COMPETITION INTENSITY AND ITS ABOVE- AND BELOW-GROUND COMPONENTS IN TWO CONTRASTING WETLAND PLANT COMMUNITIES

by

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ABSTRACT

A fundamental question in plant ecology is if and how the intensity of competition changes with productivity. This question has been the source of considerable discussion during the last two decades, yet few experiments have tested whether competition intensity changes with productivity in nature. Even fewer studies have separated competition into its above- and below-ground components in the field. I used a field experiment to measure total competition intensity and its above- and below-ground components in two wetlands that represent extremes in habitat productivity: an infertile sandy shoreline and a fertile bay. Transplants of *Lythrum salicaria* and *Carex crinita* were grown with no neighbours, with roots of neighbours only and with all neighbours; their growth rates were used to estimate competition intensity. The experiment was carried out to answer the following main questions:

(1) Is there a difference in total, above- and below-ground competition intensity in two wetlands that differ in standing crop?

(2) Is there an effect of standing crop on total, above- and below-ground competition intensity when the data from the two wetlands are combined?

Both total and above-ground competition intensity were found to be greater in the high standing crop wetland but below-ground competition did not differ between wetlands (CI_{TOTAL}: $p<0.00001$, CI_{ABOVE}: $p=0.0013$, CI_{BELOW}: $p=0.58$). Mean total competition increased from 0.16 to 0.43, the above-ground component increased from -0.063 to 0.21 and the below-ground component was close to 0.20 in both wetlands. Total and above-ground competition intensity

were significantly affected by standing crop in the wetlands studied but below-ground competition intensity was not (CI_{TOTAL}: p=0.0001, CI_{ABOVE}: p=0.0001, CI_{BELOW}: p=0.89). The result that competition was predominantly below-ground in the low standing crop wetland supports previous work in agricultural pot experiments (Wilson 1988) and terrestrial field studies (Wilson and Tilman 1991, Putz and Canham 1992, Wilson and Tilman 1993, Wilson in press). The result that root and shoot competition were roughly equal in the high standing crop wetland is not typical of past studies.

Additional field measurements and analyses were conducted to answer secondary questions related to species effects on measures of competition intensity, resource availability and wetland community production and species composition. In summary, the results of this study suggest that the total amount of competition increases with productivity in wetlands and that this increase is primarily due to an increase in competition for above-ground resources.

RÉSUMÉ

Y a-t-il et comment l'intensité de la compétition varie en fonction de la productivité est une question fondamentale en écologie végétale. Au cours des vingt dernières années cette question a généré beaucoup de discussion et, jusqu'à présent, peu d'études en milieu naturel ont testé les variations de l'intensité de la compétition en fonction de la productivité. De plus, parmi celles-ci, peu ont fait la distinction entre les deux composantes de la compétition, soit la compétition au-dessus du sol et celle sous le sol. Cette étude, en milieu naturel, mesure l'intensité de la compétition totale, de même que celle de ses deux composantes (au-dessus et sous le sol) dans deux sites de terres humides qui représentent les deux extrêmes de productivité; une rive sablonneuse infertile et une baie fertile. Des plants de *Lythrum salicaria* et *Carex crinita* ont été cultivés soit sans voisins ou avec des voisins au niveau des racines seulement ou avec des voisins au niveau des racines et des parties aériennes. Le taux de croissance de ces plants a été utilisé comme mesure de l'intensité de la compétition. Cette étude a été conduite afin de répondre à deux questions principales:

1) Y a-t-il une différence entre l'intensité de la compétition totale, celle au-dessus et celle sous le sol dans ces deux sites de terres humides dont la biomasse totale est différente?

2) Y a-t-il un effet de la biomasse totale sur l'intensité de la compétition totale, celle au-dessus et celle sous le sol quand les données des deux sites de terres humides sont combinées?

L'intensité de la compétition totale (CI_{TOTAL}) et celle au-dessus du sol (CI_{ABOVE}) sont plus élevées dans les terres humides dont la biomasse totale est élevée (CI_{TOTAL}: $p< 0.00001$, CI_{ABOVE}: $p=0.0013$). La compétition sous le sol (CI_{BELOW}) n'est pas différente quel que soit la biomasse totale (CI_{BELOW}: $p=0.58$). La compétition totale moyenne augmente de 0.16 à 0.43, celle au-dessus du sol augmente de -0.063 à 0.21 et celle sous le sol est près de 0.20 aux deux sites de terres humides. L'intensité de la compétition totale au-dessus du sol est significativement influencée par la biomasse totale des terres humides mais l'intensité de la compétition sous le sol ne l'est pas (CI_{TOTAL}: $p=0.0001$. CI_{ABOVE}: $p=0.0001$, CI_{BELOW}: $p=0.89$).

Dans le but de répondre à des questions supplémentaires concernant l'effet des espèces sur les mesures de l'intensité de la compétition, la disponibilité des ressources, la productivité de la communauté des terres humides et la composition taxinomique, des analyses et des mesures supplémentaires ont été effectuées. De façon générale, les résultats suggèrent que la compétition augmente avec la productivité des terres humides et cette augmentation est reliée à une augmentation de la compétition pour les ressources au-dessus du sol.

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INTRODUCTION

Background

Competition, defined here as the negative effects that one organism has upon another by consuming or controlling access to a resource that is limited in availability (Keddy 1989a), has been shown to occur in nature (Connell 1983, Schoener 1983, Gurevitch *et al.* 1992) and is believed to be an important biotic process affecting the distribution and abundance of organisms (Grubb 1985, Keddy 1989a). Since one of the first plant competition studies was done (Clements *et al.* 1929), plant competition has been well documented (Gurevitch *et al.* 1992) through observation and experimentation. Field experiments yield realistic results and permit the manipulation of independent variables (Diamond 1986), and may therefore provide the best way to resolve questions about competition between organisms (Gurevitch *et al.* 1992). Most field experiments involving plants have addressed the question of whether competition occurs, and it does occur with high frequency in natural communities (Goldberg and Barton 1992). There is now a need for plant field experiments that address the question of whether the magnitude of competition varies in time and space (Keddy 1989a, Goldberg and Barton 1992).

Total competition intensity

It has long been observed that plant species composition, plant species diversity and plant growth forms vary in nature with productivity (Whittaker 1975, Grime 1979, Tilman 1988). Productivity in this case and hereafter refers to primary productivity, defined here as the rate at which energy is bound or organic material created by photosynthesis, per unit area of the earth's surface per unit time (Whittaker 1975). One fundamental question is if and how productivity influences the role of competition in determining community structure (Grime 1979, Tilman 1988, Keddy 1989a, Turkington *et al.* 1993). There are two prevalent views in the literature. Some ecologists believe that competition intensity increases with productivity (Huston 1979, Keddy 1989a, 1990, Wisheu and Keddy 1992, Grime 1973, 1974, 1979, Thompson and Grime 1988, Campbell and Grime 1992). According to this view, species composition in unproductive habitats is controlled mainly by abiotic processes, and a plant's survival in such a habitat depends on its ability to minimize resource demands. In productive sites, species composition is thought to be primarily controlled by biotic processes, such as competition, and a plant's survival in such a habitat results from its high competitive ability. It is thought that increased productivity will lead to higher growth rates, increased amounts of biomass, greater demand for resources and increased chances for plant interactions and therefore to an increase in the amount of competition. Others believe that competition intensity remains constant as productivity changes (Newman 1973, Tilman 1982, 1988, Grubb 1985). It is thought that plants compete intensely for soil resources in unproductive soils and for light resources in productive sites leading to a qualitative change in total competition intensity, as opposed to a quantitative change. According to this view, competition is important regardless of the productivity level and a species is specialized for and has a high competitive ability at a particular resource ratio along the productivity gradient. More recently, some have suggested that competition is not necessarily correlated with productivity because it depends on the ratio of resource supply to demand which may be unrelated to productivity (Taylor *et al.* 1990).

Until recently, this issue has been complicated by a number of factors. Different definitions for competition and competitive success have been used (Grace 1991) and the intensity of competition has not been distinguished from the importance of competition (Weldon and Slauson 1986, Grace 1991). There has also been a lack of consideration for whether competition intensity refers to the per gram, per plant or per community effect of competition (Grace 1991) and there has been a failure to distinguish between resource and non-resource productivity gradients (Grace 1991). Finally, there have been few field experiments designed to test directly whether the magnitude of competition varies with productivity (Grace 1993, Taylor *et al.* 1990, Wilson and Keddy 1991) (**Table 1**).

Previous field experiments

The results of field experiments that have tested whether competition varies with productivity are contradictory (**Table 1**). If one tries to compare existing field results to make generalizations, one finds that competition has been evaluated along a range of productivity gradients such as soil depth, nutrient availability, standing crop, and topography in a range of vegetation communities including alvars, mixed-grass prairies, abandoned pastures, old fields and shorelines (**Table 1**). In addition, the intensity of competition has been calculated in two different ways. In some studies, it has been calculated as the absolute reduction due to competition while in others it has been calculated as the relative reduction, which tends to be less sensitive to changes in productivity (Campbell and Grime 1992, Turkington *et al.* 1993, Reader *et al.* in press).

My experiment

Given the importance of this problem and the contradictory results of previous experiments, I used a field experiment involving introduced transplants to measure plant competition intensity in two communities that differ in standing crop. Final standing crop is used here as an estimate of the production of the community (Chapman 1976, Whigham *et al.* 1978) because net primary productivity is difficult to measure directly in the field (Whittaker and Lieth 1975).

This study was designed to yield 30 measures of competition intensity in each wetland community, which were used to answer the following main question:

(1) Is mean total competition intensity different in two wetlands that differ in standing crop?

There was natural variation in standing crop within and among wetlands and, to obtain a predictive and general result that focused solely on the differences in standing crop, I also asked:

(2) Is there an effect of standing crop on total competition intensity?

These two questions were translated into the following hypotheses:

(1)Ho: mean total competition intensity is not different in two wetlands that differ in standing crop.

(2)Ho: there is no effect of standing crop on total competition intensity.

The components of competition

Competition among plants occurs primarily for light, soil nutrients and water (Clements *et al.* 1929) and to a lesser extent for carbon dioxide, oxygen, space and pollinators (Newman 1981). Competition for light occurs above-ground and competition for soil nutrients and water occurs below-ground. To gain more information about the nature of competitive interactions one needs to quantify the relative amounts of competition occurring above- and below-ground by separating competition into these two components.

As well as determining if and how competition intensity varies with productivity it is important to determine if and how the above- and the below-ground components vary with productivity. Again, there are different views in the literature. Some ecologists believe that both above- and below-ground competition increases with increasing productivity (Grime 1979). The low nutrient supply in unproductive habitats is thought to decrease the chance that neighbours will interact. An increase in soil resources may then lead to an increase in plant growth and demand on both above- and below-ground resources, which in turn may lead to increased competition among plants. This would result in a positive correlation between the two components of competition along a productivity gradient. Others argue that there is a trade-off between above- and below-ground competition. Above-ground competition is thought to be greater where productivity is higher because light is limiting. Similarly, below-ground competition is higher where productivity is less because soil resources are limiting (Tilman 1988). This would result in an inverse relationship between the two components along a productivity gradient.

Previous field experiments

Field measurements are required to properly test predictions concerning patterns of above- and below-ground competition intensity with productivity (Wilson and Tilman 1993), yet the number of field experiments that have separated the intensity of competition into above- and below-ground components is low (**Table 2**). To date these studies have all been done in terrestrial plant communities, they have used different kinds of productivity gradients in different types of plant communities and their results have varied.

My experiment

The separation of competition into its above- and below-ground components in wetland communities has not previously been done. My design permits the separation of total competition intensity into its two components to yield 30 measures of above-ground competition intensity and 30 measures of below-ground competition intensity in two different wetlands. These measurements are used to answer the following questions:

(3) Is mean above-ground competition intensity different in the two wetlands?

(4) Is mean below-ground competition intensity different in the two wetlands?

(5) Is there an effect of standing crop on mean above-ground competition intensity?

(6) Is there an effect of standing crop on mean below-ground competition intensity?

The remaining main questions were translated into the following hypotheses:

(3)Ho. mean below-ground competition intensity is not different in two wetlands that differ in standing crop

(4)Ho: there is no effect of standing crop on below-ground competition intensity.

(5)Ho: mean above-ground competition intensity is not different in two wetlands that differ in standing crop

(6)Ho: there is no effect of standing crop on above-ground competition intensity.

Although it would be ideal to test for an effect of standing crop on competition intensity and its two components in a large number of wetland communities, this is not feasible when using an experimental design that requires continual supervision and field measurements. An alternative is to establish the experiment in two communities that represent two extremes in standing crop, which is what I have done. The design is simple and involves a large number of replicates and thus provides ecological data that can be easily interpreted (Gurevitch *et al.* 1992) using standard statistical techniques.

Wetlands as a study system

I used wetlands for four main reasons. First, there are clear patterns of variation in wetland vegetation with productivity. Vegetation is known to change with standing crop (Day *et al.* 1988, Moore *et al.* 1989, Wilson and Keddy 1988, Vermeer and Berendse 1983, Wisheu and Keddy 1989) and soil fertility (van der Valk 1981, Vermeer and Berendse 1983, Moore *et al.* 1989, Wilson and Keddy 1988, Day *et al.* 1988, Wisheu and Keddy 1989). Second, competition has been found to be an important biotic force in the structure of wetland plant communities (Buttery and Lambert 1965, Grace and Wetzel 1981, Wilson and Keddy 1986a, Wilson and Keddy 1986b, Gaudet and Keddy 1988, Keddy 1989b). Third, wetlands are important ecosystems and information about the processes involved in plant community structure is essential for proper conservation and management. Wetlands provide habitat for diverse flora and fauna (Mitsch and Gosselink 1986, National Wetlands Working Group 1988). They are hydrologically important for providing natural sinks, sources and transformers of biological, chemical and genetic materials, cleaning polluted water, preventing floods, protecting shorelines (Mitsch and Gosselink 1986) and the storage and slow release of water (National Wetlands Working Group 1988). Wetlands are also extensively used for recreational activities and are economically valuable (National Wetlands Working Group 1988). Finally, wetlands are suitable for transplant experiments because standing water and moist soil at the beginning of the growing season help to reduce the risk of transplant shock.

The use of indicator species

This experiment also addresses some secondary issues. One of these relates to the use of indicator species or phytometers (Clements and Goldsmith 1924, Clements 1935) to measure competition intensity. An indicator species can be planted into a community and the total effect of neighbouring plants on indicator plant traits, such as relative growth rate, final biomass, survivorship, basal area etc., can be measured. It is a realistic index of competition because a plant competes with all surrounding plants simultaneously in nature and not with one plant at a time (Wilson and Keddy 1986a). This method has two primary advantages. First, it provides a general and comparative approach to measuring the magnitude of competition occurring in a community. Second, it is a practical alternative to the formidable task of measuring the amount of competition between each pair of individuals or species.

In some studies it has been found that the choice of indicator species has had no effect on the results (Gaudet and Keddy 1988). Others have found that the choice of indicator species affects measures of the magnitude of competition (DiTommasio and Aarrsen 1989, Wilson and Keddy 1986a, Wilson in press), the relative importance of below- and above-ground competition (Putz and Canham 1992) and the importance of competition (Reader and Bonser 1993). For this reason, I decided to base my measures of competition intensity on the mean results for two common wetland species. These wetland species were chosen because they represent two very different wetland plant guilds (Boutin and Keddy 1993), both of which typify common wetland morphologies.

A further question posed here is whether the results are the same using two very different indicator species. The previously stated six questions are repeated for both species separately to determine whether the choice of indicator species affected the results.

Field measurements

The remaining secondary issues addressed in this study relate to the two wetland communities studied and assumptions involved in the experimental design. Field measurements were done to aid in the interpretation of the competition results and provide practical background for future work. Measurements including initial standing crop, final standing crop, litter, species composition, light intensity, soil nutrient content and climatic information were collected to make three sets of comparisons at increasing scales:

(1) Between treatments:

Do the following differ among treatments:

(a) light availability?

(b) concentrations of soil macronutrients and soil pH?

(2) Between wetlands:

Do the following differ between the two wetland communities:

(a) standing crop?

(b) amount of standing crop produced during the growing season?

(c) amount of litter?

(d) plant community composition?

(e) light availability?

(f) concentrations of soil macronutrients and soil pH?

(3) Across years:

Are the number of sunlight hours, air temperature and total precipitation in the summer months of 1992 different from those of the previous 30 summers?

These secondary questions were translated into the following hypotheses:

Standing crop, production of standing crop and litter

(1)Ho: there is no difference in mean standing crop in the two wetlands.

(2)Ho: there is no difference in mean production of standing crop in the two wetlands.

(3)Ho: there is no difference in mean litter in the two wetlands.

Light intensity and soil data

Between-subject hypotheses:

(1)Ho:there is no effect of wetland community on mean light penetration, [NO_3], [P], [K], [Mg], and pH.

(2)Ho: there is no effect of experimental treatment on mean light penetration, [NO_3] etc.

(3)Ho: there is no interaction between wetland community and experimental treatment.

Within-subject hypotheses:

(4)Ho: there is no effect of sampling time on mean light penetration, [NO_3] etc.

(5)Ho: there is no interaction between wetland community and sampling time.

(6)Ho: there is no interaction between experimental treatment and sampling time.

(7)Ho: there is no interaction among wetland community, experimental treatment and sampling time.

Weather data

(1)Ho: mean bright sunshine hours, mean air temperature and total precipitation during June, July August and September of 1992 are not different from the monthly means for the 30 previous years.

Table 1. Summary of field studies that have measured total competition intensity along environmental gradients.

Author(s)	**Gradient studied**	**Indicator trait(s)**	**Competition increased with increasing productivity**
Belcher *et al.* (submitted)	soil depth in alvar	shoot biomass	no
Gurevitch (1986)	topographic/moisture in grassland	# flowers/plant, RGR of basal area, seedlings established, seedlings survived,	yes
Reader (1990)	nutrient in abandoned pasture	recruitment of rosettes, survival of rosettes	yes
Reader & Best (1989)	nutrient, light & standing crop in abandoned pasture	population growth rate, # rosettes established, # rosettes survived,	yes
Reader *et al.* (in press)	standing crop in grassland	RGR of shoot biomass	no&yes*
Wilson & Keddy (1986a)	fertility on shoreline	total biomass	yes
Wilson & Shay (1990)	nutrient & disturbance in mixed grass prairie	basal area, growth in basal area, tiller #	no
Wilson & Tilman (1991)	nitrogen in old field	% flowering per individual, % flowering stems/plant, leaf #, mean tiller length, RGR of shoot biomass, root biomass, % survival, tiller #, total tiller length,	no
Wilson & Tilman (1993)	nitrogen & disturbance in old field	proportion of biomass dead, proportion of biomass = tillers, RGR of stem biomass, total biomass	no&yes**

*Results depend on biomass range.
**No variation along nitrogen gradient but variation along disturbance gradient.

Table 2. Field studies that have separated competition intensity into its above and below-ground components.

Author(s)	System	Traits measured	Variation in CI_{ABOVE}	Variation in CI_{BELOW}
Belcher *et al.* (accepted)	soil depth in alvar	final biomass	no	no
Putz and Canham (1992)	nutrient in shrublands	RGR of above-ground biomass, RGR of basal area, RGR of height	increases with productivity	decreases with productivity
Wilson & Tilman (1993)	nitrogen and disturbance in old field	proportion of biomass=tillers, proportion of biomass dead, RGR of stem biomass, total biomass	increases with productivity	decreases with productivity
Wilson (1993)	standing crop in prairies & forest	above-ground biomass, survivorship		decreases with productivity
Wilson (in press)	nitrogen and moisture in heath and grasslands	RGR above-ground biomass, % survival	no	decreases with productivity

METHODS

Study site

The experiment was carried out in two wetland communities at Westmeath Provincial Park (lat.:45° 47.8', long.:76° 53.5') which is located 16.5 km west of the city of Pembroke, Ontario and 110 air km northwest of Ottawa. One wetland is a low standing crop wetland that was located along the shoreline of the Ottawa River. The other is a high standing crop wetland that was located in Bellow's Bay, a bay of the same river. These sites were chosen for two main reasons. First, the biomass of these wetlands was already known (Day *et al.* 1988, Moore and Keddy 1989, McCanny *et al.* 1990) and it was known that they represented two extremes in wetland biomass for eastern Ontario and western Quebec wetlands (Day *et al.* 1988, Moore and Keddy 1989, McCanny *et al.* 1990, Shipley *et al.* 1991, Lee 1993, Gaudet 1994). Second, the wetlands were approximately one km apart making the environment similar in most respects other than those factors related to productivity.

Experimental design

A vegetation removal experiment involving introduced transplants (Aarrsen and Epp 1990) was conducted to measure competition intensity in the field. The design involved a "press" type perturbation experiment (Bender *et al.* 1984) where the density of neighbours was reduced and held at a new level throughout the experiment. The competition intensity values obtained reflect the total effect of neighbouring plants on an indicator plant. They therefore include both interference effects such as allelopathy and exploitative effects such as the depletion of shared resources (Connell 1990). Thirty experimental plots, each 2 X 8 m, were established in each wetland community on June 1 and 2, 1992. Each plot was divided into four equal subplots, 2 X 2 m. The four subplots were randomly assigned to three competition treatments and a control treatment using random numbers. The four treatments were as follows (**Figure 1**):

(1) Control (C) and (2) All Neighbours (AN): These were established by leaving all natural vegetation untouched.

(3) Roots Only (RO): This was established by using a square piece of black plastic netting (mesh size:1cm^2), which was 2.6 X 2.6 m in the low standing crop wetland and 2.8 X 2.8 m in the high standing crop wetland, to hold the shoots and leaves of the surrounding vegetation at an angle towards the outside of the subplot. The net was secured with string in the centre of the subplot by six 1 cm diameter aluminum rods which were arranged in two sets of three and inserted all the way into the ground. At the outside four corners of the subplot, the net was secured with string by four 1 cm diameter aluminum rods. Holes were cut in the netting between the two sets of central rods to allow for transplanting (**Appendix 1**).

(4) No Neighbours (NN): This was established by clipping all standing crop at soil level (June 3 - June 9) and applying a non-selective herbicide (Round Up; 38gL^{-1} glycophosphate; 500 ml in 25 L of water for 50 square meters) to all shoots that were not killed by clipping. All roots were cut around the outside of the subplot to a depth of approximately 30 cm.

Transplants

The two species used as indicator species or phytometers were *Lythrum salicaria* and *Carex crinita*. *Lythrum salicaria* belongs to the Lythraceae and is a large, purple flowered species which is rapidly spreading across North American wetlands (White and Haber 1992). *Carex crinita* belongs to the Cyperaceae, grows in swamp forests, ponds, ditches and wetland hollows in deciduous woods, river borders and marshes (Voss 1972) and is found from Newfoundland to Manitoba, south to Georgia and Missouri (Roland and Smith 1969). According to recent comparative studies, *Lythrum salicaria* is a ruderal facultative annual and *Carex crinita* is an interstitial tussock perennial (Boutin and Keddy 1993). They are both common wetland plants that naturally occur at Westmeath Provincial Park (Hough, Stansbury and Michalski, 1983). *Lythrum salicaria* occurred in the experimental plots in both wetlands when sampled at the end of the experiment. *Carex crinita* did not occur in the experimental plots when sampled at the end of the experiment but was found nearby in slightly drier sites in the high standing crop wetland.

The plants were started from seed on April 7, 1992 in the University of Ottawa greenhouse. The *Carex crinita* seeds were collected in August 1988 at Breckenridge, Quebec and the *Lythrum salicaria* seeds were collected in September 1988 at Luskville, Quebec; all seeds were stored moist at 4°C. They were planted in multipot trays using 98% organic, pH adjusted potting soil with sphagnum peat moss (Premier Soil, Dorval, Quebec). Once seeds had germinated and become established seedlings, they were transported to an outdoor compound at Carleton University, Ottawa, Ontario. When seedlings started to show signs of nutrient stress, they were fertilized using 0.08 g of Nutricote 14-14-14, a slow release fertilizer, which was approximately equal to 1 slow-release pellet per seedling container. The pellets were removed from the soil surrounding the plants before the plants were transplanted into the experiment.

Prior to transplanting, 210 transplants of each species that were most similar in size were selected from the seedlings grown. The height and the number of leaves of all 420 plants were measured. Thirty plants of each species were harvested, dried and their above- and below-ground biomass measured. The remaining 360 plants were transported to the field site and used in the experiment. From June 12-14 one transplant of each species was planted into the middle of all competition treatment subplots; the transplants were placed 50 cm apart. The transplanting process was completely randomized. A *Lythrum salicaria* and a *Carex crinita* transplant were randomly chosen for each treatment subplot within each experimental plot to reduce between wetland, among treatment and among plot variability in transplant initial biomass. The transplant species planted into each experimental plot was randomly planted by either my assistant or myself to prevent one of us always planting the same species. All transplanting was done on overcast days. The orientation of the plants in each experimental plot was randomly chosen from eight possible directions, north, northeast, east, southeast, south, southwest, west and northwest.

To prevent possible transplant shock, plants were partially shaded using inverted bottomless plastic pails and watered for a period of two weeks. During this time period, any transplants that died were replaced. Survivorship was very high; only two *Lythrum salicaria* and three *Carex crinita* seedlings needed to be replaced. The *Lythrum salicaria* transplants, especially those in the high standing crop NN treatments, showed signs of insect damage in August. A powder insecticide containing 1% Rotenone (tradename: SEVIN) was dusted on all *Lythrum salicaria* transplants every few days to reduce the effects of insectivory. Transplants in the fertile wetland were temporarily flooded in late July as a result of beaver activity. This was prevented from occurring again through regular removal of a section of a beaver dam at the mouth of the bay. The transplants were grown in the experiment until September 2-10, at which time they were harvested. The above-ground portion of the plants were cut off at soil level and bagged. The below-ground portion of the plants was harvested by removing a soil core from the ground that was 10 cm in diameter and 20 cm deep. The soil was washed from the below-ground structures which were then bagged separately. All plant material was dried to constant biomass and weighed. Six *Lythrum salicaria* and six *Carex crinita* transplants that were either greatly affected by herbivory or died of unknown causes were excluded from the analysis.

Relative growth rate calculations

The relative growth rate of the indicator plant was the dependent variable used to measure competitive effect. The final biomass of the transplants was obtained directly and the initial biomass of the transplants was estimated non-destructively using simple linear regression.

The equation used to calculate relative growth rate is :

$$r=\frac{\ln(B2/B1)}{T}$$

where B1 is the initial biomass of the transplant (in g)

B2 is the final biomass of the transplant (in g)

T is the growth period (in days)

Competition intensity equations

The equations used to calculate total competition intensity and its two components are:

Total competition intensity $(CI_{TOTAL})=\frac{(r_{NN}-r_{AN})}{r_{NN}}$

Below-ground competition intensity $(CI_{BELOW})=\frac{(r_{NN}-r_{RO})}{r_{NN}}$

Above-ground competition intensity $(CI_{ABOVE})=\frac{(r_{RO}-r_{AN})}{r_{NN}}$

where r_{NN}, r_{RO} and r_{AN} are growth rates of the transplant in the NN, the RO and the AN treatment respectively. All equations include the quotient r_{NN} to standardize the measurements to account for different relative growth rates between species and among experimental plots and thus they yield relative measures of competition intensity (Keddy 1989a, Campbell and Grime 1992, Grace 1993, Turkington *et al.* 1993). These equations were calculated separately for each indicator species and then averaged to calculate mean competition intensity for each experimental plot. Therefore, each plot yielded one CI_{TOTAL}, one CI_{BELOW} and one CI_{ABOVE} value, which are based on two wetland plant species. Initial and final total biomass of the transplants and the calculated competition intensity values are given in **Appendix 2.**

Standing crop, litter and species composition

Initial standing crop was measured in each plot by clipping and bagging the inside 1 m^2 area of each NN treatment subplot during initial experimental set up (June 3-9). The final standing crop was measured by clipping and bagging all biomass in the inside 1m^2 area of the C treatment subplot at the end of the experiment (September 13-19). The rate of production of biomass in $gday^{-1}$ over the course of the experiment was calculated as:

$$grsc = \frac{sc2 - sc1}{T}$$

where sc1 is the initial standing crop (in g)

sc2 is the final standing crop (in g)

T is the growth period (in days)

To describe the species composition of the communities, the final standing crop was separated by species, the species' biomass were bagged separately, dried to constant biomass and weighed. This was done for a random sample of 15 plots in each of the two wetlands. Litter was collected for the same two sets of 15 plots at the same time that final standing crop was collected.

Light measurements

Light intensity was measured in the same random sample of 15 plots in each wetland using a LICOR Photosynthetically Active Radiation Sensor. Light measurements were taken above the vegetation and 15 cm above the soil (the height of the light meter sensor) at five locations in each subplot. In the NN, AN and the C treatments, light was measured at the four corners of the central $1m^2$ square area of the subplot and in the centre of the subplot. This could not be done in the RO treatment because of the net so measurements were taken on both sides of each transplant and at three points in the centre of the subplot. Light measurements were done at three times during the experiment June 22-30, Aug. 5-Aug. 6 and Sept. 2-9 and done within three hours of noon. Light penetration was calculated as follows:

$$\text{light penetration} = \frac{I_B}{I_A}$$

where I_B is the light intensity at soil level (in microamps per 1000 umole $s^{-1}m^{-2}$)

I_A is the light intensity above the vegetation (in microamps per 1000 umole $s^{-1}m^{-2}$).

The five light penetration values per subplot were averaged to obtain one estimate for the amount of light available to the indicator plants in each experimental subplot at each sampling time.

Soil analysis

Soil samples were collected in the same random sample of 15 experimental plots in each wetland. Soil samples approximately 3 cm in diameter and 8 cm in depth were taken from the four corners of the central $1m^2$ square of each subplot and at the centre of each subplot. This was done for all four treatments in the experimental plots. The soil samples per subplot were then placed in one bag and thoroughly mixed. This was necessary to reduce the cost of analysis by four-fifths (from 1800 units to 360 units). Therefore, the experiment yielded one estimate of soil nutrient content per subplot. Soil sampling was done three times during the experiment; June 22-24; Aug. 4-8; Aug 31-Sept 1. The soil samples were stored at -15°C in a freezer until March 1993 at which time they were shipped to Agri-food Laboratory in Guelph, Ontario for analysis. A basic soil test was conducted on each soil sample. Soil nitrate concentration was measured using specific ion electrode techniques and soil phosphorous concentration was determined by measuring the amount of phosphorous per litre of filtrate. Soil potassium and magnesium concentrations were measured by using an atomic absorption spectrophotometer and pH was measured with a pH meter.

Weather data

Weather data were obtained from the Pettawawa National Forestry Institute located 35 air kilometres north northwest of the field experiment. The variables for which data were obtained were monthly bright sunshine hours, mean air temperature and total precipitation for May through September for the years 1961-1992. Standing crop, standing crop production, litter, soil data and light intensity data are given in **Appendix 3**.

Statistical analysis

Prediction of initial biomass of transplants

Simple linear regression was used to predict total biomass from leaf number and height (independent variables) of *Lythrum salicaria* seedlings. The linear regression equation which explained the most variation (had the highest r^2 value) was then used to predict the total biomass (dependent variable) of the 180 *Lythrum salicaria* seedlings used in the experiment. The same was done for *Carex crinita*. The linear equation used to predict the initial biomass of the *Lythrum salicaria* seedlings used in the experiment was logbiomass = 1.11 ± 0.092(logheight) - 1.60 ± 0.11 ($F=149.18$, $p=0.0001$; $r^2=0.84$) and that used to predict the initial biomass of *Carex crinita* seedlings was logbiomass = 1.83± 0.21(logheight) - 2.91 ± 0.29 ($F= 75.54$, $p=0.0001$; $r^2=0.73$). The estimates of variance for the slopes and intercepts are standard errors.

Competition intensity based on the mean of two indicator species

A two-tailed student's t-test was used to determine if mean total competition intensity was different in the two wetlands. Data from both wetlands were then combined to use a more general and predictive approach to determine whether there was a relationship between standing crop and total competition intensity. Simple linear regression was used to test for an effect of standing crop on total competition intensity. The same analyses were used for above- and below-ground competition intensity. When comparing means, a t-test adjusted for unequal variance was used when the assumption of equal variances was not satisfied. Power analyses were done for statistical tests when the null hypothesis was accepted. The results of these analyses are summarized in **Appendix 7**.

Competition intensity for each indicator species

All statistical analyses were repeated for each species separately to determine whether two very different wetland indicator species yielded similar results.

Standing crop and standing crop production

Two-tailed student's t-tests were used to determine whether mean standing crop, mean litter and the amount of standing crop produced during the experiment were different in the two wetlands.

Light measurements and soil analysis

Six two way ANOVA's with repeated measures were used to test for significant effects of wetland community, experimental treatment and sampling time on light penetration, four soil macronutrient concentrations and soil pH. SNK, Tukey and Bonferroni multiple comparisons were performed for significant between-subject main factors at each sampling time and the results were compared to determine which means differed. The SNK test tends to be liberal, the Bonferroni test is conservative and the Tukey test is intermediate between the other two (Zar 1984) so a comparison of the results from all three tests was thought to be more reliable than using the results for one test only.

When assumptions of normality and homoscedasticity of residuals were not satisfied, the dependent variable was transformed and the assumptions re-tested. When assumptions were satisfied after transformation, transformed data were used in the repeated measures ANOVA. When the assumptions were still not satisfied the original data was used because sample sizes were large and a non-parametric two-way ANOVA with repeated measures was not available.

Community composition

Mean abundance and the frequency of occurrence were calculated for each species in both of the wetlands. As well, the mean species richness (alpha diversity) and the total number of species were calculated for each wetland. As a further description, detrended correspondence analysis, which is an indirect gradient analysis, was used to search for major gradients in the species data irrespective of environmental data.

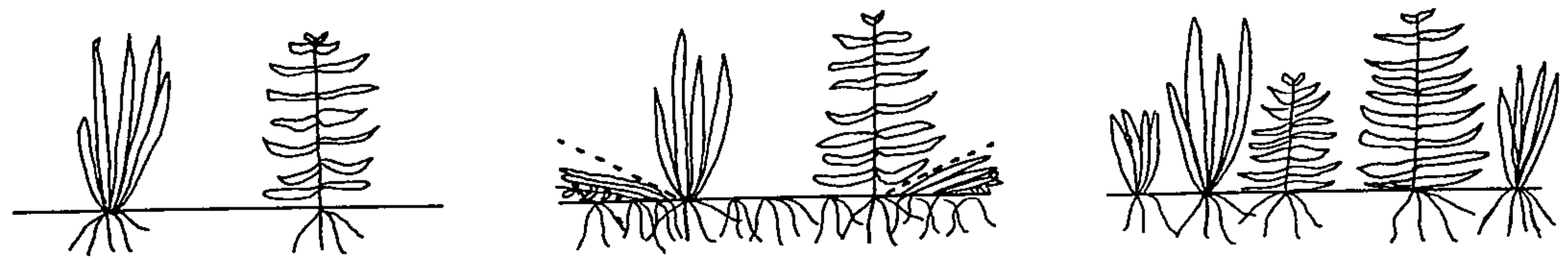
Weather data

To test whether bright sunshine hours, mean air temperature and total precipitation for the summer of 1992 differed from previous years, data for the summer 1992 was compared to that for the summers of 1962-1991. T-tests were used to test whether the 1992 observations differed significantly from the means for the past 30 years (Sokal and Rohlf 1981, pp. 228-231).

Statistical software

All statistical analyses were done using SAS 6.04 (SAS Institute 1990), Sigmastat 1.01 (Jandel Corporation 1992) and CANOCO (ter Braak 1992).

Figure 1. The treatments used to measure total competition intensity and its two components.



No neighbours Roots only All neighbours

RESULTS

Total competition intensity and its components

Both mean total competition intensity and mean above-ground competition intensity were different between the low and the high standing crop wetlands (total: $t=-4.93$, $p<0.00001$; above-ground: $t=-3.41$, $p=0.001$). **Figures 2a** and **2b** shows that mean total and above-ground competition intensity values were greater in the high standing crop wetland. In contrast, mean below-ground competition intensity was not different between the two wetlands ($t=-0.56$, $p=0.58$; **Figure 2c**). Total competition intensity was strongly related to standing crop ($F=31.96$, $p=0.0001$, $r^2=0.36$; **Figure 3a**). A significant relationship was also found between above-ground competition intensity and standing crop ($F=17.69$, $p=0.0001$, $r^2=0.24$; **Figure 3b**). There was no effect of standing crop on below-ground competition intensity ($F=0.018$, $p=0.89$, $r^2=0.0003$; **Figure 3c**).

Competition results for each indicator species

Carex crinita results

The two wetlands were significantly different in all three competitive interactions (total:

t=-5.92, p=0.0001; above-ground: t=-2.39, p=0.021; below-ground: t=-2.22, p=0.033). In all cases, mean competition intensity was greater in the high standing crop wetland (**Figures 4a**, **4b** and **4c**). Simple linear regression analysis detected a significant relationship between standing crop and total competition intensity (F=34.76, r^2=0.40, p=0.0001; **Figure 5a**). Similarly, a significant relationship was found between standing crop and above-ground competition intensity (F=8.77, r^2=0.14, p=0.005; **Figure 5b**). No significant effect of standing crop on below-ground competition intensity was detected (F=2.40, r^2=0.044, p=0.13; **Figure 5c**).

Lythrum salicaria results

Mean total competition intensity was not significantly different between the two wetlands based on *Lythrum salicaria* (Figure 6a) but differences were found for the above-ground and the below-ground components of competition (total: t=-0.38, p=0.70; above-ground: t=-2.38, p=0.022; below-ground: t=2.32, p=0.022). The above-ground component was greater in the high standing crop wetland but the reverse was found for the below-ground component (**Figures 6b** and **6c**). A relationship between standing crop and above-ground competition intensity was detected using linear regression (F=6.09, r^2=0.11, p=0.017; **Figure 7b**). Simple linear regression analysis failed to detect a significant relationship between standing crop and total competition intensity (F=0.78, r^2=0.014, p=0.38; **Figure 7a**). Nor was a significant relationship between standing crop and below-ground competition intensity found (F=3.79, r^2=0.070, p=0.057; **Figure 7c**).

Field measurements

Standing crop, standing crop production and litter

Mean standing crop, mean standing crop produced during the experiment and mean litter content in the two wetlands were different (**Table 3**). For all three environmental variables, the means were greater in the high standing crop wetland.

Light intensity

Light penetration was significantly affected by wetland community type (F=475.45, p=0.0001), experimental treatment (F=319.19, p=0.0001) and sampling time (F=170.31, p=0.0001) using a repeated measures analysis of variance. All interactions in the repeated measures ANOVA model were also significant. A summary of the repeated measures ANOVA is given in **Appendix 4a(a)** and the wetland, treatment and sampling time means and multiple comparison results are given in **Appendix 4a(b)**. Mean light penetration in each treatment in both wetlands at all three sampling times are plotted in **Figure 8a**. Most importantly mean light penetration was significantly greater in the low standing crop wetland and significantly greater in the NN and the RO treatments compared to the AN and the C treatments at all sampling times.

Soil nutrients

Nitrate: Soil nitrate concentration was significantly affected by wetland community type (F=393.84, p=0.0001) and the interaction between time and wetland was the only significant interaction term in the model (F=22.3, p=0.0001). A summary of the repeated measures ANOVA, the wetland, treatment and sampling time means and multiple comparisons are in Appendices **4b(a)** and **4b(b)**. Most importantly, mean [NO_3] was greater in the high standing crop wetland than in the low standing crop wetland at all three sampling times. Mean [NO_3] for all wetland, treatment and sampling time categories are plotted in **Figure 8b**.

Phosphorous: Wetland community type (F=2057.59, p=0.0001) and sampling time (F=16.5, p=0.0001) significantly affected soil [P] using an ANOVA with repeated measures (**Appendix 4c(a)**). The interaction between time and wetland was the only significant interaction term in the ANOVA model (F=57.23, p=0.0001). Mean [P] for all wetland, treatment and sampling time categories are plotted in **Figure 8c**. Most importantly, mean [P] was significantly greater in the high standing crop wetland at all three sampling times (**Appendix 4c(b)**).

Potassium: Soil potassium concentration was significantly affected by wetland community type (F=633.43, p=0.0001), experimental treatment (F=2.71, p=0.048) and sampling time (F=93.46, p=0.0001) (**Appendix 4d(a)**). The interaction between time and wetland was the only significant interaction term in the model (F=14.12, p=0.0001). Mean [K] in all wetland, treatment and sampling time categories are plotted in **Figure 9a**. Most importantly, mean soil [K] was greater in the high biomass wetland for each sampling time (**Appendix 4d(b)**. For sampling time 2, mean [K] was significantly greater in the NN treatment than in the AN and the C treatments, but the mean potassium concentration was not significantly different between the RO treatment and any other treatment.

Magnesium: Community wetland type (F=3392.06, p=0.0001) and sampling time (F=25.32, p=0.0001) significantly affected soil magnesium concentration using a repeated measures ANOVA (**Appendix 4e(a)**). The interaction between time and wetland was the only significant interaction term in the model (F=9.12, p=0.0002). Mean [Mg] in all wetland, treatment and time categories of the model are plotted in **Figure 9b**. Most importantly, for each sampling time, the mean [Mg] of the soil was significantly greater in the high standing crop wetland (**Appendix 4e(b)**).

pH: A significant effect of sampling time on pH was found using a repeated measures ANOVA (F=18.79, p=0.0001) (**Appendix 4f(a)**). The interaction between time and wetland was the only significant interaction term in the model (F=5.26, p=0.006). The wetland, treatment and time means are given in **Appendix 4f(b)** and mean pH for all wetland, treatment and time categories are plotted in **Figure 9c**.

Community composition

The vegetation varied greatly between the two wetland sites with only three species occurring in both wetlands (**Appendix 5a** and **5b**). Both mean and total species richness were greater in the low standing crop site. A detrended correspondence analysis revealed two distinct wetland communities. Sample scores for the experimental plots are plotted along the two main theoretical axes in **Appendix 5c** and along the three main axes in **Appendix 5d**.

Weather information

A summary of the t-test results are given in **Appendix 6**. July and August of 1992 had significantly less sunlight hours than the thirty previous July and Augusts. As well, July 1992 had a significantly lower mean temperature and greater monthly precipitation than the thirty previous Julys.

Assumption testing and power analysis

Appendix 7a summarizes the results of all tests of normality and homoscedasticity done during data analysis. Power analysis results for non-significant differences are in Appendix 7b.

Table 3. Mean final standing crop, standing crop produced during the growing season and litter in the two wetland communities.

Variable	Low standing crop wetland mean	High standing crop wetland mean	T	df	p
Final standing crop (gm^{-2})	201.27	462.03	-11.42	58.0	<0.0001
Standing crop produced during the growing season (gm^{-2}/day)	1.84	4.08	-9.82	58.0	<0.001
Litter (gm^{-2})	10.44	102.77	-6.47	14.2	0.0001

Figure 2. (a) Mean total competition intensity, (b) mean above-ground competition intensity, and (c) mean below-ground competition intensity based on *Carex crinita* and *Lythrum salicaria* in a low and high standing crop wetland. Vertical error bars give 95% confidence intervals.

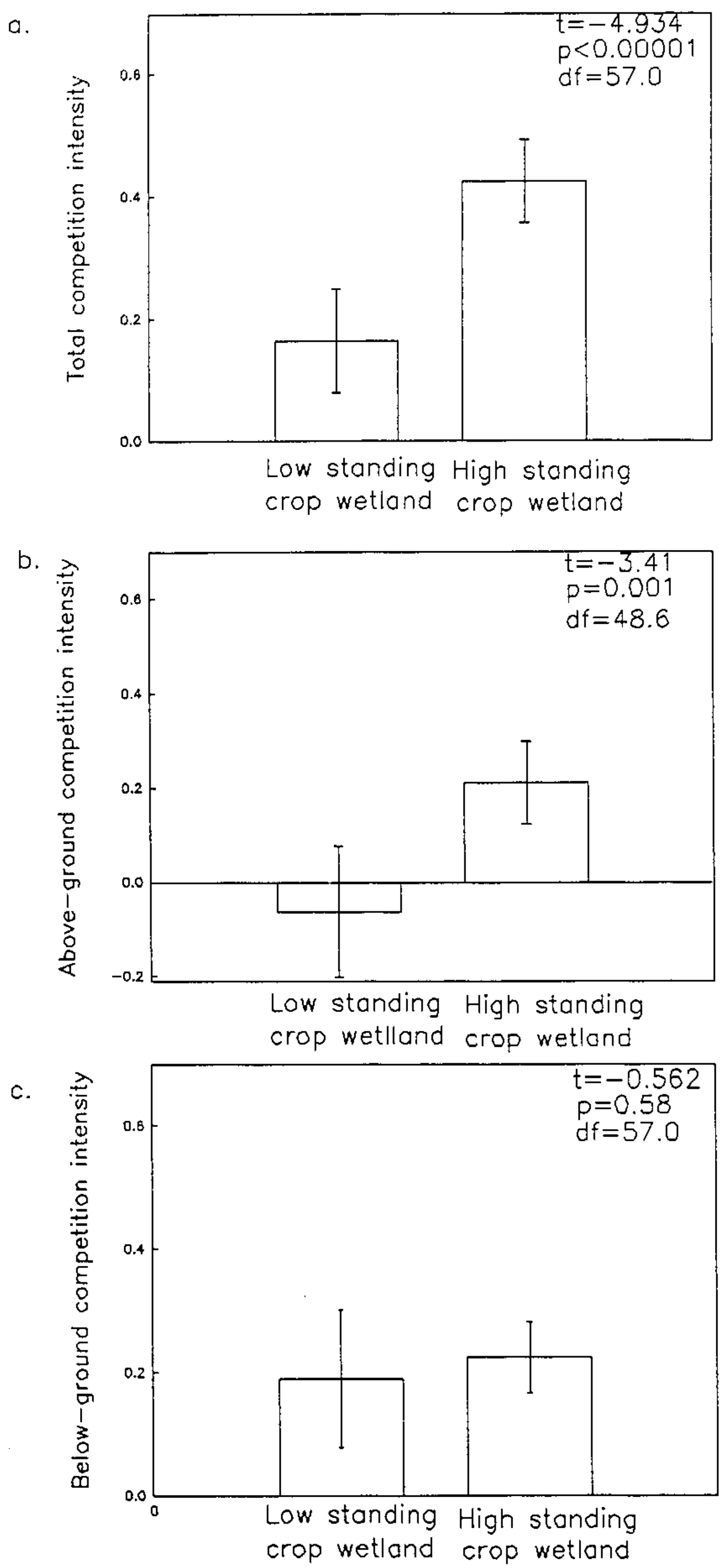

a.
Total competition intensity
0.0
0.2
0.4
0.6
t=−4.934
p<0.00001
df=57.0
Low standing crop wetland
High standing crop wetland
b.
Above−ground competition intensity
−0.2
0.0
0.2
0.4
0.6
t=−3.41
p=0.001
df=48.6
Low standing crop wetlland
High standing crop wetland
c.
Below−ground competition intensity
0.0
0.2
0.4
0.6
t=−0.562
p=0.58
df=57.0
Low standing crop wetland
High standing crop wetland

Figure 3. Relationship between standing crop and (a) total competition intensity (regression equation: CI_{TOTAL}=0.00092 ± 0.00016(standing crop) - 0.0091 ± 0.059), (b) above-ground competition intensity (regression equation: CI_{ABOVE}=0.0011 ± 0.00025(standing crop) - 0.27 ± 0.090) and (c) below-ground competition intensity (regression equation: CI_{BELOW}=0.000027 ± 0.00020(standing crop) + 0.20 ± 0.073). Broken lines given 95% confidence bands and estimates of variance for slopes and y-intercepts are standard errors.

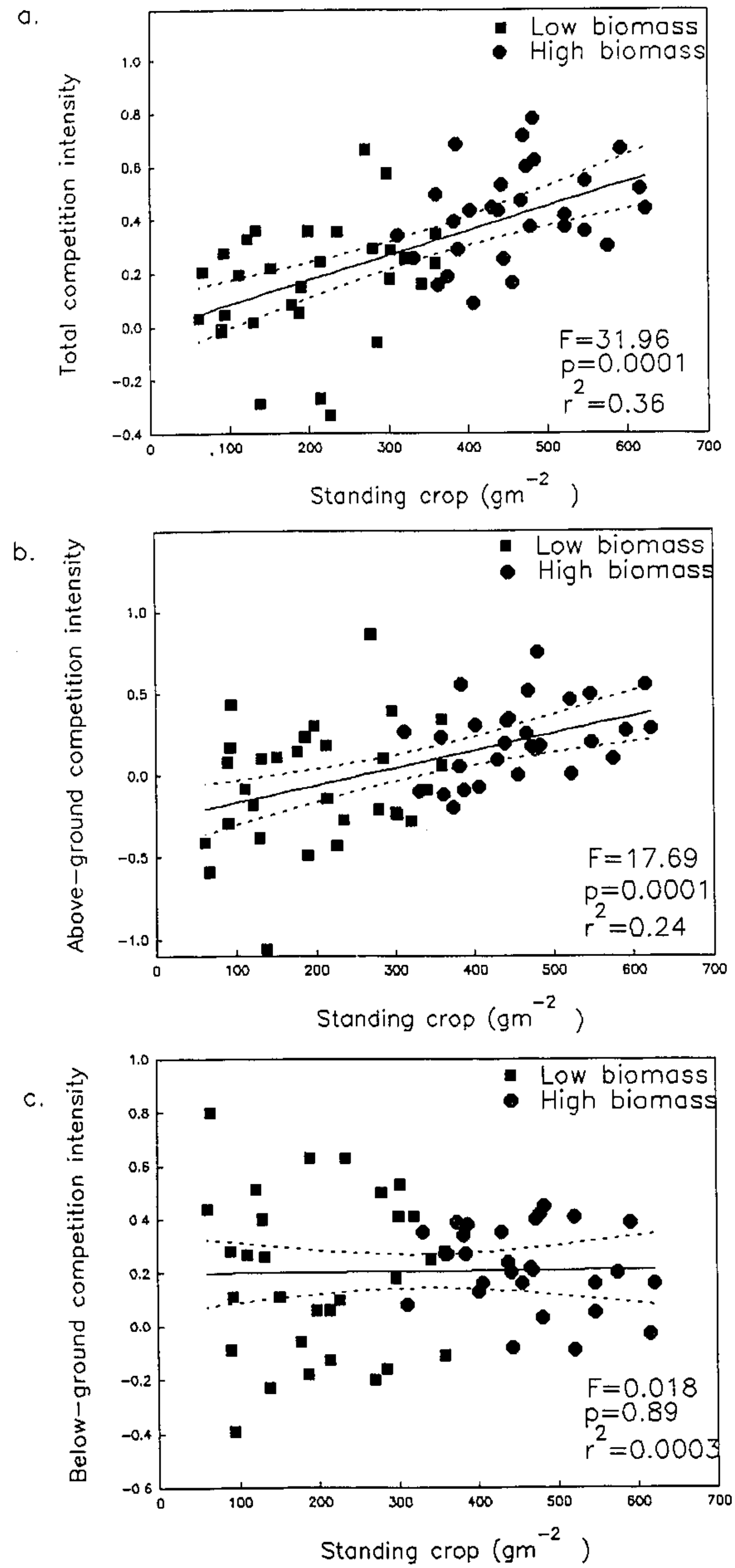

a.
Low biomass
High biomass
Total competition intensity
F=31.96
p=0.0001
r2=0.36
Standing crop (gm-2)
b.
Low biomass
High biomass
Above-ground competition intensity
F=17.69
p=0.0001
r2=0.24
Standing crop (gm-2)
c.
Low biomass
High biomass
Below-ground competition intensity
F=0.018
p=0.89
r2=0.0003
Standing crop (gm-2)

Figure 4. (a) Mean total competition intensity, (b) mean above-ground competition intensity, and (c) mean below-ground competition intensity measured using *Carex crinita*. Vertical error bars give 95% confidence intervals.

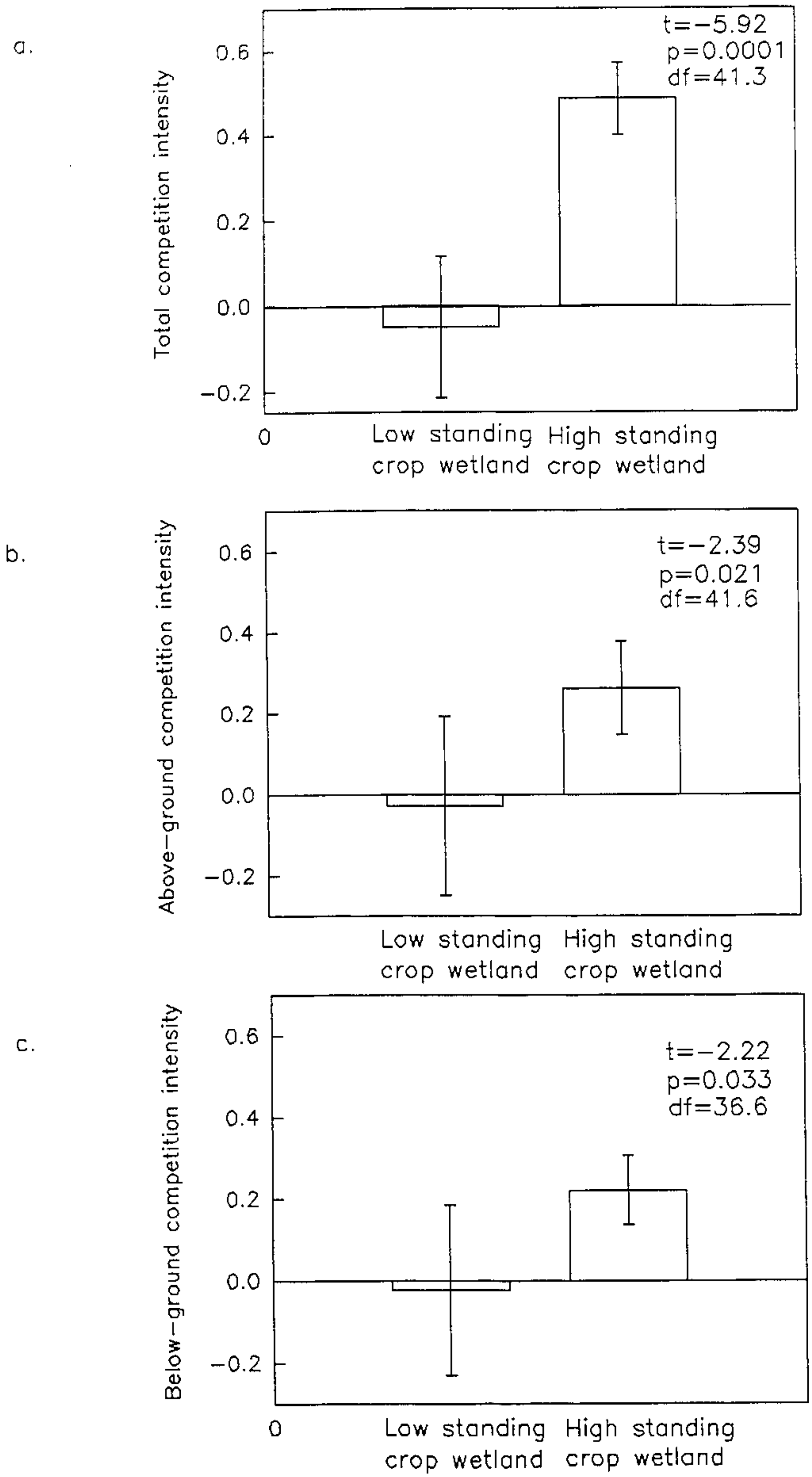
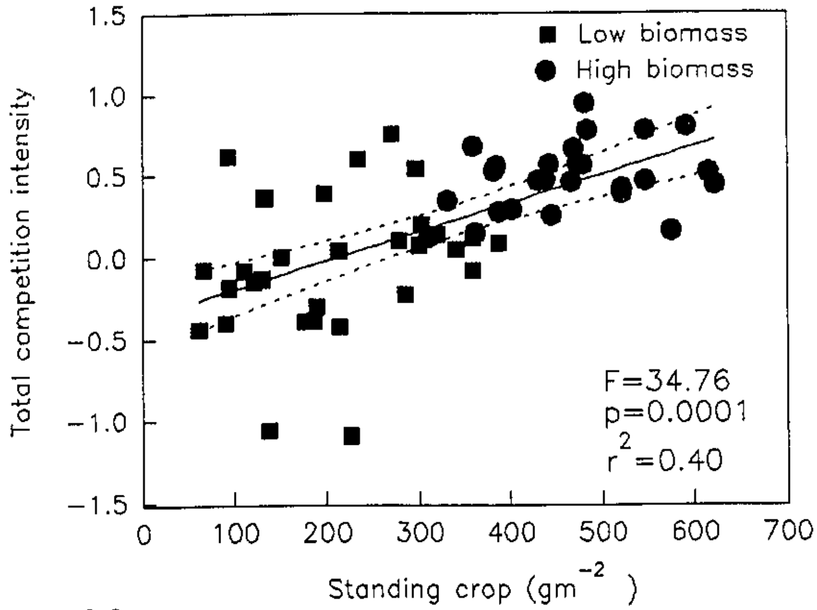
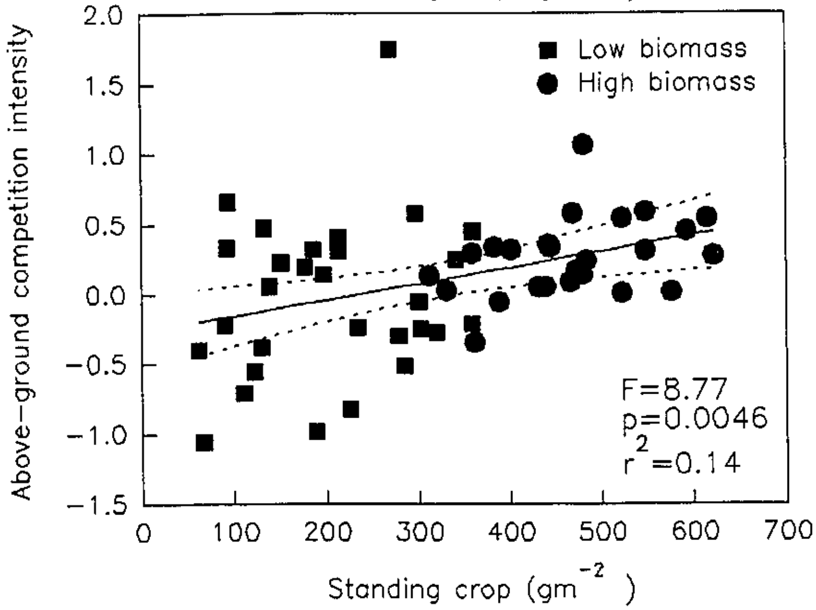

a.
Total competition intensity
t=−5.92
p=0.0001
df=41.3
0.6
0.4
0.2
0.0
−0.2
0
Low standing crop wetland
High standing crop wetland
b.
Above-ground competition intensity
t=−2.39
p=0.021
df=41.6
0.6
0.4
0.2
0.0
−0.2
Low standing crop wetland
High standing crop wetland
c.
Below-ground competition intensity
t=−2.22
p=0.033
df=36.6
0.6
0.4
0.2
0.0
−0.2
0
Low standing crop wetland
High standing crop wetland

Figure 5. Relationship between standing crop and (a) mean total competition (regression equation: CI_{TOTAL}=0.0017 ± 0.00030(standing crop) - 0.37 ± 0.11, (b) mean above-ground competition intensity (regression equation: CI_{ABOVE}=0.0012 ± 0.00039(standing crop) - 0.27 ± 0.14 (c) mean below-ground competition intensity (regression equation: CI_{BELOW}=0.00058 ± 0.00037(standing crop) - 0.10 ± 0.14) using *Carex crinita*. Broken lines give 95% confidence bands and estimates of variance for slopes and y-intercepts are standard errors.

a.


Low biomass
High biomass
Total competition intensity
Standing crop (gm⁻²)
F=34.76
p=0.0001
r^2=0.40
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
0
100
200
300
400
500
600
700

b.


Low biomass
High biomass
Above-ground competition intensity
Standing crop (gm⁻²)
F=8.77
p=0.0046
r^2=0.14
2.0
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
0
100
200
300
400
500
600
700

c.

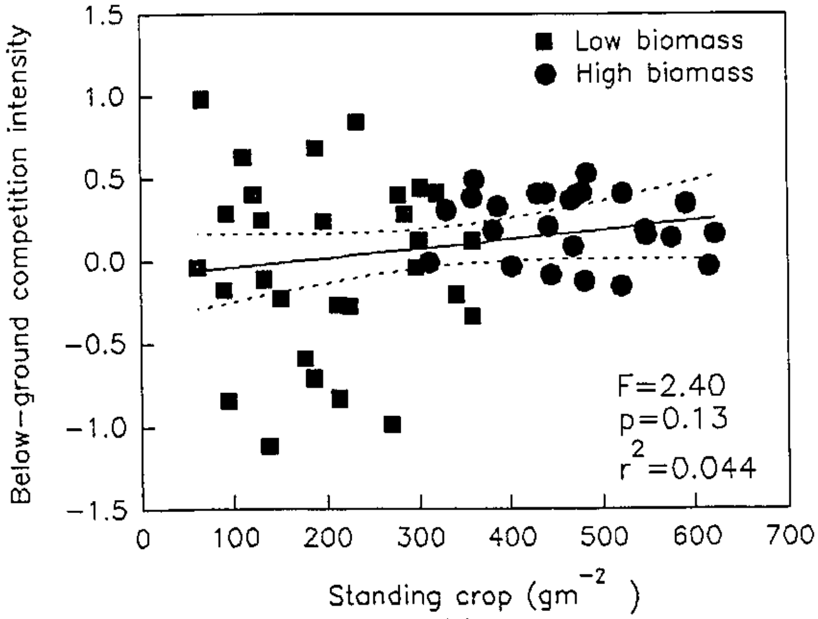

Low biomass
High biomass
Below-ground competition intensity
Standing crop (gm⁻²)
F=2.40
p=0.13
r^2=0.044
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
0
100
200
300
400
500
600
700

Figure 6. (a) Mean total competition intensity, (b) mean above-ground competition intensity, and (c) mean below-ground competition intensity measured using *Lythrum salicaria*. Vertical error bars give 95% confidence intervals.

a.

b.

c.

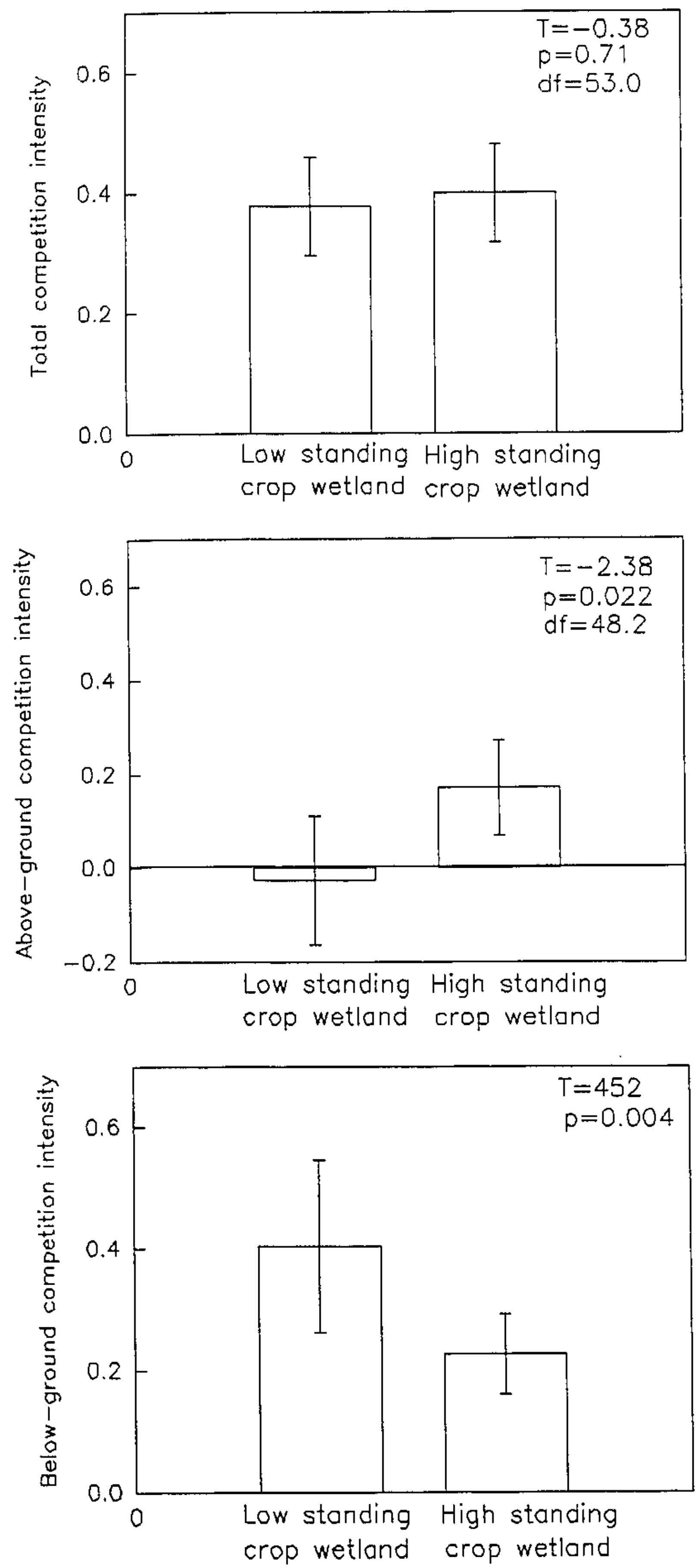
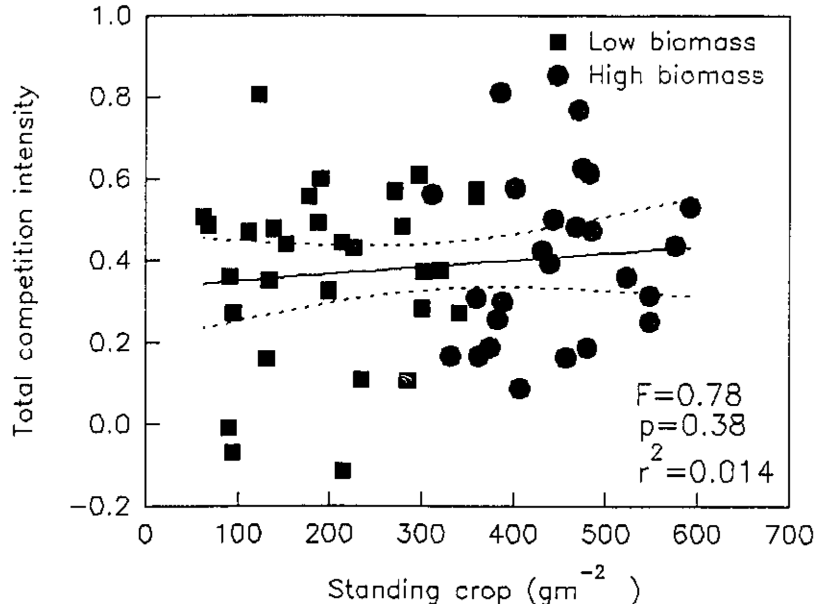

T=-0.38
p=0.71
df=53.0
Total competition intensity
0.6
0.4
0.2
0.0
0
Low standing crop wetland
High standing crop wetland
T=-2.38
p=0.022
df=48.2
Above-ground competition intensity
0.6
0.4
0.2
0.0
-0.2
0
Low standing crop wetland
High standing crop wetland
T=452
p=0.004
Below-ground competition intensity
0.6
0.4
0.2
0.0
0
Low standing crop wetland
High standing crop wetland

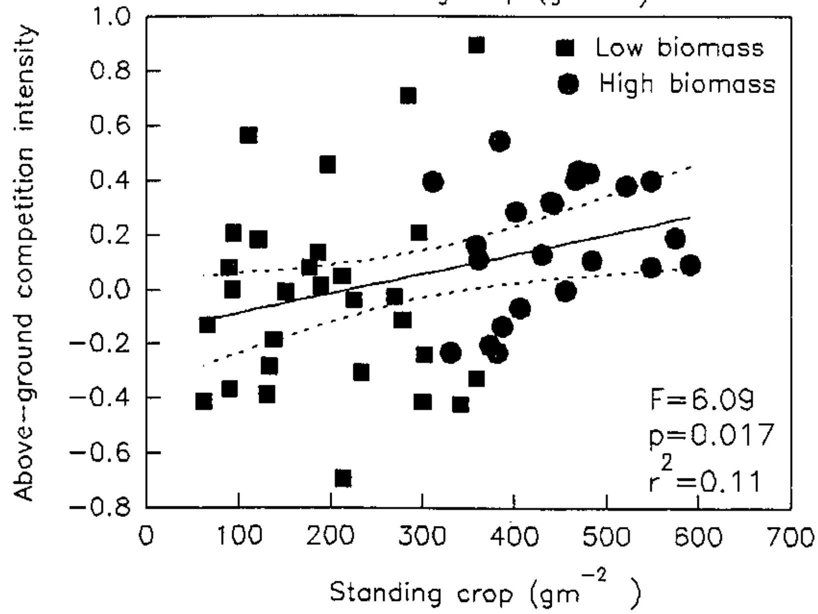
Figure 7. Relationship between standing crop and (a) total competition intensity (regression equation: CI_{TOTAL}=0.00017 ± 0.00019(standing crop) + 0.34 ± 0.065), (b) mean above-ground competition intensity (regression equation: CI_{ABOVE}=0.00071 ± 0.00029(standing crop) - 0.16 ± 0.098) and (c) mean below-ground competition intensity (regression equation: CI_{BELOW}=-0.00055 ± 0.00028(standing crop) + 0.49 ± 0.095) using *Lythrum salicaria*. Broken lines give 95% confidence bands and estimates of variance for slopes and y-intercepts are standard errors.

a.



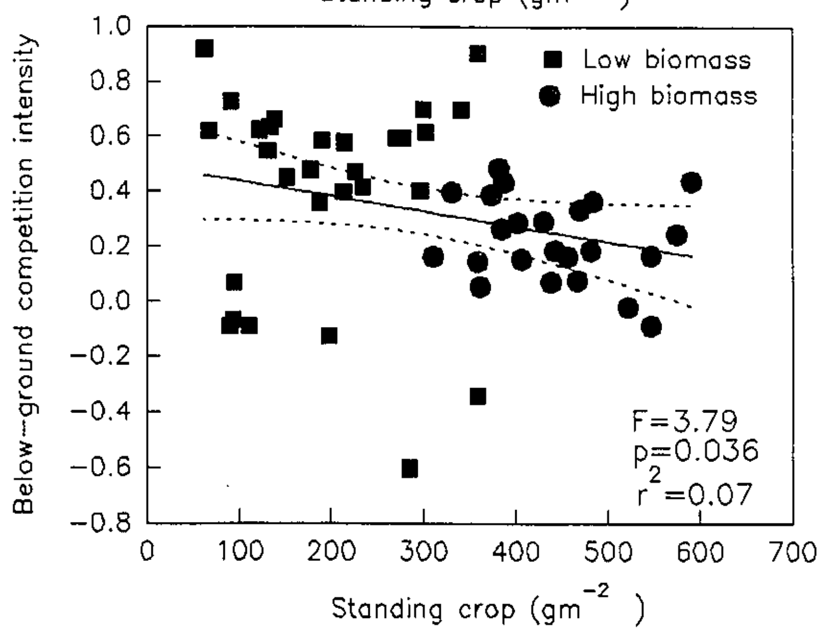
Low biomass
High biomass
Total competition intensity
F=0.78
p=0.38
r^2=0.014
Standing crop (gm^{-2})

b.



Low biomass
High biomass
Above-ground competition intensity
F=6.09
p=0.017
r^2=0.11
Standing crop (gm^{-2})

c.



Low biomass
High biomass
Below-ground competition intensity
F=3.79
p=0.036
r^2=0.07
Standing crop (gm^{-2})

Figure 8. Mean (a) light penetration, (b) soil nitrate concentration, and (c) soil phosphorous concentration in four treatments in a low and a high standing crop wetland at three sampling times. Filled symbols refer to the low standing crop and hollow symbols refer to the high standing crop wetland. The treatments are designated as follows: No Neighbours (circle), Roots Only (triangle down), All Neighbours (square) and Control (triangle up). Vertical error bars give 95% confidence intervals.

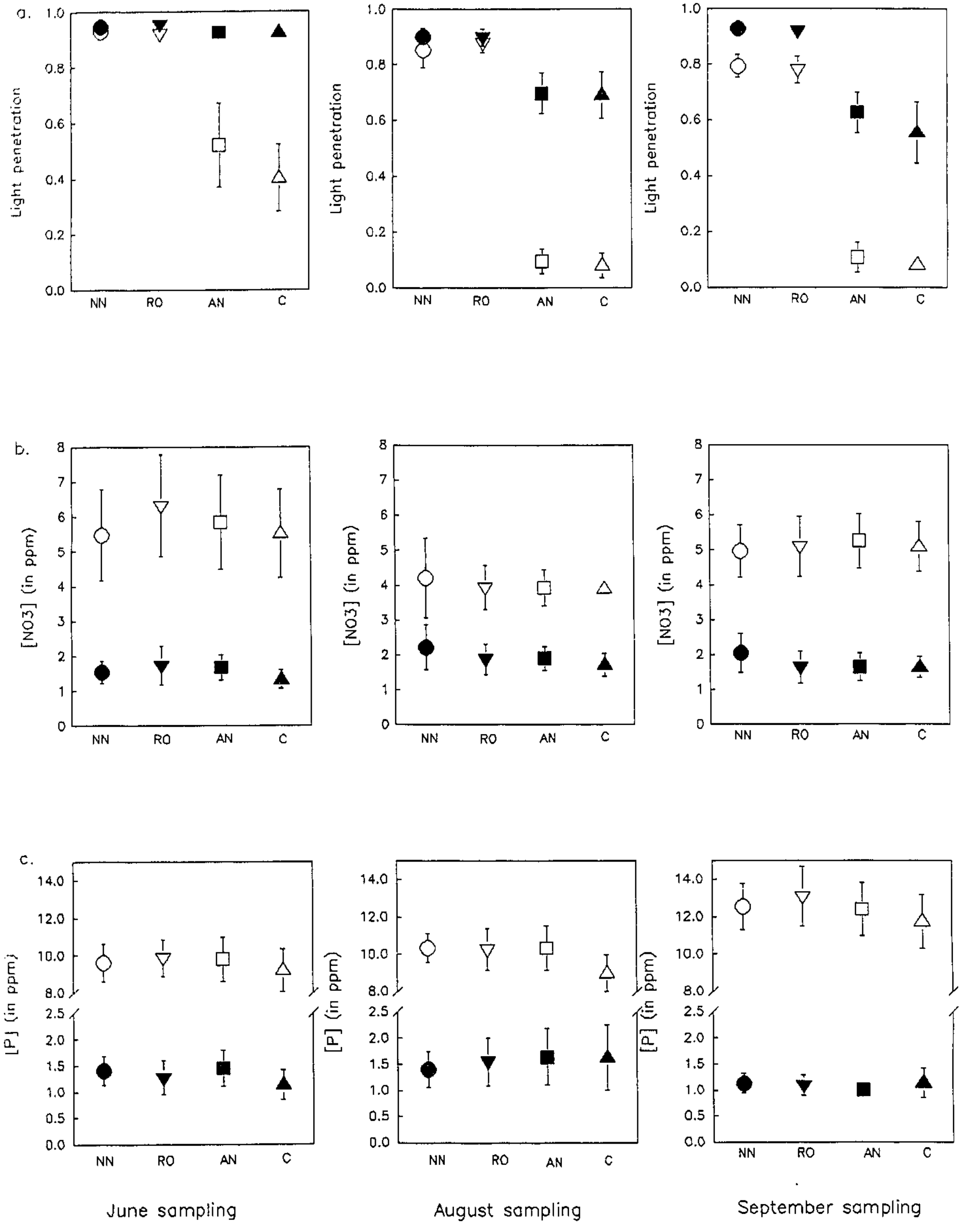
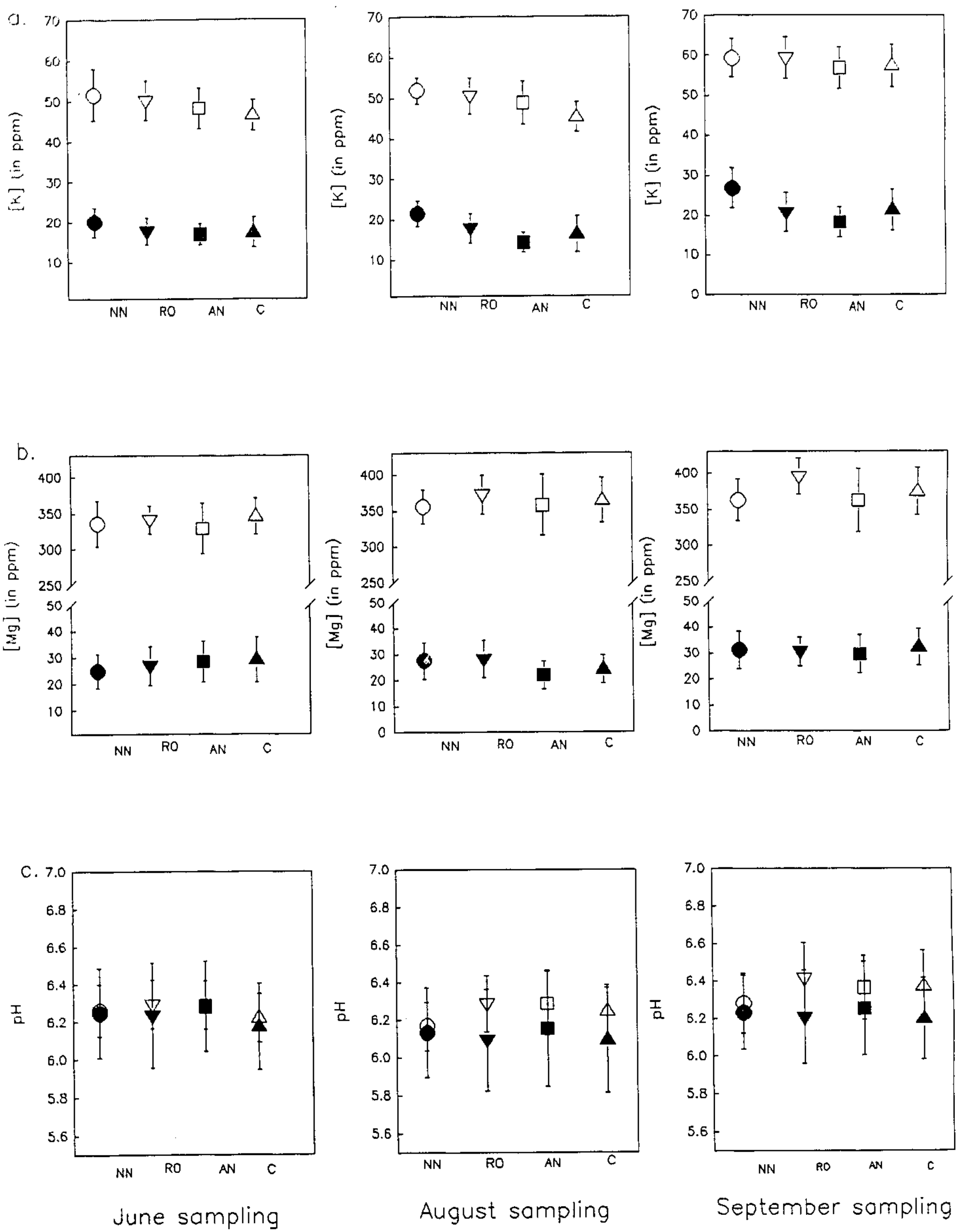

a.
Light penetration
b.
[NO3] (in ppm)
c.
[P] (in ppm)
NN
RO
AN
C
June sampling
August sampling
September sampling

Figure 9. Mean (a) potassium soil concentration, (b) magnesium soil concentration, and (c) soil pH in four treatments in a low and a high standing crop wetland at three sampling times. Filled symbols refer to the low standing crop wetland and hollow symbols refer to the high standing crop wetland. The treatments are designated as follows: No Neighbours (circle), Roots Only (triangle down), All Neighbours (square) and Control (triangle up). Vertical error bars give 95% confidence intervals.


a.
[K] (in ppm)
NN RO AN C
b.
[Mg] (in ppm)
NN RO AN C
c.
pH
NN RO AN C
June sampling
August sampling
September sampling

DISCUSSION

General implications

In the literature two main views prevail on the role of competition in structuring plant communities along productivity gradients. They predict different patterns of competition. The patterns emerging from one view are an increase in both the total amount of competition and an increase in both above- and below-ground competition. This increase in competition is thought to result from increased productivity leading to increased plant growth rates, increased biomass and an increase in the demand for resources. An increase in the intensity of both components of competition causes the relative importance of below-ground to above-ground competition intensity to be constant as productivity increases. These patterns are depicted in **Figure 10a**. The general patterns emerging from the second view are an increase in above-ground competition as above-ground resources become limiting and a decrease in below-ground competition as below-ground resources become more available. This qualitative change in competition results in a decrease in the relative importance of below- to above-ground competition intensity and no net change in the total amount of competition **(Figure 10b)**. My results suggest that a hybrid of these two alternatives is what actually occurs in wetlands (**Figure 10c**). Mean total competition intensity increased from 0.16 in the low standing crop wetland to 0.43 in the high standing crop wetland. Mean above-ground competition intensity increased from an overall facilitative effect (CI_{ABOVE}=-0.063) in the low standing crop wetland to 0.21 in the high standing crop wetland, where light was more limited. Mean below-ground competition intensity was close to 0.20 in both wetlands, even though soil fertility was higher in the high standing crop wetland. This resulted in an overall decrease in the relative importance of below-ground to above-ground competition intensity; competition was predominantly among roots in the unproductive wetland and occurred to an equal extent among roots and shoots in the productive wetland (see confidence levels in **Figures 2b** and **2c**).

My study is one of the few field studies designed to specifically test the patterns emerging from current theory using a natural gradient. Related work in old fields and mixed-grass prairie (Wilson and Shay 1990, Wilson and Tilman 1991, 1993) involved artificially created nutrient gradients. My work does not completely support either of the two prevalent views in the literature and it does not explain why past field experiments yielded different results (Tables 1 and 2). It does however suggest that the two main views in the literature represent only two alternatives out of many and reinforces the need for experiments designed to test all possible hypotheses. The issue of whether competition increases with productivity has gone unanswered partly because of debates arising from false dichotomies and partly because of the lack of experimental tests.

Comparison to previous experiments

Total competition intensity: Results of this experiment are consistent with the work by Wilson and Keddy (1986a) in which diffuse competition (now called competition intensity) was found to increase along an increasing fertility gradient on a lake shoreline. The results are also consistent with the findings of Gurevitch (1986), Reader and Best (1989) and Reader (1990), all of whom found total competition intensity to increase along productivity gradients (Table 1). In contrast, the results contradict those of Wilson and Tilman (1991,1993) done in old fields, that of Wilson (in press) done in heath and grasslands and the work by Belcher *et al.* (submitted) in alvars. As well, the results do not support the findings of Reader *et al.* (in press) where data from 12 locations across the world were combined to test for an effect of neighbour biomass on total competition intensity. Nor do they support the results of a meta-analysis that found competition intensity was not different in high and low productivity habitats (Gurevitch *et al.* 1992). It appears no generalizations about total competition intensity are yet possible.

Above-ground competition intensity: The results are consistent with the work of Wilson and Tilman in old fields (1993) who found that above-ground competition intensity increased with productivity and with the work by Putz and Canham (1992) who found that above-ground competition was more severe in sites with more productive soils. In contrast, Belcher *et al.* (submitted) found that above-ground competition intensity was similar in the two halves of a soil depth gradient in alvars, and Wilson (in press) found that above-ground competition intensity was similar in heath and grasslands. Therefore no generalizations are yet possible.

Below-ground competition intensity: My results are not consistent with any of the five studies that have measured below-ground competition intensity. All previous studies found that below-ground competition intensity increased as productivity levels decreased (Putz and Canham

1992, Wilson 1993, Wilson and Tilman 1993, Wilson in press, Belcher *et al.* submitted). It appears that wetlands are fundamentally different from the published results of terrestrial sites in terms of below-ground competition intensity.

Ratios of below-ground to above-ground competition: Root competition was predominant in the infertile wetland; in the fertile wetland root competition equalled shoot competition. The results in the infertile wetland are typical of both agricultural pot experiments (Wilson 1988) and experimental field results in old fields (Wilson and Tilman 1991, 1993, Wilson in press) and shrublands (Putz and Canham 1992). The fact that the relative importance of below-ground to above-ground competition intensity changes with productivity suggests that the relative importance of root to shoot competition intensity may indeed depend on the environment (Wilson 1988, Putz and Canham 1992). I know of no published examples where the intensities of root and shoot competition were not statistically different; however the fact that the high standing crop wetland was fertile and wet may explain the inordinant importance of shoots competition in this site. Infertile sandy shorelines are exceptional and unusual wetlands (Moore *et al.* 1989); most wetlands are more fertile. Tnerefore the wetland site with higher shoot competition may be typical of the majority of wetlands, even if it is not typical of agricultural experiments and terrestrial habitats.

Some comments on mechanism

This study was not designed as a mechanistic study yet some comments on mechanism are necessary when attempting to account for differences in the results of this field experiment and those previously done. My total competition results support the findings of previous work in wetlands but not some of the experiments done in terrestrial systems. Similarly, my results for the two components of competition differ from previous studies done in terrestrial communities. Differences in water availability may explain why total competition increased with productivity in wetlands and not in old fields, heath, grassland and alvars and why below-ground competition increased with decreasing nutrient availability in terrestrial communities and not in wetlands. Wetlands are different from terrestrial systems in that plants are not limited by water (Gosselink and Turner 1978). As well, loss though water evaporation may be substantial in areas where the soil surface is moist causing neighbour effects on water depletion to be minimal (Newman 1981). Both of the wetlands used in this study and those used in Wilson and Keddy (1986a) were flooded in the spring. When the water levels decreased in mid June the soil was left moist to wet for the duration of the experiments. It is therefore unlikely that water was a limiting resource in the wetlands studied. It may be that an increase in below-ground competition for resources only occurs when plant roots compete for water and nutrients (i.e. in terrestrial areas) and not when plant roots compete only for nutrients (i.e. in wetlands). This could explain why there was no change in below-ground competition intensity along a wetland standing crop gradient but there was a change in total competition intensity.

Water availability may also affect nutrient availability (Ponnamperuma, 1972, 1984, Mitsch and Gosselink 1986). Water is thought to increase the nutrient availability to plants (Reader and Bonser 1993) by increasing the movement of nutrients in soil solution. Large increases in water availability, such as flooding, have various effects on fertility (Ponnamperuma 1984). Flooding decreases oxygen in the soil and leads to anaerobic conditions (Ponnamperuma 1972, Gosselink and Turner 1978, Ponnamperuma 1984). This in turn decreases nitrate availability through denitrification, favours the accumulation of ammonia and increases nitrogen fixation (Ponnamperuma 1972, 1984). Flooding also increases the concentration of water soluble and available phosphorous, increases the concentration of potassium in soil solution, increases dissolved and suspended nutrients and decreases decomposition rates (Ponnamperuma 1972, 1984, Mitsch and Gosselink 1986, Gosselink and Turner 1978). These differences in nutrient availability in terrestrial and wetland systems may be related to the observed differences in competition for soil resources in terrestrial and wetland systems. It also may be significant that the infertile wetland had patterns of root to shoot competition most similar to terrestrial studies.

Differences in limiting nutrients may also be a reason for differences in the relationship between competition intensity and productivity in wetland and terrestrial communities. It has been shown that N is the major limiting soil nutrient for the growth of plants in old fields (Tilman 1984, Tilman 1987), dunes (Willis 1963), chalk grasslands (Bobbink 1991) and upland heath (Haag 1974) whereas phosphorous has been shown to be more strongly correlated with wetland vegetation variables such as plant height, standing crop and species richness than nitrogen (Lee 1993). Phosphorous is also thought to be limiting in freshwater marshes (Klopatek 1978), northern bogs (Heilman 1986), deep water swamps (Brown 1981, Mitsch *et al.* 1979) and coastal plain pocosins (Wilbur and Christensen 1983). Wetlands may therefore be more similar to aquatic systems, where phosphorous has also been shown to be the most limiting nutrient (Schindler 1971, Thomas 1973, Kohler and Labus 1985 and references therein, Hutchison 1957). When roots of adjacent plants intermingle, the density of roots is usually great enough for competition for nitrogen to occur but this may not be the case for phosphorous (Newman 1981). If the depletion zones for phosphorous do not overlap, there may be no competition for this nutrient (Newman 1981). This could explain why plants in the unproductive wetland do not appear to compete below-ground any more than in the productive wetland.

Practical considerations for future work

Choice of indicator species

Competition intensity varied with the choice of species. Mean total competition intensity based on *Carex crinita* was significantly greater in the high standing crop wetland. When the results for *Lythrum salicaria* were analyzed, mean total competition intensity was greater in the high standing crop wetland but the difference was not significant. As well, total competition intensity increased with standing crop for *Carex crinita* but not for *Lythrum salicaria*. The results for above-ground competition intensity were the same with both of the indicator species -- above-ground competition intensity was significantly greater in the high standing crop wetland. The results for below-ground competition intensity were quite different. Mean below-ground competition intensity based on *Carex crinita* was significantly greater in the high standing crop wetland but the reverse was found for below-ground competition intensity based on *Lythrum salicaria*. It should be noted that the probabilities associated with these differences were close to the critical level of 0.05 and linear regression analyses failed to detect a significant relationship between standing crop and below-ground competition intensity for either of the indicator species. It is also interesting that the competition intensity measures varied more between species in the low standing crop wetland. As well, *Carex crinita* showed more evidence of overall facilitative effects in the unproductive habitat than did *Lythrum salicaria*.

This study suggests that species vary in their sensitivity to competition occurring in a community, especially to below-ground competition, and may vary in the overall type of biotic interaction detected. Furthermore, this difference in sensitivity maybe most pronounced in an infertile environment. For instance, if a model, like that in **Figure 10c**, were presented for *Lythrum salicaria* and *Carex crinita*, they would be different. Therefore, basing competition intensity on the results for more than one species maybe preferable because it represents average effects measured using two species. Increasing the number of species might lead to a more accurate measurement of competition intensity but using a large number of species defeats the primary advantage of using indicator species. The main advantage being the ability to measure the magnitude of competition in a community without measuring the effects on each species. One strategy is to ensure that each guild of plants in the community is represented by one indicator species and the mean of the results for the indicator species averaged as was done by Wilson and Keddy (1986a).

Facilitation

Some plants in the experiment had higher growth rates when grown in the presence of competition than in the NN treatment. This resulted in competition intensity values less than one. This study is not alone in this respect; other experiments designed to study negative competitive interactions have shown facilitation (Stone and Roberts 1991 and references therein, Connell 1983, Belcher *et al.* submitted). Facilitation has been shown to be an important biotic process in various plant communities. For instance, facilitation is important in the germination and survival of cacti (Cody 1993), in the growth of *Quercus douglasii* and its understory in central California (Calloway *et al.* 1991, Calloway 1992), in the establishment of tree seedlings in sand dune communities (Kellman and Kading 1992) and in the establishment of woody plants in old fields (Gill and Marks 1991). Facilitation is also thought to be an important process in controlling community structure of plant communities on granite outcrops (Houle and Phillips 1989), in the establishment of forb seedlings in chalk grasslands (Keizer *et al.* 1985) and it is thought to increase *Fucus* recruitment via association with ephemeral blue-green algae (McCook and Chapman 1993). In spite of the importance of facilitation, there has been a tendency to focus on negative interactions such as competition or predation and to place less emphasis on facilitative interactions such as mutualism (Boucher *et al.* 1982, Keddy 1989a).

In the present study most positive interactions occurred for *Carex crinita* in the low standing crop wetland. Figure 5 appears to suggest that both above- and below-ground effects of facilitation are occurring for this species. *Carex crinita* may have benefitted from neighbours by the provision of shade. It may also be that *Carex crinita* benefitted from the presence of neighbours through elevated amounts of litter, which may lead to increases in nutrient availability, and through exposure to mycorrhizae. Vesicular-arbuscular mycorrhizae have been found in a wide range of vegetation communities including marshes (Read *et al.* 1976) and macrophyte communities (Sondergaard and Laegaard 1977, Farmer 1985). Mycorrhizae benefit plants most in infertile conditions (Read *et al.* 1976, Boucher *et al.* 1982) where they can increase diffusion of nutrients to root surfaces (Chapin 1980) by increasing the width of the zone from which the roots extract nutrients (Hayman and Mosse 1972).

Previous studies have shown that both facilitation and competition may occur in a plant community (Callaway *et al.* 1991, Callaway 1992, Houle and Phillips 1989, Morris and Wood 1989, Gill and Marks 1991). Because the positive interactions occurred where fertility was lowest, it is possible that a natural transition from competition to facilitation may occur in wetlands. Figure 5 shows that *Carex crinita* changes from facilitative effects to competitive effects when standing crop approximately equals 250 gm^{-2}. It is interesting and perhaps significant that this is similar to the standing crop range at which alpha diversity peaks in herbaceous wetlands (280 gm^{-2}). It is also interesting that *Carex crinita*, which has shown evidence of facilitation, naturally occurs in wetland with much lower mean standing crop than *Lythrum salicaria* (250gm^{-2} compared to 450 gm^{-2}) (Gaudet 1994).

In this study, all experimental data have been analyzed together. One could argue that the term competition intensity is no longer appropriate and that a term such as interaction intensity should be used instead. This is a valid point but the introduction of a new term could cause confusion, especially when trying to relate my work to previous studies and relevant theory. This study suggests that facilitation is important to some species under infertile conditions. Therefore, facilitation should be incorporated into future theoretical work related to productivity gradients. As well, future experimental work should include specific tests for the occurrence of both negative and positive biotic interactions.

Standing crop

Field studies that have measured competition intensity have used a wide range of biomass levels (Belcher *et al.* submitted) and it is thought that the biomass level may affect the conclusions (Shipley *et al.* 1991, Reader *et al.* in press, Belcher *et al.* submitted). For instance, Reader *et al.* (in press) did not detect a relationship between competition intensity and standing crop when a standing crop range of 150 gm^{-2} was used but a relationship was found at a site where the range spanned 567 gm^{-2}. Similarly, a significant relationship was detected in this study where the biomass range was 560 gm^{-2}. This indicates that standing crop may be a more useful predictor of competition intensity over a wide range of standing crop (Reader *et al.* in press). Similar conclusions have been made for the relationship between standing crop and alpha diversity in wetlands (Moore and Keddy 1989). The biomass range is important in interpreting competition intensity results and should be measured and incorporated into any future work in this area of study.

Light intensity

Nutrient availability has often been experimentally manipulated in the field (i.e. nutrient addition) whereas very few experiments have manipulated the availability of light to plants (DiTommasio and Aarrsen 1989). This experimental design assumes that light availability is greater in the low standing crop wetland, that the transplants growing in the RO treatment receive equivalent light to those in the NN treatment and that light penetration through the vegetation canopy is equivalent in the AN and the C treatments. On average, light availability in the high standing crop wetland was 20 - 40 % less than that in the infertile wetland and therefore plants in the fertile bay were more likely limited by light. Light penetration did not differ between the NN and the RO treatments, which indicates that the RO treatment did prevent shading of the indicator plants by surrounding vegetation. Similarly, light penetration in the AN and the control treatments did not differ which suggests that the introduction of the transplants into the AN treatment did not measurably affect the light regime. Finally, light penetration in the AN and the C treatments was approximately 20-45 % less than in the other two treatments suggesting that transplants in the AN treatment were more likely to be limited by light. The use of a net to create a RO treatment appears to be effective and should be considered a feasible field technique for future experimentation.

Soil analysis

This experiment assumed that fertility differed in the two wetlands; concentrations of soil nitrate, phosphorous, potassium and magnesium were all significantly greater in the experimental plots of the high standing crop wetland. This indicates that plants in the low standing crop wetland were more likely limited by soil nutrients than those in the high standing crop wetland. The net used in the RO treatment might have increased self-shading and thereby reduced plant growth rates leading to decreased nutrient uptake and a simultaneous increase in both soil nutrients and light availability (Wilson and Tilman 1991). Because soil nutrient concentrations in the four treatments did not differ significantly, it appears that this did not occur. Soil nutrient availability may increase following root death and decomposition. In some cases this has occurred fairly quickly (Eason and Newman 1990) and in other cases it has occurred after three to four months (Seastedt 1988). This experimental design assumed that indicator plants in the NN treatments have greater growth rates due to decreased neighbour effects and not to increased soil nutrient availability following the herbicide application (Aarrsen and Epp 1990). No significant differences in soil nutrient concentrations were found among competition treatments and so it appears that any root decomposition in the NN treatment did not increase nutrient levels measurably. Creating RO and NN competition treatments using netting and herbicide does not appear to adversely affect soil nutrient availability and should be considered feasible field techniques for future work.

Limitations of the experiment

One weakness of this study is its short time scale. It is not possible to determine if the same results would be obtained had the experiment been run longer, which is a common weakness of field experiments. In a review of competition field experiments, experiments lasted from 1-36 months with a median of four months (Gurevitch *et al.* 1992). There was no tendency for greater competitive effects in longer studies but longer experiments showed less variation in competitive effect (Gurevitch *et al.* 1992). This experiment was carried out during the period of highest growth for wetland plants in this geographical area (Auclair *et al.* 1976) when effects on community structure and species composition are most likely to occur. Therefore, the biotic effects observed during this experiment provide good estimates of the biotic interactions naturally occurring in these wetlands.

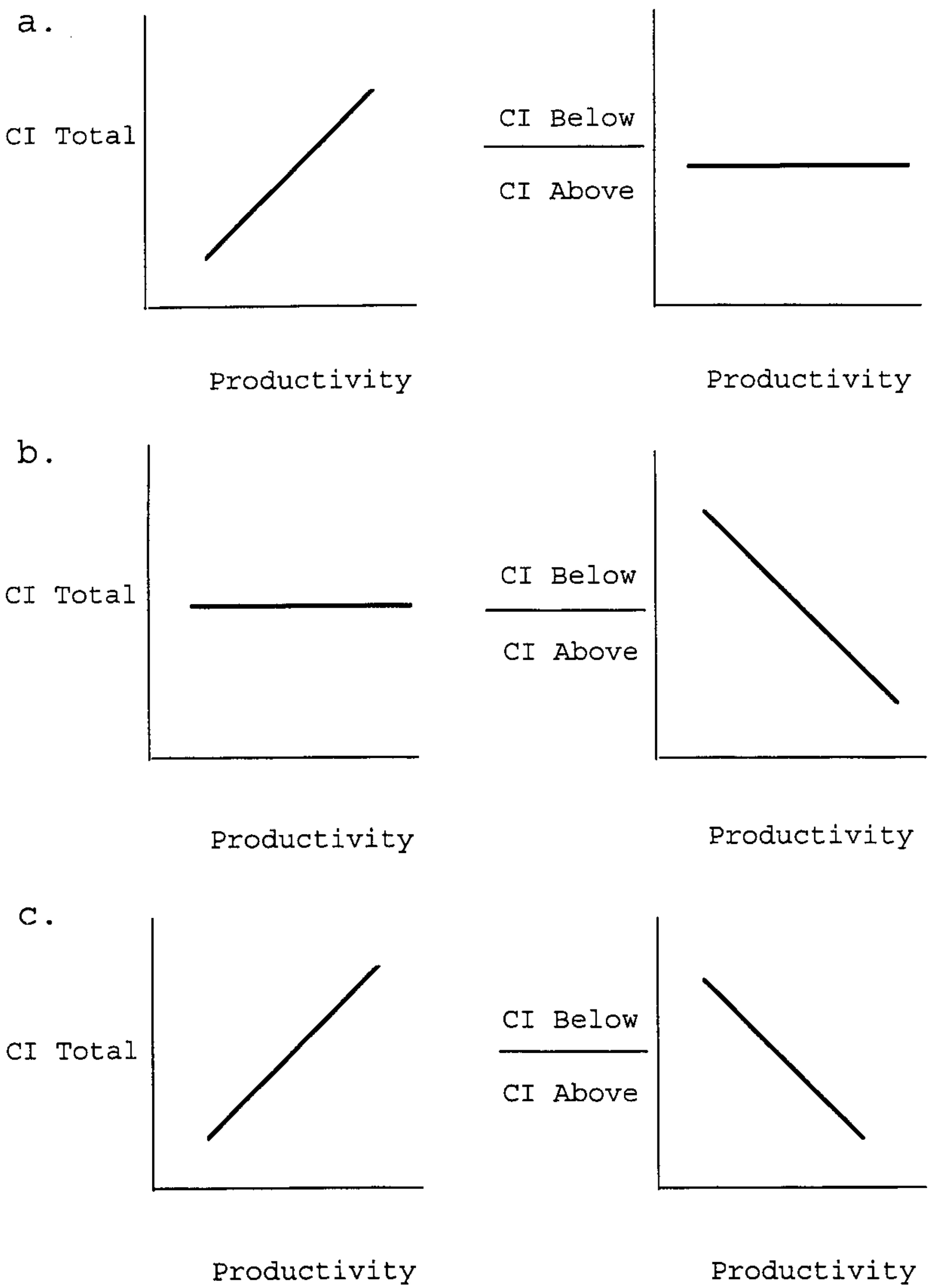
This study was done in one low and one high standing crop wetland. It could be argued that the statistics used in this study are appropriate only for determining whether these two wetlands differ from each other. If I used them to decide whether low standing crop wetlands as a group differ from high standing crop wetlands as a group, it is pseudoreplication (Hurlbert 1984). The reasoning behind this view is that this study offers no estimate of between-wetland variability. This is essentially a question of extrapolation (i.e. how far can I extrapolate from a study based on two wetlands?). There are some reasons for expecting that this pattern does apply to the two classes of wetlands in general. First, the wetlands used in this study are representative of natural extremes in wetland standing crop and are typical of low and high standing crop wetlands. Indeed, this is why they were chosen for the study. As well, the wetlands are close together and so the environment in the wetlands is largely similar except for factors relating to productivity. In addition, an exploratory analysis of covariance of the data in Figures 3, 5 and 7 (not shown) revealed that the slopes and the intercepts of the linear equations for the low and high wetlands were not significantly different. Therefore, the relationships between competition intensity and standing crop are similar for both wetlands. The above three points tend to confirm the contention that the patterns observed in my study are likely representative of patterns between standing crop and competition intensity in wetlands in general.

A large number of similarly sized transplants was needed for this experiment, so seedlings were used instead of adult ramets. The effects of plant dominance are most profound during the seedling stage (Grime 1979) and it is not known whether competition changes after the initial phase of growth of seedlings (Newman 1981). It has also been shown that competition among seedlings and among adults may be different (Shipley *et al.* 1989). The interactions observed reflect the amount of competition experienced by seedlings from established neighbour plants and this should be kept in mind when comparing these results to studies using adult ramets.

The experimental design used in this study assumes that above- and below-ground competition intensity are additive and therefore do not interact. Light and nutrient supply are interactive (Grubb 1985) and above- and below-ground competition may enhance each other (Clements *et al.* 1929, Donald 1958, Wilson 1988) or may have different effects (Newman 1981, Wilson 1988). If the components interacted positively in this study, the above-ground competition intensity values would be overestimated. If the components interacted negatively, the values would be underestimated. My study focused on comparing competition intensity at different levels of standing crop and any such interaction would presumably occur at all levels of standing crop. Interactions between the components of competition are relatively rare (Wilson 1988). It is therefore unlikely that the main conclusions of this study are affected by such interactions.

This study involved a complex gradient with low standing crop, low fertility and high light availability at one end and the opposite at the other end (Reader and Best 1989). In contrast to artificial nutrient gradients where only soil fertility changes, a natural productivity gradient can vary with respect to fertility and disturbance (Wilson and Keddy 1986a, Wilson and Tilman 1993). I attempted to minimize the effects of disturbance by establishing experimental plots in areas where disturbance appeared minimal (i.e., not in an area subject to wave action or intense ice scour). Productivity gradients are naturally complex and even though one cannot quantify all factors that change along such a gradient, one is at the very least using a gradient that does indeed occur in nature.

Figure 10. Three alternative models of total competition intensity and the ratio of below- to above-ground competition intensity along a gradient of increasing productivity; (a) is associated with Grime (1973, 1979), (b) with Tilman (1982, 1987, 1988) and (c) represents existing data from wetlands.


a.
CI Total
Productivity
CI Below
CI Above
Productivity
b.
CI Total
Productivity
CI Below
CI Above
Productivity
c.
CI Total
Productivity
CI Below
CI Above
Productivity

CONCLUSIONS

Total competition intensity increased from zero to nearly 0.5 as standing crop increased from 50 to 650 gm^{-2}. Standing crop explained 36% of the variation in total competition intensity and may be a useful predictor of the total amount of competition in a wetland community. These results support other work done in wetlands (Wilson and Keddy 1986a) and suggest that the community structure of highly productive wetlands is more controlled by competition, whereas abiotic factors and facilitation predominate in unproductive wetlands.

The increase in competition is primarily due to an increase in competition among neighbouring shoots. In the unproductive wetland, where light was not limited, above-ground interactions were predominantly facilitative or weakly competitive. In the productive wetland, where light was limiting, shoot interactions were mainly competitive and greater in magnitude.

Competition among neighbouring roots did not vary with standing crop. A decrease in soil resources with decreasing productivity did not appear to affect the amount of below-ground competition in the two wetlands studied. The results of the infertile wetland, where competition was primarily among roots, are typical of other agricultural pot experiments and terrestrial field experiments. In contrast, the result that root and shoot competition were similar in the fertile wetland is not typical of previous work but may represent what occurs in most wetlands.

Secondary analyses suggest that the two indicator species varied in their sensitivity to competition, especially to the effects of below-ground competition. This reinforces the need to base competitive indices on the results of more than one species. Results from field measurements suggest that the experimental design was successful in separating total competition into its above- and below-ground components and provide quantitative information about the complex wetland gradient used in this study.

I hypothesize, based on the observations of this study, that in wetlands the total amount of competition increases with productivity. I also predict that the relative importance of below-ground to above-ground competition intensity decreases with increasing productivity, primarily due to an increase in above-ground competition. More experimental work is needed to test these predictions.

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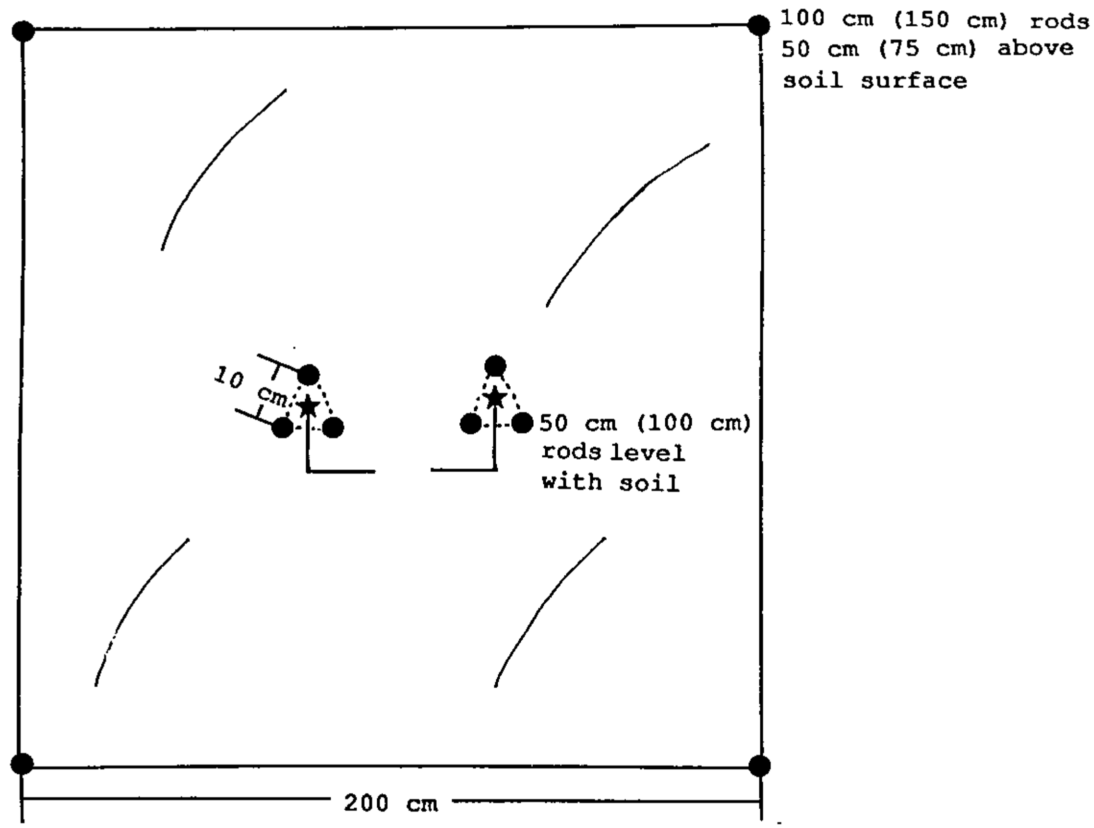
Appendix 1. The construction of the Roots Only competition treatment.


100 cm (150 cm) rods
50 cm (75 cm) above
soil surface
50 cm (100 cm)
rods level
with soil
10 cm
200 cm

Appendix 2a. Initial total biomass (in g) of the transplants grown in the experimental plots. Plots 1-30 and 31-60 correspond to the low and high standing crop wetlands respectively.

PLOT	*Lythrum*-NN	*Lythrum*-RO	*Lythrum*-AN	*Carex*-NN	*Carex*-RO	*Carex*-AN
1	0.20	0.20	0.19	0.33	0.26	0.35
2	0.27	0.24	0.18	0.24	0.28	0.31
3	0.37	0.20	0.24	0.30	0.31	0.38
4	0.25	0.29	0.18	0.16	0.23	0.27
5	0.18	0.30	0.27	0.28	0.31	0.11
6	0.21	0.17	0.13	0.32	0.16	0.43
7	0.19	0.74	0.22	0.29	0.21	0.22
8	0.18	0.20	0.17	0.32	0.26	0.19
9	0.27	0.25	0.17	0.34	0.41	0.64
10	0.22	0.20	0.24	0.36	0.50	0.37
11	0.29	0.20	0.29	0.41	0.33	0.35
12	0.27	0.33	0.30	0.56	0.24	0.32
13	0.26	0.23	0.30	0.42	0.25	0.48
14	0.37	0.29	0.26	0.23	0.48	0.25
15	0.20	0.17	0.33	0.38	0.20	0.30
16	0.19	0.16	0.27	0.44	0.34	0.30
17	0.20	0.24	0.23	0.27	0.43	0.35
18	0.23	0.24	0.20	0.34	0.32	0.23
19	0.23	0.28	0.19	0.48	0.30	0.36
20	0.19	0.20	0.18	0.29	0.32	0.16
21	0.20	0.19	0.34	0.22	0.29	0.32
22	0.20	0.22	0.22	0.34	0.13	0.37
23	0.18	0.20	0.25	0.31	0.59	0.49
24	0.17	0.20	0.22	0.32	0.29	0.47
25	0.25	0.20	0.18	0.34	0.14	0.45
26	0.24	0.35	0.21	0.10	0.35	0.30
27	0.23	0.13	0.22	0.42	0.31	0.33
28	0.23	0.29	0.19	0.39	0.14	0.25
29	0.19	0.18	0.19	0.34	0.40	0.25
30	0.24	0.34	0.33	0.35	0.41	0.32
31	0.27	0.20	0.15	0.23	0.34	0.28
32	0.26	0.34	0.19	0.45	0.56	0.34
33	0.29	0.29	0.37	0.43	0.17	0.30
34	0.23	0.19	0.36	0.20	0.34	0.16
35	0.20	0.21	0.31	0.43	0.40	0.16
36	0.18	0.17	0.24	0.13	0.45	0.44
37	0.20	0.25	0.26	0.24	0.30	0.34
38	0.21	0.21	0.38	0.49	0.43	0.31
39	0.25	0.28	0.20	0.41	0.25	0.33
40	0.24	0.29	0.22	0.32	0.47	0.36
41	0.24	0.25	0.25	0.34	0.32	0.13
42	0.17	0.24	0.23	0.51	0.38	0.19
43	0.17	0.32	0.19	0.26	0.65	0.47
44	0.23	0.33	0.19	0.24	0.34	0.57
45	0.25	0.27	0.22	0.24	0.59	0.36
46	0.25	0.30	0.25	0.41	0.25	0.48
47	0.26	0.21	0.34	0.37	0.58	0.28
48	0.32	0.18	0.12	0.37	0.28	0.62

49	0.16	0.18	0.27	0.45	0.90	0.33
50	0.35	0.20	0.25	0.19	0.30	0.16
51	0.27	0.22	0.26	0.30	0.38	0.22
52	0.15	0.21	0.23	0.37	0.27	0.43
53	0.29	0.32	0.22	0.30	0.46	0.37
54	0.26	0.24	0.22	0.39	0.28	0.33
55	0.21	0.21	0.23	0.56	0.49	0.34
56	0.37	0.22	0.36	0.32	0.35	0.32
57	0.23	0.27	0.25	0.32	0.31	0.25
58	0.17	0.25	0.34	0.39	0.43	0.29
59	0.29	0.25	0.21	0.17	0.34	0.28
60	0.23	0.25	0.23	0.31	0.36	0.39

Appendix 2b. Final total biomass (in g) of the transplants grown in the experimental plots. Plots 1-30 and 31-60 correspond to the low and high standing crop wetlands respectively.

Plot	*Lythrum*-NN	*Lythrum*-RO	*Lythrum*-AN	*Carex*-NN	*Carex*-RO	*Carex*-AN
1	2.98	0.88	0.86	1.08	1.12	1.15
2	1.15	2.45	0.66	0.65	0.57	1.05
3	1.69	0.50	0.56	0.74	0.97	0.90
4	0.64	0.47	0.51	0.26	0.56	0.54
5	0.67	1.02	0.70	0.47	0.91	0.22
6	1.32	0.45	0.37	0.68	0.42	2.09
7	1.56		0.82	2.25	0.70	1.29
8	1.15	1.62	0.59	1.75	0.94	0.54
9	2.37	0.55	0.69	0.83	1.10	1.13
10	2.77	0.46	1.47	1.07	1.30	1.01
11	2.19	3.01	0.71	0.92	0.67	0.84
12	6.08	0.48	1.13	1.94	1.26	0.96
13	5.29	0.78	1.10	1.05	1.55	0.60
14	2.45	0.71	1.27	0.82	1.25	1.05
15	3.83	0.46	1.54	0.60	0.53	0.77
16	4.49	0.38	2.03	1.02	0.92	0.98
17	2.95	0.67	0.91	1.03	0.44	1.26
18	7.69	0.32	1.12	0.81	0.79	0.81
19	3.7	0.89	0.58	1.38	0.42	1.43
20	5.21	0.77	1.00	3.41	1.40	1.48
21	1.87	2.18	1.11	1.03	0.47	1.69
22	1.35	1.77	1.51		0.77	1.46
23	1.42	1.82	2.27	1.35	1.69	0.86
24	3.27	0.61	0.39	0.91	0.54	1.56
25	3.64	0.81	0.59	0.70	0.60	1.61
26	2.01	1.22	1.39	0.88	0.49	0.71
27	9.35	0.54	2.22	0.93	0.57	0.79
28	6.73	0.81	2.19	1.03	0.45	0.63
29	4.81	1.24	0.67	1.22	1.51	0.45
30	7.80	3.19	1.94	0.74	1.47	0.90
31	11.28	2.78	1.28	5.34	2.16	1.51
32	6.18	1.74	2.00	3.33	2.81	0.87
33	14.02	3.08	8.62		0.60	1.54
34	10.95	7.30	9.00	2.51	1.24	1.40
35	8.95	1.80	4.43	3.55	1.64	0.73
36		1.84	1.95	2.53	2.59	2.47
37	2.67	2.73	1.00	2.83	1.43	1.29
38	8.28	4.78	4.82	4.92	1.78	0.65
39		5.28	2.44	2.31	1.63	1.20
40	12.43	4.02	0.55	2.83	3.42	0.75
41	3.79	2.57	3.09		2.80	1.08
42	26.66	10.72	3.98	5.30	2.81	1.35
43	6.98	7.01	3.05	3.05	5.18	1.75
44		3.38	3.22	3.35	5.11	2.04
45	8.01	4.91	4.00		3.17	1.69
46	21.51	12.34	1.77	3.64	2.27	3.26
47	9.53	0.30	1.26	2.76	1.93	0.66
48	14.91	4.08	0.53	2.68	2.59	0.69

49	20.45	6.30	0.67	5.58		1.02
50	18.83	1.38	6.36	4.73	1.96	0.66
51	5.92	1.42	3.39	4.45	2.44	1.30
52	11.7	4.65	1.46	4.56	3.61	2.57
53		1.23	2.31		3.20	1.67
54	4.15	4.06	1.29	2.76	2.67	1.09
55		4.3	2.06	6.15	3.63	1.29
56	32.57	2.72	2.95	5.84	2.33	0.57
57	5.31	8.12	1.94	3.18	2.00	0.42
58	14.52	4.17	3.53	7.93	1.76	0.57
59	15.01	9.73	2.28	5.34	2.58	1.74
60	11.24	5.95	1.61	1.79	1.44	0.84

Appendix 2c. Competition intensity based on the mean of two indicator species for all experimental plots. Plots 1-30 and 31-60 correspond to the low and high standing crop wetlands respectively.

Plot	CI_{TOTAL}	CI_{BELOW}	CI_{ABOVE}
1	0.22	0.11	0.11
2	-0.06	-0.16	0.10
3	0.24	0.06	0.18
4	-0.27	-0.13	-0.14
5	0.05	-0.39	0.43
6	-0.33	0.10	-0.43
7	0.26	0.41	-0.28
8	0.36	0.06	0.30
9	0.36	0.26	0.10
10	0.18	0.41	-0.23
11	0.24	-0.11	0.34
12	0.35	0.28	0.06
13	0.66	-0.20	0.86
14	0.02	0.40	-0.38
15	-0.29	-0.23	-1.06
16	-0.02	0.28	-0.29
17	0.21	0.80	-0.59
18	0.03	0.44	-0.41
19	0.15	0.63	-0.49
20	0.29	0.50	-0.21
21	0.20	0.27	-0.08
22	-0.01	-0.09	0.08
23	0.28	0.11	0.17
24	0.33	0.51	-0.18
25	0.08	-0.06	0.14
26	0.36	0.63	-0.27
27	0.29	0.53	-0.24
28	0.16	0.25	-0.09
29	0.57	0.18	0.39
30	0.05	-0.18	0.23
31	0.45	0.35	0.09
32	0.39	0.34	0.05
33	0.19	0.39	-0.20
34	0.16	0.27	-0.12
35	0.29	0.38	-0.09
36	0.42	0.41	0.01
37	0.47	0.22	0.25
38	0.50	0.27	0.23
39	0.25	-0.08	0.34
40	0.72	0.21	0.51
41	0.09	0.16	-0.07
42	0.30	0.20	0.10
43	0.36	0.16	0.20
44	0.52	-0.03	0.55
45	0.16	0.16	0.00
46	0.34	0.08	0.26
47	0.60	0.40	0.17
48	0.78	0.03	0.75

49	0.68	0.27	0.55
50	0.37	0.42	0.15
51	0.26	0.35	-0.10
52	0.43	0.13	0.30
53			
54	0.38	-0.09	0.46
55	0.44	0.16	0.28
56	0.67	0.39	0.27
57	0.55	0.05	0.49
58	0.62	0.45	0.18
59	0.43	0.24	0.19
60	0.53	0.20	0.33

Appendix 2d. Competition intensity based on *Carex crinita* and *Lythrum salicaria* for all experimental plots. Plots 1-30 and 31-60 correspond to the low and high standing crop wetlands respectively.

Plot	*Lythrum* CI_{TOTAL}	*Lythrum* CI_{BELOW}	*Lythrum* CI_{ABOVE}	*Carex* CI_{TOTAL}	*Carex* CI_{BELOW}	*Carex* CI_{ABOVE}
1	0.44	0.45	-0.01	0.00	-0.23	0.23
2	0.11	-0.60	0.71	-0.23	0.29	-0.51
3	0.44	0.40	0.05	0.04	-0.27	0.31
4	-0.12	0.58	-0.69	-0.43	-0.83	0.41
5	0.27	0.07	0.21	-0.18	-0.85	0.66
6	0.43	0.47	-0.04	-1.10	-0.27	-0.82
7	0.38			0.14	0.41	-0.28
8	0.33	-0.13	0.46	0.39	0.24	0.14
9	0.35	0.63	-0.28	0.36	-0.11	0.47
10	0.28	0.70	-0.41	0.07	0.12	-0.05
11	0.56	-0.34	0.90	-0.08	0.13	-0.21
12	0.58	0.90	-0.33	0.12	-0.33	0.45
13	0.57	0.59	-0.02	0.75	-0.99	1.75
14	0.16	0.55	-0.39	-0.13	0.25	-0.38
15	0.48	0.66	-0.18	-1.06	-1.12	0.06
16	0.36	0.73	-0.37	-0.40	-0.17	-0.22
17	0.49	0.62	-0.13	-0.07	0.98	-1.06
18	0.51	0.92	-0.41	-0.44	-0.04	-0.40
19	0.60	0.58	0.02	-0.30	0.68	-0.98
20	0.48	0.59	-0.11	0.10	0.40	-0.30
21	0.47	-0.09	0.56	-0.08	0.63	-0.71
22	-0.01	-0.09	0.08			
23	-0.07	-0.07	0.00	0.62	0.28	0.33
24	0.81	0.62	0.18	-0.15	0.40	-0.55
25	0.56	0.48	0.08	-0.40	-0.59	0.20
26	0.11	0.41	-0.30	0.60	0.84	-0.24
27	0.38	0.62	-0.24	0.20	0.44	-0.25
28	0.27	0.70	-0.42	0.05	-0.20	0.25
29	0.61	0.40	0.21	0.54	-0.04	0.58
30	0.49	0.36	0.14	-0.39	-0.71	0.32
31	0.43	0.29	0.13	0.46	0.41	0.05
32	0.26	0.49	-0.23	0.53	0.19	0.34
33	0.19	0.39	-0.20			
34	0.17	0.06	0.11	0.14	0.49	-0.35
35	0.30	0.43	-0.13	0.28	0.33	-0.05
36				0.42	0.41	0.01
37	0.48	0.08	0.40	0.46	0.37	0.09
38	0.31	0.15	0.16	0.68	0.39	0.29
39				0.25	-0.08	0.34
40	0.77	0.33	-0.07	0.66	0.09	0.58
41	0.09	0.15	-0.07			
42	0.44	0.25	0.19	0.16	0.14	0.02
43	0.25	0.17	0.08	0.47	0.16	0.31
44				0.52	-0.03	0.55
45	0.16	0.16	0.00			
46	0.56	0.17	0.40	0.12	-0.01	0.13
47	0.63			0.57	0.40	0.17

48	0.61	0.19	0.43	0.94	-0.12	1.07
49	0.81	0.27	0.55	0.55		
50	0.19			0.56	0.41	0.15
51	0.17	0.40	-0.23	0.34	0.31	0.03
52	0.58	0.29	0.29	0.29	-0.03	0.32
53						
54	0.36	-0.02	0.38	0.39	-0.15	0.54
55				0.44	0.16	0.28
56	0.53	0.44	0.09	0.80	0.35	0.45
57	0.32	-0.08	0.40	0.77	0.19	0.59
58	0.47	0.37	0.11	0.77	0.53	0.24
59	0.40	0.07	0.32	0.47	0.41	0.06
60	0.50	0.19	0.31	0.56	0.21	0.35

Appendix 3a. Initial standing crop, final standing crop, standing crop produced during the growing season and litter for all experimental plots. Plots 1-30 and 31-60 correspond to the low and high standing crop wetlands respectively.

Plot	Initial standing crop (in gm^{-2})	Final standing crop (in gm^{-2})	Litter (in gm^{-2})
1	11.79	151.48	
2	11.93	285.19	18.09
3	7.8	213.52	9.85
4	3.39	214.2	8.67
5	7.02	94.34	6.64
6	12.15	226.03	7.91
7	30.12	320.02	
8	14.49	198.19	
9	8.42	133.18	7.69
10	7.09	300.48	11.46
11	8.43	359.19	
12	12.39	359.42	12.07
13	8.48	270.55	15.86
14	7.86	130.37	
15	8.93	138.11	10.75
16	5.47	90.42	
17	12.8	66.54	
18	8.48	61.81	13.88
19	10.25	189.81	
20	7.83	279	
21	11.02	111.13	1.85
22	8.61	89.85	
23	4.9	93.3	7.83
24	13.05	122.07	
25	10.53	177.29	
26	5.94	234.54	
27	11	302.73	18.4
28	15.9	341.26	5.71
29	17.29	297.03	
30	3.2	187.07	
31	24.71	430.83	
32	51.73	382.43	
33	7.37	374.16	86.29
34	36.52	361.64	22.93
35	39.34	387.83	
36	27.24	522.36	
37	45	466.88	
38	26.92	359.02	
39	32.93	444.85	
40	10.73	469.38	
41	42.15	406.09	109.36
42	49.68	575.93	208.17
43	59.81	548.19	149.34
44	45.04	615.65	
45	77.29	455.96	136.47

46	44.54	311.63	43.31
47	45.66	473.5	
48	88.58	481.44	
49	21.69	384.67	41.06
50	37.72	479.26	69.52
51	36.45	331.28	
52	58.87	401.9	
53	71.01	545.91	49.32
54	44.23	522.16	121.52
55	47.36	622.23	178.07
56	86.85	592.1	
57	65.23	547.85	135.16
58	64.36	484.19	133.68
59	85.79	439.12	
60	31.53	442.45	57.35

Appendix 3b. Mean light penetration values for all treatments in one half of the experimental plots. Plots 1-15 and 16-30 correspond to the low and high standing crop wetlands respectively.

Plot	June	August	September
1-NN	0.92	0.85	0.95
RO	0.93	0.79	0.95
AN	0.87	0.84	0.71
C	0.84	0.54	0.42
2-NN	0.92	0.97	0.87
RO	0.96	0.95	0.93
AN	0.9	0.55	0.68
C	0.95	0.76	0.52
3-NN	0.93	0.93	0.93
RO	0.93	0.92	0.91
AN	0.96	0.63	0.59
C	0.94	0.6	0.5
4-NN	0.96	0.9	0.92
RO	0.88	0.95	0.9
AN	0.9	0.73	0.74
C	0.82	0.67	0.7
5-NN	0.98	0.92	0.9
RO	0.9	0.91	0.86
AN	0.9	0.48	0.35
C	0.88	0.71	0.29
6-NN	0.92	0.92	0.92
RO	0.98	0.79	0.9
AN	0.96	0.67	0.8
C	0.95	0.69	0.68
7-NN	0.94	0.93	0.93
RO	0.99	0.91	0.87
AN	0.93	0.69	0.38
C	0.95	0.7	0.28
8-NN	0.97	0.9	0.9
RO	0.97	0.91	0.92
AN	0.91	0.58	0.61
C	0.94	0.33	0.34
9-NN	0.97	0.89	0.94
RO	0.97	0.81	0.92
AN	0.98	0.6	0.67
C	0.94	0.52	0.49
10-NN	0.93	0.92	0.93
RO	0.99	0.95	0.93
AN	0.94	0.75	0.67
C	0.94	0.76	0.61
11-NN	0.96	0.95	0.97
RO	0.98	0.93	0.93
AN	0.94	0.62	0.56
C	0.97	0.87	0.89
12-NN	0.92	0.77	0.95
RO	0.94	0.91	0.95
AN	0.94	0.88	0.79
C	0.95	0.82	0.72

13-NN	0.94	0.95	0.98
RO	0.97	0.95	0.93
AN	0.92	0.94	0.58
C	0.96	0.96	0.92
14-NN	0.97	0.88	0.89
RO	0.96	0.9	0.96
AN	0.93	0.76	0.68
C	0.94	0.7	0.37
15-NN	0.97	0.85	0.93
RO	0.97	0.89	0.94
AN	0.89	0.74	0.59
C	0.9	0.72	0.59
16-NN	0.98	0.8	0.7
RO	0.96	0.82	0.86
AN	0.71	0.11	0.05
C	0.5	0.02	0.18
17-NN	0.96	0.78	0.82
RO	0.92	0.91	0.81
AN	0.91	0.2	0.4
C	0.37	0.04	0.06
18-NN	0.94	0.93	0.82
RO	0.92	0.84	0.74
AN	0.7	0.19	0.24
C	0.75	0.27	0.12
19-NN	0.96	0.9	0.82
RO	0.93	0.83	0.67
AN	0.21	0.09	0.06
C	0.39	0.05	0.07
20-NN	0.81	0.77	0.69
RO	0.89	0.83	0.63
AN	0.35	0.05	0.04
C	0.27	0.02	0.1
21-NN	0.87	0.71	0.81
RO	0.86	0.87	0.71
AN	0.68	0.09	0.08
C	0.61	0.13	0.09
22-NN	0.97	0.95	0.81
RO	0.94	0.86	0.78
AN	0.58	0.08	0.08
C	0.21	0.02	0.04
23-NN	0.95	0.58	0.9
RO	0.91	0.9	0.97
AN	0.57	0.02	0.08
C	0.54	0.03	0.05
24-NN	0.98	0.87	0.95
RO	0.91	0.97	0.89
AN	0.77	0.03	0.06
C	0.26	0.06	0.02
25-NN	0.96	0.83	0.71
RO	0.9	0.92	0.82
AN	0.82	0.01	0.08
C	0.71	0.03	0.01
26-NN	0.96	0.95	0.75

RO	0.94	0.9	0.75
AN	0.09	0.05	0.05
C	0.17	0.06	0.04
27-NN	0.92	0.95	0.82
RO	0.96	0.93	0.78
AN	0.31	0.26	0.1
C	0.05	0.12	0.07
28-NN	0.88	0.98	0.79
RO	0.96	0.88	0.72
AN	0.19	0.2	0.11
C	0.28	0.23	0.09
29-NN	0.85	0.95	0.78
RO	0.89	0.73	0.8
AN	0.17	0.02	0.08
C	0.29	0.02	0.1
30-NN	0.95	0.82	0.73
RO	0.93	0.96	0.77
AN	0.74	0.04	0.1
C	0.62	0.1	0.16

Appendix 3c. Soil data for one half of the experimental plots sampled in (a) June, (b) August and (c) September. Plots 1-15 and 16-30 correspond to the low and high standing crop wetlands respectively.

(a)

Plot	ph	bph	[NO_3] (in ppm)	[P] (in ppm)	[K] (in ppm)	[Mg] (in ppm)
NN1	6	7.3	1.2	2	20	31
RO1	5.8	7.3	1.6	2	18	41
AN1	5.6	7.3	1.39	2	14	31
C1	5.8	7.4	1.2	1	8	25
NN2	6		1.6	1	19	28
RO2	5.9	7.4	0.4	1	15	13
AN2	5.8	7.4	1.2	2	16	20
C2	5.8	7.4	1.39	1	17	11
3-NN	5.8	7.4	0.8	1	12	4
RO	6.6		4.59	1	13	23
AN	6.3		1.79	1	10	16
C	6.3		1.39	1	10	9
4-NN	6.3		1.6	1	7	13
RO	6.2		1.2	1	8	3
AN	6.2		1.6	1	10	8
C	6.4		1.79	1	7	19
5-NN	5.7	7.2	1	1	18	23
RO	5.5	7.2	1.2	1	27	25
AN	5.9	7.3	0.4	1	21	18
C	5.8	7.2	0.6	2	30	27
6-NN	6.7		1.79	1	22	23
RO	5.5	7.2	1	1	30	28
AN	6.1		2.2	1	18	24
C	5.9	7.3	0.8	1	23	23
7-NN	6		1.6	1	22	23
RO	5.9	7.4	1.39	1	22	24
AN	5.9	7.4	1.39	2	16	29
C	5.5	7.4	1	1	24	40
8-NN	5.9	7.4	1.39	2	23	17
RO	6		1.6	1	12	24
AN	6.2		1.2	1	18	47
C	5.8	7.4	0.8	1	17	30
9-NN	5.8	7.4	0.8	1	23	34
RO	6.1		1.2	1	20	40
AN	6		0.8	1	21	31
C	5.9	7.3	1	1	29	54
10-NN	6.8		1.39	2	17	49
RO	6.2		1.79	1	19	53
AN	6.9		2	2	16	60
C	6.4		1.39	2	19	64
11-NN	5.8	7.2	1	2	36	41
RO	6.2		1.2	2	21	45
AN	6.3		1.79	1	29	44
C	6.5		1.79	2	16	35
12-NN	6.7		2	1	21	25
RO	7		1.6	2	13	20
AN	7		2	2	18	23
C	6.8		1.39	2	14	30

13-NN	6.8		2	2	12	10
RO	7		1.79	2	12	11
AN	6.9		2	1	12	13
C	6.8		1.79	2	13	9
14-NN	6.9		3	2	24	28
RO	6.9		3	2	18	23
AN	6.5		2.59	2	16	24
C	6.6		1.39	1	15	32
15-NN	6.5		2	1	24	25
RO	6.7		2.4	1	18	30
AN	6.6		3	1	19	37
C	6.3		2.4	1	20	30
16-NN	5.9	6.5	2	10	35	252
RO	5.9	6.5	3.2	9	40	287
AN	5.9	6.5	2.59	9	31	164
C	5.8	6.5	1.6	8	36	300
17-NN	5.8	6.3	2.4	7	35	275
RO	5.9	6.5	2.59	7	34	311
AN	5.8	6.2	2.4	6	33	257
C	5.8	6.3	2.59	8	37	313
18-NN	6.3		3.4	11	67	389
RO	6.4		3.79	13	63	380
AN	6.3		3.2	11	57	365
C	6.4		3.2	14	58	385
19-NN	6.3		6	9	53	376
RO	6.3		7.59	9	45	360
AN	6.6		8.39	8	50	380
C	6.4		7.8	7	46	346
20-NN	6.5		6.19	8	57	355
RO	6.4		5.19	8	47	363
AN	6.5		6	7	47	376
C	6.4		4.8	6	46	370
21-NN	6.4		5.4	8	44	342
RO	6.5		8	10	58	356
AN	6.4		6.59	14	62	347
C	6.4		8.8	10	50	342
22-NN	6.6		11.39	12	71	354
RO	6.6		11	10	58	357
AN	6.6		7	11	47	337
C	6.3		7	8	50	349
23-NN	5.9	6.4	7.59	8	42	255
RO	6		7.4	10	48	312
AN	6.1		5.4	9	41	306
C	6.1		4	7	34	246
24-NN	5.9	6.4	4.19	7	35	223
RO	6		3.59	7	37	272
AN	6	6.5	3.79	7	38	258
C	5.9	6.4	3.4	9	43	262
25-NN	6.5		5.19	13	56	324
RO	6.5		5.59	12	52	333
AN	6.3		3.4	12	51	294
C	6.6		6.59	11	56	367
26-NN	6.4		3.59	11	65	389

RO	6.2	3.79	11	57	325
AN	6.3	6.19	10	50	328
C	6.3	6.4	10	52	376
27-NN	6.3	4.8	9	49	342
RO	6.4	9	12	55	364
AN	6.4	10.8	11	55	365
C	6.2	6.59	9	50	385
28-NN	6.2	6	11	58	385
RO	6.3	8	10	49	327
AN	6.2	8	11	48	390
C	6.1	8	11	46	398
29-NN	6.5	8	9	50	400
RO	6.4	6	9	45	380
AN	6.5	8	10	52	401
C	6.3	4	9	46	374
30-NN	6.4	6	11	55	378
RO	6.6	10	11	63	391
AN	6.4	6	11	59	360
C	6.3	8	11	47	376

(b)

Plot	ph	bph	$[NO_3]$ (in ppm)	[P] (in ppm)	[K] (in ppm)	[Mg] (in ppm)
NN-1	5.6	7.3	4.19	1	20	32
RO	5.8	7.2	2.2	2	23	52
AN	5.8	7.3	2.4	2	18	23
C	6.1		1	1	13	29
NN-2	6.1		2	1	22	26
RO	5.8	7.4	1.39	1	14	30
AN	5.9	7.4	1.39	1	14	15
C	5.7	7.4	1.6	1	12	27
NN-3	5.7	7.4	1.2	1	18	16
RO	5.9	7.4	0.8	1	12	17
AN	6.1		1		10	12
C	6.1		0.8		9	19
NN-4	6.4		1.2	1	9	29
RO	6.3		1	1	8	17
AN	6		1	1	10	15
C	6.5		1.2	1	7	7
NN-5	5.7	7.3	1	1	27	29
RO	5.6	7.3	1.79	1	30	31
AN	5	7.3	1.78	3	26	17
C	5.2	7.3	1.91	3	40	28
NN-6	5.9	7.5	1.79	2	23	18
RO	5.3	7.4	1.91	3	33	25
AN	5.5	7.5	1.89	1	16	22
C	5.9	7.5	2	2	27	24
NN-7	6	7.5	1.58	2	26	29
RO	5.5	7.5	1.41	2	19	30
AN	5.7	7.5	1.37	3	14	31
C	5.5	7.5	1.67	1	18	30
NN-8	5.9	7.5	1.58	3	28	38
RO	6.2		1.36	1	15	36
AN	6.4		1.6	2	11	25
C	5.6	7.5	1.2	2	13	25
NN-9	5.8	7.5	1.2	2	26	25
RO	5.9	7.5	1.39	2	18	39
AN	6		2.2	1	13	36
C	5.5	7.4	1.39	2	20	37
NN-10	6.4		1.6	1	22	65
RO	6.1		1.6		20	45
AN	6.6		1.6		14	40
C	6.5		1.79		17	47
NN-11	5.6	7.1	1.6	1	31	33
RO	6	7.3	1.39		17	40
AN	6		2		21	36
C	6.5		2		13	23
NN-12	6.7		3.59	1	18	20
RO	6.9		2.59	1	13	18
AN	6.9		2.79	1	12	13
C	6.8		2.2		12	16
NN-13	6.8		3.2	1	17	12
RO	6.9		3.2		13	4

AN	6.9		3	1	10	9
C	6.7		2.4		14	18
NN-14	6.8		4	1	18	15
RO	6.6		3	1	16	14
AN	6.9		2	1	12	15
C	6.6		1.6	1	17	20
NN-15	6.6		3.79	2	18	25
RO	6.6		3.2	2	17	25
AN	6.6		2.59	2	14	21
C	6.2		3	1	13	14
NN-16	5.8	6.4	3.2	10	42	293
RO	5.9	6.4	3	9	38	286
AN	5.9	6.5	4	7	24	133
C	5.8	6.3	3.59	7	29	256
NN-17	5.7	6.2	3.59	7	37	276
RO	5.7	6.2	3.2	6	35	277
AN	5.6	6.1	3.2	6	35	278
C	5.7	6.4	4.19	5	32	259
NN-18	6.3		4.4	12	50	330
RO	6.3		4.19	13	51	338
AN	6.3		3.79	11	49	336
C	6.3		5	10	45	305
NN-19	6.3		7.4	10	52	398
RO	6.4		5.8	9	46	412
AN	6.6		6.59	11	54	443
C	6.5		6.4	8	47	437
NN-20	6.4		4.8	9	54	374
RO	6.5		5	10	53	447
AN	6.7		4.59	12	59	446
C	6.5		4.4	8	47	419
NN-21	6.4		3.59	10	55	402
RO	6.5		3.2	9	50	397
AN	6.4		3.4	13	53	355
C	6.5		3	10	51	388
NN-22	6.4		4	11	56	368
RO	6.5		5.19	10	61	416
AN	6.4		3.2	11	55	353
C	6.4		5.4	9	53	388
NN-23	5.9	6.3	4	12	58	305
RO	6	6.3	4.8	11	55	326
AN	6		3.79	9	54	371
C	6	6.4	2.79	10	48	329
NN-24	5.8	6.4	2.4	10	53	316
RO	6	6.5	4	10	46	371
AN	5.9	6.4	3.2	9	41	344
C	6		2.4	9	42	344
NN-25	6.4		3	13	56	361
RO	6.5		2.79	12	58	410
AN	6.5		3.2	11	59	399
C	6.5		4.19	8	49	411
NN-26	6.2		3.4	10	52	393
RO	6.2		4	10	56	380
AN	6.2		4.19	10	47	364

C	6.4	4	8	48	422
NN-27	6.3	3.79	10	55	403
RO	6.5	5.59	12	54	410
AN	6.4	4.8	13	49	361
C	6.3	3.4	11	48	395
NN-28	6.2	3	10	46	391
RO	6.2	2.4	8	40	359
AN	6.4	3	8	44	417
C	6.2	2.4	9	44	354
NN-29	6.2	10.19	10	58	347
RO	6.5	3.79	14	61	404
AN	6.5	4.8	11	54	417
C	6.2	4.19	11	49	377
NN-30	6.2	2.4	11	53	375
RO	6.6	2.2	11	54	353
AN	6.5	3.2	13	56	349
C	6.4	3.2	12	46	379

(c)

Plot	ph	bph	$[NO_3]$ (in ppm)	[P] (in ppm)	[K] (in ppm)	[Mg] (in ppm)
NN-1	5.7	7.3	1	2	31	33
RO	6.1		2	1	20	37
AN	6		1.39	1	19	23
C	6.2		1.79		16	31
NN-2	6.3		1.79	2	32	27
RO	6.1		1	1	19	26
AN	5.9	7.4	1.2	1	15	32
C	5.9	7.4	1	1	19	20
NN-3	6.1		1	1	19	17
RO	5.9	7.4	0.8	1	9	23
AN	6.2		1	1	9	17
C	6.3		0.8		10	22
NN-4	6.3		1.39	1	12	29
RO	6.3		1		10	18
AN	6		1.2		10	15
C	6.5		1.6		9	28
NN-5	5.6	7.3	1.2	1	35	34
RO	5.4	6	1	2	45	40
AN	5.6	7.3	1.39	1	25	18
C	6		1.39	2	46	46
NN-6	6.2		1.39	1	27	27
RO	5.6	7.1	1.39	1	31	46
AN	5.7	7.3	1.39	1	31	23
D	5.7	7.3	2.79	1	29	47
NN-7	6	7.4	2.59	1	39	35
RO	5.8	7.3	1.2	1	21	30
AN	5.8	7.3	1.2	1	18	37
C	5.8	7.4	1.2	1	27	21
NN-8	5.9	7.4	2	1	28	32
RO	6	7.4	1.2	1	20	32
AN	6.2		1.39	1	15	25
C	5.7	7.4	1	1	24	32
NN-9	6.2		2.2	1	34	37
RO	6.8		3.2	1	19	31
AN	6.2		1.6	1	16	34
C	5.6	7.2	1.39	1	30	54
NN-10	6.5		2	1	18	59
RO	6.2		1	1	26	47
AN	6.8		1	1	24	60
C	6.6		1.79	1	24	49
NN-11	6		1.2	1	43	51
RO	6		1	1	23	36
AN	6.2		1.79	1	31	47
C	6.6		1.79	1	19	32
NN-12	6.6		3.59	1	21	25
RO	6.9		3	1	12	17
AN	7		3.2	1	13	20
C	6.8		2.2	1	17	32
NN-13	6.6		3.4	1	16	9
RO	6.8		3.2	1	13	12

AN	6.8		3.2	1	12	15
C	6.6		2.4	1	13	6
NN-14	6.8		4.19	1	19	14
RO	6.6		1.6	1	23	29
AN	6.8		1.39	1	21	44
C	6.4		1.79	1	23	38
NN-15	6.7		1.79	1	28	38
RO	6.6		2	1	21	35
AN	6.6		2.4	1	15	34
C	6.3		1.6	1	15	27
NN-16	5.8	6.5	3.4	11	50	231
RO	5.9	6.5	4	10	42	314
AN	6	6.5	3	8	33	146
C	5.8	6.6	2.79	8	36	262
NN-17	5.7	6.4	3.79	8	43	294
RO	5.7	6.2	3.79	8	47	333
AN	5.6	6.3	4	8	45	279
C	5.6	6.3	4.59	8	41	308
NN-18	6.3		8	16	65	361
RO	6.5		8.39	19	67	410
AN	6.4		5.4	14	63	381
C	6.6		6.4	19	68	391
NN-19	6.4		5	12	55	391
RO	6.6		3.4	10	47	392
AN	6.7		5.4	13	61	460
C	6.6		6.4	11	59	460
NN-20	6.5		4.8	11	63	392
RO	6.5		4.8	13	66	486
AN	6.5		4.19	12	68	461
C	6.4		4.4	11	68	447
NN-21	6.5		5	13	63	425
RO	6.7		6.19	14	64	441
AN	6.3		6.4	14	55	394
C	6.6		6.19	13	63	423
NN-22	6.6		5.8	12	63	392
RO	6.7		5.19	14	67	404
AN	6.6		6.59	15	59	391
C	6.6		5.4	11	59	367
NN-23	5.9	6.3	4.19	13	74	352
RO	6.2		4	13	61	406
AN	6.1		5	10	53	307
C	6		5.19	10	49	299
NN-24	6	6.4	3.79	9	44	290
RO	6.1		4.19	10	51	391
AN	6	6.4	4.8	9	47	361
C	6		3.59	11	58	336
NN-25	6.5		3.79	14	62	364
RO	6.8		4.4	16	62	378
AN	6.7		4	14	64	335
C	6.6		4.19	11	58	318
NN-26	6.4		6.19	12	62	365
RO	6.3		6.8	13	60	325
AN	6.4		7.8	14	57	341

C	6.6	7.19	14	71	413
NN-27	6.4	6.59	15	61	395
RO	6.6	8	14	64	417
AN	6.5	7.59	14	62	409
C	6.7	5.59	12	61	417
NN-28	6.4	3	12	52	402
RO	6.3	4	12	53	420
AN	6.6	3.59	11	55	404
C	6.5	4.59	11	54	408
NN-29	6.3	6	15	68	405
RO	6.4	4.19	13	63	400
AN	6.5	5.8	16	68	410
C	6.3	3.4	13	62	408
NN-30	6.5	5	15	65	390
RO	6.9	5.19	17	76	414
AN	6.6	5.4	14	62	360
C	6.7	6.4	13	53	366

Appendix 4a. Results for light intensity analysis. (a) ANOVA table for repeated measures analysis of light penetration. (b) Summary of light penetration means and multiple comparison results (N=60 for wetland means, N=30 for treatment and N=120 for sampling time means).

(a)

BETWEEN-SUBJECT SOURCE	df	SS	MS	F	p
Wetland	1	7.79	7.79	475.45	0.0001
Treatment	3	15.69	5.23	319.19	0.0001
Wetland*Treatment	3	4.69	1.56	95.43	0.0001
Error	112	1.84	0.016		
WITHIN-SUBJECT SOURCE					
Time	2	3.22	1.61	170.31	0.0001*
Time*Wetland	2	0.11	0.055	5.85	0.0042
Time*Treatment	6	1.35	0.23	23.8	0.0001*
Time*Wetland*Treatment	6	0.23	0.037	3.97	0.0012
Error	224	2.11	0.0094		

* probability values are Huynh-Feldt Epsilon adjusted because the test for sphericity was rejected (X^2=19.61, df=2, p=0.0001)

(b)

Category	standing crop level	Mean light penetration	Comparison
Wetland - Time1	Low	0.94	A
	High	0.69	B
Time 2	Low	0.80	A
	High	0.48	B
Time 3	Low	0.76	A
	High	0.44	B
Treatment - Time 1	NN	0.94	A
	RO	0.94	A
	AN	0.72	B
	C	0.63	B
Time 2	NN	0.88	A
	RO	0.88	A
	AN	0.40	B
	C	0.39	B
Time 3	NN	0.86	A
	RO	0.85	A
	AN	0.37	B
	C	0.32	B
Time 1		0.82	
Time 2		0.64	
Time 3		0.60	

Appendix 4b. Results for soil [NO_3]. (a) ANOVA table for repeated measures analysis of log [NO_3]. (b) Summary of [NO_3] means and multiple comparison results, (N=60 for wetland means, N=30 for treatment and N=120 for sampling time means).

(a)

BETWEEN-SUBJECT SOURCE	df	SS	MS	F	p
Wetland	1	19.15	19.15	393.84	0.0001
Treatment	3	0.072	0.024	0.50	0.69
Wetland*Treatment	3	0.074	0.025	0.51	0.68
Error	112	5.45	0.049		
WITHIN-SUBJECT SOURCE					
Time	2	0.062	0.031	1.60	0.21*
Time*Wetland	2	0.86	0.43	22.30	0.0001*
Time*Treatment	6	0.090	0.62	0.78	0.58*
Time*Wetland*Treatment	6	0.027	0.0044	0.23	0.96*
Error	224	4.33	0.019		

* probability values are Huynh-Feldt Epsilon adjusted because the test for sphericity was rejected (X^2=18.35, df=2, p=0.0001)

(b)

Category	Standing crop level	Mean [NO_3]	Mean log[NO_3]	Comparison
Wetland - Time1	Low	1.58	0.16	A
	High	5.79	0.72	B
Time 2	Low	1.94	0.25	A
	High	4.00	0.58	B
Time 3	Low	1.74	0.20	A
	High	5.10	0.69	B
Treatment - Time 1	NN	3.51	0.43	
	RO	4.02	0.47	
	AN	3.77	0.46	
	C	3.43	0.40	
Time 2	NN	3.22	0.44	
	RO	2.91	0.41	
	AN	2.29	0.42	
	C	2.81	0.39	
Time 3	NN	3.50	0.47	
	RO	3.36	0.43	
	AN	3.46	0.45	
	C	3.37	0.44	
Time 1		3.68		
Time 2		2.97		
Time 3		3.42		

Appendix 4c. Results for soil [P]. (a) Repeated measures analysis for sqrt [P]. (b) Summary of means and multiple comparisons.

(a)

BETWEEN-SUBJECT SOURCE	df	SS	MS	F	p
Wetland	1	336.38	336.38	2057.59	0.0001
Treatment	3	0.33	0.11	0.67	0.57
Wetland*Treatment	3	0.25	0.082	0.50	0.68
Error	97	15.86	0.16		
WITHIN-SUBJECT SOURCE					
Time	2	1.35	0.68	16.50	0.0001*
Time*Wetland	2	4.68	2.34	57.23	0.0001*
Time*Treatment	6	0.094	0.016	0.38	0.89*
Time*Wetland*Treatment	6	0.22	0.037	0.91	0.49*
Error	194	7.93	0.041		

* probability values are Huynh-Feldt Epsilon adjusted because the test for sphericity was rejected (X^2=0.93, df=2, p=0.030)

(b)

Category	Standing crop level	Mean [P]	Mean sqrt [P]	Compar-ison	N
Wetland - Time1	Low	1.13	1.14	A	45
	High	9.62	3.09	B	60
Time 2	Low	1.53	1.21	A	45
	High	9.98	3.15	B	60
Time 3	Low	1.09	1.04	A	45
	High	12.43	3.51	B	60
Treatment - Time 1	NN	5.50	2.93		30
	RO	6.23	2.28		26
	AN	6.27	2.30		26
	C	6.39	2.33		23
Time 2	NN	5.87	2.18		30
	RO	6.44	2.36		26
	AN	6.58	2.37		26
	C	6.65	2.38		23
Time 3	NN	6.83	2.29		30
	RO	8.00	2.51		26
	AN	7.58	2.44		26
	C	8.04	2.59		23
Time 1		5.49			120
Time 2		6.17			109
Time 3		7.00			115

Appendix 4d. Results of soil [K]. (a) Repeated measures analysis of variance. (b) Means and multiple comparisons, (N=60 for wetland means, N=30 for treatment means and N=120 for sampling time means).

(a)

BETWEEN-SUBJECT SOURCE	df	SS	MS	F	p
Wetland	1	97911.03	97911.03	633.43	0.0001
Treatment	3	1257.56	419.19	2.71	0.048
Wetland*Treatment	3	242.56	80.86	0.52	0.67
Error	112	17312.18	154.57		
WITHIN-SUBJECT SOURCE					
Time	2	3478.82	1739.41	93.46	0.0001*
Time*Wetland	2	525.6	262.80	14.21	0.0001*
Time*Treatment	6	117.71	19.62	1.05	0.39*
Time*Wetland*Treatment	6	126.98	21.16	1.14	0.34*
Error	224	4168.89	18.61		

* probability values are Huynh-Feldt Epsilon adjusted because the test for sphericity was rejected (X^2=8.79, df=2, p=0.012)

(b)

Category	Standing crop level	Mean [K]	Compar-ison
Wetland - Time1	Low	18.03	A
	High	49.02	B
Time 2	Low	17.52	A
	High	49.10	B
Time 3	Low	21.82	A
	High	58.2	B
Treatment - Time 1	NN	35.73	A
	RO	33.90	A
	AN	32.50	A
	C	31.97	A
Time 2	NN	36.67	A
	RO	34.20	BA
	AN	31.60	B
	C	30.77	B
Time 3	NN	43.07	A
	RO	40.67	A
	AN	37.53	A
	C	39.37	A
Time 1		33.53	
Time 2		33.31	
Time 3		40.01	

Appendix 4e. Results for [Mg]. (a) Repeated measures analysis of variance for sqrt [Mg]. (b) Means and multiple comparisons, (N=60 for wetland means, N=30 for treatment means and N=120 for sampling time means).

(a)

BETWEEN-SUBJECT SOURCE	df	SS	MS	F	p
Wetland	1	16920.98	16920.98	3392.06	0.0001
Treatment	3	8.14	2.71	0.54	0.65
Wetland*Treatment	3	2.90	0.97	0.19	0.90
Error	112	558.7	4.99		
WITHIN-SUBJECT SOURCE					
Time	2	27.10	13.55	25.32	0.0001
Time*Wetland	2	9.76	4.88	9.12	0.0002
Time*Treatment	6	2.98	0.50	0.93	0.48
Time*Wetland*Treatment	6	3.62	1.13	1.13	0.35
Error	224	119.85	0.54		

(b)

Category	Standing crop level	Mean [Mg]	Mean sqrt [Mg]	Comparison
Wetland - Time1	Low	27.33	5.07	A
	High	337.90	18.32	B
Time 2	Low	25.48	4.92	A
	High	362.45	18.97	B
Time 3	Low	30.92	5.45	A
	High	374.03	19.27	B
Treatment - Time 1	NN	171.43	11.55	
	RO	184.03	11.72	
	AN	180.43	11.60	
	C	187.57	11.89	
Time 2	NN	191.47	11.98	
	RO	200.30	12.20	
	AN	189.87	11.68	
	C	191.47	11.93	
Time 3	NN	197.20	12.23	
	RO	213.00	12.65	
	AN	196.10	12.12	
	C	203.60	12.43	
Time 1			11.69	
Time 2			11.95	
Time 3			12.36	

Appendix 4f. Results for soil pH (a) Repeated measures analysis for pH. (b) Means and multiple comparisons, (N=60 for wetland means, N=30 for treatment means and N=120 for sampling time means).

(a)

BETWEEN-SUBJECT SOURCE	df	SS	MS	F	p
Wetland	1	0.87	0.87	2.22	0.14
Treatment	3	0.19	0.062	0.16	0.92
Wetland*Treatment	3	0.19	0.063	0.16	0.92
Error	112	43.94	0.39		
WITHIN-SUBJECT SOURCE					
Time	2	0.72	0.36	18.79	0.0001
Time*Wetland	2	0.20	0.10	5.26	0.0059
Time*Treatment	6	0.68	0.013	0.66	0.68
Time*Wetland*Treatment	6	0.041	0.0069	0.36	0.90
Error	224	4.27	0.019		

(b)

Category	Standing crop level	Mean pH	Comparison
Wetland - Time1	Low	6.23	A
	High	6.27	B
Time 2	Low	6.12	
	High	6.25	B
Time 3	Low	6.22	A
	High	6.36	B
Treatment - Time 1	NN	6.25	
	RO	6.26	
	AN	6.28	
	C	6.20	
Time 2	NN	6.15	
	RO	6.19	
	AN	6.22	
	C	6.17	
Time 3	NN	6.26	
	RO	6.31	
	AN	6.31	
	C	6.29	
Time 1		6.25	
Time 2		6.18	
Time 3		6.29	

Appendix 5a. List of plant species occurring in the low standing crop wetland (n=15 quadrats).

Species*	Mean abund-ance (in gm^{-2})	Standard deviation	Occur-rence (/15)
Carex c.f. stricta	3.38	7.57	7
Carex veridula Michx	0.03	0.12	1
Carex c.f. vesicaria L. Stokes	0.75	2.09	3
Drosera intermedia Hayne	0.04	0.11	2
Eleocharis elliptica Kinth.	0.42	0.81	5
Eleocharis smallii Britt.	2.19	4.39	4
Eriocaulin septangulare With	0.10	0.38	2
Hypericum boreale (Britt.) Brickn	0.14	0.27	6
Hypericum ellipticum Hook	1.59	2.98	9
Iris versicolor L.	0.36	1.41	1
Juncus alpinus Vill. var. *rariflorus* Hartm.	1.06	1.75	8
Juncus filliformis L.	2.38	7.04	2
Juncus pelocarpus E. Meyer.	0.95	0.81	14
Lycopus uniflorus Michx.	0.04	0.09	3
Lysimachia terrestris (L.) BSP.	17.94	20.98	10
Lythrum salicaria L.	1.03	1.95	5
Mimulus ringens L.	0.02	0.10	1
Onoclea sensibilis L.	0.09	0.34	1
Potentilla anserina L.	0.33	1.15	5
Scirpus americanus Pers.	159.85	98.29	14
Salix discolor Muhl	0.87	3.06	2
Salix nigra L.	0.45	1.46	3
Salix rigida Muhl.	1.71	4.46	3
Solidago graminifolia (L.)	0.39	0.96	3
Spartina pectinata Link.	13.30	17.01	7
Triadenum fraseri (spach) Gl.	0.27	0.56	4

*Nomenclature follows Gleason 1952.

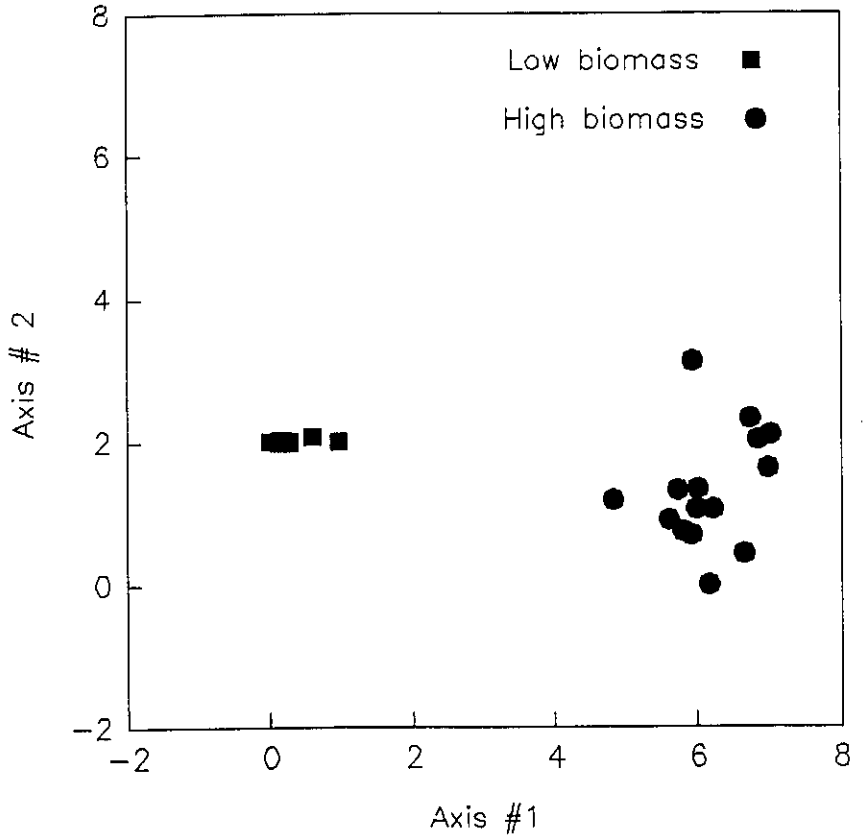
Appendix 5b. List of plant species occurring in the high standing crop wetland (n=15 quadrats).

Species*	Mean abund-ance (in gm^{-2})	Standard deviation	Occur-rence (/15)
Acorus calamus L.	109.59	71.78	15
Boehmeria cylindrica (L.) Sw.	8.29	14.81	10
Calamagrostis canadensis (Michx.)	24.39	91.51	2
Carex vesicaria L.	14.63	26.24	6
Equisetum fluviatile L.	0.16	0.51	2
Juncus filiformis L.	8.68	32.78	2
Leersia oryzoides (L.) Sw	66.10	92.25	12
Lythrum salicaria L.	2.23	0.42	2
Naumburgia thrysiflora (L.) Duby.	44.73	33.02	15
Polygonum c.f. amphibium	26.63	15.69	15
Potentilla palustris (L.) Scop.	11.59	22.47	6
Scirpus acutus Muhl./validus Vahl.	22.82	47.36	5
Scirpus Cyperinus (L.) Kunth	132.17	129.94	11
Thelypteris palustris (Salisb.) Schott.	3.74	14.49	1

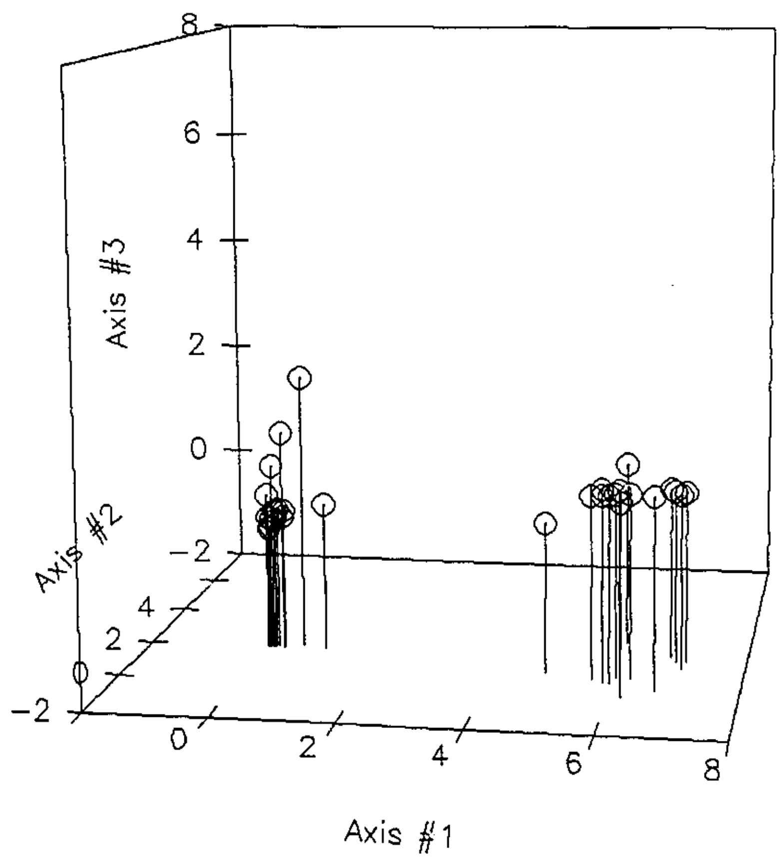
*Nomenclature follows Gleason 1952.

Appendix 5c. Ordination of species data along the (a) two and (b) three main theoretical axes.

a.


Low biomass
High biomass
Axis # 2
Axis #1
8
6
4
2
0
−2
−2
0
2
4
6
8

b.


Axis #3
Axis #2
Axis #1
8
6
4
2
0
−2
4
2
−2
0
2
4
6
8

Appendix 6. T-test results for weather data (t. theor.= 2.045, df=29).

Variable	30 year mean	Monthly mean	Obs. t	p
May sunlight (in hrs.)	237.6	248.8	0.22	>0.5
June	248.3	232.2	-0.38	>0.5
July	279.5	195.6	-2.56	0.02>p>0.01
August	235.8	164.8	-2.58	0.02>p>0.01
September	156.9	150.3	-0.24	>0.05
May temperature (in C)	11.7	11.9	0.10	>0.5
June	16.4	15.5	-0.80	0.5>0.2
July	19.1	16.4	-2.21	0.05>p>0.02
August	17.6	17.2	-0.33	>0.5
September	12.7	13.2	0.35	>0.5
May precipitation (in mm) (log)	1.8	1.9	0.49	>0.5
June (log)	1.9	1.6	-0.98	0.5>p>0.2
July	71.8	154.8	2.69	0.02>p>0.01
August (log)	1.9	2.2	1.48	0.2>p>0.1
September	79.6	98	0.85	0.5>p>0.2

Appendix 7a. Probability values associated with tests of normality and homoscedasticity assumptions conducted for (a) competition intensity t-tests, (b) competition intensity linear regressions, (c) standing crop t-tests, (d) light and soil repeated measures anova's, (e) t-tests for weather data.

(a)

Variable	normality* (sample 1)	normality (sample 2)	homoscedasticity.**
CI_{TOTAL} (mean)	0.30	0.93	0.19
CI_{ABOVE} (mean)	0.85	0.62	0.013
CI_{BELOW} (mean)	0.73	0.14	0.0006
CI_{TOTAL} (*Carex*)	0.26	0.78	0.0004
CI_{ABOVE} (*Carex*)	0.22	0.28	0.0005
CI_{BELOW} (*Carex*)	0.62	0.09	<0.00001
CI_{TOTAL} (*Lythrum*)	0.24	0.47	0.67
CI_{ABOVE} (*Lythrum*)	0.24	0.16	0.03
CI_{BELOW} (*Lythrum*)	0.0021	0.75	<0.00001

* Wilks Shapiro Test

**Test of Equality of Variance of Data

(b)

Regression	normality *	homoscedasticity**
CI_{TOTAL} (mean)	0.65	0.93
CI_{ABOVE} (mean)	0.59	0.005
CI_{BELOW} (mean)	0.93	0.004
CI_{TOTAL} (*Carex)*	0.15	0.61
CI_{ABOVE} (*Carex*)	0.10	<0.001
CI_{BELOW} (*Carex*)	0.19	0.003
CI_{TOTAL} (*Lythrum*)	0.66	0.49
CI_{ABOVE} (*Lythrum*)	0.74	0.67
CI_{BELOW} (*Lythrum*)	0.04	0.014

* Wilks Shapiro Test
**Test of Equality of Variance of Residuals

(c)

Variable	normality (sample 1)	normality (sample 2)	homoscedasticity***
Standing crop	0.09*	0.57*	0.59
Standing crop produced	>0.20**		0.66
Litter	0.73*	0.57*	<0.0001

* Wilks-Shapiro Test
**Kirmigrov-Smirnov Test
***Test of Equality of Variance of Data.

(d)

Variable	Normality -Time 1*	Homoscedasticity-Time 1**	Normality -Time 2	Homoscedasticity-Time 2	Normality -Time 3	Homoscedasticity-Time 3
Light	0.0001	0.0001	0.38	0.0048	0.0001	0.0001
[NO3]	0.098	0.92	0.32	0.056	0.015	0.064
[P]	0.0001	0.32	0.0001	0.55	0.0001	0.0001
[K]	0.069	0.018	0.49	0.34	0.76	0.97
[Mg]	0.0062	0.56	0.0001	0.61	0.0001	0.30
pH	0.014	0.0003	0.33	0.0011	0.013	0.42

*Wilks-Shapiro Test

**Levene's Test of Homoscedasticity

(e)

Variable	May	June	July	August	September
Sunlight	0.05*	0.07	0.60	0.41	0.19
Temperature	0.63	0.42	0.87	0.91	0.78
Precipitation	0.35	0.04	0.32	0.14	0.59

* Wilks-Shapiro Test

Appendix 7b. Results of power tests performed when the null hypothesis was accepted.

Test variable	Statistic	Power (α=0.05)
CI_{BELOW} (mean)	linear regression	0.034
CI_{BELOW} (Carex)	linear regression	0.33
CI_{TOTAL} (Lythrum)	t-test	0.075*/ 0.40**
CI_{TOTAL} (Lythrum)	linear regression	0.14
CI_{BELOW} (Lythrum)	linear regression	0.48

*power of test to detect the actual difference in the means
**power of test to detect a biologically meaningful difference in means equal to 0.1.