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Nitrogen and phosphorus availability, ecosystem processes and plant community dynamics in boreal wetland meadows

Erickson, Heather Elyse, Ph.D.

University of Washington, 1994

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Nitrogen and Phosphorus Availability, Ecosystem Processes and Plant Community Dynamics in Boreal Wetland Meadows

by

Heather Elyse Erickson

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1994

Approved by Dale W Cole
(Co-chairperson of Supervisory Committee)

Robert J Nai
(Co-chairperson of Supervisory Committee)

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to Offer Degree Forest Resources

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Date June 8, 1994

University of Washington

Abstract

Nitrogen and Phosphorus Availability, Ecosystem Processes and Plant Community Dynamics in Boreal Wetland Meadows

by Heather Elyse Erickson

Chairpersons of the Supervisory Committee: Professors D. W. Cole and R. J. Naiman
College of Forest Resources

The effects of nitrogen (N) and phosphorus (P) availability on above-ground primary production and plant community dynamics in wetland "beaver" meadows were examined in Voyageurs National Park in northern Minnesota, USA. Five meadows were floristically distinguished as either "sedge-dominated" or "grass-dominated" and were sampled to describe patterns of above-ground primary production, seasonal depth to the water table, N and P availability, and *in-situ* N mineralization. In two sedge meadows, production was higher, N and P were more available during the non-growing season, and water tables were closer to the soil surface than in three grass meadows. Across all meadows, productivity correlated positively with available N and P, but not with N mineralization, which was insufficient to meet the requirements of the plant communities, supporting the existence of external, presumable hydrologic, sources of N to the meadows.

Based on these and other observations, two hypotheses regarding N and P limitation to production were developed: **H1)** lower production in the grass meadows is due to a greater nutrient limitation in the grass meadows, and **H2)** wet-sedge meadows are proportionately less P limited than the grass meadows. A third hypothesis (**H3**) was developed to test a theory that plant species function with all resources equally limiting. An experiment varying ratios and amounts of N and P was conducted in all meadows. Biomass response after one year reflected ambient hydrologic and fertility conditions; production in the wetter, more nutrient-rich sedge meadows was not nutrient limited, while production in the drier, relatively less rich grass meadows was nutrient limited. Thus, while hydrologic and fertility conditions tended to co-vary, differences in production are attributed differences in fertility, supporting **H1**. As stated, **H2** assumed that biomass in the sedge meadows would respond to nutrient additions, which did not occur. The pattern of response in the grass meadows supported a Leibig model of nutrient limitation, leading to a rejection of H3.

Nutrient enhancements may alter plant community dynamics according to two theoretical predictions: 1) plant species will segregate along gradients of resource supply if their resource requirements differ (Tilman 1982) and, 2) species richness will decrease if production increases in competitive environments (Grime 1979). Two hypotheses (H4, H5) were developed to test these theories. After two years, botanical convergence with treatment was not indicated in any meadow, leading to a rejection of H4. High N and P caused a reduction in species richness in both community types but because of the lack of biomass response in the sedge meadows, mechanisms supporting changes in richness independent of changes in productivity are suggested, and H5 is rejected. Thus, while the ecosystem property of production (in the grass meadows) was affected by N and P additions, dynamics of the dominant plant species appeared to be relatively unaffected.

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I thank my three principal advisors, John Pastor (University of Minnesota), Dale W. Cole, and Robert J. Naiman, without whose assistance this research would not have been possible. Thanks also to committee members Peter Kareiva (Department of Zoology), Roger del Moral (Department of Botany), and Robert Harrison for their contributions. In addition, special thanks to Calvin Harth (University of Minnesota) for providing consistent, high-quality assistance in the field throughout the project. The research staff at Voyageurs National Park are also thanked for facilitating our endeavors.

DEDICATION

This dissertation is dedicated to my sister Hilary for her recent successes in life and in the hope that she continues to have them.

Chapter 1: Introduction

1.1 BACKGROUND

A wetland's hydrologic regime is often considered to be the major driving variable influencing plant community composition, net primary production and related ecosystem processes such as decomposition and nutrient cycling (Gosselink and Turner 1978, Mitsch and Gosselink 1993). However, other factors (e.g., nutrient availability or competition) may potentially be as equally or more important than hydrology per se, in regulating community composition and ecosystem functioning. In particular, biotic regulation of community structure (e.g., competition) can predominate in wetlands where hydrologic gradients are gradual and impacts due to disturbances are low (Wilson and Keddy 1986). Furthermore, alterations in the availability of nutrients may play a key role in affecting competitive interactions (Aerts and Berendse 1988, Tilman 1982, Huston in press). Certainly, nutrient availability and competitive interactions may correlate to, or be a consequence of, hydrologic influences, yet they have not been given as much attention as hydrologic gradients in community or ecosystem studies of wetlands (Vitt and Chee 1990).

This dissertation is an examination of the role of nitrogen and phosphorus availability in regulating plant community structure and ecosystem processes in wet meadow ecosystems in northern Minnesota. Nitrogen (N) and phosphorus (P) were chosen as the two nutrient elements most likely limiting plant growth in these systems.

1.2 OBJECTIVES AND GENERAL APPROACH

Overall Guiding Objective: To understand how nutrient availability influences ecosystem dynamics and plant community structure in wet meadow ecosystems. Several related themes are addressed in this dissertation, including: nutrient availability/productivity relationships, hydrologic regulation of nutrient availability, contribution of nitrogen mineralization to nitrogen availability, single versus multiple nutrient limitation of above-ground production, and productivity/plant community relationships.

My focus was to elucidate the often complex interactions among hydrologic regime, soil nutrient (N and P) availability, plant species composition, and primary production by making measurements of these attributes in several wet meadows located on the Kabetogama Peninsula within Voyageurs National Park in northern Minnesota. Specifically, I conducted the research in two types of wet-meadow ecosystems, floristically distinguished as "sedge-dominated" and "grass-dominated" meadows. These ecosystems occur in areas that were once flooded by beaver (*Castor canadensis*) but had been drained after beaver abandoned upkeep of their dams. On a large scale the meadows appear very similar. On a finer scale however, they represent gradients in hydrology, plant community composition, net primary production, organic matter accumulation and presumably nutrient cycling. For example, the sedge-dominated communities typically occur in wetter landscape positions than the grass-dominated communities; meadows are generally dominated by one or the other community type.

The meadows are relatively productive and are considered minerotrophic wetlands, i.e., they receive at least some nutrient supply from ground or surface waters. The degree of minerotrophy has often been used to classify wetland types at very coarse scales. For example, an ombrotrophic bog receives little to no external nutrient inputs, other than from precipitation or fixation of atmospheric N, and is characterized by low productivity and vegetation adapted to low nutrient availability. On the other hand, a fen typically receives some nutrients from additional hydrologic sources and is characterized by a productivity greater than a bog and vegetation typical of more nutrient rich sites. Borrowing the nutrient classification approach used at larger scales, I wanted to examine whether the relatively subtle differences in hydrology and plant community composition among the meadows reflected differences in nutrient availability and what the impact of differing availabilities is on productivity and competitive interactions. Furthermore, because the meadows had relatively consistent vegetation cover within them and were abundant on the landscape, they were ideal systems to conduct experiments examining influences of nutrient availability on productivity and competitive interactions.

I incorporated both observational and experimental approaches in the study. The first step was to describe the pattern of differences in ecosystem and community properties among the meadows. Specific hypotheses were then developed either to explain the patterns or to test theory. I then tested the hypotheses in an extensive field manipulation experiment. I used a plot approach for observational and experimental components. Two "grass-dominated" and three "sedge-dominated" meadows were selected, with 14 permanent plots randomly located in each of the meadows. Variables measured in the 70 plots included: species composition, end of the season above-ground biomass (used as a surrogate for net primary production), N and P availability during the non-growing season, annual N mineralization and seasonal depth to the water table. The experimental portion involved a manipulation of N and P availabilities across all 70 plots within the five meadows and continued for two years. Although rarely done, replicating experiments across similar ecosystems is critical to ascertain the generality of experimental results. Because many of the measurements made were used to test multiple hypotheses, how each measurement was used to address particular hypotheses is presented in the next section under the relevant hypothesis.

1.3 HYPOTHESES, RATIONALE AND DETAILED APPROACH TO HYPOTHESIS TESTING

Hypothesis regarding above-ground productivity and nutrient relationships:

H1: (A) Above-ground productivity is lower in the grass meadows than in the wet-sedge meadows. (B) The lowered productivity in the grass meadows is due to stronger nutrient limitations in those meadows.

A corollary hypothesis tested under **H1** is the following: (C) Nitrogen availability gradients do not correspond to rates of N mineralization and N mineralization does not provide what is required by the plant community.

Rationale for H1.

Both the "sedge-dominated" and "grass-dominated" ecosystems are highly productive minerotrophic wetlands. My observations and data collected during the first field season (1989) suggested that net production is greater in the wetter sedge meadows when compared to the drier grass meadows. I propose that the greater productivities in wet-sedge meadows are due to greater nutrient availabilities in the sedge meadows, and, correspondingly, the lowered productivities in the grass meadows are due to lower nutrient availabilities in the grass meadows.

Several lines of reasoning support this hypothesis. In general, productivity in northern wetlands may be limited by a number of resources including water, low temperatures (Gorham 1974), various nutrients, and waterlogging (Reader 1978). Isolating the effect of one resource over another is difficult because many resources have interactive effects on productivity. For example, soil saturation is known to increase the solubility of several nutrients including P (see below), which if limiting, would have a positive effect on productivity. However, soil saturation may also have a negative effect on productivity if anaerobic conditions restrict root uptake of nutrients. Because the wetter meadows are more productive than the drier meadows, consequences of hydrology and soil saturation that increase production are explored.

A number of processes theoretically contribute to more nutrients being available in the wetter systems. First, hydrologic inputs of nutrients are increased in systems having greater contact with hydrologic flows. Surface and subsurface water can contain nutrients both in dissolved and particulate form. Contact with these waters results in nutrients being transported directly to wetlands (Ingram 1967, Verhoeven 1986, Verry and Timmons 1982). For example, high soil P and plant productivity were related to sedimentation from surface flow in a *Carex* wetland (Auclair et al. 1976). Vitt (1990) however, cautions that nutrient concentrations in subsurface flows may not adequately reflect total hydrologic inputs because flows generally differ among wetlands. It is the total flux of nutrients passing through the rooting zone of a plant that defines the supply rate.

Secondly, flooding itself has a number of consequences on nutrient availability, including altered transport, modified soil chemistry and changes in decomposition. Transport of ions may be greatly facilitated with soil saturation and the subsequent reduction of air spaces. Because nutrient uptake processes in plants are generally diffusion limited (Ingram 1967, Chapin 1991a), both Ingram (1967) and Chapin (1980) argue that the movement of water in and of itself would increase the availability of ions already present in the soil. Flooding also alters the availability of nutrients due to changes in soil chemistry (Ponnamperuma 1972). In particular, sediment reduction is known to increase the availability of P (Reddy and Patrick 1984) (and see below).

Finally, flooding may change decomposition and mineralization dynamics. Because different decomposition dynamics operate between the two types of meadows, regulation of nutrient mineralization presumably varies between the meadows. Greater peat accumulations characteristic of the wet-sedge meadows are the result of anaerobic conditions restricting rates of decomposition. Yet because decomposition in anaerobic environments is thought to be less N (and possibly P) limited than in aerobic environments (Reddy and Patrick 1984), immobilization of N (and perhaps P) may be less in the wetter areas leading to potentially greater nutrient release from decomposition in the wet meadows. Support for this comes from a recent laboratory study showing that net mineralization of nitrogen was greater under flooded than under aerated conditions (Gale and Gilmour 1988). In another laboratory study, Ono (1991), found that the increase in pH due to flooding caused increases in N mineralization and N uptake by plants.

Not all studies show an increase in N mineralization with soil saturation. For example, although Grootjans et al. (1985) found greater ammonification in undrained portions of a fen meadow during wet years, total N mineralization was still greatest in drained portions. Similarly, in the Netherlands, Van Vuuren et al. (1992) found greater rates of N mineralization under relatively drier heathland soils and grasses than under wet heathland soils. Stanford and Epstein (1974) found a non-linear relationship between N accumulation in soil and soil moisture content. Generally, when more than 80 - 90% of the pore spaces were filled, N mineralization rates (or N accumulation) decreased (Stanford and Epstein 1974). Perhaps the contrasting results from the various studies examining effects of soil saturation on N mineralization are due to differences in the degree of soil anoxia. In this dissertation I examine N mineralization along the hydrologic gradient defined by the five graminoid meadows.

In terrestrial ecosystems, soil N mineralization has been equated with N availability (Keeney 1980, Binkley and Hart 1989). In minerotrophic wetlands, N mineralization, as a component of N availability, may be insufficient to meet the needs of the plant community, and the community may therefore require extra inputs from effects of hydrology. For instance, Verhoeven et al. (1988a) found lower N and P mineralization at a "rich" (i.e., more productive) wetland site in contrast to a "poor" site and that the amounts of N and P mineralized at the more productive site were insufficient to meet plant requirements, pointing to the importance of hydrologic sources in supplying necessary nutrients. In this dissertation I examine whether N mineralization in the five graminoid meadows is sufficient to meet plant community requirements.

Both correlative and experimental approaches are used to test this hypothesis. For example, a key result is that above-ground production in the five study meadows was correlated to N and P availability (I used a measure that provides a relative index of availability), suggesting that plant productivity was nutrient limited. I tested the nutrient limitation hypothesis by experimentally enhancing nutrient availability and measuring the response of plant biomass. By also providing a separate measure of the N mineralization process, I determined whether N mineralization was related to hydrology and whether N mineralization provided the N necessary to meet the requirements of the plant community.

Approach to Testing H1:

1. Measure above-ground production in the two wet-sedge and three grass meadows (Observational).

2. Estimate N and P availability, annual N mineralization and hydrology within each community (Observational).

3. Relate above-ground biomass accumulation to nutrient availability (Observational).

4. Relate plant uptake of N to N mineralization (Observational).

5. Measure change in biomass in response to N and P additions (Experimental).

Parts 1-4 of the above, describing the patterns of productivity and N and P availability, are addressed in Chapter 2 of the dissertation: **Primary productivity, nitrogen and phosphorus availability, and nitrogen mineralization along hydrologic gradients in five wetland meadows.** The experimental test of hypothesis **H1** is addressed in Chapter 3: **Nitrogen and phosphorus limitation of above-ground primary production in five wetland meadows**

Hypotheses regarding relative and multiple N and P limitations to productivity:

H2: The wet-sedge meadows are proportionately more P limited than the grass meadows due to greater organic matter accumulation under sedge which has resulted in a greater percentage of P in the unavailable organic pool.

Rationale for H2.

> P mineralization has been shown to regulate P cycling and availability in Histosols where organic forms of P dominate (Richardson and Marshall 1986, Chapin et al. 1978). Accumulations of peat are deeper in the wetter, sedge-dominated meadows than in the drier, grass-dominated meadows. With the slow mineralization rates typical of cold wet systems, and the assumed slow mineralization rates in the wet-sedge meadows, P might be more highly limited in the wet sedge meadows than in the drier grass meadows.

H2 (Alternative): (A) The wet-sedge meadows are proportionately less P limited than the grass meadows due to greater relative P availability in the wet-sedge meadows. (B) The greater P availability may be due to inorganic P release during reduction of flooded sediments.

Rationale for H2 (Alt).

A number of important chemical and biological changes take place when an inorganic soil is flooded that could affect P solubility. In that context, the reduction of Fe^{3+} to Fe^{2+} may be the most important chemical change that takes place in saturated soil (Ponnamperuma 1972). The reaction:

$$3Fe(OH)_3 + H^+ + e^- \rightarrow Fe_3(OH)_6 + H_2O$$

results in an increase in soluble Fe in solution and a rise in solution pH (Faulkner and Richardson 1989). In fact, this reaction is the primary cause of the observed increase in pH of an acidic soil upon saturation. With the reduction of Fe, adsorbed and chemically bonded P is released into solution. Furthermore, as a result of the subsequent increase in pH, P may also be made more available by hydrolysis of Fe and Al phosphates and by the release of P previously held by anion exchange. The sum of these processes would be to increase P availability in the wetter sedge-dominated meadows. This is in contrast to H2, which predicts lower P availability in the sedge meadows due to slower rates of mineralization.

Approach to Testing H2:

1. Measure proportions of P in organic vs. inorganic forms in grass and sedge meadows (Observational).

2. Indirectly evaluate potential for sediment reduction causing a release of P (Observational).

3. Contrast biomass response to experimentally increased P availability in sedge and grass meadows (Experimental).

Parts 1 and 2 of the above, describing P pools in the meadows and the potential for sediment reduction, are addressed in Chapter 2. Part 3, testing the response via a field experiment, is addressed in Chapter 3.

H3: Productivity increases will be stronger in response to a given external ratio of N and P than to absolute amounts of N and P.

Rationale for H3.

Studies on nutrient limitation of production in wetlands (and in many other ecosystems) often only examine the effect of a single nutrient limitation. For example, fens in northern Michigan (Richardson and Marshall 1986), marshes of central Alberta (Bayley et al. 1985), and the Florida Everglades (Craft and Richardson 1993), have been shown to be P limited. While bogs of northern Minnesota (Urban and Eisenreich 1988), wet meadows in the Netherlands (Vermeer 1986b), and Alaska tussock tundra (Shaver et al. 1986) were shown to be N limited. However, N and P nutrition is inextricably linked due to the high energy (ATP) requirements of N metabolism. Without N limitations or, with better N nutrition, many wetland plants can grow rapidly and are able to assimilate larger quantities of P (Chapin 1980, Vermeer 1986b, Guntenspergen et al. 1989). While several experimental studies have indicated co-limitation by N and P in wetlands (e.g., Sanville 1988, Bowman et al. 1993), the interactions of several nutrients in regulating plant growth are, in general, poorly understood (Shaver and Lechowicz 1985).

A body of theory suggests that plants have specific nutrient requirements for optimum growth at equilibrium (Ingestad 1979, Ingestad and Agren 1988). Under conditions of steady state, plants will grow at a level where all nutrient resources are equally limiting (Tilman 1982, Bloom et al. 1985). Extending this concept to the ecosystem, if the ecosystem is functioning under optimum nutrition (c.f., Ingestad 1979), a greater biomass response would be expected from an application of an optimum ratio of N and P than from an increased addition of a single nutrient alone. Experiments growing seedlings in solution have supported the optimal element ratio theory (e.g., Ingestad 1979), yet to my knowledge this has not been demonstrated in the field.

Approach to Testing H3:

1. Measure change in biomass in response to manipulated ratios of N and P vs. change in response to increases in availabilities of single elements (Experimental).

2. Evaluate uptake of N and P with fertilization against growth response (Experimental).

Both of these components are addressed in Chapter 3.

Hypotheses regarding plant species, nutrients and community responses to altered nutrient supply:

The next two hypotheses together predict how increased nutrient availability will influence presences and abundances (determined by percent cover) of plant species in the wetland meadows. In particular,

H4: Ratios of experimentally applied nutrients (N and P) select for certain species combinations. There will be a "community convergence" (i.e., botanical composition becoming more similar, c.f. Inouye and Tilman 1988) determined by the ratio of applied nutrients.

Rationale for H4.

A number of studies has demonstrated empirically that the availability of nutrient resources influences the community structure of grassland and wetland ecosystems, including prairie grasslands (Inouye et al. 1987, Tilman 1986, Tilman 1987), wet grass meadows (Grootjans et al. 1985, Vermeer and Berendse 1983), hay meadows (Silvertown 1980, Tilman 1982), *Carex* meadows (Auclair et al. 1976), and poor and rich fens (Vitt and Chee 1990). Species vary in their resource requirements (Tilman 1982, Tilman 1987) and therefore their distributions are expected to vary along gradients of resource availability. A change in the external ratio of required resources (e.g., N and P) may favor certain species over others and result in a shift in species composition (Tilman 1985, Tilman 1988). Although some field evidence is available supporting species replacement in response to changing resource ratios (Tilman 1982, for N and P ratios in the Rothamsted Park Grass Experiments in the UK, Tilman 1987 and Inouye and Tilman 1988 for N and light ratios), little information is available on how wetland species will respond to altered ratios of N and P, gradients that may be important in wetlands limited by N and P.

H5: Species diversity will decrease with experimentally increased nutrient availability if productivity is enhanced.

Rationale for H5.

Theory predicts that with increased resource availability in competitive environments, diversity should eventually decrease due to the increased dominance of the vigorously growing species (Al-Mufti et al. 1977, Grime 1979, Huston 1979, Tilman 1987). Experimentally it has been shown that increasing nutrient availability alters competitive relationships between dominant plant species (Aerts and Berendse 1988, Wedin and Tilman 1993). A number of studies has also demonstrated the negative correlation between biomass and species richness for medium to high biomass systems along natural (Day et al. 1988, Vermeer and Berendse 1983, Inouye et al. 1987, Wheeler and Shaw 1991) and experimentally-induced nutrient gradients (Huenneke et al. 1990, Tilman 1987, Pysek and Leps 1991).

The exact mechanism for the reduction in diversity with increasing productivity is still unclear. Tilman (1982, 1987) and others (e.g., Grime 1979) suggest that increased above-ground biomass decreases light availability to subcanopy plants resulting in their mortality. However the relationship between production and diversity isn't always straightforward. For example, several recent studies (Goldberg and Miller 1990, Carson and Barret 1988, Willems et al. 1993) found that experimentally increased production did not always lead to the predicted decrease in diversity. Which resource is manipulated may have consequences on diversity independent of changes in production. For example, Willems et al.

(1993) found that adding N alone to a chalk grassland did not significantly increase production (production did respond to P and N+P), but adding N alone did decrease species richness. This dissertation assesses changes in biomass and species richness along experimental gradients of N and P availability (including altered ratios) to determine relationships between increased biomass, N and P availability and species richness.

Approach to Testing H4 and H5:

1. Track species responses (percent cover) by plot and meadow to experimental additions of N and P (Experimental).

2. Monitor changes in species richness to two years of experimental additions of N and P (Experimental).

All phases of testing are addressed in Chapter 4 of the dissertation: **Response of wet meadow communities to N and P additions along fluctuating hydrologic gradients.**

Chapter 2: Primary productivity, nitrogen and phosphorus availability, and nitrogen mineralization along hydrologic gradients in five wetland meadows

2.1 INTRODUCTION

Primary production in many, if not most, terrestrial ecosystems is nitrogen (N) limited (Aber and Melillo 1991, Chapin 1980). Exceptions occur where N fixation activity is high, where atmospheric N inputs have increased or where some other nutrient is limiting. Wetlands may be either N limited (Chapin et al. 1988, Shaver et al. 1986, Vermeer 1986a, Vermeer 1986b, Verhoeven et al. 1983, Morris 1991), phosphorus (P) limited (Craft and Richardson 1993, Verhoeven 1986, Morris 1991) or co-limited by both N and P (Bowman et al. 1993, Aerts and Berendse 1988, Sanville 1988, Vitousek and Howarth 1991). Given the different hydrologic conditions in uplands and wetlands, the controls on nutrient limitation and productivity may differ substantially between these two broad types of systems. Similarly, the controls on productivity and nutrient availability may differ along gradients of hydrologic conditions within and among wetlands.

A wetland's hydrology can influence nutrient supply to the plant community through a number of direct and indirect effects, ultimately influencing net primary production (Mitsch and Gosselink 1993). Several examples from the literature illustrate the importance of hydrology to productivity. In a *Carex* marsh in Canada, Auclair et al. (1973) noted an inverse relationship between productivity and water depth. In bottomland forested wetlands, productivity was higher in stands where surface water flow rates were greater (Mitsch et al. 1991). In these two examples, the wetlands received undoubtedly significant, but unquantified, inputs of nutrients through surface or groundwater flows. In an Alaskan wet tundra, productivity and rates of nutrient cycling were greater in areas in contact with sub-surface flows compared with areas not in contact (Chapin et al. 1988).

By definition, sources of available N and P in minerotrophic wetlands include inputs from precipitation, subsurface flows and groundwater, and mineralization of organic matter (Tallis 1983, Verhoeven 1986). Ombrotrophic wetlands (e.g., bogs) however, receive nutrients from precipitation, perhaps N fixation, and organic matter decomposition and are generally less productive than more minerotrophic wetlands. Proposed mechanisms for high productivity in minerotophic wetlands therefore include: 1) elevated nutrient inputs via surface, subsurface or groundwater sources; 2) increased nutrient availability due to indirect effects of increased soil wetness; and 3) lack of plant water stress during the growing season. The net result of the first two general mechanisms is an increase in the pool of nutrients available to the plant community for production.

Despite this general understanding, it has been difficult to document nutrient availability gradients in most wetlands (Barko and Smart 1986, Verhoeven 1986, Vitt and Chee 1990). Simple concentrations of nutrients in soil water do not take into account hydrologic flow rates and underestimate the flux of nutrients through the system or to the plant roots (Vitt 1990). Hydrologic fluxes are notoriously difficult to measure. For most types of minerotrophic wetlands, the contribution of internal inputs of N (e.g., N mineralization) relative to hydrologic or other inputs is either unknown or results are contradictory. Bowden (1986), for example, found a good correlation between net N mineralization and plant demands for N in a riverine marsh, suggesting that internal inputs of N may furnish most of the N required by the plant community. Yet Verhoeven et al. (1988a) provide evidence that high rates of production are supported by external inputs of nutrients when conditions are unfavorable for high mineralization. In general, the factors regulating mineralization and limiting primary production in wetlands are not well understood (Bowden 1987).

Beaver meadows are useful systems for examining relationships among hydrology, productivity and N mineralization. As a result of expanded beaver populations over the last fifty years in Voyageurs National Park (VNP) in northern Minnesota, the extent of beaver-impacted wetlands has increased on the Kabetogama Peninsula in the park (Johnston and Naiman 1990a). Two types of minerotrophic, wet meadow communities, "grass-dominated" and "sedge-dominated", occur when beaver abandon their ponds and the dams soon collapse resulting in a catastrophic lowering of the water table (Johnston and Naiman 1990a, Pastor et al. 1993). Grass and sedge species soon occupy the exposed sediments, with sedge-dominated communities typically on wetter sites, where the water table is just at or below the soil surface. In grass-dominated communities, the water table is substantially lower. The grass and sedge communities therefore represent gradients of hydrology and potentially other ecosystem attributes. They are widely distributed across the landscape, allowing for a number of structurally similar meadows to be chosen for replicated studies.

In this chapter, I examine whether factors thought to influence above-ground net primary production (N and P availability, N mineralization and hydrology) are related to production in the two types of minerotrophic wet meadow ecosystems. My overall objective is to examine the relationship between nutrient (N and P) availability and productivity and how this relationship changes along a hydrologic gradient.

Specific objectives are to:

1) determine whether the two types of meadows differ in above-ground net primary production;

2) determine whether above-ground net primary production correlates with nutrient (N and P) availability, N mineralization, and/or hydrologic gradients;

3) examine factors influencing N mineralization in the two types of ecosystems; and,

4) assess whether internally generated N (i.e., from N mineralization) is sufficient to meet the requirements of the plant community or whether supplemental sources are required.

Meeting the objectives also provides a test of parts A and C of hypothesis **H1** (Chapter 1). **H1**(A) states that above-ground productivity is lower in the grass meadows than in the wet-sedge meadows; **H1**(C) states that nitrogen availability gradients do not correspond to rates of N mineralization and that N mineralization does not provide what is required by the plant community.

2.2 RESEARCH SITES

The Kabetogama Peninsula of VNP, located on the Minnesota (USA) - Ontario (Canada) border (48°34' N, 93°23'W), is in a region consisting of complex glaciated terrain overlying Precambrian metasedimentary and granitic bedrock (Johnston and Naiman 1990b). Clayey lacustrine sediments from glacial Lake Agassiz are extensive and form the parent material in most of the topographic depressions. The climate is cold (mean annual temperature is 1.4°C), caused by the presence of polar air masses for approximately six months of the year (Bryson and Hare 1974). Mean annual precipitation is 63 cm, with summer months generally the wettest (Johnston and Naiman 1990b).

Upland forests on the Peninsula consist of trembling aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Wetlands in the area include open *Sphagnum* bogs, coniferous bogs, forested swamps and wet meadows.

Briefly, the grass meadows are composed primarily of Canada blue joint (*Calamagrostis canadensis*); the sedge meadows are co-dominated by *Calamagrostis canadensis*, wooly grass (*Scirpus cyperinus*), and species from the genus *Carex*. These communities are classified as semipermanently and seasonally flooded, emergent wetlands (Cowardin et al. 1979) and are the two most common types of wet-meadow communities on the Peninsula (Johnston and Naiman 1990a). Both communities can occur within a single physiographic meadow forming a toposequence, with the grass-dominated communities occurring on higher ground than the sedge-dominated communities. However, because of the generally low topographic gradients in the region, most meadows are dominated by either grass or sedge communities. Johnston et al. (unpublished ms.) mapped and typed soils for several of the beaver meadows on the Peninsula; soils in those meadows included histic Ochraqualfs, typic Ochraqualfs, and typic Argiaquolls.

I selected two sedge-dominated meadows (Lower Bluefin (S1), Lower Shoepack (S2)) and three grass-dominated meadows (Upper Bluefin (G1), Upper Shoepack (G2), Found (G3)) to conduct my study (Fig. 1). A grass meadow is paired with a sedge meadow in each of two drainages (Shoepack, Bluefin); a third grass meadow (Found) is unpaired and is somewhat unique structurally due to the presence of *Salix* shrubs. Woody shrubs are rare in the other meadows and were not present in any of the study plots.

2.3 METHODS

Plot selection and description

Seventy plots were established within the five meadows during the summer of 1989. Within each of the five meadows, a qualitative delineation of the dominant community was made prior to randomly locating fourteen plots within the community. This was necessary to ensure that the plots fell within the desired vegetation type. To maintain as much plot-to-plot homogeneity as possible, plots were excluded if more than ten percent of the area was covered with dead wood from a previous stand or if soils contained sands indicating a fluvial influence.

Each plot was 8.55 m^2 and circular. The plot circumference was initially marked by inserting 12 equally spaced, 1/4" diameter PVC pipe 15 cm into the soil. Roofing rubber (45 mil thick) was hung onto the PVC and sunk approximately 10 cm into the mineral horizon to ensure a relatively impervious plot boundary.

Above-ground biomass measurements

Three 30 x 30 cm subplots were systematically located within each of the circular plots and clipped of above-ground vegetation at the end of the 1989 growing season. Where possible, vegetation was sorted to species in the field, transported from the meadows in paper bags and dried for several days under 100 W light bulbs until samples "felt-dry" and could be stored. Later, samples were oven dried at 70°C, sorting to species was completed if necessary, and weighed to the nearest 0.1 gm.

Tissue chemical analyses and uptake calculations

Tissue chemical analyses were not conducted on plant samples harvested in 1989. However, chemical analyses were conducted in 1991 and results from control plot samples from each meadow (see Chapter 3) in 1991 were used to estimate N and P above-ground uptake for 1989. Sampling occurred after growth for the year terminated, enabling above-ground uptake of N and P to be approximated as the biomass content of N and P. Samples were digested in $LiSO_4$ for analyses of total N and P colorimetrically with a Technicon Autoanalyzer II. Biomass N and P contents (g element/m^2) were calculated by multiplying mean concentrations of N and P from control plot samples (g element/g biomass) by 1989 biomass for all plots (g/m^2).

Below-ground uptake of N was based on two separate estimates of below-ground biomass, assuming a below-ground N concentration of 1%. The low estimate of below-ground production comes from Bernard (1974) who measured root production to be 25% of shoot production in *Carex* meadows. The high estimate of root biomass comes from direct measurements I made at one of the grass meadows (G3) during the fall of 1991, where total root biomass was 3.35 times greater than above-ground biomass. I assumed below-ground biomass measured in the fall was equal annual production, which may be an underestimate of total production.

Floristic data

Visual estimates of percent cover were made for all species in the plots at the end of the 1989 and 1990 growing seasons. To ensure high precision, observers obtaining cover estimates were periodically inter-calibrated. Two or three observers provided cover estimates for each plot, with observer values averaged for each species. Estimates were made to the nearest percentage; species with < 1% cover were assigned a cover of 0.5% for data analyses. Species nomenclature follows Gleason and Cronquist (1991).

Nitrogen mineralization

The most significant source of plant available nitrogen in many ecosystems is by *in-situ* decomposition of organic matter and release of nitrogen as inorganic ammonium or nitrate. Nitrogen mineralization (the conversion of organic nitrogen into inorganic ammonium and nitrate) and nitrification (nitrate production from ammonium) were assessed using an *in-situ* polyethylene bag technique (Eno 1960). The key feature of this method is that it provides a measure of the mineralization process under ambient temperature conditions in the absence of plant uptake; moisture conditions are assumed to remain consistent throughout the incubation (demonstrated by Gordon et al. 1987, although Hart and Firestone 1989 showed moisture tended to change with incubation).

Furthermore, mineralization, as an internal source of available N, is isolated from hydrologic (or external) sources of N.

Paired samples (immediately adjacent to each other) were collected from the upper organic horizons with a bulb corer (approximately 8 cm diameter), taking care to minimize disturbance of the sample. One sample in the pair was enclosed in a 1 ml thick polyethylene bag and replaced as an intact core into its original location. The other sample in the pair was also enclosed in polyethylene, but returned to the lab without incubation for determination of initial extractable nitrate and ammonium. Beginning in October 1989, three sets of samples (or "buried bags") were established in each of the 70 plots. The three bags from 11 of the 14 plots within each meadow were composited prior to extraction to reduce the analytical load; the three bags from the remaining three plots within each meadow were processed separately for an estimate of within-plot variation.

After collection, samples were stored on ice until they were processed, generally within 2-3 days. The field moist samples were sieved through a 6 mm screen to remove roots and other coarse particles, mixed well and subsampled for moisture determinations. Approximately 25 grams of the sieved, moist soil was extracted in 100 ml of 1N KCl. Samples were placed on a shaker for 30 minutes, then left to settle overnight. A 40 ml clear aliquot of the extractant was drawn from just below the surface for analysis.

Net mineralization was calculated as the difference between the incubated sum of nitrate-nitrogen (NO_3-N) and ammonium-nitrogen (NH_4-N) and the sum in the initial unincubated sample; net nitrification as the increase in NO_3-N during incubation. A decrease in NO_3-N and NH_4-N during incubation is interpreted as immobilization by microbes. Five incubation periods were used to estimate annual rates: 1) October 7 1989 - May 6 1990, 2) May 6 1990 - June 25 1990, 3) June 25 1990 -July 25 1990, 4) July 25 1990 - August 21 1990, and 5) August 21 1990 - October 7 1990. Annual net mineralization and annual net nitrification were calculated by summing the rates for each of the five periods.

The above N mineralization calculations are based on mineralization occurring in the O horizon. However the meadow soils also consist of an A horizon with decomposable organic material undoubtedly contributing to the pool of available N. To estimate the total supply of N from mineralization, I calculated mineralization from the A horizon as follows: 1) I used a direct measure of N mineralization in the A horizon based on a separate study conducted in one sedge and one grass meadow using 6 pairs of O and A samples incubated separately for one month, 2) I converted measured mineralization rates for O and A horizon soil to an areal basis by using mean depths of O and A horizons for a given meadow measured during plot installation, mean bulk densities of the O horizon for the appropriate meadow, and a bulk density for all A horizons of 1.16 (C. Johnston, pers. comm.), 3) using the areal rates, I calculated a ratio of O + A mineralization to O mineralization, 4) then I converted annual areal rates based on the O for each meadow to annual areal rates based on the A and O using the calculated ratio. These calculations assume that the ratio of N mineralization in the O and A horizons remains consistent during all periods in all meadows.

Samples from the October 1989, May 1990 and October 1990 collections had to be frozen for several months until they could be extracted. To examine the effect of freezing on extractable nitrate and ammonium levels, I conducted a separate study whereby 26 samples from the June 1990 collection were split prior to processing: one set was frozen and the other set processed as usual. After two months, the frozen samples were thawed and processed. In general, ammonium levels increased with freezing but the effect on nitrate was minimal (Appendix A). The average ratio of NH_4-N between frozen and non-frozen samples was 1.8, with 25 out of 26 samples showing increased NH_4-N. Based on this, I divided the ammonium values for all frozen samples by 1.8. Because nitrate analyses did not show a consistent pattern of differences between frozen and non-frozen samples, no adjustments were made to these values.

Nutrient (N and P) availability

Many minerotrophic wetlands, including the beaver meadows, receive additional and potentially significant inputs of nutrients from surface runoff and contact with groundwater flows. To get an estimate of total input, I used ion exchange resins placed in porous bags (Binkley and Matson 1983, Gibson et al. 1985) and buried in the organic horizons of the meadows. The resin-bag measurements provide an estimate of longer-term <u>total availability</u> of nitrate, ammonium and phosphate, integrating the input from mineralization, weathering, and hydrologic effects (Binkley 1984) over the incubation period. I emphasize that this is only an estimate of *in-situ* availability; resin bags may underestimate actual availability if competitive processes (eg., plant and microbial uptake) have stronger affinities for the nutrients or if lack of water limits transport to the bags (c.f. Lajtha 1988). Furthermore, because water fluxes are unknown, the availability estimates cannot be expressed on an areal basis. Hence their utility is limited to relative comparisons among sites.

Two sets of resin bags were used; the first from October 7 1989 to May 6 1990 and the second from May 6 1990 to October 7 1990. The period from October to May occurs during the season of little to no plant growth. Availability estimates made during this period represent what is available in the absence of significant plant uptake and may be a better indicator of relative site nutrient status.

Approximately ten grams of moist mixed-bed anion/cation exchange resins (Baker AGMI-615, ionic form H/OH) were enclosed in nylon sacs and buried approximately 5 cm deep into the organic horizons. After removal, resins were air-dried until processing could take place. For each analysis, one gram of air-dried resin was extracted in bulk with two rinses of 50 ml 1N KCl. Replication and compositing followed the same scheme used for the buried polyethylene bags. After extraction, extracts were frozen until analysis.

Resin KCl extracts were analyzed for nitrate, ammonium and phosphate; buried bag KCl extracts for nitrate and ammonium. All analyses were performed on a Technicon Autoanalyzer II.

Hydrology

Depth to the ground water table was measured approximately weekly during the growing season. Standpipes, constructed of perforated 5 cm diameter PVC tubes, were sunk into the ground at least 55 cm below the soil surface. The standpipes were located downslope from each plot towards the existing pond or stream, approximately 1 m beyond the plot boundary. Depth to the water table was measured to the nearest cm beginning in July of 1990.

Total carbon and nitrogen

To express mineralization rates on a gram of nitrogen basis, and to have estimates of the carbon (C) and N capital in the meadows, every soil sample collected as part of the buried bag study was analyzed for total C and N with a LECO 800 CHN analyzer. The oven-dried sample used for moisture determination was ground with a mortar and pestle. An approximately 1 gm subsample was obtained for analysis by sampling from three different areas of the ground sample.

Bulk density and depth of organic horizon

In four of the meadows (G2, S2, G1, S1) bulk density estimates were made by placing three 12.5 cm diameter templates on the meadow floor adjacent to a plot. A bread knife was used to cut down through the organic horizon and a roughly cylindrically-shaped hole was excavated of organic material. The holes were lined with a plastic sheet and filled with water measured to the nearest 0.1 ml. The excavated material was then sieved through the same 6 mm coarse screen used to process the buried bag samples. Material passing through the sieve and material caught by the sieve were oven dried separately at 70°C. Because calculations for measurements made on soils from the buried bag studies (e.g., total C, total N, total P, and extractable N) were all based on the mass of the sieved soil, only material passing through the screen was used to calculate the soil mass on a volume (cm^3) basis. Mean bulk densities were 0.225, 0.236, 0.209 and 0.251 for S1, S2, G1, and G2, respectively. (For G1, G2 and S2 there were no differences ($p > 0.05$) in measured bulk density among the plots. Only at S1 was there a significant difference among the plots ($p = 0.05$). I used the mean bulk density for S1 for consistency and ease in calculation.)

Depths of visually distinct horizons were measured at the time of plot installation. Because direct measurements of mass were only made on a subset of plots in the four meadows, I calculated mass for each plot by multiplying the average depth of the organic horizon measured for each plot by the mean bulk density value calculated for the meadow. For G3, the grass-dominated meadow where no bulk density measurements were made, I used the average of the bulk densities for the other two grass-dominated meadows.

Inorganic, organic and total phosphorus

Inorganic, organic and total phosphorus were determined using the ignition method of Olsen and Sommers (1982) on the initial (i.e., non-incubated) buried bag soil samples collected during June of 1990.

pH

Distilled water pH's were measured using a field moist soil to solution ratio of 1:5 on 5 g of soil. In some cases, insufficient material remained to measure pH.

Statistical analyses

Water table depths were ranked by plot and sampling date. A multiple analysis of variance (MANOVA) was conducted on the ranks to determine overall site effects on depth to the water table (Conover 1971). Hydrologic fluctuation was estimated as the standard error of the mean rank over sampling date for each plot. Differences among means of the estimate of hydrolgic fluctation and all remaining plant community and soil properties were tested with a one-way ANOVA (H_0: all meadow means are equal). Specific differences between the means of the two sedge meadows and the three grass meadows (H_0: sedge meadow means = grass meadow means) were tested using the method of linear comparisons (i.e., orthogonal contrasts) (Sokal and Rohlf 1981). A linear comparison was also used to test for the effect of community type (i.e., grass or sedge) on depth to the water table, using the Wilks' Lambda statistic to indicate significance.

Spearman's rank correlation analysis, which makes no assumptions about the underlying distribution of variables (Zar 1984), was used to examine relationships with biomass production and N mineralization to various soil parameters.

All analyses were conducted using PC SAS (SAS Institute 1988).

2.4 RESULTS

Community composition

Percent cover for the five most frequently occurring plant species from the sedge and grass communities (Table 1) shows that both communities are characterized by a high degree of dominance; only a few species contributed to a majority of the cover. Several of the dominant species are common to both community types.

Productivity and soil characteristics

Above-ground biomass at the end of the 1989 growing season was significantly higher in the two sedge meadows than in the three grass meadows (Table 2). Resin estimates of available nitrate, ammonium, and phosphate were also higher in the two sedge meadows (Table 2). A number of other soil properties were consistently higher in the sedge meadows. These include: percent organic matter, depth of the organic horizon, calculated masses of total C, N and P in the organic horizon, and inorganic P (Table 3). Over 90% of the soil P was organic in each of the meadows; organic P did not differ among the community types (Table 3). Although there were significant differences among individual meadow pH's (Table 3), pH's did not differ between grass and sedge communities.

Percent N in plant community biomass was higher in the three grass communities than in the two sedge communities (Table 4); there was no difference in P concentration in community biomass between the community types. The mass of P in plant biomass tended to be greater in the sedge meadows (Table 4); there were no differences in mass of N between the two types of meadows. The ratio of N:P in plant biomass was lower in the two sedge meadows than in the three grass meadows (Table 4).

Hydrology

Seasonal depth to the water table (when < 55 cm below the surface) was on average greater for the grass meadows during both 1990 and 1991 (Fig. 2, Table 2). In 1991 beaver returned to S1 and re-flooded a portion of the meadow, resulting in mean water levels above the soil surface for that year. Water table fluctuations differed among meadows and differed between meadow types in 1991 but not 1990 (Table 2).

Nitrogen mineralization

Annual nitrogen mineralization in the O horizon ranged from 1.1 to 3.7 g N/m^2/y (Table 5). Annual nitrification ranged from 45 to 110% of net mineralization. There were, however, no clear differences between sedge and grass meadows for either annual net nitrogen mineralization or nitrification on an areal basis. For example, the rates at S2, a wet sedge meadow, were as low as the rates measured at G3, a dry grass meadow (Table 5). Turnover of N (mineralization of N per gram of soil N), however, was greater overall in the grass meadows.

Annual N mineralization per unit area was positively correlated to soil C/N ratio, soil N/P ratio and percent loss on ignition (Spearman's $r = 0.90$, $p = 0.0374$, $n = 5$). Annual N mineralization per gram of soil was also positively correlated with soil C/N ratio and soil N/P ratio (Spearman's $r = 0.90$, $p = 0.0374$, $n = 5$), but negatively correlated with the concentration of soil P and water table fluctuation (Spearman's $r = -0.90$, $p = 0.0374$). Annual N turnover was negatively correlated with production and pH (Spearman's $r = -0.90$, $p = 0.0374$).

Rates of N mineralization in the five meadows varied seasonally (Fig. 3). Mineralization in each of the five meadows was greatest for the periods ending in August 1990 or October 1990. Rates were lowest for the winter period ending in May 1990. Net nitrification rates varied similarly to net mineralization.

To examine effects of environment and substrate quality on N mineralization, for each period in each meadow, N mineralization and nitrification rates were regressed against average initial values of soil moisture content, extractable ammonium, extractable nitrate, C/N ratio, percent N, and percent C. Initial ammonium concentrations were negatively correlated with mineralization (Spearman's $r = -0.578$, $p = 0.003$, $n = 25$) and nitrification (Spearman's $r = -0.472$, $p = 0.050$, $n = 25$). Mineralization was positively correlated with initial percent nitrogen in the soil (Spearman's $r = 0.414$, $p = 0.039$, $n = 25$), especially in the sedge meadows (Spearman's $r = 0.854$, $p = 0.002$, $n = 10$). In the grass meadows alone, there was a trend for mineralization to be negatively correlated with initial nitrate concentrations (Spearman's r = -0.479, p = 0.071, n = 15).

Moisture contents of the incubated sample did not appear to affect ammonium or nitrate production when making comparisons among the mean annual values from the meadows. However, within a meadow, when data from the individual plots were combined over all periods, moisture was moderately and negatively correlated with daily mineralization in four of five meadows (Table 6). It appeared that high moisture contents (e.g., > 500%) tended to decrease mineralization rates.

N mineralization per gm of N was significantly greater in the O horizon vs. the A horizon in both the sedge meadow and the grass meadow (Fig. 4, p = 0.007 and p = 0.022, respectively). Because there was no difference in mineralization of the A horizon between the two meadows (p = 0.997), the average ratio of O + A mineralization to O mineralization of 1.47 was used to estimate the total supply of N from mineralization in all of the meadows (see below).

Productivity relationships

Mean productivity for each of the meadows correlated positively with resin available phosphate, nitrate, and ammonium, and total soil P (Spearman's r = 0.900, p = 0.0374, n = 5 for all four of the soil properties). Biomass correlated negatively with annual N turnover (Spearman's r = -0.900, p = 0.0374, n = 5), but did not correlate with N mineralization on a soil mass (p = 0.873) or areal basis (p = 0.505).

N supply from mineralization and annual plant community demand for N

The calculated total supply of N from mineralization of the O and A horizons was less than the above-ground plant mass of N in four of five meadows (Table 7). Even with the lower, more conservative, estimates of combined above- and below-ground plant community N requirements, based on total mass of N (Table 7), N supplied via mineralization processes in the O and A horizons was less than community production requirements.

2.5 DISCUSSION

Nitrogen mineralization

Annual N mineralization rates measured for the meadows (Table 5) are of the same magnitude as rates measured for the relatively few other wetland and grassland ecosystems that have been studied in the region. For example, Grigal and Homann (1994) reported 1.9 and 1.6 g N/m^2/y N mineralization for a savanna and a lowland hardwood stand respectively, located at the Cedar Creek Natural History Area in central Minnesota. Pastor et al. (1987) and Zak and Grigal (1991) reported rates ranging from 3.5 and 4.7 g N/m^2/y, respectively, for an old field at Cedar Creek and from 4.2 and 6.5 for a nearby savanna. Zak and Grigal (1991) reported the lowest rate (1.5 g N/m^2/y) for a swamp forest. In the Netherlands, N mineralization rates in a heathland ranged from 4.4 g N/m^2/y under *Erica* to 7.8 g N/m^2/y under *Molinia* (Van Vuuren et al. 1992). In central Europe, Verhoeven et al. (1990) measured rates of 4.6 g N/m^2/y and 5.6 g N/m^2/y for bogs and fens, respectively. The rates measured in the VNP beaver meadows are of the same magnitude as rates measured in upland boreal forests at Isle Royale National Park in Lake Superior (Pastor et al. 1993).

Despite the reasonable estimates for mineralization rates at the beaver meadows, an explanation for the pattern of differences among the meadows is not readily apparent. N mineralization in wetlands is affected by a number of factors including soil temperature, pH, C/N ratio (an indicator of organic matter quality), aeration, nutrient availability, and soil texture and structure (Reddy and Patrick 1984). Annual N mineralization, expressed on either a soil mass or an areal basis, correlated to soil C/N and N/P ratio but was not correlated to N or P availability, pH or depth to the water table. Although N mineralization at the VNP meadows was poorly correlated with environmental factors measured for the meadows, turnover of N was greater in the drier grass meadows and was negatively correlated to pH, which was generally lower in the drier meadows (one grass meadow, G1 had a high pH).

Several studies have shown that net N mineralization can be greater under flooded than under aerated conditions (Gale and Gilmour 1988, Ono 1991), in particular the ammonification portion of the process. Reddy and Patrick (1984) attribute greater rates of ammonification in flooded soil to anaerobic decomposition being less N (and possibly P limited) than aerobic decomposition, leading to perhaps less immobilization under anaerobic conditions. Yet not all studies show an increase in N mineralization with soil saturation. For example, although Grootjans et al. (1985) found greater ammonification in undrained portions of a fen meadows during wet years, total N mineralization was still greatest in drained portions. In the Netherlands, Van Vuuren et al. (1992) found greater rates of N mineralization under relatively drier heathland soils and under grasses than under wet heathland soils. Verhoeven et al. (1988a) found both N and P mineralization to be less at a "rich" wetland site in greater contact with ditch water than at a "poor" site. Marrs et al. (1988) suggested that N mineralization in high altitude montane soils of Costa Rica was limited by high soil moisture. Grigal and Homann (1994) show a positive relationship between net N mineralization and depth to groundwater, with lowest rates occurring in the forest with the shallowest depth to groundwater.

Stanford and Epstein (1974) found a non-linear relationship between N accumulation in soil and soil moisture content. Generally, when more than 80 - 90% of the pore spaces were filled, N mineralization rates (or N accumulation) decreased (Stanford and Epstein 1974). When examined within a given meadow at VNP, high moisture contents appeared to limit mineralization, perhaps reflecting the percent of filled pore-space as suggested by Stanford and Epstein (1974). Initial soil moisture content did not appear, however, to be an important factor controlling differences among the meadows.

Nitrification occurred in both the wetter and drier meadows at VNP. Proportional nitrification was greater in the sedge communities, suggesting conditions in the wetter sedge communities were quite conducive for nitrification. In contrast, net nitrification was virtually absent from the wet heathland soils in the Netherlands (Van Vuuren et al. 1992). Nitrification can occur in aerated microsites in saturated soils, for example in oxidized rhizospheres (Reddy et al. 1989) or when there are fluctuations in the water table. The seasonally fluctuating water tables in the VNP meadows may have facilitated nitrate production.

N mineralization, N and P availability and productivity

Above-ground production at the five VNP meadows was correlated to the resin-based index of N and P availability, but not to N mineralization, suggesting that external sources of N may be important for the maintenance of meadow fertility. The gradient of N mineralization on a gram of N basis (turnover) at the VNP meadows was actually opposite the productivity gradient. However, because the mass of N was lower in the grass meadows, the amount of N turned over was low on a bulk soil basis and did not correspond to N availability.

Resin estimates of nutrient availability depend on transport of ions to the bags (Binkley 1984); the resin measurements therefore serve as useful indices of total nutrient availabilities, incorporating processes that contribute to increased nutrient availability in water-dominated systems. In several terrestrial ecosystems, N mineralization has been highly correlated with productivity (Pastor et al. 1984, Nadelhoffer et al. 1983, Zak et al. 1989). Because other sources of available N are relatively minor in upland ecosystems, equating N mineralization with N availability in those systems may be justified (c.f., Binkley and Hart 1989). However this model may not be appropriate for many wetlands. The poor correlations between N availability and N mineralization found in this study, corroborated with results from other recent studies, suggest that alternative sources of N are important in many wetlands. For instance, Grigal and Homann (1994) found that *in-situ* N mineralization did not reflect N availability in a forested swamp (they used plant uptake of N as an indirect measure of availability), and suggested that groundwater was an important source of N in periodically inundated forests. Verhoeven et al. (1988a) found that N (and P) mineralized faster at lower productive sites where N (and P) uptake was also low. They concluded that flowing ditch water increased the supply of N (and P) to the more highly productive sites. In some wetland systems, N mineralization has been equated with availability (Bowden 1987, Bowden 1986). The degree of hydrologic contact and the characteristics of that contact may be important in determining the influence of hydrology on nutrient availability.

Sources of nutrients in both terrestrial and wetland ecosystems include precipitation, atmospheric fixation (of N), mineral weathering, biotic recycling (i.e.,decomposition), and direct and indirect effects of surface and groundwater drainage (Reddy and Patrick 1984). Water movement in most upland systems is dominated primarily by leaching and evapotranspiration processes. Minerotrophic wetlands on the other hand, may be dominated by saturated flow conditions for a significant portion of the year, and hence are subject to a number of associated processes enhancing transport to plant root systems.

Foremost, hydrologic inputs of nutrients may be directly increased in systems in contact with hydrologic flows. Surface and subsurface waters can contain nutrients both in dissolved and particulate form. Contact with these waters results in nutrients being transported directly to wetlands (Ingram 1967, Verhoeven 1986, Verry and Timmons 1982). For example, high soil P (and plant productivity) was related to sedimentation from surface flow in a *Carex* wetland (Auclair et al. 1976). Vitt (1990), however, cautions that nutrient concentrations in subsurface flows may not adequately reflect total hydrologic inputs because flows generally differ among wetlands. It is the total flux of nutrients passing by the rooting zone of a plant that defines supply rate.

Additionally, a number of indirect effects influencing nutrient availability result from soil saturation. Flooding can alter the availability of nutrients due to changes in soil chemistry (Ponnamperuma 1972). In particular, sediment reduction is known to increase the availability of P (Patrick and Khalid 1974, Reddy and Patrick 1984) via a number of linked processes. Soil reduction results in an increase in soluble Fe in solution and a rise in solution pH (Faulkner and Richardson 1989). With the reduction of Fe, adsorbed and chemically bonded P is also released into solution. As a result of the increase in pH, P is also made more available by hydrolysis of Fe and Al phosphates and by the release of P held by anion exchange. The soil in the sedge meadows had more inorganic P than the grass meadows (Table 3), suggesting that sediment reduction may have played a role in the greater P availabilities measured in the sedge meadows.

Soil saturation may facilitate transport of ions by the reduction of air spaces. Because nutrient uptake processes in plants are generally diffusion limited (Ingram 1967, Chapin 1991a), with diffusion enhanced in saturated soils, movement of water in and of itself would increase the availability of ions already present in the soil. Verhoeven et al. (1988a) pointed to the importance of water flux rates in maintaining higher supplies of

N and P at more productive sites, although concentrations of N and P in ditch water were the same along the productivity gradient. In general, the rate of hydrologic flow appears to increase the degree of minerotrophy (Tallis 1983).

Within a species, leaf or foliar concentrations of nutrients often correlate to availabilities. A preliminary conclusion to be made from comparing tissue concentrations between grass and sedge communities is that more N is available in the grass communities, in direct contrast to the results from the resin estimates. However, species vary in their nutrient requirements and uptake patterns (Chapin 1980). If communities change along a resource gradient, tissues concentrations may not reflect availabilities. Where plant species remain the same, the comparison is valid. However, the total mass of a nutrient in community biomass may be a better indicator of availability. In this case, the masses of N in plant biomass were equal between the two communities. There was a trend for a lower mass of plant P in the grass communites than in the sedge communities. Vermeer (1986b) found the total amount of P stored in plants tended to be lower with low water tables, suggesting lower P availability with a drop in the water table.

In summary, it is the degree and nature of the hydrologic contact that regulates the level of influence of hydrology on nutrient availability. In the more productive, wetter-sedge meadows, where surface horizons were in greater contact with groundwater, N and P availabilities were greater than in the drier grass meadows.

Annual N mineralization vs. seasonal and annual uptake of N

Further evidence to support the importance of hydrologic sources of N comes from the estimates of whether net N mineralization provides enough N to meet annual plant requirements for N. My calculations (Table 7) suggest that N mineralization was insufficient to meet even the most conservative estimate of plant community requirements for N. I based the comparison on annual rates of N uptake and N mineralization. However, the majority of uptake of N in similar graminoid ecosystems has been shown to occur in spring (Auclair 1982, Bernard and Hankinson 1979, Bowden 1987, Mitchell 1987). If mineralization is to provide required N, it needs to be made available during the spring when peak uptake is thought to occur. The seasonal pattern of N mineralization at the VNP meadows shows that maximum N mineralization takes place in summer and fall (Fig. 3), further pointing to the inadequacy of N mineralization in providing the N necessary for sustained ecosystem fertility at the production rate indicated.

Limitations to production in beaver meadows

Because productivity in the five beaver meadows at VNP correlates to gradients of N and P availability, but not to measured depths to the water table, a N and/or P limitation of production in the meadows is suggested. The relative role of N or P limitation along the productivity gradient can be examined by viewing the N:P ratios in the available pool and in plant biomass. The plant biomass N:P ratio was significantly lower in the sedge communities (Table 4). While the available N:P ratio was not significantly different between grass and sedge communities (Table 2), there was a trend for the ratios in the two sedge meadows to be lower than in two of the grass meadows (G2, G3) ($p = 0.104$). These results indicate that, in the sedge systems, P tends to be relatively more available than N and that plants are taking up more P relative to N. Collectively, these data suggest that P may be relatively more limiting to production than N in the drier grass meadows. Experiments manipulating N and P availability are needed to test these hypotheses regarding N and P limitation in the meadows.

Although the measure of hydrology used in this study, the mean depth to the water table during the growing season, was poorly correlated to the ecosystem properties of productivity and availability of nutrients, clearly hydrology is important in maintaining floristic differences among the communities and presumably has a significant influence on other ecosystem properties. Perhaps a more "ecologically relevant" measure of hydrology might be depth to the water table in the spring; seed germination, plant growth and nutrient uptake are greatest during this season. Keddy (1990) describes how reduced spring flooding leads to a succession from *Carex*-dominated meadows to *Calamagrostis*-dominated meadows within about seven years time. Likewise, reduced spring flooding in *Calamagrostis* meadows changes the meadows into a low shrub community within ten years and prolonged flooding of *Calamagrostis* meadows may result in transitions to sedge meadows in one to two years time (Keddy 1990). Clearly, flooding by beaver is crucial for the maintenance of the characteristic hydrologic regime that regulates plant community composition and ecosystem processes in these systems.

2.6 CONCLUSIONS

Primary production was greater in the wetter sedge-dominated communities than in the drier grass-dominated communities. Although the sedge communities had shallower mean depths to the water table, water table depths were not highly correlated to production or to availabilities of N and P. Production paralleled the gradients of N and P availability, but not to N mineralization. Moreover, N mineralization was insufficient to meet the requirements of plant community, suggesting that external sources of nutrients and/or effects of soil saturation which may increase nutrient availability are important mechanisms supporting the fertility of the beaver meadows.

These results support hypothesis **H1(A)** which states that production is lower in the drier grass-dominated communities. Because production correlates to available N and P, hypothesis **H1(B)** was developed to explain the lower production in the grass meadows as a consequence of lower N and P availability. Hypotheses **H2** and **H2** (Alternative) address the relative role of P limitation between the two types of meadows. Although an experimental approach is the best test of this hypothesis, the observational evidence gathered does not support the mechanism behind hypothesis **H2**. **H2** states that the sedge meadows are more P limited due to greater amount of soil organic P in the sedge meadows; this was not found so **H2** is rejected. The two sedge meadows do exhibit higher absolute and relative P availability than the three grass meadows, as well as more soil inorganic P, a possible source of the available P. Thus hypothesis **H2** (Alternative), which states that the sedge meadows are relatively less P limited than the grass meadows, is accepted.

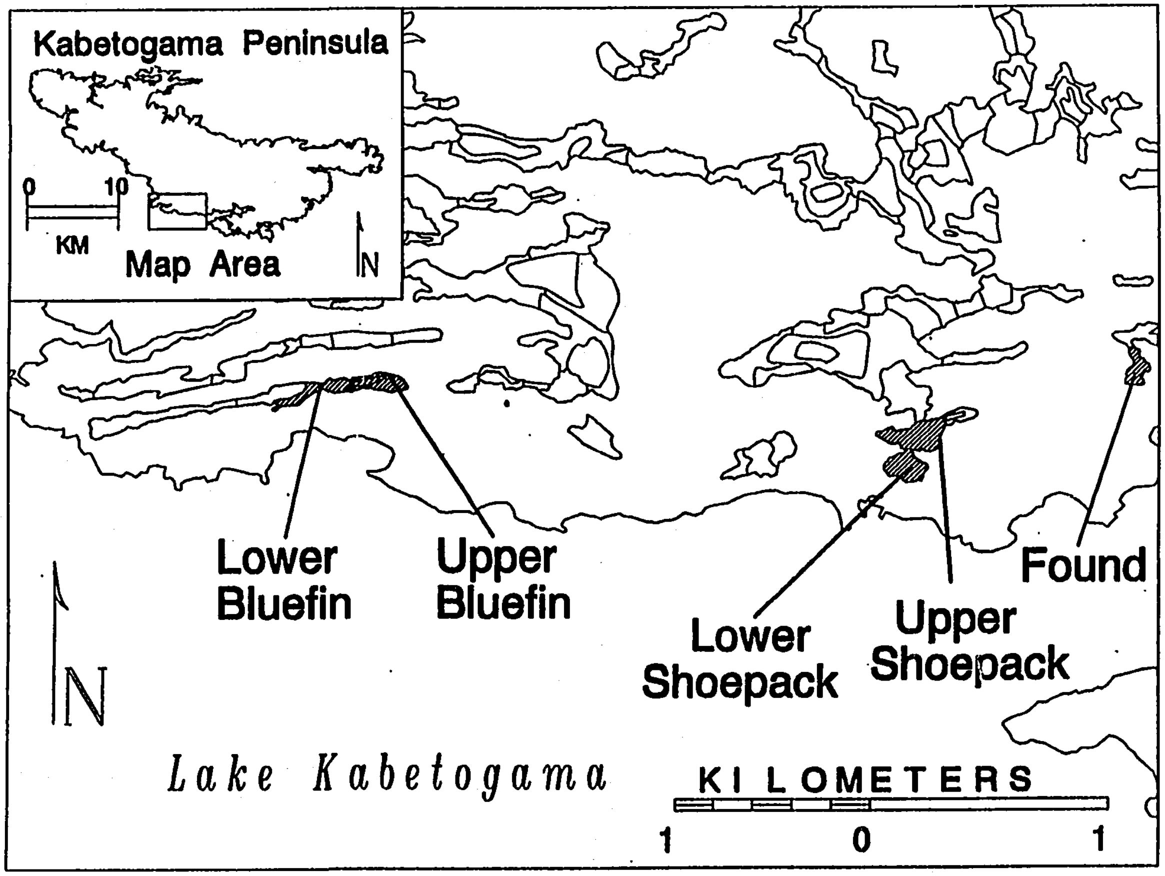
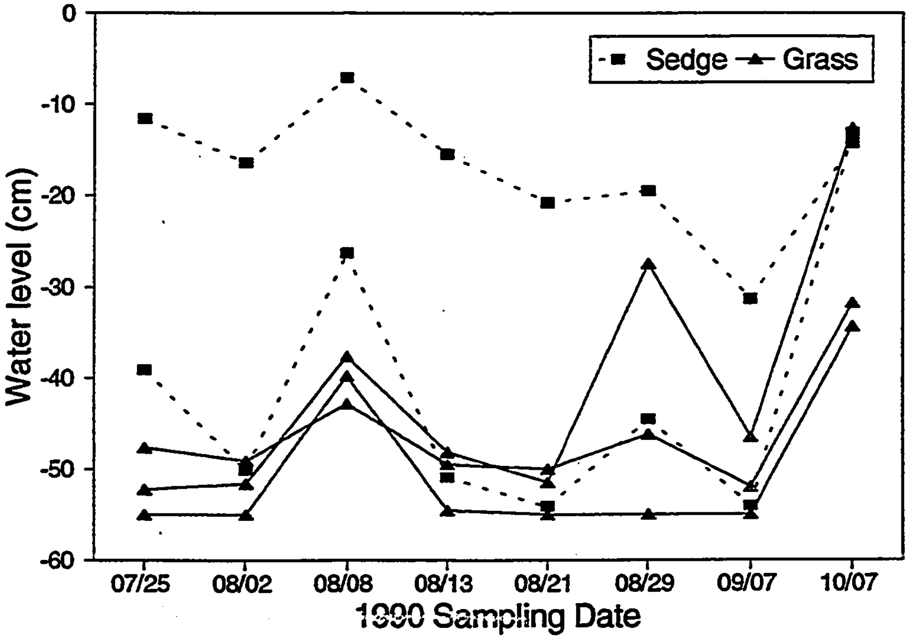


Figure 1. Location of the five study meadows (two sedge-dominated (S) and three grass-dominated (G)) on the Kabetogama Peninsula in Voyageurs National Park, MN. Lower Bluefin = S1, Lower Shoepack = S2, Upper Bluefin = G1, Upper Shoepack = G2, Found = G3.



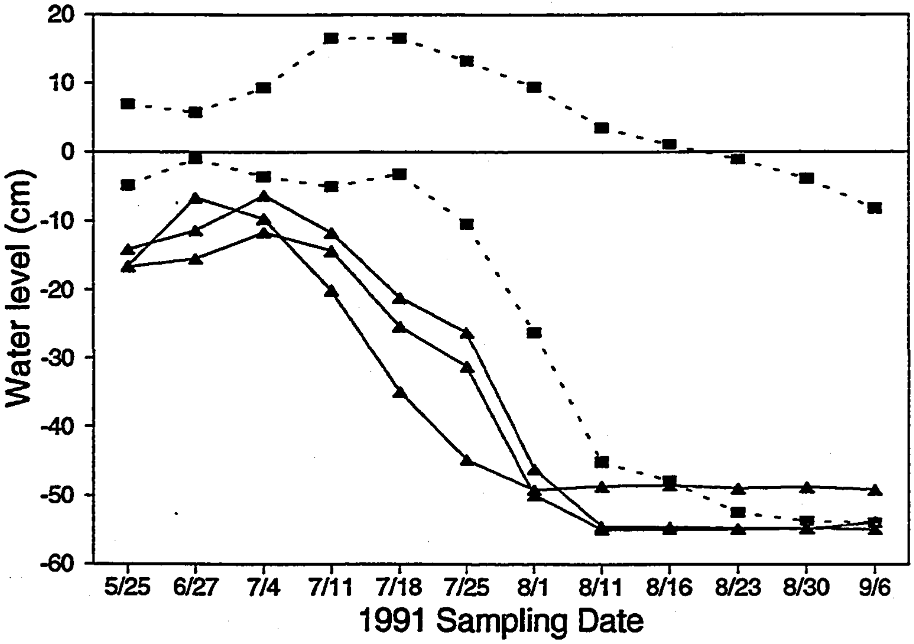


Figure 2. Seasonal water table depths in sedge and grass meadows for 1990 and 1991. Values for each sampling date are means of 14 plots per meadow.

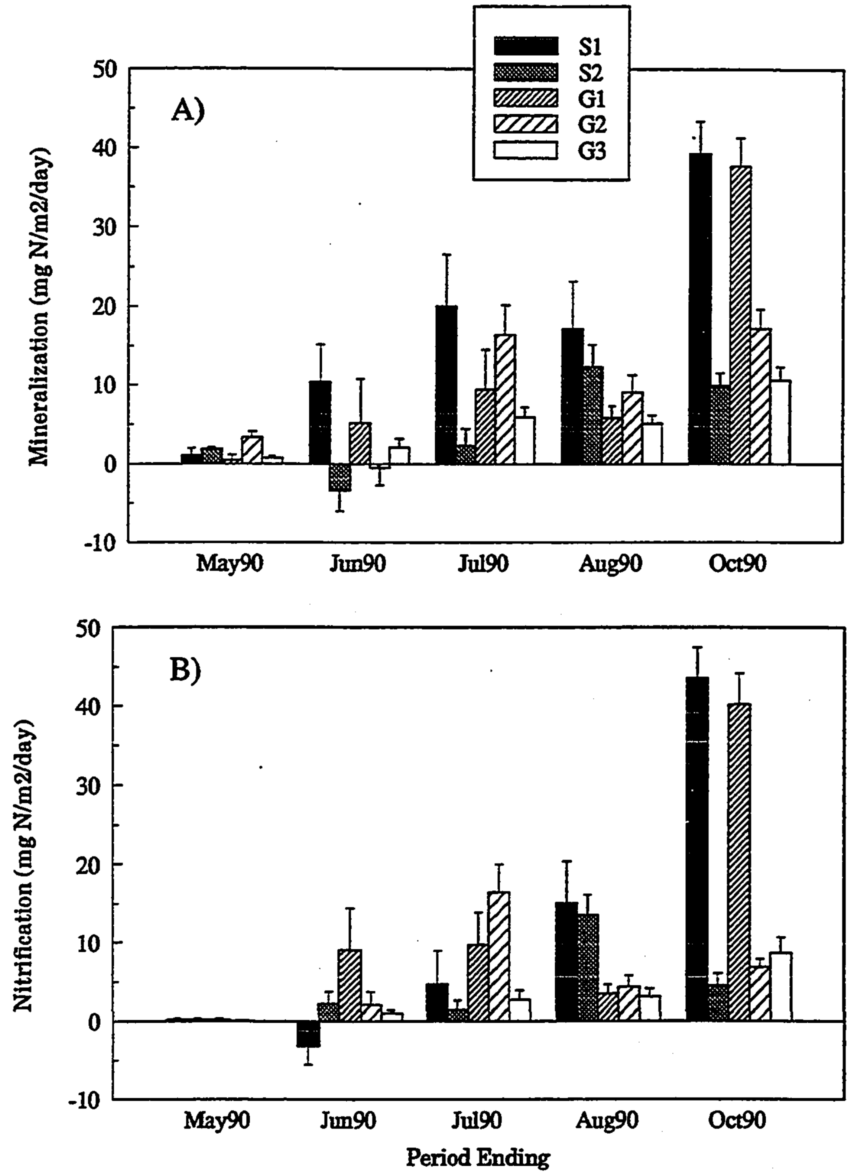


Figure 3. Rates of net N mineralization (A) and net nitrification (B) for the sedge and grass meadows over five different incubation periods. Period ending 'May90' covers October 7 1989 -May 6 1990; period ending 'Jun90' covers May 6 - June 25 1990; period ending 'Jul90' covers June 25 - July 25 1990; period ending 'Aug90' covers July 25 - August 21 1990; period ending 'Oct90' covers August 21 - October 7, 1990. Values are means of 14 plus standard errors.

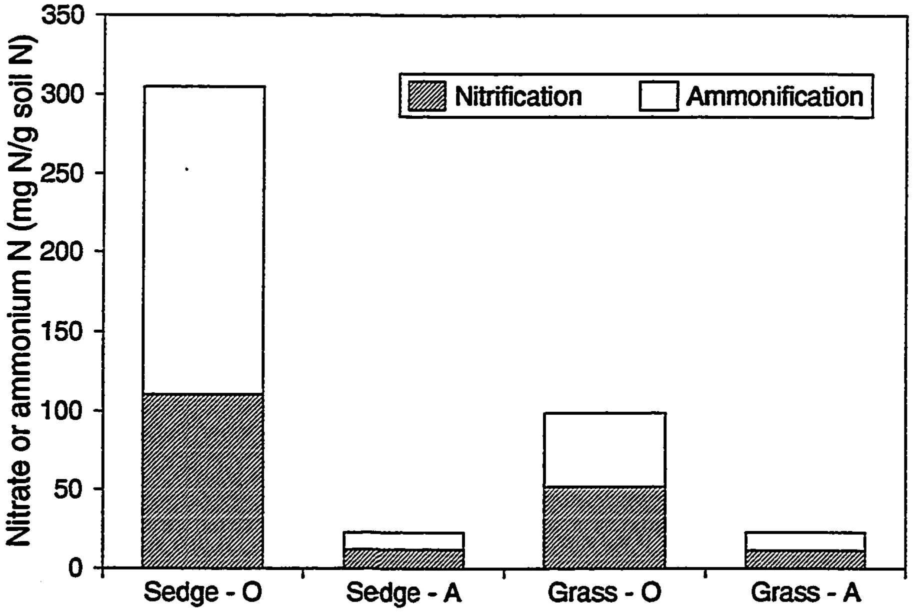


Figure 4. O vs. A horizon ammonification and nitrification for a thirty day period in a sedge (S1) and a grass (G2) meadow. "Sedge - O" = sedge meadow, O horizon; "Sedge - A" = sedge meadow, A horizon, etc. Values are means of eight replicate samples.

Table 1. Mean percent cover in 1990 of the five most frequently occurring plant species in grass and sedge-dominated beaver meadows. Relative frequency in grass meadows is percent occurrence out of 42 plots, relative frequency in sedge meadows is percent occurrence in 28 plots.

Grass-dominated meadows

Species	**Relative Frequency**	**Mean Cover***
Calamagrostis canadensis	100%	89.1%
Carex (lacustris)	85.7%	7.2%
Scirpus cyperinus	76.2%	5.3%
Carex ovales group	71.4%	1.6%
Cirsium arvense	57.2%	3.0%

Sedge-dominated meadows

Species	**Relative Frequency**	**Mean Cover***
Scirpus cyperinus	100%	59.8%
Calamagrostis canadensis	85.7%	29.2%
Lysimachia thyrsiflora	71.4%	2.6%
Carex (lacustris)	64.3%	13.2%
Carex ovales group	57.1%	9.5%

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* Mean covers are calculated by averaging non-zero abundances of a given species.

Table 2 (A). Above-ground biomass production, depth to the water table, and estimates of available nitrogen and phosphorus for sedge and grass meadows. Data are means (plus one standard error), except for water depths where medians are used. N = 14, except for resin N:P ratios where n = 12, 13, and 10 for S2, G2 and G3, respectively.

		SEDGE MEADOWS		GRASS MEADOWS		
PROPERTY	Units	S1	S2	G1	G2	G3
1989 Production	$g/m^2/y$	420 (26)	515 (44)	411 (37)	410 (31)	400 (28)
1990 Water Table Height	cm	-17.4	-42.2	-50.4	-51.8	-42.6
1991 Water Table Height	cm	5.6	-27.1	-37.2	-40.3	-33.7
1990 Water Table Fluctuation	na*	2.21	4.56	2.19	2.48	4.74
1991 Water Table Fluctuation	na*	0.86	2.73	2.51	3.55	2.99
Resin Available NO3-N	mg N/g resin	0.30 (0.06)	0.13 (0.03)	0.12 (0.07)	0.04 (0.01)	0.03 (0.01)
Resin Available NH4-N	mg N/g resin	0.23 (0.04)	0.23 (0.04)	0.17 (0.03)	0.10 (0.01)	0.15 (0.03)
Resin Available NO3-N plus NH4-N	mg N/g resin	0.53 (0.08)	0.36 (0.06)	0.29 (0.08)	0.15 (0.02)	0.19 (0.03)
Resin Available PO4-P	mg P/g resin	0.032 (0.005)	0.017 (0.005)	0.014 (0.002)	0.007 (0.001)	0.006 (0.002)
Resin N:P Ratio	na*	20.5 (4.0)	25.6 (6.0)	23.7 (4.8)	32.9 (7.1)	34.4 (8.4)

* Not applicable

Table 2 (B). Results of ANOVA (or MANOVA for water table depth) testing the two hypotheses: 1) no difference among the meadows, and 2) no difference between grass and sedge meadows for variables in 2(A). Units are the same as on Table 2 (A).

PROPERTY	1) One-way ANOVA *		2) Contrast (Grass vs. Sedge)	
	$F_{4,65}$	Probability	$F_{1,65}$	Probability
1989 Production	1.99	0.107	3.83	0.055
1990 Water Table Height *	11.21	0.0001	17.10	0.0001
1991 Water Table Height *	14.83	0.0001	44.04	0.0001
1990 Water Table Fluctuation	19.22	0.0001	0.86	0.357
1991 Water Table Fluctuation	13.22	0.0001	23.62	0.0001
Resin Available NO3-N	5.45	0.0008	13.00	0.0006
Resin Available NH4-N	2.85	0.0304	8.87	0.0041
Resin Available NO3-N plus NH4-N	6.41	0.0002	18.8	0.0001
Resin Available PO4-P	8.85	0.0001	23.39	0.0001
Resin N:P Ratio **	0.97	0.4289	1.76	0.1899

* MANOVA used to analyze ranked water table height data. Statistic is an F approximation associated with the Wilks' lambda statistic, with 32, 215 degrees of freedom (df's) for 1990 site effects and 8, 58 df's for 1990 contrast, and 48, 210 df's for 1991 site effects and 12, 54 df's for 1991 contrast.

** F df's = 4, 58 for effect of site and 1, 58 for contrast.

Table 3 (A). Soil properties for sedge and grass meadows at VNP. Data are means plus one standard error. N = 14 except for depth of the organic horizon at G3 and G2 where n = 8 and n = 9, respectively.

		SEDGE MEADOWS		GRASS MEADOWS		
PROPERTY	Units	S1	S2	G1	G2	G3
Loss on Ignition	%	54 (3)	45 (3)	48 (4)	38 (3)	28 (2)
Depth of the Organic horizon	cm	6.2 (0.7)	4.5 (0.7)	5.8 (0.6)	3.4 (0.5)	2.6 (0.5)
Soil C	g/m^2	3377 (204)	2273 (153)	2852 (199)	1848 (108)	898 (50)
Soil N	g/m^2	227 (9)	165 (0.7)	172 (10)	116 (4)	59 (3)
Soil C:N Ratio	na	16.6 (0.4)	13.7 (0.5)	16.4 (0.5)	15.8 (0.4)	15.2 (0.6)
Soil P	g/m^2	17.8 (1.4)	17.9 (1.3)	16.9 (1.4)	9.1 (0.9)	9.8 (0.8)
Inorganic P	mg/g	0.13 (0.01)	0.13 (0.01)	0.07 (0.01)	0.12 (0.01)	0.11 (0.01)
Organic P	mg/g	1.1 (0.1)	1.6 (0.1)	1.3 (0.1)	0.9 (0.1)	1.6 (0.1)
Soil pH (Organic horizon)	pH	6.01 (0.05)	6.06 (0.10)	6.30 (0.08)	5.98 (0.11)	5.66 (0.09)

Table 3 (B). ANOVA results testing the following two hypotheses: 1) no difference among the meadow means, and 2) no difference between grass and sedge meadows for variables in 3 (A). Units are the same as on Table 3 (A).

PROPERTY	1) One-way ANOVA		2) Contrast (Grass vs. Sedge)	
	$F_{4,65}$	Probability	$F_{1,65}$	Probability
Loss on Ignition	9.91	0.0001	16.10	0.0002
Depth of the Organic horizon *	4.35	0.0040	4.86	0.0318
Soil C	48.78	0.0001	67.59	0.0001
Soil N	69.98	0.0001	134.85	0.0001
Soil C:N Ratio	6.00	0.0004	2.19	0.1434
Soil P	13.50	0.0001	28.55	0.0001
Inorganic P	4.87	0.0017	9.83	0.0026
Organic P	5.35	0.0009	0.65	0.4244
Soil pH (Organic horizon)	6.37	0.0002	0.45	0.5046

* F df's = 4,54 for effect of site and 1,54 for contrast

Table 4 (A). Concentrations and amounts of N and P in above-ground biomass in grass and sedge meadows. Data are means and plus standard error. N = 2 for percent measurements, n = 14 for mass measurements.

BIOMASS PROPERTY		SEDGE MEADOWS		GRASS MEADOWS		
	Units	S1	S2	G1	G2	G3
Percent N	%	1.09 (0.155)	1.18 (0.180)	1.48 (0.050)	1.50 (0.005)	1.30 (0.065)
Percent P	%	0.13 (0)	0.12 (0.030)	0.12 (0.001)	0.12 (0.015)	0.10 (0.005)
Biomass N:P ratio	na	8.4 (1.2)	10.1 (1.0)	12.9 (0.1)	12.1 (1.4)	12.3 (0.03)
Biomass N	g/m^2	4.59 (0.28)	6.08 (0.51)	6.08 (0.55)	6.13 (0.47)	5.18 (0.36)
Biomass P	g/m^2	0.54 (0.03)	0.62 (0.05)	0.47 (0.04)	0.51 (0.04)	0.42 (0.03)

Table 4 (B). ANOVA results testing the two hypotheses: 1) no difference among the meadow means, and 2) no difference between grass and sedge meadows for biomass variables in 4 (A). Units are the same as on Table 4 (A).

BIOMASS PROPERTY	1) One-way ANOVA		2) Contrast (Grass vs. Sedge)	
	$F_{4,9}$	Probability	$F_{1,9}$	Probability
Percent N	2.50	0.171	7.76	0.039
Percent P	0.39	0.806	0.51	0.507
Biomass N:P	3.87	0.085	13.6	0.014
Mass Biomass N *	2.45	0.055	1.29	0.260
Mass Biomass P *	3.49	0.012	9.57	0.003

* F df's for effect of site = 4,65, and for contrast = 1,65.

Table 5 (A). Annual *in-situ* N mineralization rates for sedge and grass meadows at VNP. Data are means (n=14) plus one standard error.

		SEDGE MEADOWS		GRASS MEADOWS		
MINERALIZATION PROPERTY	Units	S1	S2	G1	G2	G3
Net N mineralization	g $N/m^2/y$	3.7 (0.6)	1.1 (0.2)	2.6 (0.4)	2.2 (0.2)	1.1 (0.1)
Net nitrification	g $N/m^2/y$	2.5 (0.4)	0.8 (0.2)	2.8 (0.4)	1.0 (0.2)	0.6 (0.1)
Nitrification:Mineralization Ratio	na	0.87 (0.20)	0.72 (0.19)	1.2 (0.12)	0.45 (0.06)	0.55 (0.08)
Net N mineralization	ug N/g N/y	15.1 (2.3)	7.0 (1.6)	13.5 (1.7)	15.8 (1.4)	16.9 (2.2)

Table 5 (B). ANOVA results testing the two hypotheses: 1) no difference among the meadow means, and 2) no difference between grass and sedge meadows for variables in 5 (A). Units are the same as on Table 5 (A).

	1) One-way ANOVA		2) Contrast (Grass vs. Sedge)	
MINERALIZATION PROPERTY	$F_{4,65}$	Probability	$F_{1,65}$	Probability
Net N mineralization	10.45	0.0001	1.78	0.187
Net nitrification	12.42	0.0001	0.33	0.5672
Nitrification:Mineralization Ratio	3.84	0.0073	0.27	0.6043
Net N mineralization	4.43	0.0032	6.47	0.0133

Table 6. Spearman rank correlations between daily N mineralization rates and initial sample moisture contents for each meadow over all incubation periods (n = 70 for each meadow: 5 periods x 14 plots).

Meadow	Spearman's r	Probability
S1	-0.095	0.436
S2	-0.533	<0.001
G1	-0.470	<0.001
G2	-0.256	0.032
G3	-0.327	0.006

Table 7. Comparison of annual N mineralization (g/m^2) with annual uptake of N (g/m^2) based on estimates of N mineralization in the A horizon* and belowground uptake of N**.

Meadow	O Horizon Mineralization	O + A Horizon Mineralization	Above-ground Mass of N ***	Total Mass of N (Low Estimate)	Total Mass of N (High Estimate)
S1	3.7	5.4	4.6	5.8	20.0
S2	1.1	1.6	6.1	7.6	28.0
G1	2.6	3.8	6.1	7.6	28.0
G2	2.2	3.2	6.1	7.6	28.0
G3	1.1	1.6	5.2	6.5	22.6

* O + A horizon mineralization was calculated by multiplying the average annual meadow O horizon N min by 1.47.

** Belowground estimates of N uptake assumed a 1% N concentration in roots, and belowground biomass estimates of 25% of above-ground biomass for the low estimate and 335% of above-ground for the high estimate.

*** From Table 4 (A).

Chapter 3: Nitrogen and phosphorus limitation of above-ground primary production in five wetland meadows

3.1 INTRODUCTION

Differences in supply rates of limiting resources to plant communities have a number of consequences to plant production, nutrient uptake and ultimately plant community composition (Tilman 1982). Within a community or vegetation type, lower nutrient availability poses a potentially greater nutrient limitation to production (Chapin et al. 1986). Response to nutrient additions is a metric commonly used to assess nutrient limitation. Within similar communities, a gradient of response suggests a corresponding gradient in the degree of nutrient limitation reflecting differences in resource supply rates. However, plant communities on infertile sites may not always respond to nutrient additions (Chapin et al. 1986), in part because species in nutrient poor systems may be less responsive to nutrient additions.

Simple gradients in resource supply rates may be rare in nature. Resources frequently co-vary forming more complex gradients. For example, in a central Wisconsin forest, N availability and soil water holding capacity were highly correlated and related to soil texture (Pastor et al. 1984). Many plants require resources (e.g., nutrients) in specific proportions for optimum growth (Ingestad 1979, Tilman 1982). A shift in the relative availabilities of limiting nutrients may cause a shift in whether one nutrient or another limits production, suggesting a single nutrient limitation. Correspondingly, if available nutrients occur in proportions that match what is required for optimum growth, yet are in short supply, two or more may be equally limiting, suggesting multiple nutrient limitation.

In the previous chapter, a number of important relationships were established regarding soil resource (N and P) and productivity gradients in the five beaver meadows at Voyageurs National Park (VNP). These include: 1) a positive and significant correlation between above-ground biomass and nutrient (N and P) availability as determined by ion exchange resins, 2) greater production and greater N and P availability in the two sedge-dominated meadows (S1, S2) compared to the three grass-dominated meadows (G1, G2, G3), 3) water table closer to the soil surface in the sedge meadows, and 4) lower ratios of (resin) available N:P and plant community biomass N:P in the sedge meadows. The first three relationships led to the hypothesis that above-ground production was more nutrient-limited in the drier grass meadows than in the wetter sedge meadows. The fourth relationship led to the hypothesis that the grass meadows are proportionately more P limited than the sedge meadows. To take advantage of the experimental approach used to test the two hypotheses, I also developed a third hypotheses attempting to contrast responses characteristic of single versus multiple nutrient limitation.

The main objective of this chapter is to test the three nutrient limitation hypotheses by experimentally increasing nutrient (N and P) availabilities in a field fertilization experiment conducted in each of the five beaver meadows at VNP. Despite potential drawbacks of adding nutrients to natural communities to examine nutrient limitations (c.f., Chapin et al. 1986), manipulating resources thought to limit production is an important step towards understanding controls on production in complex natural systems.

Specifically, the following hypotheses are tested:

> **H1**: Above-ground productivity is lower in the grass meadows because production is more nutrient limited in the grass meadows;
>
> **H2**: The wet-sedge meadows are proportionately less P limited than the grass meadows due to greater relative P availability in the wet-sedge meadows; and,
>
> **H3**: Where adequate (i.e., balanced) nutrition exists, productivity increases will be stronger in response to a given external ratio of N and P than to absolute amounts of N and P.

3.2 METHODS

Study sites

The experiments were conducted on the 70 research plots established within the five meadows at VNP, as described in Chapter 2. Because the experiment was based on a control-treatment approach (see below), I needed to assess whether pre-manipulation biomass differences existed among the fourteen plots within a meadow. A one-way ANOVA on 1989 clip plot biomass confirmed there were no differences among plot biomasses within a given meadow ($p > 0.05$).

Nutrient addition experiment

To test for the effect of nutrient ratios and concentrations on production, a design was necessary that varied both ratios and concentrations of N and P. Three mass ratios of N to P (1:1, 3:1, 9:1) were defined, with a "high" level of each ratio that was 3X a lower level. Although this design may appear like a standard factorial, it is not a factorial due to concentrations of N and P being imperfectly crossed. A factorial would have yielded N:P ratios less than unity, which was not desirable because plant nutrition studies have shown that N is required in greater amounts than P. The design yielded six fertilizer treatments and one control for a total of seven treatments (Table 8).

Table 8. Treatment levels of N and P ($g/m^2/y$) used in the nutrient addition experiment. Treatments are grouped by ratio, with the low level of a given ratio listed first.

Treatment	N	P	N:P
T2	3	3	1:1
T5	9	9	1:1
T4	9	3	3:1
T1	27	9	3:1
T3	9	1	9:1
T6	27	3	9:1
T7	0	0	0

Each treatment was assigned to two plots in each of the five meadows, for a total of 70 experimental plots (7 treatments x 2 replicates x 5 meadows). To ensure maximum dispersion of treatments (Krebs 1989), two blocks of seven plots within each meadow were defined based on similarity of vegetative cover. Each of the treatments was then randomly allocated to the seven plots within a block.

N was applied as NH_4Cl. Half of the P was applied as NaH_2PO_4 and half as Na_2HPO_4, to maintain pH's of the fertilizer solutions similar to surface horizons. Fertilizer was dissolved in pond water and applied with a backpack sprayer. The amount of water added to each plot per treatment time was 1 mm. Control plots were left untreated. Pond water and dissolved fertilizer samples were analyzed for nitrate, ammonium and phosphate. In all cases, water from the ponds contributed less than 1×10^{-5} g element (N or P) per m^2 to the plots.

One ninth of the annual addition was applied to the plots at the end of the 1990 growing season. The remaining eight ninths were split into two applications and applied in early May and June of 1991, to distribute the pulse of availability over the period of peak uptake.

Biomass measurements

Above-ground primary production was measured as above-ground biomass harvested at the end of the 1991 growing season. Three 30 x 60 cm subplots were systematically located within the 8.5 m^2 plots and clipped of all above-ground vegetation in late August of 1991. Live vegetation was sorted to species, transported from the meadows in paper bags and dried under 100 W light bulbs until samples "felt-dry" and could be stored. Any dead vegetation was removed at the time of cutting. Samples were oven dried at 70°C for 24 h prior to final weighing.

Tissue chemical analyses and uptake calculations

A mixed-species composite sample was made to assess treatment effects on N and P concentrations in 1991 community biomass. Species contributing to a cumulative weight of at least 95% of plot biomass were ground separately in a Wiley mill (20 mesh screen) then subsampled proportionately by weight for the composite community sample. Samples were digested in $LiSO_4$ for analyses of total N and P colorimetrically with a Technicon Autoanalyzer II. Biomass N and P contents (g element/m^2) were calculated by multiplying concentration (g element/g biomass) by 1991 biomass (g/m^2), and were assumed to equal above-ground uptake of N and P.

Statistical analyses and hypothesis testing

Within each meadow, the mean biomass calculated from the two control plots was subtracted from the biomass of each plot. This "change in biomass from the control" was used as the response variable in statistical analyses. The effects of community type (grass or sedge), treatment (T1 - T7) and community/treatment interaction on change in biomass were first tested using a fixed-effects ANOVA model. Then, because the biomass response was only significant within grass communities (see below), the effects of individual meadow (or site), treatment and site/treatment interactions were tested using a fixed effects, two-way ANOVA model within the grass communities. If the interaction was non-significant ($p > 0.10$), it was removed and a new one-way model assessing the effects of treatment (blocked by site) was run. Type III sums of squares were used for unequal sample sizes, otherwise type I sums of squares were used. Within the grass meadows, a fractional factorial analysis, used for designs with main effects that are imperfectly crossed (Cochran and Cox 1992), was employed to assess overall effects of N and P on production differences. However more than just the overall effects are of interest. For example, interactions may also be important and their identification could give insights into the existence of N or P limitation at various levels of nutrient availability. Linear or orthogonal contrasts (Sokal and Rohlf 1981) were therefore used to test specific hypotheses regarding effects of added N and P and varying ratios and levels of ratios (see next paragraph). Statistical tests of tissue nutrient responses followed the same protocol.

The design of the fertilization experiment enabled a number of orthogonal contrasts to be used to test specific hypotheses regarding levels of N and P and ratio effects on production. The following are the hypotheses and their tests (u's refer to treatment means as indicated in Table 8):

1) Do fertilizer treatment means differ from the control treatment?

C1: Control vs. others H_o: $u_1, u_2, u_3, u_4, u_5, u_6 = u_7$

2) Four of the treatments (T1, T4, T5, T6) represent a balanced 2 x 2 factorial of N x P, with N at 9 and 27 $g/m^2/y$, and P at 3 and 9 $g/m^2/y$ (Table 8). Interactions and main effects are tested as:

C2: Main effect of N H_o: $u_6 + u_1 = u_4 + u_5$

C3: Main effect of P H_o: $u_6 + u_4 = u_1 + u_5$

C4: Interaction effect H_o: $u_6 - u_4 = u_1 - u_5$

3) Another four treatments (T1, T3, T4, T6) represent a balanced factorial of two ratios (9:1 and 3:1) with a low and high of each ratio. The test of the low and high level of each ratio is essentially a test of varying amounts of N and P simultaneously.

C5: Main effect of ratio H_o: $u_4 + u_1 = u_3 + u_6$

C6: Main effect of ratio level H_o: $u_4 + u_3 = u_1 + u_6$

C7: Interaction effect H_o: $u_4 - u_3 = u_1 - u_6$

The fractional factorial analyses were performed using SYSTAT (Wilkinson 1989) for the PC. All other analyses were conducted with PC SAS statistical programs (SAS Institute 1988).

3.3 RESULTS

Overall biomass response

Mean above-ground biomass for the seven treatments within each meadow is listed on Table 9. After one year of experimental nutrient additions, the mean biomass over all treatments increased (relative to controls) by 92.9, 47.9, and 29.1% respectively for G3, G1, and G2 (the three grass meadows) and by 13.3 and 15.4% respectively for S2 and S1 (the two sedge meadows). Across all grass and sedge plots, biomass was significantly affected by community type and treatment; the community/treatment interaction was not significant (Table 10). Yet within the sedge plots, the biomass response was not significant (Overall $F_{13,14} = 0.35$, $p = 0.967$, Fig. 5), while changes within grass plots were significant (Overall $F_{20,21} = 3.26$, $p = 0.005$, Fig. 5) and revealed both highly significant treatment ($F_{6,21} = 7.30$, $p = < 0.001$) and individual meadow ($F_{3,21} = 4.85$, $p = 0.019$) effects.

Biomass response within grass communities (G1, G3, G2)

The pattern of biomass response to N and P additions differed among the three grass meadows. At G1, while overall biomass increase relative to the controls approached 50%, high among-treatment variation influenced the significance of the response and there was only a tendency for biomass to be increased by N, as revealed by fractional factorial analysis ($T = 1.66$, $p = 0.125$, Fig. 6). At G1, a one-way ANOVA of effect of treatment on biomass was non-significant ($F_{6,7} = 0.95$, $p = 0.516$). There was a trend however, ($p = 0.080$) for the control and T2, the treatment with the lowest amounts of N and P, to be different from the other treatments.

At G3, the site showing the greatest response, the fractional factorial analysis revealed an overall effect of N on change in biomass ($T = 2.52$, $p = 0.029$, Fig. 6). The one-way ANOVA of effect of treatment on change in biomass was significant at G3 ($F_{6,7} = 6.91$, $p = 0.011$). At G3, treated plots differed from the control (C1, Table 11). The main effect of N was significant (C2, Table 11), and the interaction between N and P was significant (C4, Table 11); when the highest level of N (27 $g/m^2/y$) was added, adding P also had a positive effect on biomass. There were no effects due to ratios or levels of ratios (C5 and C6, Table 11).

At G2, where the response was lowest among the grass meadows, the fractional factorial revealed an overall effect of P on change in biomass ($T = 2.32$, $p = 0.040$, Fig. 3). The one-way ANOVA of effect of treatment on change in biomass was significant ($F_{6,7} = 3.86$, $p = 0.050$). At G2, there was a trend for the control to differ from the other treatments (C1, Table 11). When T2 was included with the control and tested against the remaining treatments, a stronger significance was demonstrated ($F_{1,7} = 16.07$, $p = 0.005$). There was an effect of P at high levels of N (C3, Table 11). T2 and T4 differed ($p = 0.039$), indicating that when P was at a low level (3 $g/m^2/y$), the effect of adding N was significant. There was a trend for a ratio effect at G2 (C5, Table 11).

Response of nutrient uptake

Across all grass and sedge plots combined, there were significant community and treatment effects on concentrations of N and P and total mass of N and P in plant biomass (Table 12). The community/treatment interactions were not significant (Table 12). To examine in more detail specific responses of plant N and P chemistry in sedge and grass communities, it was necessary to perform separate ANOVA's for each type of community.

Percent N in plant biomass was affected by individual meadow (or site) and treatments in grass plots, but only by treatment in sedge plots (Fig. 7, Table 12). Significant contrasts for specific treatment effects on percent N were the same for grass and sedge communities and include: C1: control vs. others, C2: main effect of N, and C6: effect of ratio level (Table 13). Mass of N (or N content) was affected by treatment in grass plots, but not in sedge plots (Fig. 7, Table 12). For grass plots, significant contrasts on mass of plant N were the same as for percent N (i.e., C1, C2 and C6) (Table 14). None of the sedge plot contrasts on mass of N was significant.

Across all plots, percent P and mass of plant P were affected by meadow and treatment, as well as by meadow and treatment within grass and sedge communities (Fig. 8, Table 12). Only for percent plant P within the grass communities, was there a significant meadow/treatment interaction (Table 12), which invalidated combining treatment means for contrasts. For sedge plots, significant contrasts for percent P include C1: control versus others ($F_{1,21} = 30.29$, $p < 0.001$), C3: main effect of P ($F_{1,21} = 9.44$, $p = 0.006$), C5: main effect of ratio ($F_{1,21} = 16.78$, $p < 0.001$), and C6: effect of ratio level ($F_{1,21} = 7.46$, $p = 0.013$). For grass plots on mass of plant P, however, all 7 contrasts were significant (Table 15). For sedge plots, significant contrasts on mass of plant P include

C1, C4: interaction between N and P; at the highest level of N adding P had an effect on mass of P but not the intermediate level of N, and C5 (Table 15).

Grass in sedge, sedge in grass

To test how grass or sedge species responded separately within grass or sedge communities, a two-way ANOVA was used to analyze the effect of treatment on sedge and grass species as groups, blocked by individual meadow (or site). Because of the uneven distribution of grass and sedge species in the plots, especially in communities where one or the other is less dominant, rather than use change in biomass from the control as the response variable in the analyses, plot biomass was used. For grass species within grass meadows, the overall model was significant ($F_{8,33} = 3.52$, $p = 0.005$), with significant site ($F_{2,33} = 5.67$, $p = 0.008$) and treatment effects ($F_{2,33} = 2.80$, $p = 0.026$). For grass species within sedge meadows, there was a trend for overall significance ($F_{7,18} = 2.38$, $p = 0.065$); mainly due to site ($F_{1,18} = 5.07$, $p = 0.037$) rather than treatment ($F_{6,18} = 1.94$, $p = 0.130$). For sedge species within grass meadows, the overall model was not significant ($F_{8,27} = 1.22$, $p = 0.325$), with a non-significant treatment effect ($F_{6,27} = 1.36$, $p = 0.268$). For sedge in sedge meadows, the overall model tended towards significance ($F_{7,20} = 2.36$, $p = 0.061$), but there was no effect of treatment ($F_{6,20} = 0.93$, $p = 0.497$).

3.4 DISCUSSION

Biomass response

Overall, biomass responses to N and P additions were greater in the three grass-dominated meadows compared with the two sedge-dominated meadows, where the responses were lower and non-significant (Fig. 5, Table 10). These experimental results support the first hypothesis (H1), which states that production is more nutrient-limited in the drier grass meadows, where background availabilities of N and P, determined by ion exchange resins, are lower in comparison with the wetter sedge meadows. Because of the positive relationship between meadow moisture conditions and availability of N and P (see Chapter 2), another suggested hypothesis is that the drier meadows are moisture limited. While the moisture limitation hypothesis was not explicitly tested, the experiment establishes a nutrient limitation separate from a water limitation.

However, not all nutrient-limited systems can be detected by their responses to nutrient enhancements. For example, communities in nutrient-poor habitats can be adapted to low nutrient levels and may not respond to nutrient additions (Chapin et al. 1986). In those systems, if the response is somehow phenotypically limited, the "agricultural concept" of nutrient limitation (c.f., Chapin et al. 1986), presupposing an increase in production if nutrient availability increases, is not appropriate. However greater responses to nutrient additions where availabilities are lower have been documented in a number of natural wetland systems. For instance, Aerts et al. (1992) found that responses to N additions were inversely proportional to N availability in *Sphagnum*-dominated bogs of Sweden. Olff and van der Veen (1992) found greater responses to fertilizer application in less productive stages of a grassland succession in the Netherlands, where nutrient supply rates were lower than at the more productive stages. Apparently the "agricultural concept" is appropriate for the beaver meadows and may also be appropriate for other relatively productive natural ecosystems.

N vs. P limitation

Because the sedge meadows did not respond significantly to fertilization, hypothesis **H2**, which predicted that the sedge meadows would be proportionately less P limited than the grass meadows, becomes irrelevant (the assumption behind the hypothesis is that the sedge meadows are nutrient limited). N and P limitation can however, be evaluated within the grass meadows, where responses to N and P fertilization varied among the meadows. At G1 there was trend for a biomass response due to N, a significant biomass response due to P at G2, and a significant biomass response due to N at G3. Within two of the meadows, G2 and G3, there were significant responses to both N and P. At G2, N had a significant effect on production only when P was low (3 $g/m^2/y$) and when N was increased from 3 to 9 $g/m^2/y$. Otherwise, the response was dominated by P availability, indicating that P became limiting when the N limitation was eliminated. At G3, where the overall response was driven by N availability, P became limiting only at the high level of N (27 $g/m^2/y$). Apparently, after N requirements are met at the two grass meadows, P becomes the next limiting nutrient.

H3, which hypothesized a stronger response to either a change in a ratio or increase in a ratio of N:P versus an increase in an amount of N or P, could only be tested in G2 and G3, where effects due to treatment were significant. At G3, none of the ratio tests were significant. At G2, there was a trend for a change in ratio to be significant. However, a closer examination of the ratios used in this experiment shows how the ratios are confounded with amount. For example, the 3:1 treatments (T4 and T1) have 3X more P than their 9:1 counterparts (T3 and T6). At G2, where the response was driven by P, the "suggested response to ratio" may be merely due to the added P. An alternative, but inherently more complex design, would have been to also create the 3:1 and 9:1 treatments by keeping P constant and modifying N.

Critical or ideal N:P ratios have been defined for a number of plant species. Ingestad (1979), working almost exclusively with coniferous species grown in solution, determined that the optimum N:P ratio for plant growth was between 6 and 8. Shaver and Melillo (1984) found that *Carex* and *Calamagrostis* adjusted their uptake so that their N:P ratios were closest to 8. Barko and Smart (1979) suggested a critical N:P ratio of 7.5 for shoots of *Cyperus*, a sedge species. Based on the tissue N:P ratios in the control treatments at the beaver meadows (sedge communities about 8, grass communities about 12), one might have predicted the sedge communities to be operating under balanced nutrition with respect to N and P, indicating either multiple nutrient limitation, or as suggested by the lack of response, adequate nutrition.

A number of studies in wetlands, wet meadows and grassland ecosystems have indicated a co-limitation by N and P. Huenneke et al. (1990) found N and P limited production in a serpentine grassland in California. Production in a wet sedge meadow in the arctic responded more to N and P than to N alone (Haag 1974). Vascular plant production in an Alaskan wetland increased more to N and P in combination than to either nutrient alone (Sanville 1988). In an alpine wet meadow community in Colorado, N and P were found to be co-limiting (Bowman et al. 1993). In all of these cases multiple nutrient limitations are implied. Multiple nutrient limitations are indicated especially if the responses to N and P are greater than predicted due to additive effects of each nutrient alone (Chapin et al. 1987).

Other studies have indicated the development of secondary (generally P) limitation after the primary limitation (generally N) is alleviated, a type of response supporting Liebig's law of the minimum or the single nutrient limitation model. A shift from N to P limitation occurred along a successional gradient of mown fens in the Netherlands (Verhoeven and Schmitz 1991), where older fens had greater exposure to anthropogenic N inputs and more P lost through cutting of biomass. Aerts et al. (1992) also found a shift from N to P limitation in *Sphagnum* systems in Sweden as N levels increased from atmospheric deposition. Because response to P only occurred with adequate N, the responses at G3 and G2 also support the single nutrient limitation model.

Absorption and mass of N and P

Concentrations of N and P in plant tissues increased with treatment in both grass and sedge meadows (Table 12), suggesting that, in general, absorption of N and P was not limited in either community (Figs. 7 and 8). In sedge and grass plots, the linear contrasts indicated that when N was added to plots, N concentrations increased. Likewise, in sedge plots, the linear contrasts indicated that when P was added to plots, P concentrations increased. The test for the main effect of ratio also influenced P concentrations in sedge plots. Again, this was not surprising given that the test for effect of ratio is also a test of P addition. (Because the treatment/meadow interaction on P concentration in grass plots was significant, contrasts on average effects of treatments over sites were not performed.)

Mass of N and P, calculated by multiplying concentration by biomass, did not show the same pattern of response as tissue concentration of N and P. This was due, in part, to the lower biomass response in sedge communities. For example, while mass of N increased significantly in grass meadows (and reflected amount of N applied), mass of N did not increase significantly in sedge meadows. In contrast to N content, P content did significantly increase in sedge meadows. P absorption was apparently large enough to result in a significantly increased mass of P. Because community biomass in sedge meadows did not respond to P (or N) additions, luxury uptake of P is indicated. Interestingly, mass of P increased in grass meadows not only with amount of P applied (as indicated by significant contrasts where P was added), but also with amount of N applied (indicated by significant contrasts where N is added).

Several studies have documented interactions between the absorption of two or more nutrients. *Calamagrostis canadensis* and *Carex lacustris* (two of the dominant species in the beaver meadows at VNP), when grown under greenhouse conditions, were found to accumulate more N as P availability increased (Shaver and Melillo 1984). Vermeer (1986b) found adding N increased P uptake in a European fen and suggested that the additional N stimulated root growth and the subsequent absorption of P. Aerts et al. (1992) found that high N additions increased the amount of P stored in an N-limited *Sphagnum* system, indicating luxury uptake of P. Barko and Smart (1986) fertilized a marsh community and found a significant response to added P and Fe and also increased N uptake. They suggest this accumulation reflects a demand for nutrients by new growth.

Most of the evidence points to adequate nutrition in the wetter sedge communities, but species-influenced responses cannot entirely be ruled out. That absorption of N and P were not limited in the sedge communities and production did not respond to N and P additions, suggests adequate nutrition with regards to N and P in the wetter communities. If this were indeed an ecosystem property and not a species effect, grass species growing in the sedge communities should respond similarly to sedge species in the sedge communities. The lower biomass response of grasses in the sedge communities compared to grasses in the grass communities, supports the idea of adequate or at least better nutrition in the sedge community. Likewise, the conclusion of inadequate nutrition being an ecosystem property in the grass communities, should also apply equally to major species in these community. However, the response of sedge species in the grass communities was not significant. This suggests two possibilities: 1) either sedges in the grass communities already have their nutritional needs met, or 2) sedges are inherently limited in their ability to respond. Support for the latter possibility comes from the study of *Calamagrostis* and *Carex* nutrition mentioned above. *Calamagrostis* was most responsive to additions of N, P, and N plus P, while *Carex* was the least responsive (Shaver and Melillo 1984). Interestingly, *Carex* was more abundant in the meadows with greater nutrient availabilities. Alternatively, delayed responses of up to 2 years were demonstrated in a fertilized *Sparganium* / *Typha* prairie marsh (Neely and Davis 1985) and may be possible with *Carex*.

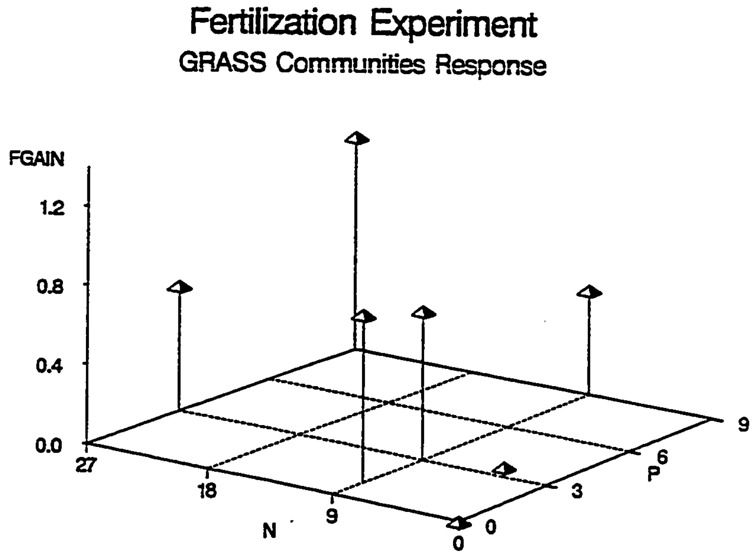
Adequate nutrition with regards to N and P does not preclude other resources from being limiting. For example, Bowman et al. (1993) propose that the lower response to N and P fertilization in a wet, nutrient-rich alpine meadow (in contrast to a drier, more nutrient-poor meadow) indicates a system heading towards light limitation. Alternatively, anoxic conditions, possibly common in the wetter, more saturated sedge meadows at VNP, may be stressful to the plants growing there and could restrict growth. Chapin (1991b) has proposed that the regulation of growth and photosynthesis in stressful environments may be independent of foliar nutrient status. More research is necessary to determine what other resource limitations or environmental constraints are operating in the sedge meadows.

Nonetheless, it is clear that hydrology influences both site fertility and responses of plant communities to nutrient additions in the beaver meadows at VNP and in other wetland systems. Bowman et al. (1993) measured greater N and P availability (as soil extractable N and P) in an alpine wet meadow in contrast to a physiognomically-similar dry meadow, where production showed a greater response to additions of N and P. In arctic tundra, response to N additions was greatest in a drier arctic tundra site and weaker in a more mesic and a wet-mesic community (Henry et al. 1986), implying greater nutrient availability in the wetter sites (availability was not measured). Bayley et al. (1985) found interesting interactions between site moisture conditions and response to P fertilization in an experimental marsh in Canada. During a dry year, the addition of sewage effluent (the source of P), increased production relative to a control. However, during a wet year, the increase in the water level above the marsh surface had the same effect on marsh production as did an application of 42 g P/m^2/y. The presumed response was due to a release of P from the soil when flooded. However, flooding may not enhance availability of N and P at all sites equally. For example, Vermeer (1986b) showed more P in soil and plants under inundated conditions, and more N in plants with a lowering of the water table. Because Vermeer's systems were N-limited, he attributed better nutrient conditions to a lower water table, in contrast to the meadows at VNP and the other examples above.

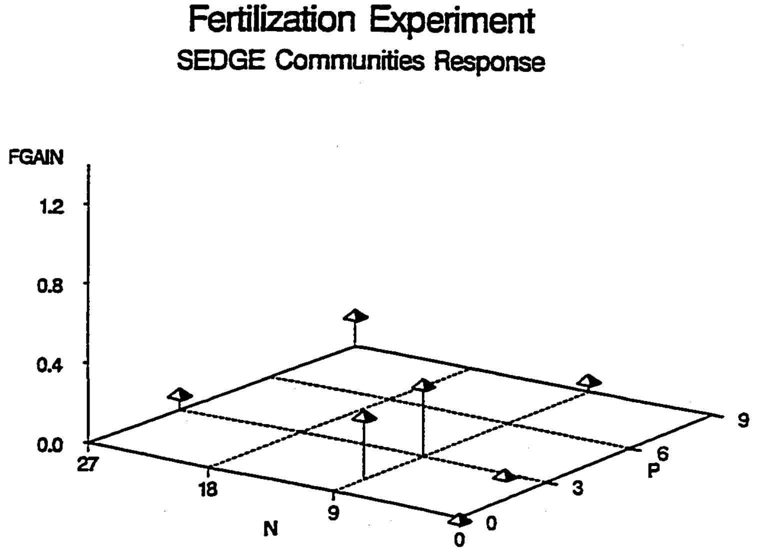
3.5 CONCLUSIONS

Nutrient limitation of above-ground production was experimentally tested with a field fertilization experiment in five wetland meadows representing a hydrologic gradient from wetter sedge-dominated meadows to relatively drier grass-dominated meadows. Production in the grass meadows, where relative availabilities of N and P were low, was shown to be nutrient limited, primarily by N and secondarily by P. Although production responses differed among the three grass meadows, the overall response patterns indicate a single nutrient limitation, with P limitation being manifested only after sufficient N supplies were made available.

Above-ground production in the two sedge communities, where relative availabilities of N and P were high, was not shown to be nutrient limited. The lack of significant response in the sedge communities implies either adequate nutrition with respect to N and P, or physiological/environmental constraints limiting potential growth responses. If physiological mechanisms preclude the sedge communities from responding to N and P additions, this would be an exception to the model of Chapin et al. (1986), which proposes that species adapted to low nutrient environments may be the least responsive to nutrient additions. The sedge communities are found in wetter and more nutrient-rich environments than the grass communities (Chapter 2). However, plant stress may be occurring as a result of soil saturation in the wetter areas, and although the sedge communities are at the high end of a N and P availability gradient, the addition of a source of stress in those systems may be affecting the communities' ability to respond. Regardless of the specific reason for the lack of response in the wetter sedge meadows, clearly hydrology appears to regulate the expression of nutrient limitation, if not nutrient limitation itself. Therefore, wetland landscapes characterized by complex hydrology may exhibit strong spatial heterogeneity in productivity responses to altered nutrient supply rates.

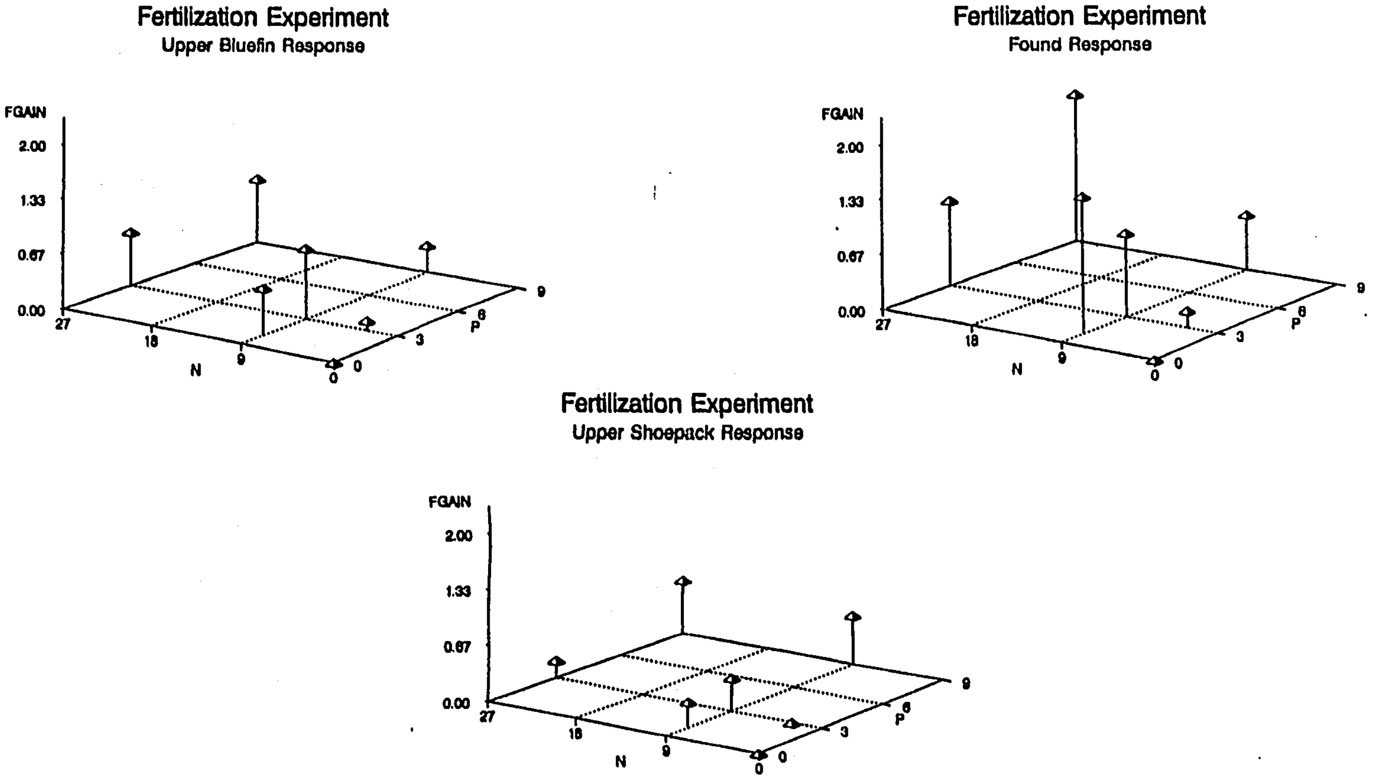


Fertilization Experiment
GRASS Communities Response



Fertilization Experiment
SEDGE Communities Response

Figure 5. Biomass response (FGAIN = proportional increase over control) after one year to N and P additions in grass and sedge communities. For grass plots, a two-way ANOVA on change in biomass was significant ($F_{20,21} = 3.26$, $p = 0.005$) and revealed both significant treatment ($F_{6,21} = 7.30$, $p = < 0.001$) and individual meadow ($F_{2,21} = 4.85$, $p = 0.019$) effects. For sedge plots, the two-way ANOVA on change in biomass was not significant ($F_{13,14} = 0.35$, $p = 0.967$). N and P axes indicate amounts applied in $g/m^2/y$.



Fertilization Experiment

Upper Bluefin Response

Fertilization Experiment

Found Response

Fertilization Experiment

Upper Shoepack Response

Figure 6. Biomass response (FGAIN = proportional increase over control) after one year to N and P additions in the 3 grass meadows: Upper Bluefin (= G1), Upper Shoepack (= G2), and Found (= G3). N and P axes indicate amounts applied in g/m^2/y.

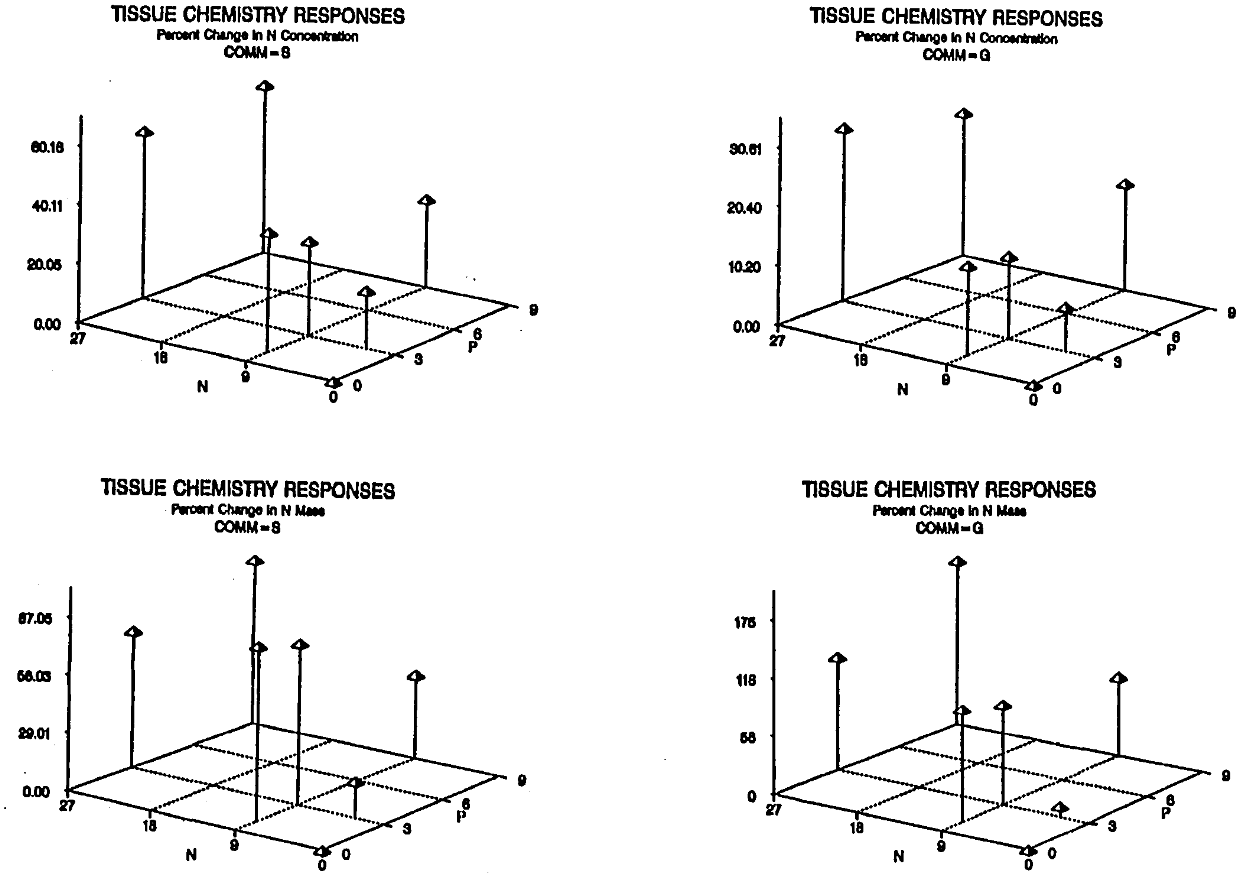
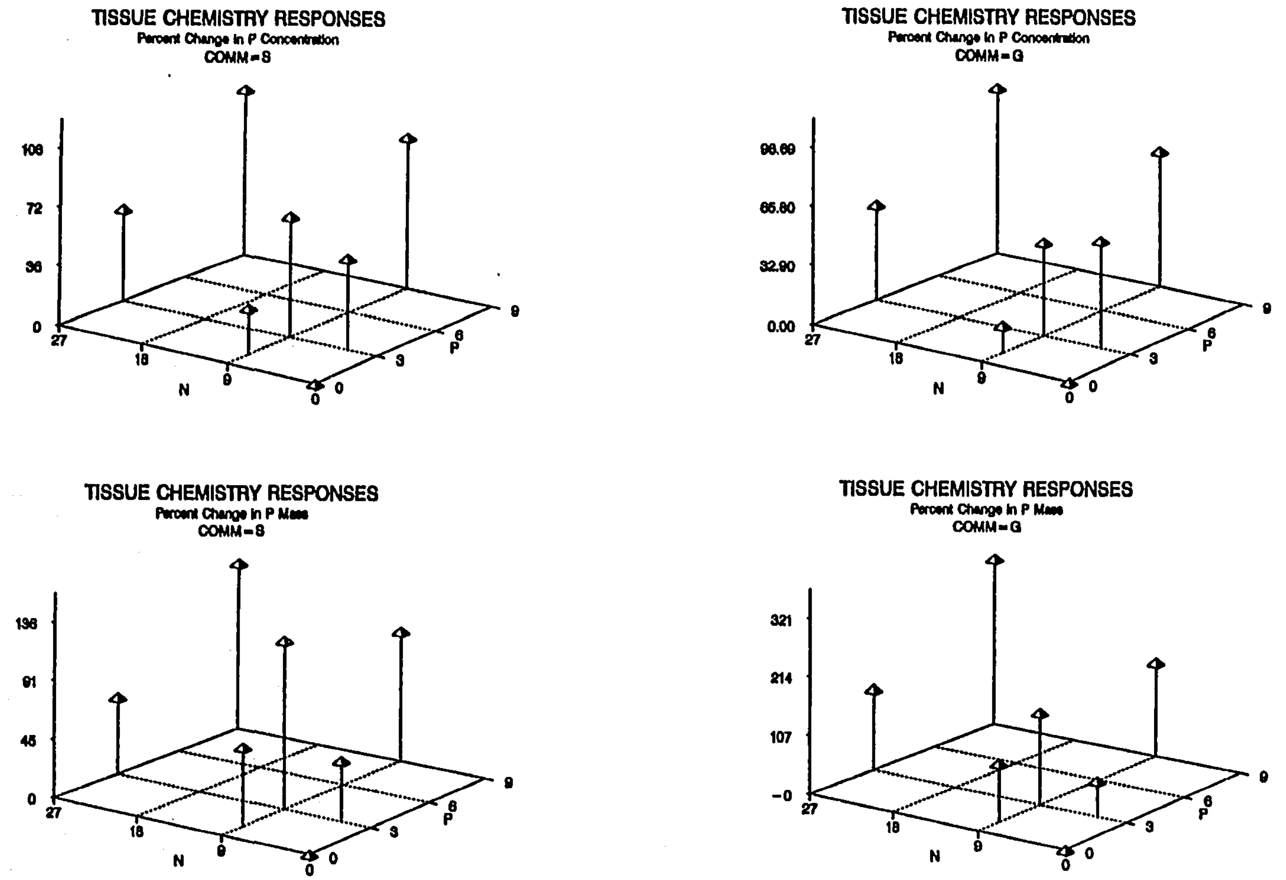


Fig. 7. Tissue N response - concentrations and mass of N in plant biomass for sedge (COMM = S) and grass (COMM = G) communities. Response is percent increase over control for all graphs. N and P axis labels indicate amounts applied in g/m^2/y.



TISSUE CHEMISTRY RESPONSES
Percent Change in P Concentration
COMM=S

TISSUE CHEMISTRY RESPONSES
Percent Change in P Concentration
COMM=G

TISSUE CHEMISTRY RESPONSES
Percent Change in P Mass
COMM=S

TISSUE CHEMISTRY RESPONSES
Percent Change in P Mass
COMM=G

Fig. 8. Tissue P response - concentrations and mass of P in plant biomass for sedge (COMM = S) and grass (COMM = G) communities. Response is percent increase over control for all graphs. N and P axis labels indicate amounts applied in $g/m^2/y$.

Table 9. Mean above-ground 1991 biomass in g/m^2 (plus one standard deviation, n = 2) for the seven treatments in each meadow. Treatments are indicated in Table 1. S1 (Lower Bluefin) and S2 (Lower Shoepack) are sedge meadows; G1 (Upper Bluefin), G2 (Upper Shoepack), and G3 (Found) are grass meadows.

Meadow	Treatment						
	T7	T2	T5	T4	T1	T3	T6
S1	385 (183)	413 (138)	439 (187)	541 (45)	423 (41)	555 (274)	346 (54)
S2	478 (216)	429 (34)	475 (35)	633 (317)	596 (90)	570 (320)	610 (172)
G1	210 (29)	234 (186)	282 (35)	388 (170)	384 (61)	327 (56)	349 (17)
G2	296 (75)	248 (34)	475 (34)	412 (51)	498 (5)	386 (26)	360 (135)
G3	188 (30)	226 (55)	319 (60)	377 (90)	546 (59)	494 (98)	387 (77)

Table 10. ANOVA table on change in biomass with community type (grass or sedge) and treatment (T1 - T7) as main effects.

Source of Variation	**df**	**MS**	**F**	**p**
Overall Model	13	34085	2.43	0.011
Community	1	59675	4.25	0.044
Treatment	6	54778	3.90	0.003
Community x treatment	6	9128	0.65	0.690
Error	56	14045		

Table 11. Tests of linear hypotheses (C1 - C7) on change in biomass at Found (G3) and Upper Shoepack (G2). See text for description of contrast hypotheses.

Contrast	**G3**		**G2**	
	$F_{1,7}$	p	$F_{1,7}$	p
C1	14.32	0.007	4.07	0.084
C2	5.65	0.049	0.11	0.752
C3	1.04	0.343	4.81	0.064
C4	4.77	0.065	0.67	0.439
C5	0.18	0.681	3.23	0.116
C6	0.38	0.555	0.42	0.538
C7	7.69	0.028	1.48	0.263

Table 12. Summary of ANOVA's on N and P concentration (%) and content (g/m^2) in 1991 above-ground biomass. Model subscripts refer to ANOVA degree's of freedom (df's).

Model	Percent N		Biomass N		Percent P		Biomass P	
	F	p	F	p	F	p	F	p
Overall$_{7,62}$	10.62	< 0.001	8.80	< 0.001	18.05	< 0.001	16.00	< 0.001
Community$_1$	8.84	0.004	12.05	0.001	12.19	0.001	40.17	< 0.001
Treatment$_6$	10.91	< 0.001	8.26	< 0.001	19.03	< 0.001	11.97	< 0.001
(Community x Treatment)		(NS)[*]		(NS)		(NS)		(NS)
Grass$_{8,33}$	5.22	< 0.001	7.62	< 0.001	7.98$_{20,21}$[**]	< 0.001	12.44	< 0.001
Site$_2$	6.34	0.005	2.80	0.075	12.54	< 0.001	4.54	0.018
Treatment$_6$	4.84	0.001	9.23	< 0.001	18.14	< 0.001	15.08	< 0.001
(Site x Treatment)		(NS)		(NS)	2.15$_{12}$	0.060		(NS)
Sedge$_{7,20}$	9.21	< 0.001	1.84	0.135	11.02	< 0.001	2.54	0.048
Site$_1$	2.16	0.158	1.93	0.180	4.70	0.042	0.51	0.485
Treatment$_6$	10.39	< 0.001	1.82	0.146	12.08	< 0.001	2.88	0.034
(Site x Treatment)		(NS)		(NS)		(NS)		(NS)

[*] Indicates a non-significant interaction effect. The interaction term was subsequently removed from the model.

[**] The interaction term (site x treatment) was significant in the model of percent P in grass meadows.

Table 13. Tests of linear hypotheses (C1 - C7) on percent N in above-ground biomass for grass and sedge communities. See text for a complete description of contrast hypotheses. For each type of community, model is a one-way ANOVA of effect of treatment on tissue N concentration, blocked by site (or individual meadow), as shown on Table 12.

Contrast	**Grass**		**Sedge**	
	$F_{1,33}$	p	$F_{1,20}$	p
C1	10.09	0.003	29.58	< 0.001
C2	4.67	0.038	17.55	< 0.001
C3	0.00	0.957	0.01	0.936
C4	0.88	0.356	0.04	0.834
C5	0.31	0.580	0.19	0.664
C6	6.44	0.016	12.51	0.002
C7	0.10	0.749	0.54	0.471

Table 14. Tests of linear hypotheses (C1 - C7) on mass of N in above-ground biomass for grass and sedge communities. See text for a complete description of contrast hypotheses. For each type of community, model is a one-way ANOVA of effect of treatment on mass of N, blocked by site (or individual meadow), as shown on Table 12.

Contrast	**Grass**		**Sedge**	
	$F_{1,33}$	p	$F_{1,20}$	p
C1	20.45	<0.001	4.77	0.041
C2	6.04	0.019	0.86	0.365
C3	1.28	0.265	0.21	0.653
C4	2.57	0.118	1.03	0.321
C5	1.51	0.228	0.04	0.836
C6	4.33	0.045	0.01	0.905
C7	2.28	0.141	0.12	0.730

Table 15. Tests of linear hypotheses (C1 - C7) on mass of P in above-ground biomass for grass and sedge communities. See text for a complete description of contrast hypotheses. For each type of community, model is a one-way ANOVA of effect of treatment on mass of P, blocked by site (or individual meadow), as shown on Table 12.

Contrast	**Grass**		**Sedge**	
	$F_{1,33}$	p	$F_{1,20}$	p
C1	34.71	<0.001	8.09	0.010
C2	5.22	0.029	0.23	0.639
C3	13.54	0.001	0.85	0.366
C4	7.31	0.011	3.04	0.097
C5	18.93	<0.001	6.37	0.020
C6	15.46	<0.001	0.09	0.765
C7	4.13	0.050	0.02	0.888

Chapter 4: Response of wet meadow communities to experimental nitrogen and phosphorus additions along fluctuating hydrologic gradients

4.1 INTRODUCTION

Wetland ecosystems are subject to a number of anthropogenic disturbances, including draining for forestry and agriculture (Mitsch and Gosselink 1993), eutrophication from agricultural runoff (Verhoeven et al. 1988b), fire, and possibly perturbations of general ecosystem function as a result of predicted global warming (Gorham 1991). These disturbances have the potential to alter the composition and dynamics of the plant community. Some of these disturbances may either directly or indirectly alter the availability of limiting nutrients. In northern latitudes for example, nutrient resources are predicted to increase with the projected rise in temperatures due to climate change, primarily as a result of increased decomposition (Hobbie et al. 1993). Enhanced atmospheric inputs may exacerbate effects due to increased decomposition. The exact magnitude of the increases are unknown however. Currently, atmospheric N deposition in the Netherlands is about 5 g $N/m^2/y$. The high N deposition in the Netherlands in particular, and in central Europe in general, has been implicated in the loss of species richness for a number of natural ecosystems (Bobbink and Willems 1987, Tamm 1991, Berendse 1993). Experimental increases in the availability of nutrients have been shown to decrease species richness and change plant community composition in several wet meadows (Berendse 1993, Vermeer 1986a, Vermeer 1986b, Henry et al. 1986) and many grassland communities (Silvertown 1980, Tilman 1987, Huenneke et al. 1990, Pysek and Leps 1991, Wilson and Tilman 1991, and Willems et al. 1993). The atmospheric inputs in Europe are nearly twice the inputs from N mineralization measured at the five beaver meadows of Voyageurs National Park (VNP) (Chapter 2). In three, relatively nutrient-poor grass meadows at VNP, biomass significantly increased in response to experimental N additions just above this level (Chapter 3). However biomass did not respond in two relatively richer sedge meadows. Because of differences in hydrology between the grass and sedge meadows, I concluded that hydrology was important in regulating nutrient availability and nutrient limitation of production. To predict the consequences of increased nutrient availability on wetland plant communities, it is important to know at what levels of increased nutrient inputs changes in species composition might occur, what the nature of those changes are, and how effects of hydrology interact to enhance or constrain community responses in a matrix of wetland community types.

Several theories attempt to explain the changes in herbaceous plant communities from increased supplies of limiting nutrients. For example, Grime (1973, 1979) and Tilman (1982, 1988) attribute the decreased number of species that occurs with increased aboveground biomass to light mortality caused by increased dominance of one or several species. However, several recent studies (Goldberg and Miller 1990, Carson and Barret 1988, Willems et al. 1993) found that experimentally increased production did not always lead to the predicted decrease in species diversity. Which resource is manipulated may have consequences on diversity independent of changes in production. For example, Willems et al. (1993) found that species richness decreased from adding N to a chalk grassland although production did not significantly increase.

Plant species may require limiting resources in different proportions (Tilman 1982). According to a resource competition model of plant community structure, a change in the external ratio of required resources may favor certain species over others, resulting in a shift in species composition (Tilman 1985, Tilman 1988). Species replacement may be predictable along light:soil N gradients (Tilman 1987 and Inouye and Tilman 1988), but only a few studies have examined species replacement along varying N:P gradients, a gradient that may be important in certain wetlands where N and P may both be limiting.

A key feature of the resource competition model of Tilman's is that the resources must be limiting to at least some species in the community and, for species replacement to occur, species must compete for the resources. In Chapter 3, I showed that aboveground production was limited by N in three grass-dominated beaver meadows at VNP. P was also found to limit production in two of the grass meadows, but only after adequate supplies of N were provided. In contrast, there were no significant responses to increased supplies of N or P in two, wetter sedge-dominated meadows. The differential pattern of biomass response to N and P additions among the grass and sedge meadows sets up a gradient of productivity response along an experimentally induced N and P availability gradient. I took advantage of these gradients to examine several theoretical predictions regarding productivity and nutrient availability effects on species richness.

Specifically, the objectives of this chapter are to provide basic descriptive information on how species in the meadow communities respond to experimentally enhanced N and P availability and to test the following two hypotheses along the hydrologic gradient of the five wetland meadows:

> **H4:** Ratios of experimentally applied nutrients select for certain species combinations. There will be a "community convergence" (i.e., botanical composition becoming more similar, c.f. Inouye and Tilman 1988) defined by the ratio of applied nutrients; and,
>
> **H5:** Experimentally increased nutrient availability will result in a decrease in species diversity if productivity is enhanced.

4.2 METHODS

Study Areas

The research was conducted in five wet meadows located on the Kabetogama Peninsula of VNP as described in Chapter 2. The two sedge-dominated meadows (S1, S2) and the three grass-dominated meadows (G1, G2, G3) represent gradients in hydrology, organic matter accumulation, nutrient availability, and net primary production (Chapter 2). Plant species in the meadows are generally robust, perennial graminoids typical of low disturbance environments. Two of the dominant species in both the sedge and grass communities, *Calamagrostis canadensis* and *Scirpus cyperinus*, form tussocks resulting in a hummocky microtopography. One of the grass meadows, G3, has a significant *Salix* component that is absent in the other meadows.

Fertilization Experiment

A nutrient enhancement experiment was begun in the fall of 1990 (Chapter 3). Treatments in the experiment varied both the amounts and ratios of N and P (Table 8 in Chapter 3). As described in Chapter 3, two blocks of 7 plots within each meadow were defined based on similarity of vegetative cover. A TWINSPAN analysis (Hill 1979), based on cover estimates made in early September 1989 for a pilot study, was used to classify the 14 plots per meadow. If the TWINSPAN analysis did not evenly divide the 14 plots into two groups, a best guess was made as to which of the 7 plots would form a block. Accordingly, a single replication of each of seven treatments was randomly allocated to one plot per block. Chapter 3 contains details of the experimental design and implementation; Table 8 in Chapter 3 should be consulted for amounts of N and P in the seven treatments (T1 - T7).

The nutrient applications were continued in 1992. Annual amounts of N and P comprising each treatment in 1992 were reduced by 1/3 of 1991 levels because foliar burning was noticed with some of the high application treatments. Half of the 1992 fertilizer was applied in early May and the remainder in early June.

Measures of production and plant species abundance

Above-ground biomass was used as a surrogate for net production. Subplots located within the experimental plots were clipped of above-ground biomass at the end of the 1991 growing season as described in Chapter 3. Visual estimates of percent cover of all species occurring in the 70 experimental plots were made at the end of the 1990, 1991 and 1992 growing seasons according to methods described in Chapter 2. While sampling with this method may have missed the few spring ephemeral species known to exist in the meadows, the majority of species in the meadows persist throughout the season and showed little indication of senescence at the time of sampling. To ensure high inter-year precision, two to three observers making cover estimates in 1992 had also made cover estimates in 1990 and 1991. Nomenclature follows Gleason and Cronquist (1991).

Species richness

Species richness was calculated as the number of plant species per 8.55 m^2 plot. When making comparisons of richness among treatments, meadows and years, "relative richness" was calculated by dividing the mean richness for each treatment in 1991 and

1992 by the corresponding mean richness in 1990, when data were collected before the fertilization experiment began. Relative richness then, is relative to the 1990 control year for all treatments.

Ordination analyses

Vegetation changes over the three years were analyzed by ordination analysis. With ordination, the relative position of plots in a two dimensional ordination space indicates similarity or dissimilarity of species composition; points close together correspond to plots that are floristically similar (Jongman et al. 1987). Data from multiple years have been combined in single ordinations to track vegetation change through time (c.f., Halpern 1988, del Moral and Wood 1988). When data from replicated experimental treatments are combined in a multiple year ordination, the effects of time and treatment on composition can be examined separately. For instance, convergence of treatments would be indicated by replicate plots moving closer together over time. Detrended correspondence analysis (DCA) was used as the ordination method. The DCA's were performed using CANOCO (ter Braak 1988), a computer program which provides an improvement of the original detrending method by segments of Hill and Gaugh (1980), by detrending with second order polynomials. Ordinations were run using percent cover data, without down-weighting rare species. Species ordinations were also performed to aid in the interpretation of plot trajectories. Abundances of major species were also examined directly for each plot. A change in abundance for species with covers of less than 20% was indicated if current years abundances differed by 30% from previous years. For species with covers over 20%, a change in abundance was indicated by an absolute increase or decrease of about 15%.

Ordinations were performed separately for each of the five meadows and included three years data for each plot, yielding a total of 42 points per ordination. The three points representing different years for each plot were connected with lines to indicate annual changes in position. Convergence was examined at two levels within a meadow: 1) within treatment, i.e., between the two replicate plots comprising a single experimental treatment, and 2) within ratio, correspondingly, between the two treatments comprising the same experimental ratio. An ordination was also performed on all 70 plots for the 1990 control year.

Statistical analyses

Relative richness was analyzed using a three-factor ANOVA with community, treatment and year as main effects. Relative richness was also analyzed within each community type with a two-way ANOVA, with treatment and year as main effects and individual meadow as a blocking factor. Data were log-transformed ($\log_e (x + 1)$) prior to analysis to normalize residuals. Orthogonal contrasts (C1 - C7, see Chapter 3), were performed to test specific hypotheses regarding the effects of levels and ratios of N and P on species richness.

4.3 RESULTS

General floristics

In 1990, the majority of the cover in grass and sedge plots was comprised of perennial grasses and sedges (Table 16). The communities are characterized by a high degree of dominance with a few of the species comprising most of the cover. Dominant species in the sedge meadows, ranked from highest mean cover, included *Scirpus cyperinus, Carex* spp. (primarily the robust *C. lacustris*), *Calamagrostis canadensis*, and *Leersia oryzoides* (Table 16). The three top dominants in the grass meadows are the same as in the sedge communities, but are ranked from highest mean cover as *Calamagrostis canadensis, Carex lacustris*, and *Scirpus cyperinus*. Perennial herbs were also common in the meadows and generally had mean covers of < 1% in most meadows. Exceptions are the two sub-canopy species *Campanula aparinoides* and *Lysimachia thysiflora* in the sedge meadows, an invasive weed, *Cirsium arvense* in the grass meadows, the rhizomatous perennial *Anemone canadensis* at G2, and a canopy herb *Solidago gigantea* at G3. Shrubs were rare in the meadows except at G3, where *Salix* spp. reached high abundances. An single annual herb, *Impatiens capensis*, was highly abundant at G2 in 1990. Of the 84 species found in the meadows in 1990, 37 occurred in both types of communities, indicating a fair amount of species overlap among the non-dominants as well. Despite this overlap, grass and sedge plots were floristically distinct, as indicated by their separation in the 1990 ordination (Fig. 9). Greater among-plot diversity of species composition in the sedge communities is indicated by the wider spread of plot locations for the sedge meadows, in contrast to the plot locations for the grass meadows (Fig. 9).

Compositional Change

Although trajectories of sedge plots through time maintained the relatively wide spacing of plots, and revealed different patterns of change for the two meadows, there was little evidence of floristic convergence between treatment replicates or identical ratios at different levels. At S1 (Fig. 10), the trajectory of plots from 1990 to 1991 reflects widespread and major reductions in the abundance of *Agrostis hyemalis*, *Leersia oryzoides* and *Scirpus cyperinus*. There was a marked tendency in 1992 for plot locations to be closer to 1990 locations, indicating a floristic return towards a community more similar to 1990. Replicate plots for T6 and T5 are an exception; the pattern there was to continue in the same direction of change initiated in 1990. Where 1992 locations returned towards the 1990 locations, *Scirpus* regained dominance that had been lost in 1991. Replicates for T2 may be converging (Fig. 10 (B)), while none of the other treatment replicates appear to be. At S2 (Fig. 11), 1992 locations for all treatments extend the DCA gradients toward the upper left hand corner of the ordination. A widespread reduction in the abundance of *Impatiens capensis* accounted for much of the pattern of change at S2; *Impatiens* cover was high in 1990 and almost non-existent by 1992. Where present, *Calamagrostis canadensis* cover increased from 1990 to 1992, regardless of treatment.

Similar fertilizer treatments did not result in floristic convergence in the grass meadows. At G1 (Fig. 12), 1992 locations for about half of the plots, representing one replicate from each treatment, extended both the horizontal and vertical ordination axes, indicating overall divergence in floristic composition. The plots extending ordination axis 1 to the right are all within a single within-meadow block (Fig. 12 - plots within one block noted by asterisks). The trajectories indicated by these plots are due to an unparalleled increase in the abundance of the weedy perennial, *Cirsium arvense*. In 1990, *Cirsium* was present in a majority of plots within the block, but had low abundances, with covers ranging from < 1 to 6%. By 1992, *Cirsium* was either the most or second most abundant species, with covers ranging from 20 to 91%. Relatively little vegetation change occurred in plots of the other block.

At G2 (Fig. 13), individual plots representing T3 and T4, extended the vertical axis in both directions and a single plot representing T2 extended the horizontal axis to the right. The rapid floristic change displayed by the single plot extending DCA axis 1 to the right was due to a dramatic and continued increase in the cover of the perennial herb, *Anemone canadensis*. The positions of plots extending DCA axis 2 reflect increases in *Cirsium* abundance, but not to the same magnitude that *Cirsium* increased in G1 or G3 (see below).

At G3 (Fig. 14), half of the plots, again representing split treatments and a single within-meadow block (indicated by asterisks in the figure), show major fluctuations in year to year locations and suggest overall divergence of composition over the three years. Plots extending the first ordination axis showed a significant increase in the dominance of *Cirsium arvense*, with covers ranging from < 1 to 5% in 1990, to covers ranging from 25 to 63% in 1992. Plots showing a return towards 1990 locations in 1992 (representing T1 and T6, Fig. 14 (A)) exhibit a decrease in *Cirsium* abundance from 1991 to 1992. *Cirsium* abundance increased at the expense of *Calamagrostis canadensis*; their covers consistently varied inversely. The position of plots extending the second DCA axis is reflected primarily by an increase in the dominance of *Salix petiolaris* in those plots (representing T2 and T5). In the T5 plot, the abundances of *Scirpus cyperinus* and *Polygonum scandens*, species which were not present in the T2 plot, increased in 1991 then decreased in 1992, accounting for the divergent trajectory of the T5 plot relative to the T2 plot. The seven plots in the other within-meadow block again, as at G1, showed little floristic change over the two year period.

Species richness

The mean number of species per 8.55 m^2 plot was 12.6 in 1990, 9.6 in 1991 and 10.5 in 1992. Mean richness per treatment ranged from a high of 19, measured at S2 in 1990, to a low of four, measured at G2 in 1992 on a plot receiving a high N treatment (Table 17). Relative richness was significantly affected by community type, treatment and year (Figs. 15 and 16, Table 18). Community type interacted significantly with year (Figs. 15 and 16, Table 18), indicating that separate analyses by community type were necessary to examine the effect of year. In the sedge communities, relative richness was affected by treatment ($F_{6,41} = 5.64$, $p < 0.001$), but not year ($F_{1,41} = 0.05$, $p = 0.829$): relative richness did not on average change from 1991 to 1992 (Fig. 15). In the grass communities, relative richness was affected by year ($F_{1,68} = 6.07$, $p = 0.016$) and treatment ($F_{6,68} = 6.06$, $p < 0.001$), with relative richness being overall greater in 1992 than in 1991 (Fig. 16). The interaction between year and treatment was non-significant for either community type ($p < 0.10$).

In sedge and grass communities, relative richness was significantly reduced by the main effect of N (C2, Table 19, Figs. 15 and 16). In the grass communities, relative richness was also reduced by adding P at high levels of N (C3, Table 19, Figs. 15 and 16). In both community types, relative richness was reduced by increasing ratio level (C6, Table 19, Figs. 15 and 16); and as discussed in the previous chapter, the ratio level tests effects due to adding N and P simultaneously.

Species that disappeared with high levels of N (i.e., 27 g N/m^2/y, T1 and T6) in the grass communities were species with original covers of generally less than 1%, and include several relatively small-statured, subcanopy annual or biennial herbs (*Polygonum sagittatum*, *Potentilla norvegica*), a trailing shrub (*Rubus idaeus*), a number of subcanopy perennial herbs (*Lycopus* spp., *Stachys palustris*, *Lysimachia thyrsiflora*, *Scuttelaria galericulata*), and a few low cover grasses and sedges (*Agrostis hyemalis*, *Poa palustris*, *Carex ovalis*, *Carex stipata*). Species that were lost with high levels of N in the sedge communities include subcanopy herbs (e.g., *Cicuta bulbifera*, *Lysimachia thyrsiflora*, *Polygonum punctatum*, *Potentilla norvegica*, *Ranunculus pensylvanicus*), grasses and sedges with low cover (*Carex stipata* and *Glyceria grandis*), and a number of species with moderate (> 5%) (e.g., *Galium trifidum*, *Glyceria borealis*, *Glyceria canadensis*, *Carex ovalis*, *Carex retrorsa*, *Leersia oryzoides*), or higher (>10%) cover (*Agrostis hyemalis*, *Impatiens capensis*). *Leersia oryzoides* and *Glyceria* spp. were lost from the control plots at S1. While no new species appeared in the grass meadows over the three years, *Lemna minor*, appeared at S1 in 1991, and disappeared again in 1992. The control plots at S2 lost species that had also disappeared in plots receiving high N treatments; these include *Bidens cernua*, *Puccinia pallida*, and *Leersia oryzoides*.

The apparent decrease in richness relative to 1990 for control plots in the sedge communities was non-significant (one-way ANOVA on effect of the three years on $\log_e$ of species numbers: $F_{2,9} = 1.52$, $p = 0.270$). There was a trend ($F_{2,15} = 2.95$, $p = 0.083$) for a year effect on species number in control grass plots.

4.4 DISCUSSION

Lack of community convergence

Nutrient supply is thought to be one of the major environmental variables influencing competitive balances between plant species (Berendse and Elberse 1990, Tilman 1982, Tilman 1988). Altering the supply rates of N and P in either the grass or sedge meadows did not result in a convergence of species composition among similar treatments or like ratios. This is in contrast to other fertilization experiments that demonstrated differential species responses and eventual floristic convergence. For instance, Inouye and Tilman (1988) showed evidence of convergence with similar resource treatments after three years of N fertilization on N-limited old field soils at Cedar Creek, Minnesota. In another example, competitive interactions between *Molinia caerulea* and *Erica tetralix*, two currently dominant species in wet heathlands of the Netherlands, are altered with N supply (Vermeer 1986b, Aerts and Berendse 1988); *Molinia*, a perennial grass, increases in abundance relative to *Erica*, a dwarf evergreen shrub, at high levels of N. In chalk grasslands of the Netherlands, *Brachypodium pinnatum* exclusively responds to N fertilization at the expense of other species (Willems et al. 1993, Bobbink 1991). However a fertilization including both N and P increased the dominance of other grasses as well, a prime example of multiple element regulation of plant community structure (Willems et al. 1993).

As suggested above, for convergence in vegetative cover to be indicated, major species invasions or replacements of dominants are not necessary. A repeatable shift in the relative abundance among existing dominants would also imply convergence. Although shifts in abundances of the dominants did occur in the meadows, the changes were not in response to N or P, and tended to show overall divergence rather than convergence. The changes that occurred are suggestive of different successional endpoints depending on the initial floristics of the individual plots and on the competitive interactions within the plots that are apparently independent of N and P availability.

An important question to ask is why treatment-induced convergence was not indicated in the beaver meadows. Because of the predominance of long-lived perennials in the meadows, there may be high degree of inertia in the plant communities; the species are slow to change to altered environmental conditions. Tilman's model of community organization requires that equilibrium be reached among the competing plant species at a given resource supply rate. At equilibrium, species adapted to differences in resource supply ratios would separate along a gradient of supply ratios (Tilman 1982, Tilman 1988). Because little overall shifts in the species composition of the dominants occurred in the meadows, high inertia is suggested instead of a movement towards equilibrium. In fact, *Cirsium*, which entered treated plots within the blocks at G1 and G3 rather indiscriminately, was the only new dominant to appear over the three years. In contrast, along the experimental nitrogen gradient in the nutrient-poor agricultural fields at Cedar Creek, Minnesota, there was a high degree of species turnover in a relatively short period of time; after 3 years over 60% of the species had been replaced in the high N treatments (Tilman 1987). At Cedar Creek, *Agropyron repens* invaded plots receiving the high N treatments regardless of initial composition.

A second explanation that is suggested is that plant species in the meadows may not be competing for N or P. The dominant species in the meadows are generally tall, erect perennials (indicating a relatively rich resource environment), many of which are tussock formers. Other than a disproportionate loss of subcanopy herbs or less dominant grasses with high N fertilization, there were no major shifts in life history characteristics along the experimental nutrient gradients. Species with similar morphological traits may have similar resource requirements (Tilman 1990, Wedin and Tilman 1993). Boutin and Keddy (1993), in an attempt to define guilds for wetland plants, classified 43 plant species into seven functional groups based on a suite of traits reflecting plant function. *Calamagrostis canadensis* and *Scirpus cyperinus* were grouped as "interstitial tussock" species, characterized by compact growth, a capability for lateral spread, relatively low flowering and a high photosynthetic area (Boutin and Keddy 1993). Conversely, *Bidens cernua, Mimulus ringens* and *Lycopus americanus*, were classified as ruderal species, characterized by high percentage of flowering and lack of above-ground lateral spread. If the dominant species in the meadows do have similar requirements for N and P, competitive displacement would be either slow, requiring many years to document, or non-existent. The results to date suggest that competition among the dominant species for limiting nutrients is not important in structuring the wet meadow communities, and that environmental fluctuations may be more important in driving the changes in relative abundances among the dominants.

Vegetational change within meadows appeared to be driven by factors equally affecting all plots in the case of S1 and S2, strongly dominated by distinctive initial floristics for the few plots that showed change at G2, and at G1 and G3, driven by factors equally affecting blocks within the meadows. In the sedge meadows, changes in the abundances of a few key indicator species suggest that hydrologic fluctuations may be driving overall vegetation changes (see below). At G1 and G3, where floristic change was dominated by a *Cirsium* invasion in a portion of each meadows, the affected portions, also corresponding to experimental blocks, represent physiographically distinct parts of the meadows. For example, the floristic division at G1 coincided with a stream that splits the meadow into a north and south portion (with a floating mat community of *Typha* in the center); the division at G3 coincides with a stream and small remnant beaver pond splitting the meadow into an east and west section. While it would certainly be both interesting and heuristic to examine more detail the causes of the different responses at either the within-meadow or whole meadow scale (e.g., variations in hydrology, microclimate, rate of spread of the invading *Cirsium*, etc.), an effort such as that was beyond the scope of this dissertation.

Dynamics of the annual herbs also appeared to be independent of treatment and may be related to meadow-wide fluctuations in hydrology. For instance, van der Valk and Davis (1978) found hydrologic drawdown was required for buried seeds of several annuals to germinate, including *Bidens*, *Polygonum*, and *Rumex*. Annuals tend to occur in areas of high fertility and high disturbances, such as mudflats (Day et al. 1988). On the Kabetogama Peninsula, exposed sediment is common in recently drained beaver ponds, where fast-growing annuals soon occupy the new surfaces. In 1991, water table levels rose in the sedge communities (Chapter 2), and remained high in 1992, particularly at S1 (personal observation). Beaver had reoccupied the sites and repaired previously abandoned dams resulting in the increased water levels. The high waters may have caused the widespread loss of *Leersia oryzoides* and *Glyceria* spp. at S1 and the loss of *Bidens* and *Puccinellia pallida* at S2; certainly the brief appearance of *Lemna minor* at S1 was in response to water tables being above the soil surface. There is also evidence of past flood disturbance in established vegetation from the occasional silt accumulation and buried organic horizons found in the meadows.

Keddy (1990) describes the following four general factors affecting plant communities in shoreline vegetation: 1) water table fluctuation, 2) mean water level, 3) wave exposure, and 4) fertility. Researchers working in ecosystems similar to the beaver meadows (i.e., wet meadow *Carex* communities) found that floristic composition is highly dependent on occasional flooding (Kenkel 1987, Keddy 1990, Keddy and Reznicek 1986), with drawdowns not only being necessary for germination of buried seeds (Keddy and Reznicek 1986), but also for removal of woody vegetation. In the absence of flooding, fire may be necessary to maintain the meadows against shrub invasion (Auclair et al. 1976, Curtis 1959). Eliminating wave exposure as significant in beaver meadows, the effects of hydrology and fertility are left as potentially important. While fertility is certainly important in determining overall meadow composition, fluctuations in fertility may not be important for species interactions in relatively nutrient-rich ecosystems such as the beaver meadows.

Because natural experiments are often time-dependent, it will be important to continue the nutrient additions and track species responses for many years. A case in point is the 14 years it took for *Arrhenatherum* to reach high levels of frequency on hayfield plots that had been fertilized annually with N, P, and K (Berendse and Elberse 1990). The long lag time was attributed to the 8 years it took for *Arrhenatherum* to establish within the hayfields.

Relationship between richness, N and P additions, and productivity

A well documented phenomenon in herbaceous communities is for species richness to vary along gradients of productivity. In particular, the number of species increases with productivity in systems of low productivity, plateaus at a medium levels of productivity, and drops at higher levels of productivity, yielding the familiar "hump-back" diversity curves (Al Mufti et al. 1977, Grime 1979, Puerto et al. 1990, Vermeer and Berendse 1983, Wisheu and Keddy 1989, Wheeler and Giller 1982, and additional references in Tilman and Pacala 1993). The "productivity corridor", i.e., the level of production where species richness reaches a peak, varies among ecosystem types (Puerto et al. 1990) and may be related to differences in environmental constraints acting on the plants. Experimentally-induced increases in productivity have generally been followed by decreases in species richness (e.g., Bobbink 1991, Huenneke et al. 1990, Tilman 1987, Silvertown 1980, Wilson and Tilman 1991, Pysek and Leps 1991), but not consistently. For example, Goldberg and Miller (1990) did not find the expected decrease in richness on experimental plots showing increased production from water additions. On the other hand, additions of N caused a reduction in richness even though productivity was not increased. Goldberg and Miller (1990) attribute the loss of richness on the N addition plots to early canopy closure which reduced light levels below critical levels for understory herbs. Willems et al. (1993) found similar effects with N additions to a chalk grassland. There, production was found to be limited by P, or by N and P in combination, but not by N alone. However richness did not decline with P additions, where the growth forms of plants allowed more spatial heterogeneity in the light environment and subsequently, greater coexistence.

Species richness was affected by N and P additions in the wet beaver meadows of VNP. In two years the number of species decreased relative to controls when high amounts of N and P were added to the grass meadows, where N and P were shown to increase production (Chapter 3). The number of species also declined in the sedge meadows with added N despite the fact that high N additions in the sedge meadows did not increase above-ground production. Perhaps an earlier season canopy closure with the N additions, as suggested by Goldberg and Miller (1990), was the reason behind the loss of species in the sedge meadows. Although a significant biomass response was not observed in the sedge meadows, the grasses and sedges did become greener and appear "thicker", suggesting mortality induced by light stress could have been the mechanism behind the decrease in richness.

I had hypothesized to find (see below) that increased P for a given level of N in the grass meadows would have allowed more species to co-exist, however this was not the case. Olff and van der Veen (1992) found that high species diversity coincided with increased multiple nutrient limitation in a series of abandoned agricultural fields in the Netherlands, and suggested that different species in the meadows became limited by different nutrients allowing for the greater diversity. The Willems et al. (1993) finding that P caused a shift in the abundance of species with different growth habits suggests that morphological differences induced by species response to different nutrient additions may allow for co-existence. While N and P were both found to limit production in two of the grass meadows, there were no species shifts, yet alone any major morphological shifts that could be attributed to the nutrient additions. Although light levels were not measured in this study, where richness declined, the loss with fertilization of primarily low cover, sub-canopy perennial herbs strongly suggests light may have been limiting. Furthermore, the loss of *Rubus idaeus*, a shade intolerant low shrub, with fertilization in the grass meadows is consistent with the hypothesis that slow growing, evergreen life forms do not perform well under conditions of high N availability (Tilman 1990, Berendse and Elberse 1990). Although *Rubus* was not a dominant, its invariable disappearance represents the only change in life form in the meadow communities. Regardless, the results from VNP, Goldberg and Miller (1990), and Willems et al. (1993) imply changes in richness that are independent from changes in productivity.

4.5 CONCLUSIONS

In conclusion, despite the positive increases in biomass to N and P additions in the grass-dominated meadows, indicating that N and P limit production, enhanced N and P availability did not select for species combinations reflecting different resource supply rates. This is in contrast to theory (Tilman 1982, Tilman 1988) and leads to a rejection of H4, which states that ratios of experimentally applied nutrients will select for certain species combinations. Other factors, perhaps related to hydrology, appear to be responsible for driving major plant community dynamics.

However species richness did change in response to fertilization over the three year period. Sub-canopy species were lost in both the grass and sedge communities with high levels of N and P. Moore and Keddy (1989) report that nutrient-rich minerotrophic wetlands, such as the beaver meadows, are less sensitive to nutrient perturbations than more-hydrologically isolated and generally more nutrient-poor wetlands. While it may be true that the loss of species is greater in more nutrient-poor systems, the results from this study indicate that with increased nutrient input in the relatively nutrient rich beaver meadows, losses of species will occur. Because species numbers also decreased in the sedge communities but without a commensurate increase in biomass, H5, which states that experimentally increased nutrient availability will result in a decrease in species diversity if productivity is enhanced, is rejected.

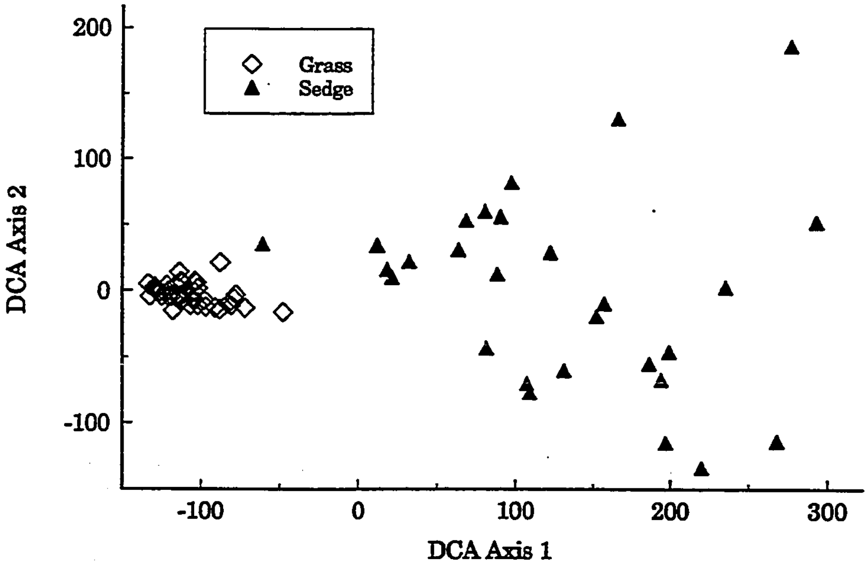


Figure 9. Detrended correspondence analysis (DCA) ordination of the seventy plots from the 3 grass-dominated and 2 sedge-dominated meadows in 1990, the control year. The ordination was performed using percent covers of plant species. N = 24 for sedge plots and N = 48 for grass plots.

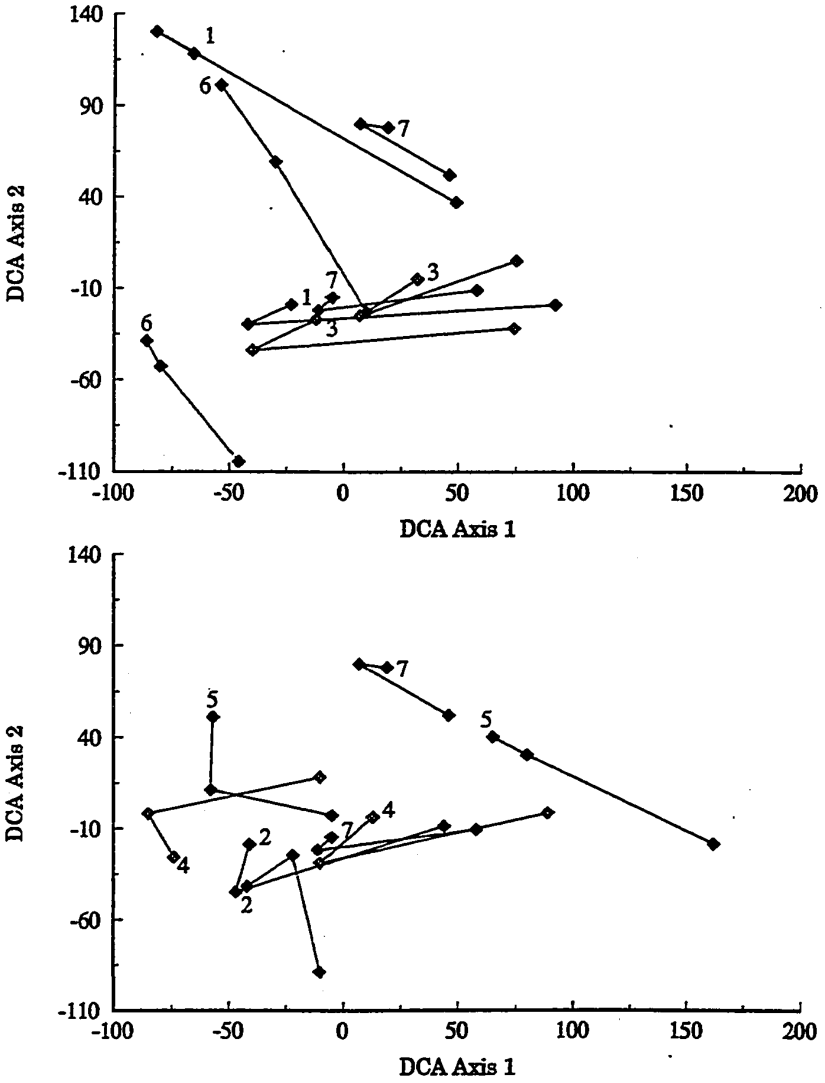


Figure 10. DCA ordinations through time for individual plots in the S1 meadow. Lines connect the same plot over the course of 3 years: 1990, 1991 and 1992. The 1992 locations are indicated by the position of the number coding for experimental treatment (1-7). The upper graph includes treatments 1, 3, 6, and 7; the lower graph treatments 2, 4, 5, and 7 (treatments were split for ease of viewing). T7, the control, is shown on both graphs for comparison. See legend in Table 17 for key to treatment codes.

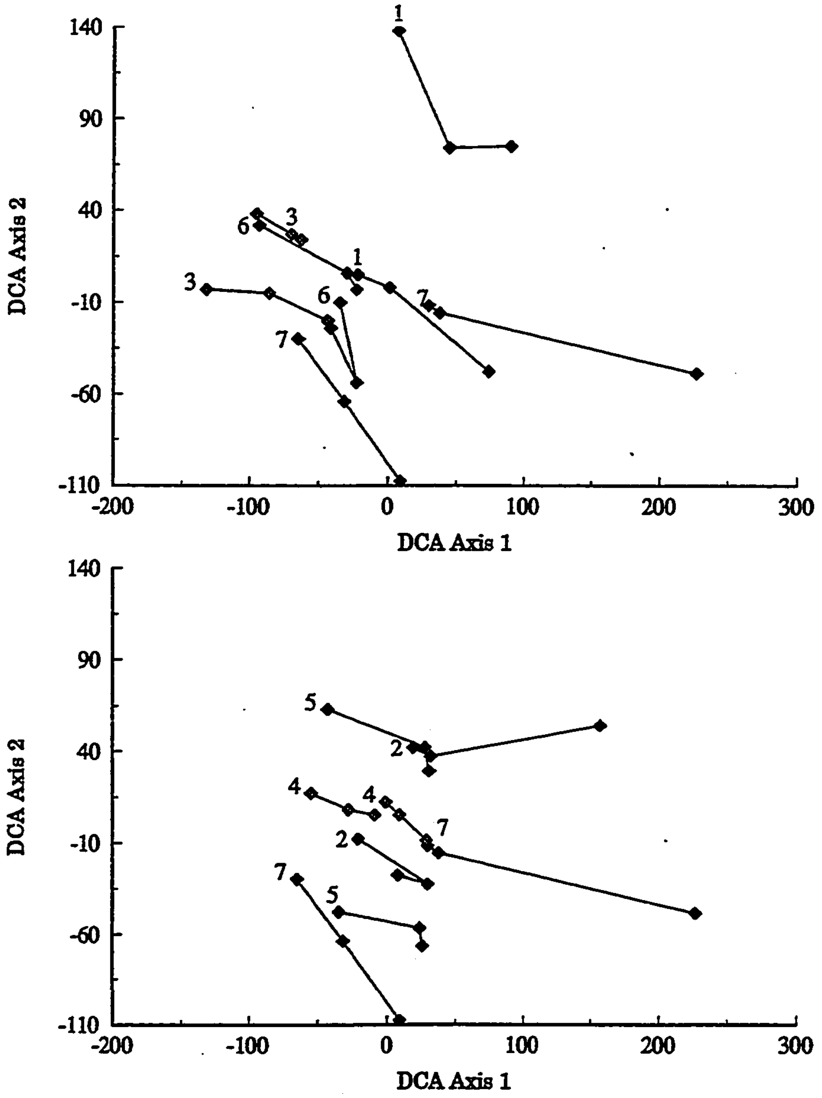


Figure 11. DCA ordinations through time for individual plots in the S2 meadow. Lines connect the same plot over the course of 3 years: 1990, 1991 and 1992. The 1992 locations are indicated by the position of the number coding for experimental treatment (1-7). The upper graph includes treatments 1, 3, 6, and 7; the lower graph treatments 2, 4, 5, and 7 (treatments were split for ease of viewing). T7, the control, is shown on both graphs for comparison. See legend in Table 17 for key to treatment codes.

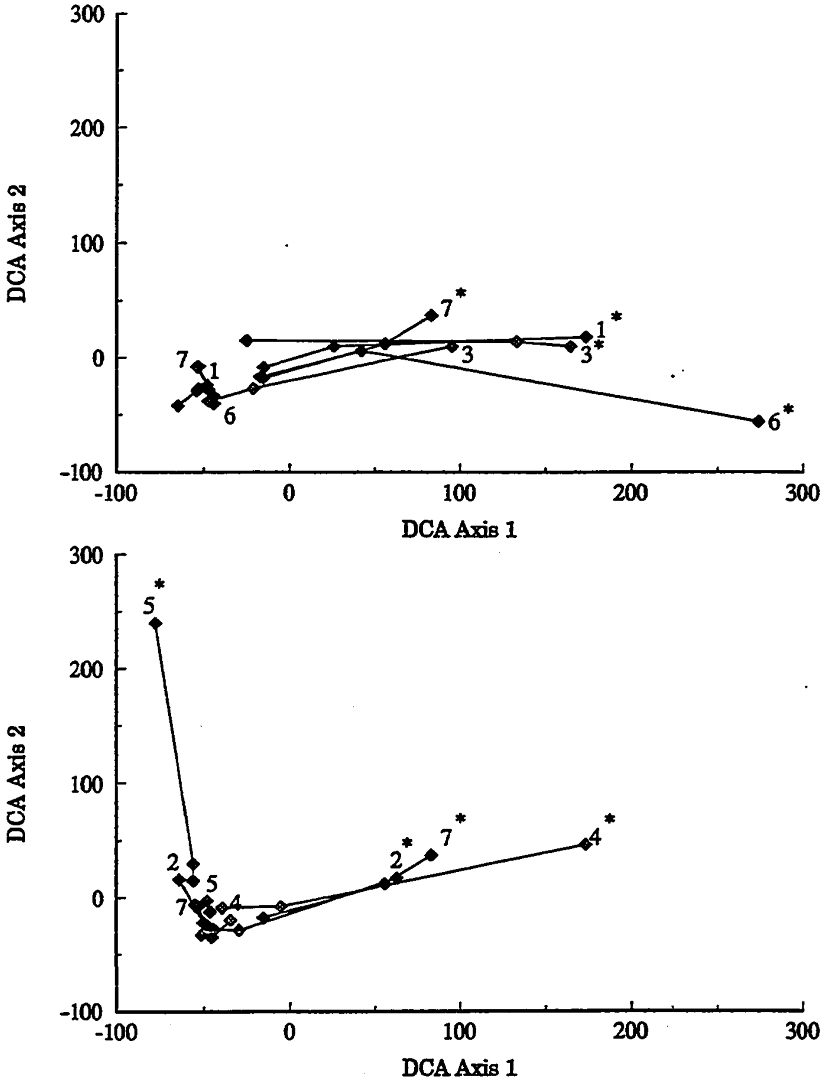


Figure 12. DCA ordinations through time for individual plots in the G1 meadow. Lines connect the same plot over the course of 3 years: 1990, 1991 and 1992. The 1992 locations are indicated by the position of the number coding for experimental treatment (1-7). The upper graph includes treatments 1, 3, 6, and 7; the lower graph treatments 2, 4, 5, and 7 (treatments were split for ease of viewing). T7, the control, is shown on both graphs for comparison. Plots marked with asterisks are located in a single within-meadow block (unmarked plots are located in the second within-meadow block).

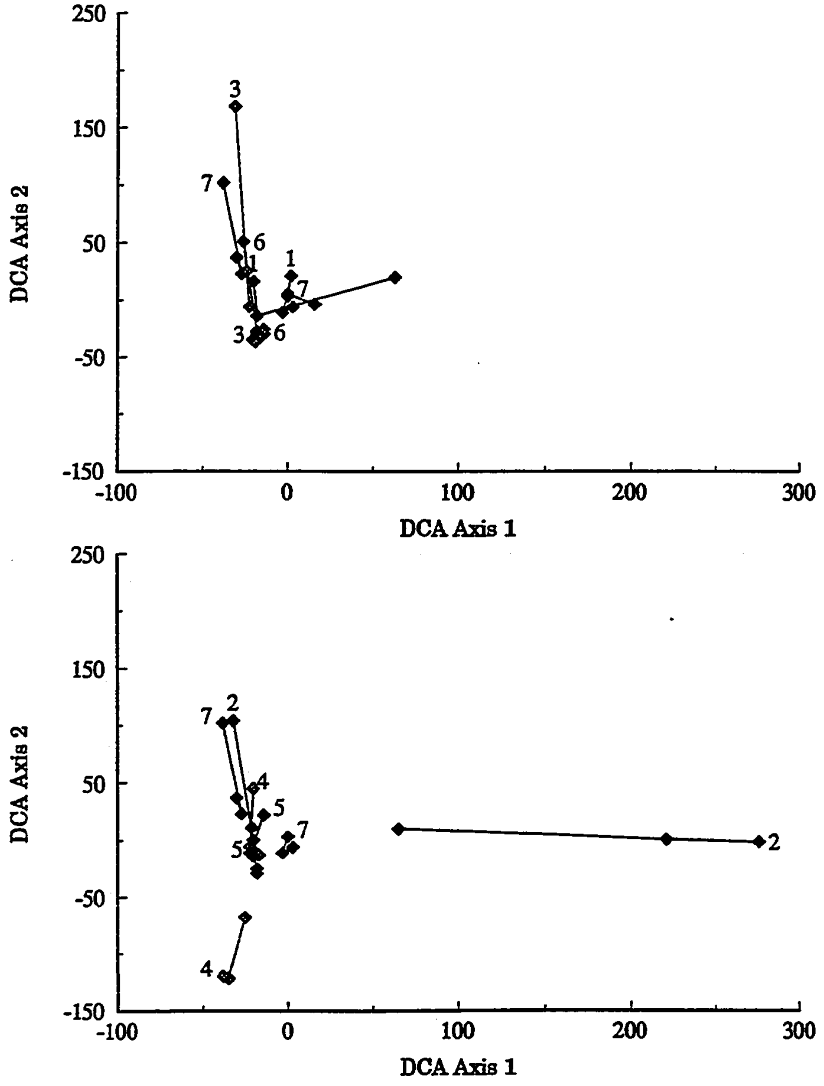


Figure 13. DCA ordinations through time for individual plots in the G2 meadow. Lines connect the same plot over the course of 3 years: 1990, 1991 and 1992. The 1992 locations are indicated by the position of the number coding for experimental treatment (1-7). The upper graph includes treatments 1, 3, 6, and 7; the lower graph treatments 2, 4, 5, and 7 (treatments were split for ease of viewing). T7, the control, is shown on both graphs for comparison.

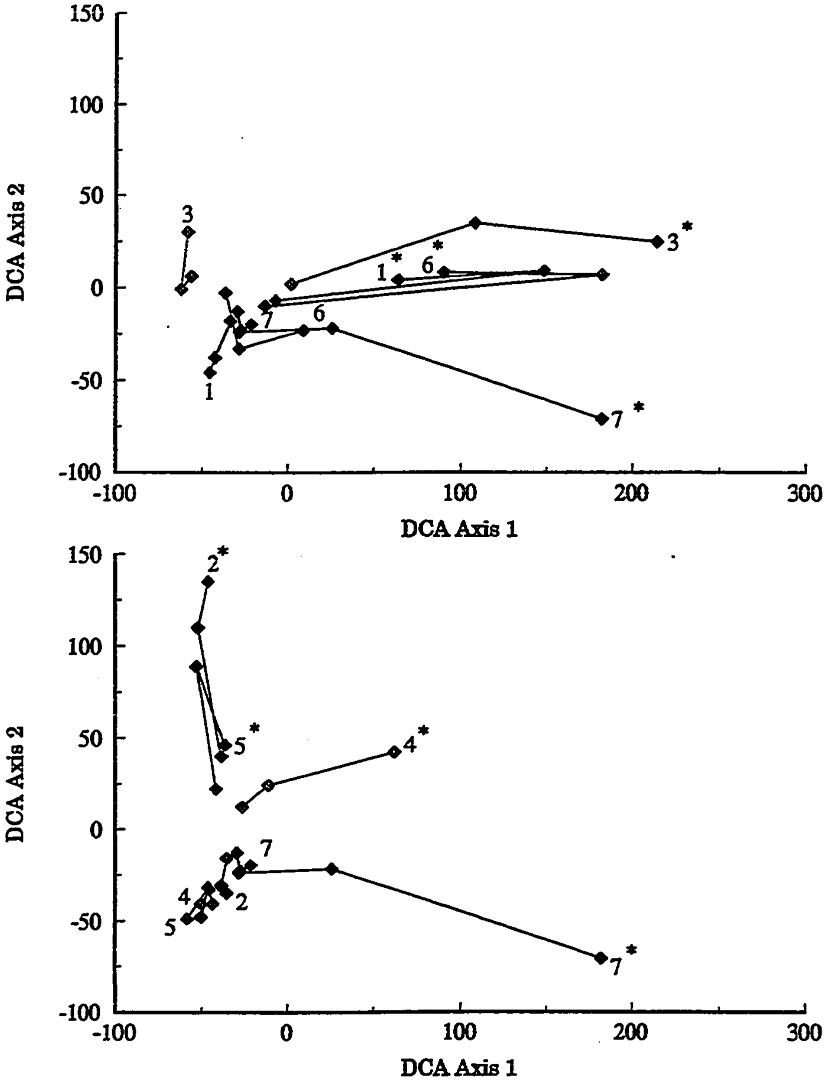


Figure 14. DCA ordinations through time for individual plots in the G3 meadow. Lines connect the same plot over the course of 3 years: 1990, 1991 and 1992. The 1992 locations are indicated by the position of the number coding for experimental treatment (1-7). The upper graph includes treatments 1, 3, 6, and 7; the lower graph treatments 2, 4, 5, and 7 (treatments were split for ease of viewing). T7, the control, is shown on both graphs for comparison. Plots marked with asterisks are located in a single within-meadow block (unmarked plots are located in the second within-meadow block).

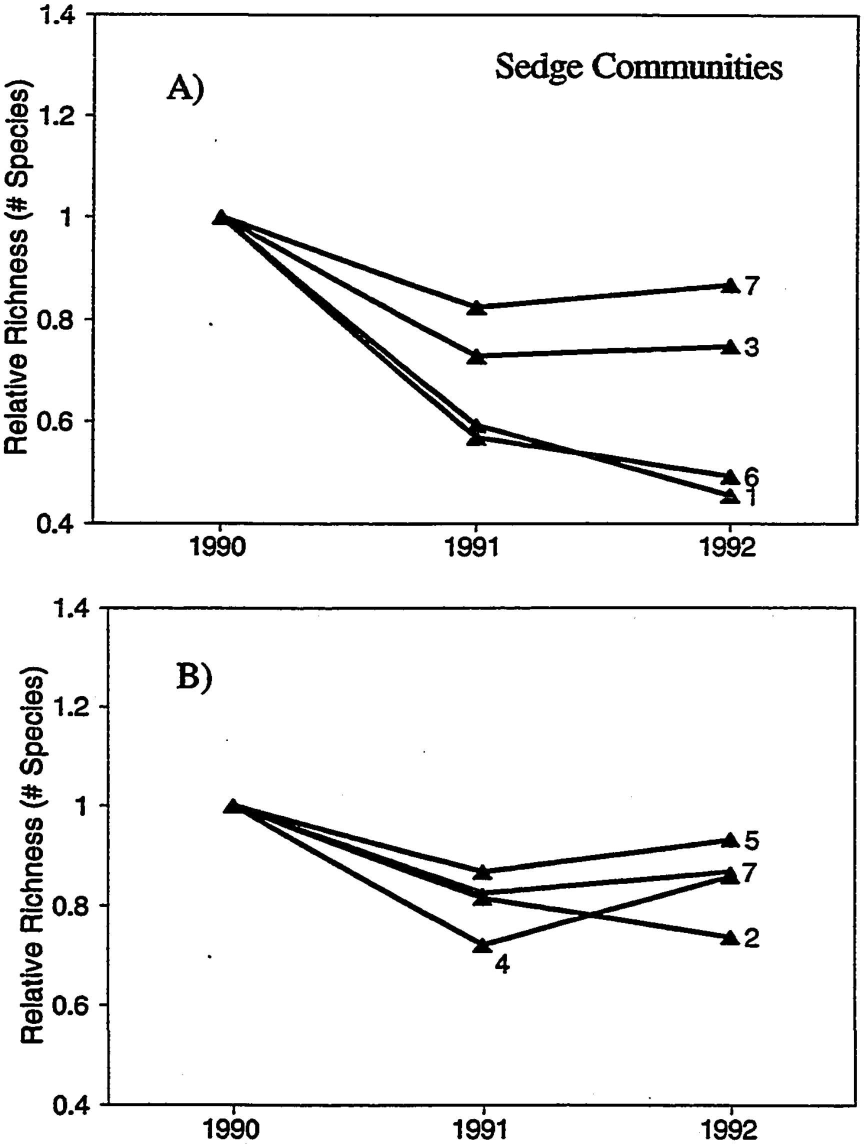


Figure 15. Mean relative richness (relative to 1990) by treatment for sedge communities in 1990, 1991 and 1992. (A) includes treatments 1, 3, 6, and 7. (B) includes treatments 2, 4, 5, and 7. (Treatments were split for ease of viewing.)

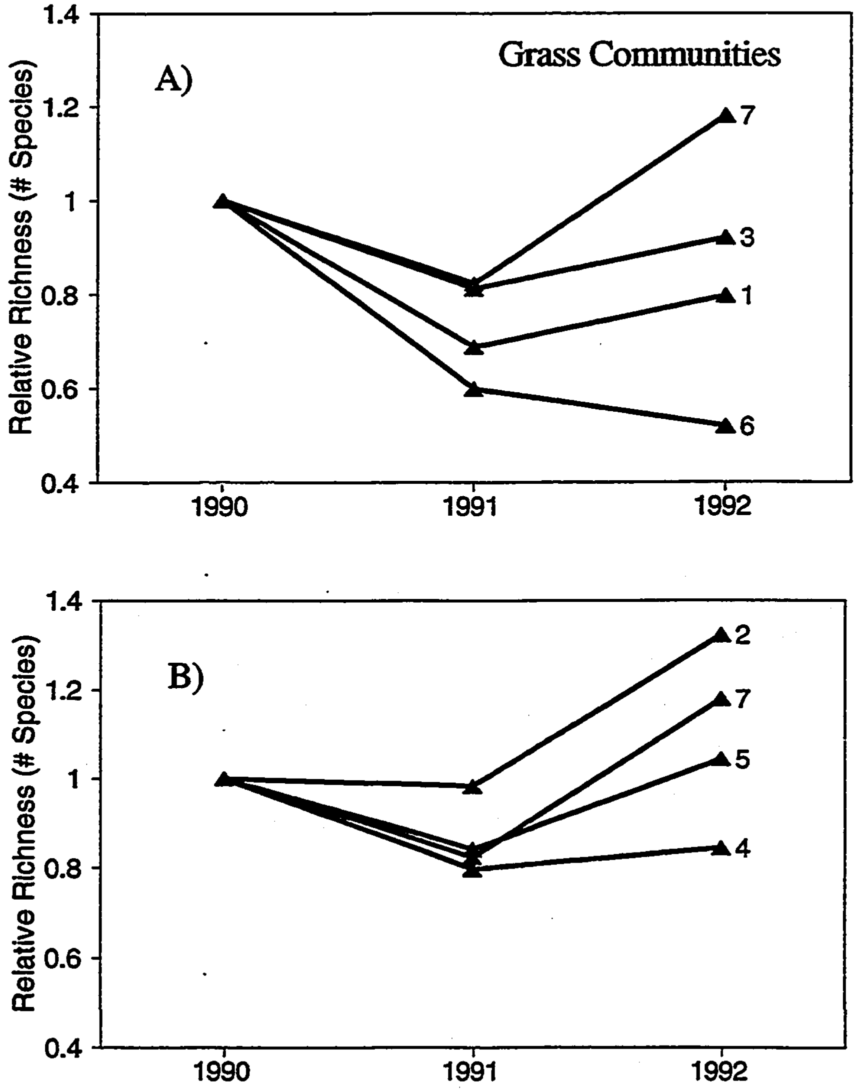


Figure 16. Mean relative richness (relative to 1990) by treatment for grass communities in 1990, 1991 and 1992. (A) includes treatments 1, 3, 6, and 7. (B) includes treatments 2, 4, 5, and 7. (Treatments were split for ease of viewing.)

Table 16. Species composition, percent cover (C) and number of plots (N) a species occurred in (out of a possible 14) in 1990 for the two sedge-dominated meadows (S1, S2) and the three grass-dominated meadows (G1, G2, G3). Mean covers greater than 1% are highlighted. S1 = Lower Bluefin, S2 = Lower Shoepack, G1 = Upper Bluefin, G2 = Upper Shoepack and G3 = Found.

	Sedge Meadows				Grass Meadows					
	S1		S2		G1		G2		G3	
Species	N	C	N	C	N	C	N	C	N	C
Annual Herbs										
Bidens cernua			3	1.07	1	0.04				
Geranium bicknellii									1	0.04
Impatiens capensis	2	0.81	13	20.57	5	0.29			1	0.04
Polygonum pensylvanicum	1	0.09								
Polygonum sagittatum	2	0.07			1	0.04	1	0.04	11	0.39
Annual, Biennial, or Perennial Herbs										
Cirsium sp.							1	0.16		
Galium sp.									1	0.04
Polygonum punctatum	13	0.79	6	0.45	5	0.21	1	0.04		
Potentilla norvegica	5	0.29	4	0.34	1	0.04	10	1.02		
Ranunculus pensylvanicus	5	0.32	4	0.25	1	0.04	4	0.37	2	0.07
Perennial Herbs										
Acorus calamus			8	4.0						

Table 16. Continued

	Sedge Meadows				Grass Meadows					
	S1		S2		G1		G2		G3	
Anemone canadensis							9	3.44	3	0.43
Aster lanceolatus			1	0.14			1	0.61	1	0.07
Aster lateriflorus	1	0.04								
Aster pubentior									3	0.41
Aster puniceus									2	0.34
Aster sp.			2	0.13	1	0.14			3	0.34
Athyrium spp.							2	0.07		
Botrychium spp.			1	0.04	1	0.04	2	0.07	1	0.04
Campanula aparanoides	1	0.04	11	5.61	1	0.04	3	0.11	2	0.09
Cicuta bulbifera	3	0.11	8	1.07	4	0.14				
Cirsium arvense					8	1.77	8	2.42	8	1.07
Epilobium ciliatum			4	0.46					1	0.04
Epilobium leptophyllum			3	0.32					1	0.04
Equisetum sylvaticum					6	1.86				
Eupatorium maculatum									1	0.12
Eupatorium perfoliatum									2	0.34

Table 16. Continued

	Sedge Meadows				Grass Meadows					
	S1		S2		G1		G2		G3	
Euthamia graminifolia									2	0.16
Fern spp.					2	0.07			1	0.04
Fragaria virginiana	2	0.11							2	0.12
Galium trifidum	2	0.07	11	1.52	8	0.29			2	0.09
Iris versicolor			3	0.57	1	0.12			5	0.44
Lycopus americanus			2	0.11	2	0.07	1	0.04	5	0.39
Lycopus rubellus	1	0.04	5	0.20	8	0.34			1	0.04
Lysimachia terrestris			8	0.77						
Lysimachia thyrsiflora	9	0.99	11	2.78	13	1.29				
Mentha arvensis			1	0.07	3	0.12			2	0.07
Mimulus ringens	1	0.04	1	0.04						
Persicaria hydropiperoides	1	0.04			1	0.16				
Unk. Mint			3	0.14						
Polygonum scandens			2	0.21	1	0.07	4	0.41	2	0.40
Rumex spp.	1	0.04			2	0.07				
Sagittaria latifolia	6	0.25	7	1.84						

Table 16. Continued

	Sedge Meadows				Grass Meadows					
	S1		S2		G1		G2		G3	
Scuttellaria galericulata	2	0.07	3	0.11	8	0.32			5	0.18
Solidago gigantea									6	2.06
Sparganium chlorocarpum			1	0.46						
Stachys palustris					3	0.12	9	0.84	6	0.21
Taraxacum sp.							1	0.04	1	0.04
Triadenum virginicum	6	1.59	8	0.71	5	0.29			3	0.21
Typha latifolia	2	0.11	2	0.46	3	0.11	1	0.05		
Urtica dioica			3	0.14	1	0.12	1	0.04		
Vicia americana	1	0.04			1	0.04	2	0.13	3	0.14
Viola sp.	1	0.04	1	0.14	1	0.04	1	0.04	3	0.11
Perennial Grasses										
Agrostis hyemalis	14	8.68					5	0.46	6	0.36
Bromus ciliatus	1	0.07								
Calamagrostis canadensis	14	37.27	10	12.70	14	91.07	14	89.46	14	86.91
Glyceria borealis	10	1.07								
Glyceria canadensis	1	0.04	1	0.07	2	0.11	1	0.04		

Table 16. Continued

	Sedge Meadows				Grass Meadows					
	S1		S2		G1		G2		G3	
Glyceria grandis	11	1.66	4	0.86	1	0.07				
Leersia oryzoides	11	5.16	4	0.86						
Poa palustris	4	0.70			2	0.13	12	0.92	3	0.11
Puccinellia pallida			3	1.57						
Perennial Sedges and Rushes										
Carex (lacustris)	12	11.42	6	5.61	14	8.32	13	8.57	9	1.73
Carex intumescens									2	0.18
Carex (ovales) group	14	10.62	2	0.21	10	0.68	11	1.95	9	0.79
Carex pseudocyperus	8	0.80							1	0.29
Carex retrorsa	9	2.96								
Unknown *Carex sp. 1*									1	0.06
Unknown *Carex sp. 3*							1	0.19		
Unknown *Carex sp. 4*							1	0.21		
Carex stipata	13	1.93	1	0.18	7	0.26	2	0.07	3	0.11
Carex utriculata			3	1.46						
Dulichium arundinaceum			1	0.04						

Table 16. Continued

	Sedge Meadows				**Grass Meadows**					
	S1		S2		G1		G2		G3	
Scirpus cyperinus	14	51.17	14	68.61	12	4.04	6	0.66	14	7.29
Shrubs										
Rubus idaeus					7	0.96	2	0.59	6	1.61
Salix bebbiana									7	0.65
Salix petiolaris									4	1.26
Unknown *Salix sp. 1*									1	0.19
Unknown *Salix sp. 2*									1	0.07
Trees										
Betula papyrifera					1	0.04				
Fraxinus pennsylvanica					1	0.07				
Picea glauca							2	0.07		

Table 17. Mean number of species by treatment (T1 - T7) and year in the two sedge-dominated (S1, S2) and three grass-dominated (G1, G2, G3) meadows. See legend in Table 1 for meadow names. Treatment codes are: T7 = control; T2 = 3N, 3P; T5 = 9N, 9P; T4 = 9N, 3P; T1 = 27N, 9P; T3 = 9N, 1P; T6 = 27N, 3P; where numbers equal amount of element applied in g/m^2/y in 1991. Treatments in 1992 were reduced by 1/3.

Treatment	S1			S2			G1			G2			G3		
	'90	'91	'92	'90	'91	'92	'90	'91	'92	'90	'91	'92	'90	'91	'92
T7	19.0	16.0	14.0	15.5	12.5	15.5	11.5	8.0	10.0	11.0	8.5	12.0	9.5	9.5	15.0
T2	16.5	11.0	11.5	13.5	13.0	10.5	11.5	10.5	15.5	9.0	8.5	10.5	11.0	12.0	16.0
T5	16.0	13.0	12.0	13.0	12.0	14.5	13.0	8.5	13.5	7.5	7.5	9.5	11.5	10.5	9.5
T4	12.5	5.5	6.5	10.0	10.0	12.0	12.0	7.0	11.0	10.5	6.5	5.5	16.0	19.0	17.5
T1	14.0	8.0	5.5	15.5	9.5	8.0	13.0	7.0	8.0	10.0	6.5	6.5	8.0	7.0	9.0
T3	13.0	7.5	8.0	12.5	11.0	11.0	12.5	7.0	8.0	8.5	8.0	9.0	15.5	14.5	16.5
T6	14.5	6.5	7.0	16.0	11.0	8.0	11.5	5.0	5.5	10.5	6.0	4.0	16.5	13.0	11.5

Table 18. ANOVA table on effects of community type, treatment and year on relative richness. Anaylses were performed on $\log_e$ transformed data.

Source of Variation	**df**	**MS**	**F**	**p**
Overall Model	24	.0853	5.26	<0.001
Community	1	.1856	11.43	0.001
Year	1	.0670	4.13	0.044
Treatment	6	.1665	10.26	<0.001
Community x year	1	.0573	3.53	0.063
Year x treatment	6	.0147	0.90	0.494
Community x treatment	6	.0131	0.80	0.569
Site	3	.1910	11.77	<0.001
Error	115	.0162		

Table 19. Tests of linear hypotheses (C1 - C7) on relative richness for grass and sedge communities. For each type of community, model is a two-way ANOVA with effect of treatment, year, and year/treatment interaction on relative richness, blocked by meadow. Analyses were performed on $\log_e$-transformed data. Contrast hypotheses are described in Chapter 3.

Contrast	**Grass**		**Sedge**	
	$F_{1,68}$	p	$F_{1,41}$	p
C1	3.43	0.068	4.79	0.034
C2	11.60	0.001	23.05	<0.001
C3	4.38	0.040	1.45	0.235
C4	0.01	0.923	1.50	0.228
C5	0.14	0.714	<0.01	0.984
C6	8.45	0.004	12.65	0.001
C7	2.65	0.108	<0.01	0.970

Chapter 5. Conclusions

The overall guiding objective of this dissertation was to understand how nutrient (nitrogen (N) and phosphorus (P)) availability influences ecosystem dynamics and plant community structure in wet meadow ecosystems. Both observational and experimental approaches were used to meet this objective. In Chapter 2, **Primary productivity, nitrogen and phosphorus availability, and nitrogen mineralization along hydrologic gradients in five wetland meadows**, patterns of differences (in the above attributes) among five beaver meadows were examined. Two types of relatively productive wet beaver meadows were sampled, "sedge-dominated" and "grass-dominated". The meadows were distinguished by differences in productivity, hydrology, and N and P availabilities. In the two sedge meadows, production was higher, N and P were more available during the non-growing season, and water tables were closer to the soil surface than in three drier grass meadows. N mineralization differed among individual meadows, but not between meadow types. N mineralization did not correlate to N availability and was insufficient to meet the requirements of the plant communities, supporting the existence of external, presumable hydrologic, sources of N to the meadows. Across the five meadows, productivity correlated to N and P availability but not to N mineralization. Because of the differences in hydrology between the meadows, hydrology is also implicated in affecting productivity, either directly through decreased water stresses on the plants, or indirectly through positive effects on soil nutrient availability. A central conclusion from Chapter 2 is that hydrologic conditions are important in maintaining the patterns of plant community composition and primary production among the beaver meadows.

Based on the observations made in Chapter 2, two hypotheses regarding N and P limitation to production in the meadows were developed: **H1)** the lower production in the grass meadows is due to a greater nutrient limitation in the grass meadows, and **H2)** the wet-sedge meadows are proportionately less P limited than the grass meadows, because of greater relative P availability in the wet-sedge meadows. A third hypothesis **H3**, was developed to test a prediction resulting from optimal allocation theory (Tilman 1982, Bloom et al. 1985). This theory states that, at equilibrium, plants will grow at a level where all (nutrient) resources are equally limiting. Assuming that N and P are limiting in the meadows, it follows that: **H3)** productivity increases will be stronger in response to a given external ratio of N and P than to absolute amounts of N and P. A manipulative experiment enhancing N and P availabilities in the meadows was used to test these and two additional theoretically-motivated hypotheses regarding the effect of varying resources on plant community dynamics.

Resource competition theory (Tilman 1985, Tilman 1988) states that plant species have different resource requirements, and, if ratios of resources that are limiting are altered, species replacement will occur and be predictable according to their resource requirements. A second theory predicts that with increased resource availability in competitive environments, diversity should eventually decrease due to the increased dominance of the vigorously growing species (Al-Mufti et al. 1977, Grime 1979, Huston 1979, Tilman 1987). The two hypothesis developed to test these theories are: **H4)** ratios of experimentally applied nutrients (N and P) select for certain species combinations. There will be a "community convergence" (i.e., botanical composition becoming more similar, c.f. Inouye and Tilman 1988) determined by the ratio of applied nutrients, and **H5)** species diversity will decrease with experimentally increased nutrient availability if productivity is enhanced.

Chapter 3, **Nitrogen and phosphorus limitation of above-ground primary production in five wetland meadows** reports the testing of **H1** - **H3**. The grass meadows responded significantly to the nutrient amendments, while the sedge meadows did not, supporting the hypothesis that primary production was nutrient limited in the drier grass meadows. The conclusion that N and P nutrition was adequate in the sedge meadows again suggests that hydrology affects nutrient limitation among the meadows. Responses to N and P in the grass meadows suggests that a single nutrient, N, limited production; P limited-production was indicated only after experimental N was supplied. Communities did not respond unequivocally to changes in nutrient ratios. These results suggest that the plant species were not operating at a level where the two nutrient elements, N and P, were equally limiting.

In Chapter 4, **Response of wet meadow communities to nitrogen and phosphorus additions along fluctuating hydrologic gradients**, the two hypotheses regarding plant communities and nutrient availabilities are tested. Species richness declined with high levels of N and P in both grass and sedge communities, regardless of whether biomass increased significantly. Thus, while a predictable decrease in richness did occur, an increase in productivity was not necessary, suggesting a need to modify the theory explaining decreases in productivity solely due to increases in productivity. While richness was affected by treatment, after two years of nutrient enhancement, convergence was not indicated for common treatments or ratios in either sedge or grass meadows, leading to a rejection of H4. On the contrary, a divergence within treatments was indicated in two grass meadows that were subject to a *Cirsium* invasion. *Cirsium* invaded all plots equally regardless of treatment. The general conclusion is that the theories based on equilibrium dynamics (tested in H3 and H4) may be inappropriate descriptors of plant communities in wetland beaver meadows.

While the emphasis of this research has been on an examination of the role of N and P availability on ecosystem dynamics and plant community structure, this is not to say that other factors do not affect vegetation in wetland meadows, especially on larger scales. For example, Curtis (1959) described wet sedge meadows as successional intermediates between marshes and hydric shrub communities, their stability being maintained by flooding or fire. By removing woody vegetation, fire returns the plant community to one dominated by graminoids. Fire has also been shown to be important in maintaining species richness of certain grasslands (Willems et al. 1993), by episodically removing foliage and increasing light availability for subcanopy species. Grazing and mowing, which also cause episodic removal of foliage, can enhance richness as well, although the effects seem to differ among ecosystems.

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Appendix A: Effects of soil freezing on nitrogen analyses

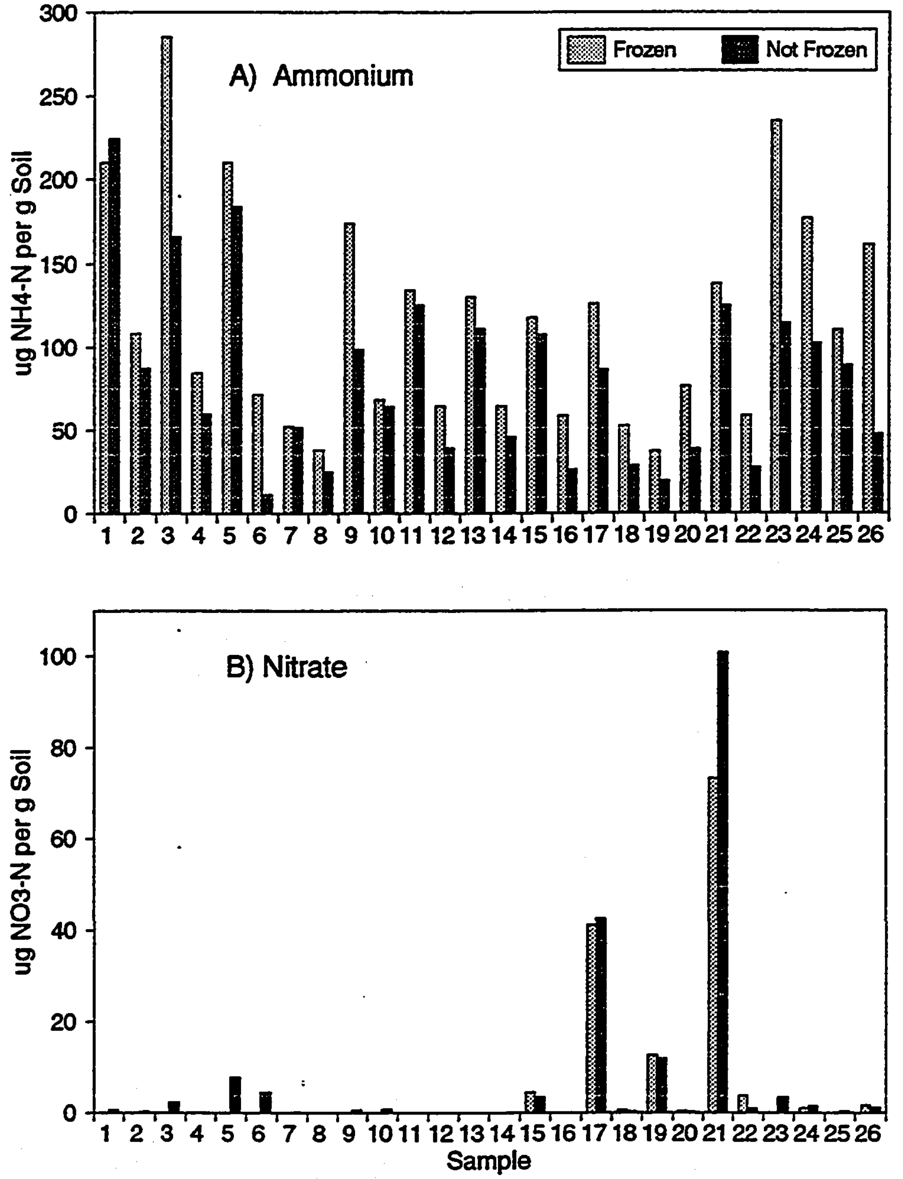

Figure 17. Concentrations of NH4 (A) and NO3 (B) in KCl extracts of frozen and non-frozen soils. Except for a sixty day freezing period, all samples were processed identically.

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EDUCATION:

Ph.D. 1994 (June) College of Forest Resources (CFR), University of Washington; Ecosystem analysis program.

M.S. 1984 University of Washington; Soil microbiology and forest ecosystems. **Thesis:** Logging residue decomposition: decay rates of woody debris in four PNW ecosystems after harvesting.

B.A. 1977 Southern Illinois University, Carbondale, IL; Biology.

RESEARCH EXPERIENCE:

Predoctoral Research Associate II, CFR, University of Washington, 1991 - 1994; Predoctoral Research Associate I, CFR, University of Washington, 1989 - 1991.

> Currently completing independent research assessing the role of nutrient availability in affecting plant species composition and primary productivity in beaver-impacted wetlands. I have taken an experimenta l approach by increasing nitrogen and phosphorus availabilities and measuring plant responses in an extensively replicated field study.

Environmental Scientist/Quality Assurance Coordinator, Acid Deposition Program, NSI Technology Services, Inc., U.S. EPA Environmental Research Lab, Corvallis, OR., May 1986 -September 1989.

> Provided technical and managerial support for the EPA-funded Watershed Manipulation Project (WMP). Interacted extensively with university cooperators for field planning, project integration and quality assurance (QA). Designed and implemented an interlaboratory comparisons program to assess bias in measurements of soil and solution chemical parameters.

Research Assistant, College of Forest Resources (CFR), University of Washington, 1980-84.

> Conducted independent research on factors influencing decomposition of wood in PNW clearcuts. Directed and participated in a field study examining the effects of Mt. St. Helens ash on litter decomposition and soil biological processes.

Field Ecologist, Old Growth Wildlife Habitat Project, Oregon State University, Corvallis, and University of Washington, Seattle, 1983, 1984, and 1985 field seasons.

Collected field data characterizing structural features of old growth Douglas-fir forests in the Cascade and Coast Mountain ranges of Oregon and Washington.

Research Assistant, Forest Science, Oregon State University, 1984.

Conducted research examining decay rates of riparian plant species.

Field Technician, CFR, University of Washington, 1980.

Implemented field research measuring above-ground biomass of Pacific Northwest hardwood species (red alder and big leaf maple).

PROFESSIONAL AFFILIATIONS:

Ecological Society of America
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HONORS:

Associate member - Sigma Xi Scientific Research Society
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TEACHING EXPERIENCE:

Teaching assistant (FRM 502), Forest Ecosystem Analysis. Lectured on structure and function of riparian forests and on forests and the global carbon cycle. Spring 1992.

Guest lecturer (UHF 475), Wetland Ecology. Topic: Nutrient cycling in wetlands. Autumn 1991.

REU Program Instructor, Voyageurs National Park, MN. Advised and assisted two undergraduate students on the design and implementation of their field projects while conducting my own research. Summer 1990.

PUBLICATIONS:

Erickson, H.E. and R.L. Edmonds. 1994. Influence of Mount St. Helens' ash on litter decomposition II: Experimental studies with Douglas-fir needles. **Canadian Journal of Forest Research.** In press.

Edmonds, R.L. and H.E. Erickson. 1994. Influence of Mount St. Helens' ash on litter decomposition I: Pacific Silver fir needle decomposition in the ash fall zone. **Canadian Journal of Forest Research.** In press.

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Erickson, H.E. 1984. Logging residue decomposition: decay rates of woody debris in four PNW ecosystems after harvesting. M.S. Thesis, University of Washington.

TECHNICAL REPORTS:

Authored or co-authored five technical reports on file at the Environmental Protection Agency's Environmental Research Lab in Corvallis, OR.

ABSTRACTS AND PRESENTATIONS:

Erickson, H.E., J.Pastor and R.J. Naiman. 1993. Two years of plant community response to enhanced nutrient supply in productive wetland meadows. Society of Wetland Scientists 1993 Annual Meeting, June 1993, Edmonton, Alberta, Canada.

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Erickson, H.E. and R.L. Edmonds. 1983. Logging residue decomposition: A comparison of woody debris weight loss in four PNW coniferous ecosystems after clearcutting. Third International Symposium on Microbial Ecology, Aug. 7-12, 1983, East Lansing, MI.

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