

# Nitrogen and phosphorus tissue concentrations in 41 wetland plants: a comparison across habitats and functional groups

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## Summary

1. Increased nutrient loading to wetlands often results in an increase in emergent plant biomass and a decrease in species diversity. While these patterns are broadly predictable, the underlying mechanisms are unknown. We tested two related hypotheses by growing plants under standardized conditions: (1) emergent plants typical of infertile wetlands have higher tissue nutrient contents than plants from fertile wetlands and (2) plants belonging to different functional groups (ruderal, interstitial and matrix) have different tissue nutrient contents.

2. Concentrations of N and P in above-ground phytomass were measured for 41 plant species, from contrasting kinds of wetlands, after one season of growth in excess fertilizer (NPK in ratios 7:11:27 and 15:0:0). Tissue nutrient concentrations ranged from 0.25 to 2.14% dry weight for N and from 0.13 to 1.07% dry weight for P.

3. There was no significant difference in nutrient content between plants from infertile sites and plants from fertile sites. However, plants with 'ruderal' life history traits (e.g. annual or functional annual/fast-growing) had significantly lower N and P tissue concentrations than plants having 'interstitial' or 'matrix' life-history traits. Interstitial perennials had significantly higher N concentrations than matrix perennials. Therefore, plant functional groups are likely to respond differently to eutrophication.

4. Plant size, estimated by maximum species biomass, explained 67% ( $r^2=0.67$ ,  $P<0.001$ ,  $n=31$ ) of the variation in N tissue concentrations but only 5% of the variation in P tissue concentrations.

*Key-words:* Ecology, eutrophication, physiology, plant nutrient content, plant traits

*Functional Ecology* (1995) **9**, 231–238

## Introduction

Eutrophication is a widespread and increasing problem for terrestrial and wetland habitats (Ellenberg 1988; Wisheu *et al.* 1991). Although the effects of eutrophication on aquatic ecosystems are well documented, the effects on wetlands are less well known (Wisheu *et al.* 1991). In general, there are usually two consequences of eutrophication on plant communities: (1) an increase in emergent plant biomass (Willis 1963; Thurston 1969; Willems 1980; Wisheu *et al.* 1991) and (2) a decrease in plant species diversity at high production levels (Thurston 1969; Al-Mufti *et al.* 1977; Grime 1977, 1978; Tilman 1982; Vermeer & Berendse 1983; Day *et al.* 1988; Wilson & Keddy 1988). Moreover, the number of rare plants in wetland

communities are known to decrease as nutrient supply increases (Ellenberg 1988; Moore *et al.* 1989).

It would be useful for management purposes to be able to predict the responses of entire groups of species to perturbations such as fertilization. The following study investigated the response of species groups to high rates of nutrient supply. We categorized 41 wetland plants belonging to 17 different taxonomic families and varying in life span, life form and habitat, in two ways: (1) by the fertility of their indigenous habitat (i.e. fertile versus infertile sites) and (2) according to the similarity of physiological, ecological and morphological traits of the species referred to as a functional group or guild (Pianka 1983) (i.e. ruderal, interstitial and matrix strategies). We focus on nitrogen (N) and phosphorus (P), because they have clear and fundamental roles in cell metabolism and are known to trigger changes in terrestrial and aquatic plant community structure (e.g. Tilman 1982; Wisheu *et al.* 1991).

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Species of infertile habitats are often under threat (Ellenberg 1988; Moore *et al.* 1989; Wisheu *et al.* 1991) and it may be useful to predict the response of such species to eutrophication. According to Chapin (1980) there may be inherent physiological differences between species whose natural habitat is infertile from those species indigenous to fertile soils. He suggests that as soil nutrients increase there is a corresponding increase in the growth rate of species from fertile sites, whereas species from infertile habitats maintain lower growth rates combined with a concomitant increase in tissue nutrient concentration. Therefore, under conditions of high nutrient availability, species from infertile habitats store excess nutrients. This strategy could increase plant survivorship if the excess nutrients could be stored until needed. Previous studies have compared populations of the same species, related species or species within the same genus or family (e.g. Hommels, Kuiper & Tanczos 1989) and have focused primarily on phosphorus (Bradshaw *et al.* 1960; Snaydon & Bradshaw 1962; Clarkson 1967; Loneragan & Asher 1967; Rorison 1968; Nassery 1970; Grundon 1972; O'Connor, Connor & Molloy 1972; White 1972; Christie & Moorby 1975; Jefferies 1977), and to a lesser extent on nitrogen (Bradshaw *et al.* 1964). Our study was designed to test the generality of this effect among a wide variety of wetland emergent plant species with respect to both nitrogen and phosphorus. Therefore, the first hypothesis is that, when grown under similar environmental conditions in excess fertilizer, species from infertile sites should have a higher tissue N and P concentrations than species indigenous to fertile habitats.

Our second objective is to determine whether functional groups of species have similar N or P tissue concentrations, thereby, discerning these elements as feasible plant traits. The term functional group relates to ecological, morphological and life-history attributes, and here we used three main functional groups: ruderal, interstitial and matrix (Boutin & Keddy 1993).

Tissue nutrient composition may be an important trait for identifying the ecological strategy of a species. Tilman (1982) notes that tissue nutrient levels are an approximate measure of resource consumption vectors, a fundamental trait for predicting the outcome of competitive interactions in plant communities. Field & Mooney (1986) have shown that leaf N content is a good predictor of the maximum photosynthetic rate. Chapin (1980) and Chapin, Vitousek & Van Cleve (1986) suggest that nutrients are as important, or more important, than carbon when exploring the allocation for plant resources. Keddy (1989) suggests that plant ecologists over-emphasize consumptive competition of resources and that resource conservation might be an overlooked aspect of plant competition in low nutrient conditions. Our second hypothesis, therefore, is that there are differences in tissue N and P concentrations between different functional groups when grown under similar environmental conditions.

## Materials and methods

The wetland plants used in this study were obtained from an outdoor screening experiment established in the spring at Carleton University, Ottawa, Canada (45° 25' N 75° 43' W). Fourteen replicates of 60 plant species of varying physiology, morphology and habitat preferences, were individually grown from seed collected in Ontario and Nova Scotia, Canada. Species incorporated in this study include two Canada-wide rare taxa, *Coreopsis rosea* Nutt. and *Panicum longifolium* Torr. (Argus & Pryer 1990). Plants were grown under standardized conditions in 11.4 dm<sup>3</sup> pots, which were designed to maintain near-flooded conditions in the spring and drier conditions in the fall. The rooting medium was a mixture of washed sand (75%) and commercial potting soil (25%). Plants were watered daily to maintain soil moisture. Fertilizer was uniformly added to all pots on 29 June and 6 July using standard hydroponic solution [7:11:27 (N:P:K) and 15:0:0 (N:Ca:Mg)] at the rate of 6 g per pot. Fertilizer was added again on 11 July and 1 August using a slow release fertilizer [10:25:10 (N:P:K)] at the rate of 3.5 g per pot. In the autumn, half the replicates of 43 species were harvested.

The leaves and stems of five replicates of 41 species (two species did not survive the summer) were dried in an oven at 65 °C and were then subsequently ground into a homogeneous powder. For phosphorus analyses, samples were then dry ashed in a muffle furnace at 500 °C and the residue was dissolved in 0.1N HCL. Phosphorus content of the acid extract was measured colorimetrically using the ascorbic acid method (Horwitz 1975; Raun *et al.* 1987). The N content of 31 plant species (the remaining 10 species had insufficient biomass) was determined using the micro Kjeldahl method (Bremner 1960; Bradstreet 1965; Horwitz 1975).

Classification of the plants according to soil fertility was determined as for previous studies using the same species (Keddy 1981; Day *et al.* 1988; Moore *et al.* 1989; Wisheu & Keddy 1989a, 1989b). Species considered native to infertile sites, were from very infertile sites, usually having sand or gravel soils, with plant biomass less than 100 mg m<sup>-2</sup> (Moore *et al.* 1989) and N and P soil levels below 10 ppm (Gaudet 1993). In our study, the following 12 species were considered typical of infertile habitats: *C. rosea*, *Cyperus squarrosus* L., *Eleocharis erythropoda* Steud., *Eleocharis palustris* L., *Euthamia galetorum* Greene., *Juncus canadensis* J. Gay ex Laharpe, *Juncus filiformis* L., *Juncus brevicaudatus* (Engelm.) Fern., *P. longifolium*, *Potentilla anserina* L., *Scirpus americanus* Pers., and *Spartina pectinata* Link.

Categorization of species into functional groups was also obtained from a study using the same species (Boutin & Keddy 1993). The functional groups were obtained by screening 43 wetland plants for 27 physiological and life-history plant traits. Examples of

traits studied include: average life span, relative growth rate, adult height, total biomass, photosynthetic area, number of tillers (or shoots), crown area, rooting depth and per cent flowering in first year. The resulting data matrix was subjected to multivariate statistical analyses (Appendix 1) and the methods and results are discussed further in Keddy (1991b) and Boutin & Keddy (1993).

Boutin & Keddy (1993) found that the primary division between species separated perennials from ruderals (Appendix 1). Ruderals (e.g. *Lythrum salicaria* L. and *Gnaphalium uliginosum* L.) are characterized by a short life span, a high flowering rate and no lateral growth. Perennials tend to expand the vegetative parts in the first year instead of flowering. The perennials further separated into interstitial species (e.g. *Carex crinita* Lam. and *E. palustris*), which vegetatively spread as discrete clumps in gaps, and matrix species (e.g. *S. pectinata* and *P. anserina*), which vegetatively cover entire gaps. The ruderals subdivided further into 'obligate annuals', which flower in the first year and die at the end of the growing season, and 'facultative annuals', which also

flowers in the first year but are perennial (Boutin & Keddy 1993). Nomenclature generally follows Gleason & Cronquist (1991).

Statistical procedures used in this study were performed using the Statsgraphics statistical package (Version 2.10). Standard one-way analyses of variance (ANOVAs) were used to test for a significant difference among the 41 species, with respect to N and P. An ANOVA was also utilized to determine whether there was a difference with respect to the ratio N:P but first the variables N and P were transformed (square root of the arcsin). ANOVAs were also used to test the hypotheses of the study. Tukey's multiple range test was employed to see whether species could be clustered into distinct functional groups based on N and P alone. A regression analysis was utilized to determine whether N or P were good predictors of the N:P ratio.

## Results

There was a significant difference among wetland plant species with respect to N ( $F=11.9$ ,  $P<0.05$ ), P ( $F=17.2$ ,  $P<0.05$ ) and N:P ( $F=10.8$ ,  $P<0.05$ ). Figures 1 and 2 show the average N and P content of the wetland plant species. *Echinochloa muricata* var. *microstachya* Wieg. had the lowest N (% dry wt=0.25,  $n=5$ ) and P concentrations (% dry wt=0.13,  $n=5$ ); whereas, *Rumex verticillatus* L. had the highest N (% dry wt=2.14,  $n=5$ ) and P contents (% dry wt=1.07,  $n=5$ ). Maximum levels of species N and P obtained were 8.6 times and 8.2 times the minimum concentrations, respectively. Ratios near 1:1 were observed for species including: *E. muricata* var. *microstachya*, *S. pectinata*, *L. salicaria*, *Mimulus ringens* L., *Lycopus americanus* Muhl. ex W. Bart., *Phalaris arundinacea* L., *Typha X glauca* Godr., *Verbena hastata* L., *E. erythropoda*, *Scirpus acutus* Muhl. ex Bigelow, *Asclepias incarnata* L. and *R. verticillatus*.

Regression analysis suggested that neither N nor P alone were good predictors of the N:P ratio, with P only accounting for 24% of the variation in N ( $r^2=0.24$ ,  $P<0.05$ , Fig. 3). Total above-ground biomass (g) of a species was negatively associated with N ( $r^2=0.67$ ,  $P<0.001$ ,  $n=31$ , Fig. 4) but did not vary with P ( $r^2=0.055$ ,  $P<0.05$ ,  $n=41$ , Fig. 5). Results from a Tukey multiple range test suggested that different species could not be clustered into distinct groups based on N or P content and/or N:P ratio alone.

There were no significant differences between plant species from fertile versus infertile habitats with respect to N, P and/or the N:P ratio (Fig. 6). However, the N content was significantly different ( $F=47.8$ ,  $P<0.001$ ) (Fig. 7) among species belonging to different functional groups. The interstitial perennials had the largest mean N content, followed by the matrix perennials and then the ruderals. When these major

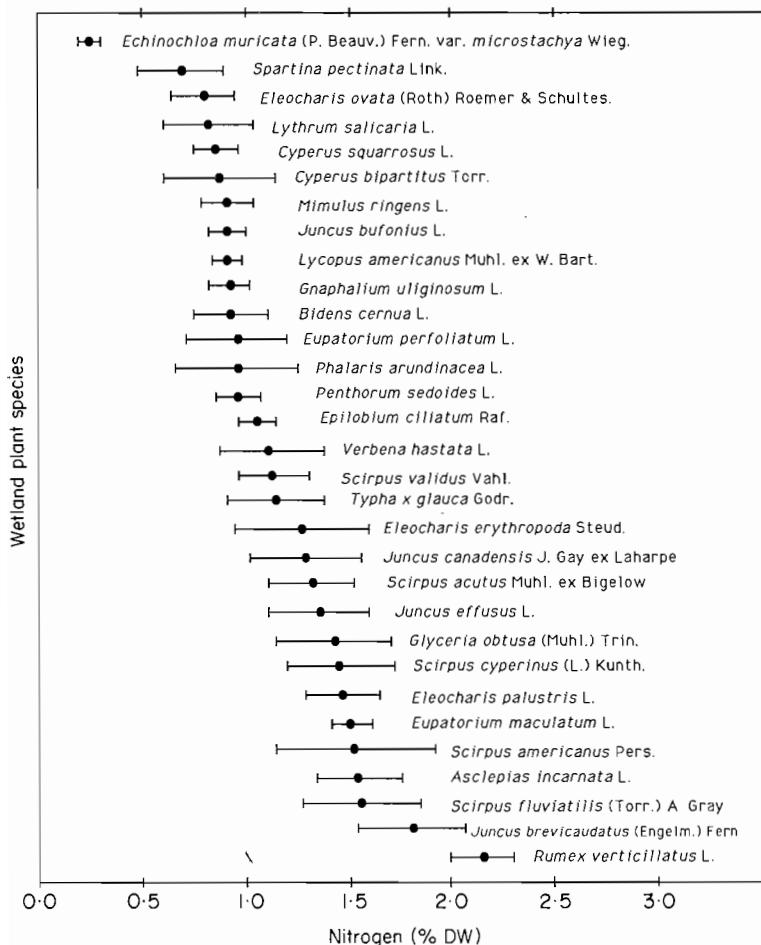


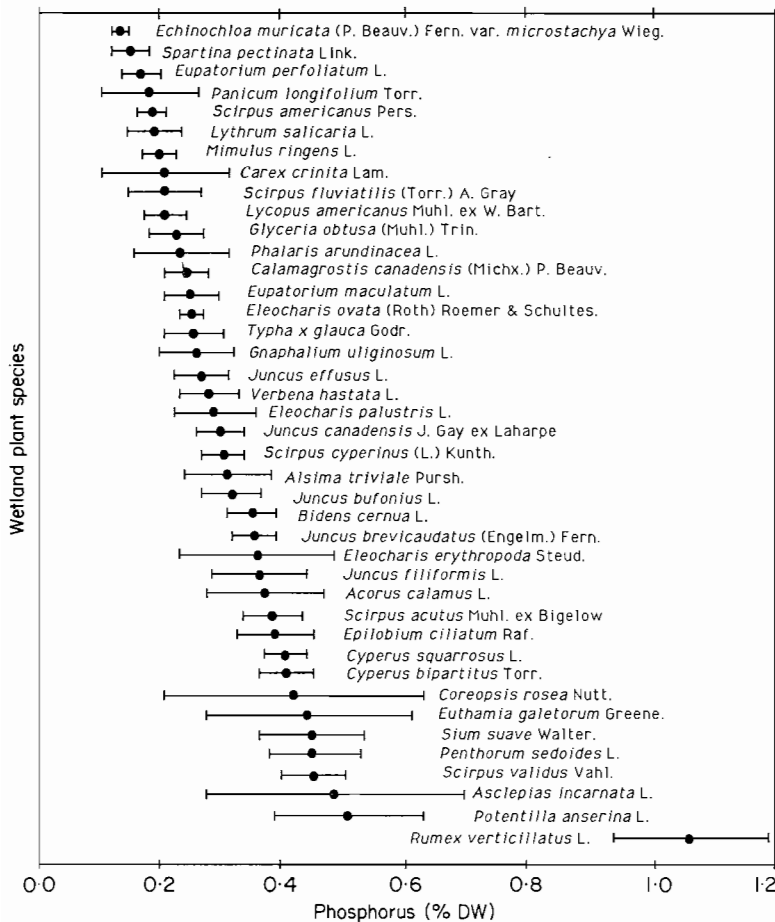
Fig. 1. Mean plant tissue N concentration (% dry wt) of emergent wetland plants grown under similar conditions with sustained fertilization. Error bars denote 1 SD ( $n=4-5$ ).

groups were further subdivided, no significant difference among subgroups was detected. P patterns were different from N. Ruderal species had significantly lower P contents than interstitial and matrix perennials but there was no difference between the interstitial and matrix groups (Fig. 7). Subdivision of the ruderal group revealed that the P concentrations of the facultative annuals (mean P % dry wt=0.20) were significantly less than the obligate annuals (mean P % dry wt=0.31). Figure 7 shows that ruderals had a lower N:P ratio than the interstitial and matrix groups.

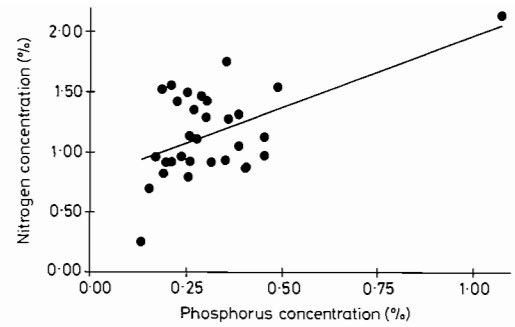
**Discussion**

INTERSPECIFIC VARIATION

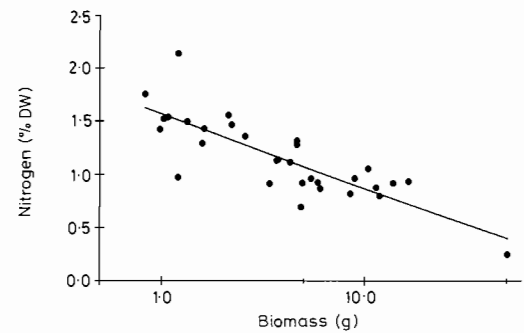
Boyd (1970, 1978) observed large interspecific variation in nutrient concentrations of aquatic plants, even among plant species with similar ecological growth habits (submersed, floating leaved and emergent). In his study, it is unclear whether such differences were related to environmental nutrient levels or to the different absorption rates of the various species because the plants were collected in the field. Our study used a



**Fig. 2.** Mean plant tissue P concentration (% dry wt) of emergent wetland plants grown under similar conditions with sustained fertilization. Error bars denote 1 SD (n=4-5).



**Fig. 3.** The relationship between the nitrogen and the phosphorus concentrations. The solid line represents the linear best fit to the data ( $r^2=0.24$ ,  $P<0.001$ ).



**Fig. 4.** The relationship between nitrogen (% dry wt) and total above-ground biomass (g). The solid line represents the linear best fit to the data ( $r^2=0.67$ ,  $P<0.001$ ,  $n=31$ ).

standard environment for all species, yet interspecific variation in tissue N and P was still observed. Adams, Cole & Massie (1973) obtained similar P values for emergent plants, although Riemer & Toth (1968) found higher values for N. Compared to the emergent macrophytes studied in this paper, forest plants have higher N levels (Gerloff, Moore & Curtis 1966; Likens & Bormann 1970) and similar (Gerloff *et al.* 1966) or lower levels of P (Likens & Bormann 1970). Prairie species have similar levels of both N and P (Gerloff *et al.* 1966) and bog species have higher N values but lower P values (Small 1972). Moreover, a negative relationship between per cent N and whole-plant biomass has been recorded in aquatic macrophytes (Polisini & Boyd 1972).

SPECIES FROM FERTILE VERSUS INFERTILE HABITATS

There is much evidence from the literature to suggest that plants indigenous to infertile sites differ in many ways from plants indigenous to fertile sites. Plants from infertile sites are not as plastic as plants from fertile sites, in root (Crick & Grime 1987) or shoot morphology (Chapin 1980) and show less phenotypic

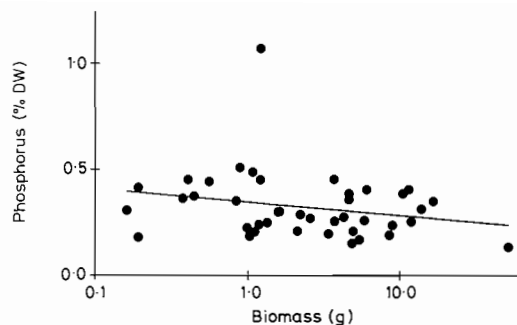


Fig. 5. The relationship between phosphorus (% dry wt) and biomass (g). The solid line represents the linear best fit to the data ( $r^2=0.055$ ,  $P<0.05$ ,  $n=41$ ).

variation in response to nutrient stresses (Chapin 1980). Species from infertile soils tend to have the following characteristics: a low relative growth rate, low photosynthetic rates, low absorption rates, high root:shoot ratio, prolonged seasonal growth, maintenance of inorganic P reserves, increased rate of luxury consumption and relatively more reabsorption of N preceding leaf fall (Small 1972; Grime 1977; Chapin 1980). By comparison, species from fertile habitats have: high relative growth rates, high photosynthetic rates, high root absorption capacities for limiting nutrients, greater plasticity in allocation patterns, low root:shoot ratios, lower rates of luxury consumption and are more responsive to an increase in nutrient supplies (Chapin 1980).

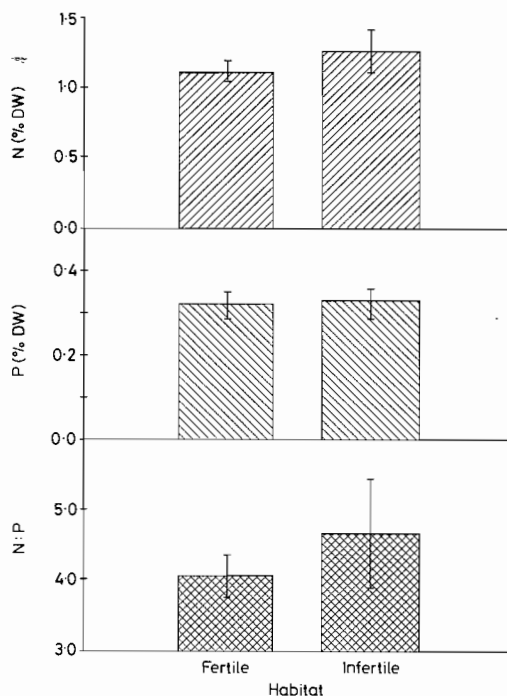


Fig. 6. The mean nitrogen, phosphorus, and N:P ratio of species from the fertile and infertile habitats. Error bars denote 95% confidence intervals ( $n=4-5$ ).

In our study, we were testing for a difference with respect to the N or P content but we found no significant difference. A previous study suggests that at high nutrient levels, species from infertile habitats may store excess nutrients (luxury consumption) to increase survivorship, whereas species from fertile habitats utilize available nutrients in order to increase growth rates (Chapin 1980). Our results suggest that luxury consumption and storage may not be a universal feature of plants from infertile sites. Even within one habitat, plants may have different strategies to cope with soil nutrient variables, and other traits such as evergreenness (Grime 1977) or CAM photosynthesis (Boston & Adams 1987), may instead adapt wetland plants to infertile conditions.

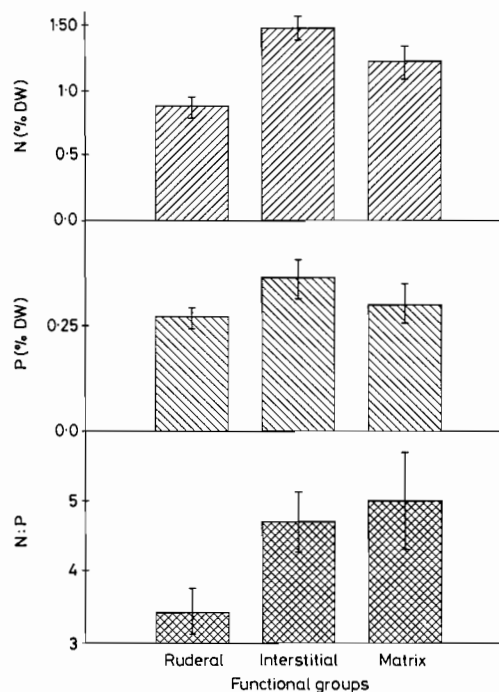


Fig. 7. The mean nitrogen, phosphorus, and N:P ratio of the three functional groups: Ruderal, Interstitial Perennial, and Matrix Perennial. Error bars denote 95% confidence intervals ( $n=4-5$ ).

Comparing a large number of species in one study requires certain assumptions and simplifications. A more precise method of categorizing habitats may reveal differences in N and P concentrations of species. This study was conducted outdoors and, not in strict laboratory conditions and therefore, it is possible that some species were exposed to suboptimal growth conditions. We assumed that species were not nutrient limited but this is not certain without doing studies for each individual species. Also, if there was significant nutrient storage in the roots, our results would be distorted because we used only the above-ground biomass to determine the P and N concentrations. There is evidence that a limiting nutrient will be

retained within the root system more at low, than at moderate or high nutrient concentrations (Williams 1948; Loneragan & Asher 1967; Barrow 1975; Veerkamp *et al.* 1980). In addition, leaf nutrient content can vary between species seasonally (Chapin, Johnson & McKendrick 1980). All of our plants were harvested near the end of the summer growing season. The trade-off between detailed knowledge of a single species or comparative knowledge about many species is inherent in screening methodology (Keddy 1992).

#### FUNCTIONAL GROUPS

Our study suggested that there may be fundamental differences between groups of species categorized according to their functional similarities. The lower nutrient concentrations of ruderal species might suggest that they are less effective at exploiting nutrients. However, ruderal plants typically occur in disturbed areas that have high soil nutrient and light levels and they have high relative growth rates (Grime & Hunt 1975). Therefore, it is more likely that the low tissue nutrient content we observed in the ruderal species is a result of high growth rates, which accelerates the conversion of photosynthate into growth. Instead of storing nutrient capital, ruderal species may immediately reinvest N and P in the production of new tissue. In contrast to the ruderal species, the interstitial and matrix species have lower growth rates and, therefore, may tend to accumulate nutrients. N and P values in interstitial and matrix plants, particularly those that are partially evergreen, may reflect a form of storage for growth in the following year.

The ultimate value of this research may be the potential for predicting the response of species to eutrophication.

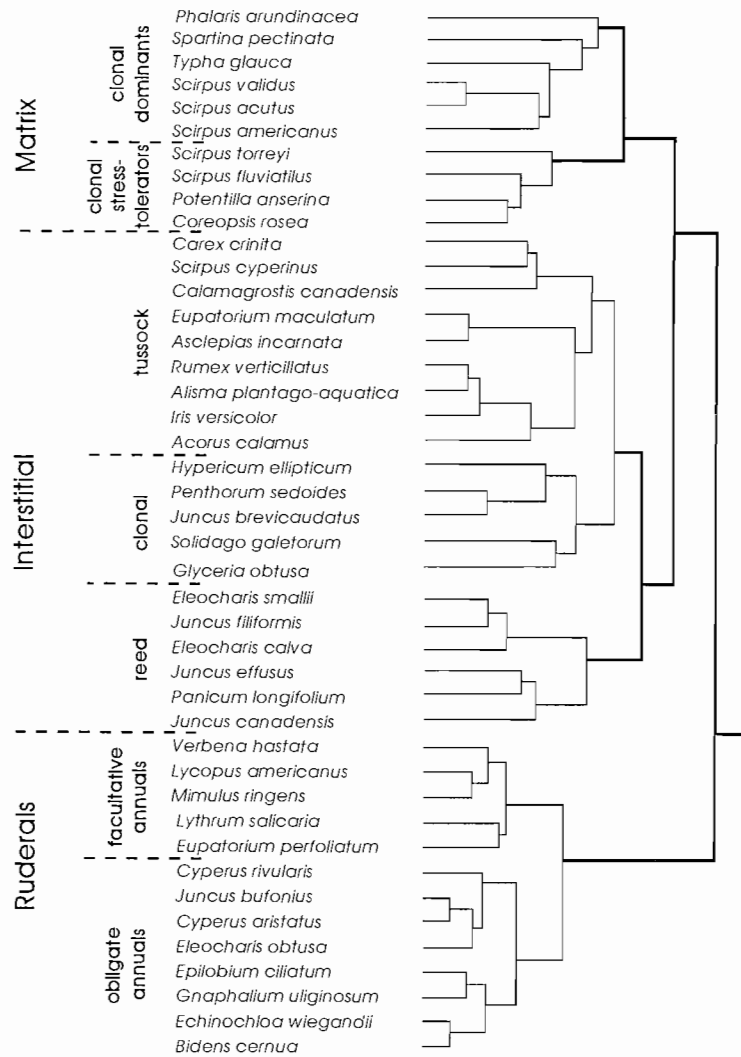
#### Acknowledgements

We wish to thank Pauline Houlihan for assistance with the nitrogen analyses. We also thank Joyce Belcher for assisting with the screening experiment and Evan Weiher and Irene Wisheu for assistance in preparing this manuscript. This work was supported by the Natural Sciences and Engineering Research Council of Canada and the Canadian Museum of Nature.

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**Appendix.**

**A dendrogram distinguishing the major functional groups after Boutin & Keddy (1993)**

*Alisma plantago-aquatica*, *A. triviale*; *Cyperus rivularis*, *C. bipartitus*; *C. aristatus*, *C. squarrosus*; *Echinochloa wiegandii*, *E. muricata* var. *microstachya*; *Eleocharis calva*, *E. erythropoda*; *E. obtusa*, *E. ovata*; *E. smallii*, *E. palustris*. Please note that *Sium suave* Walter. is not included in the dendrogram.