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**The Effects of Eutrophication on Wetland
Plant Communities**

by

Harold Thomas Lee

submitted in partial fulfilment of the requirements for the degree
of Master of Science at
University of Ottawa
Ottawa, Canada



Harold Thomas Lee, Ottawa, Canada, 1993



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UNIVERSITÉ D'OTTAWA
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Abstract

The loss of wetland quality through the indirect effects of eutrophication represents a major threat to our few remaining natural wetlands. If we are to preserve the remaining diversity of wetland habitats, it is imperative that we understand the changes arising from eutrophication and that we develop general models to predict these changes.

The first two parts of this study are concerned with a natural field project in which I measured specific plant traits, community state variables, species frequencies, and soil fertility in a large scale comparative study of eight Great Lakes wetlands. I asked the following questions:

1. Are there measurable, quantifiable differences between wetlands - with respect to plant traits, community state variables and fertility
- and 2. Are there empirical relationships between plant traits / community state variables and fertility variables.

To answer the first, I used a one way analysis of variance between two general wetland types. Significant differences (ranging from $P < 0.001$ to $P < 0.05$) between four productive and four unproductive wetlands were found across all the plant traits, except rhizome diameter, all the community state variables and all the fertility variables, except nitrogen. Productive wetlands had lower species richness and were taxonomically distinct from unproductive wetlands. For the second question, I used a model I regression analysis to find predictive relationships. After ranking all

possible relationships according to their regression correlation coefficients (r), I found that total phosphorus was the most important independent variable and that the most important dependent variables were plant height ($r = 0.92$), standing crop ($r = 0.90$), and species richness ($r = -0.85$). In the third part of this project I ran a large outdoor screening experiment for the purpose of bioassaying 40 wetland plants, at two fertility levels, to measure a trait I call 'biomass sensitivity'. In general, I found after one growing season that all species produced more biomass in the fertile treatment. By comparing species according to the proportional 'biomass sensitivity' ($P(\Delta B)$) trait, that is the proportional change in biomass between high and low nutrients, I find there are no differences between species. I propose that other traits may be more useful for explaining the field distribution of plants along nutrient gradients.

Résumé

Afin de préserver la qualité et la diversité des milieux marécageux, mises en péril par les effets indirects de l'eutrophisation, il est impératif de mieux comprendre les changements liés à ce phénomène ainsi que de développer des modèles généraux permettant de prédire les effets de l'eutrophisation.

Les deux premières sections du présent travail se consacrent à l'étude comparative de huit sites marécageux de la région des grands lacs. Les caractéristiques spécifiques des plantes, les variables décrivant l'ensemble de la communauté, la fréquence relative de chacune des espèces et la fertilité des sols sont les éléments investigués lors de cette étude comparative. Deux questions sont étudiées:

1. Existe-t-il des éléments quantifiables et mesurables qui différencient les sites marécageux au niveau des caractéristiques spécifiques des plantes, des variables décrivant l'ensemble de la communauté et de la fertilité des sols?

2. Existe-t-il une relation empirique entre les caractéristiques spécifiques des plantes, les variables décrivant l'ensemble de la communauté et la fertilité des sols?

Afin de répondre à la première question, les caractéristiques de deux types de sites marécageux (quatre sites productifs et quatre sites non productifs) furent soumises à une analyse de variance à un critère de classification. Des différences significatives (variant de $p < 0.001$ à $p < 0.05$) entre les deux types de sites furent obtenues. Toutes les caractéristiques spécifiques

des plantes (à l'exception du diamètre du rhizome), tous les éléments caractérisant les communautés ainsi que toutes les variables décrivant la fertilité des sols (à l'exception de l'azote) se sont avérés significativement différentes. Une faible diversité taxonomique et une flore spécifique différenciaient les sites productifs des sites non productifs. Pour ce qui est de la seconde question, visant à mettre en évidence les relations prédictives, une régression de type I fut utilisée. Après avoir classées toutes les relations possibles selon leurs coefficients de corrélation (r), la variable indépendante la plus importante s'est avérée être le taux de phosphore total. Les variables dépendantes principales furent la hauteur des plantes ($r = 0.92$), biomasse ($r = 0.90$) et la diversité des espèces ($r = -0.85$). Dans la troisième partie de ce projet, 40 espèces de plantes marécageuses, ont été cultivées à l'extérieur, dans deux niveaux contrastants de fertilité. La biomasse de chacune des espèces de plantes fut comparée dans le but de mesurer ce que j'ai appelé 'la sensibilité à la biomasse'. En général, après une saison de croissance, toutes les espèces avaient une biomasse supérieure en milieu fertile. En comparant les espèces selon leur 'sensibilité à la biomasse' ($P(B)$), c'est-à-dire selon la proportion de changement de la biomasse entre les milieux fertiles et non fertiles, aucune différence entre les espèces ne put être observée. À la lumière de ces résultats, l'utilisation des autres caractéristiques me semble être plus utile afin expliquer la distribution des plantes à partir des gradients nutritionnels.

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General Introduction

Much of the current effort to protect and conserve wetlands is directed at minimizing the physical loss of wetlands from drainage for agriculture and human development (Zelazny and Feierabend 1988; Bardecki and Patterson 1989; Kusler and Smardon 1992b). That is, the objective is to minimize the reduction in area of wetlands. This goal is worthwhile, since many areas of North America have losses up to or exceeding 80% of their pre-settlement wetlands (Weller 1988 from Weller et al. 1992; Kusler and Smardon 1992a). But the loss of unique wetland habitats arising from changes in wetland quality is also important. Since wetland habitats can be lost through other indirect influences, factors such as eutrophication (Keddy 1983; Ehrenfeld 1983; Morgan and Philipp 1986; Moore et al. 1989; Wisheu and Keddy 1989; Wisheu et al. 1992) or modification of water level regimes (Keddy and Reznicek 1986; Keddy 1992) also need to be considered. This study is concerned with the former. If we are to preserve the remaining diversity of wetland habitats it is imperative that we understand the changes arising from eutrophication and that we develop general models to predict these changes.

It is usually assumed that the ultimate goal of developing models is to predict species composition, and their changes in response to changing environmental conditions. However, the traditional emphasis on measuring individual species responses at specific sites is unlikely to produce general predictive models, given the vast number of species and possible environments (Rigler

1982; Wimsatt 1982; Shipley et al. 1989; Keddy 1990; Peters 1991). The development of models useful at the landscape scale will therefore require replacing taxonomic units with other variables with greater generality (Grime 1985; Keddy 1987). These variables might be either community level state variables, such as standing crop or diversity (Grime 1979; Keddy 1987; Keddy 1990) or variables describing the plant traits which are related to the functions a plant must perform to survive under specific environmental conditions (Grime 1979, 1985; Keddy 1990). By concentrating on plant traits and community state variables rather than individual species, it may be possible to develop simple empirical predictions about expected changes in wetland plant communities upon eutrophication. More generally, it may also be possible to identify the processes by which nutrients, plant traits and local species pools interact to determine the types of communities that form in particular wetland habitats (ie. Grime 1979; Shipley et al. 1989).

I have used such an approach to investigate the effects of eutrophication on wetland plant communities. In general, the work presented here is based on three different questions and will therefore be presented in three parts. The first two chapters are concerned with a large scale natural field study of eight Great Lakes wetlands. In chapter 1 I first try to establish whether there are measurable, quantifiable differences between wetlands according to the variation in specific wetland vegetation variables and fertility. Having measured both vegetation variables and

fertility variables together in the field the next logical step was to look for empirical relationships between them. In chapter 2 I adopt an empirical approach and use regression to determine if there are predictive relationships between plant traits or community state variables and fertility. Finally, in chapter 3 I ran a large screening experiment to bioassay wetland plants for a trait, 'biomass sensitivity', which may be useful for predicting differences between species in their response to eutrophication. This functional trait is not unlike the common 'relative growth rate' (as developed by Grime and Hunt 1975) and may be useful in explaining the field distributions of plants (Grime 1979).

"...we should seek methods to anticipate human actions which lead to degradation of wetlands...and be able to anticipate whether or not a site that currently is of minimal value as a wetland may...become a high value wetland site."

McCormick 1978

Effects of Eutrophication on Freshwater Wetlands:
A Comparative Study at the Landscape Scale

Introduction

Although the effects of eutrophication on aquatic ecosystems (see Vollenweider 1968; International Joint Commission 1980; Schindler 1971, 1987; Thomas 1973; Kohler and Labus 1983 for reviews) and terrestrial plant communities (Willis 1963; Jeffrey and Pigott 1973; Bakelaar and Odum 1978; Silvertown 1980; Tilman 1982, 1984, 1987; Carson and Barrett 1988; Ellenberg 1988; Tamm 1991 (and refers therein); Bobbink 1991) are well documented, comparatively little is known about the effects of eutrophication on wetland plant communities (Wisheu et al. 1992). Instead, much of the work addressing eutrophication in wetlands is concerned with plant productivity (ie. Cargill and Jefferies 1984; Neely and Davis 1985; DeLaune et al. 1986; Sanville 1988) and the use of wetlands for wastewater renovation (ie. Steward and Ornes 1975; Sloey et al. 1976; Whigham and Simpson 1976; Mudroch and Capobianco 1979; Vega and Ewel 1981; Nichols 1983; Hantzsche 1985). As a result, there are few large scale generalizations about the response of wetland plant communities to eutrophication.

One way of getting large scale generalizations about the effects of eutrophication, as opposed to species oriented site specifics, is to use generalized variables. There has been some early and promising work describing the responses of community state variables and plant traits to nutrients in plant communities. Along environmental gradients, both standing crop (Willis 1963; Al-

Mufti et al. 1978; Bakelaar and Odum 1978; Grime 1979; Tilman 1984, 1987; Moore et al. 1989; Wisheu and Keddy 1989; Bobbink 1991) and litter (Al-Mufti et al. 1977; Tilman 1987; Moore et al. 1989; Wisheu and Keddy 1989) increase with added nutrients. Similarly, specific plant traits, such as relative growth rate (Grime and Hunt 1975; Shipley and Keddy 1988) and plant height (Willis 1963; Jeffrey and Pigott 1973; Grime 1979; Austin and Austin 1980; Tilman 1984, 1987) also increase with enrichment. Species richness or diversity indices, on the other hand, decrease at higher levels of standing crop (Grime 1973, 1979; Al-Mufti et al. 1978; Moore et al. 1989; Wisheu and Keddy 1989) and fertility (Willis 1963; Jeffrey and Pigott 1973; Bakelaar and Odum 1978; Grime 1979; Tilman 1982, 1984, 1987).

To address the problem of how wetland plant communities respond to eutrophication I chose Great Lakes wetlands as a model system. My objective was to compare selected Great Lakes wetlands to find differences in selected fertility variables, plant traits, community state variables, and species distributions.

Site Selection

The Great Lakes have a diversity of wetland plant communities, making them an ideal model system to study the patterns in plant traits and community state variables. Historically, botanists and ecologists have recognized a unique wetland community type around the Great Lakes, one which supports the rare plants Fernald (1935) called "the critical plants of the upper Great Lakes". This

unusual, unproductive wetland type is characterized by a short, sparse, low standing crop plant cover, high plant species richness, and the presence of rare and endangered species (Fahselt and Maun 1980; Keddy and Reznicek 1986; Glooschenko et al. 1988; Charlton and Hilts 1989; Moore et al. 1989; Smith et al. 1991). These areas are in striking contrast to the more common productive, densely vegetated, high standing crop sedge meadows and cattail marshes found around the Great Lakes (Keddy and Reznicek 1986; Glooschenko et al. 1988; Moore et al. 1989; Reznicek and Catling 1989; Smith et al. 1991).

These differences in standing crop appear to be connected with differences in species composition and productivity. Existing relationships show that standing crop increases and species richness decreases with fertility in wetlands (Day et al. 1988; Moore et al. 1989; Wisheu and Keddy 1989) and that only infertile wetlands tend to have rare species (Moore et al. 1989; Wisheu and Keddy 1989). Based on this, the above wetland types appear to represent infertile and fertile wetlands, respectively. Therefore, in this study, wetlands were selected according to three general criteria: 1) sites represent the two aforementioned wetland types - the atypical, infertile, sparsely vegetated wetlands being Type I (as described in Fahselt and Maun 1980; Charlton 1986; Keddy and Reznicek 1986; Glooschenko et al. 1988; Charlton and Hilts 1989; Moore et al. 1989; Smith et al. 1991) or the typical, fertile, densely vegetated sedge meadows or cattail wetlands being Type II (see Glooschenko et al. 1988; Moore et al. 1989; Reznicek and

Catling 1989; Smith et al. 1991), 2) wetlands that were large, provincially significant and/or protected areas, and 3) sites that represented wetlands from a wide geographic area. The Ontario Ministry of Natural Resources publication "Provincially and Regionally Significant Wetlands in Southern Ontario: Interim Report - 1987" (Glooschenko et al. 1988) was used as the principal source for wetland selection. Eight wetlands were selected, four representing each of the aforementioned wetland types.

Study Areas

The eight wetland sites sampled are along the Canadian shorelines of the Great Lakes in southern Ontario, with four on Lake Ontario, two on Lake Erie, and two on Lake Huron and Georgian Bay (Figure 1.1). The four unproductive, sparsely vegetated, wetland sites (Type I) were represented by the pannes found near Gravelly Bay on the southern tip of Long Point (42°32'29" N, 80°07'30" W), in Sandbanks Provincial Park (43°55'55" N, 77°17'04" W), and in Presqu'ile Provincial Park (44°00'00" N, 77°43'53" W), and the Oliphant fens (44°42'18" N, 81°18'10" W) (Fig. 1.1). The pannes occur in poorly drained depressions found within the Long Point, Sandbanks and Presqu'ile sand spit peninsula's, whereas the Oliphant fens are along a gently sloping sandy shoreline and separated from Lake Huron by low sand dunes. The four productive, densely vegetated wetland sites were represented by the seasonally wet meadows found within Oshawa's Second Marsh (43°52'30" N, 78°48'23" W), Rondeau Provincial Park (42°16'38" N, 81°52'08" W),

Matchedash Bay (44°43'14" N, 79°39'24" W), and just south of Long Point Harbour, Long Point, Prince Edward County (43°55'55" N, 76°52'19" W) (Fig. 1.1). These sites are all associated with large *Typha* and *Carex* marsh complexes.

Methods

Sampling Procedures

Vegetation

The vegetation sampling was done between 23 July and 28 August, 1990. Within each site, twenty quadrats (each a 0.5 m X 0.5 m quadrat with nine equal subunits) were randomly placed along a transect of common elevation, with respect to the adjacent Great Lake water line, using a surveying level. Within each quadrat, species frequency was recorded in each of the nine subunits. Above ground biomass and litter were cut at the substrate surface, separated, and then collected to be later dried at 60°C in a forced-air oven and weighed.

Concurrent measurements of plant traits was done during the vegetation sampling. Plant height, considered an important trait for the competition for light (Givnish 1982; Westoby 1984; Tilman 1985; Keddy 1989) was the above ground trait measured. Rhizome diameter and rhizome depth, potentially important for the acquisition of space and resources (Shipley et al. 1989), were the below ground traits measured. Three individuals of each plant species were collected at each site to measure their height (cm) (main shoot measured from substrate surface), rhizome diameter (mm)

(measured largest horizontal rhizome within 5 cm of the main plant shoot), and depth to rhizome (cm) (measured from substrate surface to point at which "rhizome diameter" was measured) traits. Voucher specimens have been deposited in the herbarium of the University of Ottawa.

Substrate

Substrate samples were collected during the same period as the vegetation sampling. Once the biomass and litter were removed from the quadrat, five substrate cores (4.7 cm inside diameter, up to 4.0 cm deep; total is approx. 500 mL) were taken, one from each of the corner and centre subunits, then bagged and frozen for future analysis.

The substrate samples were thawed on 18 July, 1991, homogenized and split into four subunits. One of these subunits was sent to the Agri-Food Laboratories in Guelph (503 Imperial Rd., Guelph, Ontario) to measure Phosphorus (sodium bicarbonate extractable P method; Olsen et al. 1954) and Nitrogen (potassium chloride extractable nitrate and ammonium Nitrogen method; Keeney et al. 1982). The other substrate units were used for the three following alternative measures of fertility. Water extractable phosphorus concentrations were determined by soaking subsamples in 75 mL of double distilled water for 12 hours, and processing the supernatant (1.5 μm pore size Whatman GF/c filtered) by an established total phosphorus protocol (Johnson 1971). The percent organic content of each subsample was determined by loss of mass on

ignition at 500°C for 12 hours. Finally, a bioassay for the fertility of the substrate was done by measuring the total biomass of a *Bidens cernua* seedling (phytometer) grown from seed in 150 mL of each substrate sample. The assumption here is that the relative growth of the phytometer in the different substrate samples should be a good measure of the relative fertility of these substrates. The bioassay took place between 26 July and 19 Sept, 1991, in a growth chamber (diurnal temperature and light cycle = 6:00, 5.0°C, 800 $\mu\text{moles/m}^2/\text{sec}$; 6:30, 10.0°C, 1600 $\mu\text{moles/m}^2/\text{sec}$; 7:00, 20.0°C, 2400 $\mu\text{moles/m}^2/\text{sec}$; 18:00, 15.0°C, 1600 $\mu\text{moles/m}^2/\text{sec}$; 18:30, 10.0°C, 800 $\mu\text{moles/m}^2/\text{sec}$; 19:00, 5.0°C, 0 $\mu\text{Einsteins/m}^2/\text{sec}$), and was watered daily with double distilled water.

Data Analysis

Since a quadrat may contain many individuals of many species and since plant traits exhibit both interspecific and intraspecific variation, the traits used in the analysis were weighted variables. First, a mean was calculated for the plant traits per species per site from the field measurements. Next, species were weighted according to their relative abundance within each quadrat (individual abundance / total abundance). The sum of the products of the mean trait values and their associated species' weight for all the species found within a quadrat gave a weighted-average trait value for each quadrat. Site values, T_s , for traits were then calculated by averaging these values over the twenty quadrats per site.

$$T_s = \frac{1}{n} \sum_{j=1}^n \sum_{i=1}^m \left(\frac{X_i Y_{ij}}{Z_j} \right) \quad (1)$$

X_i = trait mean for species i , m = # species in quadrat j ,
 Y_{ij} = frequency for species i in quadrat j , n = # quadrats in site,
 Z_j = total species frequency in quadrat j .

One way analyses of variance (model I), using site means ($n=4$) as replicates and wetland types ($n=2$) as treatments, were performed to test for differences between wetland types according to all fertility and vegetation variables. Natural logarithmic transformations were used to stabilize variances where appropriate.

A hierarchical cluster analysis (SPSSx statistical package) was performed, using a Jaccard similarity coefficient matrix, to determine the relationship between wetland sites with respect to total species composition.

Results

Standing crop ($P<0.001$) and litter ($P<0.003$) in the Type II wetlands were significantly greater than the Type I wetlands (Figure 1.2; refer to Appendix 1.4 for full ANOVA results), confirming that the sites were representative of the two types of wetlands described earlier. In contrast, the species density within the Type II sites was significantly lower ($P<0.03$) than that found in the Type I sites (Fig. 1.2).

Each of the six soil fertility variables, except nitrogen,

Each of the six soil fertility variables, except nitrogen, showed significant differences between the wetland types (see Fig. 1.3, Appendix 1.4). The trend for all these variables was consistent, with the fertility values in the Type II sites being greater than those in the Type I sites.

Similarly, plant height ($P < 0.001$) and rhizome depth ($P < 0.04$) were significantly different between wetland types whereas rhizome diameter was not (Fig. 1.4). Fertile wetlands therefore have plant communities which are taller and possess deeper rhizomes than those found in infertile wetlands.

Table 1.1 gives the five most abundant species within each of the sampling sites. The infertile sites (top row) had many species in common, including *Cladium mariscoides* and the nationally rare (Priority III; Argus and Pryer 1990) *Scleria verticillata*. Similarly, many of the fertile sites (bottom row) shared *Phalaris arundinacea*, *Calamagrostis canadensis*, and large *Carex* spp. However, there were no species shared between the infertile and fertile wetlands. This floristic similarity within wetland type and dissimilarity between wetland types is supported by the hierarchical clustering dendrogram, using total species composition, shown in Figure 1.5.

Discussion

Fertility

The observed differences in fertility between wetland types is undoubtedly due to differences in land use in their surrounding drainage areas and their soil characteristics (Thompson and Troeh 1973; International Joint Commission 1980; Ehrenfeld 1983; Lewis et al. 1984; Morgan and Philipp 1986; Howarth et al. 1991). The oligotrophic nature of Type I wetlands is a result of receiving their drainage from the adjacent natural landscapes on nutrient poor limestone (Oliphant fens) or sand (Sandbanks Provincial Park, Presqu'ile Provincial Park, Long Point (CWS)) (Chapman and Putnam 1966), and having soils which are typically sandy (refer to Loss on Ignition, Fig. 1.3). In contrast, Type II wetlands receive drainage from areas dominated by agriculture (Rondeau Provincial Park), human development (Oshawa's Second Marsh), or both (Prince Edward Point, Matchedash Bay), and have soils with a small inorganic component and more dark, rich organics (refer to Loss on Ignition, Fig. 1.3). The eutrophic nature of such drainage (International Joint Commission 1980; Lewis et al. 1984; Howarth et al. 1991) therefore accounts for their higher soil fertility. In addition, the greater response of the phytometer in the fertile soils suggests that the organic nature of these soils makes them better able to retain mineral nutrients, or that they continually release them through the breakdown of organics, or both (refer to Bioassay of Fertility, Fig. 1.3). Note that I found differences in the Loss on Ignition and Bioassay of Fertility measures associated

with differences in chemical nutrients, suggesting they may be suitable alternatives to the more sensitive and costly chemical analysis for nutrients.

This difference in fertility between wetland types corresponds with differences in plant traits (Fig. 1.4), community state variables (Fig. 1.2) and species composition (Fig. 1.5). This is evidence that nutrient levels play an important role in determining vegetation types in wetlands. I found both phosphorus variables highly significantly different between wetland types whereas nitrogen was not, suggesting that phosphorus is more related to this observed vegetation response (Fig. 1.3). Experiments in aquatic communities show similar responses where, in response to various nutrient applications, phytoplankton are limited most by phosphorus (Hutchinson 1957, 1969; Schindler 1971, 1987; Thomas 1973; Kohler and Labus 1983 (and references therein)). Terrestrial vascular plant communities (Willis 1963; Bakelaar and Odum 1978; Tilman 1984, 1987, 1988; Carson and Barrett 1988; Bobbink 1991; Tamm 1991 (and references therein), and salt marsh plant communities (see Morris 1988, 1991, and Valiela et al. 1988 and references therein), on the other hand, have shown greater and more frequent responses to treatments of nitrogen. It is surprising to find the differences between freshwater vascular plant communities related more to phosphorus than to nitrogen (Fig. 1.3), making them more like phytoplankton than terrestrial vascular plant communities. Controlling phosphorus loading from in and around the Great Lakes drainage basin, be it from diffuse or point sources, is

therefore just as important for maintaining wetland quality as it is for maintaining water quality (International Joint Commission 1980; Wisheu et al. 1992).

Fertility and Plant Traits

The increase in plant height and rhizome depth in fertile wetlands (Fig. 1.4) demonstrates the relationship between available nutrients and some important plant traits. These results are consistent with described trends in terrestrial plant communities where Willis (1963), Jeffrey and Pigott (1973), Grime (1979), Silvertown (1980), and Bobbink (1991) all found increasing abundances of taller species in eutrophic areas. Gaudet and Keddy (1989) and Shipley et al. (1989) also found that plant height was correlated with fertility gradients in the field. Similarly, Austin and Austin (1980) and Tilman (1987) have shown, using experimental nutrient gradients, that there is a change from short species to tall species with increases in nutrients. With respect to rhizome depth, Shipley et al (1989) found, in a Principal Coordinate Analysis between adult plant traits and field distributions, a correlation between rhizome depth and an axis of variation believed to represent fertility.

Grime (1979), Givnish (1982), Tilman (1985, 1987), and Keddy (1989) view plant height as an adaptive trait, with competition for light selecting for greater vegetative height. That taller species were found in fertile wetlands suggests that, once nutrient limitation is removed, competition for light becomes the process

determining the species found in these areas. Supporting this contention are competition studies which consistently show taller species outcompeting shorter species under similar nutrient conditions (ie. Weiner 1986; Weiner and Thomas 1986; Mitchley and Grubb 1986; Goldberg and Fleetwood 1987). Similarly, Austin and Austin (1980) found that shorter grass species were outcompeted by tall grass species at high nutrient levels, apparently as a consequence of shading by the taller grass species. Conversely, at lower nutrient levels competitive interactions may be less intense (Wilson and Keddy 1986b) or less asymmetric (Keddy 1989), thereby preventing the exclusion of smaller species at lower nutrient concentrations. This may explain why shorter species predominate and dominance by a few species is prevented in infertile wetlands. Likewise, rhizome depth may be a trait related to the acquisition of space and resources in fertile wetlands (Shipley et al. 1989), or it may simply be a mechanical feature, with taller plants needing deeper anchors for support.

Fertility and Community State Variables

Standing crop, litter and species richness also show relationships with fertility in wetlands -- standing crop and litter increase in sites of high fertility whereas species richness decreases (Fig. 1.2). This relationship between standing crop and species richness holds true for other wetland communities (Auclair et al. 1976; Wheeler and Giller 1982; Vermeer and Berendse 1983; Day et al. 1988; Wisheu and Keddy 1989; Moore et al. 1989; Wheeler

and Shaw 1991) as well as being a general trend in terrestrial herbaceous plant communities (Grime 1973, 1977, 1979; Al-Mufti et al. 1978; Tilman 1982).

The relationship between standing crop and species richness found here is consistent with that particular component of Grime's 'humpback model' (1973, 1979) which predicts a decrease in species richness when going from moderate infertility to high fertility (decreasing stress, sensu Grime 1979) or from moderate to high standing crop. Wilson and Keddy (1986b) showed that wetland plants from fertile sites have higher competitive abilities than those from infertile sites, suggesting this reduction in species richness at high standing crop is a result of increased competition by a few competitively dominant species.

Fertility and Species Composition

Sites with similar fertility share dominant species and are taxonomically similar, whereas sites of different fertility are taxonomically distinct (Table 1.1 and Fig. 1.5). This is consistent with other studies showing that fertility is a major control of species composition in wetlands (Auclair et al 1976; Moore et al. 1989; Day et al. 1988; Walker and Wehrhann 1971). But, in addition to being taxonomically distinct from fertile wetlands, only infertile wetlands had rare and endangered plant species as dominant components of their flora (Table 1.1, Appendix 1.1), as found by Moore et al. (1989) and Wisheu and Keddy (1989). This suggests that rare species require the conditions created by

infertility, refugia from the competitively dominant species found at fertile sites, and that their rarity may be a result of the rarity of the infertile habitat (Smith et al. 1991).

Plant species of infertile wetlands share a number of similar traits such as low growth rates (Shipley and Keddy 1988), low competitive abilities (Wilson and Keddy 1986a), short stature (Grime 1979; this study), shallow rhizomes (this study), evergreenness (Boston and Adams 1987; Wisheu and Keddy 1989), and carnivory (Givnish 1987; Wisheu and Keddy 1989). This complement of traits make these plants adapted to conditions of resource limitation and can be categorized as stress-tolerators (sensu Grime 1977, 1979; Boston 1986; Boston and Adams 1987). Some examples of such plants from this study are *Cladium mariscoides*, *Scleria verticillata*, *Rhynchospora capillacea*, and *Sarracenia purpurea*. In contrast, many plants of fertile wetlands typically have high relative growth rates (Shipley and Keddy 1988), high competitive ability (Wilson and Keddy 1986a), tall stature (Grime 1979; Shipley et al. 1989; this study), and a large capacity for vegetative spread (Day et al. 1988; Shipley et al. 1989). Species such as these may have physiologies which are sensitive to suboptimal soil fertility (Shipley and Keddy 1988), thus trading off the ability to tolerate low nutrient concentrations for the ability to exploit optimal conditions. These species can be classified as competitors (Grime 1979) or clonal dominants (Day et al. 1988) and are represented here by species such as *Phalaris arundinacea*, *Calamagrostis canadensis*, and *Carex lacustris*. Thus, not only are

there species differences between wetlands of varying fertility, but there are also differences in the types of species.

The fact that we see such species compositional differences in the field -- a natural experiment sensu Diamond (1983) -- does not in itself prove that similar patterns will arise from cultural eutrophication, even if it is highly suggestive. However, similar shifts in plant community composition following eutrophication have been observed in wetlands (Sloey et al. 1978; Mudroch and Capobianco 1979; Ehrenfeld 1983; Morgan and Philipp 1986). Moreover, experiments in aquatic phytoplankton communities (Vollenweider 1968; International Joint Commission 1980; Schindler 1971, 1987; Thomas 1973; Kohler and Labus 1983) and terrestrial herbaceous communities (ie. Willis 1963; Bakelaar and Odum 1978; Jeffrey and Pigott 1973; Tilman 1984, 1987; Bobbink 1991) also show consistent, directional changes in community composition resulting from enrichment. Having established an association between wetland vegetation -- be it plant traits, community state variables, or the types of species -- and fertility, we can now make generalized predictions as to the potential species composition of wetlands based on fertility, or their changes upon eutrophication.

Conservation

If we assume that plant species composition will change in wetlands upon eutrophication, as discussed above, then infertile wetland habitats can be lost through eutrophication. This is important if we consider that infertile wetlands will be

increasingly subjected to eutrophication pressures as a result of the ever increasing urban and agricultural development around the Great Lakes. Three of the key factors influencing wetland ecosystems are water level, nutrient status, and disturbance (Keddy 1983). Eutrophication, by reducing the range of the natural nutrient gradients to just the fertile habitats, therefore acts to reduce the biological variation found along natural nutrient gradients. By removing an important environmental constraint (habitats with low nutrient levels), eutrophication will lead to the loss of those habitats essential for the persistence of the unique and often rare vegetation types found around the Great Lakes. Ellenberg (1988) and Tamm (1991) have described similar dramatic changes as a consequence of nitrogen loading in European vegetation types. From the perspective of centrifugal organization, eutrophication causes the progressive loss of distinctive peripheral habitats and vegetation types (Keddy 1990). The wide array of wetland communities becomes more and more compressed into a narrow core region consisting of species tolerant of eutrophic, high standing crop conditions. The maintenance of wetland quality and the protection of the range of plant communities, rare species and their associated wildlife will therefore require greater attention to minimizing the damage from eutrophication.

Eutrophication, however, is a natural process occurring on a geological time scale. All lakes and poorly drained depressions are subject to a natural aging process whereby they become enriched

through natural sedimentation and accumulation of organic materials (Spence 1921; Wetzel 1983; International Joint Commission 1980). This process needs to be considered since many infertile shoreline wetlands have undoubtedly been lost, through natural eutrophication, to more fertile types. More importantly, however, should be the concern for the increasing loss of infertile wetland habitats arising from accelerated, human induced, eutrophication. That is, the rate of infertile wetland loss is greatly accelerated by the effects of cultural eutrophication. The concern for such losses is much like the concern over the increasing loss of biodiversity globally, due to human influences, when species extinctions also occur as a natural process. If we are concerned about maintaining biodiversity (International Union for Conservation of Nature and Natural Resources 1980; World Commission of Environment and Development 1987), we will need increased conservation efforts directed at arresting the accelerated loss of infertile wetlands.

Natural eutrophication, on the other hand, does not work in isolation and is only one of many factors which effect the evolution of wetland ecosystems. Other factors, such as disturbance and exposure (e.g. Day et al. 1988; Wisheu and Keddy 1989) act to maintain ifertility and account for extant infertile wetlands. This understanding of the factors which influence wetland plant communities could be useful to direct conservation strategies. First, to maintain infertile wetlands, the natural processes which arrest natural eutrophication and maintain

infertility need to be identified and maintained. Secondly, if our goal is to restore infertile wetlands, we need to develop means to simulate these processes to maintain infertility.

Maintaining infertility appears to be the most logical means for conserving infertile wetlands. Reducing nutrient inputs from urban and agricultural runoff could be fairly straight forward and feasible, yet another important consideration is the increases of atmospheric deposition of phosphorus and nitrogen. The atmospheric deposition of these nutrients is a considerable component of the widespread eutrophication of ecosystems (International Joint Commission 1980; Ellenberg 1988; Tamm 1991) and the most difficult to mitigate. This form of eutrophication is especially important in those ecosystems which rely mostly on precipitation as a source of water, such as the interdunal pannes found in Sandbanks Provincial Park, Presqu'ile Provincial Park, and Long Point (Lake Erie) (this study). If the maintenance of species rich wetlands and the conservation of the range of wetland types is a desired goal, then means to mitigate this incipient eutrophication need to be sought. That species richness declines with increases in biomass (Auclair et al. 1976; Wheeler and Giller 1982; Vermeer and Berendse 1983; Day et al. 1988; Wisheu and Keddy 1989; Moore et al. 1989; Wheeler and Shaw 1991) suggests that reducing biomass could increase species richness. Removal of biomass by grazing or harvesting (Grime 1980; Wheeler and Giller 1982; Wheeler 1983; Tamm 1991), or by burning (Auclair et al. 1976; Wheeler and Giller 1982) has been found to maintain high species richness and is therefore

a possible management option (refer to Wheeler and Giller 1982 for further discussion and references). Removal of biomass in this manner would directly remove nutrients, reduce vegetation productivity and result in related species changes associated with lower biomass sites (see above discussion, Grime 1980). However, the introduction of another factor, namely disturbance, will have different ecological implications and could also result in a change in the unique, and often rare, plant communities found in infertile wetlands (Wheeler and Giller 1982; Tamm 1991). The use of such management therefore needs to be investigated further and the development of new ways to maintain infertility without added ecological consequences needs to be addressed.

Figure Captions

- Figure 1.1. Location of study sites, according to wetland type, along the northern shorelines of the Great Lakes in southern Ontario, Canada.
- Figure 1.2. Mean values (n=4) with 95% confidence limits for Community State Variables (Standing Crop, Litter and Species Density) for Type I and II wetlands. Model I ANOVA significance level between wetland types are: * = $P < 0.05$, ** = $P < 0.01$.
- Figure 1.3. Mean values (n=4) with 95% confidence limits for Fertility Variables (Phosphorus, Aqueous Extractable Phosphorus, Nitrogen, Loss on Ignition, and the biomass and biomass/soil weight for the Bioassay of Fertility) for Type I and II wetlands. Significance levels between wetland types are as in Fig. 1.2.
- Figure 1.4. Mean values (n=4) with 95% confidence limits for Plant Traits (height, rhizome diameter, rhizome depth) for Type I and II wetlands. Significance levels between wetland types are as in Fig. 1.2.
- Table 1.1. Five most frequently encountered species within each of the eight wetland sites. Top Row represents Type I wetlands and Bottom Row represents Type II wetlands. Note: *Helenium autumnale* and *Panicum flexile* for Long Point have the same frequency value. Species associated with a '*' are classified as nationally rare according to Argus and Pryer

1990.

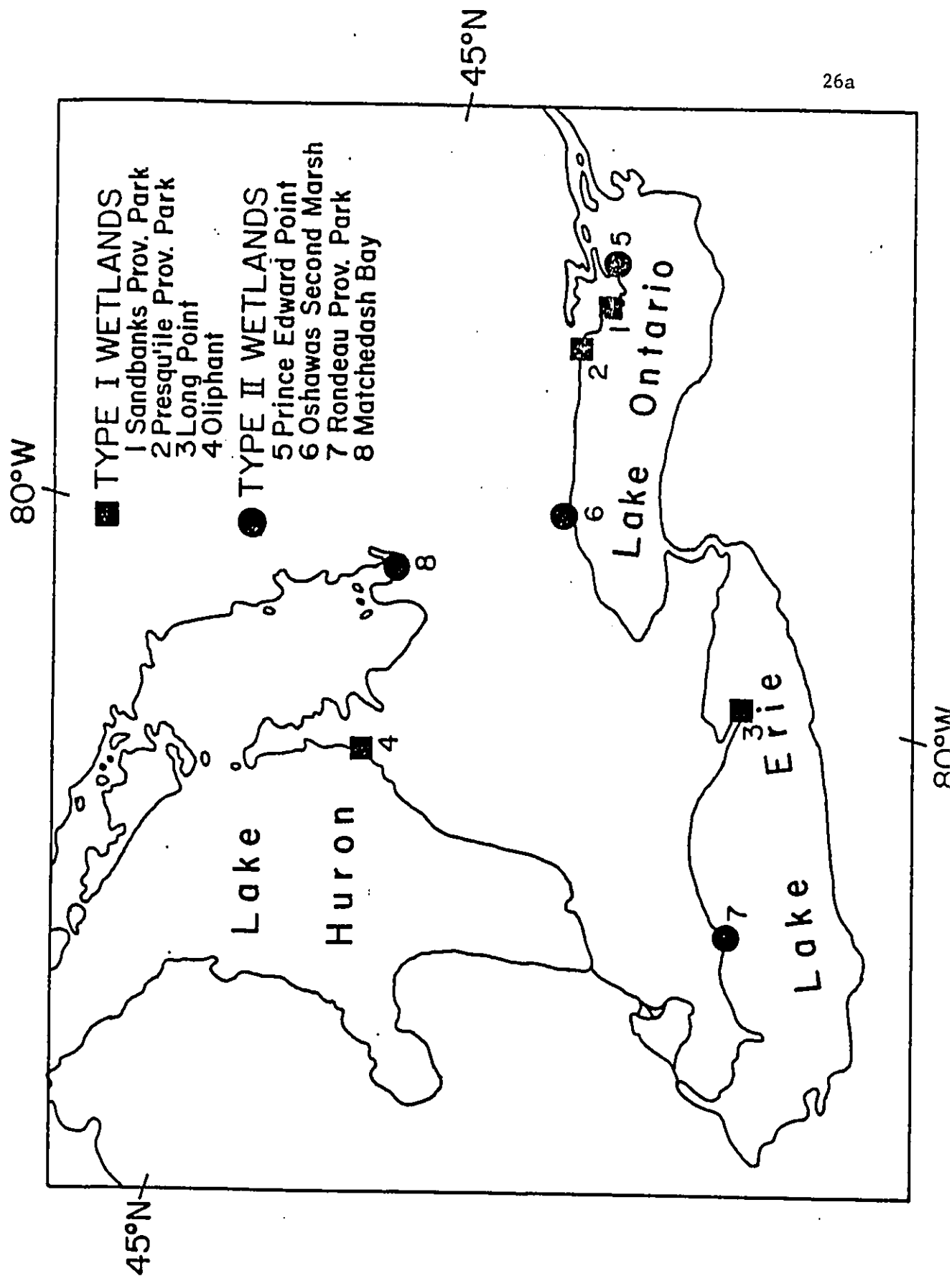
Figure 1.5. Hierarchical cluster dendrogram, using Jaccard similarity matrix for total species composition, showing per-cent similarity. Sites are as follows:

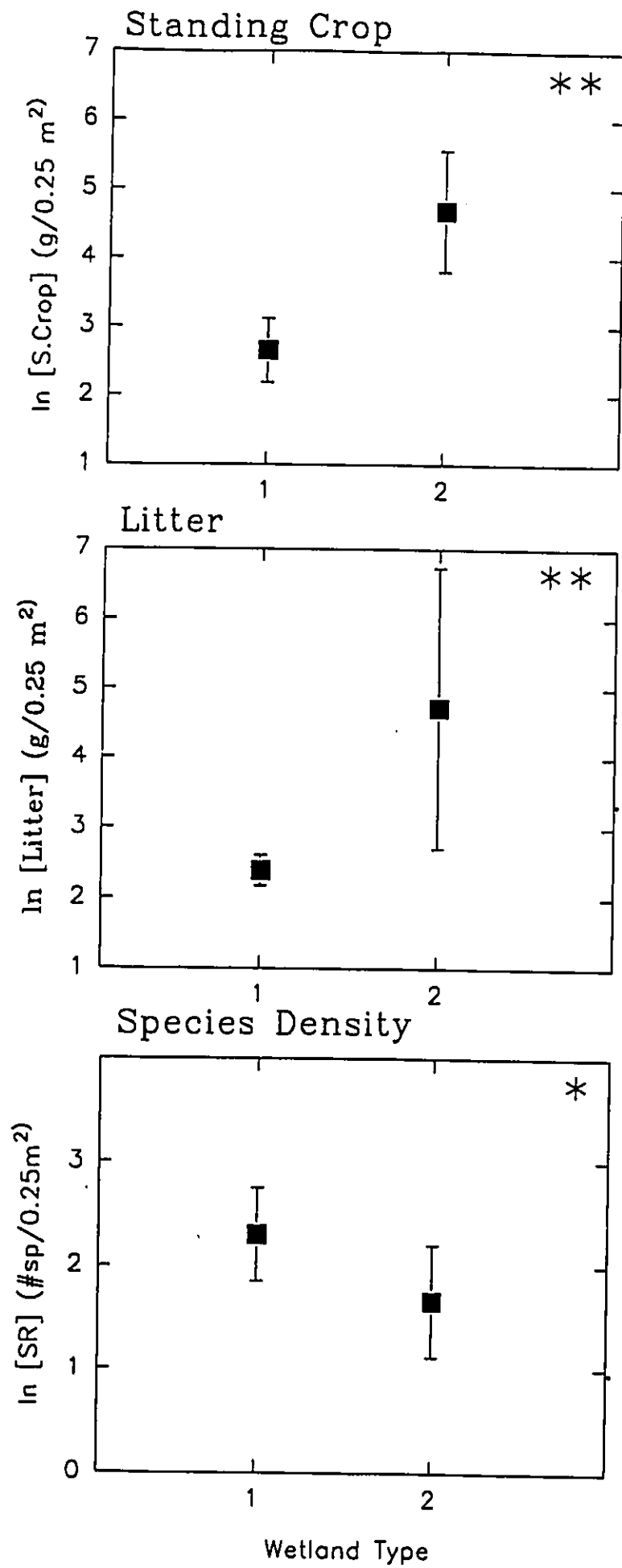
Type I

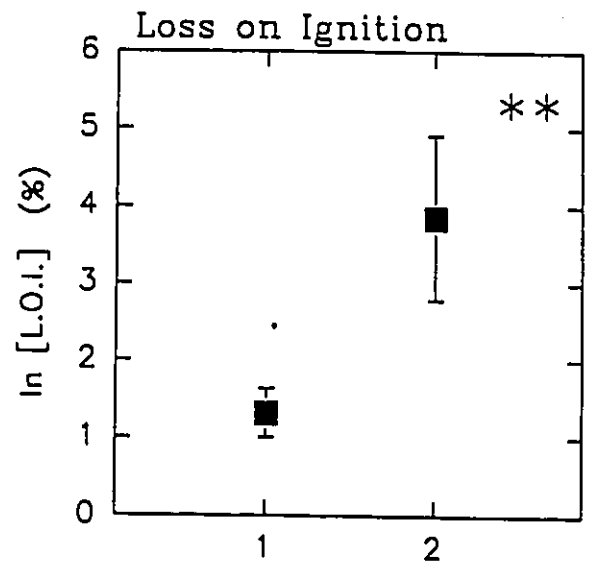
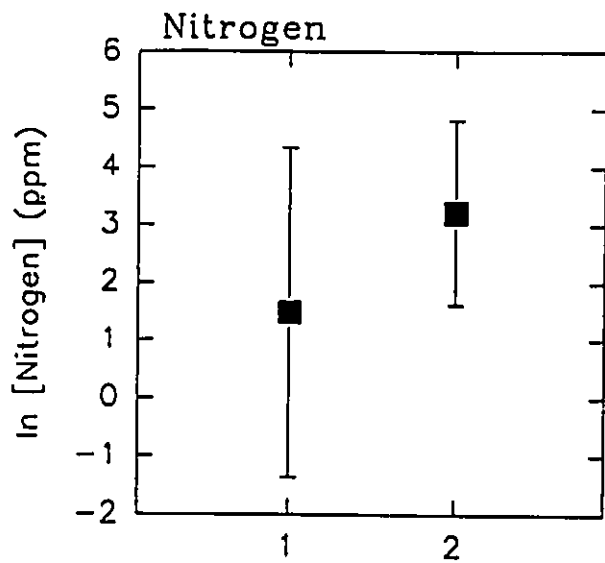
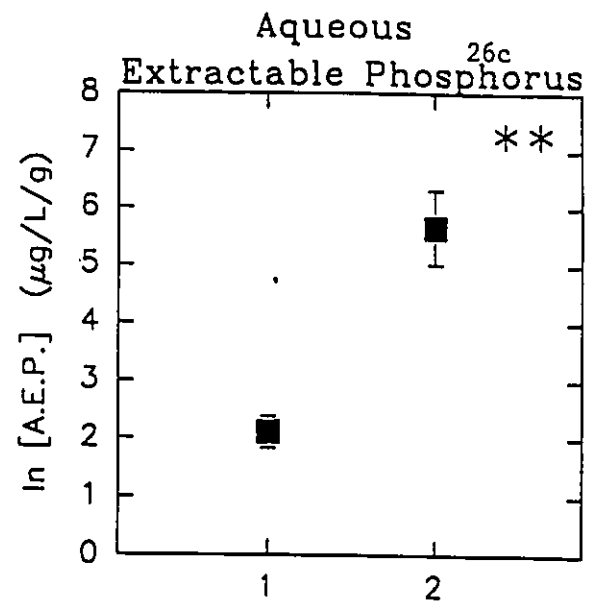
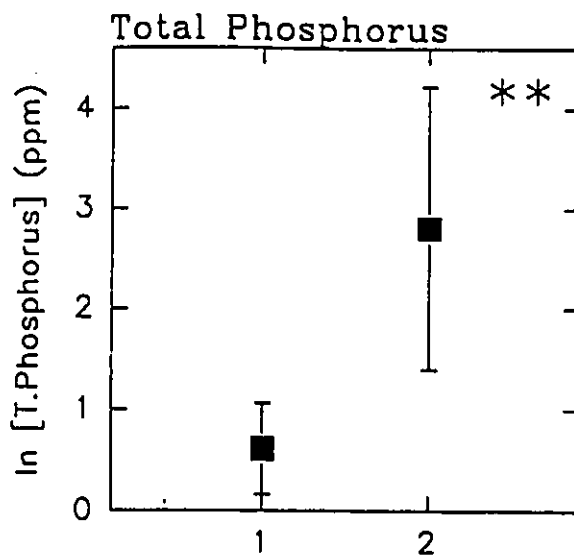
1. Sandbanks Provincial Park
2. Presqu'ile Provincial Park
3. Long Point
4. Oliphant

Type II

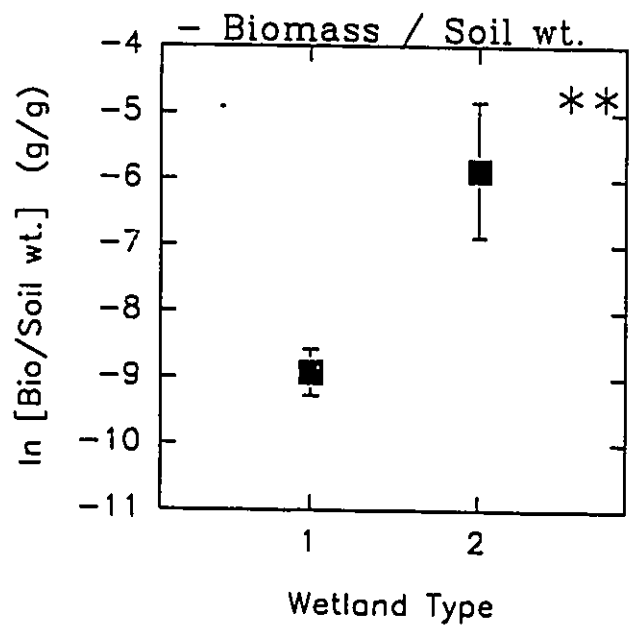
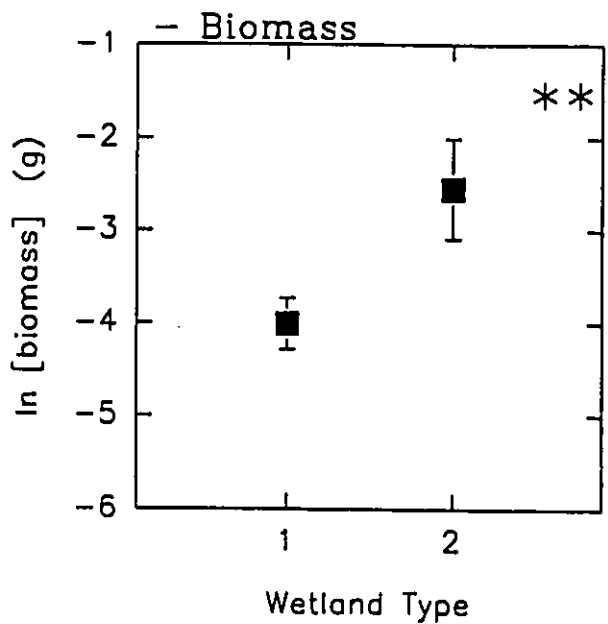
5. Prince Edward Point
6. Oshawa's Second Marsh
7. Rondeau Provincial Park
8. Matchedash Bay







Bioassay of Fertility



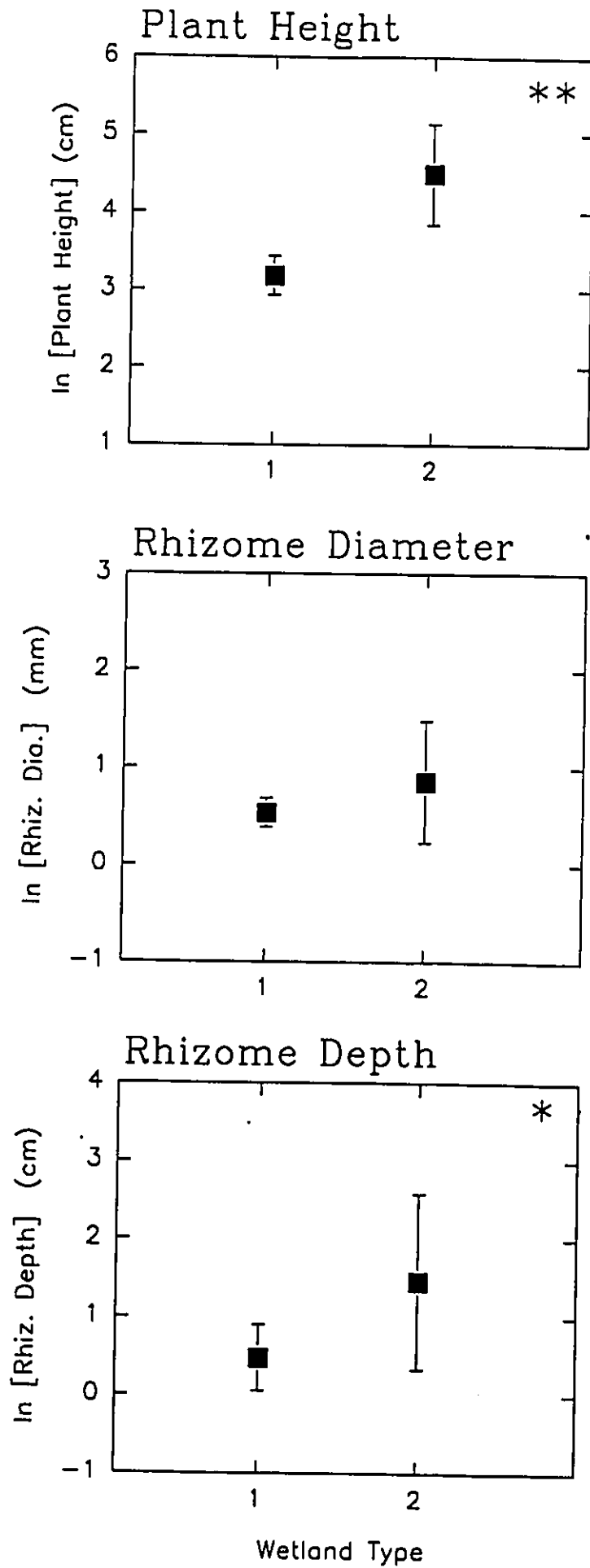
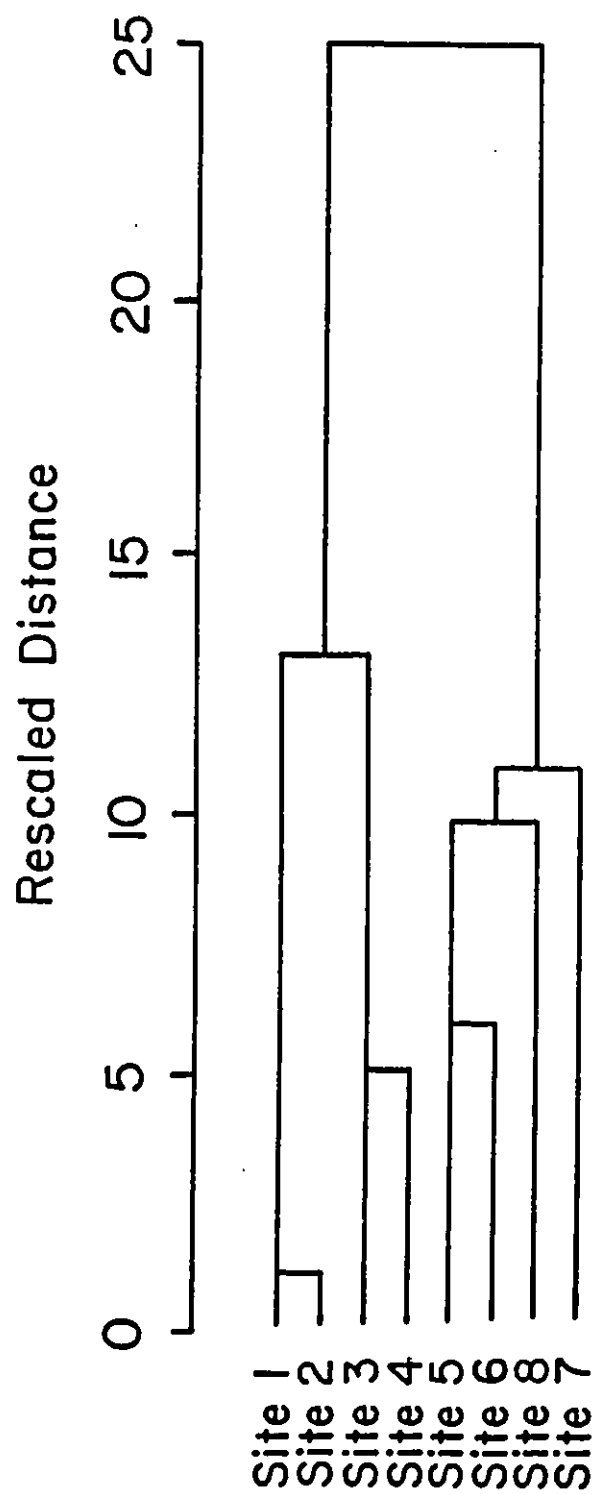


Table 1.

Sandbanks P.P.	Presqu'île P.P.	Long Point	Oliphant fens
<i>Eleocharis pauciflora</i>	<i>Eleocharis elliptica</i>	<i>Rhynchospora capillacea</i>	<i>Cladium mariscoides</i>
<i>Cladium mariscoides</i>	<i>Cladium mariscoides</i>	<i>Scleria verticillata</i>	<i>Rhynchospora capillacea</i>
<i>Potamogeton gramineus</i>	<i>Potentilla anserina</i>	<i>Cladium mariscoides</i>	<i>Scleria verticillata</i>
<i>Equisetum variegatum</i>	<i>Scleria verticillata</i>	<i>Eleocharis elliptica</i>	<i>Tofieldia glutinosa</i>
<i>Lycopus uniflorus</i>	<i>Equisetum nesonii</i>	<i>Helenium autumnale</i>	<i>Sisyrinchium montanum</i>
		<i>Panicum flexile</i>	
Prince Edward Point	Oshawa's Second Marsh	Rondeau P.P.	Matchedash Bay
<i>Carex stricta</i>	<i>Phalaris arundinacea</i>	<i>Calamagrostis canadensis</i>	<i>Calamagrostis canadensis</i>
<i>Calamagrostis canadensis</i>	<i>Calamagrostis canadensis</i>	<i>Polygonum hydropiper</i>	<i>Carex lacustris</i>
<i>Sium suave</i>	<i>Impatiens biflora</i>	<i>Leersia oryzoides</i>	<i>Carex atherodes</i>
<i>Scutellaria lateriflora</i>	<i>Lathyrus palustris</i>	<i>Eleocharis erythropoda</i>	<i>Phalaris arundinacea</i>
<i>Lycopus spp.</i>	<i>Mentha arvensis</i>	<i>Carex lasiocarpa</i>	<i>Onoclea sensibilis</i>

Hierarchical Cluster Analysis



"We feel that some emphasis should be diverted to the development of models whose value will be judged on their predictive ability alone rather than their causal or heuristic properties."

(Dillon and Rigler 1974)

Relationships among plant traits, wetland vegetation and
fertility: An empirical approach to
plant community ecology

Introduction

Prediction, as opposed to description, has been repeatedly argued as a goal for community ecology (ie. Peters 1980a, 1980b, 1991; Rigler 1982; Starfield and Beloch 1986; Keddy 1990; Keddy in press). Yet the still largely descriptive emphasis of ecology has left planners and managers with very few useful, predictive models (Dillon and Rigler 1974; Odum 1985; Schindler 1987; Keddy 1987, in press; Peters 1991). Without predictive relationships ecologists have little to contribute to the development of adequate environmental management policies.

Predictive relationships are simplest to find and most useful when the dependent variable of interest is univariate as opposed to multivariate. For example, the relationship between phosphorus and chlorophyll 'a' concentration (Dillon and Rigler 1974) has revealed an effect of eutrophication in aquatic communities and has, in part, led to remedial action plans (International Joint Commission 1980). However, no such relationship has been sought concerning eutrophication in vascular plant communities. Instead, the usual approach of seeing vegetation as a group of species complicates the search for predictive models. Here the response variables are site specific and become either multi-dimensional "species space", as in standard ordination studies (ie. Auclair et al. 1976; Gauch and Stone 1979; Orlóci and Stanek 1979; Whittaker et al. 1979; Ehrenfeld 1983; Day et al. 1988; Ben-Shahar 1991; Roberts and

Ludwig 1991; Franklin and Merlin 1992), or individual species responses along environmental gradients (ie. Willis 1963; Austin and Austin 1980; Parrish and Bazzaz 1982; Tilman 1984; Inouye and Tilman 1988; Bobbink 1991), making large scale general predictions difficult and complex. In fact, ordination is primarily used as a descriptive tool, a link between community properties and human conceptualization (Gauch 1982), rather than a predictive tool for this reason. Since ordination axes are not functions of original variables any arguments for causal relationships are tenuous, making ordination, at best, a method to generate hypotheses not test them (James and McCulloch 1990).

One way to avoid the complexity of multi-species descriptions, and their lack of predictive utility, is to emphasize traits that have to do with function (ie. Grime and Hunt 1975; Grime et al. 1981; van der Valk 1981; Givnish 1987; Shipley and Keddy 1989, Keddy 1990, 1992; Shipley and Parent 1991). Screening plants for traits provides the quantitative data necessary for ecological inquiries which are not limited to the species in a specific area (Grime 1980; Keddy 1992). Another way to avoid multi-species descriptions is to look for simple state variables that describe characteristics of assemblages of species (Keddy 1992). State variables such as standing crop and species richness have yielded important generalizations in community ecology (Al-Mufti et al. 1977; Grime 1979; Tilman 1982; Wheeler and Giller 1982; Vermeer and Berendse 1983; Day et al. 1988; Wisheu and Keddy 1989; Moore et al. 1989). Then, once one has screened a group of species for a

specific trait or measured state variables at many sites, one can search for environmental factors which best predict these traits or state variables. Some recent examples of success using this approach include Rosenzweig (1968), Dillon and Rigler (1974), Whittaker and Niering (1975), Schall and Pianka (1978), Currie and Paquin (1987), White and Miller (1988), Whillans (1989), Hill and Keddy (1992).

I used both these approaches to investigate the response of wetland vegetation to eutrophication. Eight Great Lakes wetlands were studied to determine the following: 1) the relationships between plant traits and fertility, 2) the relationships between community state variables and fertility, 3) the soil fertility variable which best predicts these dependent variables.

Methods

The study sites and variables used here are all described in chapter 1 - these are as follows; 1) Sandbanks Provincial Park, Presqu'ile Provincial Park, Long Point Harbour (Prince Edward County), Oshawa's Second Marsh, Long Point (Haldimand-Norfolk County), Rondeau Provincial Park, Oliphant, and Matchedash Bay, 2) plant traits - height, rhizome diameter, and rhizome depth, 2) community state variables - standing crop and species richness, and 3) fertility variables - total phosphorus, aqueous extractable phosphorus, nitrogen, loss on ignition, and bioassay of fertility (biomass or biomass/soil weight).

Data Analysis

Since Model II regression is inappropriate for developing predictive relationships (Sokal and Rolf 1981) a Model I simple linear regression analysis was used to find the relationships between selected variables. Site means ($n=8$) for all variables were used in the analysis. To determine which relationships were strongest and most useful I compared all dependent variables separately across all six fertility (independent) variables according to their significance levels. I used Bonferroni adjusted probabilities, 0.008 (equivalent to $P<0.05$) and 0.0013 (equivalent to $P<0.001$), to determine significance levels for such unplanned comparisons. The independent variable most frequently rated as the best predictor of the dependent variables was then used to select the best relationships. Natural logarithmic transformations were used to stabilize variances and were used with all variables.

Results

Table 2.1 shows the correlation coefficients (r) and significance levels between all variables. Among the fertility variables, total phosphorus was most frequently ranked as the best predictor of the vegetation variables whereas nitrogen was the least. In turn, plant height, standing crop and species richness were the dependent variables most strongly connected to total phosphorus. To simplify the model, only these three dependent variables and total phosphorus were used to show the significant response of plant traits and community state variables to fertility.

Figure 2.1 shows that both plant height (Ht) and standing crop (SC) are strongly positively related to soil phosphorus (TP) ($\ln(\text{Ht}) = 2.93 + 0.523(\ln[\text{TP}])$, $P < 0.0012$, $r = 0.92$; $\ln(\text{SC}) = 2.3 + 0.79(\ln[\text{TP}])$, $P < 0.000$, $r = 0.90$). Species richness (SR), on the other hand, shows a strong negative relationship with soil phosphorus ($\ln(\text{SR}) = 2.48 - 0.29(\ln[\text{TP}])$; $P < 0.005$; $r = -0.85$).

Discussion

Merits of Approach

Having demonstrated that there are strong relationships between plant traits / community state variables and fertility variables, the questions remaining here are concerned with their utility. The greatest merit of such simple empirical relationships is that prediction is now possible. I show that plant height, standing crop and species richness vary predictably with soil phosphorus (Fig. 2.1). If we assume that eutrophication could be responsible for such vegetation changes, as discussed in chapter 1, it should now be possible to predict changes in these variables with specified levels of eutrophication. In general, tall, clonal species would replace the shorter stress tolerators (*sensu* Grime 1979) upon enrichment. These patterns would be consistent with other published studies (Willis 1963; Al-Mufti et al. 1978; Bakelaar and Odum 1978; Grime 1979; Tilman 1984, 1987; Moore et al. 1989; Wisheu and Keddy 1989; Bobbink 1991). More specifically, we can now progress from these generalizations to more accurate predictions. Equation 3 (Fig. 2.1) shows that a roughly 11 fold increase in soil phosphorus will decrease species richness by half.

For example, if soil phosphorus increased from 1.8 to 20.1 ppm we could expect species richness to decline from 10 to 5 sp/0.25m². Similarly, using equations 1 and 2, to double plant height would require a roughly 4 fold increase in soil phosphorus and to double standing crop would take a roughly 2 fold increase in soil phosphorus.

With such strong relationships between specific plant traits, community state variables, and fertility, clear connections to mechanism and process now emerge. For example, I found that shorter species are replaced by taller species upon enrichment (chapter 1 Fig. 1.4, Fig. 2.1), as did Willis (1963), Jeffrey and Pigott (1973), Grime (1979), Austin and Austin (1980), and Tilman (1984, 1987). Such findings suggest that, once nutrient limitation is removed, competition for light becomes important in determining species composition in fertile sites (Grime 1979; Givnish 1982; Tilman 1985, 1987; Keddy 1989; Smith and Huston 1989). As a result, tall species, with their high relative growth rates (Grime and Hunt 1975; Grime 1979; Shipley and Keddy 1988) and other size related traits (Grime 1979; Gaudet and Keddy 1989), predominate in fertile areas where competitive interactions are more intense (Wilson and Keddy 1986b) and more asymmetric (Keddy 1989). Similarly, rhizome diameter and rhizome depth may be traits related to the acquisition of resources and space in fertile sites (Shipley and Keddy 1989) leading to higher standing crop in these areas dominated by fewer species, but these variables were of secondary importance here (Table 2.1).

Furthermore, by using simple, quantitative response variables I found such models to have broad generality. By identifying key environmental factors, along with the aforementioned link between plant traits and vegetation processes, this approach may be used in other vegetation types. Similar response patterns to eutrophication have been described for sand dunes (Willis 1963), grasslands (Jeffrey and Pigott 1973; Silvertown 1980; Bobbink 1991), old fields (Bakelaar and Odum 1978; Tilman 1982, 1984, 1987; Carson and Barrett 1988), pine barrens (Ehrenfeld 1983; Morgan and Philipp 1986), and many other terrestrial vascular plant communities in continental Europe (Ellenberg 1988). But, since most of these studies were species oriented they only provide descriptions on a site by site basis, generating many individual cases and little generality.

Finally, with its increased generality, this empirical approach could make the selection of indicators for assessing ecosystem health easier and more objective. Regression requires continuous, quantitative variables to describe the vegetation response, unlike species oriented approaches. Such variables, like plant traits and community state variables, are then necessarily general, large scale, and easily measured, and are therefore potentially suitable indicators of ecosystem health (see Keddy et al. in press). By ranking these variables according to their correlation coefficients (r), I was then able to objectively reduce this list to those which have the greatest predictive value, namely plant height, standing crop, and species richness. If we wanted to

select variables to indicate changes in ecosystem quality arising from eutrophication, then these variables appear appropriate. For example, infertile wetlands can now be identified by a plant community of low standing crop composed of short stress tolerant species and a high species richness (refer to Chapter 1). Then through monitoring, if we find taller, clonal dominant species, typical of more common wetland areas, beginning to invade as well as changes to higher standing crop and a decline in species richness, we may suspect that eutrophication is occurring. To simplify this even further, you may only want to measure the variable which is most sensitive. Then, by using the regression slope, one would select species richness. Having the greatest slope, species richness changes faster per unit phosphorus and therefore is the most sensitive to changes in soil phosphorus.

Implications

It would be simpler to manage our environment if we had the ability to know and predict the consequences of our actions. Unfortunately, present ecological models provide us with only a preliminary understanding of how communities respond to perturbation (Odum 1985; Schindler 1987; Keddy 1991). However, the research agenda set forth by the Ecological Society of America in the "Sustainable Biosphere Initiative" (Lubchenco et al. 1991), "The World Conservation Strategy" (International Union for Conservation of Nature and Natural Resources 1980), The United Nations' report "Our Common Future" (World Commission of

Environment and Development 1987), and "Canada's Green Plan" (Government of Canada 1990) all emphasize changing research priorities to understanding our effects on the environment. This will require predictive relationships. I suggest one route to progress is to place greater emphasis upon empirical approaches, using generalized variables such as traits, to investigate and predict the effects of human actions.

Figure Captions

Table 2.1. A matrix of model I correlation coefficients (r) between all variables, using site means ($n=8$). The natural logarithmic transformation has been used to stabilize variances for all variables. Refer to Appendix 1.3 for full data details. BF=Bioassay of Fertility.

Figure 2.1 i). Model I linear regression between plant height (Ht in cm) and total phosphorus (TP in ppm) using site means ($n=8$):

$$\ln(\text{Ht}) = 2.93 + 0.523(\ln[\text{TP}]), P < 0.0012, r = 0.92.$$

Refer to Appendix 2.1 for regression analysis details.

ii) Model I linear regression between standing crop (S.C. in g/0.25 m²) and total phosphorus (TP in ppm) using site means:

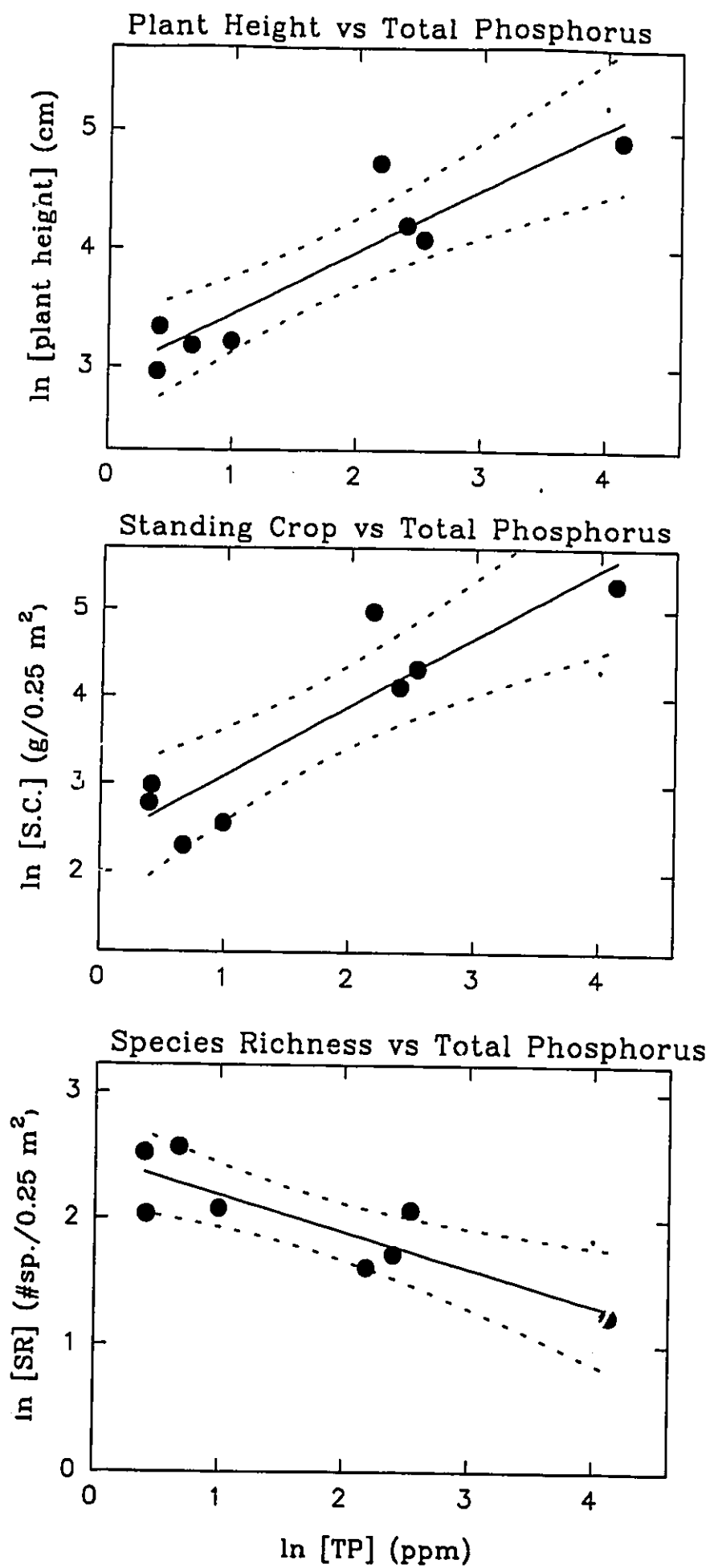
$$\ln(\text{SC}) = 1.20(\ln[\text{TP}]) - 2.62, P < 0.000, r = 0.90.$$

Refer to Appendix 2.1 for regression analysis details.

iii) Model I linear regression between species richness (SR in #sp/0.25 m²) and total phosphorus (TP in ppm) using site means:

$$\ln(\text{SR}) = 2.48 - 0.29(\ln[\text{TP}]), P < 0.005, r = -0.85.$$

Refer to Appendix 2.1 for regression analysis details



Dependent Variable

Independent Variable	Height (cm)	Rhizome Diameter (mm)	Rhizome Depth (cm)	Standing Crop (g/0.25m)	Species Richness (#sp./0.25m)
Total Phosphorus (ppm)	0.92 ** (0.0012)	0.62 (0.098)	0.79 (0.020)	0.90 * (0.002)	-0.85 * (0.007)
Aqueous Extractable Phosphorus (µg P/L/g)	0.89 * (0.003)	0.49 (0.221)	0.67 (0.068)	0.91 * (0.0016)	-0.71 (0.047)
Nitrogen (ppm)	0.60 (0.118)	0.38 (0.354)	0.46 (0.246)	0.51 (0.513)	-0.56 (0.146)
Loss on Ignition (g/g or %)	0.82 (0.013)	0.45 (0.263)	0.61 (0.109)	0.81 (0.014)	-0.61 (0.107)
BF - Biomass (g)	0.86 * (0.006)	0.40 (0.326)	0.61 (0.106)	0.88 * (0.004)	-0.63 (0.096)
BF - Biomass/soil wtL (g/g)	0.84 * (0.008)	0.43 (0.285)	0.61 (0.106)	0.85 * (0.007)	-0.62 (0.100)

A potential trait to measure interspecific differences
in plant responses to eutrophication

Introduction

Plant traits, rather than species, appear to be more useful for large scale ecological questions (i.e. Chapters 1 and 2). The use of plant traits is an approach receiving more attention lately (Grime 1977, 1979; Menges and Waller 1983; Noble and Slatyer 1980; van der Valk 1981; Givnish 1982, 1987; Tilman 1988, 1991; Keddy 1989, 1990; Grace 1989; Shipley et al. 1989). This work differs from most others dealing with plant community changes along experimental (Willis 1963; Jeffery and Pigott 1973; Bakelaar and Odum 1978; Austin and Austin 1980; Silvertown 1980; Tilman 1984, 1987; Carson and Barrett 1988; Tilman and Cowan 1989; Bobbink 1991) or natural (Walker and Wehrhahn 1971; Ehrenfeld 1983; Morgan and Philipp 1986; Ellenberg 1988; Day et al. 1988; Ben-Shahar 1991) nutrient gradients. That is, empirical relationships between plant traits and natural nutrient gradients make prediction now possible (Chapters 1 and 2). In this chapter I will further investigate the effects of eutrophication on wetland plant communities by measuring a trait which may be useful in predicting interspecific responses to changing nutrients.

Many traits which relate to the physiological and life history properties a plant must possess to survive and compete under specific environmental conditions (Grime 1979, 1985; Keddy 1990) are not obvious upon inspection of plant form. Such traits require a process called 'screening' (e.g. Grime and Hunt 1975; Grime et al. 1981) for their determination. In screening, a simple bioassay

for a particular attribute is developed and is systematically applied to a flora of interest. This systematic comparative approach was pioneered by Grime and Hunt (1975) using relative growth rate (RGR). Since then, traits such as competitive ability (Wilson and Keddy 1986; Gaudet and Keddy 1988), stress tolerance (Shipley and Keddy 1988), R^* (Tilman 1980, 1990), biomass partitioning ratio (root:shoot ratio - Chapin 1980; Tilman 1988, 1991; Shipley and Peters 1990), and palatability (Sheldon 1987) have been measured (see Keddy 1990 for further discussion).

If we assume that species changes will occur upon eutrophication, as discussed in Chapter 1, then is there a generalized trait useful for predicting such interspecific changes to enrichment in the field? My purpose here was to first screen 47 wetland species, which represent species from a wide array of shoreline habitats in north-eastern North America, for their above ground biomass response to high and low nutrients. I then compared these species according to their proportional differences in above ground biomass between low and high nutrients, the 'biomass sensitivity' trait, to see whether or not it was potentially useful for predicting or explaining their distribution in the field.

Methods

Species

Forty-seven wetland plant species were used for the screening bioassay (Appendix 2.1). They were chosen to represent the various species which are found in the different shoreline wetland habitats

in north-eastern North America. These included rare or endangered taxa from infertile lakeshores (*Coreopsis rosea*, *Panicum longifolium*, *Rhexia virginica*), annuals typical of mud flats (*Gnaphalium uliginosum*, *Cyperus aristatus*), large perennials typical of fertile areas (*Phalaris arundinacea*, *Typha glauca*), reeds from river banks (*Scirpus acutus*, *Eleocharis calva*, *Juncus brevicaudatus*), and other species representing other life forms and habitats (see Boutin and Keddy (1992) and Appendix 2.1 for further details).

Experimental set up

To establish the perennials (as listed in Appendix 2.1), seeds of each of the species were taken from cold storage on July 28, 1989 and separately sown into 11.4 L pots containing 10 L of a mixture of commercial potting soil (25%) and washed sand (75%). Ten replicates for each of these species were arranged in a common garden at Carleton University, Ottawa, Ontario, Canada. Three holes (7 mm diameter) were drilled in each pot, two were placed 5 cm from the top and the other 5 cm from the bottom, for drainage. After germination and establishment, the seedlings were thinned or transplanted to get one individual per pot. These were maintained throughout the growing season and kept under a bird netting tent to prevent herbivory. In mid-November the plants were prepared for outside winter storage by first corking all the holes and flooding the pots, then covering the pots with a single layer of clear plastic sheet, and finally covering the plastic with a thick layer of straw.

The following year the plants were uncovered and the pails uncorked on May 9, 1990. At this time the three annual species were sown into their separate pots (prepared as before) and were placed into an overall randomized block design. On May 25, five of the blocks received a high nutrient treatment (54 g fertilizer/pot) with the other five blocks receiving a low nutrient treatment (2.6 g fertilizer/pot) of Nutricote 14-14-14 controlled release fertilizer pellets (Scientific Growing Aids, Plant Products Co. Ltd., Brampton, Ontario, Canada), mixed within the top 2 cm of soil. The plants were maintained for the season by uniform watering and periodic weeding. Upon harvesting the plants on Sept. 29, 1990, the soil was carefully washed off the roots of each plant, the above and below ground biomass were separated and their dry weight (to constant weight at 60°C) determined.

Data Analysis

Of the 47 species initially selected (Appendix 2.1) only 28 survived to provide two or more replicates for each treatment (Table 3.1). Since the perennials were established the previous year, the 'biomass sensitivity' measure was derived using only the above ground biomass for each species using the following formula:

$$P(\Delta B) = \frac{(B_F - B_I)}{B_F}$$

where B_F and B_I are the mean values for the above ground biomass produced in the fertile and infertile treatments, consecutively. A two way ANOVA was used to test for interspecific and nutrient treatment effects on the above ground biomass produced.

Results:

Table 3.1 shows that all species produced more above ground biomass and therefore grew better at high fertility. There were also large differences between species in terms of the absolute amount of biomass produced. However, there appears to be very little difference between species when their proportional differences in biomass, the 'biomass sensitivity' trait ($P(\Delta B)$), are compared (Table 3.1). The similarity in proportional differences in biomass suggests that all the species responded uniformly to nutrient treatment effects.

Table 3.2 shows that both the species and nutrient treatment main effects were significant ($P < 0.0005$) as well as the interaction component ($P < 0.0005$) for the $\ln(\text{biomass})$ response variable. Note how large the nutrient main effect variance component is in comparison to those of either the species or interaction components. The significant interaction variance component for $\ln(\text{biomass})$ indicates that the species did not respond proportionally to the nutrient treatment. In other words, in order to know the response of $\ln(\text{biomass})$ to a nutrient treatment one needs to know which species is concerned. This finding contradicts the findings from Table 3.1, where $P(\Delta B)$ suggests that the biomass

response of species was proportional.

Upon further inspection of Tables 1 and 2, I reconciled their apparent contradictory results. First, the proportion of variance partitioned to the species main effect and the interaction components are very small (0.5% of that for nutrient effects) in comparison to that of the nutrient treatment effect. This suggests that there is actually very little difference between species in their $\ln(\text{biomass})$ response (Table 3.2). As well, all species, except *Juncus brevicaudatus* and *Cyperus aristatus*, had biomass sensitivity measures ($P(\Delta B)$) between 0.93 and 0.99 (Table 3.1). It is peculiar that only two out of twenty-eight species, selected to represent a wide variety of different wetland habitats, had comparatively lower 'biomass sensitivity' values. If the biomass sensitivity measure was meaningful, correlated with species distribution patterns, then one would expect a pattern of similarities and dissimilarities throughout such a list of varied species. Instead, only two species, having contrasting life histories and growth forms (refer to Appendix 2.1 and Boutin and Keddy (in press)), were found to be different. In addition, a similar study by Gaudet (1992) found that *Juncus brevicaudatus* had a $P(\Delta B)$ value not unlike the other species measured - that is $P(\Delta B) = 0.98$. I therefore suspected that some other factor, one not accounted for here (e.g. experimental error), is responsible for these species being different. I then redid the analysis with these 'outliers' removed. Table 3.3 shows that the removal of these two species made the interaction term not significant. That

there is no interaction between the species and nutrient main effects for the $\ln(\text{biomass})$ response variable means that the only component of the model affecting $P(\Delta B)$ is the nutrient treatment effect. Increases in $\ln(\text{biomass})$ at high fertility is therefore proportional across all species, making the biomass sensitivity trait unchanged across species.

Discussion

All species grew better in the fertile treatment (Table 3.1; nutrient treatment main effect in two way ANOVA, $P < 0.0005$, Table 3.3) and therefore have an inherent shared preference for fertile conditions. Although all species perform best at the same end of the nutrient gradient in isolation, they show different distributions along nutrient gradients in the field (Chapter 1; Day et al. 1988). This is consistent with the distinction between 'ecological' versus 'physiological' responses (Mueller-Dombois and Ellenberg 1974; Austin and Austin 1980; Austin 1982) or 'fundamental' versus 'realized' niches (Miller 1967) and illustrates the pattern of inclusive niches (Miller 1967; Colwell and Fuentes 1975; Wisheu and Keddy 1992). One of the basic assumptions of the 'Centrifugal Organization' model of Keddy (Keddy 1990; Wisheu and Keddy 1992) is that plant niches are inclusive, all plants having an inherent (physiological) preference for the ideal conditions of the core habitat. According to this model, plants become restricted to the peripheral habitats as a result of a tradeoff between the ability to compete and the ability to

tolerate different stresses.

If we consider the change in biomass between treatments on a proportional basis, that is the 'biomass sensitivity' measure $P(\Delta B)$, there appears to be no difference between species (Table 3.1). The very small, yet significant, variance component of the species main effect (Table 3.3) shows that there are some species that are significantly different from others. However, since it is so small, if you hold the nutrient level constant the differences are comparatively very small. Furthermore, since there was no interaction, all species respond proportionally the same. This means that $P(\Delta B)$ should not change between species, as was found. My results therefore suggest that, for adults in the absence of neighbours, species show the same proportional response in above ground biomass to changes in nutrients. That is to say, observed changes in species composition along natural nutrient gradients appear not to be because of the inherent, physiological differences of adults to exploit nutrients. This is consistent with Gaudet (1992) who found that a similar measure of stress sensitivity gave the same, proportional adult responses in a screening experiment using 21 wetland species, 10 of which were used in this study, and two nutrient levels.

Given how little variation there is in my proportional measures of biomass sensitivity ($P(\Delta B)$), some other trait apparently underlies the change in species upon eutrophication. There is increasing evidence that plant height is an important, adaptive trait, with competition for light selecting for greater

vegetative height (Grime 1979; Givnish 1982; Tilman 1985, 1987; Tilman and Cowan 1989; Keddy 1989). Plant height also varies with nutrient levels in the field (chapters 1 and 2). Simple traits such as plant height or shade tolerance may therefore be more useful in predicting plant responses to eutrophication.

Figure Captions

- Table 3.1. Above ground biomass (standard deviation) of 28 wetland plant species grown at high and low nutrient conditions, the change in mean above ground biomass ($\Delta B = \bar{B}_F - \bar{B}_I$) between nutrient treatments, and the 'biomass sensitivity' trait ($P(\Delta B)$, see text) between nutrient treatments.
- Table 3.2 Results of the two way analysis of variance for species ($n=28$) and nutrient treatment ($n=2$) effects on $\ln(\text{biomass})$.
- Table 3.3 Results of the two way analysis of variance for species ($n=26$) and nutrient treatment ($n=2$) effects on $\ln(\text{biomass})$. Note that *Juncus bevicaudatus* and *Cyperus aristatus* have been removed for this analysis, making $n=26$.

Table 1.

Species	Above Ground Biomass (g)				ΔB	P(ΔB)	52
	n	B_t	n	B_p			
<i>Acorus calamus</i> L.	4	2.23 (1.12)	5	31.24 (9.27)	29.01	0.93	
<i>Alisma plantago-aquatica</i> L.	2	0.59 (0.73)	2	99.04 (19.69)	98.45	0.99	
<i>Carex crinita</i> Lam.	5	3.95 (1.09)	5	77.16 (6.07)	73.22	0.95	
<i>Cyperus aristatus</i> Rottb.	5	1.07 (0.60)	4	4.04 (2.38)	2.97	0.73	
<i>Echinocloa crusgalli</i> (L.)Beaurv.	5	2.54 (1.49)	5	53.05 (13.56)	50.51	0.95	
<i>Eleocharis erythropoda</i> Steud.	5	1.85 (1.00)	5	47.85 (8.83)	46.00	0.96	
<i>Eleocharis ovata</i> (Roth.)R.&S.	5	1.88 (1.01)	5	63.86 (19.19)	61.98	0.97	
<i>Eleocharis palustris</i> (L.)R.&S.	4	1.44 (0.59)	3	23.75 (7.19)	22.31	0.94	
<i>Epilobium ciliatum</i> Raf.	5	1.89 (1.21)	4	58.22 (23.67)	56.33	0.97	
<i>Eupatorium maculatum</i> L.	3	1.37 (0.81)	4	39.92 (16.57)	38.55	0.97	
<i>Eupatorium perfoliatum</i> L.	2	2.53 (0.98)	2	53.15 (35.11)	50.62	0.95	
<i>Glyceria canadensis</i> (Michx.)Trin.	3	0.55 (0.02)	2	42.39 (8.41)	41.84	0.99	
<i>Gnaphalium uliginosum</i> L.	5	1.21 (0.47)	4	27.15 (9.21)	25.94	0.96	
<i>Iris versicolor</i> L.	5	1.33 (1.73)	5	19.57 (12.89)	18.24	0.93	
<i>Juncus filiformis</i> L.	4	1.99 (2.18)	5	40.38 (10.93)	38.38	0.95	
<i>Juncus pelocarpus</i> E.Meyer.	2	3.45 (1.74)	3	12.43 (3.53)	8.98	0.72	
<i>Lycopus americanus</i> Muhl.	4	1.54 (0.51)	5	91.5 (28.46)	89.96	0.98	
<i>Lythrum salicaria</i> L.	3	4.49 (1.09)	5	91.65 (28.58)	87.16	0.95	
<i>Mimulus ringens</i> L.	5	2.18 (0.68)	5	91.14 (19.85)	88.96	0.98	
<i>Penthorum sedoides</i> L.	5	2.27 (0.49)	5	86.33 (44.51)	84.06	0.97	
<i>Potentilla anserina</i> L.	2	0.29 (0.15)	3	19.54 (6.14)	19.25	0.99	
<i>Scirpus acutus</i> Muhl.	5	4.08 (0.98)	5	55.33 (22.68)	51.25	0.93	
<i>Scirpus cyperinus</i> (L.)Kunth.	3	1.02 (1.30)	2	39.44 (7.34)	38.42	0.97	
<i>Scirpus validus</i> Vahl.	4	1.73 (0.36)	3	48.76 (22.63)	47.03	0.96	
<i>Sparganium eurycarpum</i> Engelm.	3	0.93 (0.51)	3	31.11 (17.76)	30.18	0.97	
<i>Spartina pectinata</i> Link.	4	2.37 (2.39)	3	67.16 (21.36)	64.79	0.96	
<i>Typha angustifolia</i> L.	3	1.41 (1.02)	2	42.39 (23.15)	40.98	0.97	
<i>Verbena hastata</i> L.	2	1.71 (0.35)	2	77.65 (86.89)	75.95	0.98	

Table 3.2

Source	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Main effects	691.2714	28	24.6883	50.589	0.00005
species	74.0829	27	2.7438	5.622	0.00005
nutrients	582.5555	1	582.5555	1000.000	0.00005
Interaction	31.1027	27	1.1519	2.360	0.0005
Residual	77.1072	158	0.4880		
Total	799.4812	213			

Table 3.3

Source	Sum of Squares	d.f.	Mean square	F-ratio	Sig. level
Main effects	675.6907	26	25.9881	54.062	0.00005
species	53.6778	25	2.1471	4.467	0.00005
nutrients	589.9264	1	589.9264	1000.000	0.00005
Interaction	17.1640	25	0.6865	1.428	0.09980
Residual	71.1443	148	0.4807		
Total	763.9991	199			

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Appendix Captions

- Appendix 1.1. Total species list, in alphabetical order, for all eight wetland sites. Nomenclature and Authorities follow Gleason and Cronquist (1963) or otherwise noted. A '*' denotes nationally rare species according to Argus and Pryer (1990).
- Appendix 1.2. Total (out of a possible 180) and individual quadrat (out of a possible 9) species frequencies per site
- Appendix 1.3. Values for plant traits, community state variables and fertility variables within each quadrat per site, plus mean and standard deviation (STD) per site. P=phosphorus (ppm); AEP=aqueous extractable phosphorus ($\mu\text{g P/L/g}$); N=nitrogen (ppm); LOI=loss on ignition (% organics); SC=standing crop ($\text{g}/0.25 \text{ m}^2$); Lit=litter ($\text{g}/0.25 \text{ m}^2$); Ht=plant height (cm); RDia=rhizome diameter (mm); RDpth=rhizome depth (cm); SpRich=species richness ($\#\text{sp.}/0.25 \text{ m}^2$)
- Appendix 1.4. Results for ANOVA (model I) between wetlands types

for each plant trait, community state, and fertility variable. Shown are the transformations needed to stabilize variances

Appendix 1.5. Means ($n=4$), standard errors, and 95% confidence intervals for each plant trait, community state, and fertility variable, and according to wetland type. Corresponds with ANOVA between wetland types (Figure's 1.2, 1.3, 1.4, Appendix 1.).

Transformations to stabilize variances are shown.

Appendix 2.1 List of the wetland plant species (authorities follow Gleason and Cronquist (1963) sown for screening experiment. A '***' indicates species which had 2 or more replicates survive for experiment (those species in Table 3.1). All species are perennials except those indicated by a 'A', which identifies them as annuals.

Appendix 1.1

Agrostis stolonifera L.
Andropogon scoparius Michx.
Anemone canadensis L.
Asclepias incarnata L.
Aster junciformis Tydb.
Aster laevis L.
Aster ? *uniceus* L.
Aster simplex Willd.
Aster spOli1
Aster spOLi2
Aster spS1
Betula pumila L.
Bidens spPEP
Calamagrostis canadensis (Michx.) Beauv.
Calamagrostis stricta (Timm.) Koeler
Campanula aparinoides Pursh.
Carex altherodes Spreng.
Carex comosa DuRoi.
Carex crawei Dewey
Carex hystericina Muhl.
Carex lacustris Willd.
Carex lasiocarpa Ehrh.
Carex rostrata Stokes.
Carex spOli
Carex stricta Lam.
Carex tribuloides Wahl.
Carex viridula Michx.
Cicuta bulbifera L.
Cirsium vulgare (Savi) Tonore
Cladium mariscoides (Muhl.) Torr.
Convolvulus sepium L.
Danthonia spicata (L.) Beauv.
Deschampsia cespitosa (L.) Beauv.
Dulichium arundinaceum (L.) Britt.
Eleocharis elliptica Kunth
Eleocharis erythropoda Steud.
Eleocharis palustris (L.) R. & S.
Eleocharis pauciflora (Light.) Link.
Eleocharis spOli
Equisetum arvense L.
Equisetum fluviatile L.
Equisetum nelsonii (A.A. Eat.) Schaffn.
Equisetum variegatum Schlecht.
Eupatorium maculatum L.
Eupatorium perfoliatum L.
Gallium trifidum L.
Gentiana procera Holm.
Gerardia purpurea L.
Helenium autumnale L.
Hypericum kalmianum L.
Hypericum majus (Gray) Britt.
Impatiens biflora Willd.
Iris versicolor L.
Juncus alpinus Vill.
Juncus balticus Willd.
Juncus brachycephalus (Engelm.) Duch
Juncus spR.
Juncus horizontalis Moench.
Lathyrus palustris L.
Leersia oryzoides Sw.
Linum medium (Planch.) Britt.
Liparis loeselii (L.) Rich.
Lobelia kalmii L.
Lycopus americanus Muhl.
Lycopus europaeus L.
Lycopus spP1
Lycopus spP2
Lycopus spPEP1
Lycopus spPEP2
Lycopus uniflorus Michx.
Lycopus virginicus L.
Lysimachia terrestris (L.) BSP
Lythrum salicaria L.
Menha arvensis L.
Menha spP1
Onoclea sensibilis L.
Panicum flexile (Gott.) Scribn.
Panicum lanuginosum Ell.
Panicum virgatum L.
Parnassia glauca Raf.
Parthenocissus quinquefolia (L.) Planch.
Phalaris arundinacea L.
Pogonia ophioglossoides (L.) Ker.
Polygonum hydropiper L.
Polygonum natans Eaton
Potamogeton gramineus L.
Potentilla anserina L.
Potentilla fruticosa L.
Primula mistassinica Michx.
Rhynchospora capillacea Torr.
Sagittaria lancifolia L.
Sarracenia purpurea L.
Satureja glabella (Torr.) Svenson.
Scirpus americanus Olney.
Scleria verticillata Muhl.
Scutellaria galericulata L.
Scutellaria lateriflora L.
Selaginella apoda (L.) Spring.
Senecio pauperculus Michx.
Sisyrinchium montanum Greene.
Sium suave Walt.
Solanum dulcamara L.
Solidago canadensis L.
Solidago graminifolia (L.) Satisb.
Solidago ptarmicoides (Nees.) T & G
Solidago spOli1
Solidago uliginosa Nutt.
Sonchus uliginosus Bieb.
Sorghastrum natans (L.) Nash.
Sporobolus vaginiflorus (Torr.) Wood.
Stachys spR1
Thelypteris palustris Schott.
Tofieldia glutinosa (Walt.) BSP.
Triadenum fraserii (Spach.) Gl.
Triglochin maritima L.
Typha latifolia L.
Utrica dioca L.
Utricularia cornuta Michx.
Vicia cracca L.

Sandbanks Provincial Park

—

Presqu'île Provincial Park

[illegible]

Species	Total	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Asclepias incarnata</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aster junceiformis</i>	13	0	2	2	4	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Heula pumila</i>	17	0	8	1	0	0	2	0	2	0	0	0	0	0	0	2	0	0	1	1	0
<i>Carex crawei</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Carex viridula</i>	3	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladium mariscoides</i>	133	3	6	7	2	4	7	5	8	9	1	8	9	7	9	4	9	8	9	9	9
<i>Eleocharis elliptica</i>	87	1	9	0	5	7	7	0	8	0	2	2	0	9	0	4	5	9	6	4	9
<i>Equisetum variegatum</i>	78	0	0	0	7	6	1	4	2	3	8	4	7	7	2	5	4	2	5	3	8
<i>Gerardia purpurea</i>	16	4	0	1	2	0	0	2	0	0	1	0	0	1	1	0	1	0	3	0	0
<i>Helenium autumnale</i>	79	3	6	0	2	1	3	4	5	5	6	0	5	8	7	1	5	5	4	6	3
<i>Hypericum kalmianum</i>	4	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1
<i>Hypericum majus</i>	54	0	3	4	5	6	4	4	0	2	3	5	1	0	2	3	2	3	4	3	0
<i>Juncus brachycephalus</i>	14	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	2	0
<i>Juniperus horizontalis</i>	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Linum medium</i>	5	3	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lobelia kalmii</i>	50	0	0	2	1	1	1	5	3	0	6	5	0	1	5	5	4	5	3	1	2
<i>Lycopus uniflorus</i>	13	0	0	0	0	0	2	9	1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Panicum flexile</i>	79	9	7	1	9	0	3	7	0	7	5	7	0	0	9	1	5	3	1	0	5
<i>Panicum lanuginosum</i>	39	9	7	1	0	0	0	1	0	7	3	1	0	0	1	1	1	1	1	0	5
<i>Panicum virgatum</i>	4	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1
<i>Parnassia glauca</i>	8	0	0	0	1	3	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1
<i>Rhynchospora capitata</i>	110	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
<i>Scleria verticillata</i>	149	9	0	9	9	9	9	9	9	9	9	9	9	9	9	9	5	2	7	0	9
<i>Selaginella apoda</i>	17	0	0	0	2	1	1	1	3	6	1	0	0	0	0	0	2	0	0	0	0
<i>Solidago ptarmicoides</i>	12	4	0	0	0	0	0	0	1	2	0	0	0	0	2	0	1	2	0	0	0
<i>Sporobolus vaginiflorus</i>	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>Triglochin maritima</i>	22	0	0	1	5	3	3	2	1	1	0	0	0	0	1						

Cliphant

Species	Total	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Agrostis stolonifera</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aster spOli1</i>	9	0	3	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	1
<i>Aster spOli2</i>	11	0	3	0	0	0	0	0	0	0	2	0	6	0	0	0	0	0	0	0	0
<i>Calamagrostis stricta</i>	6	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
<i>Carex craxii</i>	4	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex spOli1</i>	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex viridula</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladium mariscoides</i>	161	7	0	9	9	9	9	7	9	8	9	9	9	9	9	8	9	8	8	7	9
<i>Danthonia spicata</i>	22	2	2	6	0	0	0	0	0	8	4	0	0	0	0	0	0	0	0	0	0
<i>Deschampsia cespitosa</i>	19	1	0	0	0	0	0	0	0	3	0	2	2	1	1	0	0	0	0	0	0
<i>Elocharis spOli1</i>	20	0	0	0	0	3	0	0	0	0	0	0	0	0	3	0	2	3	0	0	9
<i>Equisetum nelsonii</i>	21	9	9	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Gentiana proera</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
<i>Gerardia purpurea</i>	30	1	2	4	0	1	1	0	4	3	0	0	0	0	3	3	0	0	0	0	0
<i>Helenium autumnale</i>	20	1	0	0	0	0	2	1	4	3	3	1	3	0	1	0	0	0	1	0	0
<i>Hypericum kalmianum</i>	21	4	3	0	1	0	0	0	0	0	0	3	1	5	1	0	3	0	0	0	0
<i>Juncus balticus</i>	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lobelia kalmii</i>	15	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	1	2	4	4
<i>Panicum lanuginosum</i>	48	6	9	4	2	3	3	0	4	2	7	0	3	2	0	0	1	0	1	1	0
<i>Panicum virgatum</i>	18	1	0	1	0	0	2	0	5	1	0	0	0	6	0	1	0	0	1	0	0
<i>Parrisia glauca</i>	49	0	0	5	1	1	2	0	4	8	9	1	1	0	4	4	3	1	4	0	1
<i>Pogonia opatoglossoides</i>	13	0	0	0	0	0	0	0	0	0	6	1	3	1	0	0	0	2	0	0	0
<i>Potentilla fruticosa</i>	13	0	0	0	0	1	0	1	4	1	1	0	0	0	1	0	0	1	3	0	0
<i>Rhynchospora capillacea</i>	111	9	0	9	9	9	9	9	9	9	0	0	0	0	5	0	0	7	9	9	9
<i>Sarracenia purpurea</i>	7	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	0
<i>Stureja glabella</i>	29	0	0	0	0	0	0	0	0	0	0	0	0	0	9	3	9	1	0	3	4
<i>Schizochyrium scoparium</i> (= <i>Andropogon scoparium</i>)	30	0	0	4	0	1	0	0	0	2	0	0	0	0	5	4	5	1	3	5	0

Oilphant (continued)

Species	Total	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Scirpus americanus</i>	7	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scleria verticillata</i>	98	1	1	7	7	4	0	3	8	9	9	0	0	0	9	9	9	0	9	9	4
<i>Senecio pauperulus</i>	7	1	0	0	0	0	0	0	0	0	4	0	0	0	1	0	1	0	0	0	0
<i>Sisyrinchium montanum</i>	64	9	7	1	1	2	3	9	5	5	8	1	4	0	3	3	0	0	2	1	0
<i>Solidago uliginosa</i>	45	9	1	0	0	0	0	0	1	8	0	0	0	0	0	0	5	3	9	7	2
<i>Solidago graminifolia</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Solidago spOli1</i>	39	0	3	7	1	2	5	2	1	2	1	0	0	0	4	9	0	1	1	0	0
<i>Sorghastrum nutans</i>	14	0	1	2	0	0	0	0	0	0	6	2	0	0	1	2	0	0	0	0	0
<i>Tofieldia glauca</i>	77	5	1	5	5	5	5	1	4	5	4	0	0	1	0	6	3	6	8	7	6
<i>Triglochin maritima</i>	7	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	3

Oshawa's Second Marsh

Species	Total	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Anemone canadensis</i>	8	0	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calamagrostis canadensis</i>	112	0	8	9	8	0	4	5	7	9	7	3	2	5	5	4	2	8	9	8	9
<i>Carex spOI</i>	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
<i>Cerastium canadensis</i>	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Convolvulus sepium</i>	7	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Equisetum arvense</i>	5	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Impatiens biflora</i>	22	7	0	0	0	0	3	0	0	4	0	1	6	0	0	0	1	0	0	0	0
<i>Lathyrus palustris</i>	12	0	0	2	0	0	1	0	0	2	0	0	0	0	0	0	1	0	3	0	3
<i>Lycopus americanus</i>	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lysimachia terrestris</i>	5	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Menischa arvensis</i>	9	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phalaris arundinacea</i>	156	9	4	0	9	9	9	9	9	0	9	9	9	8	9	9	9	9	9	9	9
<i>Polygonum natans</i>	3	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Scutellaria galericulata</i>	8	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Typha latiflora</i>	5	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
<i>Urtica dioica</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vicia cracca</i>	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Prince Edward Point

[illegible]

Rondeau Provincial Park

Species	Total	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Calamagrostis canadensis</i>	175	9	9	7	9	9	9	9	9	9	9	7	9	9	8	9	9	9	9	9	9
<i>Campanula sparinoides</i>	4	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Carex tribuloides</i>	36	1	0	0	1	1	3	5	0	0	0	0	5	2	0	0	8	9	1	0	0
<i>Carex comosa</i>	4	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Carex hystericina</i>	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Carex lasiocarpa</i>	46	0	0	0	0	1	2	0	9	2	3	0	8	5	0	2	3	1	4	3	3
<i>Carex rostrata</i>	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Carex spR1</i>	5	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cicuta bulbifera</i>	4	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cirsium vulgare</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dulichium arundinacea</i>	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	5	0	1	0	8
<i>Eileocharis erythropoda</i>	70	0	0	0	0	0	0	9	7	9	0	9	0	0	0	9	0	0	9	9	9
<i>Galium trifid. n.</i>	6	0	0	0	0	0	0	4	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>Impatiens biflora</i>	3	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Juncus spR1</i>	12	0	0	0	9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leersia oryzoides</i>	102	3	3	0	6	1	2	7	8	4	3	7	4	3	8	7	9	9	2	8	8
<i>Lycopodium americanus</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lysimachia terrestris</i>	3	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Mentha arvensis</i>	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parthenocissus quinquefolia</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phalaris arundinacea</i>	13	0	0	0	4	2	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0
<i>Polygonum hydropiper</i>	104	9	9	0	8	1	0	0	0	6	9	5	9	0	9	8	9	9	0	9	4
<i>Polygonum natans</i>	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0
<i>Sagittaria lancifolia</i>	34	0	0	0	0	0	0	7	1	6	2	2	3	0	0	1	6	3	0	2	1
<i>Scutellaria galericulata</i>	8	0	3	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Solidago canadensis</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sonchus uliginosus</i>	11	0	0	1	0	0	0	4	5	0	0	0	0	0	1	0	0	0	0	0	0
<i>Suchys spR1</i>	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thelypteris palustris</i>	18	0	0	4	1	0	0	1	0	1	1	0	0	5	0	2	0	0	1	2	0
<i>Triadenum fraserii</i>	13	0	0	0	0	0	0	2	0	0	3	5	0	0	0	1	0	0	0	2	0

Matchedash Bay

Species	Total	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Aster puniceus</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Aster simplex</i>	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calamagrostis canadensis</i>	153	9	8	8	1	9	9	6	7	3	5	9	9	8	9	9	9	9	9	9	8
<i>Campanula spirooides</i>	6	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0
<i>Carex albertensis</i>	59	0	2	9	9	2	6	9	9	8	0	2	2	0	1	0	0	0	0	0	0
<i>Carex lacustris</i>	82	3	6	2	1	9	0	1	0	5	9	5	0	2	7	5	2	5	2	9	9
<i>Equisetum fluviale</i>	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>Eupatorium maculatum</i>	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lycopus virginicus</i>	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Lysimachia terrestris</i>	38	2	0	2	5	4	1	0	1	0	1	1	0	1	7	1	0	2	2	2	6
<i>Mimulus arvensis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Onoclea sensibilis</i>	11	5	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0
<i>Phalaris arundinacea</i>	53	6	0	0	8	0	0	9	0	9	8	7	0	5	1	0	0	0	0	0	0
<i>Polygonum natans</i>	9	1	0	2	0	0	0	1	1	1	0	0	0	0	0	1	0	1	0	0	1
<i>Scutellaria galericulata</i>	9	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	2	0	4	0

Appendix 1.3 (8 pages - 8 sites)

Sandbanks Provincial Park

Sample	P	AEP	N	B	B/Swt	LOI	SC	Li	It	RDia	RDph	SpRich
s1	2.00	11.17	1.60	0.028	0.00020	4.28	24.97	3.75	28.24	1.77	2.14	8.00
s2	2.00	11.56	1.40	0.010	0.00008	4.91	18.26	14.76	23.27	1.65	1.50	11.00
s3	2.00	12.57	4.40	0.012	0.00009	4.01	36.59	8.48	25.71	1.45	1.61	10.00
s4	1.00	7.01	1.80	0.015	0.00010	1.64	15.79	1.03	18.60	1.75	1.84	7.00
s5	2.00	5.06	2.20	0.017	0.00010	3.90	43.21	33.93	32.95	1.87	2.64	8.00
s6	1.00	2.43	0.60	0.011	0.00008	2.77	10.86	5.42	34.52	2.02	2.56	4.00
s7	2.00	11.83	1.00	0.035	0.00028	3.63	16.96	19.68	37.28	1.87	2.77	8.00
s8	1.00	10.57	1.00	0.008	0.00006	3.96	17.39	19.79	31.03	1.68	2.24	6.00
s9	2.00	14.72	0.80	0.008	0.00006	4.02	25.39	5.17	26.04	1.85	2.01	13.00
s10	1.00	16.08	2.00	0.015	0.00013	5.14	36.23	18.45	26.30	1.70	1.77	8.00
s11	2.00	9.94	0.80	0.012	0.00008	3.09	18.00	1.82	19.08	1.76	1.97	9.00
s12	1.00	17.50	0.60	0.009	0.00008	3.55	11.49	3.11	26.01	1.84	2.09	7.00
s13	1.00	13.83	0.60	0.028	0.00021	4.33	29.61	13.83	36.09	1.90	2.20	8.00
s14	1.00	8.76	0.80	0.003	0.00002	3.82	9.15	5.31	25.65	1.67	2.01	7.00
s15	1.00	11.15	2.40	0.068	0.00050	4.08	19.81	9.15	26.31	1.61	2.04	8.00
s16	2.00	6.75	2.80	0.015	0.00011	4.43	5.23	2.55	25.56	1.41	1.43	4.00
s17	2.00	9.31	0.40	0.009	0.00007	4.00	16.45	3.75	26.65	1.59	2.10	7.00
s18	1.00	2.31	2.60	0.008	0.00005	1.29	10.43	7.56	30.64	1.87	2.58	5.00
s19	1.00	15.56	1.40	0.020	0.00014	3.57	10.24	6.48	33.06	1.82	2.43	5.00
s20	2.00	12.23	0.40	0.075	0.00017	2.64	19.81		30.96	2.03	2.77	10.00
MEAN	1.50	10.52	1.48	0.018	0.00013	3.65	19.79	9.67	28.20	1.76	2.14	7.65
STD	0.50	4.11	0.99	0.014	0.00010	0.94	9.89	8.23	4.95	0.16	0.39	2.22

Presqu'île Provincial Park

Sample	P	AEP	N	B	B/SWt	LOI	SC	Li	It	RDia	RDph	Splch
p1	6.00	8.77	39.60	0.048	0.00006	2.54	14.72	1.10	25.00	1.98	1.55	11.00
p2	3.00	8.44	76.60	0.005	0.00004	3.10	15.14	19.60	24.62	2.72	1.65	8.00
p3	3.00	12.08	57.00	0.013	0.00010	2.77	6.55	2.92	22.92	2.08	1.77	10.00
p4							17.85	54.41	27.43	2.55	2.04	7.00
p5	3.00	7.64	79.00	0.026	0.00020	2.62	9.93	15.57	18.58	1.60	1.40	9.00
p6	2.00	8.61	52.80	0.026	0.00020	4.21	15.80	27.67	30.12	2.27	2.08	6.00
p7	2.00	8.86	55.20	0.034	0.00030	3.00	11.00	8.21	20.12	1.29	1.09	10.00
p8	1.00	8.42	69.00	0.017	0.00015	4.37	17.10	8.82	24.76	1.58	1.47	10.00
p9	3.00	5.63	50.80	0.017	0.00012	3.27	19.62	8.51	23.47	1.52	1.44	9.00
p10	3.00	8.56	37.00	0.036	0.00032	4.03	11.91	10.73	26.06	1.69	1.58	10.00
p11	2.00	10.23	5.40	0.013	0.00006	4.47	13.84	8.07	33.67	2.07	2.04	4.00
p12	1.00	11.13	9.60	0.010	0.00008	6.00	16.18	16.90	26.25	2.41	2.02	6.00
p13	2.00	8.86	5.80	0.010	0.00009	3.47	12.99	13.84	27.28	2.49	2.09	6.00
p14	2.00	7.98	21.20	0.006	0.00004	3.24	19.75	12.64	29.64	2.28	2.07	6.00
p15	6.00	6.82	2.40	0.005	0.00003	3.13	8.50	8.26	22.12	1.59	1.46	7.00
p16	3.00	10.57	39.40	0.006	0.00005	5.68	10.63	15.97	30.33	1.84	1.76	7.00
p17	2.00	4.03	57.40	0.039	0.00028	4.92	15.13	14.92	30.58	2.13	2.09	6.00
p18	3.00	8.13	39.60	0.008	0.00006	4.38	8.46	6.54	22.78	1.49	1.45	11.00
p19	2.00	7.26	45.60	0.006	0.00005	4.41	6.24	3.17	20.60	1.29	1.19	8.00
p20	2.00	3.69	68.20	0.018	0.00013	3.73	6.85	6.44	15.37	1.22	0.96	9.00
MEAN	2.68	8.20	42.72	0.016	0.00013	3.86	12.91	13.21	25.09	1.88	1.66	8.00
STD	1.30	2.08	23.57	0.011	0.00009	0.96	4.16	11.28	4.44	0.41	0.35	1.95

Long Point

Sample	P	AEP	N	B	BjSWt	LOI	SC	I _{at}	Ill	RDia	RDph	SpRich
LP1	2.00	7.17	0.60	0.014	0.00009	3.40	10.27	7.90	18.35	0.83	0.81	10.00
LP2	2.00	10.49	1.20	0.053	0.00010	4.62	13.28	3.59	22.24	1.91	1.38	11.00
LP3	1.00	9.92	0.20	0.007	0.00004	1.89	7.79	2.38	16.71	0.79	1.07	12.00
LP4	1.00	8.81	0.20	0.005	0.00004	3.36	11.83	13.85	16.37	1.11	1.48	15.00
LP5	1.00	10.43	0.20	0.012	0.00007	2.47	10.56	8.66	18.13	1.27	1.31	12.00
LP6	1.00	11.10	0.40	0.005	0.00003	4.50	14.57	6.66	18.64	1.63	1.27	14.00
LP7	1.00	6.98	0.20	0.011	0.00007	2.03	10.29	13.29	16.76	1.76	1.10	15.00
LP8	1.00	7.52	0.20	0.026	0.00016	3.02	10.90	14.12	19.58	1.77	1.04	13.00
LP9	2.00	9.29	0.40	0.024	0.00016	3.20	28.35	12.75	17.76	1.25	0.76	14.00
LP10	1.00	6.44	0.60	0.015	0.00009	2.09	15.75	1.73	19.77	1.45	1.14	13.00
LP11	1.00	6.82	0.60	0.010	0.00006	2.18	18.38	6.02	16.02	0.81	1.18	11.00
LP12	1.00	9.53	0.60	0.033	0.00019	2.40	19.54	20.17	20.15	1.70	0.85	6.00
LP13	1.00	1.58	0.40	0.013	0.00008	4.03	19.46	8.24	22.79	2.16	1.08	9.00
LP14	4.00	10.45	4.20	0.011	0.00006	1.98	16.45	17.08	18.79	1.55	0.95	13.00
LP15	3.00	5.57	2.20	0.016	0.00009	1.07	9.44	6.54	19.30	1.21	1.18	16.00
LP16	2.00	6.61	1.00	0.008	0.00005	2.61	17.60	6.08	20.99	1.70	1.18	16.00
LP17	1.00	7.87	0.60	0.029	0.00023	5.33	18.91	18.81	21.36	1.91	1.19	12.00
LP18		3.17	0.60	0.006	0.00003	2.31	18.96	5.57	20.05	1.59	1.18	13.00
LP19	1.00	7.39	0.80	0.012	0.00008	2.19	17.56	17.93	22.46	2.28	1.18	11.00
LP20	1.00	6.31	0.40	0.018	0.00010		33.67	15.35	19.72	1.41	1.12	13.00
MEAN	1.47	7.67	0.78	0.016	0.00011	2.88	16.18	10.34	19.30	1.50	1.12	12.45
STD	0.82	2.40	0.91	0.011	0.00009	1.07	6.23	5.57	1.97	0.41	0.18	2.36

Chiphart

Sample	P	AEP	N	B	B/SWt	LOI	SC	I _{it}	I _{lk}	RD _{ia}	RD _{ph}	SpRich
OLI1	2.00	8.38	9.00	0.021	0.00014	3.52	16.64	22.80	20.40	1.69	1.58	17.00
OLI2	1.00	6.48	7.20	0.016	0.00009	2.80	25.00	13.45	18.27	1.72	1.58	19.00
OLI3	1.00	6.23	5.20	0.016	0.00012	7.31	10.46	12.11	20.12	1.80	1.68	15.00
OLI4		7.39	6.60	0.009	0.00006	4.88	6.96	10.80	23.54	1.49	1.73	9.00
OLI5		3.10	6.60	0.008	0.00005	6.95	25.33	12.63	21.89	1.56	1.71	12.00
OLI6	1.00	6.05	7.60	0.024	0.00016	4.06	6.71	3.91	23.68	1.88	2.09	10.00
OLI7	1.00	5.96	6.20	0.016	0.00011	2.96	4.57	5.69	22.05	1.63	1.72	8.00
OLI8	1.00	8.78	34.60	0.032	0.00023	4.31	15.41	8.62	22.49	1.63	1.58	14.00
OLI9	1.00	6.67	6.20	0.026	0.00022	4.80	8.21	7.46	18.76	1.62	1.19	19.00
OLI10	4.00	9.81	16.80	0.009	0.00008	8.09	11.04	13.84	23.74	1.73	1.73	15.00
OLI11	2.00	12.49	4.80	0.022	0.00018	4.69	12.89	24.60	45.16	2.02	2.70	8.00
OLI12	2.00	3.57	18.40	0.051	0.00040	5.65	10.34	14.52	28.73	2.27	2.28	9.00
OLI13	2.00	11.87	4.40	0.120	0.00108	7.15	12.11	17.76	39.98	2.02	2.46	8.00
OLI14	2.00	5.54	2.60	0.016	0.00012	3.69	3.62	5.19	19.76	1.24	1.38	16.00
OLI15	2.00	7.05	3.00	0.014	0.00010	4.19	4.01	5.70	23.47	1.74	1.79	12.00
OLI16	2.00	5.09	2.00	0.012	0.00008	3.09	2.78	3.51	22.57	1.36	1.38	12.00
OLI17	3.00	7.42	2.00	0.013	0.00009	4.58	9.17	12.90	24.18	2.04	1.74	14.00
OLI18	2.00	10.72	2.80	0.011	0.00007	3.75	9.32	13.92	22.32	1.86	1.30	18.00
OLI19	4.00	4.18	3.20	0.016	0.00012	4.12	2.60	3.18	20.78	1.63	1.21	14.00
OLI20	2.00	6.13	2.60	0.015	0.00009	2.41	2.20	3.65	21.00	1.18	1.22	12.00
MEAN	1.94	7.15	7.59	0.023	0.00018	4.65	9.97	10.81	24.14	1.71	1.70	13.05
STD	0.91	2.50	7.54	0.024	0.00022	1.57	6.50	6.09	6.58	0.26	0.40	3.56

Prince Edward Point

Sample	P	AEP	N	B	H/SWt	LOI	SC	Li	It	RDia	RDpth	SpRich
PEP1	11.00	156.89	17.20	0.038	0.00141	58.86	62.95		59.80	2.06	2.85	6.00
PEP2	13.00	408.16	4.60	0.011	0.00051	64.41	54.27		64.95	1.50	1.34	4.00
PEP3	13.00	421.36	23.60	0.027	0.00166	70.44	80.12		74.37	2.16	2.92	5.00
PEP4	11.00	420.95	4.20	0.054	0.00308	76.23	93.98		65.62	2.08	2.01	6.00
PEP5	13.00	802.35	3.40	0.057	0.00409	78.30	37.34		78.54	2.12	2.07	5.00
PEP6	9.00	247.11	4.20	0.054	0.00305	68.78	125.13		86.14	2.18	2.79	4.00
PEP7	10.00	257.26	8.00	0.088	0.00412	63.45	84.25		81.22	2.37	2.17	3.00
PEP8	8.00	181.26	3.40	0.037	0.00146	53.07	52.10		71.14	2.11	2.33	5.00
PEP9	11.00	80.51	18.00	0.171	0.00557	44.27	49.94		58.11	2.05	2.69	7.00
PEP10	11.00	542.01	6.00	0.068	0.00235	51.49	80.07		53.56	2.16	3.65	6.00
PEP11	9.00	293.97	5.80	0.042	0.00278	67.96	89.40		88.22	2.31	2.08	4.00
PEP12	7.00	236.50	30.00	0.030	0.00193	81.17	101.45		61.81	1.84	4.66	6.00
PEP13	6.00	121.05	4.60	0.030	0.00198	81.78	26.73		61.36	1.93	6.41	5.00
PEP14	12.00	196.22	20.20	0.016	0.00079	59.45	41.31		62.51	2.23	5.07	7.00
PEP15	12.00	70.17	6.40	0.028	0.00109	53.63	47.83		79.24	2.16	2.04	4.00
PEP16	21.00	67.97	8.80	0.017	0.00111	70.89	70.98		68.21	2.23	4.95	6.00
PEP17	15.00	157.05	3.60	0.097	0.00455	64.32	33.80		68.13	2.17	5.77	10.00
PEP18	12.00	222.13	9.20	0.018	0.00124	63.15	27.44		42.96	2.26	6.75	5.00
PEP19	8.00	143.69	3.20	0.090	0.00271	46.23	29.44		61.88	1.73	2.67	6.00
PEP20	8.00	102.12	1.80	0.106	0.00320	44.56	33.14		36.33	2.55	3.38	8.00
MEAN	11.00	256.44	9.31	0.054	0.00243	63.12	61.08	0.00	66.20	2.11	3.43	5.60
STD	3.22	179.58	7.79	0.039	0.00134	11.38	27.57	0.00	12.85	0.22	1.5	1.56

Oshawa's Second Marsh

Sample	P	'AEP	N	B	B/SWt	I.OI	SC	Lit	It	RDia	RDph	SpRich
O1	19.00	83.72	73.20	0.058	0.00086	18.39	211.60		118.39	3.57	7.94	2.00
O2	29.00	61.12	83.20	0.085	0.00115	16.17	104.90		92.01	2.23	6.43	9.00
O3	15.00	68.87	28.00			13.14	83.41	97.26	71.33	2.28	6.29	9.00
O4	62.00	174.54	21.20	0.030	0.00041	17.11	324.56		147.47	2.82	8.59	2.00
O5	62.00	9.83	19.00	0.031	0.00040	17.86	217.53		164.11	3.55	10.22	1.00
O6	72.00	149.31	30.40	0.049	0.00073	21.01	241.16		134.42	3.07	8.13	4.00
O7	77.00	242.83	44.60	0.061	0.00129	24.53	210.90	258.13	151.48	3.00	8.98	2.00
O8	29.00	11.51	12.80	0.036	0.00043	16.53	160.80		148.64	2.87	8.70	2.00
O9	76.00	255.62	99.00	0.137	0.00198	14.15	104.74	174.64	105.51	2.39	6.42	5.00
O10	82.00	52.64	26.80	0.058	0.00084	19.50	169.96	224.00	147.90	2.91	8.51	3.00
O11	44.00	240.74	88.60	0.059	0.00082	13.01	141.05	265.50	147.91	3.20	9.02	3.00
O12	131.00	461.98	129.40	0.145	0.00212	15.01	226.30		145.55	7.73	8.54	4.00
O13	97.00	218.95	106.40	0.102	0.00162	12.42	141.77	230.02	150.51	2.95	8.89	2.00
O14	33.00	66.09	95.20	0.084	0.00127	12.50	253.92	224.76	151.48	3.00	8.98	2.00
O15	66.00	687.64	112.40	0.072	0.00205	19.57	239.60	190.59	153.23	3.07	9.15	2.00
O16	34.00	109.68	98.40	0.081	0.00130	17.38	207.18	194.90	145.93	3.03	8.76	5.00
O17	93.00	143.70	86.20	0.067	0.00117	11.69	215.27		147.47	2.82	8.59	2.00
O18	8.00	41.46	91.40	0.081	0.00163	19.14	229.90	198.50	137.16	2.51	7.72	4.00
O19	111.00	179.61	103.60	0.117	0.00296	23.75	182.02	157.93	147.47	2.82	8.59	2.00
O20	96.00	112.62	103.60	0.078	0.00160	19.08	307.06	179.57	141.59	2.62	7.77	4.00
MEAN	61.80	168.62	72.69	0.075	0.00123	17.40	198.68	199.65	137.48	3.12	8.31	3.45
STD	33.57	158.55	36.34	0.031	0.00070	3.36	62.60	44.03	22.53	1.11	0.97	2.16

Rondeau Provincial Park

Sample	P	AEP	N	B	B/SWt	LOI	SC	Lit	It	RDia	RDph	SpRich
R1	12.00	414.86	29.80	0.108	0.00399	53.17	39.58	31.16	53.89	1.29	1.57	5.00
R2	21.00	314.16	19.00	0.063	0.00248	56.69	62.86	23.82	46.37	1.44	2.17	8.00
R3	23.00	2111.80	48.00	0.502	0.02508	67.06	28.89	75.75	51.02	1.52	2.32	7.00
R4	9.00	266.67	19.00	0.065	0.00239	54.94		15.31	44.68	0.96	1.32	10.00
R5	16.00	720.33	102.00	0.081	0.00490	79.76	155.87	66.68	69.79	1.64	2.09	9.00
R6	8.00	8.72	23.60	0.042	0.00205	59.40	66.93	127.28	75.31	1.54	1.77	5.00
R7	7.00	331.74	14.00	0.057	0.00270	61.58	72.09		61.58	1.44	2.21	13.00
R8	12.00	359.03	32.00	0.076	0.00394	75.11	47.84	35.51	70.36	1.64	1.65	10.00
R9	17.00	420.53	109.60	0.066	0.00383	81.95	61.32	23.45	56.70	1.53	1.96	10.00
R10	16.00	418.63	12.00	0.079	0.00321	55.37	93.12	60.00	54.35	1.36	1.48	7.00
R11	17.00	813.60	26.00	0.028	0.00189	80.96	93.36	40.62	55.84	1.40	1.79	7.00
R12	11.00	326.69	60.20	0.147	0.00452	49.17	82.96	27.50	64.76	1.44	1.58	7.00
R13	9.00	271.74	59.80	0.066	0.00234	47.96	63.72	41.32	65.21	1.47	1.40	6.00
R14	11.00	422.45	23.40	0.686	0.02494	55.43	74.22	89.06	54.29	1.20	1.46	5.00
R15	11.00	424.22	36.40	0.077	0.00396	75.67	82.24	12.74	51.73	1.39	1.70	10.00
R16	9.00	176.63	61.40	0.026	0.00084	42.83	105.38	22.48	60.21	1.36	1.78	8.00
R17	17.00	93.93	83.60	0.111	0.00276	29.44	88.72	9.12	62.54	1.26	1.67	7.00
R18	9.00	131.35	93.80	0.080	0.00293	39.65	55.67	55.56	64.98	1.60	1.79	9.00
R19	7.00	405.84	43.60	0.049	0.00212	59.96	75.67	58.41	56.19	1.34	1.56	8.00
R20	10.00	164.61	44.20	0.062	0.00155	23.71	74.12	29.07	59.43	1.53	1.86	7.00
MEAN	12.60	417.68	47.07	0.123	0.00512	57.49	74.98	44.47	58.96	1.42	1.75	7.90
STD	4.53	435.86	29.24	0.162	0.00671	15.91	26.62	29.15	7.79	0.16	0.27	2.00

Machedash Bay

Sample	P	AEP	N	B	B/SW ₀	LOI	SC	Lit	It	RDia	RDph	SpRich
M1	9.00	293.05	54.00	0.019	0.00133	81.14	102.18	100.43	113.03	3.51	6.61	6.00
M2	12.00	493.51	14.00	0.175	0.0106	78.88	193.38	207.43	119.49	3.64	7.36	3.00
M3	13.00	334.24	20.20	0.057	0.00323	74.81	125.22	95.85	97.80	2.96	6.50	6.00
M4	13.00	569.43	4.20	0.031	0.00189	85.96	164.47	161.91	113.91	2.93	6.26	5.00
M5	9.00	209.79	10.80	0.080	0.00319	64.76	170.66	172.72	105.37	3.48	6.80	6.00
M6	9.00	321.18	26.40	0.018	0.00094	69.70	177.70	215.44	101.57	3.11	6.35	4.00
M7	8.00	56.73	6.40	0.050	0.00291	72.68	121.78	168.72	124.81	3.11	6.73	6.00
M8	4.00	133.65	3.40	0.082	0.00309	49.41	148.68	136.76	98.94	3.64	6.44	6.00
M9	4.00	195.15	1.00	0.041	0.00258	83.48	188.92	130.95	131.17	3.31	6.96	6.00
M10	5.00	257.96	18.60	0.079	0.00550	83.84	186.16	140.23	140.50	3.61	7.32	5.00
M11	7.00	465.80	15.80	0.004	0.00021	80.27	140.64	137.98	127.16	3.20	7.10	6.00
M12	11.00	459.79	20.20	0.095	0.00531	79.85	134.00	221.60	106.00	2.89	6.83	3.00
M13	11.00	423.88	17.60	0.038	0.00245	81.89	117.98	195.49	132.46	3.17	7.04	4.00
M14	11.00	511.89	2.00	0.172	0.00949	74.90	157.73	153.42	102.05	3.20	6.57	7.00
M15	11.00	575.40	4.60	0.139	0.00867	84.53	122.47	179.22	112.21	3.31	7.08	5.00
M16	13.00	474.62	5.40	0.122	0.00716	78.77	99.31	199.72	112.91	3.12	6.83	3.00
M17	7.00	435.29	6.60	0.054	0.00352	81.49	153.98	177.87	106.78	3.21	7.21	5.00
M18	7.00	354.19	1.40	0.101	0.00546	59.37	160.12	153.46	94.69	3.59	6.41	5.00
M19	6.00	480.67	8.00	0.025	0.00185	86.57	108.64	134.88	106.58	3.27	7.12	5.00
M20	7.00	369.24	1.00	0.107	0.00658	80.65	124.72	126.84	98.59	3.58	6.93	5.00
MEAN	8.85	370.77	12.08	0.074	0.00430	76.65	144.94	160.55	112.30	3.29	6.82	5.05
STD	2.87	140.99	12.17	0.049	0.00237	9.27	28.74	35.09	12.74	0.24	0.32	1.12

Appendix 1.4 (2 pages - 12 variables)

	Source	Sum of Squares	d.f.	Mean Square	F-ratio	Sig. level
(Log) Phosphorus (ppm)	Between grp.	9.6587	1	9.6587	22.242	0.0033
	Within grp.	2.6055	6	0.4343		
	Total	12.2643	7			
(Log) Aqueous Extractable Phosphorus ($\mu\text{g/L/g}$)	Between grp.	25.0772	1	25.0772	256.450	0.0000
	Within grp.	0.5867	6	0.0978		
	Total	25.6639	7			
Nitrogen (ppm)	Between grp.	980.8953	1	980.8953	1.492	0.2678
	Within grp.	3945.4479	6	657.5747		
	Total	4926.3432	7			
(Log) Bioassay of Fertility - Biomass (g)	Between grp.	4.2623	1	4.2623	58.165	0.0003
	Within grp.	0.4397	6	0.0733		
	Total	4.7020	7			
(Log) Bioassay of Fertility - Biomass/Soil wt. (g/g)	Between grp.	18.8120	1	18.8120	81.527	0.0001
	Within grp.	1.3845	6	0.2307		
	Total	20.1964	7			
(Log) Loss on Ignition (%)	Between grp.	12.8837	1	12.8837	52.519	0.0004
	Within grp.	1.4719	6	0.2453		
	Total	14.3555	7			

	Source	Sum of Squares	d.f.	Mean Square	F-ratio	Sig. level
(Log) Standing Crop (g/0.25m ²)	Between grp.	8.1427	1	8.1427	41.496	0.0007
	Within grp.	1.1774	6	0.1962		
	Total	9.3200	7			
(Log) Litter (g/0.25m ²)	Between grp.	9.3187	1	9.3187	33.978	0.0021
	Within grp.	1.3713	6	0.2743		
	Total	10.6900	7			
Species Richness (#sp/0.25m ²)	Between grp.	45.8403	1	45.8403	7.933	0.0305
	Within grp.	34.6719	6	5.7786		
	Total	80.5121	7			
(Log) Height (cm)	Between grp.	3.3916	1	3.3916	35.369	0.0010
	Within grp.	0.5754	6	0.0959		
	Total	3.9669	7			
(Log) Rhizome Diameter (mm)	Between grp.	0.2076	1	0.2076	2.556	0.1610
	Within grp.	0.4873	6	0.0812		
	Total	0.6949	7			
(Log) Rhizome Depth (cm)	Between grp.	1.9225	1	1.9225	6.723	0.0410
	Within grp.	1.7156	6	0.2859		
	Total	3.6381	7			

Appendix 1.5

	Wetland Count Type	Mean	Std Error (internal)	Std Error (pooled s)	95 % C.I. for mean
(Log) Phosphorus (ppm)	1 4 2 4	0.6114 2.8090	0.1404 0.4443	0.3295 0.3295	-0.1951 - 1.4179 2.0025 - 3.6155
(Log) Aqueous Extractable Phosphorus (µg/L/g)	1 4 2 4	2.1152 5.6562	0.0841 0.2045	0.1564 0.1564	1.7325 - 2.4979 5.2735 - 6.0389
Nitrogen (ppm)	1 4 2 4	13.1414 35.2875	9.9760 15.1415	12.8216 12.8216	-18.2414 - 44.5243 3.9046 - 66.6704
(Log) Bioassay of Fertility - Biomass (g)	1 4 2 4	-4.0089 -2.5490	0.0870 0.1705	0.1354 0.1354	-4.3402 - -3.6776 -2.8803 - -2.2178
(Log) Bioassay of Fertility - Biomass/Soil wt. (g/g)	1 4 2 4	-8.9275 -5.8606	0.1087 0.3218	0.2402 0.2402	-9.5154 - -8.3396 -6.4484 - -6.9783
(Log) Loss on Ignition (%)	1 4 2 4	1.3100 3.8480	0.0989 0.3360	0.2476 0.2476	0.7038 - 1.9161 3.2419 - 4.4542
(Log) Standing Crop (g/0.25m ²)	1 4 2 4	2.6566 4.6744	0.1476 0.2763	0.2215 0.2215	2.1145 - 3.1987 4.1322 - 5.2165
(Log) Litter (g/0.25m ²)	1 4 2 3	2.3918 4.7233	0.0672 0.4685	0.2618 0.3024	1.7185 - 3.0651 3.9458 - 5.5008
Species Richness (#sp/0.25m ²)	1 4 2 4	10.2875 5.5000	1.4288 0.9208	1.2019 1.2019	7.3456 - 13.2294 2.5581 - 8.4419
(Log) Height (cm)	1 4 2 4	3.1763 4.4786	0.0793 0.2041	0.1548 0.1548	2.7974 - 3.5553 4.9960 - 4.8575
(Log) Rhizome Diameter (mm)	1 4 2 4	0.5341 0.8563	0.0466 0.1961	0.1425 0.1425	0.1853 - 0.8829 0.5075 - 1.2051
(Log) Rhizome Depth (cm)	1 4 2 4	0.4777 1.4581	0.1335 0.3538	0.2674 0.2674	-0.1768 - 1.1321 0.8037 - 2.1125

Appendix 2.1

Acorus calamus L. **	Lycopus americanus Muhl. **
Alisma plantago-aquatica L. **	Lythrum salicaria L. **
Asclepias incarnata L.	Mimulus ringens L. **
Aster nemoralis Ait.	Panicum longifolium Torr.
Calamagrostis canadensis (Michx.) Beauv.	Penthorum sedoides L. **
Carex crinita Lam. **	Phalaris arundinacea L.
Coreopsis rosea Nutt.	Potentilla anserina L. **
Cyperus aristatus Rothb. ***	Rhexia virginica L.
Echinocloa crusgalli (L.) Beauv. ***	Rhynchospora capitellata (Michx.) Vahl.
Eleocharis erythropoda Steud. **	Rumex verticillata
Eleocharis palustris (L.) R.&S. **	Sabatia kennedyana Fern.
Eleocharis ovata (Roth.) R.&S. ***	Sagittaria latifolia Willd.
Epilobium ciliatum Raf. ***	Sium suave Walt.
Eupatorium maculatum L. **	Scirpus acutus Muhl. **
Eupatorium perfoliatum L. **	Scirpus cyperinus (L.) Kunth. **
Glyceria canadensis (Michx.) Trin. **	Scirpus torreyi Olney.
Gnaphalium uliginosum L. ***	Scirpus validus Vahl. **
Gratiola Aurea Pursh.	Sparganium euycarpum Engelm. **
Iris versicolor L. **	Spartina pectinata Link. **
Hypericum ellipticum Hook.	Typha angustifolia L. **
Juncus Breviceaudatus (Engelm.) Buch. **	Verbena hastata L. **
Juncus canadensis J. Gay	Xyris caroliniana Walt.
Juncus filiformis L. **	