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The Effects of River Connectivity on Floodplain Wetland Ecology in Jasper National Park, Alberta, Canada

By

Julie K. Guimond ©

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Abstract

Floodplain wetlands are characterized by seasonal flood disturbance. River flooding increases water level fluctuations, brings dissolved nutrients, and removes plant litter. A railroad embankment in 1915 altered the natural connections to the Athabasca River by bisecting the floodplain in Jasper National Park. Diversity, community structure, productivity and nutrient availability were investigated in floodplain marshes with varied river connectivity. Unique vegetation community types were observed in the disconnected, partially river-connected and fully river-connected marshes. Lack of flooding resulted in peat development, increased moss growth, and wetland succession to a fen. Moderately flooded marshes had the highest diversity (45 species), supporting the Intermediate Disturbance Hypothesis, and highest productivity. A high flood year resulted in decreased productivity in all floodplain wetlands and increased nutrient concentrations in river-connected marshes. Large flood disturbance, rather than low nutrients, may be more important in determining vegetation communities, diversity, productivity, and ecosystem stability in the fully river-connected marshes.

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1. Introduction

Floodplain wetlands are on fluvial floodplains and receive annual flooding and sedimentation (National Wetlands Working Group 1988). Floodplain wetlands are important features in the landscape because they control flooding, prevent downstream erosion, recycle nutrients and function as breeding and nursing grounds for fish, breeding and migratory resting sites for waterfowl, and wildlife corridors for larger mammals (Poff *et al.* 1997, Amoros *et al.* 2000). Despite their small area, floodplain wetlands support high biodiversity.

By rapidly changing the water levels in floodplain wetlands, seasonal floodwaters scour organic sediment, deposit suspended sediments, decrease water temperature, and increase turbidity, thereby acting as a natural disturbance (Poff *et al.* 1997, Amoros *et al.* 2000). Disturbance can be beneficial to a community by increasing diversity, removing excess organic matter, or inhibiting competitive exclusion (Connell 1978, Wilson and Keddy 1985).

The Intermediate Disturbance Hypothesis states that the highest diversity will be found at intermediate frequencies, durations, and intensities of disturbance (Connell 1978). At intermediate disturbance, diversity is highest due to an equilibrium between strongly competitive species and disturbance tolerant species (Huston 1979). At low disturbance, diversity is lower since less competitive species are excluded. At extreme disturbances, diversity is low since harsh conditions limit the species able to inhabit the area. Flood disturbance can also influence community structure by limiting flood intolerant species (Richter *et al.* 1997, Lenssen *et al.* 1999) and resetting successional patterns (Jean and Bouchard 1993).

Wilson and Keddy (1988) and Wisheu and Keddy (1989) found that disturbance directly limited plant net primary productivity (NPP) and standing crop. Disturbance can limit plant NPP by removing biomass (Grime 1973) and creating unfavourable conditions for growth (Resh *et al.* 1988). Nutrient limitations have been extensively studied as a variable controlling plant growth (Verhoeven and Arts 1987, Wisheu and Keddy 1989). Flooding can strongly influence nutrients in wetlands, by removing litter, increasing internal nutrient cycling, depositing sediments and dissolved nutrients, and as a result, should have an indirect influence on plant NPP. Many variables shown to influence plant

NPP are also influenced by river flooding, such as water levels (van der Valk 1994), temperature (Bernard and Gorham 1978), and species composition (Pérez-Corona and Verhoeven 1996).

Throughout history, beavers have altered natural hydrologic regimes by building dams. However, over this past century, anthropogenic development has also extensively altered river systems. Anthropogenic alterations include upstream damming, channel straightening, embankments, wetland drainage, and loss of lateral flow (Poff *et al.* 1997). Changes in timing of floods can be as important as loss of flooding and cause changes in ecological processes (Poff *et al.* 1997).

In Jasper National Park (JNP), the Athabasca River is a turbid river with peak flows in late-June and July from snowmelt and high discharge continuing through the summer from rain and glacial melt. River water enters the floodplain wetlands at peak flow. However, distances from the river and barriers to river water limit the amount of river water each wetland receives. A railway and highway (previously a second railway) have bordered the Athabasca River for 80 years and have cut off river water from the adjacent wetlands and lakes in several places. In contrast to the littoral zone in lakes, and stream and riparian studies, there have been few studies done in montane emergent marsh communities to determine the influence of flood disturbance.

The main objective of this thesis was to determine how flood disturbance affects several ecological parameters in wetlands with varying degrees of river connectivity. Specifically, diversity, community structure, NPP and nutrient availability of vegetation were investigated. Three areas were studied: riverine marshes (RM), which are fully connected to the river and reacts quickly to fluctuations in the river; beaver impounded marshes (BIM), which are partially blocked to the river by beaver dams but those dams are easily surpassed at high water levels; and railway impounded marshes (RIM), which are completely blocked from river water by a railway and water levels are stable due to impoundment by the railbed and beaver dams.

Chapter two examines the community structure and diversity of the floodplain wetlands. Multivariate analysis was used to determine the most important environmental variables separating species, sites and community types. The range of flood conditions in the study wetlands should lead to a range of community types. Relationships between diversity and the natural flood disturbance gradient were examined to test the Intermediate Disturbance Hypothesis.

Chapter three focuses on the effect of river flooding on aboveground plant standing crop and nutrient availability in floodplain wetlands of varying river connectivity. Nutrient limitations are assessed based on nutrients in the water column, nutrients in the sediment and reaction to experimental nutrient addition in the Jasper study wetlands. The occurrence of two hydrologic extremes, a year of low river discharge and a year of high river discharge, provided the opportunity to compare the effect of annual variation in flow regimes.

Chapter four summarizes the main findings from this study and makes some brief concluding remarks, including management implications for Parks Canada.

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2. The Effect of River Connectivity on Community Structure and Diversity of Montane Floodplain Wetlands in Jasper National Park, Alberta

Introduction

Floodplain wetlands are valuable features in the landscape. They provide high biodiversity, nutrient cycling, wildlife habitat, fish spawning grounds, and flood control (Poff *et al.* 1997, Pollock *et al.* 1998, Rundel and Sturmer 1998, Amoros *et al.* 2000). The ecological characteristics of floodplain wetlands are governed by their interaction with the main river channel (Gore and Shields, Jr. 1995). Fluvial processes (e.g. floods, meanders, sedimentation, incision) maintain dynamic floodplain structures such as side channels, oxbow lakes, and backwaters. This diversity in structure leads to diverse and productive aquatic vegetation (Bornette and Amoros 1991, Smith 1996, Abernethy and Willby 1999).

In fluvial systems, seasonal river flooding can act as a natural disturbance (Poff *et al.* 1997, Pollock *et al.* 1998, Amoros *et al.* 2000). Disturbance has been defined as a condition that removes biomass (Grime 1973) and can cause an abrupt change in natural communities (Resh *et al.* 1988). The Intermediate Disturbance Hypothesis states that highest species diversity will be found at intermediate frequency, intensity and duration of disturbance (Connell 1978, Ward and Stanford 1983, Bornette and Amoros 1996). In stable environments superior competitors can eliminate their competitors leading to decreased diversity (Huston 1979). At intermediate disturbance intensities, an equilibrium is reached between species of superior competitive ability in stable environments and species adapted to frequent disturbance. Thus, intermediate disturbance can maintain high diversity as has been found in several wetland studies (Day *et al.* 1988, Wilson and Keddy 1988, Wisheu and Keddy 1989, Bornette *et al.* 1998a).

Diversity in floodplain ecosystems varies greatly. Pollock *et al* (1998) had extremely high total species richness, 233 species but they sampled a wide variety of microhabitats in the Alaskan floodplains. Bornette *et al*'s (1998a) study of riverine wetlands in France had species richness counts ranging from 10-38 species, while other French riverine wetlands had lower species richness counts, 4-24 species (Bornette and Amoros 1996). Diversity can be examined at several scales (i.e. plot, site, landscape). Alpha (α) diversity is the measure of the diversity in each site, while gamma (γ) diversity is the measure of the total number of species in the landscape (i.e. all the Jasper study wetlands). From those values beta (β) diversity can be calculated, which is a measure of the rate of change of habitat or species turnover between the site and the landscape scale (Whittaker 1972).

Seasonal flood disturbance can also affect community structure. Flood frequency and magnitude are a major influence on the distribution of vegetation species in floodplains (Barnes 1978, Richter *et al.* 1997, Lenssen *et al.* 1999) but not all species in a community will be influenced by flooding in the same way (Wilson and Keddy 1988). Variation in hydrology at seasonal and annual time scales is a disturbance that maintains the earlier successional stages of wetland plant communities (Jean and Bouchard 1993) and thus, alteration of hydrologic disturbances can allow for succession to proceed. Changes in timing of floods can be as important as loss of flooding and causes changes in community composition (Wilcox 1995).

Hydrologic regimes can be changed through natural or human induced alterations. Beaver dams have a large effect on wetland areas by blocking inflows or impounding outflows (Naiman *et al.* 1988). Changes in channel morphology through sediment erosion or deposition, movement of woody debris, and channel incision will alter the flow regimes and ecological communities (Resh *et al.* 1988). If sufficient sediment is deposited a secondary channel may become isolated and eventually undergo wetland succession, as in the case of oxbow lakes.

Human alteration to river floodplains is common throughout the world and include upstream damming, channel straightening, embankments, groundwater pumping, wetland drainage, and loss of lateral flow (Bornette and Amoros 1991, Henry and Amoros 1995, Poff *et al.* 1997, Girel and Manneville 1998). As a result, the natural dynamics of floodplains are diminished and new floodplain wetlands are unable to form. Naiman *et al* (1993) estimate that 80% of riparian corridors have been lost over the past 200 years in North America. Roads and railways often follow river valleys since they have the gentlest grade (Patten 1998).

In the mountains near the headwaters of rivers, the impact of the hydrologic regime is more extreme and unpredictable than further downstream (Rundel and Sturmer 1998). The wetlands in this study are floodplain wetlands along the Athabasca River in

Jasper National Park (JNP) in the Rocky Mountains of Alberta, Canada. Within the Rocky Mountains, the floodplain wetlands are typically constrained to the montane zone (valley bottom to ~1350m in elevation). In JNP, the small area of the montane zone is valuable to a large number of plant and animal species and possesses the highest biodiversity of any ecosystem in the region. In Banff National Park, the Vermillion Lakes Wetland is home to 227 species of animals and plants but cover 0.2% of the park area (Banff-Bow Valley Study 1996). There have been very few studies of the wetlands of the Canadian Rocky Mountains (Cooper and Andrus 1994, Banff-Bow Valley Study 1996).

Similar to other floodplain systems, the cold floodwaters of the Athabasca River raise water levels and carry large quantities of suspended sediments and nutrients to the riverine wetlands. Water levels can rise quickly, going from dry sediment to 1.5 m in less than a week in some well connected wetlands. River floodwaters arrive in mid June with snowmelt and last about two months. Typical floodplains have base flows from groundwater and gradual snowmelt, while rapid spring snowmelt and intense storms can cause periodic flooding (Patten 1998). Melting of the glaciers in midsummer adds to the flood peak. Even with large amounts of river inputs, these wetlands are extremely nutrient poor with limited nitrogen availability.

There has been a combination of natural and human induced alterations to the river-flooding regime in JNP. Wetlands with fully connected channels can receive large amounts of river water. Other wetlands have floodwater inflows partially blocked by beaver dams that are surpassed at higher water levels, and still others are cut-off from the river floodwaters by the railway that has few culverts or bridges to allow for river water inflow. This produces a gradient of river connectivity that coincides with a gradient of flood disturbance. This provides an opportunity to examine the impact of disturbance on community structure and to assess if the diversity of these wetlands supports the Intermediate Disturbance Hypothesis.

All the Jasper study wetlands are sedge dominated with shrub hummocks in all but the fully connected wetlands. The wetlands are close to open water, bordering small lakes and channels of the Athabasca River floodplain but the amount of river water each wetland receives is dependent on distance from the main river, barriers to the inflow, and the magnitude of flooding. Considering the range of conditions found in the Athabasca

River floodplain wetlands, I would expect a range in communities in those wetlands. Thus, communities would be adapted to the degree of disturbance encountered at that site.

The specific objectives of this paper are threefold. First, to document the dominant plant community types in the Jasper montane wetlands. Second, to determine relationships between individual plant species, community types, and environmental variables. Finally, to examine the differences in the diversity of the Jasper wetlands, as measured by species richness, and to define relationships with environmental variables. Based on the Intermediate Disturbance Hypothesis, I expected diversity to be lowest in the open riverine sites receiving large amounts of river floodwaters and highest in the beaver-impounded sites receiving moderate amounts of floodwaters.

Site Description

Jasper National Park (JNP) is located in the Canadian Rocky Mountains in western Alberta (Figure 2.1). This area is characterized by a climate of long cold winters with high snow pack in the mountains and short cool summers with occasional hot spells (Holland and Coen 1982). The mean annual temperature is 3.1°C, with 95 frost-free days, and the mean precipitation is 393.7 mm, with 281.6 mm as rainfall and 143.9 mm as snowfall (Environment Canada 1994).

Three wetland areas, each with three study sites, were measured in 1998 and 1999 and represent the main montane floodplain wetland types in the Athabasca River valley in JNP. These sites differ in degree of connectivity to the Athabasca River. The wetland areas include riverine, beaver-impounded and railway-impounded marshes. Within each area there were three representative sites. Thus, sampling included three marsh areas (riverine, beaver-impounded and railway-impounded) each with three representative sites, with each site sampled in ten plots, for total of 90 plots.

Riverine Marsh Area

The riverine area is located in the east end of JNP by the Pocahontas warden station (53° 12' N and 117° 56' W) and is freely connected to the main Athabasca River by a secondary river channel (Figure 1). All these marshes are classified as floodplain marshes since they are adjacent to the main river and are seasonally inundated by river flooding (National Wetlands Working Group 1988). All three marsh sites are sedge dominated with no shrub cover and negligible moss growth.

Riverine Marsh 1 (RM1):

This marsh site is located closest to the inflow of the main river and has a mineral substrate with at least three metres of fine sediment deposits from the river. Tall *Salix* shrubs surround the marsh on all sides with a small channel entering the marsh.

Riverine Marsh 2 (RM2):

This marsh site, located further along the same inflow channel, is surrounded on two sides by channels. A thin line of Salix shrubs borders the back. The sediment in this site is largely mineral substrate with small amounts of organic deposits and undecomposed litter.

Riverine Marsh 3 (RM3):

This marsh site is even further along the same inflow channel and is surrounded on three sites by elevated *Picea glauca* forest and the fourth side is open water. The sediment is mineral with a thin, well-decomposed, organic layer on top.

Beaver-impounded Marsh Area

The beaver-impounded and railway-impounded areas are part of the same wetland complex that was bisected by the railway in 1912 (Figure 2.1). These are located further west in the park (53° 01' to 53° 02' N and 118° 05' to 118° 06' W). This wetland complex, consisting of channels, marshes, shallow lakes and forested sand dunes, is connected to the main Athabasca River by a secondary channel. Several beaver dams (<1 m high) are located along the inflow channel. The beaver dams are easily surpassed at high water levels and the outflow is unblocked. These marshes are classified as floodplain marshes since they are adjacent to the main river and are seasonally inundated by river flooding (National Wetlands Working Group 1988).

Beaver-impounded Marsh 1 (BIM1):

This marsh site is adjacent to a shallow lake with open water on one side and with *Salix* shrubs bordering the marsh the other side. The sediment has a well-decomposed organic layer overlaying alternating layers of mineral and organic sediment. The marsh is sedge-dominated with some hummocks with *Salix* shrubs and some hollows with more submersed cover and less emergent cover. Bryophytes are restricted to the drier edges and the hummocks.

Beaver-impounded Marsh 2 (BIM2):

This marsh site, adjacent to a shallow lake, is located at the outflow from the lake, although, there is no definite channel or substantial flow. It is bordered on two sides by elevated *Picea glauca* forest and by open water on the other two sides. The sediments are mostly fine minerals topped with a thin organic layer. The marsh is sedge-dominated with bryophyte cover restricted to the shallower edges.

Beaver-impounded Marsh 3 (BIM3):

This marsh site is along the outflow of the wetland complex. Two sides are bordered by *Salix-Picea* forest. The sediment is a mixture of mineral and organic matter. The marsh is sedge-dominated with a mixture of *Equisetum-Scirpus* in the wetter centre with. Bryophytes are more common at the edges and on hummocks.

Railway-impounded Marsh Area

The railway-impounded area is in the same area as the beaver-impounded marshes but is completely disconnected from the main Athabasca River by a railway embankment (Figure 2.1). This marsh complex consists of channels, marshes, shallow lakes and forest. These marshes are classified as shore marshes since they border permanent lakes and are subject to water level rise with the lake and wave action (National Wetlands Working Group 1988).

Railway-impounded Marsh 1 (RIM1):

This marsh is at a convergence of two streams. A beaver dam along one of those streams causes slow water to flow through the marsh. The back edge of the marsh is a sand dune with a drier *Picea* forest. Thick organic sediment is typical of most of the marsh. The marsh is sedge-dominated with floating *Scorpidium scirpoides* as the dominant bryophyte.

Railway-impounded Marsh 2 (RIM2):

This marsh is bordered by open water and Salix shrubs on one side. The plants are rooted in a bryophyte layer, which overlays a poorly decomposed peat layer, approximately 50 cm deep. It is a sedge- and bryophyte-dominated marsh.

Railway-impounded Marsh 3 (RIM3):

This marsh is located along the same lake as the previous marsh and has similar characteristics. The sedge and bryophyte dominated marsh covers poorly decomposed peat that is approximately 45 cm deep.

Methods

Diversity Survey

Each marsh site was set up with a grid design within the defined boundaries and was equally divided into 100 plots. Ten plots were then randomly chosen and marked. This method removed the bias of transect placement and also ensured that all sites measured 10% of the marsh area. Plots varied in size from 16 to 81 m^2.

The diversity survey was conducted in July 1998 to find most plants with flowers intact. All species were identified within the plot and a rank cover value was assigned (2- rare; 3- <25%; 4- 25-75%; 5- >75%). Since the plots varied in size between sites, an additional 20-minute survey was conducted around each plot. Any new species found in the additional survey were recorded and assigned a value of one on the rank scale. All plants were identified to species. The moss nomenclature follows Vitt *et al* (1988) and Ireland *et al* (1987). The emergent and submersed vascular plants follow the nomenclature of Moss (1983) except for most *Carex* spp., which follow Taylor (1983).

Several environmental variables were also measured within each plot. The percent cover of each vegetation stratum (moss, submersed, emergent and shrub) was estimated. In addition, an estimate was recorded of percent cover by water, litter, open sediment, rocks and deadfall. The height of the dominant vegetation, depth of the water, water temperature, conductivity and turbidity were also measured. Since some sites were dry when the survey was completed the conductivity and turbidity values were transformed into categories and dry sites were assigned a separate category from the other readings.

Environmental Variables

At each marsh site a permanent gauge was established for water level readings and water chemistry sampling location. Water levels were taken on a weekly basis starting in May. At each of those sampling times a water sample was taken for turbidity and conductivity analysis using a Hach® Pocket Turbidimeter™ and an Orion® Model 115 Conductivity, TDS, and Salinity Meter, respectively.

From May to the end of October, a water sample was collected for chemical analysis every three weeks from a location in the main Athabasca River and at each of the nine marsh sites. Samples were collected in acid washed 1 L Nalgene and 75 mL polypropylene bottles. The samples were analysed for nitrate (NO_3-N and NO_2-N), ammonia (NH_4-N), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP) and total phosphorus (TP). Nitrate samples were filtered using a 0.45 µm HAWP millipore filter, while ammonia samples were not filtered. TDN was digested with 4N H_2SO_4 and H_2O_2. Nitrate, ammonia, and TDN were analysed on a Technicon Auto Analyser II. TDP and TP were analysed using the methods described in Bierhuizen and Prepas (1985). SRP was analysed using the method of Menzel and Corwin (1965).

Sediment samples were collected in August of 1999 with a metal corer 4.4 cm in diameter. Three cores were taken from each of the nine study sites in randomly determined plots. The 10 cm core was separated in the field into upper and lower 5 cm segments and the lower layer was kept. The upper layer was not analysed since flooding caused scouring and sediment deposition in the top layer and the objective was to determine the nutrient concentration of the rooting zone. Cores were frozen at -10°C until analysed.

Cores were freeze dried, sieved to 2mm and larger material was homogenized with a Wiley mill to 2 mm. The ground sample was analysed for total nitrogen (TN) and total carbon (TC) using a HCN auto-analyser. Total phosphorus (TP) was analysed by persulfate oxidation digestion (Menzel and Corwin 1965). All concentrations are expressed as % of dry weight. Bulk density was determined using dried samples and organic content was determined by combustion at 550°C, then the ash was weighed.

Many researchers have used water level fluctuations (Johnson and Leopold 1994, Wilcox 1995) or flood frequency (Weiher *et al.* 1996, Pollock *et al.* 1998) as a measure of disturbance. In this study, water level fluctuations were highest in the most river-connected sites and lowest in the most disconnected sites. Therefore, a measure of the disturbance gradient was created using the amplitude of water level fluctuation, defined as the difference between the highest and lowest water levels at each site.

Statistical Analyses

Species abundance data were analysed using two-way indicator species analysis (TWINSPAN) using PC-ORD (Version 3.17: McCune and Mefford 1997) to determine if vegetative differences occurred between sites. This is a divisive hierarchical method of yielding a classification of both sites and species (Hill 1979). Direct gradient ordination was used to determine potential relationships between species and environmental variables. Canonical correspondence analysis (CCA) was used for direct ordination with the program CANOCO (Version 4.0: ter Braak and Smilauer 1998a). Direct gradient analysis constrains the site and species scores to a linear combination of the environmental variables. A CCA Monte Carlo test with forward selection was used to determine significant environmental variables. With this method, all environmental variables were retained in the ordination. For simplification of the CCA graph, the only environmental variables included had t-values greater than 2.1 for the first two axes (ter Braak and Smilauer 1998b).

Differences in diversity between all nine sites and between the three wetland areas were determined using analysis of variance (ANOVA) with a post-hoc test (Tukey's HSD) to determine which factors were significantly different. Relationships between diversity and environmental variables were determined using linear and quadratic regressions. Homogeneity of variances, an assumption of ANOVA's, was tested using Bartlett's test and when heterogeneity occurred the data was log transformed (Sokal and Rohlf 1995). This transformation should also remedy non-normality in the data. All statistical procedures were completed in SYSTAT Version 8.0.

Results

Community classification

The TWINSPAN classification of the 90 plots yielded eight community types after three levels of division (Figure 2.2). In general, riverine marshes had unique community types compared to the beaver and railway-impounded marshes. The beaver-impounded marshes and RIM1 together had three unique community types, while RIM2 and RIM3 were grouped together with high moss cover and different vascular plants. Refer to Appendix I for full species list with authorities and cover values.

The first level of division, with an eigenvalue of 0.320, separated the riverine marshes from the beaver and railway-impounded marshes (Table 2.1 and Figure 2.2). The second and third levels of division further divided the riverine marshes into community types that coincided with the individual study sites. At the same time, the second level of division separated the beaver-impounded marshes and RIM1 from RIM2 and RIM3. The third level of division separated these community types based on landscape position, wet versus dry.

Eight distinct community types, defined by the TWINSPAN classification, are described below with indicator species, dominant species and characteristics.

1) Dry *Drepanocladus-Carex aquatilis*: Indicator species for this community type included high cover of *Carex aquatilis*, high cover of *Drepanocladus aduncus*, and presence of *Aster borealis*. This group also typically had high cover of *C. utriculata* and low cover of *Cornus stolonifera, Equisetum fluviatile, Salix* spp. and *Utricularia intermedia*. This group tended to have minimal natural disturbance, which led to moss growth but no peat development. It was commonly found close to shrub edges or hummocks. It was found in only three plots that were from RIM1 and BIM2 (Table 2.1).

2) Wet *Drepanocladus-Carex aquatilis*: Indicator species for this community type included high cover of *Carex aquatilis*, high cover of *Drepanocladus aduncus*, and absence of *Aster borealis*. Other dominant plants included *Equisetum fluviatile* and *Utricularia intermedia* and common plants included *Carex diandra, Potamogeton pectinatu,s* and *Bryum pseudotriquetrum*. This community type was only found in RIM2 and RIM3 (Table 2.1) and had minimal natural disturbance, which led to moss growth and peat development.

3) Wet *Carex utriculata-Equisetum fluviatile*-submersed aquatics: There were many indicator species for this community type. The indicator species were high cover of *Carex aquatilis*, moderate cover of *Potamogeton pectinatus*, presence of *Potamogeton filiformis*, presence of *Sium suave,* and absence of *Drepanocladus aduncus*. This community type was also dominated by *C. utriculata*, *Equisetum fluviatile*, *Utricularia intermedia* and *U. vulgaris*. This community type was found in the beaver-impounded

marshes and RIM1 (Table 2.1) and had moderate natural flood disturbance and was relatively wet, which lead to high submersed vegetation cover.

4) Dry *Carex utriculata-Equisetum fluviatile*: The indicator species for this community type were high cover of *Carex aquatilis*, and absence of *Potamogeton pectinatus*, *Potamogeton filiformis*, *Sium suave*, and *Drepanocladus aduncus*. Other dominant vegetation included *C. utriculata*, *Equisetum fluviatile* and common, less dominant plants included *Equisetum palustre*, *Salix* spp. and *Aster borealis*. This community type had similar dominant vegetation to community type 3 but the drier environment lead to the absence of submersed species. This group was also restricted to beaver-impounded marshes and RIM1 (Table 2.1).

5) *Eleocharis palustris-Carex utriculata*: Several species were indicators for this community type. They included high cover of *Eleocharis palustris*, moderate cover of *Utricularia minor*, presence of *Ranunculus reptans*, *Mentha arvensis*, and *Deschampsia cespitosa*, and absence of *Equisetum fluviatile*. Dominant vegetation in this community type also included *Carex utriculata* and *Carex saxatilis*, and common but less dominant was *Scirpus acutus* and *Juncus alpinoarticulatus*. This community type was found entirely in RM3 (Table 2.1).

6) *Carex utriculata-Eleocharis palustris-Equisetum fluviatile*: Several species were indicators for this community type. They included high cover of *Eleocharis palustris*, moderate cover of *Utricularia minor*, presence of *Ranunculus reptans*, *Mentha arvensis*, *Deschampsia cespitosa*, and *Equisetum fluviatile*. This was a very mixed community type with many of the same plants as community type 5, previously described. However, *Bryum pseudotriquetrum*, *Triglochin maritima* and *Sium suave* were common with low cover. This community types was found entirely in RM2 (Table 2.1).

7) Wet *Carex saxatilis*: Several species were indicators for this community type. They included high cover of *Eleocharis palustris*, moderate cover of *Ranunculus reptans*, presence of *Mentha arvensis* and *Deschampsia cespitosa*, and absence of *Utricularia minor*. This community type was also dominated by *Carex saxatilis* and has low cover by *Carex aquatilis*. This community type was restricted to RM1 (Table 2.1) and was

typically in a wetter environment, which explains the higher cover of the submersed plant *Ranunculus reptans*.

8) Dry *Carex saxatilis-Equisetum fluviatile*: Several species were indicators for this community type. They included high cover of *Eleocharis palustris*, presence of *Mentha arvensis*, *Ranunculus reptans* and *Deschampsia cespitosa*, and absence of *Utricularia minor*. This community type was also dominated by *Carex saxatilis*, *Equisetum fluviatile* and *Carex utriculata*. In addition, two mosses, *Bryum pseudotriquetrum* and *Campylium stellatum*, were also common with low cover. This community type as found exclusively in RM1 (Table 2.1) and was common at the drier edge compared to community type 7.

Direct Gradient Ordination

A canonical correspondence analysis (CCA) was used for the direct gradient ordination. The first axis expresses the best relationship between species and the environment and each subsequent axis expresses the next best relationships. The first axis separated community types 5-8, found only in the riverine marshes, from community types 1-4, found in the beaver-impounded and railway-impounded marshes (Figure 2.3). The second axis separates community types 1 & 2, wet and dry *Drepanocladus* dominated marshes, from community types 3 & 4, wet and dry *Carex utriculata-Equisetum fluviatile* dominated marshes. The first two axes contributed to the majority of the variation explained by this analysis (Table 2.2). In addition, the environmental variables used in this ordination were good indicators of the species variation in this ecosystem (Table 2.2).

The first four axes of the ordination explained 26.6% of the variance in the species dataset (Table 2.2). The high eigenvalue of the first axis suggests this axis explains most of that variation. A large decline in the eigenvalue of the second and even greater decline in the third and fourth axes indicates that they do not contribute to the variation in the species data.

Based on the high species-environment correlation values of the first two axes ($R^2_{axis\ 1}$= 0.853 and $R^2_{axis\ 2}$= 0.859), the measured environmental variables explained a large proportion of the species variations along those axes (Table 2.2). The lower correlation values of the third and fourth axes suggest that the environmental variables did not explain the species variation as adequately. Based on the low eigenvalues and the low species-environment correlation values, the third and fourth axes will not be discussed further.

The importance of each environmental variable can be determined by the canonical correlation and the t-values, the higher the values the more important the variable. The most important variables for defining the first axis were water conductivity and amount of organic sediment (Table 2.3). These variables were in opposite directions. Thus plots and species on the right side of the ordination had high conductivity and low organic sediments (Figure 2.3). The second axis was defined by water depth, amount of hummocks and amount of organic sediment (Table 2.3). Again, these were in opposite directions; the plots and species at the top of the ordination had shallower water, high organic sediments, and lot of hummocks (Figure 2.3). Water depth in the beaver-impounded and riverine marshes varied greatly through the year and the water depths in this analysis were taken only one point at the end of July after the floods had almost completely receded. Fluctuation in individual plot water levels over the whole summer may be a better environmental variable but could not be measured in this study.

The first axis of the ordination of plots categorized by community types separated community types 5-7, found exclusively in the riverine sites, from community types 1-4, found in beaver- and railway-impounded sites (Figure 2.3). Thus, the first axis appears to define the unique riverine community types based on high water conductivity and low organic sediments. The second axis effectively spread community types 1-4. Community types 1 & 2, wet and dry *Drepanocladus aduncus* dominated plots, are separated from community types 3 & 4, wet and dry *Carex utriculata-Equisetum fluviatile* dominated plots. The *Drepanocladus aduncus* dominated plots have higher organic sediments, more hummocks, and lower water levels than the *Carex utriculata-Equisetum fluviatile* dominated plots. The first two axes then separated these community types into three main groups: community types 1 & 2, which have almost no flood disturbance, community types 3 & 4, which have moderate flood disturbance, and community types 5-8, which have high flood disturbance. Thus, the ordination coincides well with the natural disturbance gradient existing in these wetlands and with the order of separation in the TWINSPAN classification.

The ordination provided some information on individual species (Figure 2.3). The common species tended to be in the centre of the ordination, e.g. *Carex aquatilis, C. utriculata, C. utriculata,* and *Equisetum fluviatile.* Indicator species (e.g. *Mentha arvensis, Ranunculus reptans,* and *Deschampsia cespitosa*) and common species (e.g. *Carex saxatilis*) of community types 5-8, found in the riverine sites, were restricted to the far right of the ordination, which is also where these community types were located in the ordination. Mosses (e.g. *Drepanocladus aduncus, Campylium stellatum,* and *Bryum pseudotriquetrum*) were found in the upper half, which means they are associated with hummocks and organic sediments. Although mosses were dominant in community types 1 & 2, found in the upper, left portion of the ordination graph, they are found in most sites, which would explain why the mosses were near the centre of the graph. For simplicity, only the common and indicator (as defined by TWINSPAN) species are labelled in Figure 2.3.

Vegetation Cover Characteristics

Percent cover of the emergent stratum was lowest in RIM2 and RIM3, the most disconnected marshes, while bryophyte cover was significantly higher in RIM2 and RIM3 (Figure 2.4). Submersed vegetation cover was slightly higher in RIM2 and RIM3. Shrub cover was negligible in all sites. Most shrubs encountered were *Salix* spp. that were extremely dwarfed, most likely due to saturated roots, and thus, were unable to be identified to species.

The differences in cover between sites in the emergent stratum were not significant. Bryophyte cover was significantly higher in RIM2 and RIM3 than all other sites except RIM1, which was intermediate ($p<0.05$). Submersed vegetation cover was variable but overall, was highest in the railway-impounded sites. RM1 had significantly lower submersed vegetation cover than RIM2, RIM3, and BIM3 and BIM2 had significantly lower submersed vegetation cover than RIM2 ($p<0.05$).

Species Richness and Diversity

There were 95 plant species identified in the 90 sample plots from nine study sites (Table 2.4, see Appendix for full species list). Vascular plants contributed to most of that number (66 emergent species and 17 submersed species), while non-vascular plants contributed the remaining species (1 submersed and 11 bryophytes). Most of the species were emergent (Table 2.5). There was little variability between sites and none between areas in the number of submersed species. The bryophyte layer varied slightly between sites but with no clear trends. There was a higher total number of bryophyte species in the beaver-impounded area (Table 2.5), although the abundance of bryophytes was higher in the railway-impounded area (Figure 2.4).

Site diversity was measured by species richness. Species richness was a good representation of the existing species in this study due to the large plot sizes and the additional species survey surrounding each plot. Alpha (α) diversity is a measure of the total number of species in each site, gamma (γ) diversity is a measure of the total number of species in the landscape (i.e. all the Jasper study wetlands), and beta (β) diversity is a measure of the rate of change or species turnover between the alpha and gamma diversity (Whittaker 1972). Beta diversity is calculated as $\beta = \gamma/\alpha$.

Mean plot species richness was not significantly different between sites (Table 2.4, Plot SR). On the other hand, site alpha diversity was highest for BIM1 and BIM2 (Table 2.4, Site SR α). Total species encountered in the beaver-impounded area was highest (66 species), while the riverine area had the lowest area species richness (37 species) (Table 2.4, Area SR). The railway-impounded area was intermediate in diversity. Site beta diversity was highest for the most river-connected site (RM1) and lowest for partially river-connected sites (BIM1 and BIM2) (Table 2.4). Thus, there was little turnover of species within the beaver-impounded area but a high turnover of species in RM1.

A total of 61 species were unique to one of the three study areas, comprising 64.2% of the species in the Jasper study wetlands. The number of unique species in each site significantly increased as the site alpha diversity increased (Figure 2.5, R^2=0.83, $p<0.05$). On a site basis, the highest numbers of unique species were found in BIM1 and BIM2 and also, on an area basis the highest number of unique species was found in the beaver-impounded area (Table 2.5). Twenty-four species, or 25% of all species, were ubiquitous to all three areas.

Diversity comparisons between TWINSPAN community types were not possible since total community type species richness was strongly related to the number of samples in each group (R^2=0.7024, $p<0.05$). Group sizes varied from 3 to 21 samples.

Relationship Between Diversity and Environmental Variables

Simple relationships between environmental variables and site alpha diversity were few. Site alpha diversity had a significant linear relationship with peak water nitrate concentration, and maximum water depth (Figure 2.6). Both mean seasonal and peak water nitrate concentration showed a significant relationship with site alpha diversity (mean: R^2=0.479, $p<0.05$, $y = 37.72 - 0.44x$, and peak: R^2=0.504, $p<0.05$, $y = 38.12 - 0.46x$). Since the trend was very similar to that of peak water nitrate concentration, only peak water nitrate concentration is shown (Figure 2.6). There was a significant quadratic relationship between peak water N:P and site alpha (Figure 2.6). Mean N:P ratio showed the same trend ratio (R^2=0.731, $p<0.05$, $y = 43.96 - 7.82x + 0.93x^2$) but the data is not shown. However, the far right data point was a statistical outlier for both mean and peak N:P and when it was removed, the remaining data gave a negative linear relationship (Figure 2.6, dashed line).

Water level amplitude, which was highest in the riverine sites, was used to estimate the natural flood disturbance gradient. This derived gradient effectively represented the distance of each site from the river (i.e. the source of disturbance). The relationship between diversity and this measured disturbance gradient produced a quadratic relationship. Although the relationship as not significant, it suggests that maximum diversity exists at intermediate levels of disturbance (Figure 2.7). However, 1998 was a relatively low water level year. Flood magnitude would strongly influence the disturbance gradient and thus, the amplitude of water level fluctuations in 1998 may not properly reflect the true gradient of disturbance.

Discussion

Community classification

The TWINSPAN community classification showed the differences between the three main groups of marshes studied (riverine, beaver-impounded and railway-impounded marshes) (Figure 2.2). The eight community types defined by TWINSPAN closely coincide with the nine study sites. Most importantly, the riverine sites were separated in the first division indicating that their community structure is very unique. These sites were fully connected to the river and respond quickly to river flooding. Dry, exposed sediments in spring and fall and high water levels in mid-summer have produced unique community types.

Riverine marshes were defined as four community types. The high degree of river connectivity and thus, flood disturbance, is strongly influencing the vegetation structure (Mitsch and Gosselink 1993, Bornette *et al.* 1998a, Lenssen *et al.* 1999). *Carex saxatilis* and *Ranunculus reptans* were species unique to the riverine sites and appear to be adapted to extensive flooding. *Carex saxatilis* grows in clumps with litter retained at the base of the clumps while the surrounding litter is removed. *Ranunculus reptans* grows well either submerged or exposed and is a short plant growing from runners. Little is known about flood tolerances of individual emergent plant species (Amoros *et al.* 2000).

The second level of division separate most of the beaver-impounded sites, along with RIM1, into two community types, based on moisture (wet vs. dry habitats). This suggests that microtopography is important in these marshes. Small hummocks with drier community types and even shrub growth were common in the beaver-impounded area. Several studies have found microtopography to be important in determining community structure (Barnes 1978, Day *et al.* 1988) and diversity (Vivian-Smith 1997). The species in these community types are common to other wetlands in Alberta (Thormann and Bayley 1997, Mewhort 2000) except that the more nutrient-loving species such as *Typha angustifolia*, *Phragmites communis*, and *Carex lasiocarpa* were not found.

The dry *Drepanocladus-Carex aquatilis* community type had high moss cover but also a higher prevalence of drier species, e.g. *Aster borealis*. The presence of drier species indicates that this community type is the drier edge habitat that receives less floodwater due to higher elevation within the site. Day *et al* (1988) also found elevation within sites to be an important factor determining vegetation structure.

TWINSPAN classified RIM1 differently from the other railway-impounded sites. Two plots from RIM1 were included in the dry *Drepanocladus-Carex aquatilis* community type but the remaining eight plots were part of the two beaver-impounded community types. Although, water levels were stabilized in this marsh, it was more similar to the beaver-impounded sites than the other two railway-impounded sites. This is likely due to a beaver dam, which forces water through this marsh. The flow may prevent large quantities of moss from developing. Higher water velocity can act as a disturbance to aquatic plant communities by removing sediment (Henry *et al.* 1994) and litter (Wilson and Keddy 1985).

The wet *Drepanocladus-Carex aquatilis* community type had high moss cover but had less emergent plant cover, a developing peat layer, and species more indicative of fens. A study of fens of the eastern Rocky Mountain Foothills of Alberta found that *Menyanthes trifoliata*, *Campylium stellatum*, *Drepanocladus* spp., *Carex limosa*, and *Tomenthypnum nitens* are indicator species (Slack *et al.* 1980); the first three of those are found this community type. A similar study of fens in the Rocky Mountain Ranges of Wyoming found the *Isoetes* sp., *Menyanthes trifoliata*, *Carex utriculata*, and *C. aquatilis* were common (Cooper and Andrus 1994).

The wet *Drepanocladus-Carex aquatilis* community type was exclusively found in RIM2 and RIM3. Characteristics of those sites (i.e. dominant plant species, importance of bryophyte cover, lack of river flooding, increased importance of groundwater, and some peat development) suggest succession from a marsh to a fen community due to stabilization of water levels by the railway. Successional processes that lead to terrestrialization in wetlands are due to organic sediment deposition (Henry and Amoros 1995). Floods prevent terrestrialization by removing organic material. Stabilization of water levels caused anoxic conditions in the sediment and decreased decomposition leading to peat development (Zoltai and Vitt 1990, Nicholson and Vitt 1994, Amoros *et al.* 2000). Attempts were made to quantify decomposition rates in the marshes but sediment accumulation due to flooding with sediment-laden water caused problems with the decomposition experiment. Peat stratigraphy should be examined to confirm this hypothesis of fen succession (Nicholson and Vitt 1994).

This trend of increasing moss cover is common in wetland succession from marsh to fen and typically, the first mosses were *Campylium stellatum* and *Drepanocladus* spp (Glime *et al.* 1982, Mitsch and Gosselink 1993). It is known that mosses become increasingly prevalent and peat becomes much thicker in fens, but it is not well documented whether moss leads to peat development or whether peat development causes moss growth (Glime *et al.* 1982). In this study we were able to see large moss cover without substantial peat development, supporting the theory that moss starts submerged, slowly becomes emergent, and further buffers minor water level fluctuations, thus creating an environment for peat development.

Direct Gradient Ordination

The similar order of separation of the community types in the TWINSPAN (Figure 2.2) and in the CCA ordination (Figure 2.3) indicates the environmental variables used in the ordination are good indicators of the true environmental gradient affecting vegetation. This was supported by the high species-environment correlations for the first two axes (Table 2.2). Work in riverine marshes of the Ottawa River (Day *et al.* 1988), the Nile Delta sand dunes (Shaltout *et al.* 1995) and Egyptian alluvial fans (Moustafa and Zayed 1996) found strong relationships between community classification and ordination.

The most important environmental variables defining the first axis are water conductivity and sediment organic content (Table 2.3, Figure 2.3). Riverine sites tended to have extremely high conductivity values due to groundwater inputs. Although all three areas have groundwater sources, the diverse geology of the area creates highly variable ionic concentrations in groundwater. Thus, the community types 5-8, which are found exclusively in the riverine sites, are associated with high water conductivity values. The riverine community types (#5-8) are associated with large fluctuations in water levels due to river inputs. Those fluctuations lead to the removal of litter and thus, the sediments have low organic content (Table 2.6 & 2.7). Those community types with very low organic contents were separated from the other community types on the first axis (Figure 2.3).

The second axis was defined by a positive relationship with organic sediments and hummocks, and a negative relationship with water depth. The second axis spread community types 1-4 along the axis. The wet and dry *Drepanocladus aduncus* dominated community types (1 & 2), which are almost restricted to the railway-impounded area and have stable water levels and peaty soil, were at the top with high organic sediments and hummocks. The wet and dry *Carex utriculata- Equisetum fluviatile* community types (3 & 4), which have moderate flood disturbance and thus, well decomposed sediments, are at the bottom with high water depth, low organic sediment and few hummocks (Figure 2.3).

Day *et al* (1988) found that litter accumulation and microhabitat elevation were important variables in the distribution of species in their ordination. Jean and Bouchard (1993) also found water depth and peat thickness to be important variables in determining plant composition in riverine wetlands. However, in this analysis, water depth was not representative of the beaver-impounded and riverine sites, both connected to the river, since water levels can fluctuate greatly and the reading was taken on a single day (Table 2.6). Since 1998 was a dry year, water levels had already receded by the time of the diversity survey in the riverine sites but had earlier peaked at 60cm. Fluctuation of water levels is known to be an important variable determining plant distribution (van der Valk 1994, Bornette *et al.* 1998a, Lenssen *et al.* 1999).

Diversity

Species richness in this study appears to be within the range of other riverine wetlands. Pollock *et al* (1998) had extremely high total species richness, 233 species compared to our 96 species, but they sampled a wide variety of habitats in the Alaskan floodplains. Bornette *et al*'s (1998a) study of French riverine wetlands had similar species richness to this study, 10-38 species, while other French riverine wetlands had lower species richness counts, 4-24 species (Bornette and Amoros 1996). Wisheu and Keddy (1989) also had lower species richness counts, 0-23 species, on Nova Scotia, lakeshores but they also had smaller plot sizes than this study.

Emergent species represented the largest group, which is similar to other studies that found forbs to have the largest representation (Pollock *et al.* 1998, Rundel and Sturmer 1998). Also, sites with high total alpha diversity also had more species unique to that site (Figure 2.5). Bornette *et al* (1998a) found no relationship between species richness and the number of rare species. Variation in disturbance can influence community structure but will not influence all species in a community the same way (Wilson and Keddy 1988). Thus, some species are ubiquitous while others are found only at the extremes. In this study, 25% of the species were ubiquitous to all sites and those were the plants that tended to be dominant and common in marshes and fens, e.g. *Carex aquatilis*, *C. utriculata*, *Equisetum fluviatile*, *E. palustre*, and *Eleocharis palustris* (Slack *et al.* 1980, Holland and Coen 1982, Cooper and Andrus 1994, Thormann and Bayley

1997, Mewhort 2000). In contrast, 64.2% of the species were unique to one of the three wetland areas.

The mean plot diversity was not significantly different between sites (Table 2.4). Moore and Keddy (1989) found that the relationships between diversity and disturbance were scale dependent, and relationships that were true among vegetation communities were not true within vegetation communities. Thus, a better relationship should be seen at the site and area diversity scales instead of the plot scale in this study.

However, site alpha diversity was highest in the two beaver-impounded marshes, followed by the railway-impounded area, while riverine area had the lowest alpha diversity (Table 2.4). Species richness of each of the three areas showed the same trend of increasing from riverine to railway-impounded to beaver-impounded. Wilson *et al* (1993) found that species richness decreased with increasing organic matter, similar to the decrease in species richness from the beaver-impounded to the railway-impounded marshes. Wilcox (1995) found that water level fluctuations on a seasonal and an annual basis could increase diversity, which supports the higher diversity in the river-connected beaver-impounded sites than the disconnected railway-impounded sites. However, Bornette *et al* (1998a) found excessive flood disturbance, associated with strong connectivity to the river, decreased diversity, similar to my findings.

Diversity and Environmental Variables

Maximum water depth was highest in areas with high connectivity to the river. Riverine sites had high maximum water depths (Figure 2.6), which may have eliminated many species less adapted to flooding, resulting in low diversity (Grime 1973). The highest site alpha diversity occurred in sites with low mean nitrate and peak nitrate concentrations (Figure 2.6). Nitrates are carried by snowmelt (Lewis and Grant 1979) and were high in the fully connected riverine sites. In a higher flood year the nitrates would be higher in the partially connected beaver-impounded sites and thus, may change the relationship.

The ratio of biologically available N:P had a curvilinear relationship with diversity (Figure 2.6). This relationship is driven by the peak value in BIM2, where the ammonium concentrations of this marsh site were higher than the other sites (Table 2.6) and resulted in a higher N:P ratio. Since BIM2 is a moderately flooded wetland, there maybe higher N-mineralization by soil microbes, which yields ammonium. When that data point was removed, the resulting linear relationship supported past findings of decreasing diversity with increasing fertility (Day *et al.* 1988, Moore *et al.* 1989, Best *et al.* 1993). Nutrient limitation in water can control diversity in wetlands but most literature has found sediment nutrients to be a more limiting factor for plants (Bedford *et al.* 1999). Sediment nutrients were not related to diversity in the Jasper floodplain wetlands. Very few relationships were found between species richness and environmental variables. Grace and Pugesek (1997) also found very few relationships between species richness and individual variables but found multivariate relationships were much stronger.

Natural Disturbance Gradient

Analysis of the diversity along a natural flood disturbance gradient suggested that diversity was highest at intermediate levels of disturbance (Figure 2.7). Since beaver-impounded sites have moderate connections to the river and by definition, intermediate seasonal disturbance, the high diversity in this area supports the Intermediate Disturbance Hypothesis (Connell 1978, Ward and Stanford 1983, Bornette and Amoros 1996). Moderate flood disturbance allows for movement of materials and increased spatial heterogeneity, which leads to increased species richness (Gosselink and Turner 1978). Intermediate disturbances, in this case river flooding, allows for co-existence of poorly competitive, flood tolerant plants and highly competitive, less flood tolerant plants and thus, increased diversity (Grime 1973). The high natural disturbance in the riverine marshes results in exclusion of flood intolerant species and thus, lower species diversity was found. Similarly, lack of flood disturbance allows for competitive exclusion and thus, lower diversity in the railway-impounded sites.

The relationship between diversity and disturbance was not significant. There is a large difference in the water level amplitudes between riverine and the other marshes but not between the railway- and beaver-impounded marshes. This is due to low water levels in 1998. A dry year seems to have the largest effect on the magnitude of the disturbance gradient in the moderately connected sites. It is possible that other variables would be better measures of the disturbance gradient. Other researchers have used organic content or bulk weight of sediment as a measure of disturbance (Wilson and Keddy 1985, Abernethy and Willby 1999). High organic matter content or low bulk density indicates low disturbance since floods remove accumulated litter and organic matter. In addition, the proportion of the sediment total carbon sequestered in organic and inorganic forms would differ with flood disturbance. Organic carbon would be high in low disturbance sites while inorganic carbon, which is deposited from the river floodwater, would be low. The opposite would be true in flood disturbed sites. However, these variables do not incorporate annual variation in the magnitude of disturbance. No other individual variable had a strong relationship with diversity. The best way to resolve this problem would be to use multivariate regressions but low sample size in this study prevents its use.

Conclusions

There appears to be a distinction between the riverine marshes and the other two marsh areas. This distinction was evident in community structure, diversity and environmental variables. The beaver-impounded marshes were more diverse and were defined by two distinct community types. The three railway-impounded sites were not consistent in their characteristics. RIM1 appears more similar to the beaver-impounded sites than RIM2 and RIM3. These latter two sites had an increase in moss cover and a decrease in emergent cover. Their community types were distinct from the other sites. Increased moss cover, decreased emergent cover, peat development, stable water levels, and increased importance of groundwater inputs all suggest that these sites are in succession to fens. Variation in hydrology at seasonal and annual scales is a disturbance that maintains successional stages of wetland plant communities, prevents terrestrialization (Jean and Bouchard 1993) and causes diverse communities (Wilcox 1995).

On the other hand, the riverine sites have fully intact flows with the river. Water levels fluctuate greatly, even in low water years like 1998, leading to a harsh environment. Sediments are dry from early fall to late spring, resulting in plants' exposure to winds at low water levels. During floods, the water levels rise quickly, the water is very turbid and cold, and the plant litter is removed. Consequently, many plants were unique to the area and diversity was low since few plants are adapted to extreme flooding.

Finally, the beaver-impounded areas received moderate amounts of river flooding due to beaver dams. Flood tolerant species and competitive species adapted to stable environments were in equilibrium leading to higher diversity (Huston 1979, Bornette and Amoros 1996). Thus, the Intermediate Disturbance Hypothesis is supported.

Plant communities in floodplain wetlands respond to flood disturbance. River flooding causes changes in the physical environment such as deposition of fine sediments, removal of organic matter or litter, and exposure of sediments changing soil conditions to promote internal nutrient cycling. As a result, nutrient availability increases and species composition and competitive abilities of individual species change. This was evident in the river-connected Jasper wetlands, riverine and beaver-impounded. The impact of the loss of this flood disturbance is visible in the disconnected wetlands, railway-impounded.

Overall, the diversity in hydrologic regimes between the three wetland areas has created high landscape-level species diversity. However, the railway-impounded areas are a response to human induced changes to river flooding and are not natural. The fens that are forming in this area are a response to the railroad impoundment. Parks Canada management is required to maintain and restore natural biodiversity and ecological integrity (Government of Canada 1988). Ecological integrity has been defined as when an ecosystem has the characteristics of native species and biological communities, rates of succession, and supporting processes (Parks Canada Agency 2000). Therefore, the management of these wetlands needs to consider the communities and diversity due to human alteration of flooding separately from the communities and diversity in naturally flooded areas. Management of riverine ecosystems, by managing the range of natural variability, is the most appropriate way to maintain and diverse, resilient and productive systems (Richter *et al.* 1997, Poff *et al.* 1997, Bornette *et al.* 1998b). To maintain ecological integrity and biodiversity we must maintain natural hydrologic regimes.

Table 2.1: The number of plots from each of the nine study sites that are included in the eight community groups defined by TWINSPAN.

Sites	Community Types							
	1	2	3	4	5	6	7	8
RIM1	2	--	--	--	--	--	--	--
RIM2	--	10	--	--	--	--	--	--
RIM3	--	10	--	--	--	--	--	--
BIM1	1	--	2	7	--	--	--	--
BIM2	--	--	3	7	--	--	--	--
BIM3	--	--	9	1	--	--	--	--
RM1	--	--	--	--	--	--	7	3
RM2	--	--	--	--	--	10	--	--
RM3	--	--	--	--	10	--	--	--

Table 2.2: Summary of canonical correspondence analysis (CCA).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.247	0.166	0.104	0.075
Species/environment correlation	0.853	0.859	0.761	0.765
Cumulative % variance of species data explained	11.1	18.6	23.2	26.6

Table 2.3: Regression coefficients and t-values of the significant environmental variables with the first two axes of canonical correspondence analysis (CCA).

	Canonical coefficients		t-Values	
Variables	Axis 1	Axis 2	Axis 1	Axis 2
Water depth	-0.1981	-0.5633	-1.9092	-5.5757
Temperature	0.1356	-0.0438	1.8596	-0.6177
Turbidity	-0.0824	0.1115	-1.0995	1.5276
Conductivity	0.6392	-0.0721	7.3168	-0.8476
Height of vegetation	-0.1369	-0.0719	-1.6736	-0.9025
Litter	0.0264	0.0395	0.3508	0.5383
Open water area	-0.1531	0.0994	-1.6666	1.1113
Hummocks	-0.0834	0.1938	-1.1924	2.8471
Organic sediment	-0.4129	0.6784	-5.3117	8.9647

Table 2.4: Species richness (SR) numbers for the Jasper study sites. Plot SR is the average number of species per plot (n=10). Site SR is the total species encountered in each of the nine sites. Area SR is the total number of species encountered in each of the three wetland areas. Jasper SR is the total species encountered in all study sites. α diversity is the measure of the number of species in each site, γ diversity is landscape diversity, and β diversity is the species turnover between α and γ.

Sites	Plot SR ± se	Site SR		Area SR	Jasper SR (γ)
		(α)	(β)		
RIM1	11.9 ± 1.43	29	3.31		
RIM2	17.3 ± 0.99	36	2.67	48	
RIM3	20.4 ± 0.83	32	3.00		
BIM1	16.5 ± 0.78	44	2.18		
BIM2	16.0 ± 1.16	43	2.18	66	95
BIM3	15.3 ± 0.86	28	3.31		
RM1	13.9 ± 0.99	24	4.00		
RM2	18.1 ± 0.72	32	3.00	37	
RM3	14.5 ± 0.99	31	3.10		

Table 2.5: The number of unique species (i.e. only found in that site or area), the number of species belonging to each strata (emergent, submersed and bryophyte), and the number of ubiquitous species (i.e. found in all the sites) for the nine study sites and the three wetland areas.

	Site				Area				Jasper
Sites	Unique	Emergent	Submersed	Bryophyte	Unique	Emergent	Submersed	Bryophyte	Ubiquitous
RIM1	4	14	9	6					
RIM2	3	21	12	3	17	29	13	6	
RIM3	3	18	13	3					
BIM1	13	26	11	6					
BIM2	13	29	10	4	33	45	13	8	24
BIM3	4	14	12	2					
RM1	0	15	6	3					
RM2	2	18	11	3	11	21	13	3	
RM3	3	17	11	3					

Table 2.6: Mean (± se) nutrient concentrations in the water column and sediment measured in the marsh study sites. The ratio of biologically available N:P (NH_4-N + NO_3-N / SRP) is expressed on a molar basis.

Environmental	Railway-impounded			Beaver-impounded			Riverine		
Variable	RIM1	RIM2	RIM3	BIM1	BIM2	BIM3	RM1	RM2	RM3
Ammonium,	2.9	1.5	2.0	3.1	14.4	9.2	3.8	7.6	3.2
NH_4-N (μg/L)	(1.0)	(0.8)	(0.7)	(1.0)	(6.7)	(5.0)	(1.4)	(3.2)	(1.1)
Nitrate, NO_3-N	7.7	0.8	1.8	0.7	0.6	0.7	8.8	6.2	3.6
(μg/L)	(1.8)	(0.4)	(0.5)	(0.2)	(0.2)	(0.3)	(6.2)	(3.3)	(1.9)
TDN	101.2	172.0	142.5	312.3	242.0	311.0	196.1	199.1	281.8
(μg/L)	(8.5)	(17.9)	(16.0)	(28.8)	(34.9)	(56.5)	(46.0)	(38.6)	(76.9)
SRP	2.4	3.8	3.1	4.3	2.1	4.1	3.2	5.7	5.4
(μg/L)	(0.2)	(0.5)	(0.2)	(0.9)	(0.5)	(1.0)	(0.6)	(2.2)	(1.4)
TP	16.3	10.8	19.9	17.5	28.0	27.2	23.3	27.0	24.9
(μg/L)	(4.5)	(1.1)	(5.2)	(2.6)	(6.0)	(4.9)	(3.4)	(6.3)	(2.1)
TDP	3.5	4.4	4.3	6.6	5.4	8.1	6.9	7.3	11.4
(μg/L)	(0.5)	(0.5)	(0.5)	(0.7)	(0.8)	(1.4)	(1.3)	(1.5)	(3.4)
N:P, available	5	0.7	1.4	0.9	9.7	2.4	4.8	4.5	2.1
	(1.2)	(0.4)	(0.4)	(0.2)	(3.4)	(0.6)	(2.4)	(1.5)	(1.3)
Sediment TN	0.53	1.43	1.26	0.32	0.20	0.28	0.12	0.17	0.16
(%)	(0.12)	(0.16)	(0.08)	(0.07)	(0.05)	(0.06)	(0.02)	(0.02)	(0.02)
Sed. TP	0.058	0.074	0.074	0.051	0.058	0.056	0.057	0.063	0.057
(%)	(0.004)	(0.002)	(0.004)	(0.003)	(0.005)	(0.007)	(0.001)	(0.001)	(0.001)
Sed. TC	14.4	32.8	29.4	11.2	8.4	9.0	8.1	7.8	7.6
(%)	(3.5)	(1.5)	(5.9)	(1.2)	(0.6)	(0.8)	(0.8)	(0.3)	(0.09)
Sed. Bulk	0.18	0.07	0.06	0.30	0.47	0.32	0.61	0.47	0.40
Density (g/cm^3)	(0.005)	(0.01)	(0.02)	(0.03)	(0.07)	(0.07)	(0.07)	(0.04)	(0.02)
Sed. Organic	21.1	66.6	60.3	11.7	8.0	11.7	5.5	6.6	6.1
Content (%)	(2.2)	(4.5)	(13.3)	(2.2)	(1.9)	(2.5)	(1.5)	(0.4)	(0.9)

Table 2.7: Mean (± se) physical variables measured in the marsh study sites. Amplitude is the difference between maximum and minimum water level and conductivity is corrected for temperature and pH.

Environmental	Railway-impounded			Beaver-impounded			Riverine		
Variable	RIM1	RIM2	RIM3	BIM1	BIM2	BIM3	RM1	RM2	RM3
Conductivity (µS)	321.7 (6.6)	327.5 (10.1)	330.5 (11.9)	354.1 (36.0)	176.0 (16.7)	209.7 (19.9)	272.4 (40.0)	536.3 (44.3)	523.1 (34.1)
Turbidity (NTU)	4.4 (1.5)	3.4 (0.6)	2.7 (0.5)	9.4 (2.5)	6.7 (1.6)	6.5 (1.7)	8.4 (1.9)	7.1 (1.6)	5.4 (2.0)
Water Depth (cm)	26.7 (1.2)	32.8 (1.3)	25.7 (1.2)	31.0 (1.6)	27.9 (1.6)	37.9 (1.5)	26.4 (5.8)	31.0 (6.2)	40.7 (7.5)
Max–Min Water Depth (cm)	38.2-23.4	40.7-22.1	34.8-16.7	30.3-9.6	27.3-6.5	37.7-18.6	59.2-0	52-0	60-0
Amplitude (cm)	14.8	18.6	18.1	20.7	20.8	19.1	59.2	52	60

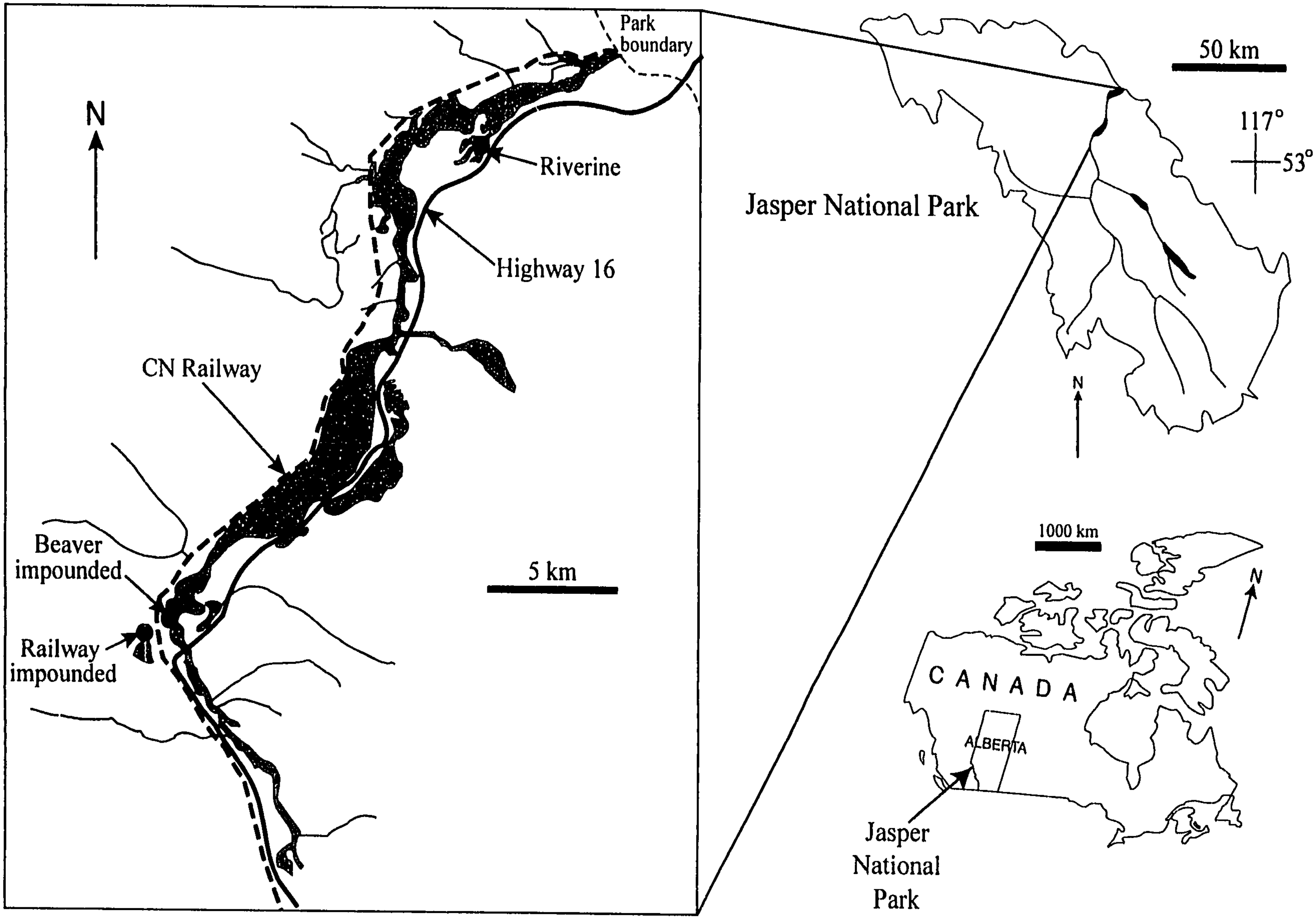

Figure 2.1: Location of the three study areas (riverine, beaver impounded, and railway impounded) in Jasper National Park, Alberta, Canada.

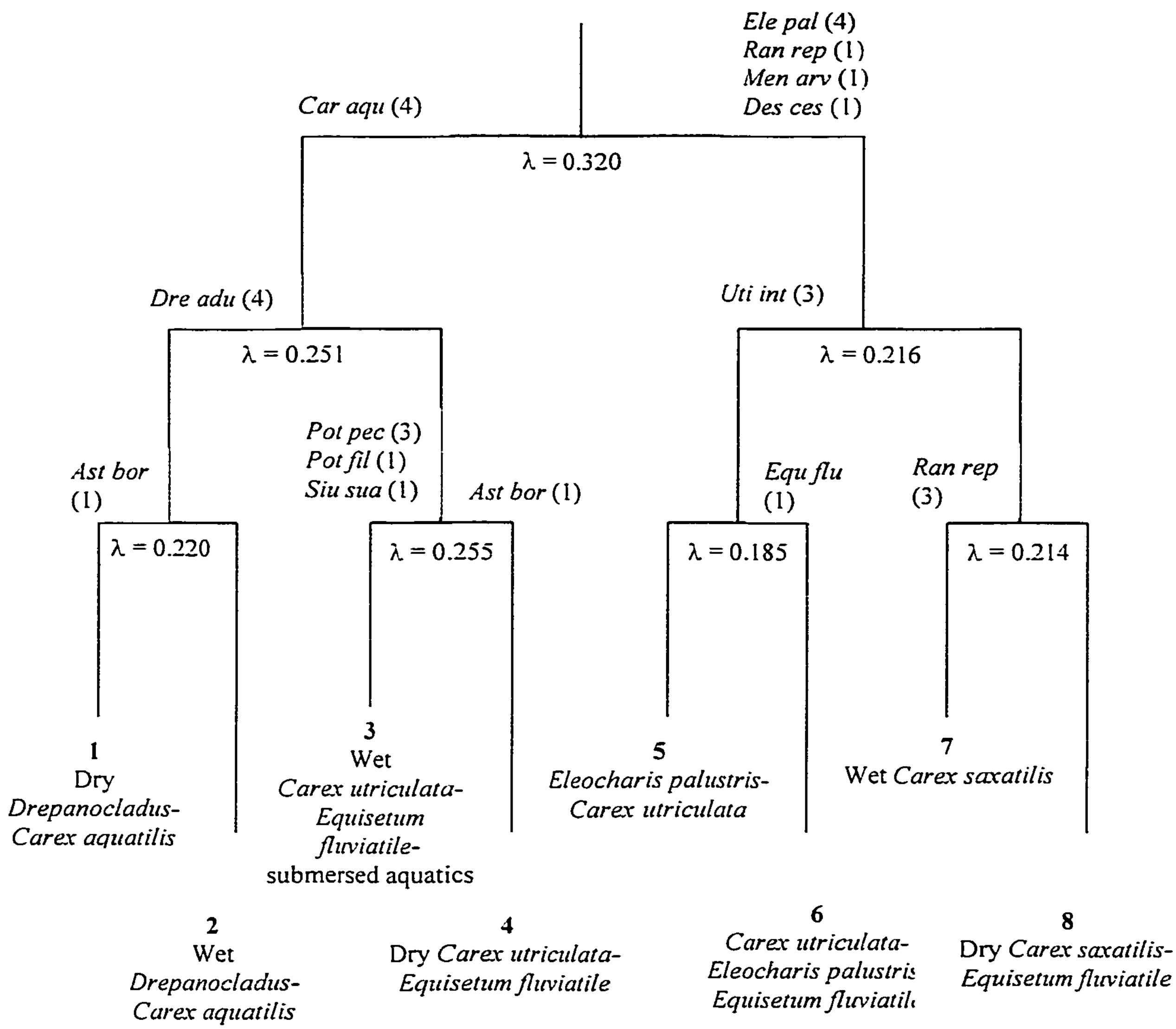

Figure 2.2: The TWINSPAN classification for the vegetation communities in the marsh study sites in Jasper yielded eight community types (the bold numbers) after three levels of division. Indicator species are abbreviated, full names below, with ranked cover values in brackets.
Note: Full species names are *Aster borealis* (Ast bor), *Carex aquatilis* (Car aqu), *Deschampsia cespitosa* (Des ces), *Drepanocladus aduncus* (Dre adu), *Eleocharis palustris* (Ele pal), *Equisetum fluviatile* (Equ flu), *Mentha arvensis* (Men arv), *Potamogeton filiformis* (Pot fil), *Potamogeton pectinatus* (Pot pec), *Ranunculus reptans* (Ran rep), *Sium suave* (Siu sua), and *Utricularia intermedia* (Utr int).

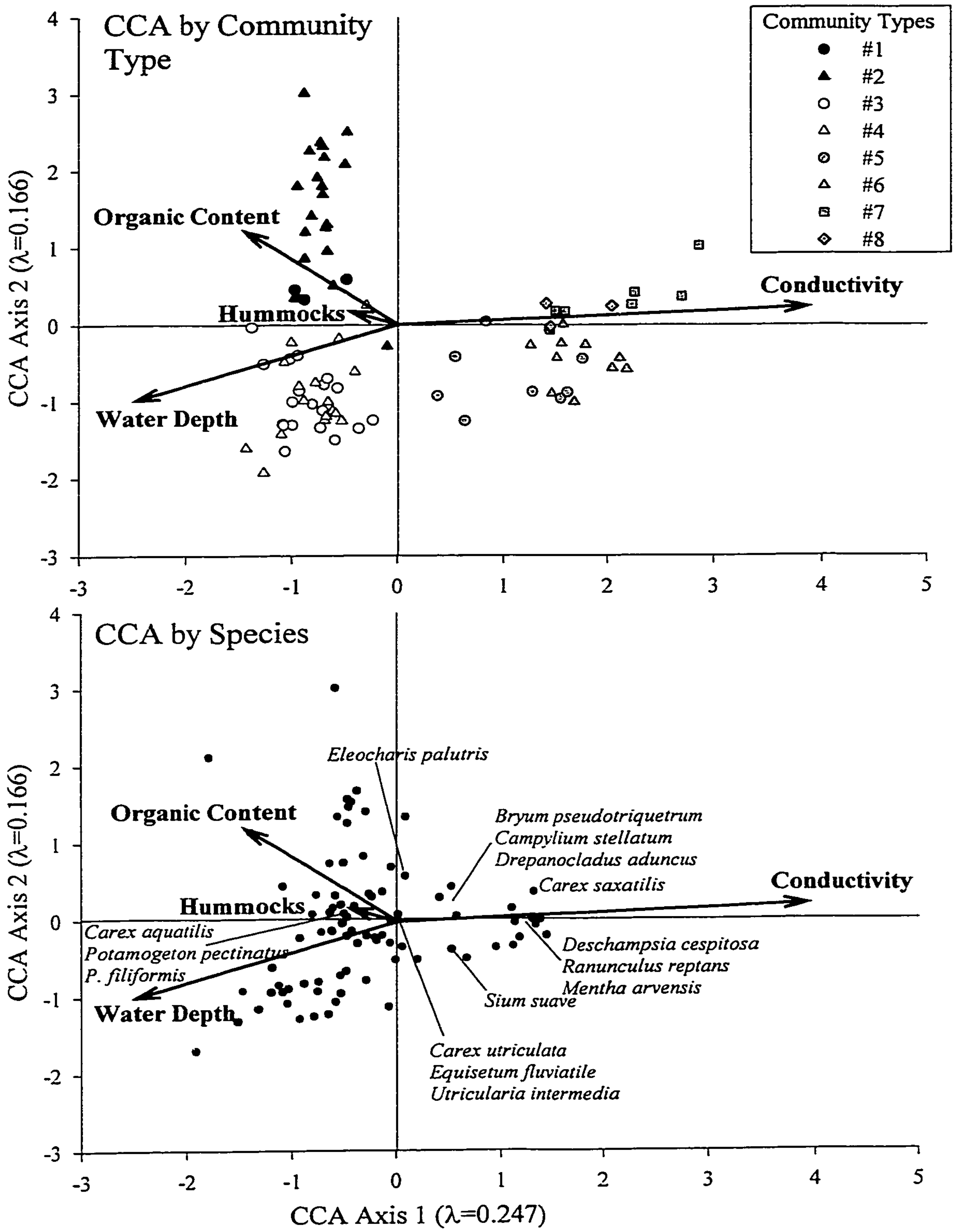

Figure 2.3: Canonical correspondence analysis (CCA) of vegetation cover in Jasper wetlands. The plots are categorized by community types and are expressed separately (top) from the species (bottom). Only dominant and indicator species, as determined by TWINSPAN, are labelled. The significant environmental variables are indicated by the arrows, the length of the arrow portrays the relative importance of that variable.

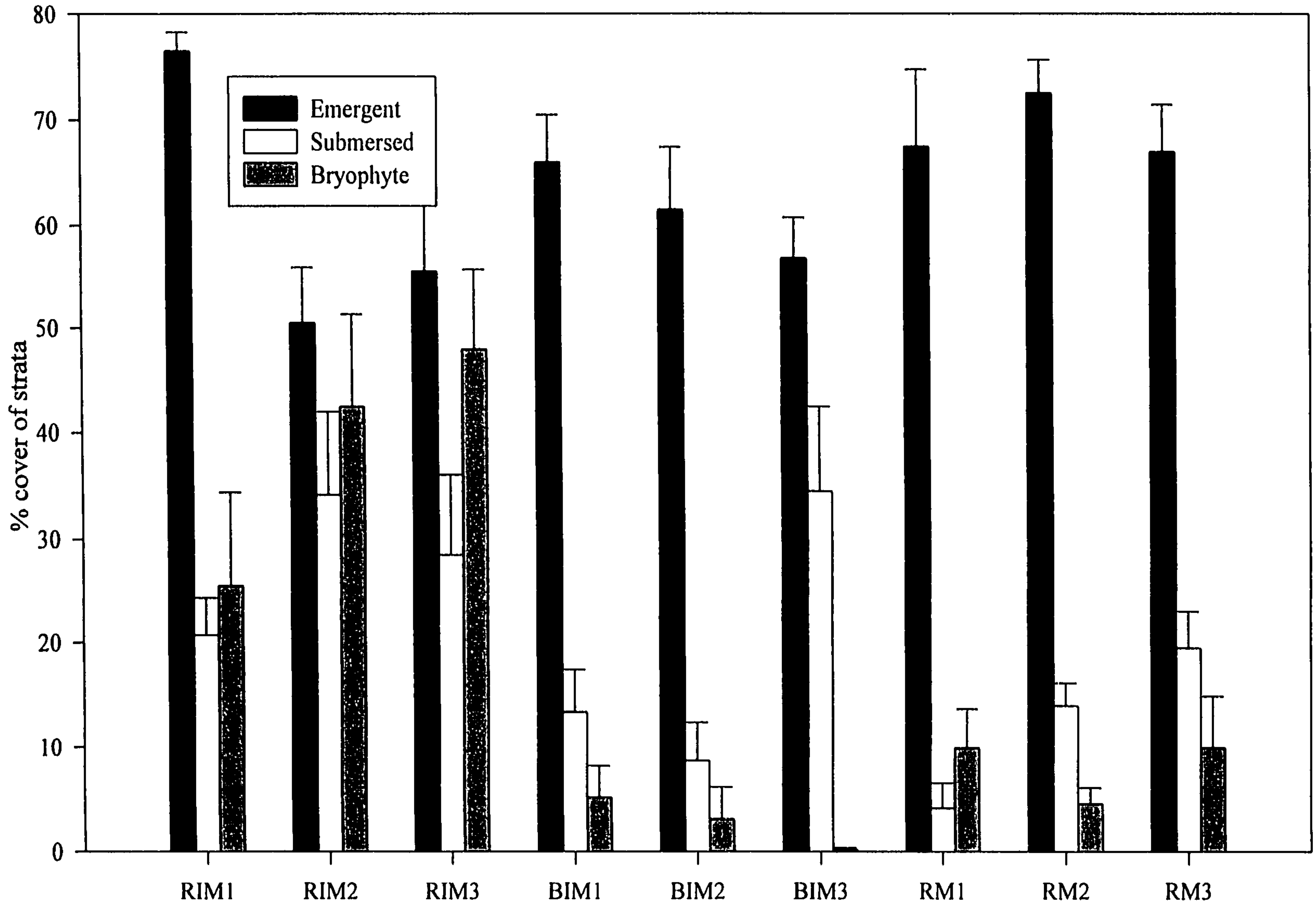

Figure 2.4: Mean percent cover (± se) for each stratum (emergent, submersed and bryophyte) in the nine study sites (disconnected RIM, partially river-connected BIM, and fully river-connected RM).

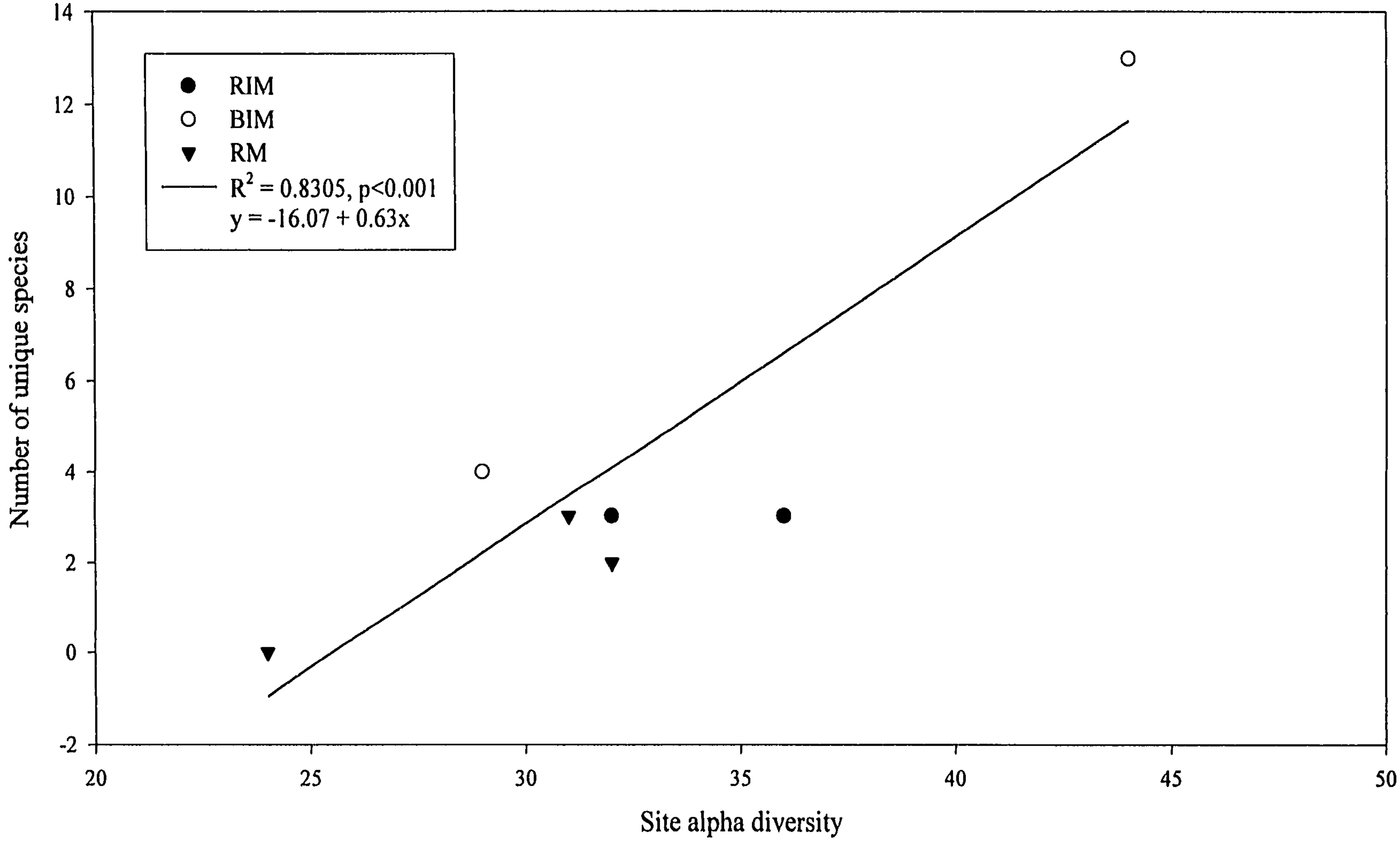

Figure 2.5: The relationship between site alpha diversity and the number of unique species of the nine study sites. There are two data points hidden at the 29 and 44 alpha diversity points.

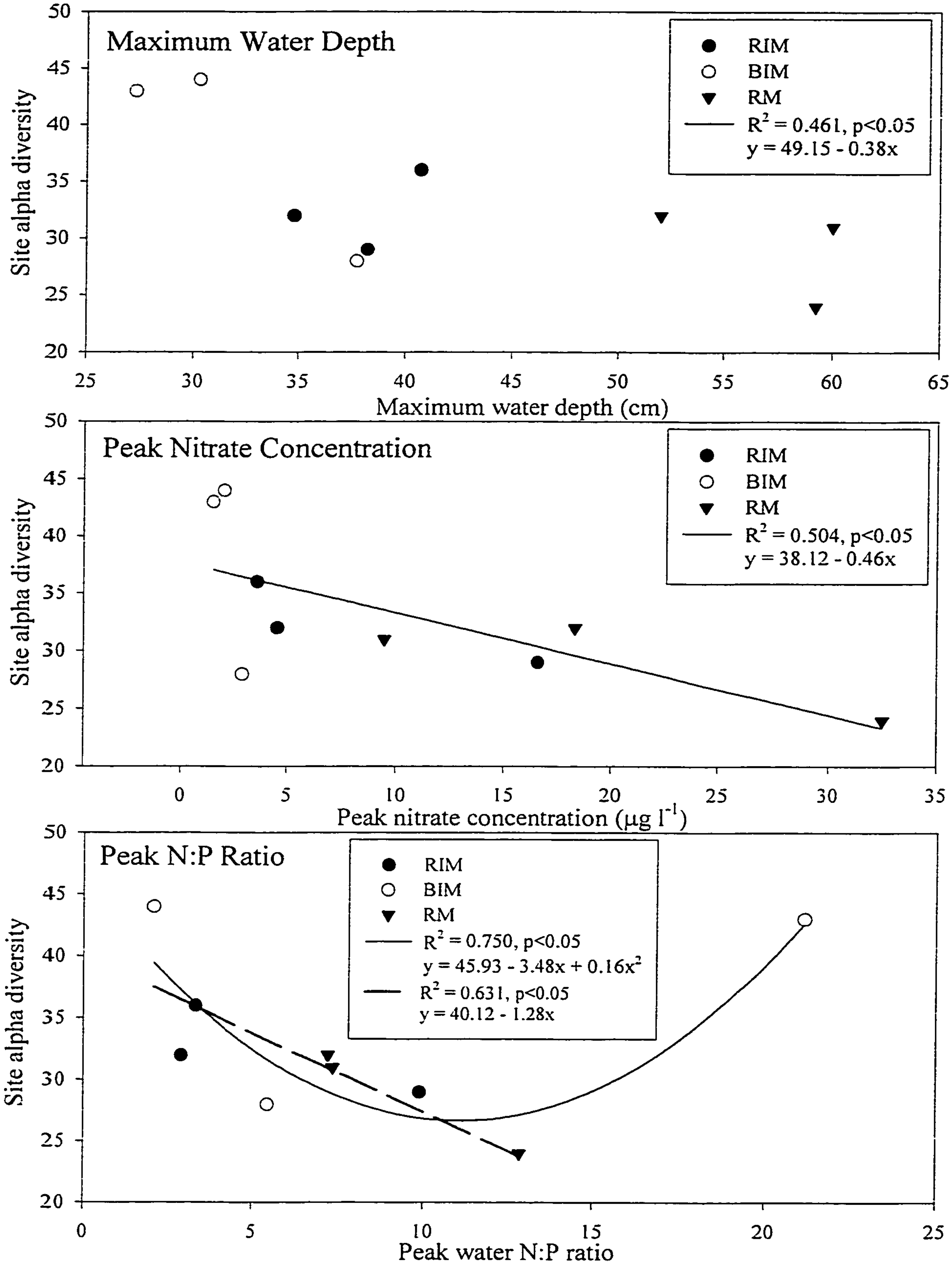

Figure 2.6: Relationships between water chemistry variables and site alpha diversity. Peak N:P ratio graph has quadrat line with the outlier and linear line without the outlier.

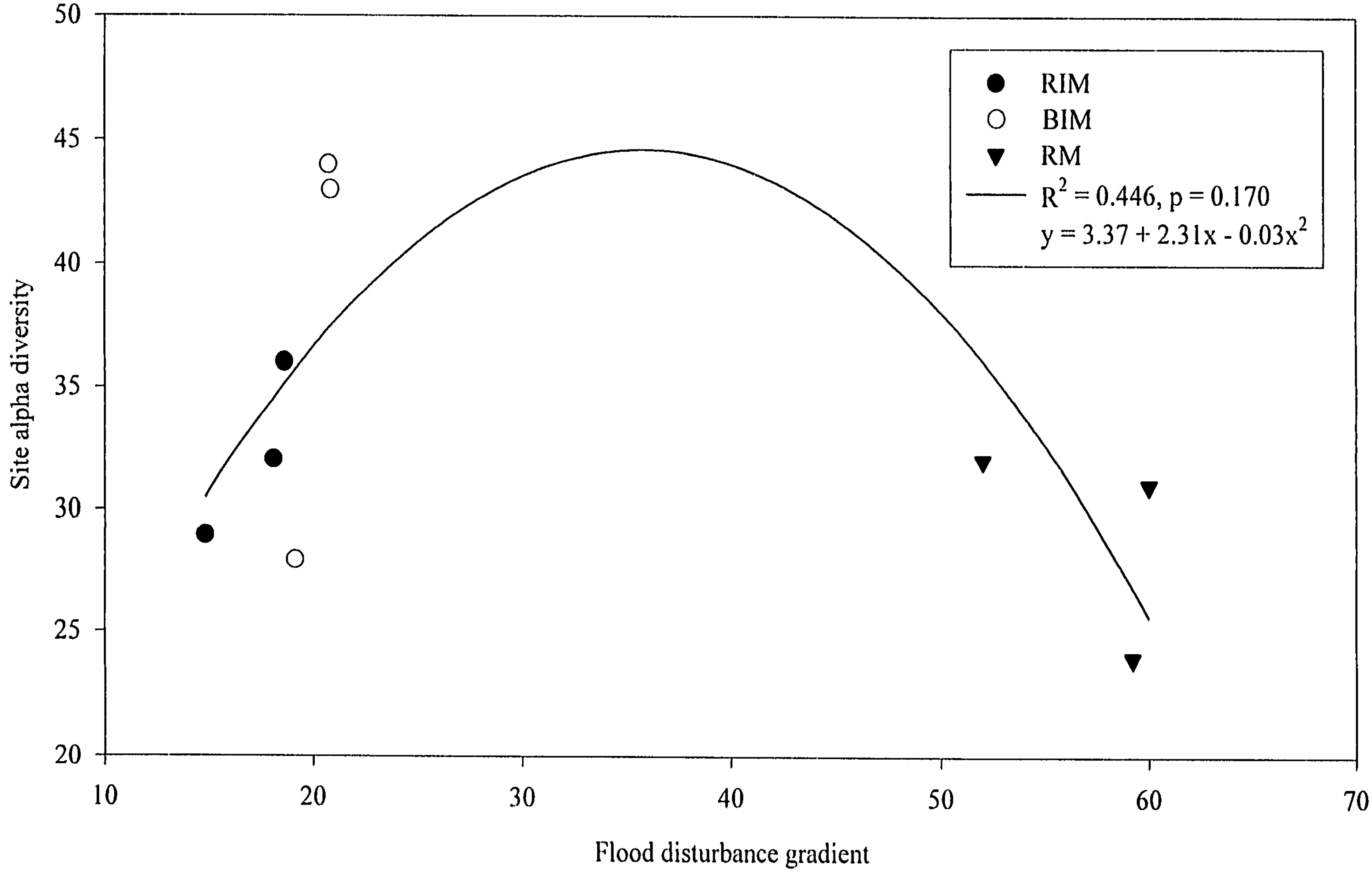

Figure 2.7: Site alpha diversity along a natural disturbance gradient. The disturbance gradient is estimated using amplitude of water level fluctuations the 1998 season.

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3. Aboveground Standing Crop and Nutrients Limitations in Floodplain Marshes in Jasper National Park, Alberta

Introduction

Freshwater marshes are amongst the most productive communities in the world and the most productive in the temperate zone (Auclair *et al.* 1976). Water levels (Bayley *et al.* 1985, Hultgren 1989, van der Valk 1994, Szumigalski and Bayley 1996) and nutrient availability (Auclair 1982, Verhoeven and Arts 1987, Wisheu and Keddy 1989) are commonly studied as environmental factors influencing net primary productivity (NPP). However, other influential variables include temperature (Bernard and Gorham 1978, Solander 1983, Szumigalski and Bayley 1997), latitude and altitude (Auclair *et al.* 1976), disturbance (Wilson and Keddy 1988, Wisheu and Keddy 1989), and species composition (Pérez-Corona and Verhoeven 1996).

Floodplain marshes are on fluvial floodplains and receive annual flooding and sedimentation (National Wetlands Working Group 1988). Within floodplain marshes, seasonal flooding drives water level fluctuations and acts as a natural disturbance to vegetation (van der Peijl and Verhoeven 1999). Disturbance can be beneficial to a community by increasing diversity, removing excess organic matter, or inhibiting competitive exclusion (Connell 1978, Wilson and Keddy 1985). Diversity has been shown to be highest at intermediate levels of disturbance (Connell 1978, Wilson and Keddy 1985, Moore and Keddy 1989, Pollock *et al.* 1998), while less evidence exists for the effect of disturbance on production.

River hydrology can affect several ecosystem characteristics including species composition, diversity, primary production, organic deposition, and nutrient cycling (Gosselink and Turner 1978). Unfortunately, many rivers in North America have had flow regimes altered by dams, channelization, and water withdrawal resulting in changes in biodiversity, productivity and ecological integrity (Poff *et al.* 1997). Ecological integrity is defined as the state of an ecosystem when the compositions and abundance of native species and biological communities together with supporting processes are intact (Parks Canada Agency 2000). The magnitude, frequency, duration, timing, and rate of flooding can affect the ecological processes, including productivity, of a floodplain. The ability of floodwaters to spread throughout the floodplain system will have a large effect on ecological processes (Henry and Amoros 1995). Many natural (e.g. beaver dams, riverbanks) and human made (e.g. roads, dams, culverts) impediments can restrict the extent of flooding.

Nutrients are also brought in with floodwaters; the amount of nutrients depends on the source and volume of floodwater (Gosselink and Turner 1978, Amoros *et al.* 2000). Very little is known about biogeochemical cycling of floodplain lakes and marshes on major rivers compared to well-studied lake complexes (Lesack *et al.* 1998). In the MacKenzie Delta, Lesack *et al* (1998) found lakes connected to river channels had chemistry more similar to river water than to disconnected lakes. Hydrologic connectivity between the river and its floodplain is important for nutrient recycling, decomposition, and sediment transport (Henry and Amoros 1995). River floodwater is a source for dissolved nutrients and suspended sediments (van der Valk 1994) and tends to have higher nutrients than other sources such as groundwater (Amoros *et al.* 2000). River floodwater is often derived from snowmelt, which is typically high in nitrates. Sediments brought in with flooding are usually phosphorus sources (Lewis and Grant 1979, Stednick 1989). Flooding can also indirectly increase nutrient supply through decomposition of plant litter, which is increased with water level fluctuations changing oxidation-reduction conditions (van Oorschot *et al.* 1997). Frequent and high flooding scours organic debris, consequently removing nutrients from the wetland (Poff *et al.* 1997). However, flooding can cause either an increase or a decrease in sediment nitrogen and phosphorus and thus, sediments of heavily flooded wetlands may be poor indicators of nutrient availability (Bedford *et al.* 1999).

Uptake of nutrients from sediment and water will differ depending on the plant species. In general, submersed plants sequester phosphorus more efficiently from water than from sediment (Robach et al 1995). Emergent macrophytes take up nutrients most efficiently from the sediment interstitial water (Auclair et al 1976). Mosses are known to take up nutrients from precipitation more quickly than vascular plants (Jonasson and Shaver 1999) but are limited by a much less extensive rooting system. Mosses tend to have lower dominance in marshes due to factors like fluctuating water levels and shading by vascular plants, particularly emergent macrophytes.

Although the fertility or the amount of nutrients available in a community will control plant standing crop (Day *et al.* 1988), the most limiting nutrient will restrict plant standing crop. Koerselman and Meuleman (1996) suggested that the ratio of N:P ratio of the plant tissue is indicative of nutrient limitations during growth. The ratio of N:P > 16 are P-limited, N:P < 14 are N-limited and N:P between 14 to 16 are co-limited. Several researchers have found that production is better correlated with the N:P ratio than absolute nutrient concentration (Koerselman and Meuleman 1996, Bedford *et al.* 1999). A recent review of nutrient limitations in North American wetlands found that marshes and swamps were N-limited (Bedford *et al.* 1999). They also found that mineral soils had lower N:P ratios than peat soils. Studies in Alberta marshes and fens found nitrogen to be the limiting nutrient (Thormann and Bayley 1997b, Mewhort 2000).

Although much work has been done on the effects of nutrients on productivity in wetlands, the interaction of natural disturbance regimes with wetland nutrients and productivity has been less studied. This study investigated a natural gradient of river flood disturbance in floodplain wetlands in Jasper National Park (JNP), Alberta. The Athabasca River in JNP is characterized by late spring or early summer flooding that brings cold, turbid river water to the floodplain. The floodplain, in some areas, is disconnected from the main river channel, and thus seasonal flooding, by beaver dams, railways, and roadbeds. A gradient of river connectivity among the floodplain wetlands is determined by the distance of the wetland to the main river and the extent of natural and artificial barriers.

The objectives of this study were 1) to determine how the degree of river connectivity, thus the amount of flood disturbance, affects standing crop and other ecological processes in Jasper floodplain marshes; 2) to estimate the nutrient limitations of Jasper floodplain marshes (sediment and water) and how that nutrient limitation affects the productivity of the marshes; and 3) to compare natural variation in the flow regimes (i.e. a wet year and a dry year) on standing crop and nutrient status.

Site Description

Jasper National Park (JNP) is located in the Canadian Rocky Mountains in western Alberta, Canada (Figure 3.1). The area is characterized by a climate of long cold winters with high snow pack in the mountains and short cool summers with occasional hot spells (Holland and Coen 1982). The mean annual temperature is 3.1°C, with 95 frost-free days, and the mean precipitation is 393.7 mm, with 281.6 mm as rainfall and 143.9 mm as snowfall (Environment Canada 1994).

Three wetland areas, each with three study sites, were measured in 1998 and 1999 and represent the main montane floodplain wetland types in the Athabasca River valley in JNP. These sites differ in degree of connectivity to the Athabasca River. The wetland areas include riverine, beaver-impounded and railway-impounded marshes. Within each area, three representative sites were studied.

Each marsh site was set up with a grid design with randomly placed plots selected. For the grid design, all the marsh area within the defined boundaries was equally divided into 100 plots. Ten plots were then randomly chosen and marked. These plots were used for all measurements in this study except water chemistry and water levels. This method removed the bias of transect placement. Plots varied in size from 16 to 81 m^2. New plots were established for the 1999 field season to avoid excess trampling within plots.

Thus, sampling included three marsh areas (riverine, beaver-impounded and railway-impounded) each with three representative sites, with each site sampled in ten plots, for total of 90 plots.

Riverine Marsh Area

The riverine area is located in the east end of JNP by the Pocahontas warden station (53° 12' N and 117° 56' W) and is freely connected to the main Athabasca River by a secondary river channel (Figure 1). All these marshes are classified as floodplain marshes since they are adjacent to the main river and are seasonally inundated by river flooding (National Wetlands Working Group 1988). All three marsh sites are sedge dominated with no shrub cover and negligible moss growth.

Riverine Marsh 1 (RM1):

This marsh site is located closest to the inflow from the main Athabasca River. It has a mineral substrate with at least three metres of fine sediment deposits from the river. Tall *Salix* shrubs surround the marsh on all sides with a small channel entering the marsh.

Riverine Marsh 2 (RM2):

This marsh site is located further along the same inflow channel as Riverine 1 and is surrounded on two sides by channels. A thin line of Salix shrubs borders the back. The sediment in this site is largely mineral substrate with small amounts of organic deposits and undecomposed litter.

Riverine Marsh 3 (RM3):

This marsh site is even further along the same inflow channel and is surrounded on three sites by elevated *Picea glauca* forest and the fourth side is open water. The sediment is mineral with a thin, well-decomposed, organic layer on top.

Beaver-impounded Marsh Area

The beaver-impounded and railway-impounded areas are part of the same wetland complex that was bisected by the railway in 1912 (Figure 1). These are located further west in the park (53° 01' to 53° 02' N and 118° 05' to 118° 06' W). This wetland complex, consisting of channels, marshes, shallow lakes and forested sand dunes, is connected to the main Athabasca River by a secondary channel. Several beaver dams (<1 m high) are located along the inflow channel, the beaver dams are easily surpassed at high water levels and the outflow is unblocked. These marshes are classified as floodplain marshes since they are adjacent to the main river and are seasonally inundated by river flooding (National Wetlands Working Group 1988).

Beaver-impounded Marsh 1 (BIM1):

This marsh site is adjacent to a shallow lake with open water on one side and with *Salix* shrubs bordering the marsh the other side. The sediment has a well-decomposed organic layer overlaying alternating layers of mineral and organic sediment. The marsh is sedge-dominated with some hummocks with *Salix* shrubs and some hollows with less emergent cover and more submersed cover. Bryophytes are restricted to the drier edges and the hummocks.

Beaver-impounded Marsh 2 (BIM2):

This marsh site is adjacent to a shallow lake in this area and is the outflow from the lake, although, there is no definite channel or substantial flow. It is bordered on two sides by elevated *Picea glauca* forest and by open water on the other two sides. The sediment is mostly fine mineral topped with a thin organic layer. The marsh is sedge-dominated with bryophyte cover restricted to the shallower edges.

Beaver-impounded Marsh 3 (BIM3):

This marsh site is along the outflow of the wetland complex. Two sides are bordered by *Salix-Picea* forest. The sediment is a mixture of mineral and organic. The marsh is sedge-dominated with a wetter centre with an *Equisetum-Scirpus* mixture. Bryophytes are more common at the edges and on hummocks.

Railway-impounded Marsh Area

The railway-impounded area is in the same area as the beaver-impounded marshes but is completely disconnected from the main Athabasca River by a railway embankment (Figure 3.1). Prior to construction of the railway in 1912, this area received river floodwaters and floods due to local snowmelt and precipitation. It no longer receives river floodwaters. This marsh complex consists of channels, marshes, shallow lakes and forest. These marshes are classified as shore marshes since they border permanent lakes and are subject to water level rise with the lake and wave action (National Wetlands Working Group 1988).

Railway-impounded Marsh 1 (RIM1):

This marsh is at a convergence of two streams. A beaver dam along one of those streams causes slow water to flow through the marsh. The back edge of the marsh is a sand dune with a drier *Picea* forest. Thick organic sediment is typical of most of the marsh. The marsh is sedge-dominated with floating *Scorpidium scirpoides* as the dominant bryophyte.

Railway-impounded Marsh 2 (RIM2):

This marsh is along the edge of a lake and is bordered on the other side by *Salix* shrubs. The plants are rooted in a bryophyte layer, which overlays a poorly decomposed peat layer, approximately 50 cm deep. It is a sedge- and bryophyte-dominated marsh.

Railway-impounded Marsh 3 (RIM3):

This marsh is located along the same lake as the previous marsh and has similar characteristics. The poorly decomposed peat is approximately 45 cm deep.

Methods

Environmental Variables

Athabasca River discharge was collected by Environment Canada from the main river channel, data station #07AA002 from 1915 to the present (Environment Canada

1999). Water levels and chemical sampling were taken at a permanent gauge established in each marsh site. Water levels were measured on a weekly basis starting in May and finishing in October, or until no water was remaining. At each of those sampling times turbidity and conductivity analysis was measured using a Hach® Pocket Turbidimeter™ and an Orion® Model 115 Conductivity, TDS, and Salinity Meter, respectively.

From May to the end of October, a water sample was collected for chemical analysis every three weeks from a location in the main Athabasca River and at each of the nine marsh sites. Samples were collected in acid washed 1 L Nalgene and 75 mL polypropylene bottles. The samples were analysed for nitrate (NO_3^- and NO_2^-), ammonia (NH_4^+), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP) and total phosphorus (TP). Nitrate samples were filtered using a 0.45 μm HAWP millipore filter, while ammonia samples were not filtered. TDN was digested with 4N H_2SO_4 and H_2O_2. Nitrate, ammonia, and TDN were analysed on a Technicon Auto Analyser II. TDP and TP were analysed using the methods described in Bierhuizen and Prepas (1985). SRP was analysed using the method of Menzel and Corwin (1965).

Sediment Characteristics

Sediment samples (10 cm deep x 4.4 cm diameter) were extracted in August 1999. Three cores were taken from each of the nine study sites from randomly selected plots. The 10 cm core was separated in the field into upper and lower 5 cm segments and the lower layer was analysed to determine the nutrient concentration of the rooting zone. The upper layer was discarded due to possible flood disturbance. Cores were frozen at -10°C until analysis.

Cores were freeze-dried, sieved to 2mm and larger material was homogenized with a Wiley mill to 2 mm. The ground sample was analysed for total nitrogen (TN) and total carbon (TC) using a HCN auto-analyser. Total phosphorus (TP) was analysed using persulfate oxidation digestion (Menzel and Corwin 1965). All concentrations are expressed as a percent of dry weight. Bulk density was determined using dried samples and organic content was determined by combustion at 550°C then the ash was weighed.

Plant Standing Crop

Herbs

The aboveground standing crop of emergent macrophytes was estimated three times during the growing season, end of June, July and August, in 1998 and 1999. A quadrat, 0.5 m x 0.5 m (0.25 m^2), was placed randomly within each of the established plots. All aboveground vegetation was removed, dried at 60°C to constant weight, and sorted into live and dead material. The dead plant material from the previous year(s) was discarded, and the live plant material was separated into individual taxa and weighed.

Mosses

Peak biomass of moss was estimated in marshes where moss cover was >25%, therefore, only RIM2 and RIM3 were measured. Three random cores, 10.5 cm in diameter, were taken at the end of the growing season in 1998 and 1999. The year's growth, determined by rhizome growth and new leaf activity, was clipped, dried at 60°C and weighed. The production was converted to weight of moss/m^2 using the area of the core.

Fertilization Experiment

A fertilization experiment was established in 1999 to determine if production was limited by nutrient availability. Within each site, nine plots were randomly chosen from the pre-established grid. One of three replicates of three treatments (nitrogen, phosphorus and nitrogen-phosphorus) was assigned to each plot. Control plots were the same plots used for productivity analyses.

The plots were fertilized in mid-May and five weeks later in mid-June. Neill (1990b) found that the fertilizer added in two doses eliminated the burning effect of phosphorus and had higher biomass increases. Fertilizer was applied to the central 1 m x1 m quadrat of the plot. The fertilizer was added in granular form in 10 portions evenly distributed over the quadrat through a 2-cm diameter piece of copper tubing inserted 10-cm into the sediment (Neill 1990b). This prevents spreading of nutrients outside the plot, especially in flooded sites. Others (Chambers and Fourqurean 1991, Clevering and van Gulik 1997, Gough and Grace 1998) have successfully used methods that pushed the fertilizer into the sediment to various depths, typically the rooting zone. It was found that this method retained fertilizer within the plot (Neill 1990a).

Nitrogen, as granular NH_4NO_3, was applied at a rate of 50 g N m^{-2} yr^{-1}. Phosphorus, as granular P_2O_5, was applied at a rate of 5.56 g P m^{-2} yr^{-1}. The concentrations are similar to Vermeer (1986). The combined nitrogen-phosphorus treatment has a ratio of 9:1 by weight. At the end of July, ten weeks after the first fertilization and five weeks after the second, all aboveground herbaceous biomass in the central 0.25 m^2 quadrat was removed. After drying at 60°C to constant weight, it was sorted and weighed. The experiment was completed at the end July because that was peak biomass for most sites in 1998.

Disturbance Gradient

The natural disturbance gradient was based on distance from the river and the number and extent of barriers along the inflow channel. Also, amplitude of water level fluctuations (calculated as the difference between maximum and minimum water levels) is an excellent indicator of connectivity to river floodwaters in this system. Many researchers have used water level fluctuations (Johnson and Leopold 1994, Wilcox 1995) or flood frequency (Weiher *et al.* 1996, Pollock *et al.* 1998) as a measure of disturbance. In this study, water level fluctuations were highest in the most river-connected sites and lowest in the most disconnected sites.

Statistical Analyses

All statistics were run in SYSTAT Version 8.0. One-way ANOVA's were used for statistical comparisons between sites for standing crop, sediment characteristics water depth, and water chemistry variables, and between treatments for the fertilization experiment. T-tests were used for statistical comparisons between years for the above variables. Moss production was compared between years and sites with t-tests. Linear and quadratic regressions were used to compare production to the disturbance gradient. Homogeneity of variances, an assumption of ANOVA's, was tested using Bartlett's test and when heterogeneity occurred the data was log transformed (Sokal and Rohlf 1995). This transformation should also remedy non-normality in the data.

Results

Water Levels

Water levels in the riverine marshes changed rapidly with river flows, while the railway-impounded marshes remained fairly stable over the season. Maximum water depth, in both 1998 and 1999, was highest in the riverine marshes, next highest in the beaver-impounded marshes, and lowest in the railway-impounded marshes (Figure 3.2). In addition, the amplitude of water levels (difference between minimum and maximum water levels) was greatest in the riverine and beaver-impounded areas (Table 3.1). However, mean water depth over the ice-free season was not significantly different between sites in 1998 or 1999 (Table 3.1).

During the study, two extremes in water levels were observed, with 1998 a dry year and 1999 a wet year. The amplitude of fluctuation was greater in 1999 in beaver-impounded and riverine marshes (Table 3.1). The floods of 1999 were much higher and more frequent (three vs. one flood peak) than in 1998 (Figure 3.2). The river floodwaters never reached the railway-impounded wetlands in either year. In the river-connected sites (beaver-impounded and riverine), the floods of 1999 were high enough to cause overbank flow directly into the marshes, while during the dry year, 1998, river floodwaters were received only from inflow channels.

Total annual discharge of the Athabasca River was significantly lower in 1998 and significantly higher in 1999 than the historical record from 1913-1995 (Figure 3.3, $t_{1998}=2.741$ and $t_{1999}=3.120$, $p<0.01$). Similarly, river discharge during the growing season (May-October) was significantly lower in 1998 and higher in 1999 compared to the historical record (Figure 3.3, $t_{1998}=3.278$ and $t_{1999}=3.581$, $p<0.01$). 1998 had higher than average discharge in May but all other months were at or below average. 1999 had slightly lower than average discharge in May and June and higher than average discharge for the remainder of the growing season. Thus, 1999 had a late spring followed by a very high flood year, while 1998 was a lower than average flood year.

Water Chemistry

The Athabasca River had relatively high mean concentrations of ammonia (NH_4-N), nitrate (NO_3-N), total phosphorus (TP) and turbidity compared to the floodplain marshes (Table 3.1 & 3.2). In the wet year (1999), turbidity and TP peaked simultaneously and the peak coincided with high river discharge in the Athabasca River, while in the dry year (1998), peak turbidity and TP were not simultaneous and occurred after the peak discharge (Figure 3.4 & 3.5). The variability in NO_3-N concentrations appeared unrelated to discharge (Figure 3.6). TDN and SRP were higher in the marshes than the river, indicating that the river floodwaters were not a source for these nutrients (Table 3.2). For the Athabasca River, most chemical variables were higher in the dry year (1998) than the wet year (1999) suggesting concentrations were diluted with the extreme floods.

The riverine and beaver-impounded marshes had higher peak concentrations of turbidity, NO_3-N, and TP, and higher N:P ratios than the railway-impounded marshes (Figure 3.4-3.7). Similar to the river, the initial peak concentrations in the wet year (1999) coincided with high water levels, indicating river floodwater inputs, but did not show the same trend in the dry year (1998) (Figure 3.2, 3.4-3.7). Riverine and beaver-impounded marshes received a greater volume of river floodwater at high water levels in 1999 than in 1998. As a result, peak concentration of chemicals was higher in riverine and beaver-impounded marshes in 1999.

Peak turbidity was highest in the riverine marshes and in the wet year (1999), it coincided with the peak water levels. Peak turbidity was higher in 1999 than 1998 in all marshes (Figure 3.4). Nitrate concentrations peaked in the beaver-impounded and riverine marshes in June and July of 1999 coinciding with high water levels (Figure 3.6). The remainder of the 1999 season had similar concentrations to those in 1998.

Total phosphorus peaked with the first June flood of 1999 in the riverine and beaver-impounded sites but otherwise, was similar between years and between sites (Figure 3.5). SRP was consistently low in all nine marshes suggesting that bioavailable phosphorus is not from river sources rather from sources common to all sites (e.g. groundwater). The surface water of all nine marshes were N-limited ($N:P<16$) in 1998 while the river was P-limited ($N:P>16$) (Figure 3.7). In 1999, most marshes were N-limited except in the first June flood when the riverine and beaver-impounded marshes (beaver-impounded and riverine) were P-limited as was the Athabasca River (Figure 3.7). Given the seasonal changes in nitrate concentration and the stable SRP concentrations, nitrates are more likely to be limiting in the water column than SRP.

Sediment Chemistry

Organic content was highest and bulk density was the lowest in the sites most disconnected from the river (i.e. RIM2 and RIM3), while the opposite was true of the sites most connected to the river (i.e. BIM2 and RM1) (Figure 3.8). Sediment nutrients, except for TP, tended to be higher in the sites with the highest organic content (Figure 3.8). Based on the N:P ratio of the sediments, all river-connected marsh areas (RM and BIM) were N-limited while the disconnected marsh area (RIM) was co-limited by N and P (Table 3.2).

Bulk density was significantly lower in RIM2 and RIM3 than all other sites, and RIM1 is significantly lower than BIM2, RM1 and RM2 (Figure 3.8, $p<0.0001$). Organic content was significantly higher in RIM2 and RIM3 than all other sites and significantly higher in RIM1 than BIM2 and all three riverine marshes (Figure 3.8, $p<0.0001$). TN and TC followed the same pattern as organic content, with RIM2 and RIM3 significantly higher than all other sites (Figure 3.8, $p<0.0001$). There were no significant differences between any of the sites for TP.

Plant Standing Crop

<u>Herb</u>

Peak aboveground standing crop of herbaceous plants was highest in the beaver-impounded marshes, lower in the riverine marshes and lowest in railway-impounded marshes in both years. In addition, aboveground herb peak standing crop was significantly lower in the wet year than the dry year.

In 1998, herb peak standing crop, an estimate of herb NPP, was significantly lower in RIM2 and RIM3 than all other sites (Table 3.3, $p<0.001$). In 1998, aboveground herb biomass peaked in July for beaver and railway-impounded sites and in August for riverine sites (Table 3.3). In contrast, all sites reached peak aboveground herb biomass in August in 1999 (Table 3.3). Plant growth was delayed in 1999 compared to 1998 and remained lower all season (Table 3.3). In 1999, herb peak standing crop was only significantly lower in RIM2 and RIM3 than BIM2 and RM2 (Table 3.3, $p<0.01$). When the three areas are grouped and compared, the railway-impounded area had significantly lower herb peak standing crop than the other two areas in both years (Figure 3.9, $p<0.001$).

Aboveground herb peak standing crop was significantly higher in 1998 than 1999 for all marshes except the most river-connected marsh, RM1 (Figure 3.9, $p<0.05$). Comparisons between areas revealed that all areas had significantly higher production in 1998, the dry year (Figure 3.9, $p<0.05$). High water levels in the wet year decreased the standing crop.

Moss

Moss contributed less than 10% cover in most sites (Chapter 2) and thus, moss production was only estimated in RIM2 and RIM3, which had 42.3% and 48% cover, respectively. Although mosses did cover 25.5% of RIM1, the moss was floating *Scorpidium scorpioides* that drifted out of the site in the fall after plant senescence. As a result, I was unable to estimate moss production for that site.

There were no significant differences between the moss production of RIM2 and RIM3 (Figure 3.9). There was also no significant difference between 1998 and 1999 for each site (Figure 3.9).

Total Plant Production

In most sites moss cover, and thus moss production, was negligible but in the two sites with measurable moss growth it contributed to the overall plant NPP of the marsh. When total plant NPP was taken into account, there was still lower production in the railway-impounded sites than the beaver-impounded sites (Figure 3.9). In all marshes, herb aboveground standing crop comprised most of the plant standing crop. Total plant NPP was lower in the wet year, 1999, than the dry year, 1998.

Fertilization

Nitrogen and nitrogen+phosphorus fertilization produced higher standing crop in July, the end of the experiment, than the control treatments for most sites. The beaver-impounded area had significantly higher standing crop in N and NP treatments (Figure 3.10A, $p<0.01$). The railway-impounded area had significantly higher standing crop in the N treatment (Figure 3.10A, $p<0.05$). The riverine area had no significant differences.

When compared between sites, RIM1, BIM2, and BIM3 had significantly higher production in the N treatments than in the controls, while BIM1, BIM2, and BIM3 had significantly higher production in the NP treatments than in the controls (data not shown). Visible changes (taller, greener vegetation) in all N and NP treated plots were observed, but not all showed a statistical biomass increase. This may be due to the low sample size (n=3).

Gradient of River Connectivity

Aboveground herb peak standing crop was highest at moderate levels of river flood disturbance in 1999 (Figure 3.11). In 1999, herb peak standing crop is best explained by a quadratic relationship along the natural flood disturbance gradient (R^2=0.695, $p<0.05$). In 1998, this relationship is not significant (R^2=0.098, p= 0.733). This lack of significance is likely due to the lack of flooding in 1998 and thus, low water level fluctuations in the beaver-impounded sites. Total plant NPP also has a quadratic relationship with the natural flood disturbance gradient but it is not significant for either year (data not shown). Moderate to high flood disturbance prevents extensive moss growth, and in sites with moss growth, moss productivity is likely controlled by environmental variables other than the disturbance gradient.

Discussion

Effect of River Connectivity

The first objective of this study was to describe the relationship between river connectivity and the peak standing crop of floodplain marsh vegetation. The three main wetland areas have a gradient of increasing river connectivity from railway-impounded marshes to beaver-impounded marshes to riverine marshes. In the river-connected sites (RM and BIM), water levels rise rapidly with river flooding but drain in the fall, while water levels remain fairly stable all year in disconnected marshes (RIM) (Figure 3.2). Thus, amplitude of fluctuation is a good estimate of natural flood disturbance.

Water Chemistry

Athabasca River water was higher in ammonia-nitrogen, nitrate-nitrogen, total phosphorus, and turbidity than the floodplain marshes (Tables 3.1 & 3.2). Thus, these variables should be indicators of river connectivity. TP concentrations were moderately high (>40 $\mu g\ l^{-1}$) in the river, but most of that phosphorus was bound by the glacial-flour suspended sediments (Lewis and Grant 1979) and therefore, was unavailable to plants. Turbidity and TP had peaks coinciding with high river discharge in the wet year (1999), while NO_3-N did not. Lewis and Grant (1979) found that some chemical variables increase with discharge in subalpine streams, while others become diluted or remain the same.

Turbidity (Figure 3.4) and nitrate concentration (Figure 3.6) were both highest in the riverine and beaver-impounded marshes and appeared to have initial peaks coinciding with the Athabasca River in the wet year but not the dry year. Lesack *et al* (1998) found lakes that were connected to the river channels each year were similar in solute concentrations to each other and to the channels, while disconnected lakes had variable solute concentrations. Nitrates are high in snowmelt but are readily taken up by algae and plants (Lewis and Grant 1979), which may explain why levels do not remain high after the floods and why there was no peak seen in the beaver-impounded sites in the dry year. Stednick's (1989) study of alpine and subalpine stream chemistry in the Colorado Rocky Mountains found nitrates to be higher in concentration than phosphates, and at lower elevations, nitrates are taken up by biota more readily than at high alpine elevations.

The Athabasca River was P-limited (Table 3.2 & Figure 3.7) but most marshes were N-limited in the water column. However, at peak river discharge there was a shift to P-limitation of the water column in the river-connected sites (Figure 3.7), likely due to the increased nitrates from the river.

Sediment Chemistry

Sediment bulk density was highest in the most river-connected sites due to mineral sediments and lowest in the disconnected sites due to build up of peat (Figure 3.8). Organic content showed the opposite trend with highest values in the disconnected, railway-impounded marshes. Other studies have found organic content to be highest in areas with low disturbance and have used it as a measure of disturbance (Wilson and Keddy 1985, Lesack *et al.* 1998, Abernethy and Willby 1999). The organic content of the riverine and beaver-impounded marsh sediments are equivalent to Great Lakes marshes, which receive disturbance through wave action, but lower than most other marshes reviewed by Mitsch and Gosselink (1993). This suggests that natural disturbance, in both these marshes and the Great Lakes marshes, is removing organic debris.

The high organic content of two of the railway-impounded marshes are equivalent to those in the literature (Mitsch and Gosselink 1993), and other marshes in Alberta that are known to have peat development (Thormann and Bayley 1997a, Mewhort 2000). The community structure (Chapter 2) of these railway-impounded wetlands suggests they are in succession to fens due to lack of river flooding, stable water levels, and lack of sediment scour (Nicholson and Vitt 1994, Amoros *et al.* 2000). Sediment TN and TC were highest in the railway-impounded marshes due to the higher organic content of those sediments (Bedford *et al.* 1999).

Peak Standing Crop

Aboveground herb peak standing crop was highest in the moderately flooded, beaver-impounded sites, lower in riverine sites, and lowest in railway-impounded marshes (Figure 3.9). The decrease in herb peak standing crop of riverine sites relative to beaver-impounded sites was also found by Auclair *et al* (1976), Wilson and Keddy (1985) and Wisheu and Keddy (1989), who found decreased production with increased natural disturbance. Moss production was negligible in all but RIM2 and RIM3 (the disconnected sites with the lowest herb production). Moss production added to the aboveground herb peak standing crop makes the total aboveground community productivity only slightly lower in the railway-impounded marshes than the other sites. Bernard *et al* (1988) found that the presence of a bryophyte layer reduces standing crop of *Carex* due to competition for nutrients.

Aboveground plant NPP in the beaver-impounded and riverine marshes of this study is substantially lower than most published productivity values, particularly in the riverine marsh (Table 3.4). The lower productivity can likely be attributed to the influence of river flooding in the Jasper wetlands. Productivity of these riverine marshes is comparable to the riverine marsh in Thormann and Bayley's (1997a) and Mewhort's (2000) studies. Increases in elevation can have a substantial impact on productivity. Bernard *et al* (1988) found an elevation gain of 700m can lead to a two-thirds decrease in standing crop. My study was in the montane, lower elevation zone of JNP but still higher in elevation than most of North America. The productivity is comparable to the montane *Carex* marshes of Gorham and Somers (1973). The railway-impounded sites, which may be in succession to fen (see Chapter 2), are comparable to literature values for herb, moss and total aboveground production in fens (Table 3.4).

Peak standing crop has been shown to underestimate net primary productivity due to shoot mortality over the growing season, and due to different times of peak biomass for individual species (Bernard and Gorham 1978, Bernard *et al.* 1988). However senescence of individual species was not observed until the entire community senesced at the end of the growing season. As a result, peak standing crop is a good estimate aboveground NPP.

Disturbance Gradient

Aboveground herb peak standing crop had different trends along the disturbance gradient, based on distance from river sources and barriers along the inflow, in the wet year and the dry year (Figure 3.11). This suggests that the magnitude of a flood event has a large effect on the relationship between plant productivity and the natural disturbance gradient. Moderate flood disturbance leads to the highest productivity in wet years. In the dry year the disturbance gradient was smaller than the wet year, and there was very little difference between the disconnected railway-impounded sites and the partially connected beaver-impounded sites.

River flooding is known to bring in nutrients (Amoros *et al.* 2000), to promote internal nutrient cycling by changing anoxic sediment conditions (van Oorschot *et al.* 1997), and to remove excess plant litter build up (Poff *et al.* 1997). All these factors may promote plant productivity with moderate flooding, while extreme flooding, as in the riverine marshes, can limit productivity. This is probably due to the cold turbid water when flooded or the harsh winds when the sediment is dry. Understanding these productivity changes along a disturbance gradient is important since it can have a large effect on the community structure and diversity (Day *et al.* 1988, Naiman *et al.* 1993, Chapter 2).

There was a stronger relationship between the disturbance gradient and herb peak standing crop than there was between the disturbance gradient and total plant peak standing crop. Other research has shown that bryophytes are not affected as strongly by a nutrient gradient as vascular plants (Vitt *et al.* 1995b). Since the relationships between productivity and disturbance in a dry year were not significant, there may be other factors affecting production, such as the relationship with belowground production and nutrient supply.

In the dry year, there is a large difference in the water level amplitudes between riverine and the other marshes but not between the railway- and beaver-impounded marshes. Riverine wetlands still receive floodwaters in a dry year, and railway-impounded wetlands never receive floodwaters, in wet or dry years. However, beaver-impounded wetlands did not receive measurable floodwaters in the dry year, but did in the wet year. Thus, a dry year seems to have the largest effect on the magnitude of the disturbance gradient in the moderately connected sites. It is possible that other variables would be better measures of the disturbance gradient. Other researchers have used organic content or bulk weight of sediment as a measure of disturbance (Wilson and Keddy 1985, Abernethy and Willby 1999). High organic matter content or low bulk density indicates low disturbance since floods remove accumulated litter and organic matter.

In this study, I found a strong relationship (exponentially decreasing) between amplitude of water level fluctuations and sediment organic matter in the wet year (Figure 3.12). This is evidence that even moderate disturbance can lead to a large decrease in organic matter accumulation. There is one anomalous site with low amplitude (my measure of flood disturbance) and low organic matter. This is RIM1, a site where flow from a creek channel removes organic matter, despite the minimal change in water level.

Nutrient Limitations

The second objective of this study was to estimate nutrient limitations in the marshes and to determine the effects of nitrogen and phosphorus limitation on herb standing crop.

<u>Water Chemistry</u>

Nutrient concentrations in water in these wetlands (Table 3.2) was extremely low compared to other Alberta wetlands (Thormann and Bayley 1997b, Mewhort 2000). Based on N:P ratios of the surface water, most of the marshes were N-limited (Table 3.2 & Figure 3.7). This is consistent with the review by Bedford *et al* (1999), who found that most marshes in North America were N-limited. However, the most river-connected sites shifted to P-limitation at peak water levels in extremely high flood events (Figure 3.7). The river was P-limited and contained higher NO_3-N levels. Nitrates peak in the river-connected marshes (RM and BIM) with peak water levels in the river in the wet year (Figure 3.5). Nitrates are high in snowmelt but are readily taken up by algae and plants (Lewis and Grant 1979) especially during the dry year(Stednick 1989). Thus, phosphorus was limiting in the riverine and beaver-impounded wetlands when floodwaters first come in but the nitrogen is quickly consumed and the wetlands return to N-limitation. Denitrification can decrease nitrogen concentrations when conditions are anoxic (Mitsch and Gosselink 1993), which may arise during extremely high water levels associated with floods.

Sediment Chemistry

TN in sediment was significantly higher in the disconnected, railway-impounded marshes, which were the sites with the higher sediment organic content, than most other sites. However, TP had no statistical differences between sites (Figure 3.8). This finding is supported by Bedford *et al* (1999), who found mean N in sediment is higher in moderate- and extreme-rich fens than in marshes but there is no significant difference in P between wetland types. Sediment TN content is lower than literature values for all sites except the railway-impounded sites (Mitsch and Gosselink 1993, Mewhort 2000). Comparison of TP and TN is difficult because it is dependent on soil bulk density, which is rarely published (Bedford *et al.* 1999). The railway-impounded sites had significantly lower bulk densities (Figure 3.8).

N:P ratios of sediments are more important to emergent plant growth than absolute nitrogen and phosphorus concentrations (Auclair *et al.* 1976). The sediment N:P ratio of the riverine and beaver-impounded marshes suggests N-limited (N:P<14), while the railway-impounded marshes appear to be co-limited by N and P (Table 3.2). However, sediment N:P ratio is a measure of total sediment nutrients not biologically available sediment nutrients. The plants will be limited by the nutrients that are readily available to the roots, such as nitrate-nitrogen. The lack of N-limitation in the sediment of the railway-impounded sites may be due to more nitrogen available in the undecomposed peat, higher N-mineralization, and lower denitrification in the sediments under stable water levels of the railway-impounded area.

N:P ratio of the plant tissue is an excellent indicator of nutrient limitation (Koerselman and Meuleman 1996) and is less affected by other variables such as flood scour, sedimentation and internal nutrient cycling. Potentially that would provide a clearer picture of nutrient limitations in these wetlands. However, we did not measure tissue nutrient concentration.

Standing Crop

The aboveground herb peak standing crop was lower than most marshes in North America (Table 3.4). However, the productivity values are similar to those of riverine marshes in central Alberta even though nutrient concentrations are substantially lower than those marshes (Thormann and Bayley 1997b, Mewhort 2000). Nitrogen was more limited in the water column of the railway-impounded sites and more limited in the sediment of riverine sites (Table 3.2). Both of those areas had lower aboveground productivity relative to the beaver-impounded area (Figure 3.9).

It is difficult to separate the importance of nutrient limitations relative to other environmental variables, such as flood disturbance. Boyd (1971) found that in relatively infertile sites, standing crop of *Typha* was not as closely related to nutrient supply as other site factors such as wave action (removal of debris) and acidity/alkalinity of water supply. Moss production also responds more to alkalinity-acid gradient than to nutrient availability gradient (Vitt *et al.* 1995a). Given the greater difference in productivity between wet and dry years in the river-connected sites, it appears that flood disturbance is a more important driving variable than direct nutrient limitation.

Nutrient Limitations

Sediment concentrations, water column concentrations, as well as fertilization experiments suggest extremely low nutrient concentrations and nitrogen-limitation in the Jasper floodplain marshes. Gosselink and Turner (1978) found that inland marshes tended to be N-limited, but streamside marshes could be P-limited. Bedford et al (1999), in a review of North American wetlands, found that marshes were predominantly N-limited while fens were P-limited.

Nitrogen treatments produced significantly greater standing crop in the railway-impounded and beaver-impounded marshes but not the riverine marshes (Figure 3.10a). This provides further support that these marshes were nitrogen limited and were low in nutrients as a whole. Standing crop did not change in riverine marshes with any treatment, this may be an indication that flood disturbance has greater control than nutrient limitation for riverine marsh productivity. By comparing the N-fertilization treatment to standing crop from the same month in 1998, the dry year, it is evident that reduced flood disturbance produced much higher standing crop of vegetation than did any fertilization regime (Figure 3.10b).

Not all the results were significant even though visible differences were evident. The natural variability in this system was too great for a small sample size (n=3). Finally, increases in nutrients in fertile sites leads to increases in productivity, but in infertile sites, it leads to increases in tissue concentration (Ohlson 1988, Aerts *et al.* 1992).

Despite the low nutrient concentrations, nutrient limitations may not be driving the productivity of the riverine marsh system. Instead, degree of flood disturbance may be a more important factor. There were no significant correlations between herb or total plant NPP and environmental variables other than the natural disturbance gradient (data not shown). Low sample size (nine marshes) prevents the use of multiple regressions to compare several environmental variables.

Flooding can cause both increases and decreases in surface sediment N:P making the sediment of these systems less reflective of the nutrient availability (Bedford *et al.* 1999). Other studies have found that productivity of relatively infertile sites is driven by other factors than nutrient supply (Boyd 1971). Laitenen (1990) found that flood stresses could be more important than nutrient status for productivity and structure of mire vegetation.

Impact of Extreme Hydrologic Events on Ecological Variables

The last objective of this study was to compare the ecological effects of two extreme hydrologic years. The first study year, 1998, was considered a dry year and 1999 was considered a wet year.

<u>Water Levels</u>

Long-term discharge data from the Athabasca River shows that 1998 was a dry year while 1999 was a wet year (Figure 3.3). The later flood pulse in 1999 indicates a later spring, which is common in high snow pack years (Hudon 1997). Although several marsh systems exhibit a cyclic nature, for instance the prairie potholes (van der Valk and Davis 1978) and delta marshes (Pollock *et al.* 1998, Lesack *et al.* 1998), few freshwater wetlands show as extreme fluctuations as those in Jasper. In one afternoon of sampling during peak water levels in July 1999, the water level dropped >30 cm in less than two hours.

Amplitude of water level fluctuations showed large differences between years in the riverine and beaver-impounded marshes (Table 3.1). The river flood pulses did not reach the railway-impounded sites, and the small increase in water level in those marshes was due to local snowmelt. The three flood peaks extending over most of the summer in the river-connected sites (RM and BIM) in 1999 indicate that the intensity, magnitude and duration of the 1999 flood were greater than the 1998 season. These are three important factors in determining the impact of a disturbance (Sparks *et al.* 1990, Poff *et al.* 1997).

Water Chemistry

Nitrates had peaks in river-connected sites in June and July 1999 (Figure 3.6) that coincided with high water levels (Figure 3.2) but the Athabasca River had similar concentrations of nitrates between years (Figure 3.6). Thus, the difference between years was the volume and frequency of river water entering the wetlands, not the concentration of nitrates in the floodwaters. Turbidity had similar trends as nitrates with peaks in river-connected wetlands corresponding with high water levels in the wet year (Figure 3.4).

Lewis and Grant (1979) found there to be three responses in chemical variables to increases in discharge along subalpine streams, 1) dilution, 2) no change (possibly due to biological demand depleting resources as it becomes available), and 3) increased concentration (flushing from upstream or bioactivation). Stednick (1989) found dilution of chemical concentrations at peak flows in alpine and subalpine streams to be the most common response. Nitrates and turbidity appear to correspond with the second case of no change in the Athabasca River and other chemical parameters, such as SRP, appear to be unaffected by the flood event.

Standing Crop

Aboveground herb peak standing crop was significantly lower in 1999 compared to 1998 in all sites except the most river-connected, RM1 (Figure 3.9). Plants in the riverine marshes are likely better adapted to extreme floods (Amoros *et al.* 2000). Hultgren (1989) found that high water levels, particularly in early summer, could affect *Carex* production. Inter-annual differences in productivity are common but appear to be dependent upon wetland type. Groundwater fed fens with constant water supply have very little inter-annual differences in production, while South African floodplain wetlands with extremely seasonal hydrologic conditions had very high inter-annual variation (Whigham and Simpson 1992).

Peak aboveground herb standing crop was reached later in the wet year than the dry year (Table 3.3), probably delayed due a late spring and higher water levels. It is unlikely that dry year of 1998 caused a decrease in productivity in 1999. Hudon (1997), in a comparison of a dry year followed by a normal hydrologic year, suggested that drought did not have a long-term effect on emergent vegetation distribution and abundance due to the extensive root system of emergent vegetation. Over time, however, the flooding or lack of flooding will affect sediment deposition and the biogeochemical cycles of the river-connected wetlands.

Conclusions

It is evident that natural flood disturbance is a driving force in this system. Aboveground herb peak standing crop is highest in sites with a moderate degree of river connectivity and lowest in sites with high degree river connectivity. This indicates that moderate natural disturbance of floods combined with nutrient inputs from floodwaters provide optimal growing conditions for marsh plants in the Athabasca River floodplain in JNP.

The floodplain marshes were nitrogen limited. Nitrogen limitations are common in marshes and fens in North America (Thormann and Bayley 1997b, Bedford *et al.* 1999). The main channel of the Athabasca River was phosphorus limited, which is common in streams and rivers (Amoros *et al.* 2000),(van der Valk 1994) and the river-connected marshes (RM and BIM) switched to P-limitation in the water column at peak river flows. Increasing nutrients in river-connected marshes associated with flooding indicates that the river is the main source of some nutrients, such as nitrate. Despite the N loading from the river, the nutrient concentrations were extremely low in all the Jasper floodplain marshes.

I found nutrients to be limiting plant production in all sites except the riverine sites. Several authors have found nutrients to be the most limiting factor in plant production in wetlands (Bernard *et al.* 1988), (Wisheu and Keddy 1989). In JNP, it appears that seasonal flood disturbance also plays an important role in controlling plant production. Not only is plant peak standing crop lower in wet years but the relationship between peak standing crop and the disturbance gradient changes with flood magnitude. In addition, annual variation in river flooding can strongly affect ecological processes such as mineral sediment and litter deposition, nutrient input, internal nutrient cycling and possibly community structure (Chapter 2).

The variation in river connectivity in Jasper is partly natural, i.e. beaver dams, and partly human-created, i.e. the railbed. Alterations to flow regimes can lead to changes in nutrient supply and sedimentation, which may change production and species composition of the floodplains (Boggs and Weaver 1994). It was evident that aboveground herb peak standing crop was reduced, mosses were more productive, and peat was developing in the railway-impounded marshes. Lesack (1998) found that infrequently flooded lakes have different biogeochemical controls than frequently flooded lakes but a large flood can easily reset the status of disconnected lakes. This is very unlikely to occur in the marshes impounded by the railbed.

In Canada, the National Parks Act (Government of Canada 1988) requires Parks Canada to maintain the natural ecological integrity. Ecological integrity has been defined as when an ecosystem has the characteristics of native species and biological communities, rates of succession, and supporting processes(Parks Canada Agency 2000). This study and others (Henry and Amoros 1995, Poff *et al.* 1997) have shown that ecological integrity is linked to hydrologic connectivity. Since the railway-impounded wetlands have been hydrologically disconnected due to human construction, the productivity, nutrient status, and sediment chemistry in the impacted wetlands is significantly different from those wetlands that maintained some measure of river connectivity. Natural flow regimes should be restored in the disconnected wetlands to restore ecological integrity.

Table 3.1: Mean (± se) physical environmental variables in the three study areas (disconnected RIM, partially river-connected BIM, and fully river-connected RM) and the Athabasca River for 1998 and 1999. Conductivity is corrected for temperature and pH. Amplitude is the difference between maximum and minimum water levels. There was no water depth gauge in the Athabasca River.

Environmental Variables	**Year**	**Athabasca River**	**RIM**	**BIM**	**RM**
Turbidity	1998	203.0 ± 59.8	3.4± 0.5	7.5 ± 1.1	6.9 ± 1.1
	1999	66.7 ± 20.4	8.0 ± 1.7	21.5 ± 6.8	22.6 ± 6.2
Conductivity (µS)	1998	189.5 ± 16.1	323.6 ± 5.6	246.6 ± 20.8	443.9 ± 32.4
	1999	227.0 ± 5.3	361.8 ± 9.7	301.3 ± 15.5	463.6 ± 22.7
Water Depth (cm)	1998	N/A	28.4 ± 0.8	32.3 ± 1.1	32.3 ± 3.8
	1999	N/A	33.1 ± 0.8	37.1 ± 3.4	52.3 ± 5.7
Amplitude (cm)	1998	N/A	18.3 ± 0.2	20.2 ± 0.6	78.5 ± 2.6
	1999	N/A	17.9 ± 0.7	83.2 ± 7.8	122.1 ± 6.9

Table 3.2: Concentrations of nutrients in surface water (mean ± se) in the three study areas (disconnected RIM, partially river-connected BIM, and fully river-connected RM) and the Athabasca River in 1998 and 1999. N:P ratios are based on weight.

Environmental Variables	**Year**	**Athabasca River**	**RIM**	**BIM**	**RM**
NH_4-N (µg/L)	1998	20.4 ± 14.7	2.2 ± 0.5	8.9 ± 2.9	4.9 ± 1.2
	1999	9.7 ± 1.5	9.1 ± 1.7	8.7 ± 1.3	10.1 ± 3.1
NO_3-N µg/L)	1998	44.1 ± 3.4	3.4 ± 0.9	0.6 ± 0.1	6.2 ± 2.3
	1999	56.8 ± 3.2	6.7 ± 1.8	12.0 ± 5.0	17.8 ± 2.3
TDN (µg/L)	1998	79.0 ± 6.1	138.5 ± 10.1	288.4 ± 24.1	225.7 ± 31.9
	1999	91.4 ± 13.9	104.8 ± 18.0	108.2 ± 15.0	110.2 ± 16.6
SRP (µg/L)	1998	1.8 ± 0.2	3.1 ± 0.2	3.5 ± 0.5	4.8 ± 0.9
	1999	2.0 ± 0.2	2.4 ± 0.2	2.2 ± 0.4	3.0 ± 0.3
TP (µg/L)	1998	65.2 ± 22.5	15.7 ± 2.3	24.2 ± 2.8	25.1 ± 2.3
	1999	44.7 ± 21.8	14.1 ± 1.5	17.0 ± 3.8	21.9 ± 5.2
TDP (µg/L)	1998	2.0 ± 0.2	4.1 ± 0.3	6.7 ± 0.6	8.5 ± 1.3
	1999	2.1 ± 0.1	2.7 ± 0.2	3.1 ± 0.4	4.5 ± 0.6
Water column N:P	1998	37.4 ± 12.5	2.4 ± 0.6	3.9 ± 1.2	3.8 ± 1.0
	1999	34.5 ± 3.7	7.2 ± 1.2	11.9 ± 3.1	10.9 ± 3.3
Sediment N:P	1999	N/A	15.4 ± 1.7	4.9 ± 0.7	2.5 ± 0.2

Table 3.3 The aboveground herbaceous standing crop (mean ±se) in the nine study sites (disconnected marshes RIM, partially river-connected marshes BIM, and the fully river-connected marshes RM) at three harvest periods in 1998 and 1999.

Year	Harvest Date	Railway-Impounded			Beaver-Impounded			Riverine		
		RIM1	RIM2	RIM3	BIM1	BIM2	BIM3	RM1	RM2	RM3
1998	June	361.44 ± 48.53	186.22 ± 25.56	175.54 ± 17.40	258.04 ± 25.03	373.58 ± 74.71	245.42 ± 42.01	235.11 ± 24.74	218.54 ± 16.22	173.65 ± 13.99
	July	339.17 ± 28.87	190.12 ± 24.57	212.55 ± 32.95	423.11 ± 32.17	522.27 ± 70.81	393.16 ±33.67	348.39 ± 53.12	338.40 ± 21.97	289.14 ± 34.21
	August	34.87 ± 34.87	22.64 ± 22.64	31.05 ± 31.05	40.62 ± 40.62	35.28 ± 35.28	24.82 ± 24.82	54.44 ± 54.44	15.63 ± 15.63	46.31 ± 46.31
1999	June	134.29 25.23±	115.44 ± 18.10	80.95 ± 13.88	81.07 ± 11.71	149.17 ±13.08	81.24 ± 15.20	113.90 ± 12.29	119.51 ± 13.88	91.50 ± 18.25
	July	187.87 ± 23.38	102.78 ± 17.06	105.32 ± 24.58	150.04 ± 10.44	217.89 ± 22.35	139.38 ± 22.26	134.83 ± 27.89	177.88 ± 18.67	88.82 ± 17.12
	August	189.66 ± 33.15	109.20 ± 25.59	105.65 ± 26.70	214.42 ± 20.37	247.24 ± 30.30	216.38 ± 29.47	226.36 ± 51.23	268.39 ± 34.39	176.57 ±44.45

Table 3.4: Aboveground net primary productivity (g m^{-2} yr^{-1}) of different strata for North American marshes and fens. Columns may not round up to total since shrub and tree productivity is not displayed. Data from this study are average for areas. Peak standing crop was used as an estimate of net primary productivity when it was not calculated directly.

Wetland Type	Source	Location	Moss	Herb	Total
MARSHES					
Riverine marsh	Thormann and Bayley (1997a)	Alberta	0	323	323
Lacustrine marsh	Thormann and Bayley (1997a)	Alberta	0	757	757
Lacustrine marsh	Mewhort (2000)	Alberta	0	884	884
Riverine marsh	Mewhort (2000)	Alberta	0	208	208
Riverine marsh (dry year)	This study	Alberta (Rockies)	0	367	367
Riverine marsh (wet year)	This study	Alberta (Rockies)	0	135	135
Beaver-impounded marsh (dry year)	This study	Alberta (Rockies)	0	446	446
Beaver-impounded marsh (wet year)	This study	Alberta (Rockies)	0	226	226
Carex marsh	Gorham and Somers (1973)	Alberta (Rockies)	0	640	640
Carex marsh	Gorham and Somers (1973)	Alberta (Rockies)	0	380	380
Lacustrine marsh	Neill (1993)	Manitoba	0	955	955
Carex meadow	Auclair et al (1976)	Quebec	0	820	820
Carex meadow	Bernard (1974)	Minnesota	0	738	738
Marsh	Bray (1963)	Minnesota	0	1360	1360
Carex sedge meadow	Gorham and Bernard (1975)	Minnesota	0	941	941
Marsh	Getz (1960)	Michigan	0	465	465
Carex marsh	Bernard and MacDonald (1974)	New York	0	857	857
FENS					
Lacustine sedge fen	Szumgalski and Bayley (1996)	Alberta	42	163	213
Extreme rich fen	Szumgalski and Bayley (1996)	Alberta	149	89	245
Lacustrine sedge fen	Thormann and Bayley (1997a)	Alberta	74	190	277
Riverine sedge fen	Thormann and Bayley (1997a)	Alberta	0	409	409
Sedge fen	Mewhort (2000)	Alberta	0	328	328
Railway-impounded (dry year)	This study	Alberta (Rockies)	61	247	308
Railway-impounded (dry year)	This study	Alberta (Rockies)	49	224	273
Rich fen	Bartsch and Moore (1985)	Quebec	41	233	335
Transitional fen	Bartsch and Moore (1985)	Quebec	39	90	176

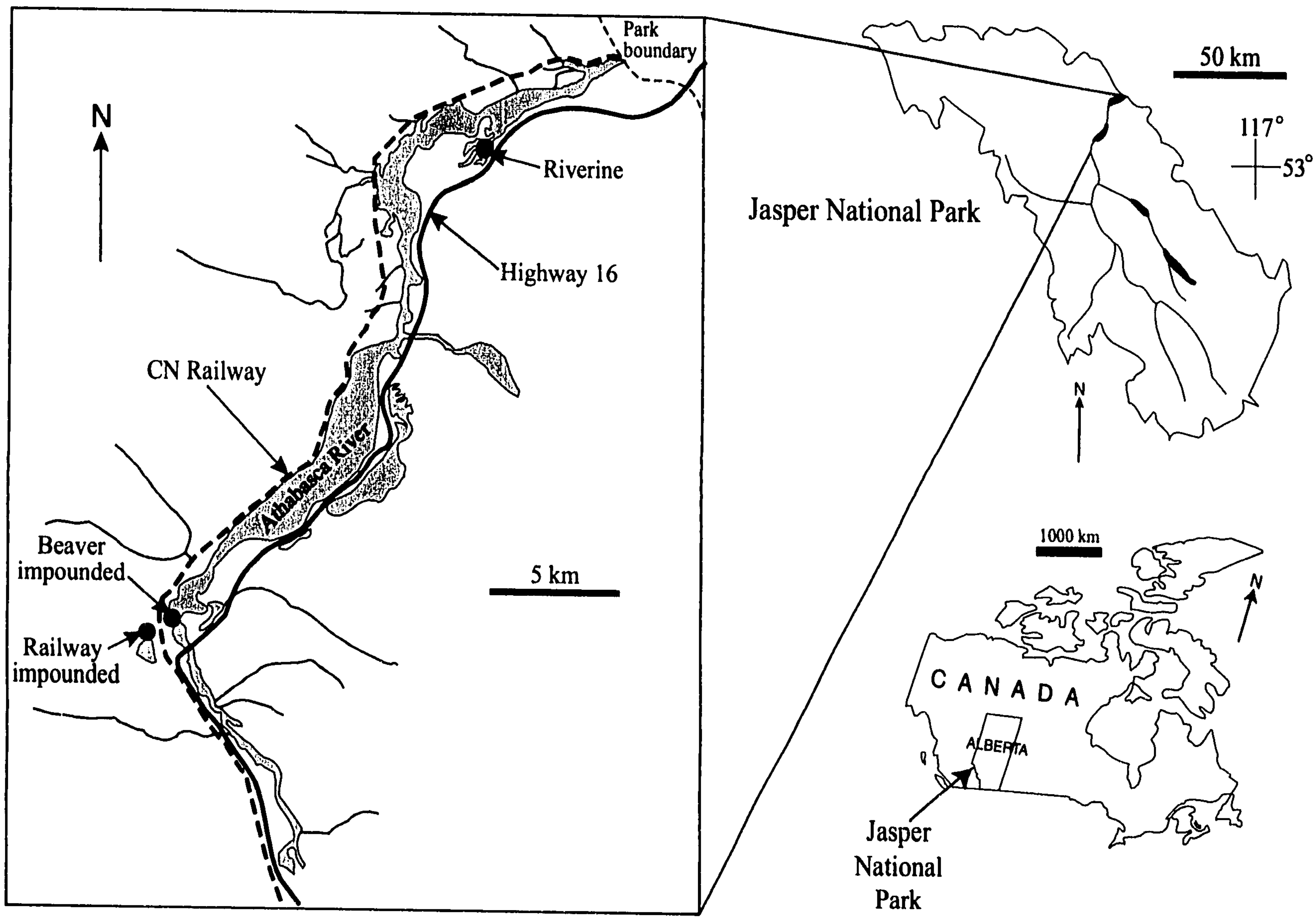
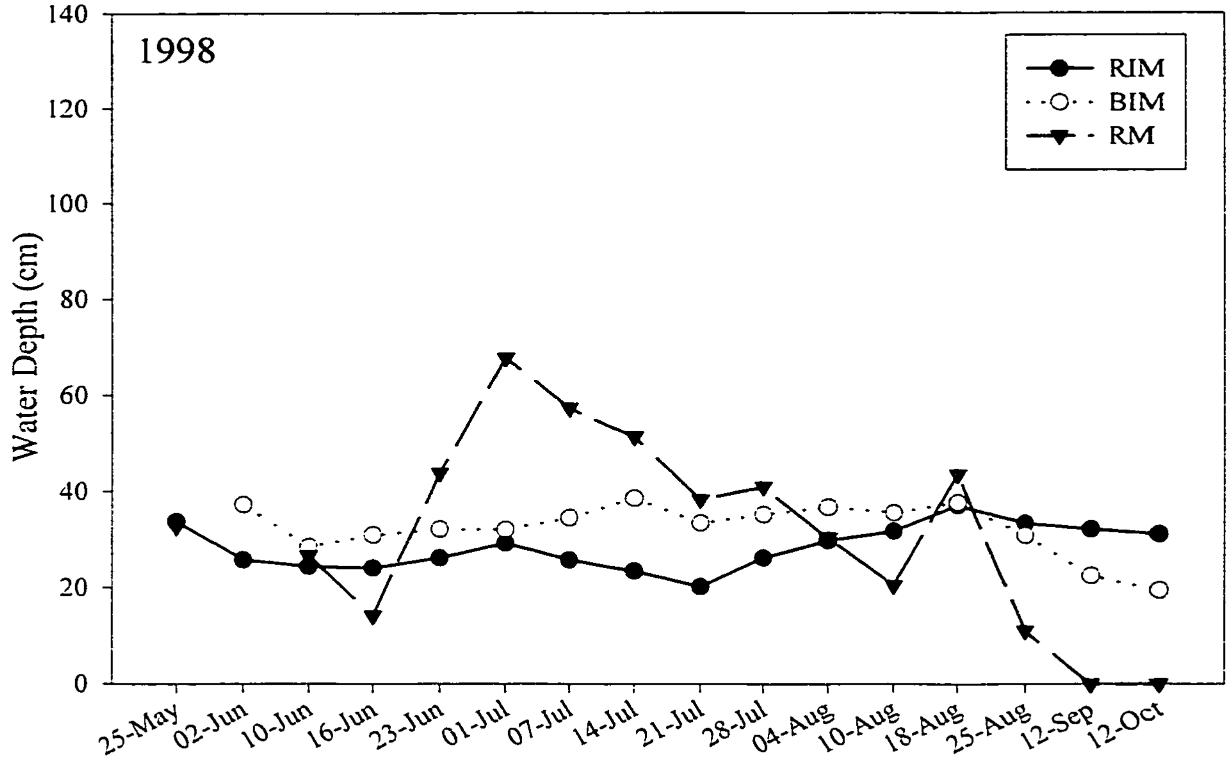


Figure 3.1: Location of the three study areas (riverine, beaver impounded, and railway impounded) in Jasper National Park, Alberta, Canada.



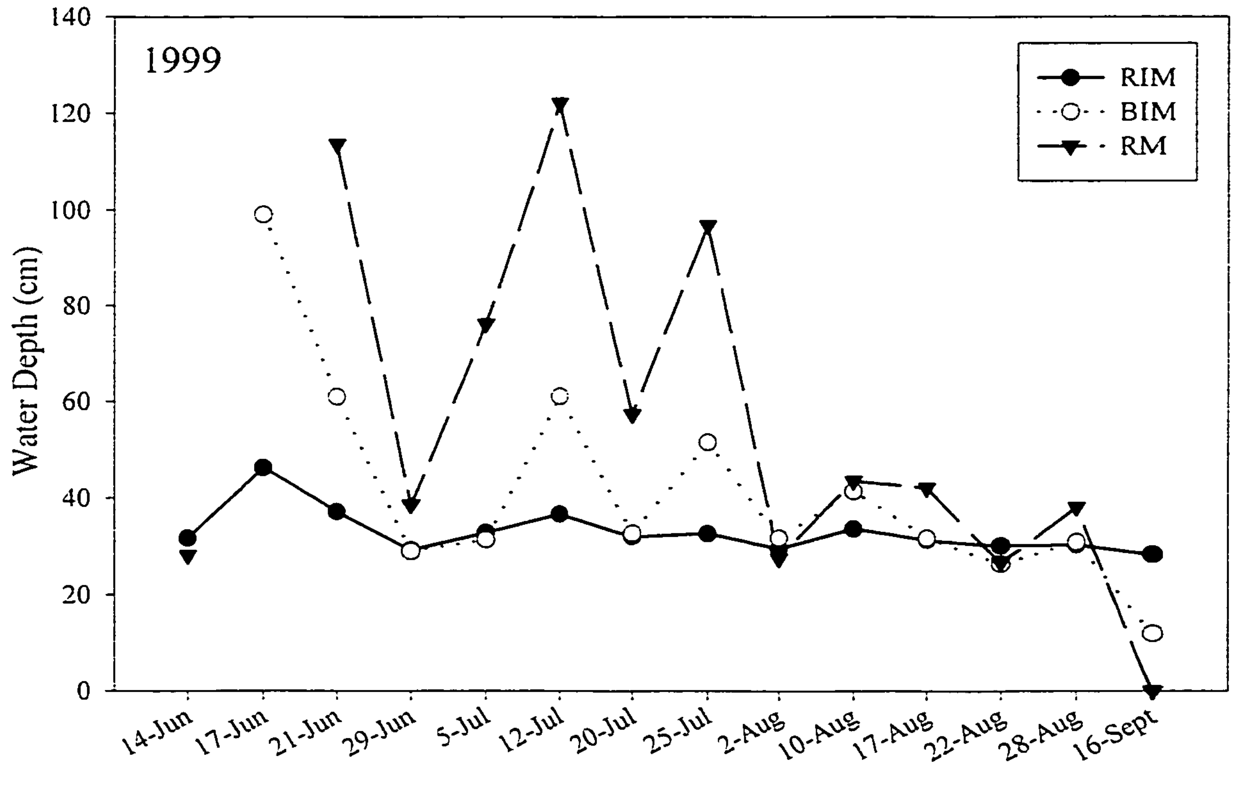


Figure 3.2: Seasonal changes in water depth in the three study areas in 1998 (top) and 1999 (bottom). The three study areas are disconnected marsh area (RIM), partially river-connected marsh area (BIM), and fully river-connected marsh area (RM).

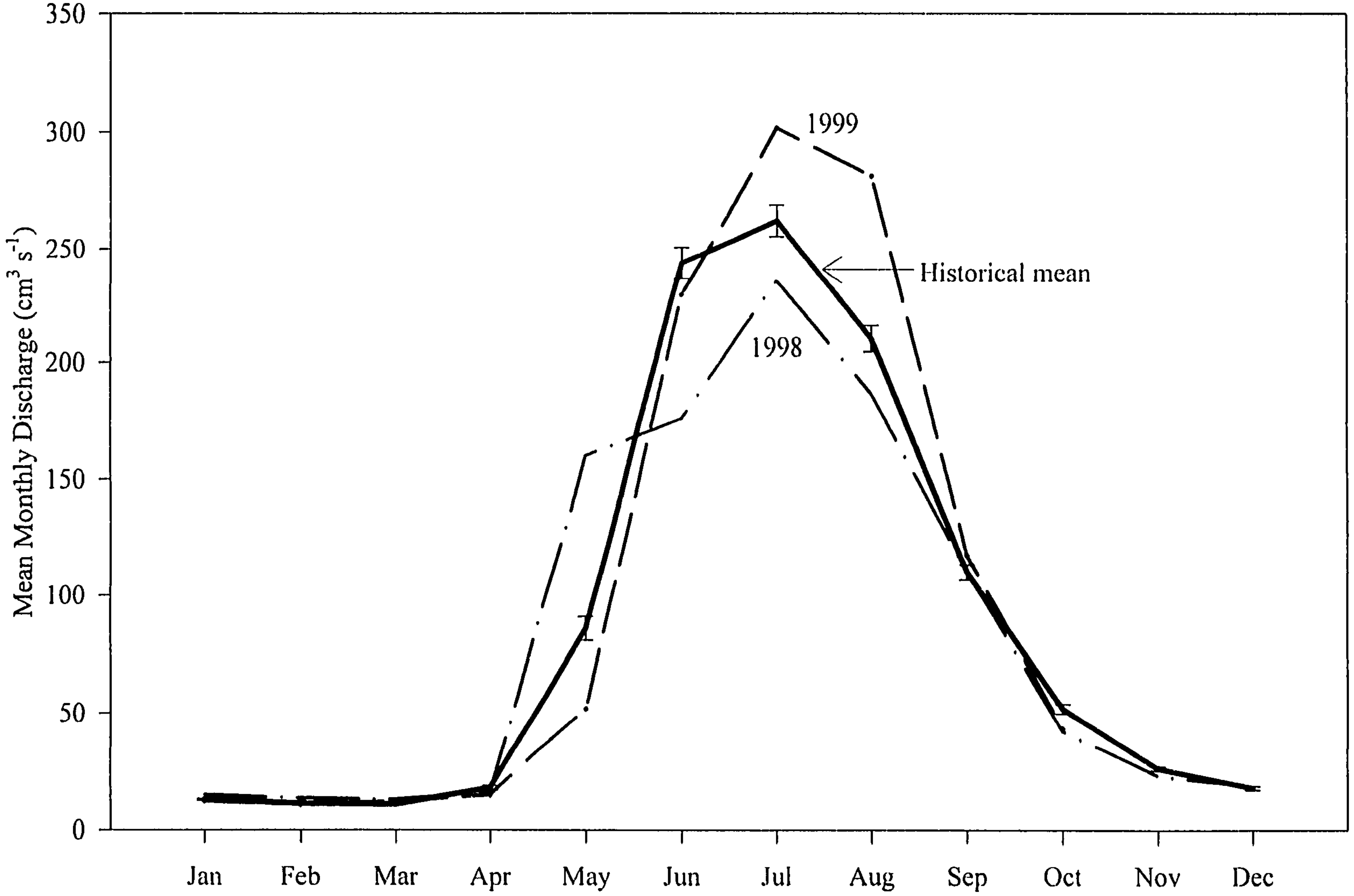


Figure 3.3: Mean monthly discharge data (cm^3 s^{-1}) for the Athabasca River near Jasper Townsite for 1998, 1999 and the mean (± se) over the historical record of 1913 to 1995.

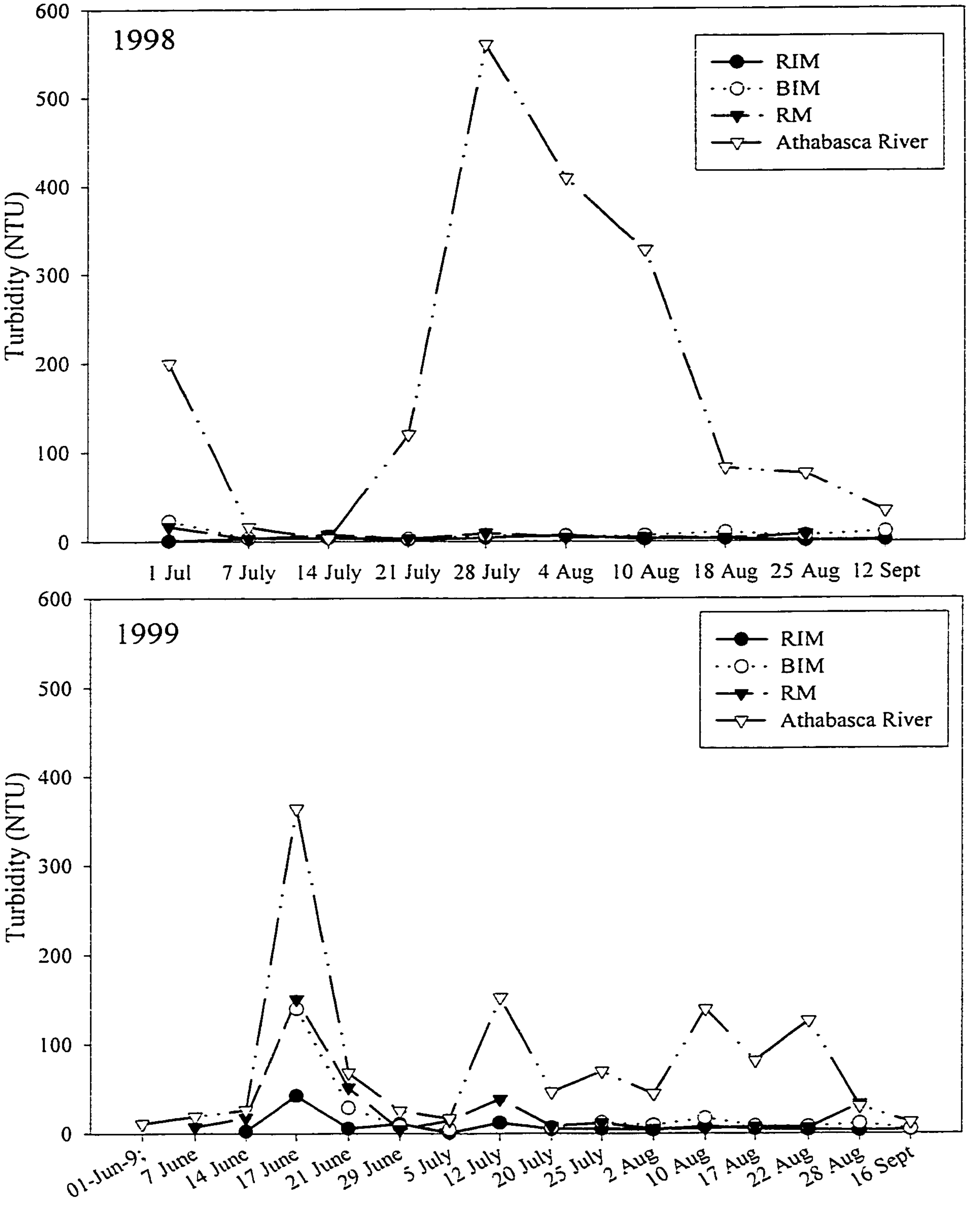


Figure 3.4: Seasonal changes in turbidity in the three study areas and the Athabasca River in 1998 (top) and 1999 (bottom). The three study areas are disconnected marsh area (RIM), partially river-connected marsh area (BIM), and fully river-connected marsh area (RM).

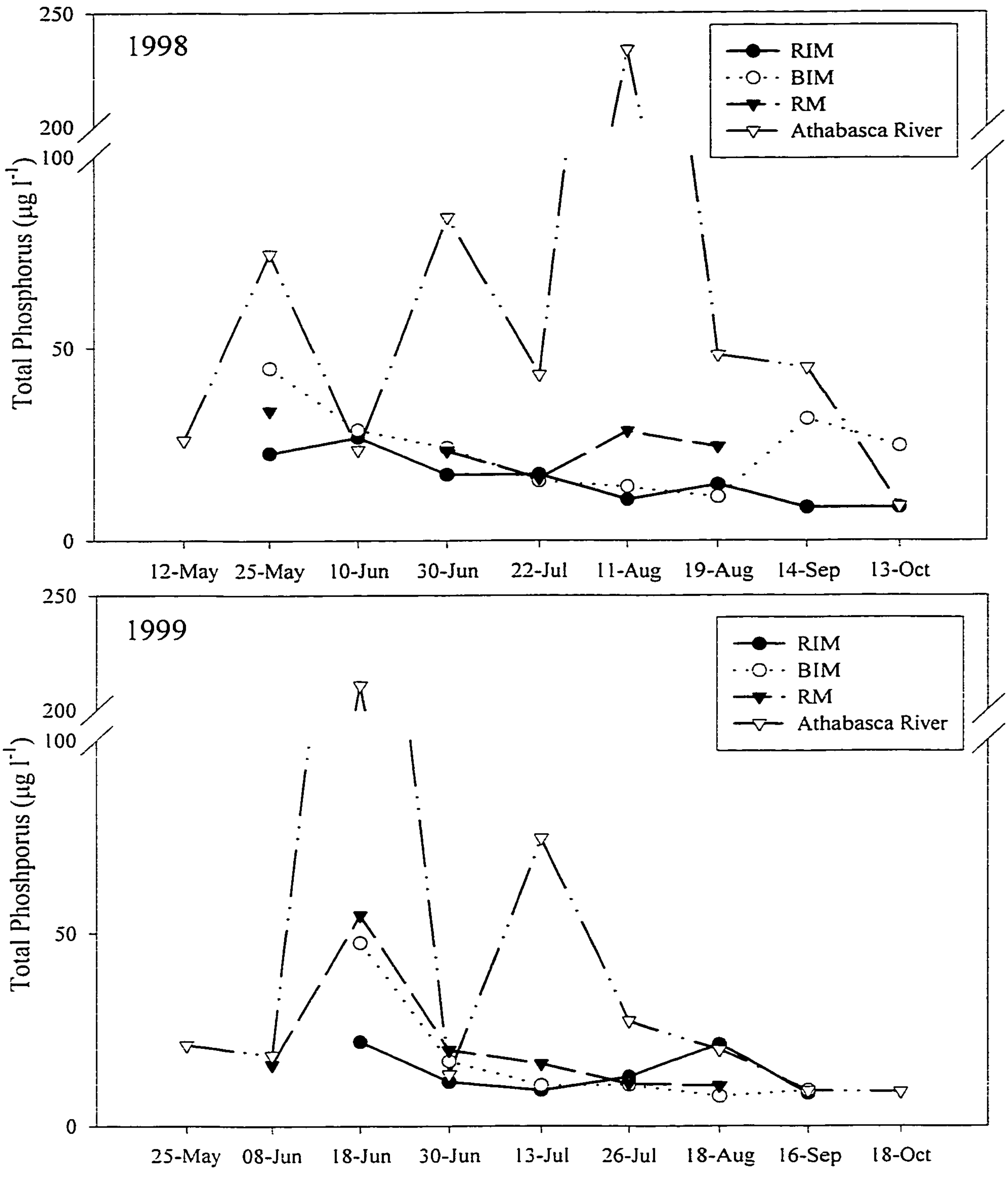


Figure 3.5: Seasonal changes in TP in the surface water of the three study areas and the Athabasca River in 1998 (top) and 1999 (bottom). The three study areas are disconnected marsh area (RIM), partially river-connected marsh area (BIM), and fully river-connected marsh area (RM).

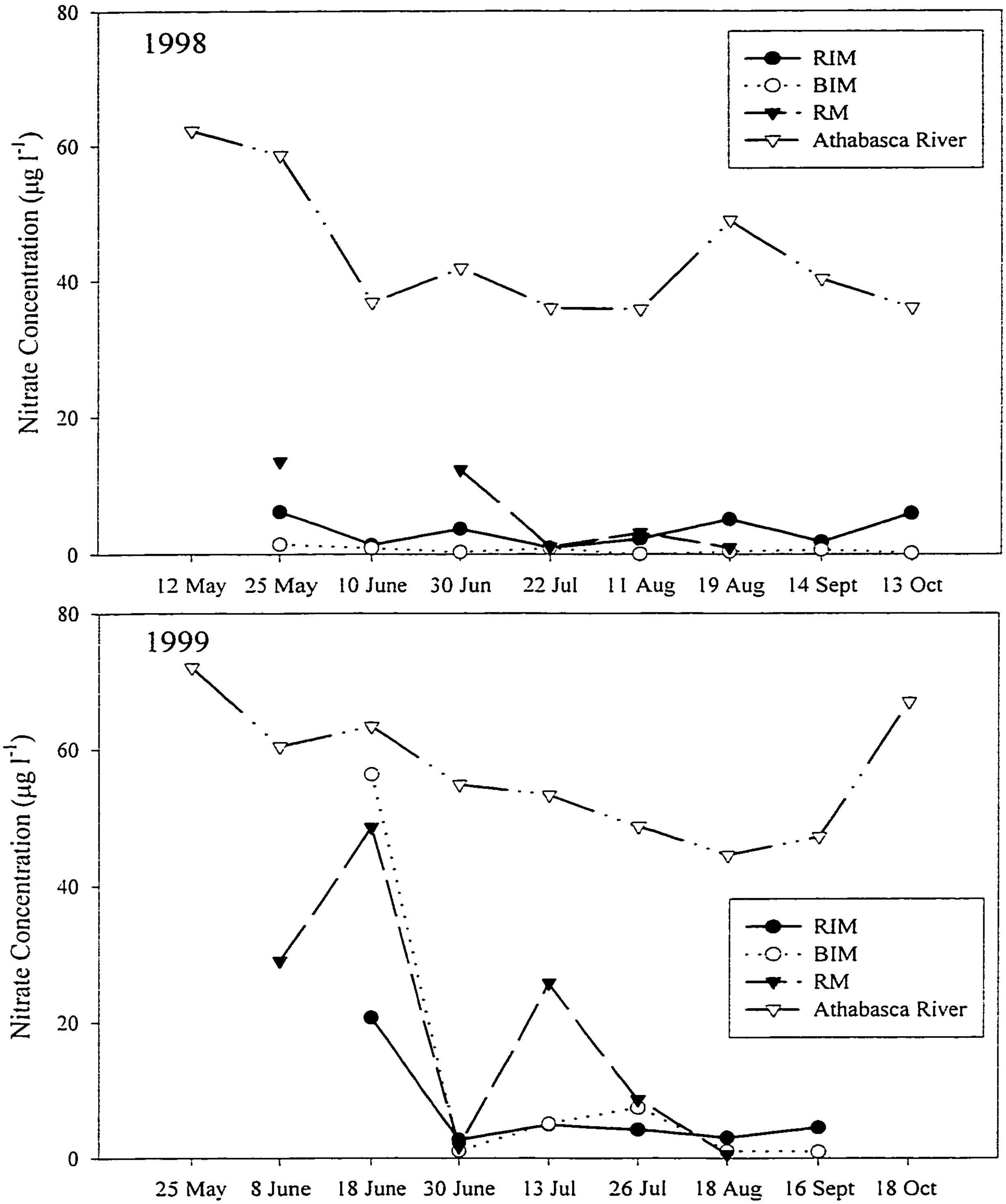


Figure 3.6: Seasonal changes in nitrate concentrations in the three study areas and the Athabasca River in 1998 (top) and 1999 (bottom). The three study areas are disconnected marsh area (RIM), partially river-connected marsh area (BIM), and fully river-connected marsh area (RM).

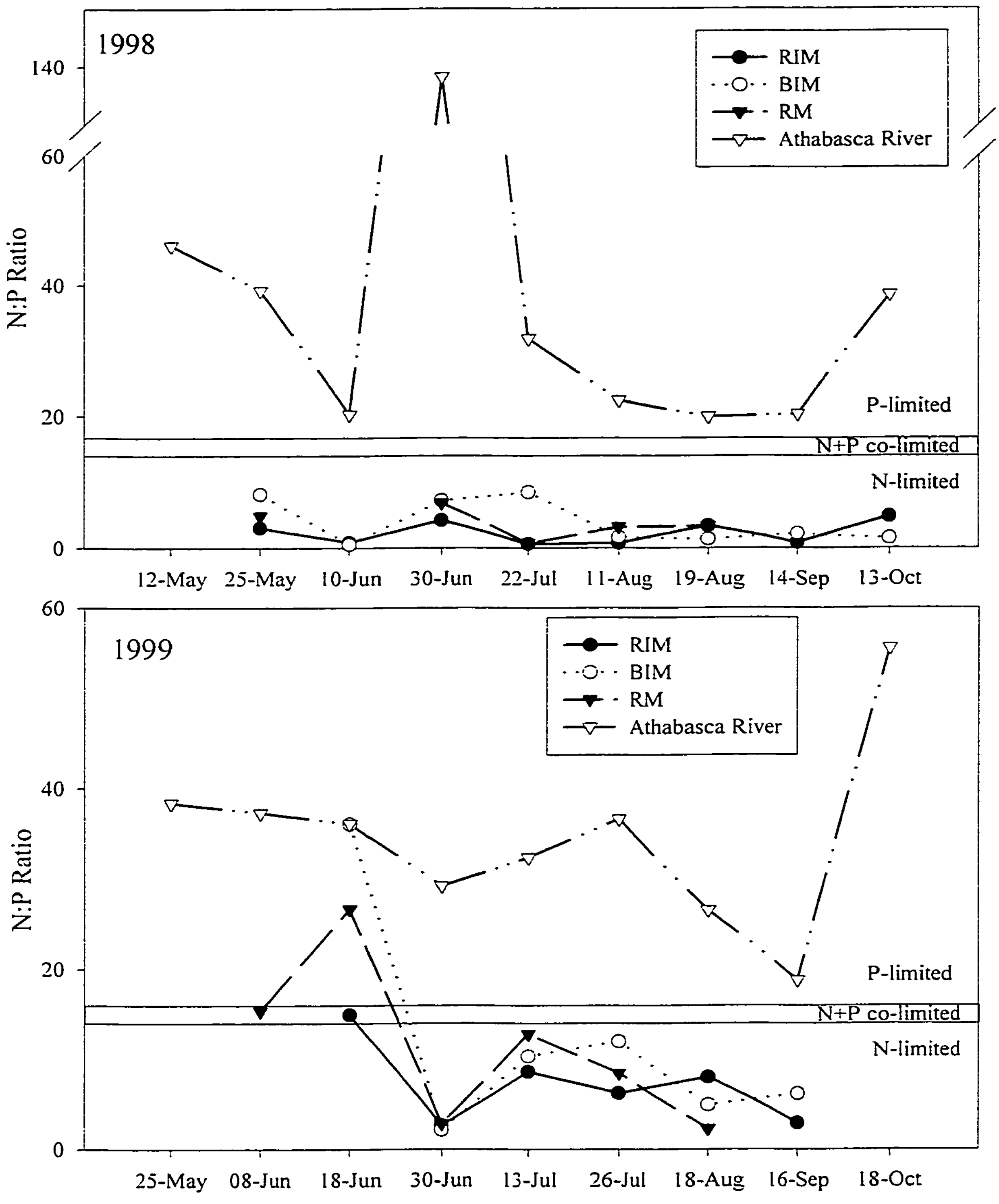


Figure 3.7: Seasonal changes in N:P ratio of the water column in the three study areas and the Athabasca River in 1998 (top) and 1999 (bottom). The three study areas are disconnected marsh area (RIM), partially river-connected marsh area (BIM), and fully river-connected marsh area (RM). The area within the double horizontal line is co-limited by nitrogen (N) and phophorus (P), while the area below the line is N-limited (N:P<14), and the area above the line is P-limited (N:P>16).

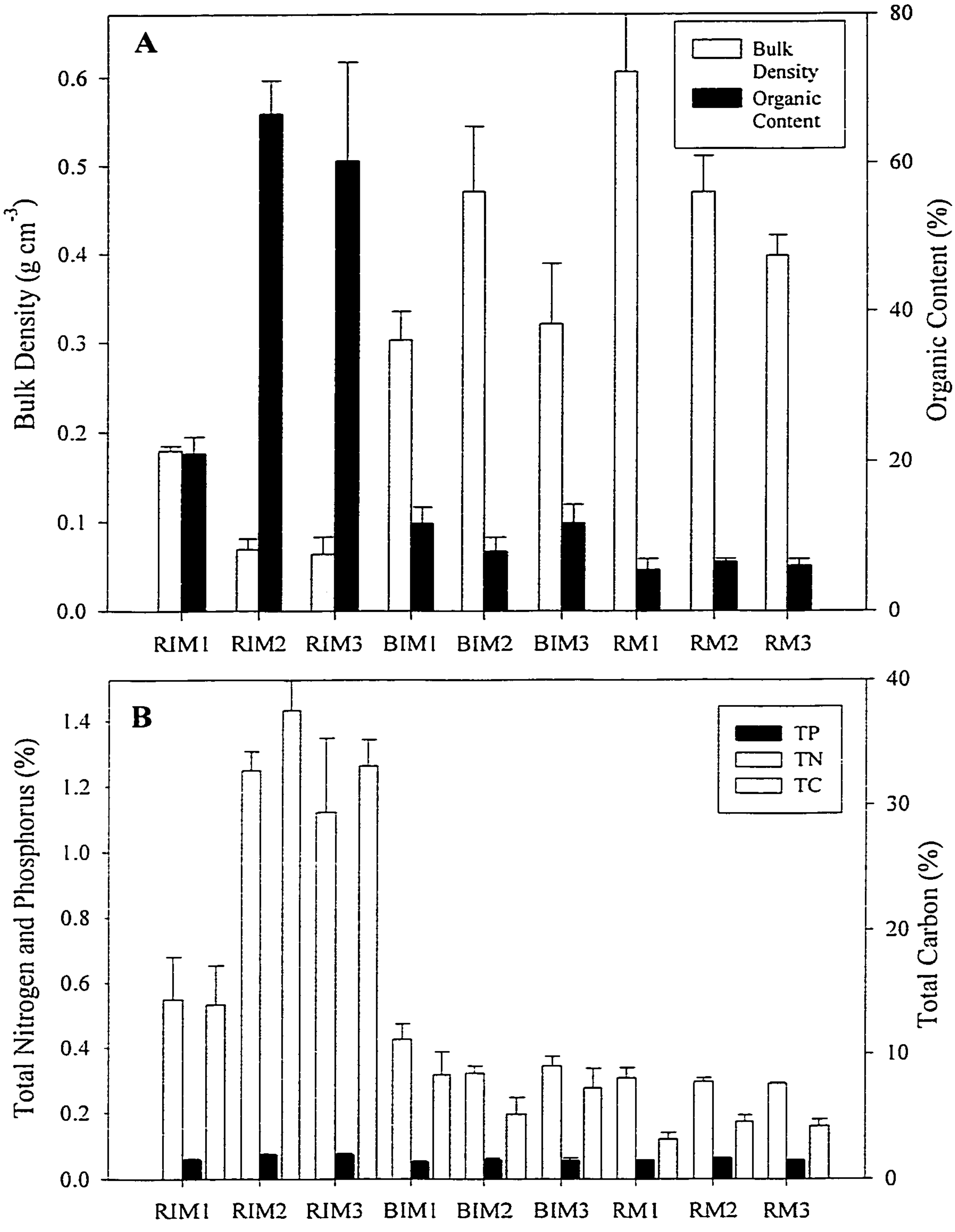


Figure 3.8: Sediment characteristics (mean ± se) from the nine marsh sites (disconnected marshes RIM, partially river-connected marshes BIM, and fully river-connected marshes RM). Bulk density and organic content (A), and total nitrogen, total phosphorus, and total carbon (B) are displayed.

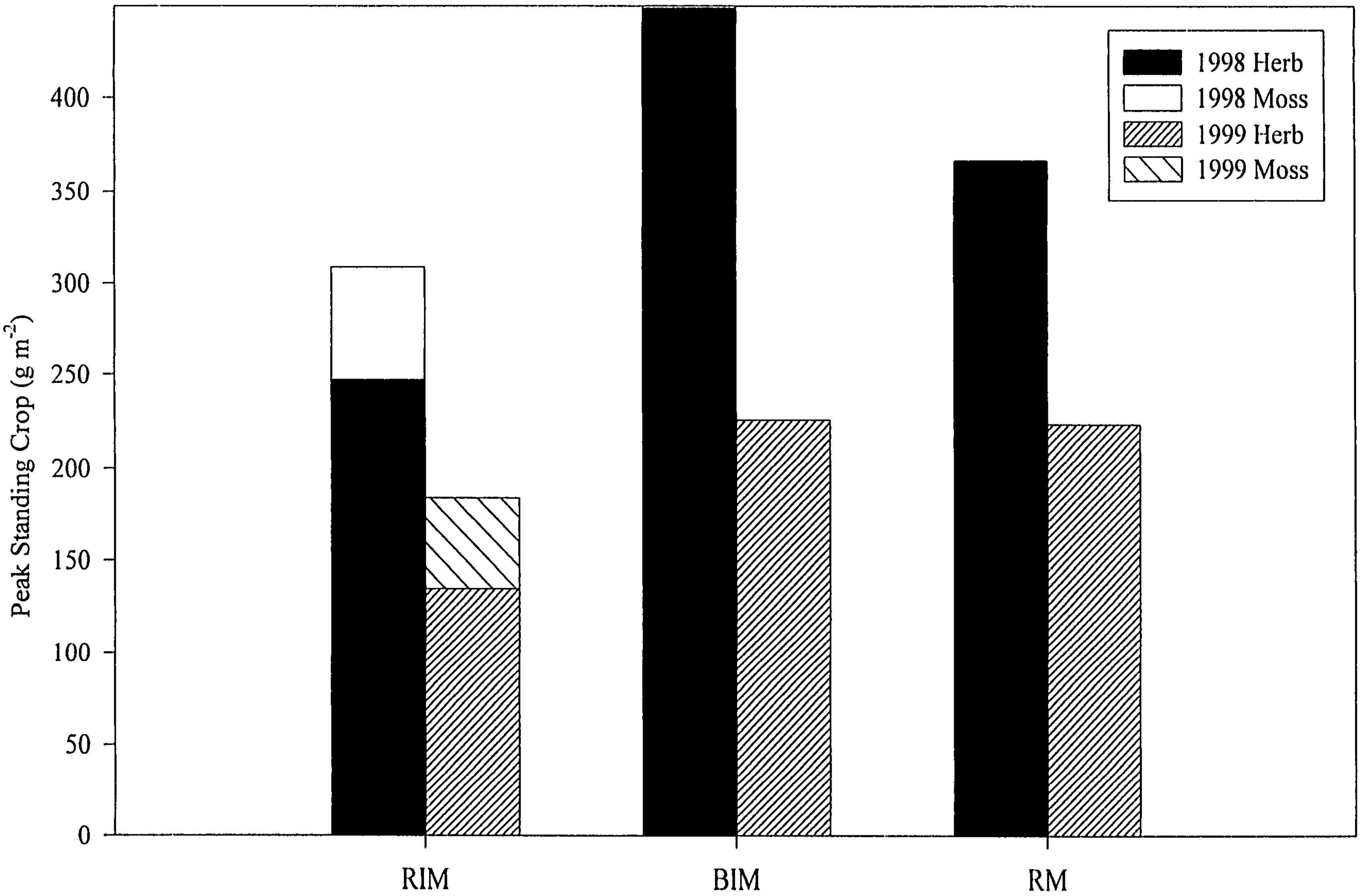


Figure 3.9: Peak standing crop for herb and moss strata, as an estimate of total plant NPP, for the three study areas (disconnected marsh area RIM, partially river-connected marsh area BIM, and fully river-connected marsh area RM) in 1998 and 1999.

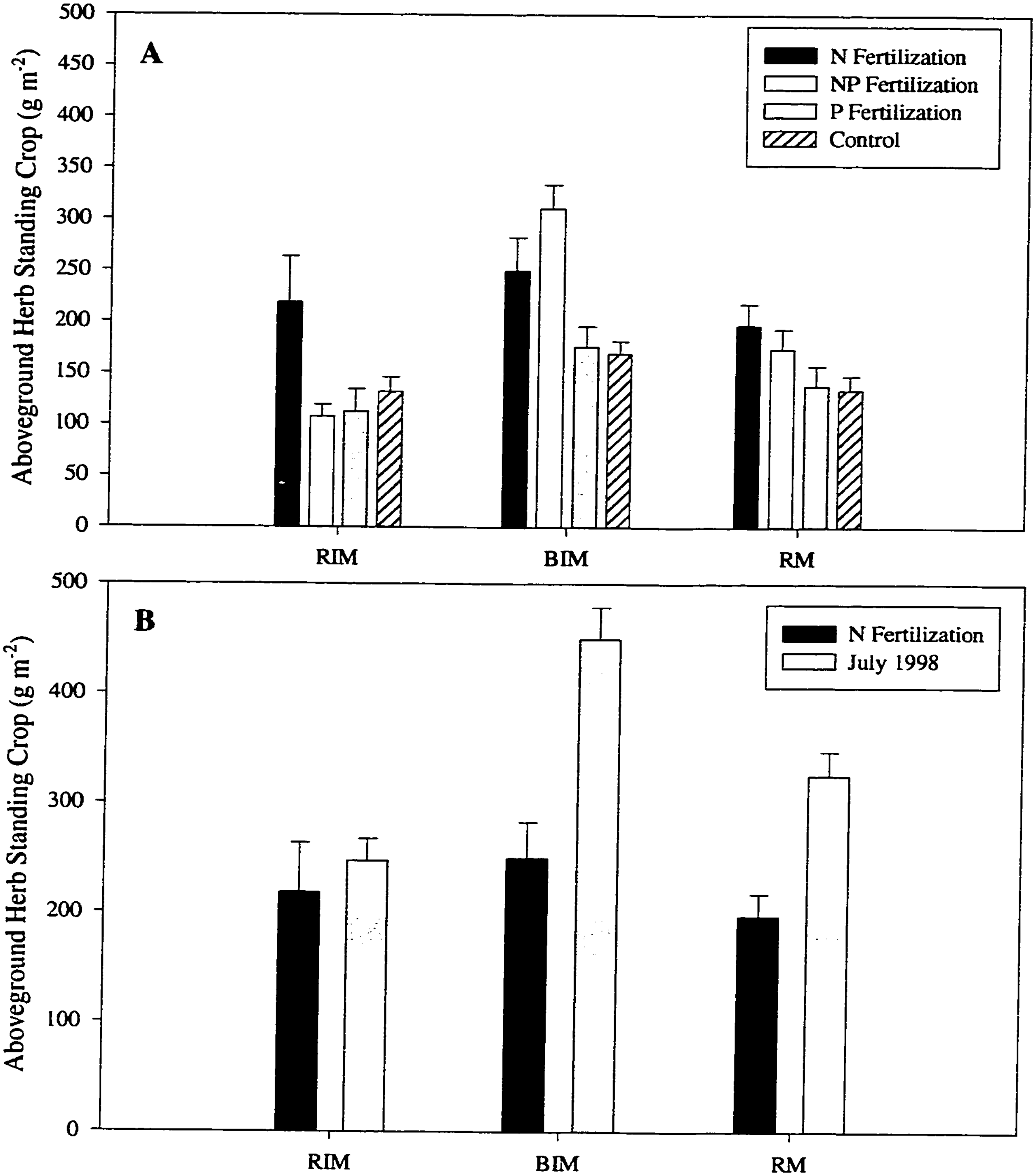


Figure 3.11: Aboveground herb standing crop collected July 30, 1999 (mean ± se) of the three fertilization treatments and the control (A) for the three wetland areas. Part B compares standing crop with N fertilization treatment in the wet year (July 1999) and standing crop with no fertilization treatment in the dry year (July 1998) the three wetland areas.

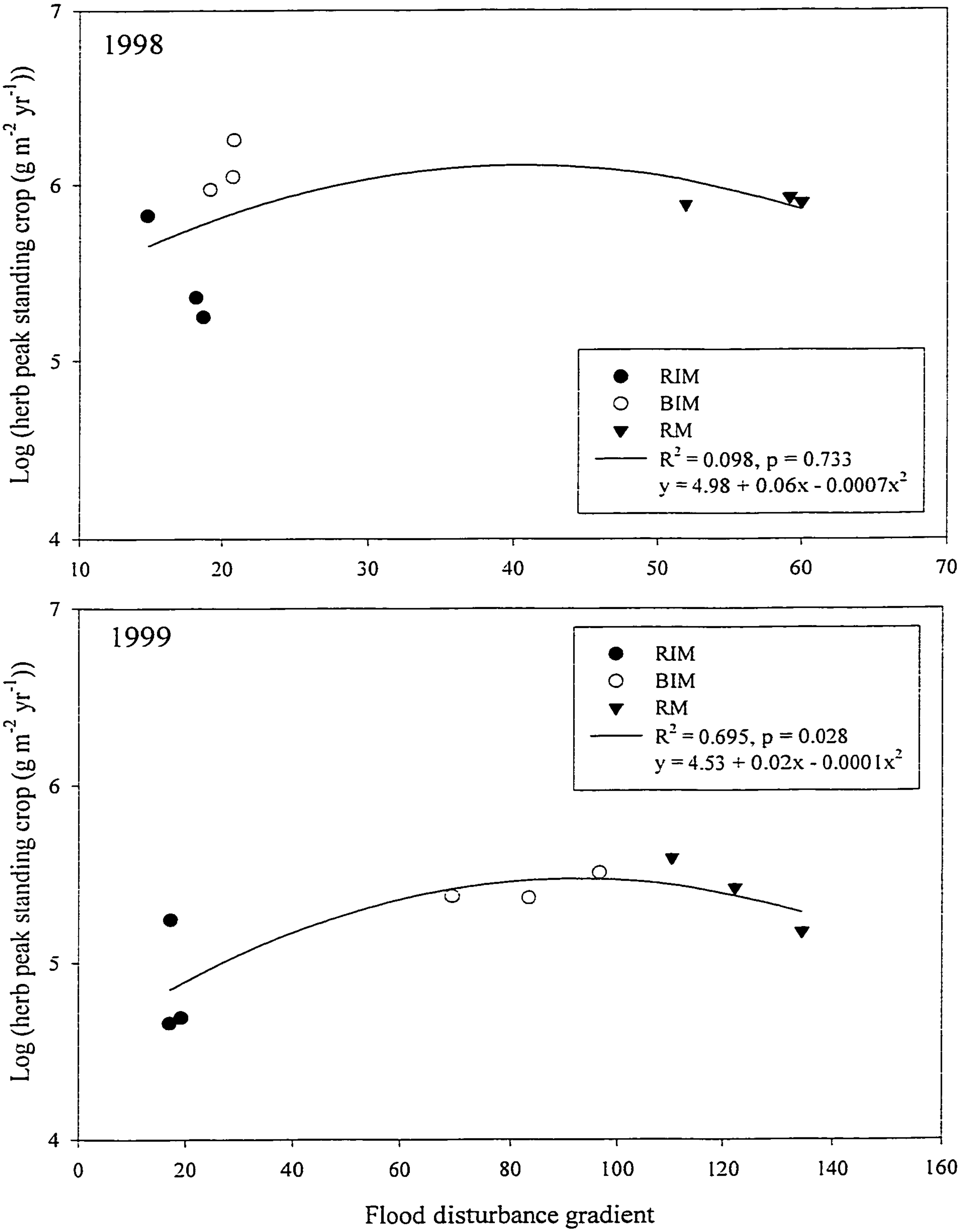


Figure 3.11: Herb peak standing crop along the natural disturbance gradient in 1998 (top) and 1999 (bottom). The disturbance gradient is estimated using amplitude of water level fluctuations. In the dry year (1998), river water did not flood the beaver-impounded sites, hence there were no significant relationship.

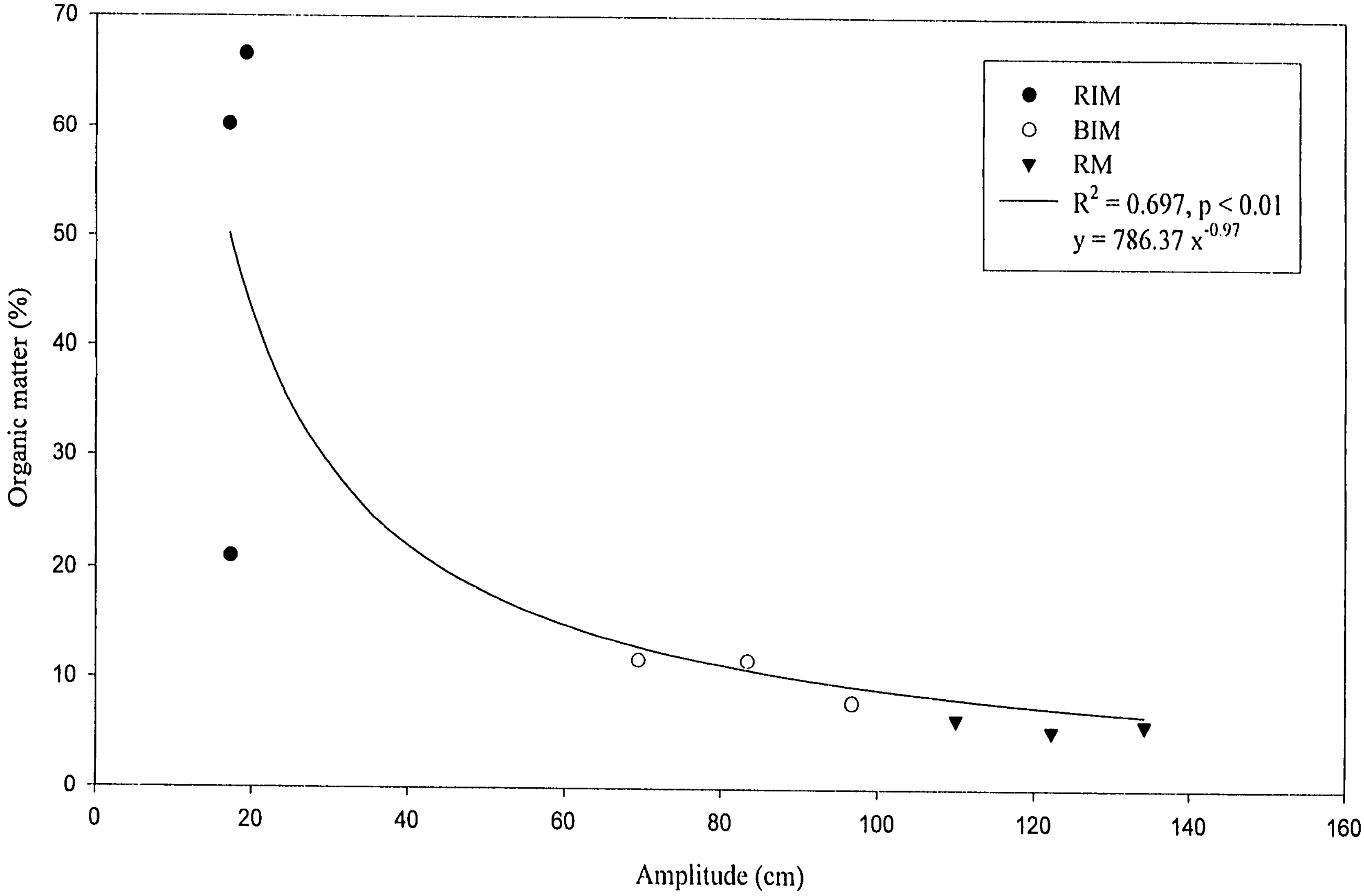


Figure 3.12: The relationship between amplitude of water level fluctuations and sediment organic content, both measures of flood disturbance, in the wet year (1999). There is a strong relationship between amplitude and organic matter except for one site. The railway impounded site with low organic matter is adjacent to a flowing channel.

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4. Conclusions

The floodplain wetlands of Jasper National Park are highly influenced by the Athabasca River. The wetlands vary in the degree of river connectivity; the lower the connectivity and the more muted the floods. River connectivity decreases with increasing distance from the main river and increasing number of barriers (beaver dams and embankments) along the inflow path. River connectivity and in turn, flood disturbance has had a large effect on the diversity, community structure and productivity of the study marshes.

The Athabasca River was a source for suspended sediments, nitrate, and TP with higher concentrations than local stream and marsh water. Flooding increased the turbidity and nitrate concentrations of surface water in the riverine and beaver impounded marshes. Nitrates are commonly found in snowmelt and suspended sediments are often high in phosphorus (Lewis and Grant 1979, Stednick 1989). Both nitrates and turbidity peaked in the riverine and beaver-impounded wetlands when water levels peaked. River discharge was significantly lower in 1998 and higher in 1999 than the historical mean discharge. Thus, the two study years were hydrologic extremes. Amplitude of water level fluctuations and maximum water depth was highest in the riverine and beaver-impounded marshes, and was higher in the wet year (1999) than the dry year (1998).

Similar to other wetlands (Thormann and Bayley 1997b, Bedford *et al.* 1999), the marshes were N-limited in the surface water, while the Athabasca River was P-limited. However, at peak discharge, the riverine and beaver-impounded marshes switched to P-limitation, providing further evidence that the river is the main source of nutrients (van der Valk 1994). Sediment chemistry also showed that all areas were N-limited. However, sediments of the disconnected, railway-impounded marshes had significantly higher organic content, total nitrogen and total carbon concentrations. The lack of flood disturbance has allowed organic sediment to accumulate and peat to develop. This was not seen in any other marsh site. Disturbance is known to remove litter (Poff *et al.* 1997) and promote decomposition (van Oorschot *et al.* 1997). Although attempts were made to quantify the differences in decomposition between the wetlands, sediment deposition made it impossible.

Even in a dry year like 1998, differences were evident in marsh species between sites with different river connectivity in JNP. Site diversity was found to be highest at intermediate values along the flood disturbance gradient. Given the intermediate flooding of the beaver-impounded area, this supports the Intermediate Disturbance Hypothesis (Connell 1978, Stanford and Ward 1993). In total, 95 species were found in the floodplain study marshes, which is slightly higher than in other studies of floodplain marsh communities (Bornette and Amoros 1996, Bornette *et al.* 1998a). A large proportion of the species, 64.2%, were unique to only one wetland area. However, a quarter of the species were ubiquitous to all study marshes. This suggests that the majority of the species are adapted to a specific environment and disturbance regime and a small number of the species, usually the dominant species, are very plastic and adapted to several environmental regimes.

Both community classification (TWINSPAN) and direct ordination analysis (correspondence analysis, CCA) support the initial classification of the floodplain wetlands as three distinct areas. The riverine sites are separated from the other sites at the first level of division in the classification and produce four unique community types with low diversity. Several dominant species (e.g. *Carex saxatilis* and *Ranunculus reptans*) in the riverine area are restricted to that area, suggesting adaptation to extreme flooding. The beaver-impounded area along with one railway-impounded site has wet and dry (associated with edges and hummocks) community types. The beaver-impounded area also has high diversity due to moderate flooding. A unique wet *Drepanocladus aduncus* dominated community type was found exclusively in two of the railway-impounded sites. Those railway-impounded marshes (with stable water levels) had increased moss cover, decreased emergent cover, and peat development indicating that these sites are in succession to a fen. However, the other railway-impounded site (RIM1) possesses few brown mosses and shows no successional trends, likely due to a flow through the marsh from an adjacent creek. I demonstrated that flood regimes are important determinants of vegetation community types, diversity, and ecosystem stability.

Aboveground herb peak standing crop was highest in the beaver impounded marshes. However, standing crop in this study was lower than in most wetland studies in North America. Only riverine sites in central Alberta (Thormann and Bayley 1997a, Mewhort 2000) and montane studies in the Canadian Rockies (Gorham and Somers 1973) had similarly low values. Herb standing crop was significantly lower in the wet year of 1999 in all sites. The railway-impounded sites were the only sites with moss productivity and it contributed 1/6 of the total site aboveground productivity. A fertilization experiment (N addition) showed increased standing crop in the railway-impounded and beaver-impounded marshes but not the riverine marshes. Lack of response to nutrient addition in the riverine marshes suggests that flood disturbance is limiting plant production more than nutrient limitation.

The gradient of river connectivity has a large effect on sediment, water chemistry, diversity, community structure and productivity. Even moderate amounts of flood disturbance resulted in a substantial decrease in sediment organic matter. Floodwaters scour litter, resulting in peaty, high nutrient sediments in disconnected, railway-impounded sites. The higher nutrient concentrations in the peat sediment did not increase productivity in railway-impounded marshes but created a community with fen characteristics (such as abundant brown mosses). Moderate degrees of natural flood disturbance led to the highest diversity in the beaver-impounded marshes and in wet years, the same is true for herb peak standing crop. However, dry years did not produce a strong relationship between peak standing crop and disturbance. In dry years, there is almost no flooding in the beaver-impounded wetlands, while there still is some flooding in riverine wetlands. Vegetation is adapted to high flood disturbance in fully river-connected, riverine marshes and productivity is controlled by disturbance more than nutrient limitation.

Even though the diversity in hydrologic regimes has created high landscape diversity between the three wetland areas, the railway-impounded sites are altered due to an anthropogenic barrier. Ecological integrity is defined as the state of an ecosystem when the compositions and abundance of native species and biological communities together with supporting processes are intact (Parks Canada Agency 2000). The National Parks Act (Government of Canada 1988) mandates Parks Canada to maintain natural ecological integrity and biodiversity. Therefore, altered processes not natural processes are leading to the high landscape scale diversity and influence the management of these wetlands by Parks Canada.

This study and others (Henry and Amoros 1995, Poff *et al.* 1997) have shown that ecological integrity is linked to hydrologic connectivity. Management of riverine ecosystems by managing the range of natural hydrologic variability is the most appropriate way to maintain diverse, resilient and productive systems (Richter *et al.* 1997, Poff *et al.* 1997, Bornette *et al.* 1998b). Since the railway-impounded wetlands are disconnected due to human construction, and that has altered the natural wetland and hence, reduced the ecological integrity, the railroad should install bridges and culverts to permit natural flow regimes.

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Appendix I

Full species list and mean cover values for community types

Species Name	**1 (n=3)**	**2 (n=21)**	**3 (n=20)**	**4 (n=17)**	**5 (n=9)**	**6 (n=10)**	**7 (n=7)**	**8 (n=3)**
Emergent plants								
Agrostis scabra Willd.	--	--	0.05	--	--	--	--	--
Agrostis stolonifera L.	--	--	--	--	--	0.10	--	--
Aster borealis (T. & G.) Prov.	2.33	--	0.05	0.88	0.11	0.10	--	0.67
Aster sp. 1 L.	--	0.05	--	--	--	--	--	--
Beckmannia syzigachne (Steud.) Fern.	--	--	0.15	--	--	--	--	--
Betula glandulosa Michx.	0.67	0.05	--	0.18	--	--	--	--
Calamagrostis canadensis (Michx.) Beauv.	1.00	0.86	0.05	0.47	0.11	0.60	0.43	0.33
Calamagrostis inexpansa A. Gray	--	1.14	--	--	--	--	--	--
Calamagrostis stricta (Timm) Koeler	--	--	--	0.12	--	--	--	--
Carex aquatilis Wahlenb.	4.67	4.43	2.70	3.41	0.89	0.20	1.86	0.33
Carex aurea Nutt.	--	--	--	0.06	--	--	--	--
Carex sp. 1 L.	--	0.05	--	--	--	--	--	--
Carex diandra Schrank	0.67	2.00	--	--	--	--	--	--
Carex interior Bailey	--	0.48	--	--	--	--	--	--
Carex keloggii Boott	--	--	--	--	0.22	--	--	--
Carex saxatilis L.	--	--	--	--	--	1.10	4.71	3.67
Carex sp. 2 L.	--	--	0.10	--	--	--	--	--
Carex utriculata Boott.	3.33	1.86	3.95	4.12	3.67	3.50	1.71	4.00
Carex viridula Michx.	--	0.05	--	0.06	--	--	--	--
Cornus stolonifera Michx.	2.33	--	--	0.12	--	--	--	--
Deschampsia cespitosa (L.) Beauv.	--	--	--	--	0.56	2.50	1.43	1.67
Elaeagnus commutata Bernh. ex. Rydb.	--	--	0.05	--	--	--	--	--
Eleocharis palustris (L.) R. & S.	1.00	1.81	0.65	0.35	4.00	3.90	3.00	3.00
Epilobium palustris L.	1.67	0.19	0.05	0.71	--	--	--	--
Equisetum fluviatile L.	3.00	3.29	4.20	4.24	0.11	4.80	2.86	4.00
Equisetum palustre L.	1.33	0.10	2.15	3.29	2.00	2.30	1.43	3.00
Eriophorum polystachion L.	0.67	0.05	0.10	--	--	--	--	--
Fragaria virginiana Duchesne	--	--	--	0.06	--	--	--	--

Species Name	**1 (n=3)**	**2 (n=21)**	**3 (n=20)**	**4 (n=17)**	**5 (n=9)**	**6 (n=10)**	**7 (n=7)**	**8 (n=3)**
Galium trifidum L.	--	0.05	--	--	--	--	--	--
Grass sp. 1	--	--	0.10	--	--	--	--	--
Grass sp. 2	--	--	0.05	--	--	--	--	--
Grass sp. 3	--	--	--	--	--	0.10	--	--
Habenaria hyperborea (L.) R.Br.	--	--	--	0.24	--	--	--	--
Herb sp. 1	--	--	--	0.12	--	--	--	--
Herb sp. 2	--	--	--	0.06	--	--	--	--
Herb sp. 3	--	0.10	--	--	--	--	--	--
Herb sp. 4	--	0.10	--	--	--	--	--	--
Herb sp. 5	--	0.10	--	--	--	--	--	--
Herb sp. 6	--	--	--	0.12	--	--	--	--
Herb sp. 7	0.33	--	--	--	--	--	--	--
Herb sp. 8	--	--	--	0.06	--	--	--	--
Herb sp. 9	--	--	--	0.06	--	--	--	--
Isoetes echinospora Dur.	--	0.95	--	--	--	--	--	--
Juncus alpinoarticulatus Chaix	--	0.05	--	--	1.22	0.40	1.57	0.67
Juncus balticus Willd.	--	--	--	0.12	--	--	--	--
Juncus nodosus L.	--	--	--	--	0.11	--	--	--
Melica subulata (Griseb.) Scribn.	--	--	0.10	--	--	--	--	--
Mentha arvenses L.	--	--	--	0.06	2.67	3.10	0.14	2.00
Menyanthes trifoliata L.	--	0.38	--	--	--	--	--	--
Parnassia palustris L.	--	--	--	0.06	--	--	--	--
Picea sp. A. Dietr.	1.00	--	--	0.18	--	--	--	--
Poa palustris L.	--	--	0.10	0.35	--	--	--	--
Polygonum amphibium L.	--	--	0.15	0.12	--	--	--	--
Potentilla fruticosa L.	1.33	0.10	--	0.24	--	--	--	--
Prunella vulgaris L.	--	--	--	--	0.11	--	--	--
Ranunculus macounii Britt.	--	--	0.05	0.06	--	--	--	--
Ranunculus sp. 2 L.	--	--	--	0.06	--	--	--	--
Rumex occidentalis S.Wats.	--	--	0.05	0.47	--	0.50	--	0.33
Salix spp. L.	2.33	0.86	0.15	1.00	0.44	0.10	0.14	0.67
Scirpus acutus Muhl. ex. Bigel.	--	0.33	1.50	0.59	2.33	1.70	1.14	0.67
Senecio sp. 1 L.	--	--	--	0.06	--	--	--	--
Shepherdia canadensis (L.) Nutt.	--	--	--	0.06	--	--	--	--

Species Name	1 (n=3)	2 (n=21)	3 (n=20)	4 (n=17)	5 (n=9)	6 (n=10)	7 (n=7)	8 (n=3)
Sium suave Walt.	0.33	0.10	0.85	0.06	1.00	2.50	--	--
Smilicina stellata (L.) Desf.	--	--	--	0.06	--	--	--	--
Solidago canadensis L.	--	--	--	0.06	--	--	--	--
Triglochin maritimus L.	--	--	--	--	0.11	1.70	0.71	0.67
Bryophytes								
*Amblystegium varium (*Hedw.) Lindb.	--	--	0.10	--	--	--	--	--
Aulocomnium palustre (Hedw.) Schwaegr.	1.00	--	0.05	0.12	--	--	--	--
Bryum pseudotriquetrum (Hedw.) Gaertn. et al	1.33	1.70	0.05	0.47	3.00	2.40	2.86	3.33
Campylium stellatum (Hedw.) C. Jens	1.67	1.14	0.05	0.59	3.67	1.70	0.29	3.00
Cinclidium stygium Sw. *in* Schrad.	0.33	--	--	--	--	--	--	--
Didymondon rigidulus Hedw.	--	--	--	0.06	--	--	--	--
Drepanocladus aduncus (Hedw.) Warnst.	3.33	4.62	0.20	0.53	0.78	1.40	0.43	2.00
Kindbergia praelonga (Hedw.) Ochyra	--	--	0.05	0.41	--	--	--	--
Meesia triquetra (Richt.) Ångstr.	0.33	--	--	--	--	--	--	--
Plagiomnium ellipticum (Brid.) T. Kop.	--	--	--	0.12	--	--	--	--
Preissia quadrata (Scop.) Nees.	0.67	--	--	--	--	--	--	--
Scorpidium scorpioides (Hedw.) Limpr.	--	--	0.90	0.24	--	--	--	--
Submersed plants								
Callitriche hermaphroditica L.	--	--	--	--	--	0.70	--	--
Ceratophyllum demersum L.	--	0.57	0.50	0.06	--	--	--	--
Chara sp.	--	1.67	1.00	0.24	0.56	0.40	2.57	0.67
Hippuris vulgaris L.	--	1.57	0.40	1.18	1.11	0.70	--	--
Myriophyllum exalbescens Fern.	--	0.86	0.15	--	--	--	--	--
Potamogeton filiformis Pers.	--	0.95	1.00	--	--	--	0.43	0.33
Potamogeton gramineus L.	--	1.24	0.70	--	--	0.10	--	--
Potamogeton pectinatus L.	--	1.81	2.30	0.24	0.22	0.30	--	--
Potamogeton richardsonii (Benn.) Rydb.	--	1.00	0.65	0.76	0.22	0.10	0.14	0.33
Potamogeton sp. 1 L.	--	0.05	--	--	--	--	--	--
Potamotgeton sp. 2 L.	--	--	--	0.65	--	--	--	--
Ranunculus circinatus Sibth.	--	--	0.95	0.18	--	--	--	--
Ranunculus reptans L.	--	--	--	--	1.67	2.90	2.86	0.67

Species Name	1 (n=3)	2 (n=21)	3 (n=20)	4 (n=17)	5 (n=9)	6 (n=10)	7 (n=7)	8 (n=3)
Ranunculus sp. 1 L.	--	--	--	--	0.11	0.80	--	--
Sparganium angustifolium Michx.	1.33	1.52	0.85	0.59	0.22	--	--	--
Utricularia intermedia Hayne	3.33	3.95	2.65	1.88	4.11	3.70	0.29	--
Utricularia minor L.	0.33	1.71	1.85	1.76	2.44	1.10	--	--
Utricularia vulgaris L.	2.33	1.86	2.40	1.59	1.22	1.10	1.43	--