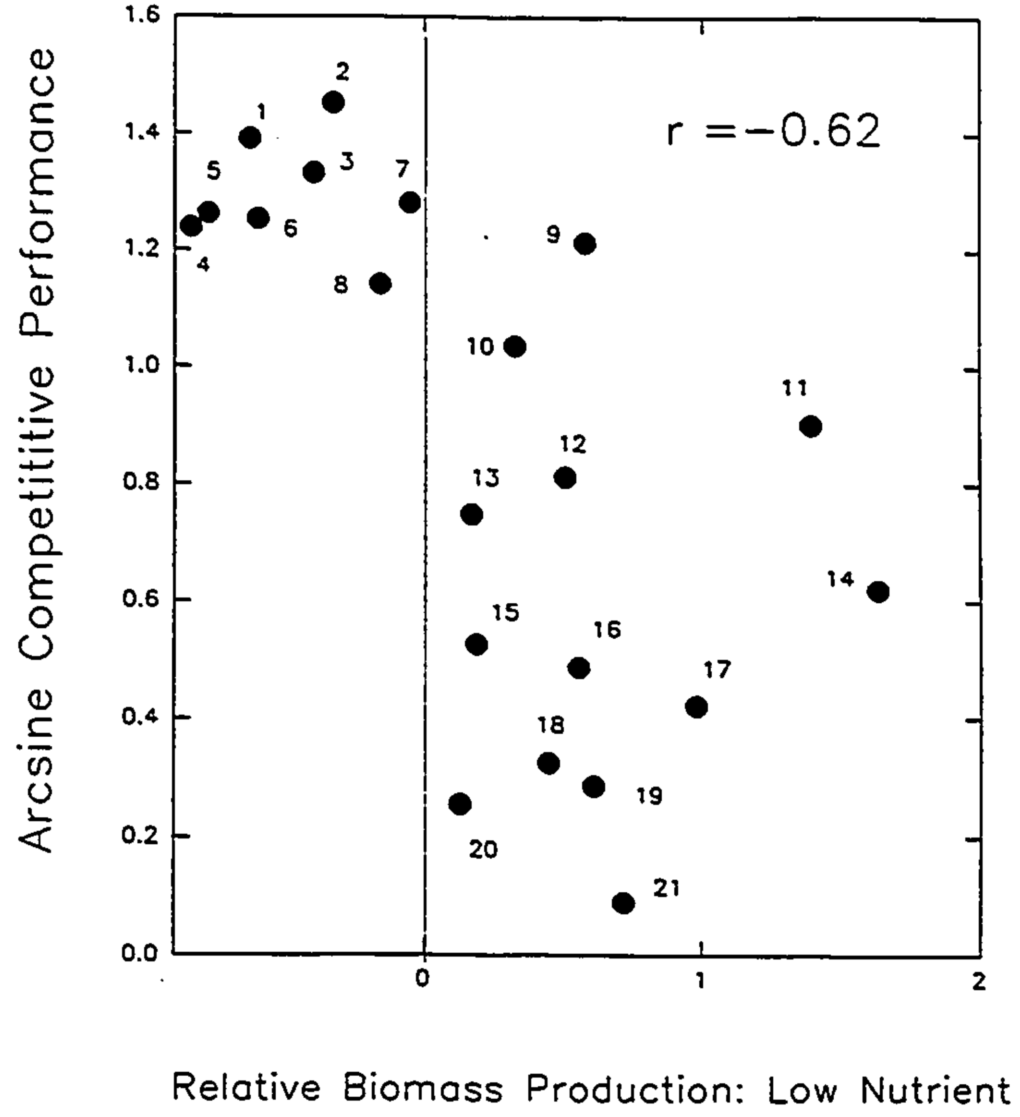
Table 4.6 Correlation (r) between measures of species stress tolerance/sensitivity and mean position on the standing crop gradient.(n = 21 species). Values in bold are significant at the 0.01 level.

	Correlation (r) with position on the standing crop gradient[2]
Below to above-ground biomass (g/g)[1]	
low nutrient	0.45 p=0.0385
high nutrient	0.35 p=0.1219
Stress Tolerance (relative biomass production (RBP) under low nutrient conditions)	**-0.68** p=0.0008
Stress Sensitivity (relative decrease in biomass between high and low nutrient conditions)	0.39 p=0.0822
Maximum growth rate (relative biomass production (RBP) under high nutrient conditions)	0.24 p=0.3048

1 - arcsine transformed
2 - log transformed

Figure 4.1 The relationship between competitive performance (expressed as percent reduction in phytometer biomass) under high nutrient conditions and relative biomass production under low nutrient conditions (n = 21 species). The dashed line represents the point at which species are not replacing tissue lost to senescence (i.e. negative biomass accumulation). Species names are as follows: 1 - *L. salicaria*; 2 - *T. xglauca*; 3 - *P. arundinacea*; 4 - *S. eurycarpum*; 5 - *S. pectinata*; 6 - *M. arvensis*; 7 - *S. fluviatilis*; 8 - *R. verticillatus*; 9 - *E. galetorum*; 10 - *A. calamus*; 11 - *E. calva*; 12 - *L. terrestris*; 13 - *C. crinita*; 14 - *J. filiformis*; 15 - *D. arundinaceum*; 16 - *H. ellipticum*; 17 - *E. acicularis*; 18 - *J. pelocarpus*; 19 - *T. Fraseri*; 20 - *S. torreyi*; 21 - *V. lanceolata*.

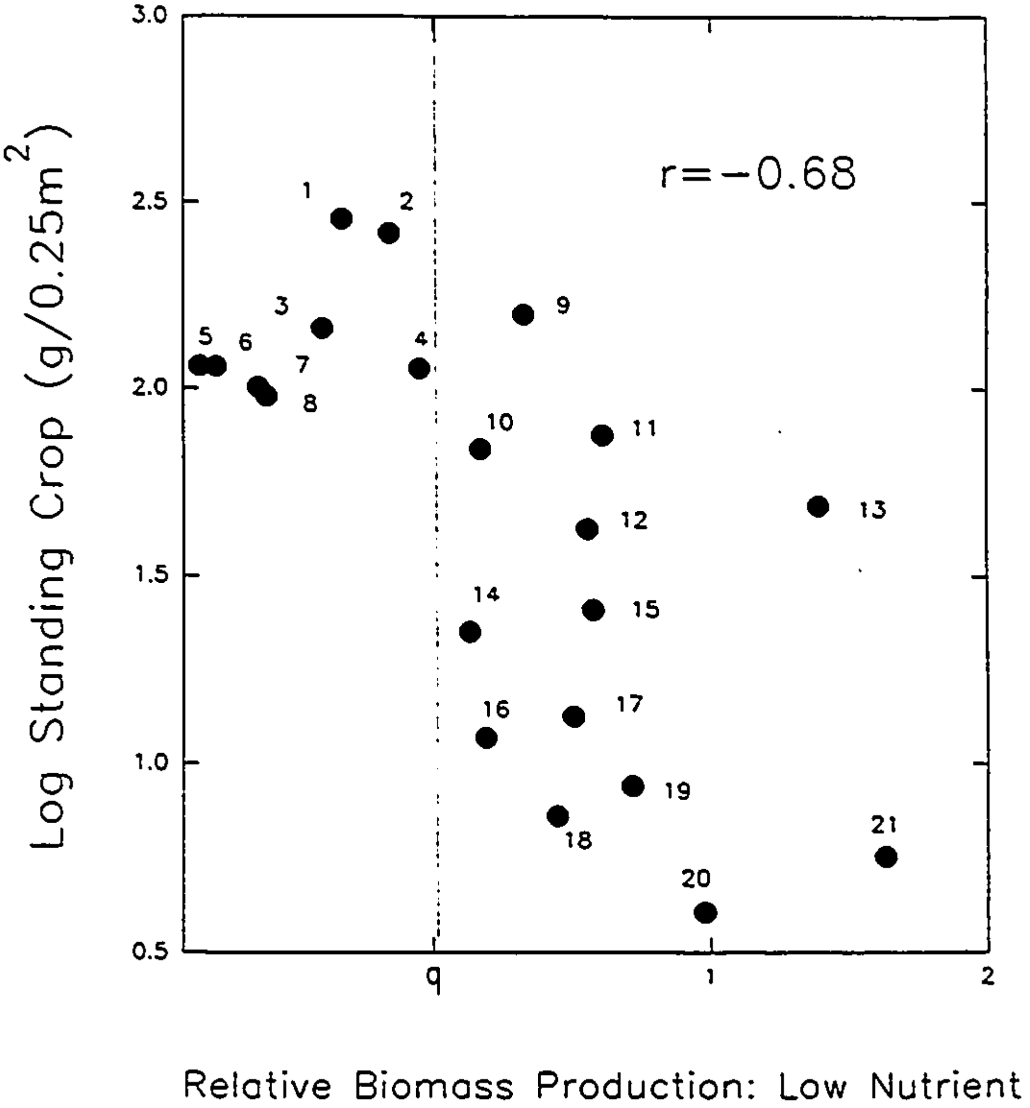
Figure 4.1



Arcsine Competititive Performance
Relative Biomass Production: Low Nutrient
r =−0.62
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

Figure 4.2 The relationship between mean position on the standing crop gradient and relative biomass production under low nutrient conditions for 21 shoreline plant species. The dashed line represents the point at which species are not replacing tissue lost to senescence (i.e. negative biomass accumulation). Species names are as follows: 1 - *T. xglauca*; 2 - *R. verticillatus*; 3 - *P. arundinacea*; 4 - *S. fluviatilis*; 5 - *L. salicaria*; 6 - *S. pectinata*; 7 - *S. eurycarpum*; 8 - *M. arvensis*; 9 - *A. calamus*; 10 - *C. crinita*; 11 - *T. Fraseri*; 12 - *H. ellipticum*; 13 - *E. calva*; 14 - *V. lanceolata*; 15 - *E. galetorum*; 16 - *D. arundinaceum*; 17 - *L. terrestris*; 18 - *J. pelocarpus*; 19 - *S. torreyi*; 20 - *E. acicularis*; 21 - *J. filiformis*.

Figure 4.2



3.0
2.5
2.0
1.5
1.0
0.5
Log Standing Crop (g/0.25m^2)
r=−0.68
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
q
1
2
Relative Biomass Production: Low Nutrient

DISCUSSION

All species, with minor exceptions, show a marked increase in biomass accumulation under fertile conditions. This is consistent with the view that plants have overlapping fundamental niches along nutrient gradients (Colwell and Fuentes 1975; Austin and Austin 1980; Keddy 1989; Wilson and Keddy 1988). This may in part explain why measures of stress sensitivity (*sensu* Shipley and Keddy 1988) that emphasize differences in growth under optimal versus nutrient poor conditions, or direct measures of relative growth under optimal conditions, are poor predictors of either field distribution or competitive performance at this broad community scale. It may be that other measures of relative growth would have yielded different results. However, when this possibility was explored using published data on the maximum growth (R*max*) under optimal conditions of over 30 shoreline plant species (published data from Shipley and Peters 1990); and data on field distribution and relative competitive performance from Chapter 1, there was still no significant relationship found. It may be that in shoreline plant communities, the capacity for rapid growth when nutrients are available is generally adaptive along a broad spectrum of the gradient, enabling species to respond quickly to fluctuating environmental conditions characteristic of these communities (Day *et al.* 1988). This shared response may however, mask minor differences in stress sensitivity which may have important implications for fine scale pattern in the field.

Only relative biomass production under low nutrient conditions was significantly related to competitive performance and field distribution of species. This relationship provides support for the suggestion that there is an evolutionary trade-off between stress tolerance on the one hand and relative competitive ability on the other hand (Grime 1979; Shipley and Keddy 1988). However, when all species are considered, the relationship is relatively weak. This is not be surprising when one considers that many variables affect the distribution and relative competitive performance of species other than nutrient stress.

In shoreline communities, stress and disturbance may be inextricably tied (Day *et al.* 1988; Keddy 1983). In transplant experiments along a combined gradient of stress and disturbance, Moore (1990) concluded that disturbance may be more important in limiting distribution than nutrient stress. In this context, it is noteworthy that highly competitive species typical of undisturbed, fertile habitats such as *Typha* sp. and *Scirpus fluviatilis*, showed a similarly low degree of stress tolerance after the second growing season. These species do not appear to be able to compensate for losses to senescent tissue, presumed to be an important factor in stress tolerance (Tilman 1990). The remaining species formed a much more diffuse group. Relative to the species of sheltered, undisturbed habitats, these species occur in habitats subject to relatively high rates of both stress and disturbance (Day *et al.* 1988). This might explain the degree of variation in the observed relationship between stress tolerance and distribution along the standing crop gradient. Measures of "disturbance tolerance" may explain much of this residual variation. Stress is thought to be accompanied by disturbance across a range of communities (Tilman 1988; Oksanen 1990). Further analysis of this relationship at the community scale is needed to reconcile conflicting theory about the relative roles of stress, disturbance and competitive ability in community pattern.

In shoreline communities, evergreen species tend to dominate habitats of extreme nutrient stress (Berendse *et al.* 1987; Boston and Adams 1987; Keddy and Wisheu 1987) as would be predicted by several authors (Chapin 1980; Tilman 1990; Keddy 1990; Grime 1979) due to the increased efficiency under low nutrient conditions. Because there is little loss to senescent tissue, these species would presumably have high relative biomass production (RBP) under low nutrient conditions. Unfortunately, evergreen species were not well represented in the current study. It is not know how inclusion of this guild of "stress-tolerant" evergreen species would have affected results.

Also, nutrient stress is clearly not the only stress relevant in natural shoreline communities. For example, Grace and Wetzel (1981) found an apparent trade-off between stress tolerance and competitive ability in two species of *Typha* that largely explained their distribution patterns at the fine scale. Water level, not nutrient level, was the relevant stress and it may therefore not be surprising that in the current study, only about 30-40% of the variation in competitive ability and field distribution could be explained by nutrient stress tolerance alone.

Below to Above-Ground Ratios

The allocation of photosynthetic to non-photosynthetic tissue has been suggested as an important determinant of pattern in natural plant communities with presumed links to enhanced competitive ability under conditions of nutrient stress (Oksanen 1990; Tilman 1988, 1987; Chapin and Shaver 1985). It is implied that simple, direct measures of species traits, specifically the ratio of below to above-ground biomass, could serve as a simple, measurable surrogate of stress tolerance. This would provide an important predictive tool for exploring pattern and mechanism in the field. There is only limited and indirect examination of this relationship for a large number of species (Shipley and Peters 1990). In this study, I directly examined the relationship between below to above-ground biomass allocation of plant species, field distribution and competitive performance.

Results of this study show that, in general, species respond similarly to nutrient stress through a shift in biomass allocation below-ground. This would superficially seem to support suggestions (e.g., Tilman 1988) that improved foraging for nutrients below-ground is an important predictor of competitive performance under limiting nutrient conditions. However, results of this study show that, at least at this broad community scale, this response is generalized across species, and shows no clear relationship to either competitive performance or distribution of species. In fact species such as *E. acicularis*, which are characteristic of low nutrient habitats (Keddy 1983), had low below to above-ground ratios. The lack of consistent relationship between root to shoot ratios and growth rate has been shown by Shipley and Peters (1990). It may be that a more precise measure of nutrient uptake or efficiency of uptake per unit biomass would offer a more accurate explanation (e.g., Tilman and Wedin 1991). The capacity for rapid adjustment in below to above-ground biomass allocation may be characteristic of communities subject to fluctuating environmental conditions, such as shorelines. Implications for other communities remain to be explored at this scale.

These results do not enable a mechanistic interpretation of stress tolerance. However, the comparative design of this study enabled a number of different measures of stress tolerance/sensitivity to be explored at the coarse community scale and points to important areas for future study. The importance of relative performance under conditions of nutrient stress as a predictor of community pattern requires more detailed examination, especially as efforts have traditionally focused on the role of R*max* rather than what might be termed "**R*min***". It is also important to once again emphasize the importance of scale. These results apply at the coarse community scale and the same traits may not be important determinants of fine-scale pattern. It is becoming increasingly apparent that questions of scale must be clearly addressed in designing and interpreting experiments if empty debate is to be avoided.

GENERAL CONCLUSIONS

This study has demonstrated that there are general relationships between experimentally determined measures of the competitive performance of shoreline plant species, plant traits and field distribution, that clearly emerge at the community scale. A species relative competitive performance under fertile conditions is related to it's distribution along environmental gradients of standing crop and fertility (Chapter 3) thus supporting the hypothesis that interspecific competition is an important determinant of community pattern.

The results of Chapter 2, showing a relationship between plant traits and competitive performance under conditions of high fertility, provides an important tool not only in the ability to generalize results of the current study beyond the particular species examined, but in interpreting observed patterns in the field. Previously, patterns of plant height or other size related measures along environmental gradients had been linked with competitive ability, but only through inference. The results of Chapter 2 clearly establish this link. The demonstrated relationship between plant size, competitive performance under high nutrient conditions, and distribution of species along natural environmental gradients provides a unifying framework for development of general predictive models of community pattern.

There remain however, several important unanswered questions. Simply put, results of Chapter 1 show that species with relatively high competitive performance under optimal conditions are abundant in areas of high productivity/ fertility but have a relatively low abundance in infertile areas. Two divergent hypotheses have been proposed to explain such patterns: 1) the relative competitive ability of species changes with changing conditions such that the species that is the superior competitor under high nutrient conditions is an inferior competitor under low nutrient conditions; and 2) species of inherently high competitive ability have low stress and/or disturbance tolerance and are therefore restricted from areas of prevailing stress. Results of Chapter 3 show that competitive performance is correlated under both high and low nutrient conditions across this range of species, and that competition is less intense under low nutrient conditions. This suggests that changing patterns of species abundance along environmental gradients of fertility are not adequately explained by changing patterns of relative competitive performance. However, shifts in competitive performance were apparent when species were considered in isolation. Though these shifts show no clear relationship to coarse-scale pattern at the multi-species level, they may be critical in explaining fine-scale pattern in the field. The results of Chapter 3 suggest that the alternative hypothesis, i.e. a trade-off between stress tolerance and competitive ability, may afford a more adequate explanation of distribution patterns. Though the results of Chapter 4 provide some support for this conclusion, in that there is a weak inverse relationship between stress tolerance and competitive ability, there remains a great deal of variation that is not explained. I suggest that this may in large part be due the importance of disturbance and "disturbance tolerance" which have not been measured and may play a key role in determining the distribution of shoreline plant species.

This study represents one of the first systematic attempts to address the importance of competition in shaping plant community structure at this scale of generality, and results are based on relatively novel techniques. There exists a great deal of controversy over appropriate methods of measuring competitive ability and interpretation of results is subject to the limitations inherent in the experimental approach. I have provided one measure that appears to have broad utility in systematically exploring the role of competition in natural plant communities at the coarse scale. Further empirical work at this scale, and in other vegetation types, is needed to evaluate the utility of this comparative approach and the generality of these conclusions in unravelling complexity at the coarse community scale. Finally, I suggest that much of the controversy surrounding the role of competition in community structure could be resolved if the scale at which the results apply were clearly defined.

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APPENDIX 1.1

Soil macronutrient levels (ppm), organic content and standing crop (g/0.25m^2) for all quadrats sampled (n = 217). Locations are idenitified in the text.

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
Luskville							
IA	74	151	6	1.3	7	6.6	13
IA	82	290	8	3	9	7.8	36.5
IA	51	235	12	1.1	9	8.7	26.1
IA	37	134	10	0.6	6	8.4	37
IA	67	226	8	1.4	9	8.2	19.7
IA	61	236	10	1.6	8	8.4	27.6
IA	83	243	6	2	8	7.5	35.4
IA	66	228	6	1.2	7	7.7	26.4
IA	50	146	4	1.3	6	7.7	57.1
IA	38	94	4	0.7	6	7.7	33.3

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
IA	48	201	6	4.8	8	7.7	34.5
IA	52	210	6	2.8	8	7.8	38.6
IA	59	202	8	1.3	8	8	32.5
IB	49	201	10	1	9	8.5	29.6
IB	57	173	6	1.1	10	8.4	63.2
IB	53	188	8	1.3	9	8.1	29.2
IB	54	166	6	2.4	7	8	33
IB	52	134	4	2.2	8	7.3	32.1
IB	79	286	6	2.4	8	8	51.4
IB	57	209	4	1.4	10	7.9	25.9
IB	59	179	4	1.9	11	7.7	18.4
IB	52	116	4	1.4	12	7.5	45.4

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
IB	60	111	2	1.5	11	7.4	52.2
IB	50	104	2	1.4	8	6.8	45.1
IB	55	152	2	2.4	8	7.3	36.4
IB	79	259	4	2.6	9	7.7	44.7
IB	82	285	6	2.3	8	7.8	41.3
IB	92	246	6	2.5	9	7.8	51.6
IC	143	292	6	5.6	7	6.1	97
IC	140	319	6	6.7	4	6.2	103.9
IC	117	273	4	5.2	4	6.4	64.2
IC	120	316	4	5.1	4	6.3	112.8
IC	118	273	4	5.4	5	6.3	114.8
IC	117	266	4	4.5	5	6	89.5

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
IC	94	246	6	4.2	8	5.9	126.2
IC	120	296	6	5.3	6	5.9	107.8
IC	134	309	6	5.5	6	5.9	81.5
IC	132	343	6	5	6	6.2	81
IC	146	353	4	6.6	6	5.9	106
IC	130	351	4	5	6	6	70.5
IC	145	352	4	4.5	7	6.2	71.5
IC	161	463	6	6.3	9	6.6	67.9
IC	167	447	6	7.1	7	6.3	90.6
ID	138	380	8	14.1	8	5.5	104.6
ID	159	438	10	11.5	10	5.6	66.4
ID	152	421	10	19	11	5.7	97.2

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
ID	176	472	12	16.6	13	6	127.5
ID	182	404	12	15.7	19	5.7	100.7
ID	135	430	16	15.5	9	5.7	135.5
ID	175	399	12	12.6	12	5.5	96.5
ID	137	428	16	12.7	8	5.4	176.9
ID	151	433	16	14.5	10	5.4	127.6
ID	143	316	12	14.5	8	5.7	101.5
ID	140	314	8	16.2	8	5.6	119.5
ID	161	356	18	14.2	9	5.5	143.4
ID	125	341	14	12.8	10	5.3	148.8
ID	152	308	6	13.9	9	5.5	152.5
ID	128	305	4	13.8	8	5.4	170.6

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
IE	125	350	12	19.5	14	6.3	265.2
IE	120	398	18	18	19	6.3	295.2
IE	147	359	18	21.4	19	5.8	289.6
IE	154	431	26	16.9	21	5.9	287.6
IE	137	425	18	22	18	5.8	343.9
IE	128	363	14	15.7	14	5.6	272.8
IE	136	346	16	14.8	13	6.4	264.5
IE	147	419	18	15.4	16	6	263.5
IE	152	359	14	18	16	5.4	251.2
IE	162	334	16	15.9	15	5.2	241.3
IE	150	428	18	13.8	15	5.5	311.6
IE	146	419	18	15.1	13	5.4	226.8

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
IE	201	403	38	16.6	17	5.9	190.7
IE	267	377	26	19	19	6	325
IE	219	392	22	16.6	15	5.6	335

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
Westmeath							
wA	43	61	2	0.7	6	7.3	7.5
wA	37	69	8	0.6	7	8.1	1
wA	38	60	6	0.6	3	8.4	12.1
wA	36	67	2	0.7	3	8.5	5.1
wA	29	40	8	0.5	3	8.2	2.1
wA	41	57	4	0.6	4	8.6	3.4
wA	30	75	2	0.7	3	8.5	13.6
wA	39	88	4	0.7	4	8.3	1.4
wA	36	83	6	0.9	4	8.5	1.8
wA	40	102	2	0.7	5	7.3	7.6
wA	41	101	4	0.6	6	8.7	1.3

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
wA	40	100	10	0.6	4	8.4	1.2
wA	35	59	4	0.7	3	8.3	1.7
wA	30	62	12	0.6	3	8.5	4.5
wA	36	91	4	0.7	3	8.6	1.1
wB	33	99	2	1.7	6	7.2	48.6
wB	30	107	4	2.6	5	6.5	49.2
wB	35	100	4	2.4	5	7	48
wB	27	85	2	1.6	5	7.4	108.9
wB	37	132	4	2.5	7	7.2	120.5
wB	34	139	4	1.9	7	7.4	70.3
wB	34	139	6	1.6	8	7.8	30.8
wB	38	151	4	1.5	8	8	55.7

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
wB	29	109	4	0.9	4	8	64.5
wB	35	96	6	1.2	4	8.1	26.8
wB	45	165	6	1.9	7	8	43.9
wB	50	167	6	2.1	5	7.9	42.3
wB	77	260	12	1.7	4	7.9	36.5
wB	35	91	8	1.8	7	7.4	27.6
wB	35	117	4	2.3	7	7.1	43.2
wC	72	303	6	25.2	11	5.3	179.9
wC	66	394	6	19.5	8	5.4	154.8
wC	72	388	6	26.4	10	5.3	189.7
wC	84	312	10	22.4	18	5.5	114.4
wC	71	380	10	23.9	10	5.5	160.2

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
wC	48	294	8	27.9	12	5.5	169
wC	47	341	12	25.2	10	5.5	145.3
wC	52	348	12	31.7	10	5.5	174.2
wC	57	353	16	30.4	13	5.7	140.9
wC	52	344	18	25.9	12	5.9	186.8
wC	50	245	14	30.7	10	5.7	212.6
wC	54	280	24	36.2	13	5.9	152.1
wC	59	423	8	30.6	10	5.4	152.3
wC	49	399	16	22.4	12	5.8	163.5
wC	52	371	18	31.1	12	5.9	148.7
wD	42	244	10	39.1	13	5.5	121.7
wD	52	231	6	39.7	16	5.5	142.1

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
wD	62	195	10	54.3	19	5.6	128.8
wD	77	194	14	44.6	22	5.6	88.3
wD	70	243	10	36.5	22	5.7	129.4
wD	62	257	8	35.6	16	5.6	116.1
wD	65	261	8	30.3	23	5.7	103.6
wD	66	268	8	33.4	19	5.7	156.9
wD	68	237	6	40.2	23	5.8	148
wD	64	249	6	35.2	23	5.8	123.2
wD	61	263	6	30.6	20	5.6	50.8
wD	56	232	6	37	21	5.9	137.6
wD	55	264	6	30.6	16	5.6	185
wD	68	274	6	22	21	5.7	215.3

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
wD	69	243	8	27.6	21	6.9	320
wE	97	256	24	17.8	23	7.2	320.8
wE	97	285	22	37.8	18	7.4	327.8
wE	75	237	28	38.2	14	7.6	383
wE	101	253	34	34.7	21	7.5	216.2
wE	112	271	28	20.4	33	7.7	369.1
wE	102	237	26	22.6	20	7.7	227.1
wE	125	249	22	26.1	26	7.8	260.3
wE	145	222	8	25.2	37	7.5	285
wE	65	276	22	38.2	17	7.6	427
wE	61	215	30	31	33	7.4	385.6
wE	79	210	28	41.9	34	7.8	432.9

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
wE	97	193	34	34.8	60	7.9	194.4
wE	87	204	30	37.9	22	8	321.9
wE	68	163	28	38.1	16	7.5	277.2
wE	90	282	46	43.9	20	7.7	308
Axe Lake	44	38	4	4	5	5.5	4.47
	59	29	4	9	7	5.2	13.72
	27	22	2	4	4	5.4	8.62
	11	20	2	2	2	6.4	6.03
	17	36	2	7	2	6.7	3.87
	14	22	2	3	2	6.7	3.22

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
	19	19	2	1.26	2	5.7	3.44
	12	17	4	1.63	2	5.7	4.34
	22	20	4	1.09	2	6.1	5.49
	30	21	2	2.04	3	5.7	33.97
	36	24	4	1.08	2	5.4	26.93
	31	22	2	0.55	2	5.7	6.67
	20	20	4	0.26	2	5.9	16.94
	15	19	4	0.33	1	6.3	1.86
	57	25	4	4.04	4	5.8	21.8
	52	25	4	11.65	4	4.9	23.8

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
Breckenridge	174	532	20	21.47	23	6.2	82.12
	184	568	18	16.51	16	6.3	80
	193	562	10	22.26	22	6.3	92.1
	167	521	8	17.46	14	6.4	200.55
	178	518	10	20.9	17	6.2	157.14
	169	600	14	12.52	16	6.4	66.27
	182	530	10	20.84	13	6.5	39.15
	197	600	14	14.79	16	6.6	23.7
	178	600	28	25.7	25	6.2	15.84

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
Lucerne	160	196	12	13.91	9	6.4	149.21
Blvd.	143	144	8	12.11	10	7	164.76
	151	175	10	17.43	9	7	172.43
	166	187	8	12.45	9	6.5	140.02
	139	192	12	11.67	10	6.5	156.75
Ottawa	132	228	6	6.67	8	6.7	84.85
Beach	188	223	10	7.82	11	6.5	126
	113	230	6	8.94	10	7.5	94
	193	232	8	12.42	10	7.5	143.4
	162	238	8	11.02	9	7.7	90.9

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
Stony	123	196	6	15.66	11	6.5	91.96
Swamp	108	196	6	14.99	8	6.8	64.18
	117	276	10	23.06	9	6.8	55.78
	98	183	8	25.53	7	6.6	100.73
	121	140	6	11.08	7	6.1	92.4
	98	220	8	35.29	17	6.3	120.39
	87	133	6	77.12	14	6.2	82.56
	62	105	6	75.6	13	6.5	71.16

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
Nova Scotia	82	63	4	2.78	7	5.5	16.95
	82	63	4	14.05	7	5.5	35.74
	82	63	4	2.63	7	5.5	7.13
	42	39	4	1.64	3	5.8	1.57
	42	39	4	2.84	3	5.8	2.32
	42	39	4	1.34	3	5.8	2.33
	76	25	4	2.46	5	4.8	6.56
	76	25	4	6.58	5	4.8	35.29
	76	25	4	6.82	5	4.8	49.19
	61	43	4	1.7	5	6.8	4.36
	61	43	4	0.74	5	6.8	2.62
	61	43	4	1.36	5	6.8	35.89

location	potassium	magnesium	nitrate	% organic matter	phosphorous	pH	standing crop
	61	43	4	0.87	5	6.8	4.97
	80	47	4	28.85	8	5.1	76.5
	80	47	4	36.54	8	5.1	73.44
	80	47	4	36.72	8	5.1	48.95
	125	46	6	42.03	7	5.2	98.27
	125	46	6	31.98	7	5.2	58.87
	51	38	6	6.06	4	5.4	9.42
	51	38	6	0.42	4	5.4	7.31
	89	40	4	9.42	7	5.2	50.64
	68	43	4	21.29	7	5.2	89.04
	78	40	4	18.85	8	5.2	76.50
	51	38	6	1.54	4	5.4	5.6

APPENDIX 1.2

Multiple Regression Analysis for Relative Competitive Performance as a function of Position on th
Environmental Gradient

Model Fitting Results for Relative Competitive Ability

Independent variable	coefficient	st. error	t-value	sig. level
CONSTANT	-1.17	0.72	-1.62	0.11
standing crop	0.39	0.11	3.65	0.0009
phosphorous	0.41	0.27	1.52	0.14
nitrogen	-0.11	0.33	-0.33	0.75
potassium	0.14	0.29	0.49	0.63
magnesium	-0.29	0.20	-1.44	0.16
% organic content	0.64	0.45	1.41	0.17
pH	1.46	0.80	1.83	0.08

Analysis of Variance for the Full Regression

Source	Sum of Squares	DF	Mean Square	F-Ratio	P-value
Model	2.78	7	0.40	12.29	.0000
Error	1.03	32	0.03		
Total (Corr.)	28446	39			
R-squared = 0.73 R-squared (Adj. for d.f.) = 0.67			Stnd. error of est. = 0.18 Durbin-Watson statistic = 1.99		

APPENDIX 2.1

Mean + standard error (indicated in brackets) for above and below-ground biomass and height for 44 species of herbaceous wetland plants (five replicates per species) grown with phytometer (test) and singly (control). All plants were grown in a high nutrient sterile organic medium (Promix^{R})

SPECIES	Species Grown Singly		Species Grown with Phytometer		
	Above-ground Biomass (g)	Below- ground Biomass (g)	Above-ground Biomass (g)	Below-ground Biomass (g)	Height (c m)
Acorus calamus	4.14 (0.67)	6.22 (2.21)	8.09 (0.83)	14.83 (1.13)	77.60 (2.71)
Anenome canadensis	0.49 (0.03)	0.01 (0.01)	1.22 (0.39)	1.89 (0.64)	22.00 (3.30)
Bidens cernua	17.65 (0.76)	8.22 (1.38)	20.27 (1.38)	9.84 (1.86)	76.20 (2.40)
Carex crinita	4.56 (0.07)	10.07 (1.22)	6.24 (.87)	9.37 (0.77)	55.25 (4.14)
Carex rostrata	8.12 (1.81)	7.42 (1.21)	12.16 (2.07)	10.20 (2.04)	64.50 (8.25)
Drosera intermedia	0.08 (0.03)	0.01 (0.00)	0.02 (0.01)	0.01 (0.01)	1.00 (0.03)
Dulichium arundinaceum	1.61 (0.28)	3.79 (0.96)	2.38 (0.47)	2.32 (1.03)	38.50 (4.25)
Eleocharis erythropoda	2.04 (0.27)	4.70 (1.47)	1.13 (0.38)	1.00 (0.28)	52.00 (8.14)
Eleocharis palustris	2.21 (0.80)	2.81 (0.43)	1.19 (0.35)	1.58 (0.36)	59.20 (2.98)
Eriocaulon septangulare	0.02 (0.01)	0.02 (0.01)	0.09 (0.02)	0.01 (0.01)	1.04 (0.01)
Eupatorium maculatum	7.57 (1.49)	13.98 (5.08)	12.27 (2.01)	27.06 (2.10)	79.25 (7.97)
Gallium palustris	2.66 (0.47)	3.79 (1.11)	2.73 (0.14)	3.31 (0.03)	41.75 (4.97)
Hypericum ellipticum	2.81 (0.51)	3.43 (0.81)	3.53 (0.08)	6.86 (0.98)	45.75 (2.14)
Impatiens capensis	0.98 (0.17)	0.09 (0.04)	1.33 (0.27)	0.71 (0.18)	50.50 (4.17)
Iris versicolor	3.53 (0.29)	10.15 (2.81)	5.52 (1.48)	5.54 (1.18)	58.00 (2.52)
Juncus filiformis	1.96 (0.30)	13.20 (1.46)	1.80 (0.31)	3.69 (0.20)	57.80 (4.66)
Juncus militaris	0.37 (0.03)	0.92 (0.57)	0.59 (.25)	1.58 (0.44)	43.00 (8.95)
Juncus pelocarpus	0.24 (0.12)	0.11 (0.02)	0.30 (0.04)	0.13 (0.02)	16.33 (3.71)

SPECIES	Species Grown Singly		Species Grown with Phytometer		
	Above-ground Biomass (g)	Below- ground Biomass (g)	Above-ground Biomass (g)	Below-ground Biomass (g)	Height (cm)
Leerzia oryzoides	2.50 (0.47)	1.26 (0.31)	3.35 (0.27)	1.93 (0.60)	58.33 (4.84)
Lobelia dortmanna	0.03 (0.01)	0.02 (0.00)	0.05 (0.02)	0.04 (0.01)	2.13 (0.13)
Lysimachia ciliata	3.81 (0.52)	5.03 (0.83)	4.93 (0.30)	9.09 (0.51)	43.80 (1.83)
Lysimachia nummularia	5.20 (2.29)	1.14 (0.28)	4.42 (0.39)	0.53 (0.06)	14.00 (5.03)
Lysimachia terrestris	2.43 (0.37)	5.85 (1.13)	3.63 (0.67)	5.91 (0.27)	53.67 (2.96)
Lysimachia thrysiflora	4.39 (0.33)	7.38 (1.06)	4.76 (0.41)	12.45 (1.23)	41.00 (1.63)
Lythrum salicaria	16.04 (1.47)	10.70 (1.17)	24.08 (3.47)	32.23 (6.09)	(125.00) 2.12
Mentha arvensis	3.74 (0.10)	7.42 (0.44)	5.68 (0.72)	7.46 (0.38)	50.60 (2.79)
Onoclea sensibilis	1.76 (0.41)	11.78 (2.92)	1.42 (0.30)	4.52 (1.10)	17.60 (1.69)
Polygonum hydropiperoides	2.67 (0.53)	4.45 (1.07)	2.99 (0.45)	5.52 (0.63)	41.20 (3.04)
Panicum longifolium	2.71 (0.95)	1.19 (0.78)	1.81 (0.30)	3.33 (0.52)	48.80 (1.98)
Phalaris arundinaceae	6.53 (1.12)	6.66 (1.96)	12.09 (1.36)	14.05 (1.32)	75.80 (3.02)
Pilea pumila	7.61 (2.01)	8.14 (2.46)	8.42 (1.34)	12.79 (1.75)	50.25 (2.29)
Potentilla anserina	7.35 (1.35)	1.79 (0.64)	4.33 (0.56)	1.84 (0.32)	28.67 (2.96)
Ranunculus reptans	0.44 (0.34)	0.54 (0.07)	0.02 (0.01)	0.05 (0.02)	2.63 (0.89)
Rhyncospora fusca	0.19 (0.05)	0.09 (0.02)	0.23 (0.03)	0.15 (0.06)	27.00 (3.21)
Rumex verticillatus	3.14 (0.07)	13.46 (3.24)	4.40 (0.63)	13.68 (1.50)	47.67 (2.73)

Appendix 2.1 cont'd

SPECIES	Species Grown Singly		Species Grown with Phytometer		
	Above-ground Biomass (g)	Below- ground Biomass (g)	Above-ground Biomass (g)	Below-ground Biomass (g)	Height (c m)
Sabbatia kennedyana	0.47 (0.11)	0.37 (0.11)	0.23 (0.04)	0.38 (0.04)	3.50 (1.54)
Scirpus fluviatilis	6.79 (1.30)	18.41 (2.50)	8.14 (0.78)	27.17 (3.35)	81.00 (4.79)
Scirpus validus	5.56 (0.79)	12.91 (1.58)	6.54 (0.83)	15.73 (2.35)	104.75 (2.57)
Spartina pectinata	3.71 (0.63)	7.92 (0.67)	7.02 (0.45)	16.64 (0.52)	94.67 (6.49)
Stachys palustris	7.48 (0.16)	12.70 (2.83)	6.91 (0.52)	9.72 (2.23)	52.20 (3.51)
Triadenum fraseri	4.17 (0.31)	6.69 (0.76)	3.36 (0.44)	4.32 (1.78)	47.75 (1.80)
Typha glauca	10.78 (1.19)	23.41 (5.58)	17.62 (1.86)	34.00 (7.31)	119.00 (7.77)
Viola lanceolata	3.43 (0.93)	2.71 (0.48)	2.29 (0.58)	2.00 (0.37)	27.66 (2.84)
Xyris difformis	0.08 (0.03)	0.09 (0.01)	0.02 (0.01)	0.02 (0.00)	5.88 (1.30)

APPENDIX 2.2

Mean + standard error (indicated in brackets) for canopy diameter, leaf length, leaf width, leaf are leaf mumber and leaf shape for 44 species of herbaceous wetland plants (five replicates per species Leaf width and canopy diameter were taken at the widest point. Leaf shape was estimated as the rati of length to width and relates generally to the degree of attenuation of the leaf. All plants were grow in a high nutrient sterile organic medium (Promix^R). All measurements are from species grown with th phytometer.

Appendix 2.2 cont'd

Species	Canopy Diameter (cm)	Leaf Length (cm)	Leaf Width (cm)	Leaf Area (cm)	Leaf Number	Leaf Shape
Acorus calamus	14.40 (0.87)	77.60 (2.71)	0.86 (.09)	66.98 (7.39)	12.00 (0.00)	94.00 (9.88)
Anenome canadensis	13.40 (3.57)	8.40 (0.54)	8.60 (1.57)	54.80 (14.58)	10.20 (2.58)	1.40 (0.15)
Bidens cernua	19.60 (1.91)	10.10 (0.75)	1.64 (0.10)	16.73 (1.97)	59.20 (13.22)	6.16 (0.39)
Carex crinita	30.20 (6.93)	53.24 (6.64)	0.43 (0.02)	23.02 (3.50)	88.00 (17.34)	124.70 (14.49)
Carex rostrata	21.75 (1.69)	71.75 (3.84)	0.60 (0.09)	43.65 (4.67)	36.25 (11.06)	122.30 (24.23)
Drosera intermedia	2.00 (0.10)	1.50 (0.01)	0.10 (0.00)	0.15 (0.02)	4.00 (2.00)	15.00 (0.04)
Dulichium arundinaceum	9.00 (1.19)	6.38 (0.55)	0.43 (0.03)	2.74 (0.37)	314.25 (88.29)	15.25 (1.05)
Eleocharis erythropoda	0.10 (0.01)	58.30 (3.51)	0.10 (0.00)	6.00 (0.35)	82.30 (36.04)	600.00 (35.12)
Eleocharis palustris	9.00 (0.10)	60.00 (4.06)	0.10 (0.00)	6.10 (0.41)	42.80 (8.15)	610.00 (40.62)
Eriocaulon septangulare	1.70 (1.67)	1.00 (0.00)	0.12 (0.02)	0.12 (0.02)	74.00 (23.13)	8.90 (1.10)
Eupatorium maculatum	14.50 (0.50)	11.25 (0.48)	4.00 (0.03)	45.00 (1.91)	142.00 (19.08)	2.80 (0.12)
Gallium palustris	58.50 ((3.77)	1.05 (0.13)	0.30 (0.07)	0.32 (0.10)	502.50 (56.33)	4.10 (1.03)
Hypericum ellipticum	11.75 (1.18)	2.14 (0.12)	1.36 (0.21)	2.98 (0.58)	320.00 (16.33)	1.67 (0.20)
Impatiens capensis	14.50 (0.87)	1.63 (0.38)	0.80 (0.18)	1.50 (0.61)	12.50 (2.50)	2.00 (0.02)
Iris versicolor	23.00 (5.68)	61.67 (4.67)	1.57 (0.07)	97.00 (10.90)	19.33 (7.84)	39.33 (2.19)
Juncus filiformis	0.11 (0.01)	63.00 (6.16)	0.11 (0.01)	6.87 (0.73)	52.00 (8.83)	592.00 (79.85)
Juncus militaris	0.47 (0.18)	45.25 (7.92)	0.20 (0.02)	9.05 (1.58)	6.50 (1.71)	226.25 (39.60)
Juncus pelocarpus	2.33 ((0.33)	16.33 (3.71)	0.10 (0.00)	1.63 (0.37)	40.67 (5.93)	163.33 (37.12)

Appendix 2.2 cont'd

Species	Canopy Diameter (cm)	Leaf Length (cm)	Leaf Width (cm)	Leaf Area (cm)	Leaf Number	Leaf Shape
Leerzia oryzoides	20.40 (7.79)	20.00 (1.15)	0.77 (0.88)	15.20 (1.44)	102.00 (21.38)	27.33 (4.84)
Lobelia dortmanna	3.50 (0.54)	3.28 (0.24)	0.18 (0.01)	0.62 (0.07)	28.75 (7.18)	12.50 (1.44)
Lysimachia ciliata	14.00 (1.14)	7.60 (0.24)	3.14 (0.22)	23.98 (2.24)	97.60 (9.41)	2.46 (0.14)
Lysimachia nummularia	99.30 (15.71)	2.62 (0.48)	2.00 (0.18)	6.38 (1.28)	16.67 (2.83)	1.13 (0.03)
Lysimachia terrestris	11.67 (0.89)	6.00 (0.29)	1.73 (0.15)	10.48 (1.38)	133.33 (8.82)	3.53 (0.12)
Lysimachia thrysiflora	17.50 (1.32)	9.50 (0.74)	3.00 (0.46)	29.53 (6.54)	99.00 (8.23)	3.30 (0.26)
Lythrum salicaria	24.75 (4.49)	9.13 (0.59)	1.63 (0.16)	14.63 (1.09)	97.50 (17.96)	5.86 (0.87)
Mentha arvensis	17.00 (2.57)	6.60 (0.24)	2.90 (0.10)	19.20 (1.20)	151.60 (26.58)	2.32 (0.07)
Onoclea sensibilis	13.00 (1.41)	12.20 (0.75)	12.20 (1.07)	146.00 (7.81)	16.40 (1.17)	1.04 (0.15)
Polygonum hydropiperoides	17.60 (1.60)	8.90 (0.56)	1.75 (0.14)	17.02 (2.15)	56.00 (5.78)	4.90 (0.28)
Panicum longifolium	8.00 (1.09)	42.4 (7.14)	0.54 (0.02)	23.16 (4.53)	24.20 (3.02)	78.28 (9.96)
Phalaris arundinaceae	30.80 (3.28)	20.60 (2.26)	1.18 (0.07)	24.58 (2.66)	164.20 (15.89)	17.70 (0.40)
Pilea pumila	11.00 (2.45)	5.38 (0.47)	3.13 (0.24)	17.13 (2.60)	95.50 (13.18)	1.70 (0.04)
Potentilla anserina	15.67 (2.67)	26.67 (0.88)	6.00 (0.84)	160.00 (5.29)	19.67 (2.03)	4.43 (0.12)
Ranunculus reptans	3.38 (1.40)	1.75 (0.25)	0.20 (0.00)	0.35 (0.05)	4.75 (2.06)	8.75 (1.25)
Rhyncosporaa fusca	5.67 (1.45)	18.67 (0.33)	0.15 (0.03)	2.83 (0.58)	40.67 (14.62)	134.00 (24.83)
Rumex verticillatus	18.67 (1.20)	9.33 (0.88)	2.17 (0.17)	20.17 (2.09)	15.67 (2.33)	4.37 (0.57)
Sabbatia kennedyana	9.38 (2.59)	6.05 (1.89)	0.73 (0.08)	4.70 (1.72)	37.00 (7.15)	7.93 (2.06)

Appendix 2.2 cont'd

Species	Canopy Diameter (cm)	Leaf Length (cm)	Leaf Width (cm)	Leaf Area (cm)	Leaf Number	Leaf Shape
Scirpus fluviatilis	40.00	32.38	0.73	23.55	49.75	46.63
	(8.16)	(2.48)	(0.09)	(3.90)	(5.72)	(6.53)
Scirpus validus	0.50	83.18	0.53	57.98	12.00	208.25
	(0.04)	(6.76)	(0.03)	(6.54)	(2.19)	(4.37)
Spartina pectinata	11.67	41.33	0.83	34.07	16.33	51.00
	(1.88)	(4.67)	(0.09)	(3.72)	(2.18)	(10.01)
Stachys palustris	13.80	5.20	1.45	7.68	190.00	3.59
	(1.62)	(0.56)	(0.10)	(1.18)	(25.21)	(0.31)
Triadenum fraseri	16.75	4.50	2.28	10.35	86.00	2.00
	(3.15)	(0.42)	(0.13)	(1.28)	(9.90)	(0.12)
Typha latifolia	30.80	94.20	0.74	68.32	33.20	139.00
	(4.87)	(5.99)	(0.09)	(7.42)	(5.74)	(24.96)
Viola lanceolata	30.33	20.67	2.17	44.67	27.60	9.67
	(0.33)	(1.22)	(0.17)	(2.91)	(3.93)	(0.88)
Xyris difformis	3.13	5.87	0.20	1.18	13.20	29.38
	(0.55)	(1.30)	(0.02)	(0.26)	(5.06)	(6.49)

Appendix 2.3 Spearman rank correlation (r_s) between plant traits for 44 herbaceous plant species (five replicates per species). Values in bold lettering are significant at p <.001.

	Below-ground biomass	Height	Leaf Number	Leaf Area	Leaf Length	Leaf Width	Canopy Diameter	Canopy Area
Above-ground Biomass	**0.92** **p<.00001**	**0.80** **p<0.00001**	0.35 p=.0228	**0.65** **<.00001**	0.36 p=0.0195	**0.52 ·** **p<.0007**	**0.64** **p=<.00001**	**0.74** **p<.00001**
Below-ground Biomass		**0.80** **p<.00001**	0.32 p=.0353	**0.67** **p<0.00001**	0.41 p=.0068	0.48 p<.0015	**0.51** **p=.0007**	**0.64** **p<.00001**
Height			0.24 p=.1120	**0.51** **p<.0009**	**0.61** **p=.0001**	0.12 p=.4279	0.32 p=.0340	0.44 p=.0041
Leaf Number				-0.07 p=.6450	-0.17 p=.2674	0.18 p=.2366	0.23 p=.1370	0.45 p=.0032
Leaf Area					**0.65** **p<.00001**	**0.64** **p<.00001**	0.43 p=.0046	**0.73** **p<.00001**
Leaf Length						-0.10 p=.5008	0.04 p=.7943	0.30 p=.0501
Leaf Width							**0.53** **p=.0005**	**0.70** **p<.00001**
Canopy Diameter								**0.63** **p<.00001**

Appendix 2.4

Mean above-ground biomass of test species grown with the phytometer *Penthorum sedoides* (five replicates per species).

Species	**Above-ground Biomass (g)**	**Standard Error**
Juncus filiformis	1.14	0.14
Lysimachia nummularia	6.28	0.81
Onoclea sensibilis	1.44	0.23
Panicum longifolium	3.12	0.44
Ranunculus reptans	0.02	0.001
Rhyncospora fusca	0.22	0.05
Rumex verticillatus	3.52	0.34
Scirpus fluviatilis	9.08	0.63
Spartina pectinata	4.67	0.58
Xyris difformis	0.02	0.01

APPENDIX 3.1

Composition of stock solution used to prepare full-strength Hoagland's solution: the one-tenth Hoagland's solution was prepared by adding one part of full-strength solution to nine parts of water. Note that the combined stock for minor elements was always prepared immediately before use from separate stocks of each minor element to prevent precipitation.

Stock solution composition ($g\ dm^{-3}$)		**Full strength solution** (cm^3 made to 1.0 dm^3 with distilled water)
KNO_3	101.1	5.0
$Ca(NO_3)24H_2O$	236.2	2.0
$MgSO_4.7H_2O$	246.5	5.0
KH_2PO_4	136.0	1.0
Minor element (volume of stock)		1.0

Minor element stock composition ($g\ dm^{-3}$)		**Combined stock** (cm^3 made to 1.0 dm^3 with distilled water)
H_3BO_3	2.9	2.9
$MnCl_2.4H_2O$	18.1	10.0
$ZnSO_4.7H_2O$	22.0	1.0
MoO_3	0.7	10.0
$CuSO_4.5H_2O$	1.25	6.4

APPENDIX 4.1

Mean + standard error (indicated in brackets) for starting biomass of species (10 replicates per species).

SPECIES	Starting Above-ground Biomass (g)	Starting Below-ground Biomass (g)
Acorus calamus	0.39 (0.023)	0.94 (0.072)
Carex crinita	0.62 (0.085)	0.41 (0.059)
Dulichium arundinaceum	0.26 (0.036)	0.27 (0.042)
Eleocharis acicularis	0.07 (0.006)	0.06 (0.009)
Eleocharis calva	0.08 (0.014)	0.14 (0.025)
Euthamia galetorum	0.04 (0.005)	0.07 (0.009)
Hypericum ellipticum	0.02 (0.005)	0.01 (0.009)
Juncus filiformis	0.07 (0.005)	0.06 (0.007)
Juncus pelocarpus	0.01 (0.005)	0.01 (0.007)
Lysimachia terrestris	0.12 (0.027)	0.13 (0.036)
Lythrum salicaria	0.19 (0.039)	1.35 (0.249)
Mentha arvensis	0.11 (0.028)	1.04 (0.071)
Phalaris arundinaceae	0.44 (0.101)	0.45 (0.097)
Rumex verticillatus	0.10 (0.042)	0.53 (0.145)

SPECIES	Starting Above-ground Biomass (g)	Starting Below-ground Biomass (g)
Scirpus fluviatilis	0.07 (0.016)	2.40 (0.457)
Scirpus torreyi	0.05 (0.012)	0.09 (0.025)
Sparganium eurycarpum	0.24 (0.041)	0.92 (0.127)
Spartina pectinata	1.14 (0.232)	1.27 (0.477)
Triadenum fraseri	0.02 (0.002)	0.01 (0.003)
Typha xglauca	1.47 (0.173)	1.23 (0.181)
Viola lanceolata	0.05 (0.006)	0.12 (0.034)