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PATTERNS IN ENVIRONMENTAL DRIVERS OF WETLAND FUNCTIONING AND SPECIES COMPOSITION IN A COMPLEX PEATLAND

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by

Jeremy A Graham

B.S., Southern Illinois University Carbondale, 2010

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
Master of Science.

Department of Plant Biology
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THESIS APPROVAL

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for the Degree of

Master of Science

in the field of Plant Biology

Approved by:

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AN ABSTRACT OF THE THESIS OF

Jeremy Alan Graham, for the Master of Science degree in Plant Biology, presented on 30 October 2012, at Southern Illinois University Carbondale.

TITLE: PATTERNS IN ENVIRONMENTAL DRIVERS OF WETLAND FUNCTIONING AND SPECIES COMPOSITION IN A COMPLEX PEATLAND

MAJOR PROFESSOR: Dr. Dale H. Vitt

The boreal peatlands that cover much of western Canada are immense reservoirs of organic carbon and nitrogen, serving as long-term sinks for atmospheric carbon, while providing habitat for flora and fauna. These ecosystems are generally believed to be nitrogen limited. Due to regional increases in industrial activities in the Athabasca Oil Sands Region (AOSR), atmospheric deposition of nitrogen is projected to increase, with unknown effects on peatland functioning. The results of this study provide baseline data for a nitrogen fertilization experiment with an accurate site description of the entire peatland complex, providing a reference for the experimental plots. This study also examines patterns of production and nitrogen usage along a moisture gradient. To give an accurate characterization of the study site I asked if species assemblages within a constant sphagna cover could be sorted into communities and how these were related to environmental gradients. Additionally, using a common peatland moss, I asked how variable primary production is across a moisture gradient while exploring seasonal patterns in nitrogen utilization for the moss.

In chapter two, four statistically distinct communities were identified, each with clear indicator species. In addition to differing in floristic composition, these communities had differences in several abiotic factors. These abiotic factors had clear spatial patterning and formed gradients across the peatland, influencing the distribution of species arrangements in the peatland complex. *Sphagnum angustifolium* thrived in all four communities and across the entire range of gradients. This species is a foundation of species of bogs and poor fens and was studied in more detail in chapters 3 and 4.

In chapter three, I found that primary production of *S. angustifolium* varied along the moisture gradient, with the highest values in the wettest habitats. Cranked wires, used to measure linear growth, became less reliable in wetter habitats, missing over 50 % of growth measure by innate time markers. The usage of cranked wires may therefore underestimate NPP in boreal peatlands. Capitula increased in biomass throughout the course of the growing season, suggesting that after vertical elongation, *S. angustifolium* begins to accumulate branches and leaves in the capitula to close the growing season.

In chapter four I found that the nitrogen concentrations in annual growth decreased as production increased. Despite the lower tissue quality, wet habitats had higher nitrogen requirements to support growth due to higher NPP. Inputs of atmospheric deposition fulfilled <5% of annual N requirements and nitrogen saturated capitula in the beginning of the season was found to be an important source of nitrogen for growth, as capitula nitrogen storage declined over the season. Across the moisture gradient 62% of nitrogen assimilated into growth is retained in the subsequent growing season. The nitrogen not retained proves to be an important source to production of *S. angustifolium.* The results of this study suggest that in drier peatland habitats, there is an insufficient supply of water to deliver nitrogen and to support continuous growth during the growing season. Consequently, in wetter habitats, *S. angustifolium* production is limited by nitrogen while in drier habitats I propose that moisture is limiting.

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To my family and loved ones, even though I’m not sure if you ever fully realized what I have been doing, other than being a student for a long time, the support, love and joy that you have brought to me not just during my time at SIUC, but for my entire life must not go without thanks and love back. Without having your care I may have lacked the ambition or desire to go and achieve any task.

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There is simply not enough time or space to give thanks to all the people and events that I am truly thankful for, so a final message to anyone that I haven’t mentioned, or not realized your assistance, thank you so much for helping me finish this thesis!

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CHAPTER 1: PEATLANDS, COMMUNITY DESCRIPTIONS, *SPHAGNUM* ECOLOGY AND NITROGEN IN PEATLANDS

Introduction

Peatlands

Peatlands are differentiated from other wetland systems by their ability to sequester large masses of carbon in the form of peat, partly decomposed organic matter. The immense storage of carbon in peatlands is equal to 25–33% of the world's terrestrial carbon (Roulet et al. 2007) despite occurring on only 2-3% of the world's surface (Maltby and Proctor 1996). Two major criteria for peatlands are a high, stable water table and for primary production to be greater than decomposition (Vitt 2006; Wieder and Lang 1983). As a whole and in contrast to other northern ecosystems, peatlands have low productivity (Frolking et al. 1998; Moore et al 2002). The accumulation of carbon as peat is more attributed to extremely low decomposition rather than high production (Vitt 1990; Moore and Basiliko 2006). These slow decomposition rates can be attributed to a number of factors, including low temperatures; anoxic, water-logged conditions; acidity; few decomposers; and/or recalcitrant plant litter (Johnson and Damman 1993; Braggaza et al. 2006; Moore and Basiliko 2006).

As a result of the imbalance between primary production and decomposition, peatlands now store between 270 – 450 Gt C (Gorham 1991; Turunen et al. 2002) and recent models estimate up to 547 Gt C stored since the beginning of the Holocene (Yu et al. 2010). The approximate long term rates of carbon accumulation are near 20 g m^{-2} yr^{-1} (Vitt et al. 2001; Gorham 1991; Turunen et al. 2002); however, the balance has been shown to vary substantially from acting as a carbon sink 89 g m^{-2} yr^{-1} to a source -14 g m^{-2} yr^{-1} over a six year period (Roulet et al. 2007). The boreal peatlands, 87% of all peatlands (Vitt 2006), occupy 3.46×10^6 –

4.00×10^6 km^2 throughout the northern hemisphere (Gorham 1991; Yu et al. 2010). In Canada, which is second only to Russia in extent of peatlands, peatlands occur on 14% of the landscape and 21% of the province of Alberta (Natural Wetlands Working Group 1988). The abundance of peatlands in Canada, along with their considerable carbon stock, demonstrates the importance of their management and intimate understanding of the functioning of these precious ecosystems.

Divisions of Peatlands

Just as peatlands are a division of wetlands, there exist divisions among peatlands. The general classes of peatlands are bog, poor fen, moderate rich fen, and extreme rich fen. The division of these peatland types occur along three main gradients: hydrologic, chemical (nutrient content of N and P, alkalinity and base cations) and biotic (differentiating types by species composition) (Zoltai and Vitt 1995). The hydrologic gradient is determined by source of incoming water. Bogs and fens differ in this aspect as bogs are ombrogenous, in that water enters only from the atmosphere, whereas fens are geogenous, having water from both the atmosphere and ground or surface water. As a result of their hydrological differences, fens have more nutrient and mineral inputs in the water making them minerotrophic, while bogs have much lower inputs, thereby termed ombrotrophic (Vitt 2006). The term nutrient usually refers to nitrogen and phosphorus and determines trophic status, whereas mineral refers to pH and dissolved ions and determines base richness (Wheeler and Proctor 2000). Vitt et al. (1995) determined that nutrient content of pore water did not vary significantly between peatland types, though flowing water has the ability to bring in additional nutrients that may be sequestered in plant material (Vitt 2006).

Chemically, bogs are on the lower end of the gradient of pH, base cations, and anions increasing to extreme rich fens (Sjörs 1950; Vitt and Chee 1990). Floristically the different types of peatlands have differing species composition as well as indicator species that can be used for classification, such as species of *Sphagnum* and *Drepanocladus sensu lato*. Moderate rich fens have the highest species diversity as they include some members of both poor fens and extreme rich fens (Vitt and Chee 1990). Another important distinction is between that of *Sphagnum*-dominated peatlands and brown moss-dominated peatlands. The switch from *Sphagnum* to brown moss typically occurs around a pH of 5.5 with bogs and poor fens being *Sphagnum* dominated and rich fens having more brown mosses (Vitt 2006). The different types of peatlands can exist adjacent to each other in peatland complexes (Vitt et al. 2003a; Vitt 2006), with the complexity of internal (autogenic) and external (allogenic) factors interacting over time (Charman 2002). These peatland types change position in the peatland complex as well as change in time owing to successional processes (Glaser 1981).

Historical approaches to community analysis

Rarely in natural ecosystems does one species grow alone, separate from all other species. Instead species are generally found growing in the presence of other species. The existence of one species in one particular location at a specific time is the consequence of dynamic processes including diaspore availability and timing, existing resources, and a species' ability to compete with other species for space and resources while tolerating the prevailing environmental conditions (Connell and Slatyer 1977). A species can only occur in a location if its dispersal mechanisms allow it to move into that position and that there are no geographic barriers to its arrival. The ability of a species to spread rapidly may allow it to initially thrive, only to be out competed later by another species that is better suited to the conditions. Conversely, a species that is first able to populate an area may exclude all other arriving species by filling all available niche space (Connell and Slatyer 1977). The existence of a plant community is by no means static and is the result of multiple complexities over time. The occurrence of two or more species living concomitantly is a phenomenon that has been well observed, studied and critiqued.

Around the turn of the 20th century, the work of earlier plant geographers gave way to new ideas surrounding the local associations of plant species rather than their broad geographic distribution, leading to a new field, phytosociology or later, community ecology. In European phytosociology, Becking (1957) presented two principles upon which the study is based: a) plants are not randomly distributed, and b) there are complex interactions between both plants and habitat as well as among individual plants. As time progressed many different ideas about the organization of plant associations emerged, leading to different central concepts, often originating by individuals or in local geographic areas.

One of the greatest debates among community ecologists is what the definition of a community is and whether or not communities actually exist. The problem that leads to much of the discrepancies between community ecologists is well described by Oosting (1948) in that recognizing or separating out communities is easier than expressing what factors distinguish the community itself. Early contributions to this debate stems from the work of Frederic Clements and Henry Gleason. Clements (1936) viewed communities as a kind of “superorganisms” in which groups of species grow with each other and over time give way to other groups of species in a predictable successional trajectory, ultimately culminating in a static climax community. The foremost opposition to this climax community concept was that posed by Gleason (1926), where species independently respond to the environmental conditions and exist according to their own physiological tolerances to their surroundings. Initially many North American ecologists were more in support of the superorganismal view of communities, but as the century progressed work by Curtis (1957) and Whittaker (1967) tended to have more support for Gleasonian concepts.

While debates in opinions over the fundamentals of community concepts continued in North America, the Europeans also had a related and long history of clashes over proper vegetation classification schemes and terminology. The divergence of concepts placed Europe with three geographically separated schools of thought: the Uppsala school in Scandanavia, the Zurich-Montpellier (Z-M or Braun-Blanquet) school popular in much of continental Europe, and the British school. Both the Zurich-Montpellier and Uppsala schools sought to base communities on floristic composition and arrange them into a hierarchical structure, yet they differed on their basic unit, definitions, and indicators of community delimitations. The methods and principles of the British school shifted from descriptive surveys to autoecological approaches focusing on physiological relationships between plant species and the environment (Poore 1955).

The term association is often used in phytosociology. Its original appearance in literature seems to be its usage by Alexander von Humboldt for categorizing vegetation (Daubenmire 1968). In 1910 during The Third International Botanical Congress, an association was defined as "the fundamental unit of phytosociology being a plant community of definite composition, of uniform habitat conditions and of uniform physiognomy," yet it was soon to be construed by different schools to fit desired standards (Becking 1957). Daubenmire (1968) pointed out that usage of words such as "definite" and "uniform" are relative terms and can be interpreted in a variety of ways by different people. Throughout the historical literature one must be careful in interpreting an author's usage of the term association. Complications involving semantic differences in definitions of terminology are one of the reasons for the division of theories of the various schools of phytosociology, including the Z-M and Uppsala schools. The complex details of the Braun-Blanquet and Uppsala schools require a further discussion.

Shortly after the turn of the 20th century, the Z-M school, in the rich floristic setting of central and southern Europe, created a system based on naming communities by the dominant species and separated themselves from British and American "ecologists" and referred to themselves as "phytosociologists." Soon afterwards though, the school evolved into three different views of communities: physiognomic, floristic, and ecological. Of these schools the floristically based Braun-Blanquet system (also referred to as the Zurich-Montpellier, or Z-M school) garnered the largest following (Whittaker 1962). The Braun-Blanquet approach is not just a theory of community assembly, but a complete set of methodological instructions to measure, classify, and organize plant communities into a tabular format. It is important to note that the Braun-Blanquet approach is not a pure construct of Braun-Blanquet, but rather an amalgamation of ideas and methods of those before him, ranging from von Humboldt to many of his existing peers in the early 20th century (van der Maarel 1975). The plant community theory of Braun-Blanquet takes an intermediate approach that accepts the heterogeneous assortment of plant species, but stresses the importance of species interactions in a community, which is to a degree unique because of the discontinuity of communities in the field (Westhoff and van der Mareel 1978). In Braun-Blanquet phytosociology there is an acceptance that not all collections of plants can form a definite community and that there are mixtures and accidental arrangements as well (Poore 1955). The three fundamental ideas are concisely summarized by Westoff and van der Mareel (1973) as follows: "1. Plant communities are conceived as types of vegetation, recognized by their floristic composition. 2. Amongst the species that make up the floristic composition of a community, some are more sensitive expressions of a given relationship than others. The approach seeks to use those species whose ecological relationships make them most effective indicators; these are diagnostic species. 3. Diagnostic species are used to organize communities into a hierarchical classification, of which the association is the basic unit." The usage of association from the Braun-Blanquet view is an abstraction based on characteristic species compositions and can be likened to that of the concept of species in taxonomy and is only described after numerous samplings have been analyzed (Becking 1957). Braun-Blanquet modified the previously defined association to meet his specific ideals, "The association is a plant community characterized by definite floristic and sociological features which shows, by the presence of character-species a certain independence" (Braun-Blanquet 1921).

Braun-Blanquet also developed a clear concise replicable outline for his methods of community surveys. As a result of the attention following the Braun-Blanquet school and the detailed methodology, numerous areas of vegetation throughout Europe were classified in a manner that allowed them to be compared and discussed (Poore 1955). A complete account of Braun-Blanquet's methods would require far too much space and will only be summarized briefly. Becking (1957) provided, in detail, a complete account of the method, including the field analytic phase and the synthetic phase, which deals with the preparation of synthesis tables. In his review of the Braun-Blanquet system, Poore (1955) put forth three main elements of the methods required to delineate associations: choice of site, description of the stand, and tabular comparisons of the species lists. The choice of site for the area requires that several plots (or relevés) be placed throughout uniform stands. There has been some critique of the subjectivity of these methods and a lack of testing for homogeneity. Moore (1962) defended these critiques suggesting that a “quasi-objective” test is performed while compiling the association tables and that had any non-homogeneous stands been selected, there would be a long list of species with isolated events and that is a signal of a poorly chosen stand for the description. The methodology of the stand description begins with measuring environmental factors that may have any ecological relevance, ie. coordinates, altitude, slope, aspect, substrate, etc. In short the next step involves listing all the species within the pre-defined homogenous area and assigning ranks of cover-abundance and sociability to all species. A more comprehensive review of this step can be found in Poore (1955). The final step involves creating association tables. The creation of these tables, as Moore (1962) pointed out, is perhaps the highlight of the method, comparable to a fine art, and requires a very skilled phytosociologist. During the preparation and organization of the tables new synthetic variables, such presence, constancy, and fidelity are assigned to each species. Species demonstrating a high degree of fidelity are used as characteristic species in delimiting the association. According to Moore (1962), a properly constructed table should allow a reader to quickly grasp the structure of an association, its diagnostic species and sub-units as well as a grasp of the habitat features of the stand. Braun-Blanquet also created a nomenclature to be used in naming vegetation hierarchical vegetation units, based on adding suffixes to Latin names of the diagnostic species (Becking 1957). The basis of the hierarchy begins with the most basic rank, the association, and increases as alliance, order, and finally class (Braun-Blanquet 1921),

Literature referring to the Uppsala school of phytosociology is sparser than that of Braun-Blanquet. Malmer (1974) admitted that for non-Scandinavians it may be difficult to understand the evolution of their phytosociology as a number of significant relevant papers have never been published in a language other than a Scandinavian one, if at all. Like the Z-M school, the Uppsala approach has been refined from historical methods beginning in the mid 19th century. To comprehend the ideas behind the Uppsala school it is helpful to conceive the regularity of limited species in the plant communities that exist in the relatively harsh conditions of Scandinavia. The differences between the two prevailing schools may be more due to floristic diversity rather than geographic distance. In the species rich regions of central and Mediterranean Europe, where fidelity was of importance and dominance had a small role, the less diverse Scandinavian flora eventually led phytosociologists to place a greater emphasis on dominant species (Moravec 1993).

Originally Du Rietz et al. (1920) of the Uppsala school proposed the association be defined as follows, "An association is a plant community with certain constants and a certain physiognomy" (Whittaker 1962; Moravec 1993). At that time the basic unit of the Uppsala school was the association (Du Rietz et. al 1920), but the term was later amended to "sociation" in order to distinguish it from the "association" as defined by the Z-M school. Realizing the shortfalls of an emphasis on constancy, Du Rietz later used sociations as the basic units of the Uppsala school, which stressed a plant community with constant dominants in each layer (Becking 1957; Moravec 1993). A sociation is analogous to Braun-Blanquet's hierarchical unit of the alliance (Moravec 1993). To summarize the concepts of the Uppsala school, Du Rietz had four laws of vegetation; abridged from Becking (1957). 1. Each sociation, or socion, requires a minimal specific area for its existence and is dependent on size of plants, degree of taxa mixtures, and variability in species composition. 2. Every sociation has a number of dominant species and will have at least one constant species that is present in every sample plot of the sociation. 3. In sample plots of the same sociation there will be certain phytosociological affinities amongst the constant species. 4. Socions and sociations border on each other with distinct boundaries. Reviewing the methods can further illustrate the idiosyncrasies of the Uppsala school.

Like the Z-M school, the goal of the Uppsala school was to delimit plant communities and organize them into hierarchical units, and this was also achieved by compiling tables (Malmer 1974). One of the departures from the Z-M school was that Scandinavian phytosociologists treated each stratum of vegetation independently (Becking 1957). Each layer defined by a dominant species was referred to as a socion, and the vertical collection of the stratified individual socions was considered the sociation. Further hierarchical terms exist for combinations different socions.

The field methods of the Uppsala school were centered on the use of small sampling areas of defined size while stressing the importance of homogeneity and capturing a complete species list (Malmer 1974). Sample plots used by the Uppsala school were comparatively smaller than those following Braun-Blaunquet methodology (Moravec 1993). The placement of the quadrat could be considered rather subjective as their sampling quadrats were only placed after a scrupulous search for ideal homogenous plots. As tables were organized, the Scandinavians sought after the dominant species of each layer to name their sociations (Malmer 1974).

It cannot be said that any school is perfect in its methodology and each school had critiques from their counterparts. For example, Z-M phytosociologists point out constant dominants as having ecological value is at times misleading due to the occurrence of some plants such as *Vaccinium myrtillus* which can be found in almost every Scandanavian ecosystem (Becking 1957). The use of character species outlined by the Z-M school was attempted to be found by Scandinavian phytosociologists, but very few species were discovered to have sufficient fidelity to form associations (Whittaker 1962). Phytosociologists of the Z-M school also criticize the layered approach because all plants start out at the same ground layer although some plants outgrow the ground layer they are still part of the same community (Becking 1957).

When dealing with peatland vegetation, common to Scandinavia, the Braun-Blanquet system treats microtopographic variation as two distinct classes: the hummocks as Oxycocco-Sphagnetea and the hollows as Scheuchzerio – Caricetea nigrae (Pakarinen 1995), whereas the Uppsala school would consider them consociations. The two schools' main difference is the usage of their respective basic units as Braun-Blanquet uses associations defined by qualitative measures and Uppsala uses sociations based of species of constant dominance. Regardless of their differences the schools have the similarity that they are both based on the usage of floristic composition to delineate vegetation units. Dahl and Hadac (1941) pointed out that the theoretical differences between the two schools may be harder to see in practice, citing two studies of the two schools that treated the same community with their respective basic unit. Malmer (1974) noted that many of the Uppsala phytosociologists were influenced by the Braun-Blaunquet system and Moore (1962) points out that even the Uppsala school was evolving towards the widely regarded views of the Zurich-Montpellier school.

The arrangement of species in peatlands is as subject to modern competition theories as other species in any other ecosystem. Two of the dominant theories in community ecology applicable to plants are Grime's CSR (Grime 1977) and Tilman's resource ratio hypothesis (1985). Grime's theory suggests tradeoffs in a species' physiological ability to compete against other species for space and resources, tolerate environmental stressors, and colonize after a disturbance. Tilman’s theory, which is based more on models of resource requirements, predicts the points at which species will outcompete each other, or coexist.

When addressing peatland vegetation, one notices a few striking characteristics, most notably a mélange of bryophyte species, and what some may call a balance and others an eternal battle between bryophytes and vascular plants. These coexisting species and guilds are the result of different resource utilization tactics and physiological traits and abilities of the present species. Vitt and Slack (1984) present seminal findings, quantifying the actual and possible arrangement of *Sphagnum* species based on resources requirements and physiological abilities. Many other papers have reported the intricacies of small scale species distributions along the hummock-hollow gradient (Clymo and Hayward 1982; Luken 1985; Rydin 1993 and more). The arrangement of true mosses among peatlands follows similar patterns to the sphagna for resource partitioning, utilization, and physiological abilities.

Whether mutualistic or competitive, the interactions between *Sphagnum* and vascular plants are critical for peatland community patterns. The presence of shrubs in hummocks provides a framework for hummock occupying *Sphagnum* species to grow while vascular plants in the hollows, namely sedges, do not provide this structural assistance, therefore preventing hummock formation (Malmer et al. 1994). The differences in vascular plant coverage along the hummock-hollow gradient with aerenchymous species occupying the hollows and dwarf shrubs restricted to hummocks creates an autonomous balance between species of both habitats (Rydin, Gunnarsson and Sundberg 2006). While it appears that there is a balance between the vascular plants and sphagna, this relationship is fragile. Vascular plants have a clear advantage for light, however due to the absorption capacity of *Sphagnum*, under normal conditions, they only get mineralized nutrients from below the moss layer. Juvenile plants or emergent shoots must grow faster than the rising moss layer. If prevailing conditions change in such a manner that *Sphagnum* is at a disadvantage or vascular plants have improved conditions then the delicate balance may be at risk, resulting in a community change and a cascading alteration to the functioning of peatland ecosystems.

Sphagnum

Sphagnum mosses cover a great extent of boreal peatlands (Rydin et al. 2006) and as a result much of the research on peatland production has focused on this particular genus (Wieder 2006). *Sphagnum* mosses are considered by some to be more ecologically important than any other group of mosses in the world because they store more carbon than any other plant genus, garnering much attention (Clymo and Hayward 1982; Andrus 1986). *Sphagnum* mosses possess several key features contributing to their importance. They create and tolerate an acidic, nutrient poor environment; resist decay; hold large quantities of water; and have different species specializing across environmental gradients (Vitt and Andrus 1977; Rydin et al. 2006). The diverse sphagna include 250 – 450 species, yet fewer than 50 are thought to contribute to peat formation and accumulation (Shaw 2000). This genus is unique in that it does not just take over available niches, it is thought to be an ecosystem engineer (van Breeman 1995) and to create conditions suitable to its persistence (Andrus 1986; Rydin et al 2006). *Sphagnum* mosses are able to achieve various ecological niches and functions in part to their interesting morphology and ecology.

Sphagnum Reproduction, Morphology and Strategies

As with all plants, sphagna consist of two generations; the conspicuous haploid gametophyte and the diploid sporophyte, which occurs as a dark capsule and a very short seta, both raised, on a haploid pseudopodium. Spores are released from the capsule via an explosive mechanism that projects the operculum into the air (Vitt and Andrus 1977). Spore dispersal is aided by wind. Plants can either be monoicous or diocious. Sphagna also have the ability to reproduce asexually by fragmentation of branches and stem or by the dichotomous splitting of the main stem (Rydin et al 2006).

Possibly the most notable feature of sphagna to the naked eye is the presence of the capitulum, a cluster of branches at the uppermost portion of the stem, containing the meristemic bud. Two types of leaves are present in sphagna; stem leaves and branch leaves. The leaf cells contain small chlorophyllose cells intermixed with the large non-chlorophyllose dead hyaline cells. Stem leaves are usually less crowded and differ from branch leaves in shape, size, porosity and fibrils (Vitt and Andrus 1977). *Sphagnum* mosses are able to hold water 10 – 25 times their dry weight because of the hyaline cells (Andrus 1986). Branches occur in clusters, or fascicles, on the stem becoming less clustered as the stem lengthens (Vitt and Andrus 1977). Branches are of two kind: spreading and hanging, or pendant.

As with most bryophytes, sphagna have been reported to have limited ability to actively transport water upwards; however *Sphagnum* may be an exception with a particular arrangement of the leaves and branches that forms a capillary network in the spaces between these features (Clymo and Hayward 1982; Rydin et al. 2006). The two kinds of branches, (spreading and hanging), facilitate the direction of water movement both horizontally and laterally (Clymo and Hayward 1982). In sphagna, photosynthesis and mineral nutrient accumulation can take place on the entire plant surface (Malmer et al. 2003). These plants are able to operate efficiently by translocation of nutrients both symplastically and through their capillary network (Rydin and Clymo 1989, Aldous 2002b).

Sphagnum Ecology

Degree of minerotrophy and nutrient availability, water chemistry, moisture, and distance to water are the gradients with the most influence on *Sphagnum* distribution (Clymo and Hayward 1982; Vitt and Slack 1984; Andrus 1986; Damman 1986; Malmer 1986; Gignac and Vitt 1990; Gignac 1993). The combination of these factors plays a role in the type of peatland in which a species is found, its position within that peatland, and its ability to reproduce. Sphagna are generally limited to pH levels less than 5.5, in bogs, poor fens and to a lesser degree in moderate rich fens (Vitt 2006). However, the presence of moving water allows species to exist in pH levels above of their normal range (Andrus 1986). Additionally, Malmer et al. (1992) noted that within rich fens, ombrotrophic hummocks are able to exist (termed 'mixed mires'). Due to the close range of individual plants, light penetration and photosynthesis are limited to areas near the top of *Sphagnum* plants (the capitula) creating a two dimensional competition between plants (Clymo and Hayward 1982; Rydin et al. 2006). The closeness of the plants also gives the *Sphagnum* priority to atmospherically deposited nutrients over the rooted vascular plants (Malmer et al. 1994; 2003; Rydin et al. 2006). This may also make sphagna more vulnerable to changes in precipitation chemistry.

The ability of *Sphagnum* to manipulate its environment is closely tied with its morphological and chemical characteristics. *Sphagnum* is able to create acidic environments by releasing H^+ ions from its numerous cation exchange sites and from the release of organic acids (Hemond 1980; Clymo and Hayward 1982; Andrus 1986). It is estimated that between 10 – 30%

of the dry mass of *Sphagnum* is uronic acids (Clymo 1963; Rydin et al. 2006). Recent evidence suggests that *Sphagnum* mosses have similar cation exchange capacities as other bryophytes and drops in pH can be attributed to their high acidification capacity, a function of both ability to bind cations and the quantity of available cations (Soudzilovskaia et al. 2010). The ability of *Sphagnum* to hold large quantities of water restricts water flow in fens, inducing waterlogging and reducing nutrient supply (Zoltai and Vitt 1995). These processes are also key in the expansion of peatlands through paludification (Charman 2002). *Sphagnum* remains are highly resistant to decay, in part due to their production of phenolic compounds, referred to as "sphagnols" (Verhoven and Liefveld 1997; Moore and Basiliko 2006). Decomposition between species based on microhabitats differs due to differences in carbon allocation, as hummock species grow slower, building more structural carbohydrates, whereas hollow species create simpler carbohydrates to support the metabolism required for their faster linear growth (Turestky et al. 2008). Thus, hollow species decompose faster due to higher litter quality. *Sphagnum* species have adapted to create and survive in true nutrient poor conditions, yet these adaptations give *Sphagnum* little tolerance to changes in nutrient status (Gunnarsson and Rydin 2000).

Sphagnum angustifolium

Abundance of a species in a given area is a function of that species' ability to persist along a wide range of environmental gradients. Throughout Alberta, *S. angustifolium* is among the most commonly found species (Vitt and Andrus 1977). *Sphagnum angustifolium* is a member of the section Cuspidata, and commonly forms lawns and occurs in hollows below *S. magellanicum* and *S. fuscum*. It can also be found growing as individuals within *S. fuscum* on hummocks. *Sphagnum angustifolium* is a highly variable species with a broad ecological niche within peatlands (Vitt and Andrus 1977; Andrus 1986; Gignac 1993). Depth to water table is possibly the largest constraint on *S. angustifolium* distributions (Vitt and Slack 1984), due to its limited ability to control water loss (Mulligan and Gignac 2001). One strategy to avoid water loss is shoot density in which *S. angustifolium* grows more densely as habitats are raised above the water table (Luken 1985). Water availability not only limits *S. angustifolium* distribution but may also limit growth. Under different moisture regimes *S. angustifolium* outgrew both *S. fuscum* and *S. magellanicum* under moist conditions whereas *S. angustifolium* grew less than the hummock species under dry conditions (Luken 1985). Short term studies have shown *S. angustifolium* to be fairly resilient to both increased nitrogen and carbon dioxide, exhibiting no negative effects even at extremely high treatments over 71 days (Jauhiainen et al. 1998). In response to different environmental gradients *S. angustifolium* was shown to have genetic variation, possibly indicating that genotypic adaptation to differing conditions exists (Såstad et al. 1999).

Primary Production

The fixing of atmospheric carbon is responsible for perpetuation of life in all terrestrial ecosystems. In peatlands, the accumulation of stored organic matter ultimately depends on inputs to the system via primary production, potentially the single most important function of these ecosystems (Wieder 2006). Primary production of boreal peatlands is low in comparison to other ecosystems (Frolking et al. 1998). Rates of production in peatlands can vary substantially spatially (Ohson and Økland 1998), and temporally (Wallen et al.1988). Spatial variation can be partially explained by peatland surface depth to water table (Belyea and Clymo 2001) as well as other variables such as shrub and lichen abundance (Pakarinen 1978) and mineral (ie. Ca^{2+} and Mg^{2+}) and nutrient (N, P and K) availability (Gunnarson 2005). Much of the temporal vegetation can be explained by climatic variables, temperature and precipitation (Gunnarson 2005). The considerable year to year variation can create problems for extrapolating production data gathered over just one year (Wallén et al. 1988). Due to difficulty in collection, belowground primary production data has been deficient, making accurate results of total productivity difficult (Wallén 1992). In some cases aboveground net primary productivity can vary as much within a site as between sites (Campbell et al. 2000; Vitt et al. 2001). In a study of total aboveground production along a bog – fen gradient Thormann and Bayley (1997a) found that total production was similar among different peatland types but that different production classes were related to different variables, namely shrub and herb production with surface water and mosses with climate (Thormann and Bayley 1997b). Vitt (1990b) found that moss production of bogs and poor fens is similar if not greater than that of extreme-rich fens. Peat accumulation will remain higher in the bogs and poor fens as decomposition increases along the bog – rich fen gradient (Bayley et al. 2005). A general trend of increasing peat production with decreasing latitude is reviewed in Thorman and Bayley (1997a), yet Damman (1979) pointed out that the largest peat stores are at high latitudes, suggesting that the decomposition gradient may be more important than production for overall peat accumulation. *Sphagnum* production rates are at least equal to or higher than those of brown mosses (Vitt 1990). As species diversity increases moving toward more true mosses, the productivity of *Sphagnum* appears to decrease (Thormann and Bayley 1997b; Gunnarsson 2005).

The microtopography of peatlands varies as well in terms of productivity and has been well researched (Moore 1989; Rochefort et al. 1990; Vitt 1990; Hajek and Adamec 2009). The effects of microtopography are important when attempting to extrapolate production values across a larger scale, as the undulations formed by hummocks and hollows increase actual surface area (Vitt 2007). On a global scale, Gunnarsson (2005) combined all research on *Sphagnum* production and sorted productivity by microhabitat finding that productivity increased from hummocks to lawns to carpets, nearly doubling. Findings from Vitt (1990) partially agree with this conclusion, as much as in bogs, where production in hollows was double hummocks, but in both poor and rich fens hummock production was equal or greater than in the hollows. Deviations from the global pattern also differed with nutrient status where over a four year period hummocks in oligotrophic zones had less production and in minerotrophic zones hummocks had higher productivity (Rochefort et al. 1990). Hajek (2009) concluded that while linear growth is higher in pools and hollows compared to hummocks, primary production is similar due to higher bulk density in hummocks. However, over long periods of time hummocks can exhibit higher peat production and accumulation than hollows (Ohlson and Økland 1998). There are species-specific strategies as hollow species need to have greater linear growth to maintain its position at the water table, whereas hummock species form denser shorter growth to prevent desiccation (Jauhiainen et al. 1998). Differences in capillary water transport capability between species can explain some of the patterns of productivity and distribution (Wallén et al. 1988). Summaries of peatlands reveal that on average aboveground primary production is bogs are somewhat higher than for fens (Thormann and Bayley 1997a; Bedford et al. 1999), however a review by Campbell et al. (2000), suggested that Canadian bogs and fens have similar productivity. The controls on net primary production in peatlands are highly variable on a range of scales influencing differences both between and within sites. In addition to the aforementioned factors, the role of nitrogen to peatland production is of keen interest as it may have a strong influence on productivity (Aerts et al. 1992; Gunnarsson & Rydin, 2000; Vitt et al. 2003b; Bragazza et al. 2006).

Nitrogen

Nitrogen is an important and limiting nutrient to the functioning of many peatlands (Rochefort et al. 1990; Aerts et al 1992; Bedford et al. 1999; Gunnarsson and Rydin 2000). Phosphorus also has been known to be a limiting factor in areas that receive high inputs of nitrogen (Aerts et al. 1992); however, based on nutrient ratios provided by Koerselman and Meuleman (1996) and data compilation (Walbridge and Navaratnam 2006), peatlands in the continental province of Alberta seem to be limited by nitrogen alone. As a result of nitrogen scarcity in peatlands there is a highly competitive environment for the nutrient between plants and microbes. The deficient supply of nitrogen into peatlands is too small to account for necessary primary production of peatmosses (Damman 1988; Aldous 2002a). Due to some of the special characteristics of peatlands (acidic, anoxic, slow decomposition) the patterns of nitrogen movement can be complex.

Inputs

Primary inputs of nitrogen to peatlands are atmospheric deposition, nitrogen fixation (Hemond 1983; Limpens et al. 2006), and inflow of dissolved forms of nitrogen. Due to their hydrology, the inflow of dissolved nitrogen, mainly organic, is restricted to fens only, however studies on these inputs are limited (Limpens et al. 2006). Inputs from all three sources have substantial variation from site to site (Waughman and Bellamy 1980; Hemond 1983; Urban and Eisenreich 1988). Atmospheric deposition of nitrogen (NO_x and NH_x) can be divided into wet and dry categories, while wet deposition is readily measured, while dry deposition can be difficult to quantify (Limpens 2006). In boreal peatlands with long winters, nitrogen from atmospheric deposition accumulates in snow resulting in a potentially large nitrogen spike in spring during snowmelt. Nitrogen fixation by microorganisms has an important role in the nutrient balance in most peatland ecosystems and may be limited by temperature, pH, trace micronutrients and/or moisture (Waughman and Bellamy 1980; Urban and Eisenreich 1988; Limpens et al. 2006). Fixation is highest in rich fens declining towards bogs with extreme rich fens being similar to moderate rich fens (Waughman and Bellamy 1980). Nitrogen fixing cyanobacteria have been found living symbiotically with *Sphagnum* and *Drepanocladus* species (Basilier et al. 1978). Recent studies reveal high diversity of nitrogen-fixing bacteria in *Sphagnum* (Opelt et al. 2007), and a recent study suggested that *Sphagnum* appears to fix nitrogen at higher rates than the common feather moss *Pleurozium schreberi* (Prša 2012) and possibly other true mosses. Increased rates of inorganic nitrogen deposition was found to reduce nitrogen fixation occurring in symbiosis with mosses (Zackrisson et al. 2009).

Internal processes and storage

Nitrogen movement in peatlands has numerous possibilities including plant uptake, immobilization, mineralization, leaching, and storage. An asymmetrical competition for inorganic nitrogen between the bryophytes and vascular plants exists due to the vertical differences between their uptake mechanisms (Malmer 1994; 2003). Upon deposition of atmospheric nitrogen, the moss cover is able to retain much of the nitrogen before it moves down to deeper zones for uptake by vascular plants (Aldous 2002a). *Sphagnum* mosses are able to assimilate NO_3^- almost immediately due to the ability to quickly activate nitrate reductase, in contrast to most vascular plants (Woodin et al. 1985.)

In areas where annual nitrogen inputs are not sufficient to account for primary production of the moss cover, namely *Sphagnum*, the nitrogen needs can partly be met by translocation (Aldous 2002a). Potential sources for nitrogen translocation are; metabolically inactive *Sphagnum* tissue, microbial turnover, mineralized nitrogen from fine roots, and NH_4^+ released from cation exchange cites (Aldous 2002b). Translocation of nitrogen in *Sphagnum* is not related to the amount of labile N (Aldous 2002b).

As *Sphagnum* lacks the ability to retain 100% of aerially deposited nitrogen, some is passed below the moss layer (Aldous 2002a). Vascular plants and microbes rely on the mineralization of peat in addition to nitrogen that passed through from above (Malmer 1994; Damman 1988). Immobilization of NH_4^+ released by mineralization will occur until the microbial community demand for N is satisfied, which is dependent upon environmental factors such as temperatures, oxygen, and acidity (Damman 1988). After the microbial requirements are met nitrogen mineralized from peat becomes available for plant uptake; however, new studies have suggested that plant uptake is able to compete directly with immobilization (Schimel and Bennet 2004). If this is the case then competition for nitrogen produced via mineralization occurs simultaneously between microbes, vascular plants, and *Sphagnum* translocation. Mineralization and decomposition are closely related processes, related to the amount of initial nitrogen available in peat and size of the microbial pool, and occur at highest rates in the uppermost areas of peat (Damman 1988; Bayley et al. 2005). Differences in these processes may be attributed to the peat forming plant communities explaining variations across peatland types (Aerts et al. 1999; Bayley et al. 2005). The presence of nitrate in peatlands is usually very small due to the uptake efficiency of *Sphagnum* upon deposition, scarce free ammonium, and adverse environmental conditions for nitrifying bacteria (Urban et al. 1988; Bridgham et al 1998; Bayley et al 2005; Limpens et al. 2006)

Over long periods of time, peatlands have served as large nitrogen sinks with estimates of 8-15 Pg stored in peat (Moore et al. 2004; Limpens et al. 2006). Within peatlands there are considerable spatial variations of nitrogen accumulation, particularly between hummocks and hollows (Ohlson and Økland 1998; Moore et al. 2004). These variations are explained by differences in productivity and nitrogen fixation (Moore et al. 2004) as well as the ability for hummocks to uptake more NH_4^+ due to increased number of cation exchange sites (Juahiainen et al. 1998).

Outputs

Pathways for nitrogen to leave a peatland ecosystem are denitrification, runoff of dissolved nitrogen, and NH_3 volatilization (Hemond 1983). As peatlands are nitrogen sinks, a majority of nitrogen that enters the system remains (65 – 80%) (Hemond 1983; Urban and Eisenreich 1988). Fens are more susceptible to losing nitrogen through outflow due to their hydrological characteristics, compared to bogs that have little drainage and outflow (Waughman and Bellamy 1980). Dissolved nitrogen leaving systems is usually in the organic form due to the high efficiency peatland vegetation of the mineral forms of nitrogen (Urban et al. 1988; Limpens 2006). Denitrification is considered small to insignificant due to the aforementioned lack of nitrate (Hemond 1983; Urban et al. 1988; Verry and Urban 1992; Bayley and Thorman 2005). Hemond (1983) concluded that only a trace amount of NH_3 is lost to volatilization.

Increased nitrogen deposition

At the turn of the century nitrogen fixation through human activities surpassed that of natural biological fixation, resulting in increased nitric acid in precipitation (Jefferies and Maron 1997; Vitousek et al. 1997). The nitrogen content in precipitation depends on wind direction and the proximity of an area to major human activities, namely fossil fuel combustion and agriculture (Fenn et al. 2003). In some areas increases in N deposition have saturated ecosystems that were once N limited (Aerts et al. 1992). Wetlands in particular have had a multitude of negative effects from increased nitrogen deposition (Jefferies and Maron 1997; Bedford et al. 1999). While deposition rates vary from place to place the highest known rates are in western Europe, ranging from 30 – 170 kg ha^{-1} yr^{-1}, often with deleterious effects (Berendse et al. 1993). Gorham et al. (1984) pointed to the susceptibility of peatlands to increases in anthropogenic acidification and the need for focused research.

Effects of increased nitrogen deposition

The importance of *Sphagnum* has led most research of increasing nitrogen deposition to focus on *Sphagnum* dominated peatlands, in particular bogs because of their isolation from adjacent nutrient flow. Few studies have examined the response in fens (Rochefort et al. 1990; Li and Vitt 1997), yet their results appear to be in concert with others. Most studies, depending on the duration of the study, are in agreement with a triphasic response, or at least within one of the three phases (Rochefort et al. 1990; Aerts et al. 1992; 2001; Li and Vitt 1997; Jauhiainen et al. 1998; Gunnarsson and Rydin 2000; Lamers et al. 2000; Berendse et al. 2001; Heijmans et al. 2002; Limpens and Berendse 2003; Wieder 2006; Limpens et al. 2006). Phase one of this response is a period of increased growth and productivity of *Sphagnum*. Phase two occurs as nitrogen deposition continues to the point that nitrogen is no longer the limiting factor and *Sphagnum* begins to accumulate excess nitrogen in tissue, followed by phase three, wherein nitrogen is able to pass by the saturated *Sphagnum* and move deeper into the peat column (Lamers et al. 2000).

In areas where nitrogen deposition is high to the point that nitrogen is not limiting the first phase may be bypassed (Aerts et al. 1992). In extremely oligotrophic conditions phosphorus and potassium may be close to limiting nutrients (Damman 1986). Until a new limiting factor is encountered, *Sphagnum* will continue to take up nitrogen and grow concomitantly resulting in no change to the C:N ratio (Aerts et al. 1992). Therefore concentration of nitrogen in tissue is limited by growth (Malmer 1988). In areas of low nitrogen deposition *Sphagnum* responds quickly with uptake growth and retention (Aerts et. al 1992; Li and Vitt 1997). Depending on the levels of nitrogen deposition and other limiting factors, the increased growth phase can last for several years (Vitt et al. 2003b)

As mentioned, *Sphagnum* uptake of nitrogen will occur even as nitrogen is no longer limiting with much of this nitrogen converted to amino acids (Lamers et al. 2000; Limpens and Berendse 2003). Amino acid content was not directly related to growth (Limpens and Berendse 2003), suggesting that hampered growth is related to another aspect of excess nitrogen (Limpens et al. 2006). Aldous (2002b) showed a reduction of translocation of nitrogen at high levels, perhaps an adaptation to avoid excessive amounts of nitrogen. As nitrate is reduced to ammonium prior to uptake and the efficient uptake of nitrogen is faster than assimilation, reduced growth may be the result of toxic levels of ammonium (Juahiainen et al. 1998; Limpens and Berendse 2003). While an exact reason for excessive nitrogen tissue content causing

Sphagnum growth decline is unclear (Limpens et al. 2006), accumulation does reach a critical point in which growth is reduced (Gunnarsson and Rydin 2000).

As nitrogen retention at high levels of nitrogen deposition are less than 100%, nitrogen is able to move below the moss layer (Malmer et al. 1994, Juahianinen et al. 1998; Heijmans et al. 2002; Aldous 2002a). The passing of nitrogen beyond the moss layer has significant effects in 1) giving vascular plants advantageous access to nitrogen (Gunnarsson and Rydin 2000; Malmer et al. 2003), and 2) increasing available nitrogen to the microbial pool (Li and Vitt 1997; Basiliko et al. 2006). When vascular plants have increased access to nitrogen a positive feedback occurs in which the taller vascular plants begin to shade out *Sphagnum*, reducing their growth, in addition to the negative effects of nitrogen saturation (Clymo 1973; Berendse et al. 2001; Heijmans et al. 2002). While response to excessive nitrogen varies between species (Juahiainen et al. 1998; 1999), saturation of tissue and subsequent movement down the peat column is inevitable. Aerts et al. (2001) put forward that the results of nitrogen addition to *Sphagnum* can increase the susceptibility of carpets to drought/water table lowering as the *Sphagnum* mat loses its integrity and falls apart. When nitrogen becomes available within the moss layer, microbial decomposition is favored by removing nitrogen limitations on microbial populations (Bragazza et al. 2006; Basiliko et al. 2006). The change in species composition from extensive *Sphagnum* cover to vascular plants will reduce the system's ability to sequester carbon as vascular plants will shade the *Sphagnum* layer and vascular plant litter decomposes at a higher rate than *Sphagnum* (Verhoeven and Liefveld 1997; Berendse et al. 2001; Moore and Basiliko 2006).

A critical load can be defined as "a quantitative estimate of an exposure to deposition of nitrogen as NH_x and/or NO_y below which empirical detection of changes in ecosystem structure and function do not occur according to present knowledge" (Jefferies and Maron 1997). In a review of nitrogen deposition rates, Vitt et al. (2003) suggested critical levels for *Sphagnum* between 14.8 – 15.7 kg ha^{-1} yr^{-1}. Despite these numbers (Rochefort et al. 1990) noted production lower than control plots just after four years, after having increased production in the first two, using a treatment of 4.6 kg ha^{-1} yr^{-1}. Results of this nature indicate that more research into critical loads is necessary.

Insights into internal variability of complex peatlands

The few studies that have investigated internal variability in peatland complexes have found differences in water chemistry e.g., (Vitt et al. 1975), in addition to plant communities (Wood 2009). In a broad sense, the distribution of vegetation is controlled by its surrounding environmental conditions and at any point vegetation response is indicative of the prevailing conditions that exert influence. Knowing that intra-site variation of controlling factors occurs within a peat complex, it can be supposed that vegetation response to perturbations will also vary throughout the complex creating patterns of assorted response variables.

As nitrogen is an important factor in many peatlands, controls of its distribution are of upmost importance, as variability in its accessibility to plants may lead to patterns of vegetation response. Additional factors that could potentially lead to response differences are water availability, microhabitat, light, surface water chemistry and flow, all of which vary spatially across a peatland complex. Investigating correlations between vegetation responses to environmental variables allows for a variety of questions into the underlying nature of internal peatland variability. From these questions possible patterns in vegetation response parameters such as community assemblage, primary production, and nutrient usage may be revealed.

Scaling issues

Unlike many other studies, ecology is intimately tied to scale. Large scale patterns and processes are the consequence of many more small scale processes and actions, and the reverse can be said as well. As a result of its unifying approach there is no one scale that ecological phenomena should be studied (Levin 1992). For complete understanding of patterns and processes at individual scales there needs to be an understanding of peatland ecology at all scales. Amongst these issues is the complexity of increasing spatial variation with increasing scale.

Most studies of peatland variability have focused on gradients of microtopography, ombrotrophy to minerotrophy, peatland expanse to margin (Horton et al. 1979; Malmer 1986) and in addition, acidity to alkalinity (Wheeler and Proctor 2000). These studies have provided the basis for comparisons of site types. Peatland ecologists now have a plethora of knowledge pertaining to the small scale hummock-hollow gradient (Rydin et al. 2006), as well as what the drivers are for creating different peatland types across large scale regional landscapes. The historical focus of small sample plots for peatland vegetation has made comparisons of vegetation on scales larger than the hummock-hollow micro-scale and smaller than macro-scale site type differences incomplete. To date, few studies have investigated meso-scale spatial variation of plant communities, water chemistry, plant production, plant chemistry, and nutrient availability in a single complex peatland.

Project Significance

This study seeks to provide baseline data for an ecosystem manipulation study as well as provide insights to peatland ecology at a scale not often studied. The narrower, more immediate goal is to properly characterize and describe a study site in which a nitrogen fertilization experiment is taking place. Due to the difficulties in fertilizing an entire site and having different fertilization regimes there are many individual plots within one peatland complex. Characterization of this site provides a reference for the plots chosen for the experimental applications to understand how representative they are of the study site. Additionally this study aims to provide data pertaining to production, decomposition, and patterns in nitrogen processes for comparisons with the experimental plots.

The broader more theoretical approach to this project is to provide more additional details on the relevance of scale in peatland ecology, as well as to explore spatial variability by using an robust spatial sampling scheme. As aforementioned the bulk of peatland studies have focused on the small scale and regional comparisons. This study intends to provide a complete description of a boreal peatland at the meso-scale to bridge the gap between large-scale and small scale patterns in processes. Understanding the variation of one peatland can provide insights into the results of comparisons between peatland at larger scales, in addition to providing insights into the usage of spatial sampling in ecological studies. To assess these goals, one study site was selected with the following umbrella question. How are plant communities arranged in a large complex peatland and do patterns of carbon sequestration and nitrogen utilization relate to these plant communities? The subsequent questions were addressed to describe how patterns in the structure of plant assemblages relate to functional attributes across a highly variable complex peatland – a peatland dominated by one species – *Sphagnum angustifolium*.

Question 1: Can species assemblages be sorted into communities and if so do they differ from each other in terms of abiotic factors? (Chapter 2)

Question 2: What are the ranges of abiotic parameters in the bog/fen complex and what is the extent of the spatial variation of these parameters? (Chapter 2)

Question 3: How are environmental gradients related to those of species, vegetation and communities in the bog/fen complex? (Chapter 2)

Question 4: Does *S. angustifolium* production and growth habits differ in between the different communities? (Chapter 3)

Question 5: How does the cranked wire method compare with the innate time marker method? (Chapter 3)

Question 6: Do *S. angustifolium* capitula nitrogen concentrations, biomass and nitrogen storage stay constant throughout the growing season? (Chapter 4)

Question 7: Do tissue nitrogen concentrations differ between early and late season growth of *S. angustifolium*? (Chapter 4)

Question 8: How much nitrogen is assimilated into one years' production of *S. angustifolium*? (Chapter 4)

Question 9: How much nitrogen is retained in one years' growth after the subsequent growing season? (Chapter 4)

CHAPTER 2: PATTERNS OF ENVIRONMENTAL GRADIENTS AND COMMUNITY COMPOSITION OF A WESTERN CANADIAN PEATLAND COMPLEX

Introduction

As peatlands hold an equivalent of 80% of the present atmospheric carbon quantity (Prentice et al. 2001; Yu et al. 2010), they have been recognized as valuable ecosystems. Since their widespread initiation following the last glacial maximum, primary production by peatland plant species has been greater than decomposition rates, resulting in an immense stock of organic remains (peat). Like many ecosystems, peatlands are undergoing constant change. Modern peatland literature suggests that there are a number of successional pathways of peatland development over time (Charman 2002). In any peatland, the plant species that exist now are surely different than the species present during peatland initiation and are the result of long competition for resources in a landscape subject to both complex internal (autogenic) and external (allogenic) influences.

Pathways of peatland initiation and succession include hydroseral succession (terrestrialization), paludification, ombrotrophication, and more rarely primary peatland formation. Terrestrialization is a process in which shallow water bodies are slowly filled in with graminoids, eventually creating conditions suitable for peatmosses (Rydin and Jeglum 2001). Paludification, the most common peatland forming process (Kuhry and Turunen 2006), occurs when conditions create a more moist, water-logged environment, resulting in the encroachment of peat forming species directly onto mineral soil. Ombrotrophication, defined as the transition of a peatland from minerotrophy to ombrotrophy by upward peat formation and isolation from ground fed mineral water (Rydin and Jeglum 2001), produces drier conditions that become more suitable for bog and poor fen species. Transitions from rich fen to bog can happen in as little as 350 years (Kuhry et al. 1993). There is, however, no single trajectory a peatland takes during its succession (Kubiw et al. 1989). In the boreal north where repeated glaciation has left a carved landscape, with irregular hydrology and many shallow basins, conducive to peatland formation, ongoing succession at different rates has left a dazzling mosaic of continuous peatlands of differing types throughout the boreal landscape.

Species-poor bogs are isolated from groundwater inputs and are solely dependent upon precipitation for nutrient input (ombrotrophic). A suite of fen types exist along a minerotrophic (receiving some inflow) gradient, varying on the chemistry of groundwater inputs. At the lowest end of minerotrophy, poor fens, also species-poor, are considered to be slightly less acidic and less nutrient deficient than bogs. These two peatland types are dominated by near continuous *Sphagnum* cover and by a $pH< 5.5$. *Sphagnum* is of great ecological importance as it contains more stored carbon than any other genus (Clymo and Hayward 1982). In the middle of the minerotrophic gradient are moderate-rich fens, that are relatively rich in species composition and are true moss-dominated; however, *Sphagnum* species can be present in these fens as well. At the highest end of the minerotrophic gradient are extreme-rich fens, which are calcareous and alkaline (HCO_3^-). The different peatland types often have unique indicator species and different floristic combinations (Vitt 2006). Peatland vascular plant species composition in North America is dominated by ericaceous shrubs and sedges. An assortment of interconnected differing peatland types is commonly referred to as a peatland complex.

Throughout the boreal forest in western Canada, these peatland complexes form a spectacular landscape associated together within a patchwork upland forests. Peatlands provide an excellent opportunity to study patterns and interactions between the plants and their environment because of their intimate relationship with the water table, water source, and water chemistry. Initially descriptive analysis of peatland vegetation was carried out in the earlier decades of the 20th century; primarily by Scandinavian phytosociologists belong to the Uppsala school of phytosociology such as Du Rietz (1921) and Osvald (1923). Like their contemporaries in the phytosociology schools of continental Europe (Braun-Blanquet 1921) and America (Daubenmire 1959), the Scandinavians sought to use small plots in homogenous patches of vegetation (Malmer 1974). With small sample plots, most studies have led to comparisons between small scale microtopographic differences as well as between large scale contrasts of entire peatland site types on a regional scale.

Early studies of how environmental gradients related to peatland vegetation began with Sjörs (1950) who concluded that peatland types exist along pH and electric conductivity gradients. Further research led to the acceptance of three primary gradients or "directions of variation" in peatlands (Sjörs 1950; reviewed in Horton et al. 1979; Malmer 1986). These gradients are i) microtopographic variation creating the hummock-hollow topography, ii) peatland expanse to margin, and iii) degree of minerotrophy, or nutrient inputs. Here the second gradient involves the variation found between the center of the peatland interior and the edge of the peatland adjacent to the margins. The third gradient is centered on the incoming source of water carrying essential nutrients into the ecosystem. In addition to floristic indicators (Chee and Vitt 1989), chemical and nutrient gradients have been used to delineate peatland types (Zoltai and Vitt 1995, Vitt 2006).

When addressing peatland vegetation one notices a few striking characteristics, most notably a mélange of bryophyte species, and what some may call a balance and others eternal competition between bryophytes and vascular plants. Whether mutualistic or competitive, the interactions between *Sphagnum* and other bryophytes, and vascular plants are an interesting example of species and guild coexistence. The presence of shrubs in hummocks provides a framework for hummock species to grow while vascular plants in the hollows, namely sedges, do not provide this structural assistance, therefore preventing hummock formation (Malmer et al. 1994). The differences in vascular plant coverage along the hummock-hollow gradient, with aerenchymous species occupying the hollows and dwarf shrubs restricted to hummocks, create an autonomous balance between species of both habitats (Rydin, Gunnarsson and Sundberg 2006). While it appears there is a balance between the vascular plants and sphagna, the relationship is fragile. Vascular plants have a clear advantage for light, however due to the high absorption capacity of *Sphagnum* for incoming nutrients (Li and Vitt 1997), under normal conditions, they only get mineralized nutrients from below the moss layer. Juvenile plants or emergent shoots must grow faster than the rising moss layer. If prevailing conditions change in such a manner that *Sphagnum* is at a disadvantage or vascular plants have improved conditions then the balance may be at risk, resulting in a community change and a cascading alteration to the functioning of peatland ecosystems.

These coexisting species and guilds follow modern competition theories such as Grime's CSR (Grime 1977) and Tilman's resource ratio (Tilman 1981) of different resource utilization tactics and physiological traits and abilities of the co-occuring species. The presence of an individual at a given time requires the individual of that species to be able to disperse to that spot and persist in the competitive surroundings provided by nearby species (Connell and Slatyer 1977). In the harsh climate and nutrient limited conditions of boreal peatlands the plants must compete for resources while tolerating the environmental stressors. Of Grimes C-S-R, there is suggestion that these plants are specially adapted to the 'C' (competition) and 'S' (stress), more so than the 'R' (ruderal, high disturbance) parts of the triangle. The plants that are present long after the most common peatland disturbance, fire, are different than those immediately following, suggesting low tolerance to disturbance (Vitt and Benscoter 2008). Instead, these species, most notably *Sphagnum* species, are well equipped to compete and persist in the harsh conditions of peatlands (van Breeman 1995). After a disturbance there are habitat openings and more available resources. As Tilman (1981) suggested, the species that can outcompete while resources are drawn to a critical level will persist. These are the species that are found in peatlands well after disturbances. Vitt and Slack (1984) present seminal findings, quantifying the actual and potential arrangement of *Sphagnum* species based on resources requirements and physiological abilities. Many other papers have reported the intricacies of small scale species distribution along the hummock-hollow gradient (Clymo and Hayward 1982; Luken 1985; Rydin 1993 and more). The arrangement of true mosses and sedges among peatlands follows these patterns in resource partitioning, utilization and physiological abilities (Gignac 1992; Gignac et al. 2004). The combination of species arrangements in peatlands is the result of complex interactions between plants and the surrounding environment. As Braun-Blanquet (1921) stated, these species combinations may form “definite floristic and sociologic features” that can be classified as associations.

Studies of these systems, their plant-plant (Heijmans et al. 2002; Malmer 2003) and plant-environment interactions (Vitt and Slack 1984; Vitt et al. 1990; Gignac et al. 1993), and the delineation of different types (Sjörs 1950; Vitt and Chee 1990) have been numerous. Yet most have focused primarily on regional scale site type comparisons (Malmer et al. 1992; Zoltai and Vitt 1995; Vitt et al. 1995) or small scale micro-site patterns (Luken 1985; Rydin 1993). While thoroughly researched, most studies that have utilized a multivariate approach to peatland community data (Chee and Vitt 1989; Gerdol 1995; Bubier et al. 1995) used methods of analysis (PCA, DCA) with linear assumptions that can cause data distortions (Minchin 1987). New non-metric techniques are considered to be more reliable than past eigenvalue-based approaches (Kenkel & Orlóci 1986, Minchin 1987).

To my knowledge, few studies (e.g.Vitt et al. 1975; Tahvanainen et al. 2002; Wood 2009) have examined intra-site variability and how the directions of variation play a role at a continuous meso-scale. To properly describe variation of flora in a stand, Daubenmire (1959) suggested that a series of small plots is superior to a few large plots. Peatland community ecology has historically been approached with small sample plots as well (Malmer 1974). This has allowed plant communities to be differentiated at the hummock-hollow micro-scale, allowing the representation of the dominant *Sphagnum* species at that scale. Studies on the hummock-hollow gradient are numerous and have covered a range of issues, even though there are conflicting results in some (Clymo and Hayward 1982; Vitt and Slack 1984; Rydin 1993; Rydin et al. 2006). My study aims to use a different sampling approach to investigate community variation and functional relationships within a single peatland complex. I chose to use sufficiently large plots to bypass this small-scale gradient and focus on meso-scale patterns and variation of the plants and their environment. This allows for the inclusion of the constant cover of the three dominant *Sphagnum* species (*S. fuscum, S. magellanicum, and S. angustifolium*) along the hummock-hollow gradient into the community analysis. This approach allows for the determination of distinct communities within the peatland complex while focusing at the meso-scale, regardless of hummock-hollow community differences. Objectives for the study are (i) to determine whether peatland communities are distinct with boundaries defined by flora, or if they slowly transition from one to another, and (ii) to intensively explore intra-site variability of plant assemblages and their relationship with environmental gradients in a peatland complex.

Research Questions

Question 1: Can species assemblages be sorted into communities and if so do they differ from each other in terms of abiotic factors?

Question 2: What are the ranges of abiotic parameters in the bog/fen complex and what is the extent of the spatial variation of these parameters?

Question 3: How are environmental gradients related to those of species, vegetation and communities in the bog/fen complex?

Study area

Location

The site for this study is situated in Alberta, Canada, near the unincorporated community of Mariana Lake, within the Regional Municipality of Wood Buffalo, approximately 101 km southwest of Fort McMurray on Highway 63 (N 55.89, W 112.09). The site includes a large poor fen, two bogs and two upland islands, totaling 233,750 m^2. The fen is the largest component at 164,000 m^2, the two bogs combined measure 65,600 m^2 and the upland islands 4175 m^2. The perimeter of the study site itself is not limited by a transition from peatlands, but is contained within an even larger peatland complex. The boundaries of the site were delineated by attempting to exclude uplands and recently burned bog, while remaining cognizant of the desired scale of the study. The location and surrounding are shown in figure 2.1. This area was chosen for its relatively abundant representation of peatlands in the boreal forest.

Geology

The study area rests on the Lea Park Formation of the late Cretaceous Age nearby the Snowbird Tectonic Zone (AGS 1999). The Lea Park Formation consists primarily of medium-dark shales with silt, fine grained tan colored sand and clay-ironstone with calcite venation (LCGU 2005). The study area rests upon a large plateau, the Stoney Mountain Upland which contains many peat complexes, elevated about 180 meters above the neighboring landscape (Nicholson and Vitt 1990). Glacial retreat around 11,300 years BP (Hutton et al. 1994) has left the area with irregular hydrologic patterns and it appears that the entire complex peatland is situated upon a drainage divide, which separates the poor fen in the study site from an adjacent poor fen. In the study site, east of the drainage divide, water flows eastward and eventually to the north into a small lake. The till remaining after the glacial retreat is primarily sand, gravel and clay.

Vegetation

The bogs at Mariana Lakes are dominated by *Sphagnum* species, namely *Sphagnum fuscum* (Schimp.) Klinggr., *S. angustifolium* Jensen, *and S. magellanicum* Brid. The dominant vascular cover is the tree *Picea mariana* (Mill.) BSP., ericaceous shrubs *Ledum groenlandicum* Oeder, *Vaccinium vitis-idaea* L., and *Kalmia polifolia* (Hook.) A. Heller, and the herb *Rubus chamaemorus* L. The large poor fen shares dominant *Sphagnum* species with the bog and consists primarily of the graminoids *Eriophorum vaginatum* L., *Scheuchzeria palustris* L, *Carex aquatilus* Wahlenb., *Carex limosa* L., and *Carex paupercula* Lam. ssp. irrigua (Wahlenb.) Hulten, the shrubs *Andromeda polifolia* L., and *Chamaedaphne calyculata* (L.) Moench. The substrate of the upland islands is moist, sandy soil covered largely by the mosses *Pleurozium* *schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., and *Dicranum polysetum* Sw. Forbs and shrubs found on the island include *Vaccinium myrtilloides* Michx., *Ledum groenlandicum* Oeder., and *Equisetum pratense* Ehrh. *Picea mariana*, and *Pinus banksiana* Lamb., comprise the tree cover of the islands.

Climate

Climate in the Mariana Lakes region is typical of the boreal forest Zonobiome VIII (Walter 1979). Mean monthly temperatures range from -16.7 to 16.5 °C. There are consistently five months each year with below freezing temperatures. The implications of this are a relatively low number of growing degree days. Average annual precipitation is around 475 mm.

Historical disturbance

The region is susceptible to disturbance by wildfire. Two fires of recent history have occurred at the study site. The Mariana Lakes Fire of 1995 which burned 135,150 ha and the House River fire of 2002 burning well over 240,000 ha (SRD 2010). These fires never made it to the fen and the majority of the bog area. The southernmost bog was partially burned from the south yet a cutline appears to have stopped the fire from continuation into the study area. All the uplands surrounding the area have been burned yet the upland islands are intact. The large fen appears to not have been burned for some time.

Methods

Sampling

In 2010, 100 points were selected within the predefined study area. Rather than attempting to demonstrate different communities, I used a combination of systematic, restricted random and subjective sampling designs to allow the communities to present themselves. Because the perimeter of the study site is not of ideal shape for complete systematic sampling, some subjectivity was used in placing the points along edges that attempted to fit the contour; also points were placed on direct edges of the peat margins and approximately 5 m from the peat margin in an attempt to embody the expanse-margin gradient. Within the interior of the peatland, points were placed approximately 30 – 50 m apart, loosely following a stratified sampling approach that was at times modified to create transects equidistant from margins. To avoid direct bias at each point a random number of steps in a random direction were taken before the plot location was finalized. Each point was assigned a plot ID, marked with surveying flags and GPS were recorded for repeated measurements (Figure 2.3).

Community surveys were carried out in 9 m^2 meter plots. To rank abundance the plot was visually gridded into smaller squares, roughly 0.5 by 0.5 m and scores were recorded based on frequency of species coverage within the subplots. Classes were divided as follows; 0-not present, 1 – 1 or 2 occurrences, 2 - <10%, 3 - 10-24%, 4 – 25-49%, 5 – 50-80% and 6 - >80% (modified from Phillips 1959).

In June (spring) and October (fall) pore water samples were collected and analyzed for pH, electrical conductivity reduced for H^+ ions (Miller et al. 1998), DON, NH_4^+ and NO_3^-, DOC, and in June only deuterium excess. Prior to analyses, samples were filtered through Whatman 541 filters followed by 0.45µm filters. All nitrogen and carbon water samples were analyzed by Jeremy Hartsock at Villanova University. NH_4^+-N was measured following the phenol protocol and NO_3^--N with the hydrazine reduction method on a Seal III colorimetric analyzer. Total dissolved nitrogen and carbon were measured on a Shimadzu flow/combustion analyzer. Dissolved organic nitrogen was calculated as inorganic nitrogen subtracted from total nitrogen. Deuterium excess was analyzed by John Gibson at the University of Victoria. Deuterium excess is used to differentiate water slow moving evaporatively enriched water from through-flowing water (Whitefield et al. 2010) Fall samples for nitrogen contained trace amounts of nitrate that were not able to be analyzed separately from DON. Shade and average depth to water from the moss surface was measured in June. Shade was measured using a spherical densiometer held at chest height. Average depth to water was measured in 5 randomly selected locations within the plot.

Statistical Analyses

For each plot, species richness, Shannon-Wiener and Simpson's diversity indices and Pielou's evenness were calculated. Gamma diversity and mean plot alpha and beta diversity were also calculated. To explore relationships of environmental gradients and species composition, ordinations were done using non-metric multidimensional scaling based on Bray-Curtis dissimilarities (Bray and Curtis 1957) and all measured variables were fitted to the ordination. Moran's *I* was calculated in ArcGIS 9.3 to detect spatial autocorrelation and clustering for all parameters. If points exhibit significant positive spatial autocorrelation points with similar values tend to be located near each other. Conversely, with little or negative spatial autocorrelation points close together have random or dissimilar values. All maps in this thesis were created using ArcGIS 9.3 software by ESRI. The aerial photo of the study location was obtained from the Air Photo Distribution branch of the Alberta Environment and Sustainable Resource Development. Continuous cover maps were created for all environmental variables with the nearest neighbor interpolation in the spatial analyst extension in ArcGIS 9.3. These continuous surfaces were classified into five classes using Jenk's natural breaks algorithm, which forms groups of like values by maximizing variance between groups and minimizing variance within groups. Because this classification algorithm was used on each variable independently, class ranges will vary between the spring and fall maps.

Complete linkage clustering was completed and groups were formed at 0.6 dissimilarity to form communities using the `vegan` package in R (Oksanen et al. 2011). ANOSIM was conducted using DECODA (Minchin 1989) to confirm that groups formed by cluster analysis were significantly different in community composition. Comparisons of all parameters were made between the different communities. Normally distributed data were analyzed using one-way ANOVA and non-normally distributed data with Kruskall-Wallis rank sum test. Post-hoc multiple comparisons were made using Tukey's HSD for normal data and pairwise Wilcoxon rank sum tests for non-parametric data. Because there may be some spatial autocorrelation of communities the independence assumption of ANOVA may be violated to compare environmental variables between communities.

With the exception of ANOSIM all other analyses used the R software (2011). NMDS, vector fitting and community clusters were calculated using the `vegan` package (Oksanen et al. 2011) and multi-level indicator species analysis were performed using the `indicspecies` package (De Caceres and Legendre 2009). Additionally, contoured surface fitting was applied to the depth to water and Shannon-Weiner diversity index to more closely examine their relation to the ordination. This was done using the `ordisurf` function in the `vegan` package. With the exception of spatial maps all other figures were created in R using `ggplot2` (Wickham 2009) or the base package. No data were standardized prior to analysis.

Results

Species diversity

Throughout the peatland complex there are 81 species, including 23 mosses, 4 hepatics, 37 vascular plant species of which 2 are carnivorous, and 17 lichen species. Mean plot alpha and beta diversity are 18.0 and 4.5, respectively. All plots exhibited an extremely high degree of evenness and lacked variability (0.98 ±0.01), most likely caused by the plot size resulting in the inclusion of many of the species from a variety of elevations. For further analyses, lichens of the genera *Cladonia* and *Cladina* were grouped together due to their high diversity but small portion of cover. Of the moss species there are 9 belonging to the genus S*phagnum* and 14 true moss species. The majority of the vascular plant cover is ericaceous shrubs and sedges along with few herbaceous species. The most frequent species is the bryophyte *Sphagnum angustifolium,* occurring in every plot. Other frequent bryophyte species were *Sphagnum magellanicum* and *Pohlia nutans,* present in 92 and 91 of the plots, respectively. The regionally rare *Sphagnum lindbergii* (Vitt and Andrus 1977) was found in 6 plots and *S. majus and S. riparium* both occurred in only 2 plots. Frequent vascular plant species were *Oxycoccos microcarpus* and *Chamaedaphne calyculata,* which occurred in 95 and 94 of the plots, respectively. Seven species are present in >80% of the plots, 18 plant species present in >40% of the plots and 35 species occur in <10% of the plots (fig 2.4). Despite the high evenness (0.98 ±0.01), there were numerous species that occurred only once or twice (fig 2.4). The high degree of evenness is driven by the high constancy and abundance of the few species that occurred ubiquitously throughout the peatland complex, overshadowing the presence of many locally rare species. In the Mariana lake peatland complex few species are common and many species are rare.

Communities

Complete linkage cluster analysis cut at 0.6 dissimilarity created 4 groups, or communities (fig 2.5). There were significant differences between the communities tested by the ANOSIM (R=0.668, p<0.0001). Pairwise comparisons between groups based on ANOSIM indicated significant differences between all groups. Sheppard's diagram (fig 2.6) indicates a strong fit of the NMDS solution. Figure 2.7 illustrates the dissimilarity of the groups in ordination space while also providing spatial reference by plotting sample unit identity numbers in the ordination. The reported stress value (0.14) allows for a fair ecological discussion of the plots in ordination space (Kruskal 1964). Groups 1, 2 and 4 have a relatively continuous transition across the ordination, while group 3 is more scattered and disjunct from the other 3 groups. Plots in group 3 are all plots that are near, (within 10 meters) from the peat margin. The remaining groups represent the interior of the peatland complex. Group 1 exists in the wettest part of the fen and is thusly named, wet fen. Group 2 represents the bulk of the interior fen and will be named peatland expanse. Group 3, along the transition between upland and fen will be referred to as fen margin. Finally, Group 4 is identified as bog. Spatial clustering of community groups was also significant (I=0.23, p<0.0001) (fig 2.8). The species composition of these plots is summarized in table 2.1.

Community indicator species

Multilevel indicator species analysis (ISA) was used to build a hierarchy of indicator species for all combinations of groups. In the Mariana Lake peatland complex at least one species, and in most cases multiple species were identified as indicators species at community hierarchies (table 2.2). Here multilevel ISA demonstrates *Andromeda polifolia* as the indicator species of the entire peatland interior, being the only species associated to the bog, fen expanse and wet fen. *Rubus chamaemorus* was the only other indicator species of three groups being indicative of every group except for the wet fen. Significant indicators for two groups were more plentiful. *Scheuchzeria palustris* was the only indicator of both fen types. The wet fen and fen transition had more indicators in common, namely *Carex aquatilis, Polytrichum strictum, Carex utriculata,* and *Betula glandulosa.* The bog and the fen expanse had only two indicators, *Kalmia polifolia* and the liverwort *Leiomylia anomala*. Of the indicators belonging to two groups the bog and the fen margins had the most shared species, namely *Vaccinium vitus-idaea, Ledum groenlandicum, Pleurozium schreberi, Aulacomnium palustre* and to a lesser degree species belonging to the genus *Cladonia.* With the exception of the peat margins there were few indicators for individual groups. Indicator species of the wet fen were *Carex limosa* and *Menyanthes trifoliata.* The peatland expanse had just one indicator being the regionally rare *Sphagnum lindbergii*. Two mosses, *Dicranum undulatum* and an unknown moss were indicator species for the bog. There is a plentitude of indicators for the fen margins with the most significant being *Salix pedicellaris, Sphagnum russowii, Equisetum* spp.*, Polytrichum commune, Calamagrostis canadensis, Carex disperma* and *Vaccinium myrtilloides.*

Patterns of environmental gradients and diversity

Several vectors were fit significantly to the NMDS ordination (fig 2.9). The orientation of the vector signifies the direction of increasing values in the ordination and the length of the vector is indicative of the strength of relationship of the variable to the ordination. While not shown vectors should be interpreted as decreasing values in the opposite direction of the fit. The relevance of the vector fits will be further considered in the discussion.

Most of the environmental parameters fit significantly to the ordination, demonstrated some variability, and exhibited a patterning that was significantly different from random (table 2.3). Diversity indices display some variation throughout the site yet there is no significant spatial clustering of areas with high or low diversity. Shrub and sedge abundances were summed to derive a value for dominance of the respective guild. As vectors, both shrub and sedge abundances fit significantly to the ordination and also exhibited a large degree of spatial patterning (table 2.3). Amongt the environmental vectors with the highest fit to the ordination, were pH (both seasons), shade, depth to water, DON (both seasons), and total dissolved nitrogen (both seasons). Of environmental variables, spring nitrate and shade had the most extreme variability (CV% 160 and 158 respectively), and with the exception of pH and diversity indices (CV% <8 for all), most other variables exhibited considerable variability (CV% 21-72).

Spatial patterns of all environmental variables can be seen in the maps created by spatial interpolation figs (2.10-2.28). All parameters exhibited clustering that was significantly different from random patterning with the exceptions of spring total carbon, spring reduced conductivity and all diversity measures (Table 2.4).

There were significant differences for all measured parameters between the four community groups (wet fen, fen expanse, fen margin and bog) with the exception of spring DOC, evenness, and fall reduced conductivity (table 2.3). Values and comparisons of measured parameters between the groups are displayed in figures 2.29-2.50.

While the linear vector fits to the ordination were similar the contour fitting of depth to water and Shannon-Weiner diversity (H') demonstrated a complex nonlinear relationship to each other (fig 2.51). Depth to water and H' increased concomitantly from the wettest areas to halfway up the moisture gradient, before becoming almost perpendicular to each in the ordination.

Discussion

Description of groups

In poor fens and bogs with a pH <5.5 there is a near continuous cover of *Sphagnum,* with emergent vascular plants (Vitt 2006). The very common peat mosses*, S. angustifolium, S.magellanicum,*and *S. fuscum* form almost a continuous cover across the study site. The dominance of *S. angustifolium* across a wide range of habitats has been previously documented (Horton et al. 1979; Wood 2009), and is representative of the large niche breadth of this robust species across several gradients (Vitt and Slack 1984). Within this nearly continuous *Sphagnum* layer and *S. angustifolium* dominance, species assemblages were separated into 4 communities. While seemingly a gradual turnover of species these groups represent distinct floristic units with clear indicator species, suggesting that several unique associations exist within the Mariana Lake peatland complex.

The fen margin, located adjacent to the uplands, had the greatest dissimilarity, while the remaining three groups, representing the peatland interior, were separated at lower dissimilarity (fig 2.5). The interior groups (wet fen, fen expanse and bog) form a unidirectional gradient signifying a gradual turnover in species (fig 2.7) and are aligned along the depth to water gradient (fig 2.9). The larger spread of the peatland margin community in the ordination represents the diverse nature of the species assemblages within this group. The margin areas appear to be subject to paludification, where the peatland is encroaching upon the mineral soil. The mineral soil underlying the organic soil allows vascular plants to root directly into mineral soil, which may explain the diversity of species found in these areas. Often these communities contain a mixture of sphagna and true mosses at the ground layer and vascular species not found in the peatland interior such as *Sphagnum russowii, Polytrichum commne*, *Salix pedicellaris,* and *Calamagrostis canadensis*. Additionally the peat margin also contains the majority of species demonstrating infidelity, in that it contains the most shared species with the other groups, for example *Rubus chamaemorus, Vaccinium vitis-idaea, Ledum groenlandicum* and *Aulacomnium palustre*. In addition to species unique to the fen margins, the margin group also shared several species with the peatland interior. The numerous species found on the margins are representative more available resources, niche space and a more tolerable environment, created by the combination of soil types and a patchwork of shade from the overstory canopy.

The wet fen, found at the wettest end of the gradient represents the community with the next largest spread in ordination space (fig 2.7), contained a *Sphagnum majus – Menyanthes trifoliata* association found in a few plots but, nowhere else in the study site. Interestingly these plots did not separate out at 0.6 dissimilarity and had enough similar species with the remaining wet fen plots to remain as the same community. Spatially, these plots are located in the SE area of the peatland near the protruding upland peninsula (plots 53-55). The remainder of these communities are typified by large lawns and carpets of *S. angustifolium* and occasionally *S. fallax*, with *Carex aquatilis* as the dominant sedge. This wet fen also contains hummocks with *S. magellancium* on the sides and topped by *S. fuscum* and *Polytrichum strictum.* There appears to be strong spatial configuration with these communities being just interior from the margin plots (fig 2.8), most likely affected by runoff from the uplands through the margins. If this is indeed a peatland spreading via paludification, these areas may be the most recently formed and thus have a lower accumulation of subsurface peat, resulting in their low, wet nature.

The fen expanse communities represent the largest number of the sample units in the study. These are found halfway along the wet/dry gradient and have some overlap with the groups found on either end of their location in ordination space. The main floristic distinction of this group from the bog is the lack of *Ledum groenlandicum*, mature *Picea mariana* and true mosses, and from the wet fen by lacking the more robust sedges *Carex aquatilis* and *C. utriculata.* One may propose that these areas are on the trajectory of becoming a bog as it faces further ombrotrophication, yet the presence of sporadic tall tree snags suggests that in recent history this area has supported mature *P. mariana*. Moving to the drier end of the water gradient there is a gradual increase in the size and cover of *P. mariana* as the fen expanse slowly transitions into bog vegetation. This occurs moving from north to south in the study area. Unlike the hummock-hollow topography of the bogs, and the *S. fallax* and *S. angustifolium* flarks and lawns in the wet fen, the peatland expanse is typified by extensive carpets of *S. fuscum* and dwarf shrubs, occasionally interrupted with hollows of *S. lindbergii, S. angustifolium* and more rarely *S. riparium.* Vascular plant species common to these pools were *Scheuchzeria palustris, Carex paupercula* and *C. livida.* Often these pools would be filled with a mixture of the liverworts *Leiomylia anomala* and *Cladopdiella fluitans*, and occasionally the bryophyte *Warnstorfia fluitans*.

The cluster group found at the driest end of the gradient represents the two bogs found in the peatland complex. The most prominent feature of these plots is the presence of mature *P. mariana.* Tree ring analysis suggests that this bog has not been recently burned and that the trees are between 100 and 110 years old. The cut line seen at the southern edge of the aerial photo may have prevented a recent fire (House River fire, 2005) from spreading into the bog within the study site. The heavy cover of *Polytrichum* spp. in the burned area suggests that the fire occurred 10 – 15 years ago (Benscoter and Vitt 2008). This may have resulted in a local water table rise leaving the bog in the study site slightly wetter than in the past. The mean depth to water in the bog (18.5 cm) is markedly higher than the range for bogs (20 – 70 cm) from other studies (Vitt and Slack 1984; Thormann and Bayley 1997a; Turetsky et al. 2008; Wood 2009). Wetter conditions in this bog would have likely slowed the spread of mature dry bog species such as *Pleurozium schreberi* and *Dicranum undulatum,* while still favoring sphagna. Nevertheless, the bog still contains these characteristic species of mature bogs, along with several members the lichen genera *Cladonia,* which prefer drier habitats. The bog near the road was slightly wetter compared to the southern bog. While grouped as bog, these sample units 49, 50 and 57-61, were grouped along the top of the bog cluster in the ordination, and slightly away from the southern bog plots. This bog lacked the same abundance of *Cladonia* species and also harbored *Carex pauciflora*, which was not present in the southern bog. Regardless of these minute differences, the tight clustering of the bog sample units in the ordination demonstrates the relatively consistent species composition found throughout the bog plots. Some overlap with the drier fen in ordination space reveals the slow gradual shift in species composition moving along the moisture gradient (figs 2.7 and 2.9).

Of the sphagna, *S. angustifolium* had the highest abundance in the bog community. The common hummock-hollow topography still exists with *S. fuscum* crowning the hummock tops and *S. angustifolium* in the hollows. While both *S. magellancium* and *S. angustifolium* have large niche breadths, *S. magellanicum* is slightly more restricted by depth to water (Vitt and Slack 1984). When given wetter conditions *S. angustifolium* is able to achieve higher growth rates than *S. magellanicum* and *S. fuscum* (Luken 1985). If indeed these bogs experienced a local rise in water table as a result of recent fire and road installation, the water thriving *S.*

angustifolium may be to outcompeting *S. magellancium* for space and resources, a possible reason for the dominance of *S. angustifolium* in these bogs.

Patterns of physical parameters and relationships to vegetation

As exemplified in the previous section, the role of water level is paramount to the arrangement of plant communities in this peatland complex. The spatial pattern of the surface water depth is well correlated with the pattern of the interior communities (figs 2.10 and 2.8), as would be expected from the direction of the vector (fig 2.9). While the communities between the wet fen and the fen expanse were different, their depth to water differences from the ANOVA were not significant. However, a two sample t-test (df=51.66, t=2.12, p=0.039) suggested that these two communities do differ in their mean depth to water. As a result of this close difference in water depth, other additional factors can be further attributed to the compositional differences between communities.

The other physical gradient, shade, is also highly significant in the single peatland complex. Vitt and Slack (1984) and Malmer (1986) also reported the shade gradient and considered it to be comparable to the margin-expanse gradient. Here the shade gradient is also indicative of the aforementioned gradient where trees on adjacent uplands provide some shading, but is also correlated with the drier portion of the peatland expanse where mature *Picea mariana* provided shading in the bog interior (fig 2.11). The bog and margins were the only communities with any appreciable shade and did not differ (fig 2.30). In this setting, it is difficult to understand the true nature of the shade gradient. It is quite likely that shade is autocorrelated with depth to water and peat margins as these communities contain larger tracheophytes. The shade vector bifurcates the margins and the bog plots in the ordination, suggesting a shared response to the gradient. It is possible that this is the gradient responsible for the many shared species between the bog and fen margins. Marshall and Proctor (2004) indicated that *Aulacomnium palustre,* an indicator for both communities, is more common in open sunny areas and only tolerates rather than prefers shady habitats. Information on *Pleurozium schreberi*, the other shared bryophyte, was not reported in their study. It is entirely possible that shade and depth to water, which was closely aligned with the shade gradient, are co-responsible for the shared species, including the ericaceous *Ledum groenlandicum* and *Vaccinium vitis-idaea.*

Patterns of pore water nitrogen and relationships to vegetation

Nearly all of the water nitrogen parameters were positively associated with the drier parts of the peatland complex, namely the bog and to a slightly lesser degree the margins. Total dissolved nitrogen in the spring was highest in the margins and bog (fig 2.31) and highest in the bog in the fall (fig 2.40). This finding of higher total dissolved nitrogen in the bog may contradict much of the belief that ombrogenous bogs generally are more nutrient limited than fens. Prepas et al. (2001) found that at a landscape level bogs generally export nitrogen, but the findings of my study suggest that nitrogen concentrations are higher in the water of the more raised bogs than in the wetter fen regions throughout the duration of the season. Possible causes for this phenomenon could be that surface water nitrogen could be potentially unavailable to bryophyte species raised above the water table, despite their ability to wick water upwards through capillary action. However this hypothesis does not account for mechanisms of vascular plant nitrogen uptake. Stagnation of water in the bog is also likely, as declining water levels would indicate a lack of water to flow outwards from the bog. It is also possible that nitrogen is just as labile in the wetter end of the gradient but that species living there are able to assimilate it more effectively, thus removing it from the surface water pool. This could also be a signal of co-limitation of *Sphagnum* growth by water and nitrogen, a topic explored in chapter 4. As *Sphagnum* growth is higher in the wetter areas of the fen if its growth is uninhibited by water shortages, then it is free to take up all forms of nitrogen, thus removing it from the surface water. Conversely, it is possible that nitrogen available in surface water of areas further from the water table could be the cause for the dense shrub cover of deeply rooted vascular plants not found in the wetter fen area. *Andromeda polifolia* and *Rubus chamaemorus,* two of the more common species of the peatland was reported to have root to shoot ratios of 13 (Wallén 1992), which would allow for uptake of deeper available nitrogen not able to be transferred to the mosses via capillary transport.

Throughout the study area forms of surface water nitrogen were higher in the fall and less in the spring. Vitt et al. (1995) also noted this trend for ammonium and nitrate in a bog and poor fen in Alberta. While in small amounts this latent nitrogen supply is counterintuitive to the notion that nitrogen should be most available immediately after snowmelt and in the nutrient poor conditions be used up in satisfying the microbial population and plant assimilation during the growing season. In addition to a co-limitation by water another explanation for higher nitrogen levels in the fall are climatic conditions (light, temperature) limiting both plant and microbial activity, thusly limiting immobilization of nitrogen.

Most of the nitrogen found in the complex was in organic form, with lesser amounts of ammonium and trace amounts of nitrate. This is of importance amongst mounting evidence that that plants compete directly with microbial populations for organic nitrogen (Kielland 1994, 1997; Lipson and Nasholm 2001; Schimmel and Bennet 2004; Limpens et al. 2006). *Sphagnum* is able to rapidly reduce and take up nitrate (Woodin et al. 1985), making it a better competitor for nitrate than many vascular plants (Rudolph et al. 1993; Juahianian et al. 1998). Because the entire plant surface of *Sphagnum* is able to adsorb nutrients (Clymo and Hayward 1982) nitrogen uptake occurs almost immediately and effectively after receiving nitrogen inputs (Rudolph et al. 1993; Juahianian et al. 1998). The trace amounts of nitrate in the water reflect the efficiency of *Sphagnum* uptake and may represent a scenario in which vascular plants and microbes compete for amino acid and NH_4^+-N before nitrification can occur, resulting in DON as the dominant nitrogen form (fig 2.52).

A conspicuous feature of nitrogen patterning, within the study site, is the high concentration of all nitrogen forms in the spring just SE of the two upland islands (figs 2.12-2.16). Nitrate in particular appears to be confined to only to this area and along the margins. While there may have been more nitrate in the fen margin and expanse, only the margin was significantly higher than the wet fen (fig 2.32). On a site average the nitrate levels found here (40 μg/L) fall well above the spring numbers reported by Vitt and Chee (1990) for poor fens (7 μg/L), moderate rich fens (3.1 μg/L) and extreme rich fens (16.5 μg/L) as well as a bog (15.7 μg/L) reported in (Li and Vitt 1997). Yet these levels of nitrate concentrations do align with the averages of three poor fen complexes (31.3 μg/L) measured by Whitfield et al. (2010). The most compelling find is that the nitrate in the aforementioned area and along the margins ranges for (180 – 280 μg/L), four times the site average. Visually, there are no surficial prominent features in this area that would lead one to believe that a surface water pattern such as this exists. Along the margins it is most likely that surface water runoff of the adjacent uplands is responsible for the higher levels of nitrate, which in turn could fuel the higher diversity of plants found in the margin communities.

Site mean ammonium levels (160 µg/L) were also higher than the poor fens, moderate rich fens and extreme rich fens reported by Vitt and Chee (1990) (22.7, 16.8, 67.3 µg/L respectively) and appreciably higher than the 1.7 µg/L at a bog (Li and Vitt 1997). Of the three poor fens measured by Whitfield et al. (2010) this site falls well above two (18 and 45 µg/L) and far below the third (260 µg/L). It is interesting to note that had only a few samples been taken from the Mariana Lake site, depending on location, this site could have been characterized by ammonium levels both above and below other studies. Ammonium in both seasons was not a significant vector on the ordination, and differences between communities were marginal (figs 2.33 and 2.41). Only the bogs had significantly lower ammonium levels in the spring and the margins in the fall.

Dissolved organic nitrogen in the spring is mainly present in the small area of the fen expanse SE of the upland islands and highest in the bogs and the margins (figs 2.15and 2.34) The values here were only slightly smaller than those found by Vitt and Chee (1990) for poor fens and far lower than the moderate and extreme rich fens. The pool of DON represents the largest of the nitrogen forms in both spring and fall. As Vitt and Chee (1990) reported, there was an increase in DON over the growing season. Few other studies have looked at the seasonal differences of water chemistry in peatlands. As mentioned in the methods nitrate dropped to undetectable levels into the fall. At the site level, ammonium levels appear only to stay relatively equal, but broken into the community groups there were only slight seasonal differences between the wet fen and fen expanse. However there were noticeable decreases along the margins and increases in the bog. As seen from the histograms as the season went on ammonium in the peatland went from a near normal distribution to a near Poisson distribution, with mostly low values, and isolated areas with high concentrations (figs 2.14 and 2.22). Total dissolved nitrogen increased in all site types as the season progressed, with the exception of the margins, where it stayed constant. The largest increases were in the bog communities, particularly high accumulation in the southern bog. As the northeastern bog now runs adjacent to a road there may be some functional differences due to a disturbance in the water table (Wood 2009). As the summer season progresses there is a general decrease in the water table. During this time it is expected that runoff from the bog ceases, resulting in stagnant waters and the accumulation of DON.

The dynamic nature of these surface water nitrogen patterns may be the result of patterns of internal processing of nitrogen. Mineralization of organic nitrogen ranges from nearly non-existent in the bog, to very rapid in the wettest parts of the fen (Hartsock 2012, pers. comm.). As many of the nitrogen transformations are pH and temperature dependent they will also be expected to exhibit both spatial and temporal variation. This may also partially explain the lack of nitrate in the fall. Across all forms and both seasons, perhaps the most striking pattern is the low concentration nitrogen in the wettest areas of the fen. These areas correlate well with both low deuterium excess and low depth to water, suggesting that through flow in these areas is more considerable. The relationship between nitrogen and flow is of much uncertainty in peatlands (Limpens et al. 2006). In fens, it is generally assumed that the inflow brings in nutrients, yet here the general lack of nitrogen creates a paradox; either there is little nitrogen coming in via inflow, any incoming nitrogen is quickly immobilized, or nitrogen is expedited through these systems. The two former scenarios would provide support and reasoning for the findings by Prepas et al. (2001) that fens generally retain nitrogen. Reasons for the latter scenario are unclear and if true could further convolute theories of nitrogen patterns in peatlands. Investigation of nitrogen content and production of the species in the wet fen compared with those of the fen and expanse and bog could add more clarity to this issue.

Patterns of chemical parameters and relationships to vegetation

Of water chemistry gradients, pH had the strongest fit to the ordination, increasing in the direction of the peat margins and the wetter part of the complex (fig 2.9). These subtle patterns in pH in the site are partially responsible for the distribution of species throughout the complex. The seasonal averages of pH were consistent with common measurements of poor fens and bogs of western Canada (Vitt and Chee 1990, Malmer et al. 1992; Vitt 2006 and Wood 2009). Unlike Vitt et al. (1995), who found very little seasonal change in pH, the Mariana Lake complex demonstrated an overall decline in pH over the course of the growing season (4.09 Spring; 3.93 Fall) perhaps due to a buildup of organic acids created by the slow decomposition of peat. This decline was common across all communities and the differences in pH between each groups remained constant, with the wet fen and margins having a higher pH than the fen expanse and bog (figs 2.38 and 2.44). Higher pH along the peat margins and wet fen areas could be due to faster decomposition in these areas associated with more nutrient rich runoff, inflow from adjacent uplands and possibly lower carbon to nitrogen ratios of the litter. It is apparent from the spatial pattern, that the extreme fen margins exhibited the highest pHs in the site (figs 2.19 and 2.25), another reason for the higher diversity in what becomes a more tolerable pH for many species. Of importance as well is the lack of alkalinity in waters with pH <5.5, suggesting that these systems have little to no acid buffering capacity and very few base cations.

Corrected conductivity is only slightly significant to the ordination and only demonstrated differences between communities in spring (fig 2.39). The higher conductivity values are associated with the peat margins, most likely attributed to slightly higher pH and more ions flowing in from adjacent uplands. The patterning of reduced conductivity in the complex (fig 2.20 and 2.26), is remarkably similar to the patterns of total nitrogen (figs 2.12 and 2.21) for the respective seasons perhaps indicating an underlying mechanism for the movement of ions. Despite their similarities in spatial patterning, the direction of the reduced conductivity vector in the ordination is nearly perpendicular to all nitrogen parameters with the exception of spring nitrate, suggesting unrelated influences on the community structure of the peatland. The values for this poor fen of this site corroborate well with those of Vitt and Chee (1990) (27 and 14 μS cm^{-1}), and a Finnish poor fen (Tahvanainen et al. 2002) (13.3 μS cm^{-1}), and are slightly higher than Wood (2009) (2.4 – 8.3 μS cm^{-1}). However the reported values for the bog plots were marginally higher than those reported by Thorman and Bayley (1997) (8 μS cm^{-1}) and Wood (2009) (8.8 μ cm^{-1}) and more so than Tahvanainen (2002) (2.1 μS cm^{-1}) and greatly lower than Li and Vitt (1997) (52.5 μS cm^{-1}). Differences in fen conductivity is most likely attributed to local sources of incoming groundwater. If the bogs reported here are truly ombrogeneous and precipitation chemistry is similar one would expect similar values for reduced conductivity. Likely explanations are differences in pH, and the rate and chemistry of discharged water.

The low (< 5) pH of this site indicates that bicarbonate and carbonate are absent from the water chemistry. Carbon present in these waters is expected to be predominantly in the form of dissolved organic carbon (DOC). Spring carbon levels were only weakly fit to the ordination, however fall levels fit strongly, with both vectors positive in the direction of the bog communities (fig 2.9). On a site average level it appears that there is little change in DOC between the seasons (spring 56.6, fall 57.9 mg/L). Investigation into the spatial patterning of DOC in the complex reveals interesting trends. Spring DOC patterning was non-significant, yet there does appear to be a cluster of higher values just north of the southern bog (fig 2.18). In the fall there is an obvious concentration of DOC in the southern bog, slightly less levels in the fen expanse and margins and significantly lower levels in the wet fen (fig 2.24). Bog communities had significantly more DOC than the other groups while the wet fen had significantly less (fig 2.43).

The vector fits for pH and DOC are in opposing directions, indicating that low pHs are correlated with higher levels of DOC (fig 2.9). The DOC found in peatlands is mostly comprised of humic acids, which are byproducts of slow decomposition. Slow decomposition in the bog and fen expanse as a result of low pH may be attributable to this build up of DOC. Due to seasonal lowering in the water table the drier and more ombrotrophic areas will export less water and hence accumulate DOC due to stagnation of water. It is possible that the wetter areas of the peatland generate DOC as well, but it appears here that more is discharged from the system. The pattern of low values of deuterium excess appears to be consistent with the areas deficient in nitrogen, DOC and ions. This is a possible indicator of rapid flow through these areas causing low concentration of soluble water compounds. When compared between site types the appreciable changes in DOC are noticed. There were no substantial differences in the in DOC for the fen expanse and the margins, but the wet fen decreased (51.3 to 41.8 mg/L) and the bog increased (58.0 to 75.2 mg/L). The changes in the bog here may even be diluted, as it appears that the increase in DOC that occurred was exclusive to the southern large bog. The small bog in the northeastern area of the study site did not experience these changes and may be due to a functional difference between the bogs as a result of the road.

Patterns of vegetation

The vegetation structures in this peatland are a result of the complex interactions of a variety of nutrient, chemical, and physical gradients. *Sphagnum* was abundant throughout the entirety of the site, but the arrangement of graminoids and shrubs demonstrated inharmonious interactions. These two vectors were both well fit to the ordination and nearly opposite in direction. Due to the heterogeneous nature only the peatland margins had high abundance of both graminoids and shrubs. Throughout the peatland interior there is a tradeoff between summed abundances of the respective guilds. The abundance of shrubs was positively correlated with areas higher from the water table, more shade and higher levels of dissolved nitrogen and carbon, while graminoids were more abundant in areas opposite of these characteristics and slightly correlated with higher pHs. This slow transition of graminoids to shrubs represents a response of the functioning of the different vegetation guilds to differences in the environment. Autogenic or allogenic perturbations at this site affecting these habitats would result in a change in species assemblages and ultimately an alternation in the functioning of the community.

At these latitudes, where species richness is globally low, there is less of an available species pool than more equatorial landscapes. In the harsh conditions of an acidic poor fen/bog complex there were still differences in species richness and diversity. Species richness and diversity indices were positively associated with the margin communities. As previously mentioned this is due to the intersection of mineral and organic soils, providing a range of habitats and conditions somewhat more mild than those of the acidic interior. In the ordination, richness and diversity were positively correlated with depth from water, shade and surface water nitrogen, in particular total spring nitrogen. As the depth to water gradient plays an essential role to the vegetation of peatlands (Sjörs 1950, Vitt and Slack 1984, Malmer 1986) I chose to use this vector to further examine the role that depth to water acts on species diversity at the meso-scale.

The Shannon-Wiener H’ vector fitted strongly to the ordination and the surface fitting along with the mean depth to water provides an interesting explanation (fig 2.51). Areas near the water table face more dramatic and frequent seasonal fluctuation in water table, resulting in periods of inundation and desiccation. Fewer species are able to tolerate these conditions, resulting in the low diversity associated with plots nearest the water table. The contours of H’ begin to digress nearly perpendicularly approximately halfway along the mean depth to water gradient. As conditions become more stable more species are able to exist and diversity is further increased as a result of other parameters. In this case H’ continues to increase strongly in the direction of the peat margin plots and also along the shade vector. As previously stated the combination of two different soil substrates provides an opportunity for a large mixture of species while increased shade creates a patchwork of expanded niches for species occupation. Diversity and species assemblages in a peatland complex are the result of several dynamic factors can be best studied using a multivariate approach to attempt to grasp the complexities of these unique ecosystems.

Conclusion

In this chapter I set out to answer three questions in order to complete the objectives of determining if peatland communities in a continuous peatland complex could be distinctly defined by floristic composition, and if these communities were associated with environmental gradients. In particular I asked if the present species assemblages could be sorted into communities and how those communities differed in abiotic conditions? What are the ranges of these abiotic conditions in the peatland complex, and do these abiotic conditions form gradients that have relationships with the plant assemblages?

The species assemblages found throughout the Mariana Lake peatland complex were sorted into four definitive communities, each with conclusive indicator species. These communities were differentiated amidst a continuous cover of *Sphagnum*, with dominance of *S. angustifolium.* The floristic composition of plants associated with *S. angustifolium* formed distinct floristic boundaries. In this peatland complex, these different communities differed from each other in nearly every abiotic factor including; moisture, shade, pore water, nitrogen, pH, reduced conductivity, and dissolved organic carbon.

Across the peatland complex, the ranges of these abiotic factors were considerable, and are responsible for patterning of the communities found in the Mariana Lake peatland complex. These environmental parameters also had spatial patterning that was significantly more clustered than expected from random. These four communities are the result of a balance in resource partitioning and niche separation self-imposed by the member species.

The three primary gradients that have long been considered as primary drivers of peatland communities also function at the Mariana Lake peatland complex within a local scale. The strength of the chemical and nutrient, moisture, and margin-expanse (shade) vectors all suggest that they are important in species composition and orientation of communities across this peatland complex. Within the peatland complex, the patterns of vegetation and environmental parameters are tightly controlled by a combination of both autogenic (peat accumulation, nutrient uptake), and allogenic (i.e. temperature, precipitation) factors. In the subsequent chapters, I will address how the functioning of carbon and nitrogen processes relate in the peatland interior across the moisture gradient.

CHAPTER 3: PATTERNS OF ANNUAL PRIMARY PRODUCTION OF *SPHAGNUM ANGUSTIFOLIUM* IN A BOREAL PEATLAND COMPLEX

Introduction

Despite the low frequency of peatlands across the global landscape, recent models project that roughly 600 Pg of carbon is stored in these ecosystems, with the greater part of these reserves in boreal peatlands located north of 45°N (Yu et al. 2010). This estimate is considerably higher than the previous approximations of 270 – 450 GtC (Gorham 1991; Turunen et al. 2002) and suggests that peatlands now contain an equivalent of 80% of atmospheric carbon (Prentice 2001). As the earth enters the anthropocene amongst a mounting recognition of the global carbon budget, mechanisms of inputs and storage of carbon in peatlands become increasingly important.

In peatlands, the accumulation of stored organic matter ultimately depends on inputs to the system via primary production, potentially the single most important function of these ecosystems (Wieder 2006). In comparison to other northern and global ecosystems, boreal peatlands have relatively low productivity (Frolking et al. 1998; Moore et al. 2002). In addition to inputs via primary production, accumulation of carbon as peat is further attributed to extremely low decomposition (Vitt 1990; Moore and Basiliko 2006). These slow decomposition rates can be attributed to a number of factors, including low temperatures; anoxic, water-logged conditions; acidity; few decomposers and/or recalcitrant plant litter (Johnson and Damman 1993; Braggaza et al. 2006; Moore and Basiliko 2006).

Sphagnum mosses are abundant in boreal peatlands (Rydin et al. 2006) and as a result much of the research on peatland annual primary production has focused on this particular genus (Wieder 2006). *Sphagnum* mosses are considered by some to be more ecologically important than any other group of mosses in the world as they store more carbon than any other plant genus, garnering much attention to their functioning (Clymo and Hayward 1982; Andrus 1986). The diverse sphagna include 250 – 450 species yet fewer than 50 are thought to contribute to mass peat formation and accumulation (Shaw 2000). Of particular interest of these peat forming species is *Sphagnum angustifolium.* A highly variable species with broad tolerances (Vitt and Slack 1984; Andrus 1986; Gignac 1993) *S. angustifolium* is among the most common species in Alberta. For Minnesota, Vitt and Slack (1984) found a limited range in height above water for *S. angustifolium* , but in Alberta this moss is able to grow across a broad range of microtopography (Horton et al. 1979; Wood 2010). *Sphagnum angustifolium* is considered a foundation species of lawns and carpets of bogs and poor fens, providing important services to the ecosystem (Vile et al. 2011).

There have been numerous studies comparing hummocks and hollows in regards to net primary production (NPP) (Moore 1989; Rochefort et al. 1990; Wallen et al. 1998; Hajek and Adamec 2009), species arrangements (Vitt and Slack 1984; Luken 1985; Rydin 1993a; Gerdol 1995), water relations (Titus et al. 1983; Schpperges and Rydin 1998), species morphology and physiology (Rydin 1993b; Rydin 1995; Turetsky et al. 2008) and more. Studies of *Sphagnum* NPP along the microtopographic gradient are still inconclusive. On a global scale Gunnarsson (2005) combined all data on *Sphagnum* NPP and sorted it by microhabitat, finding that production increased from hummocks to lawns to carpets, nearly doubling. Findings from Vitt (1990) partially agree with the summary, as much as in bogs, where production in hollows was double hummocks, but in both poor and rich fens hummock production was equal or greater than the hollows. The wide physiological range of *S. angustifolium* provides a unique opportunity to explore aspects of production for a single species along a moisture gradient.

It is commonly understood that nitrogen is an important and limiting nutrient to plant production and functioning in peatlands (Rochefort et al. 1990; Aerts et al 1992; Bedford et al. 1999; Gunnarsson and Rydin 2000). However, production in hollows is often limited by water availability (Rochefort et al. 1990; Rydin et al. 2006), rather than the common limiting nutrient, nitrogen. *Sphagnum* mosses are ectohydric, having no water repellent layer and exchange water and nutrients over the entire plant surface (Proctor 1982; Glime 2007). Tissue water content in sphagna is dependent upon three primary controls, the rate of precipitation, the amount of water available for capillary transport, and lastly the rates of drying (Titus et al. 1983). Given an adequate supply of water, hollow species are able to achieve high rates of linear growth during a growing season (Rydin et al. 2006; Hajek and Beckett 2008). In the natural environment, water is not always present and due to the poikilohydric nature of *Sphagnum,* it ceases carbon assimilation during periods of desiccation (Proctor 2011), causing interruptions in growth. Across the microtopographic gradient, species have morphological adaptations to deal with water, with hummock species having higher shoot density and a higher number of branches to conserve water loss, while wet hollow species generally grow in a less dense mat (Rydin 2006). These differences in morphology can contribute to differences in *Sphagnum* primary production as well. Few studies have investigated the relationships of a single species among different habitat types within a single peatland complex.

The cranked wire method is often used to study *Sphagnum* growth (Clymo 1970). This method is known to be reliable in dry, dense mosses, yet Clymo (1970) warned about inaccuracies in wetter habitats in species with open canopies. Additionally, when the moss layer thaws and growth resumes, often the water table is still frozen, creating difficulties in placing wires early in the season, resulting in some growth not recorded by the wires. Some *Sphagnum* species (i.e. *S. angustifolium*) also can be measured using innate time markers left in the moss, capturing the entire annual growth (Clymo 1970; Rochefort et al. 1990). Few studies (Benscoter 2007) have examined the amount of missing growth and none have investigated the accuracy of wires in wet habitats. Also, several assumptions are often made when calculating primary production of *Sphagnum*; namely that capitula biomass (Rochefort 1990) and that stem mass density (Vitt et al. 2003) remains constant; however these assumptions are rarely tested. The goals of this study are to investigate the production and associated parameters of *S. angustifolium* in three compositionally distinct peatland types within a single peatland complex and along a depth to water table gradient for two years, as well as inspect the reliability of cranked wires in wet habitats and to check assumptions in *Sphagnum* primary production.

Research Questions

Question 1: How does the cranked wire method compare with the innate time marker method along the wetness gradient?

Question 2: Do capitulum and stem mass remain constant through the growing season?

Question 3: Does *Sphagnum angustifolium* net primary production and population attributes differ between the three communities found in the peatland interior at Mariana Lake?

Methods

Site and Flora

The study site is a large peatland complex located near the Hamlet of Mariana Lake, approximately 115 km south of Fort McMurray via Highway 63 (N 55.89, W -112.09). Climate in this region is typical of the boreal forest Zonobiome VIII (Walter 1979), with mean monthly temperatures ranging from -16.5 to 16.5 with a mean annual temperature (MAT) of 0.2 °C. Mean annual precipitation (MAP) is around 455 mm^{-1}, and 292 mm^{-1} during the growing season between May and September. The complex contains several spatially and floristically distinct peatland types. *Sphagnum angustifolium* production measurements were taken from three of the peatland types.

The first type is a treed bog characterized by the mosses *Sphagnum fuscum* (Schimp.) Klinggr., *S. angustifolium* Jensen, *and S. magellanicum* Brid., *Pleurozium schreberi, Aulacomnium palustre* (Hedw.) Schägr., *Pohlia nutans* (Hedw.) Lindb. *and Dicranum undulatum* Brid. The vascular cover is dominated by the tree *Picea mariana* (Mill.) BSP., ericaceous shrubs *Ledum groenlandicum* Oeder*, Vaccinium vitis-idaea* L.*,* and *Kalmia polifolia* (Hook.) A. Heller, *Andromeda polifolia* L.*,* the herbs *Rubus chamaemorus* L. and *Smilacina trifolia* (L.) Desf. and the cotton grass *Eriophorum vaginatum* L. The second type is a dry poor fen with *Sphagnum* species shared with the bog, but lacking some of the abundance of the true mosses found in the bog, in particular *P. schreberi* and *D. undulatum*. The regionally rare species, *Sphagnum lindbergii* Schimp., also occurs in this second type. Vascular plant species are shared with the bog but lacking *L. groenlandicum* and mature *P. mariana*, leaving this poor fen with little shade. The third type is a wet poor fen with *S. angustifolium* being the dominant *Sphagnum* species. *Sphagnum fallax* (Klinggr.) Klinggr. is found in the wettest habitats and *S. magellanicum* and *S. fuscum* can also be found in between flarks. True mosses in this site type are nearly absent with the exception of *Pohlia nutans*. This site type lacks many of the shrubs found in the previous site types with the exception of *A. polifolia* and *Oxycoccos microcarpus* L. Instead the majority of the vascular cover consists of sedges, predominantly *Carex aquatilus* Wahlenb.*, Eriophorum scheuchzeri* Hoppe, and the emergent *Scheuchzeria palustris* L.

The bog is located at the southern extent of the study site and gradually gives way to the shrub dominated dry fen moving north which more abruptly transitions into the wetter sedge-dominated fen before the landscape gives way to a burnt upland along the northern extent of the study site. The distance from the bog to the wettest part of the fen is approximately 400 meters. Analysis of similarity (ANOSIM) performed in DECODA (Minchin 1989) confirmed significant differences in community composition ($R=0.82$, $p<0.0001$) and all tests between groups were significant. The three site types also differed in pH, reduced conductivity and distance of the bryophyte layer to the water table (Table 3.1). Plots were established in each of these types, bog ($n=10$), dry treed fen ($n=10$), and the wet sedge fen ($n=9$), all placed a minimum of 15 m apart from each other. These plots were selected randomly from the plots in the three interior communities identified in chapter 2, after plots that contained an insufficient amount of homogenous *S. angustifolium* for repeated destructive sampling were excluded.

Calculation of Production

Samples for each year were taken as close together as possible without sampling from areas that were disturbed from previous sampling. Samples for 2010 production occurred on May 22nd 2011, assuming that growth and decomposition are insignificant over the winter months, and samples for 2011 production were obtained on October 6th 2011. The calculation of production on a meter squared basis requires two measurements; linear growth, how much biomass grew vertically; and the mass of 1 cm of new growth in a known area. Often the latter is referred to as bulk density with units of (mg cm^{-3}). Here I chose to express bulk density as the weight of 1 cm deep of stems in a meter squared, and is aptly named as stem mass density (SMD) with units (g cm^{-1} m^{-2}). Thus, the weight of capitula within a meter squared is capitula mass density (CMD) with units (g cm^{-1} m^{-2}). Stem mass density and linear growth are then multiplied and reported on as the weight of biomass per meter squared per year. Mean weight values of individual stem and capitulum can be derived by dividing the stem and capitula mass densities by the number of plants per square meter.

Linear growth was measured using two different techniques, time markers and cranked wires (Clymo 1970). Linear growth of *S. angustifolium* can be measured reliably using the innate time marker method for the species (Vitt 2007) by measuring from the bend in the stem to the underside of the capitulum. These innate markers are created by the weight of overlying snow that bends the stem. During thaw the stems realign and begin to grow vertically again, resulting in an often conspicuous notch or bend in the stem. Wires were not placed at the beginning of the growing season in 2010, therefore comparisons of linear growth methods only took place for 2011. Linear growth collections for the innate time markers were taken on May 20th 2011 for 2010 growth, and on October 6th 2011 for 2011 growth. Linear growth was determined as the average length of 10 crook bearing plants. On May 22nd 2011, 20 cranked wires were set in each plot and measured on October 3rd 2011. If any disturbance occurred to the wires (animal damage, litterfall) those wires were not measured.

Samples to calculate mass densities were collected using a small sharpened steel core, open on each end with a diameter of 6.5 cm. Samples were collected on the same dates as collections for innate time markers. The depth of the each core was at minimum 8 cm in order to keep the sample intact. Cores were then brought back to the lab to be sorted and processed. Within each core all capitula were counted and removed and stems were cut 2 cm below the capitula. All capitula and stem sections were oven dried at 55° C for four days and weighed separately. The weight of stem section was then divided by 2 to obtain the weight of 1 cm vertical growth for an area of $\pi\ 6.5^2$ cm. Stem mass density is then be extrapolated to g $\mathrm{cm}^{-1}\ \mathrm{m}^{-2}$

by dividing by $\pi\ 6.5^2$ and multiplying by 10,000 cm^2. For each collection depth to water was measured from the location of the core to the surface of the water table. Annual net primary production was calculated by multiplying linear growth by the stem mass density.

Statistical Analyses

Differences between methods of linear growth (2011 only) were calculated with two-sided paired t-tests for the entire site and for each site type. Nonlinear regression was performed on the differences of measurements to depth to water table to determine accuracy of the cranked wires as a function of depth to the water table. Two-sided t-tests were used to compare seasonal differences in average stem and capitulum weight. Differences of linear growth, stem and capitula mass densities, production, stem count, stem and capitula weights were analyzed by two-way ANOVA with site type and year as factors. Because wires were only used for 2011, values derived from the innate time marker method were used for linear growth and NPP comparisons between site type and year. If the model failed Shapiro-Wilk's normality test the data were rank transformed. Post-hoc multiple comparisons were done by Tukey's HSD.

Results

Linear growth method comparisons – Significant differences of recorded growth from the two methods (innate markers and cranked wires) were present in the entire peatland complex (table 3.2). However, these differences were more pronounced in the wetter habitats, particularly the fen communities, however differences in the bog were non-significant (table 3.2). The wet fen had the largest percent of growth unaccounted for (63.8%), followed by the dry fen (42.5%) and the bog (16.5%). Using the cranked wire method, the bog had the highest recorded linear growth of the three site types, despite having less linear growth than the wet fen using the innate time markers (table 3.2). Analyzing the differences in methods as a function of depth to water using nonlinear regression following an exponential decay model was significant ($F_{1,27} = 54.19$; $R^2=0.54$; $p<0.0001$) with and a fit line following the formula $f(x)=6.976^{-0.149DTW}$ (fig 3.1).

Seasonal capitulum and stem weight differences. – Both mean capitulum and stem weights were higher in October and lower in May (table 3.3, figs. 3.2, 3.3). Only the wet fen demonstrated significant differences in mean stem weight between May and October, and both the bog and wet fen experienced significant seasonal changes in average capitulum weight. The implications of these measurements on capitulum weight normalized to the individual level may affect the analysis due to the variability in the number of plants per core, and additionally the constancy of capitulum origin (refers to forking of the main stem, creating a new capitula) Clymo (1970). When the seasonal differences were analyzed on stem and capitula mass densities, the increased mass became more pronounced, with significant differences found in the dry fen as well (table 3.3, figs 3.4, 3.5).

Net primary production (NPP) and population attributes. - There were significant differences in net primary production (NPP), linear growth and stem mass density (SMD) of *Sphagnum angustifolium* in the three communities (Table 3.4, fig 3.6). Net primary production, linear growth, and population attributes (# of plants, SMD) exhibited considerable variability (table 3.5). Plant density (# of plants m^{-2}), not differing significantly between communities, demonstrated high variation, with a grouped mean of 32,324 ±6,994 SD m^{-2}. There was no relationship between the number of stems to either depth to water or NPP ($p > 0.05$ for both

Pearson correlations). In both years, the highest linear growth was achieved in the wet fen, while the bog and dry fen did not differ (fig 3.7). Stem mass densities were different between site types, but greater differences existed between years, with higher values in 2011 than 2010 (Table 3.4; fig. 3.4). Only production had a significant site type x year interaction, most likely the consequence of differences between site type for linear growth and site type and year for SMD. Mean NPP among all site types and years was 259.4 ± 92.1 SD g m^{-2} yr^{-1} (innate time markers). For all site types production was higher in 2011 than 2010, and conspicuously so for the wet fen with respective percent increases of (21, 25, 47 %) for the bog, dry fen and wet fen (fig 3.6). On average the production declined on a wet to dry gradient of the site types.

Using data from the cranked wire method gives different results for NPP at the site with no differences in 2011 NPP between site types ($F_{2,26} = 0.81$; $p = 0.45$). With the communities grouped together, mean 2011 NPP was 166.4 ± 57.5 SD g m-^{2} yr^{-1}, considerably lower than the values derived using the innate time markers.

Climate –Climate (mean annual temperature (MAT) and mean annual precipitation (MAP) have considerable influence on *Sphagnum* production (Gignac et al. 1998; Gunnarsson 2005; Wieder 2006). Historical climatic data (1944-2011), were compiled for the site from the nearby Fort McMurray A weather station (figs 3.8 and 3.9). The hydrological effective period for a growing year begins in October of the previous year, as snow begins to accumulate and ends in September, just before freeze up. The two years in the study period, 2010 and 2011, were both drier and warmer than the long term historical means, 21 and 36 % drier (359 and 291 mm), and 1.9° and 0.6° C warmer, respectively. During the two year study period, warmer annual temperatures were largely a consequence of warmer winters rather than warmer growing seasons. As a result of these climatic differences, *Sphagnum angustifolium* depth to water in October 2010 was lower (mean = 10 ± 4.5 sd cm) than in October 2011(mean = 22 ± 6.0 sd cm). The effect of these climatic differences was more pronounced in the dry fen and bog and less so in the wet fen (data not shown).

Discussion

Method comparisons - The cranked wire method provided different linear growth values from those measured by the innate time markers, and the amount of this growth differed along the wetness gradient. Only Benscoter (2007) has investigated differences between the methods, and he reported that 39% of the growth was missed in an Albertan bog, nearly double the amount of missed growth from the bog in my study (table 3.2). The 16.5% of the missing growth in the bog is likely representative of growth that occurred prior to setting of cranked wires in the spring, while additional missed growth in the wetter habitats is likely attributed to other factors. When Clymo (1970) developed this method, he did so in raised bogs of England. These bogs are located in a climate without a winter frost, thus the wires could be left in place year-round. In this study, inaccuracies of the cranked wires became large around 10 – 12 cm from the water table (fig 3.1). Clymo (1970) warned that horizontal growth and movement of the *Sphagnum* carpet could result in inaccuracies in the cranked wire method; however, he never tested these. Negative growth of *Sphagnum* found by Damman (1978) was reported to be the result of drying and contraction of the peat mat. Moore (1989) attributed negative growth to precipitation differences between two years causing a loss of water content in *Sphagnum* also resulting in contraction of the *Sphagnum* stems.

As Clymo (1970) predicted, the poor representation by cranked wires of growth in the wet fen in this study is largely attributed to horizontal growth and movement of the *Sphagnum* carpet. In the bog and shrubby fen, the structure of the peat mat is maintained by the surrounding *Sphagnum* species (i.e., *S. fuscum*) and ericaceous shrubs. In the wet sedge fen, the carpets of *S. angustifolium* are kept partially erect by the water. The water table experienced steady declines during the growing season (data not shown) that caused the *Sphagnum* surface to subside with the declining water, falling back along the cranked wires, resulting in the small amount of growth captured by the cranked wire method in the wetter habitats. These data indicate that cranked wires used in boreal areas with frost, underestimate growth by around 17 – 42 %. Since many of the worlds' estimates of *Sphagnum* NPP come from this region, ground layer production has been considerably under-estimated.

Seasonal Changes - Assumptions of static capitula and stem biomass are often used for measurement of primary production. At the Mariana Lake peatland complex, appreciable seasonal increases were found for *Sphagnum angustifolium* capitula mass density and stem mass density (CMD and SMD) during the 2011 growing season. This same trend was noted on the mean capitula and stem weights, but was not as strong. This may be due to the large variability in plant densities (# plants m^{-2}), creating inconsistencies in mean capitula and stem weights. Increases in capitulum and stem mass in *S. angustifolium* cannot indefinitely occur, suggesting a seasonal mechanism must be present for the fluctuation of capitula and stem biomass.

A plausible explanation is the existence of two stages of growth in *Sphagnum*. The first being an early season of rapid stem elongation in the spring, followed by a period of branch and leaf accumulation in the capitula in the fall. Moore (1989) found that most linear growth in

Sphagnum occurs early. In the spring, there is no shortage of water to support stem elongation and a potential nitrogen surge; there may be more physiological emphasis on vertical growth rather than stem thickness, which may explain the less stem mass density in the spring. When water becomes more limiting it is likely that continued growth exists as increases in stem thickness and branch and leaf accumulation in the capitula, resulting in higher SMD and CMD in the fall. While less likely it is conceivable that there is some cellular degradation from freeze-thaw cycles, which may also be attributable to the lower stem and capitula mass densities post thaw in spring.

The finding of seasonal shifts in stem and capitula biomass is a novel discovery and, like errors in linear growth methods, has implications to calculations of NPP. Varying seasonal stem densities may cause confounding results of NPP measurements that are collected at different times, and therefore careful attention should be given to time of collections for SMD. Additionally, the increase of capitula biomass during the growing season represents annual growth not accounted for by using SMD alone for NPP values. In 2011, in all plots, the mean increase in capitula biomass was 59.1 g m^{-2} yr^{-1}, 20 % of the mean NPP in 2011. The seasonal fluctuation of capitula biomass presents a new complexity of NPP in *Sphagnum*. The new biomass added to capitula in the latter part of 2011 will eventually become part of 2012 stem biomass, presenting an issue of when this capitula biomass should be considered in terms of annual NPP.

Net primary production (NPP) and population attributes - At the Mariana Lake peatland complex, NPP increased from dry to wet habitats for both study years, with the highest values found in 2011 for all sites (table 3.5, fig 3.6). The values of production are dependent on the annual linear increment of the *Sphagnum* shoots, as well as population attributes.

It has been assumed that species of hollows generally grow with fewer large individuals while species on hummocks have more compact, smaller plants, a morphological mechanism for dealing with water conservation. Here when only one species is considered there were no differences in number of plants between communities along the moisture gradient (table 3.4). This lack of differences may be related to a factor that was observed but not directly measured. While the bog and dry fen plants were of fairly similar size, plants in cores from the wet fen often contained both very robust plants as well as numerous immature stringy individuals. In this analysis every individual within the top 2 cm of the core was included, with drier habitat populations having less variation in plant size compared to wetter ones.

The inclusion of all stems for derivation of stem mass density (SMD) in my study differs from most studies (Grigal 1985; Moore 1989; Rochefort et al. 1990; Camill 2001; Malhotra 2010), which count the number of plants and weigh a subsample of stems to calculate SMD. Using this sub-sampling technique may not capture actual variation of SMD and average stem mass and may ultimately influence production rates. In my study, the SMD differences between the two study years were greater than between community (table 3.4). In all communities there were higher SMD values in 2011 compared to 2010 (fig 3.4). The two fen communities had larger increases in SMD compared to the bog, with the largest change in the wet fen (table3.3, 3.5; fig 3.4). Despite having the lowest SMD in 2010, wet fen production was still highest for that year, a result of higher linear growth rates. Linear growth did not vary between years and was highest in the wet fen community. If water is not limiting and desiccation does not occur, hollows are able to achieve more rapid and sustained linear growth when compared to hummocks (Luken 1985; Hajeck and Becket 2008). At the Mariana Lake site, the effects of drought were more pronounced in the dry fen and bog, while the wet fen was able to remain wet for a longer duration. The lack of consistent differences in SMD values between communities suggests that differences in *S. angustifolium* NPP between communities is predominantly driven by differences in linear growth rates. Because linear growth did not vary by year and NPP calculations are consistently higher in 2011, the high 2011 NPP is attributed to the higher 2011 SMD values.

During this study period both years were warmer and drier than historic means, with the 2010 growing season having drought-conditions with 36% less precipitation. However, this climatic difference had little or no effect on linear growth rates that were consistent in each community between years (fig 3.7). Elucidating whether the differences in SMD between years are the result of climatic differences or due to seasonal effects is complex. Stem mass density and NPP were both higher in 2011, which was more water limited than 2010. The effect of climate driving these higher values is then intuitively dismissed. Instead, (due to sampling schedule) the effects of winterization of the biomass and the aforementioned seasonal differences in stem masses are responsible for higher SMD and NPP in 2011. These effects are more severe in the wet fen compared to the drier communities, hence the large 2011 wet fen NPP.

This study provides NPP and population attributes growth habits and values for a foundation species for a region not yet published. Linear growth and production values here fall within the range of published data and slightly above the global mean derived by Gunnarsson (2005) (table 3.6). Szumigalski and Bayley (1997) found that moss NPP was more linked to climatic variables and herb and shrub production correlated with water level and pH. Of climatic variables Moore (1989) found MAP to be of little influence on *Sphagnum* growth but that MAT was more influential of NPP. Production may be influenced by latitude (Wieder and Lang 1983) yet other factors (temp, precipitation, VPD, nutrient availability, competition) must also be explanatory. The extreme high and low published NPP values for *S. angustifolium* occurred with respective high and low temperatures. However the extremely high linear growth achieved at the lowest latitude (Grigal 1985) and highest MAT (Overbeck and Happach 1957) may be suspect. A consensus on production among microhabitats has not been reached. Vitt (1990) reported lower production in hollow species compared to *S. magellanicum* and *S. fuscum* hummocks while globally Gunnarsson (2005) found that production decreases along a wet-dry gradient from carpets to lawns to hollows. The range of production data generated from this study is closest to that of Lindholm and Vassander (1990), who used a mesh net overlain on the Sphagnum surface to measure growth, and selectively took the thickest section of sphagnum for volumetric weight. They found *S. angustifolium* NPP to be higher on hummocks and raised lawns, attributing competition amongst other sphagna for low carpet productivity, opposite of the results of this study. The closest proximity studies (Camill 2001; Malhotra 2010) had similar values of linear growth yet less production, and this pattern seems to vary amongst studies. Discrepancies in *S. angustifolium* NPP with literature data may be ascribed to a variety of reasons; including climatic differences, as well as the aforementioned differences in linear growth measurements, SMD calculations, and sampling time.

Conclusions

While seemingly simple, proper calculation of *Sphagnum* NPP is a difficult and complex process, with high possibilities for errors. Methodological differences in linear growth and bulk density derivations can lead to misleading data comparisons, namely the underestimated of linear growth by cranked wires. Previous estimates for *Sphagnum* production across the boreal region may be unreliable or at best underestimated in general. Seasonal differences in both stem and capitula mass densities are much more dynamic then previously thought and imply that time of collection for analysis may also cause noticeable differences in NPP calculations. The two years of this study had lower precipitation than normal, with 2011 being the driest. While the effects are complicated, climate has been important in determining *Sphagnum* NPP in other studies, the climatic differences between these two years did not produce a conclusive difference of *S. angustifolium* NPP.

CHAPTER 4: SEASONAL VARIATION IN UPTAKE, ASSIMILATION, AND MOVEMENT OF NITROGEN OVER A WETNESS GRADIENT IN THE MOSS *SPHAGNUM ANGUSTIFOLIUM*

Introduction

While the importance of boreal peatlands to the global carbon pool is well established (Gorham 1991; Yu et al. 2010), these ecosystems are also large reservoirs of organic nitrogen, conservatively containing 10 Pg of soil organic N (Moore et al. 2004) or 9-16 % of the global soil organic nitrogen pool (Limpens et al. 2006). Boreal peatlands play a vital role to biogeochemical pools with sizeable annual estimates of carbon 10 - 30 g C m^{-2} yr^{-1} (Vitt et al. 2001; Gorham 1991; Turunen et al. 2002) and N accumulation 0.2 g -4.5 g N m^{-2} yr^{-1} (Kuhry and Vitt 1996; Urban and Eisenreich 1988; Moore et al. 2004). With concerns about anthropogenic manipulations of the nitrogen cycle (Jefferies and Maron 1997; Vitousek et al. 1997), further research to the understanding of the functioning of nitrogen dynamics in peatlands is imperative.

Bogs and poor fens, abundant in the boreal forest, are peatlands characterized by a nearly continuous cover of *Sphagnum* mosses, distinguished by bogs being purely ombrogenous (receive nutrients via deposition only) while fens are receive some through inflow. The *Sphagnum* mosses that dominate many boreal peatlands are of crucial significance, storing more C than any other plant genus (Clymo and Hayward 1982). The source and usage of nitrogen in these peatlands, and *Sphagnum*, is of key importance, as N is often limiting NPP (Rochefort et al. 1990; Aerts et al. 1992; Vitt et al. 2003; Limpens 2006). Unlike eastern Canadian and European peatlands which have experienced chronic high N deposition (5-40 kg ha^{-2} yr^{-1}, respectively), peatlands of western Canada have low N deposition (<1 kg N ha^{-2} $year^{-1}$), and are believed to be N limited (Vitt et al. 2003). In the Athabasca Oil Sands Region (AOSR), in northern Alberta, ongoing industrial activity will continue to lead to elevated nitrogen deposition regionally (Vitt et al. 2003).

In areas with persistently high nitrogen deposition there have been deleterious effects on *Sphagnum* cover (Woodin et al. 1985; Press et al. 1986). A model of increased nitrogen deposition has suggested a three phase response of *Sphagnum* and ecosystem functioning in which initial increased N is offset by stimulated NPP, until the threshold where nitrogen is no longer limiting, coinciding with an increase in tissue concentration, until full saturation of the moss allows nitrogen to pass beyond the moss layer, becoming available to higher plants (Lamers et al. 2000). The breaching of N beyond the moss layer can lead to a cascading series of events including, alterations in species composition, physiological modifications, shifts in microbial activity and enhanced decomposition in peatlands as a result of increased nitrogen (Woodin et al. 1985; Gunnarsson and Rydin 2000; Heijmans et al. 2002; Malmer et al. 2003; Limpens and Berendse 2003; Bragazza et al. 2006; Limpens et al. 2006; Bubier et al. 2007; Wiedermann et al. 2009).

While the results of increased N in these long-term high N sites is evident, the effects of nitrogen loading at severely low N deposition sites, namely western continental Canada, has been less studied and understood (Rochefort et al. 1990; Li and Vitt 1997; Vitt 2003; Wieder et al. 2010). Due to the rising concern of N emissions in the AOSR, particular interest in these systems is the setting of a critical load, defined as “a quantitative estimate of an exposure to deposition of nitrogen as NH_x and/or NO_y below which empirical detection changes in ecosystem structure and function do not occur according to present knowledge” (Jefferies and Maron 1997). In a review of nitrogen deposition rates, Vitt et al. (2003) suggested critical levels for *Sphagnum* between 14.8 – 15.7 kg ha^{-1} yr^{-1}. Despite these numbers (Rochefort et al. 1990) noted experimentally acidified production rates to be lower than control plots after just four years, using a treatment of 4.6 kg ha^{-1} yr^{-1}. Intimate understanding of nitrogen sources and allocation for production, and retention in peatlands could aid in discovering indicators for critical loads.

Sphagnum mosses are recognized for their ability to efficiently take-up and retain aerially deposited nitrogen (Woodin and Lee 1987; Li and Vitt 1997; Aldous 2002a). In accordance with the triphasic model (Lamers et al. 2000), areas characterized by lower nitrogen regimes have had higher N retention (Li and Vitt 1997), sometimes with increased growth with higher N inputs (Vitt et al. 2003), yet the effects of incoming N retention also can be confounded by climatic factors such as drought (Aldous 2002a). In spite of this efficient uptake of nitrogen there have been striking deficits of incoming atmospheric N to meet the N-requirements primary production in peatlands (Hemond 1983; Damman 1988; Urban and Eisenreich 1988; Aldous 2002a). Only Aldous (2002a) has quantified this N-shortcoming for an individual species, *Sphagnum capillifolium*. Several studies have shown species dependent response to N loading from uptake efficiency (Juahianen et al. 1998), growth (Rochefort et al. 1990;), competition (Gunnarsson et al. 2004), photosynthetic capability (Granath et al. 2009) as well as a range of physiological measurements (Granath et al. 2012). Water availability to *Sphagnum* is equally as influential on all of the aforementioned responses as N. Before elucidating the results of N loading on peatlands, further research into the role of water on N requirements for more species of *Sphagnum* is required.

Some attempts have been made on creating a mass budget for nitrogen in peatlands and most have concluded that internal processing of N must be important (Hemond 1983; Urban and Eisenriech 1988; Limpens et al. 2006). Due to the transient and variable nature of N in peatlands many of these budgets have large associated errors. Only a few studies have concluded that mineralization and translocation of nutrients are responsible for filling nitrogen deficits in growth (Urban and Eisenreich 1988; Aldous 2002a; b). Until recently it had been thought that N fixation in peatlands was a relatively unimportant input; however, recent studies have suggested that N-fixation can actually account for a significant portion of assimilated N and growth (Burke-Scholl 2008, Vile et al. 2011; Berg et al. 2012). Forthcoming data about these processes (mineralization, fixation, and translocation) will aid in creating an N budget for mono species stands, yet there needs to be data on the nature of annual assimilation and retention of mosses to compare.

There may still be some unresolved issues in the current understanding of nitrogen dynamics in peatlands that may convolute application of general models and large scale N-budgets. The triphasic model (Lamers et al. 2000) uses apical N tissue concentrations of *Sphagnum* as the response variable, yet only Aldous (2000b) has considered seasonal variation in apical nitrogen concentrations. It is hypothesized that in areas where N is not limiting then concentrations should remain static, yet in areas where N is limiting there may be seasonal changes coinciding with inputs. In northern peatlands most N is exported during snowmelt (Urban and Eisenreich 1988; Limpens et al. 2006) suggesting an excess of available N in the spring. Considering the efficient uptake of N by *Sphagnum,* it can be assumed that there will be some luxury uptake, phase two of the triphasic model, during this time. Therefore times of collection for tissue analysis may be important in fitting to the triphasic model.

The goals of my study are to explore seasonal changes in nitrogen concentrations and to quantify annual N assimilation and retention along a wetness gradient for a single species, *Sphagnum angustifolium*. *Sphagnum angustifolium* has broad habitat tolerances (Vitt and Slack

1984; Gignac 1992) and is considered a foundation species of lawns and carpets of bogs and poor fens (Vile et al. 2011). To accomplish the goals of the study the following questions are asked:

Research Questions

Question 1: Do *Sphagnum angustifolium* capitulum nitrogen concentrations, biomass, and nitrogen storage stay constant throughout the growing season?

Question 2: Do tissue nitrogen concentrations differ between early and late season growth of *S. angustifolium*?

Question 3: How much nitrogen is assimilated into one years' production of *S. angustifolium* and are there differences in tissue N concentrations in the annual growth segments?

Question 4: How much nitrogen is retained in one years' growth after the subsequent growing season and what is the quality of the remaining tissue?

Methods

Site and Flora

The study site is a large peatland complex located near the Hamlet of Mariana Lake, approximately 115 km south of Fort McMurray via Highway 63 (N 55.89, W -112.09). Climate in this region is typical of the boreal forest Zonobiome VIII (Walter 1979), with mean monthly temperatures ranging from -16.5 to 16.5 with a mean annual temperature (MAT) of 0.3 °C. Mean annual precipitation (MAP) is around 455 mm^{-1}, with 292 mm^{-1} during the growing season between May and September. The complex contains several spatially and floristically distinct peatland types. *Sphagnum angustifolium* production measurements were taken from three of the peatland types.

The first type is a treed bog characterized by the mosses *Sphagnum fuscum* (Schimp.) Klinggr., *S. angustifolium* Jensen*, and S. magellanicum* Brid., *Pleurozium schreberi, Aulacomnium palustre* (Hedw.) Schägr., *Pohlia nutans* (Hedw.) Lindb. *and Dicranum undulatum* Brid. The vascular cover is dominated by the tree *Picea mariana* (Mill.) BSP., ericaceous shrubs *Ledum groenlandicum* Oeder*, Vaccinium vitis-idaea* L., and *Kalmia polifolia* (Hook.) A. Heller, *Andromeda polifolia* L., the herbs *Rubus chamaemorus* L. and *Smilacina trifolia* (L.) Desf. and the cotton grass *Eriophorum vaginatum* L. The second type is a dry poor fen with *Sphagnum* species shared with the bog, but lacking some of the abundance of the true mosses found in the bog, in particular *P. schreberi* and *D. undulatum*. The regionally rare species, *Sphagnum lindbergii* Schimp., also occurs in this second type. Vascular plant species are shared with the bog but lacking *L. groenlandicum* and mature *P. mariana*, leaving this poor fen with little shade. The third type is a wet poor fen with *S. angustifolium* being the dominant *Sphagnum* species. *Sphagnum fallax* (Klinggr.) Klinggr. is found in the wettest habitats and *S. magellanicum* and *S. fuscum* can also be found in between flarks. True mosses in this site type are nearly absent with the exception of *Pohlia nutans*. This site type lacks many of the shrubs found in the previous site types with the exception of *A. polifolia* and *Oxycoccos microcarpus* L. Instead the majority of the vascular cover consists of sedges, predominantly *Carex aquatilus* Wahlenb. *Eriophorum scheuchzeri* Hoppe and the emergent *Scheuchzeria palustris* L.

The bog is located at the southern extent of the study site and gradually gives way to the shrub dominated dry fen moving north, which more abruptly transitions into the wetter sedge-dominated fen before the landscape gives way to a burnt upland along the northern extent of the study site. The distance from the bog to the wettest part of the fen is approximately 400 meters. Analysis of similarity (ANOSIM) performed in DECODA (Minchin 1989) confirmed significant differences in community composition (R=0.82, p<0.0001) and all tests between groups were significant. The three site types also differed in pH, reduced conductivity and distance of the bryophyte layer to the water table (Table 4.1). Plots were established in each of these communities, bog (n=10), dry treed fen (n=10), and the wet sedge fen (n=9). These plots were selected randomly from the plots in the three interior communities identified in chapter 2, after plots that contained an insufficient amount of homogenous *S. angustifolium* for repeated destructive sampling were excluded.

Capitula and stem growth nitrogen constancy and annual N requirements

All measurements took place during the 2011 field season. Quantification of nitrogen requirements in one year's growth requires both the amount of tissue produced for a given year and the nitrogen concentration in that tissue. Net primary production was calculated as the product of linear growth multiplied by stem mass density, the weight of 1 cm length of stems in a known area. Measurements for linear growth used the innate time marker method caused from snowpack (Clymo 1970; Rochefort et al. 1990; Vitt 2007). For calculation of 2010 production, on May 20th 2011 6.5 cm diameter cores were taken from each plot. Additionally, samples for linear growth were collected. Capitula were removed and every stem snipped at 2 cm below the capitula. The same was repeated for 2011 production on October 6th 2011. Linear growth was determined as the average length of the 10 best crook bearing plants. Yearly segments were snipped. All tissue samples were dried for a minimum of 4 days at 55°C. Capitula and stem density samples were then weighed to obtain respective mass densities. All samples were then homogenized in a Thomas Wiley Mini-Mill and analyzed for C and N on a Flash EA 1112 Series NC Soil Analyzer. Collections for seasonal capitulum N concentrations also took place on July 27th 2011. To analyze for capitula N storage the weight of capitula was extrapolated to g m^{-2} and multiplied by the nitrogen concentration (May and October). Capitulum carbon to nitrogen ratios were also compared. Capitulum N concentration is represented as % N in biomass (May, July and October). Tissue N concentrations of early and late season growth used the 0-2 cm collection for stem mass density (May and October). Annual N requirements used the % N content of the entire growth segment for the corresponding year, multiplied by NPP.

Retention of nitrogen assimilated in 2010 growth after 2011 growing season

Calculation of annual N retention requires values for several unknowns; 1) the annual quantity of nitrogen assimilated in 2010, 2) the amount of the 2010 biomass that remains after decomposition and mineralization have occurred, 3) the amount of N left in the 2010 biomass at the end of 2011. The amount of N in 2010 growth is known from the previous question. To estimate loss of biomass of 2010 growth, mesh decomposition bags (n=5) containing snipped 2010 growth segments were placed just under the moss layer in May 2011, retrieved in October 2011, dried and weighed to establish a percent mass loss. The weight of 2010 biomass remaining was calculated by multiplying the 2010 production by (100 - %loss). To find the amount of N remaining in 2010 biomass in October 2011, samples were taken that included the yearly growth segments of 2010 and 2011 in October 2011. The 2010 segment was isolated clipped and its tissue N concentration is representative of N that has been retained and not lost to mineralization, DON leaching, or translocation. The amount of N remaining in 2010 growth at the end of 2011 growing season is calculated by multiplying the percent N concentration of the tissue 2010 tissue still attached to the 2011 stems by the amount of 2010 biomass remaining derived from the decomposition bags.

Statistical Analyses

All data were tested for normality (Shapiro-Wilk's) and homogeneity of variance (Bartlett's) by examination of residuals from two way ANOVA using site type and time as factors. Tukey's HSD was used for post-hoc multiple comparisons among different pairs. Data that failed to meet ANOVA assumptions were rank-transformed and ran with non-parametric ANOVA. Capitula and stem nitrogen contents were compared among site type and month. One plot in the bog was identified as a significant outlier and removed (Grubbs 1950) having an exceptionally high May N concentration for both capitula and 0-2 cm (1.87 and 1.90 %N, respectively). Production, nitrogen content of growth, and nitrogen stored in growth were compared among site types and years. When site type was not significant a Student's t test was used to compare differences between times. The amount of nitrogen in 2010 biomass was compared between site types for May and October. The percent of nitrogen retained in this biomass was compared with one way ANOVA between site types. Statistics were calculated using the R base package (R 2011).

Results

Seasonal capitula and stem N-concentrations - Differences in capitula N concentrations were detected for site type ($F_{2,77} = 3.43$; $p = 0.03$) and month ($F_{2,77} = 140.78$; $p < 0.0001$), with no significant interaction ($F_{4,77} = 0.96$; $p = 0.44$). Capitula N concentrations were highest in May and declined to the lowest in October (fig 4.1). Month was a significant effect for capitula weight ($F_{1,51} = 46.21$; $p < 0.0001$), g N capitula m^{-2} ($F_{1,51} = 17.50$; $p < 0.0005$) and capitula C:N

($F_{1,51}$ = 277.47 $p < 0.0001$), while site type was non-significant for capitula weight, g N capitula m^{-2}, and site type and type x month interaction were significant for capitula C:N ($F_{1,51}$ = 3.48; p = 0.04, $F_{1,51}$ = 3.95; p = 0.03). Student's t test demonstrated significantly higher capitula biomass in October ($t_{54.9}$ = -6.66; $p < 0.0001$), lower g N capitula m^{-2} in October ($t_{42.1}$ = 4.14; $p <$ 0.0005) and higher October C:N ($t_{44.1}$ = -15.36; $p < 0.0001$) see table 4.2.

Nitrogen concentrations in the 0-2 cm section of stems failed to met normality assumptions (Shapiro-Wilk's test, $p < 0.05$) and were examined using a two way nonparametric ANOVA based on ranks. For nitrogen in the 0-2 cm section there were no significant site type effects ($F_{1,51}$ = 2.82; p = 0.07) and significant month ($F_{1,51}$ = 145.75; $p < 0.0001$) and weakly significant interaction effects ($F_{1,51}$ = 3.26; p = 0.046). Nitrogen 0-2 cm stem concentrations were highest in May and lowest in October, with the lowest values found in the wet fen (fig 4.2).

Annual N assimilation and tissue quality - For *S. angustifolium* NPP, there were significant site type ($F_{2,52}$ = 31.92; p<0.0001), year ($F_{1,52}$ = 23.34; $p < 0.0001$) and interaction ($F_{2,52}$ = 3.61; p = 0.03) effects. Net primary production was highest in the wet fen and lowest in the bog for both years and NPP in 2011 was higher than in 2010 (table 4.3). The high production in the wet fen compared to the dry fen and bog was driven by high linear growth rates as bulk density did not vary between the site types, though was higher in 2011, causing higher NPP in 2011 (data not shown).

Tissue N concentration was significantly different by type ($F_{2,52}$ = 15.87; $p < 0.0001$) but not between year ($F_{1,52}$ = 1.59; p = 0.21) with no significant interaction ($F_{2,52}$ = 0.22; p = 0.80). For both years N concentrations in growth segments was highest in the bog and lowest in the wet fen with intermediate values in the dry fen (table 4.3). The amount of N required to support NPP differed significantly by site type ($F_{2,52}$ = 13.07; $p < 0.0001$) and year ($F_{1,52}$ = 30.09; $p < 0.0001$) with no significant interaction ($F_{2,52}$ = 1.85; $p = 0.17$). For each year the wet fen required the most N for NPP with the highest requirement in 2011 (table 4.3).

N retained in previous year's biomass - Decomposition ($F_{2,26}$ = 4.41; $p = 0.02$), amount of biomass remaining ($F_{2,26}$ = 6.05; $p = 0.007$) and percent N concentrations of remains ($F_{2,26}$ = 4.75; $p = 0.02$; non-parametric ANOVA) were all significantly different between site type (table 4.4). The percent of N retained in 2010 growth in October 2011 was analyzed with non-parametric ANOVA and did not differ between site types ($F_{2,26}$ = 1.65; $p = 0.21$) with mean retention of 62.3 % ± 2.36 SE. Thus, the bulk amount of nitrogen was highest in the wet fen, with the dry fen and bog having lower bulk retention ($F_{2,26}$ = 3.62; $p = 0.04$) yet post-hoc comparisons were between site type was ns. (table 4.4). To investigate the rate of N loss compared to decomposition, two way ANOVA of C:N of 2010 biomass in May and October was performed. There were significant differences between site type ($F_{2,52}$ = 7.14; $p < 0.005$) and month ($F_{1,52}$ = 58.05; $p < 0.0001$) with no significant interaction ($F_{2,52}$ = 2.16; $p = 0.13$)(fig 4.3).

Discussion

Seasonal capitula changes – It has often been assumed that capitula are relatively static in behaviors such as size and C:N ratios, remaining constant between seasons and years. Clymo (1970) cautioned that capitula under experimental conditions may be subject to alterations, but did not consider natural changes. This study provides clear evidence of seasonal shifts in capitulum biomass, nitrogen content, and nitrogen storage. The percent nitrogen content in capitula decreases, while capitula biomass increases along with a concomitant rise of C:N ratios.

The result is a seasonal decline of total nitrogen stored in capitula per area (table 4.2). Only Aldous (2002b) has investigated and found seasonal changes in capitula, using an ^{15}N tracer. It was found that ^{15}N found in capitula increased over the first year into October, then continually decreased over winter and through the following season. Conclusions from Aldous (2002b) should not be compared with this study, as her study was investigating movement of nitrogen applied only once and it should be expected that this labeled nitrogen should leave the capitula as it becomes assimilated into growth and that the capitula ^{15}N concentration should increase after application. This aims of my study differed in that the goal was to elucidate natural shifts in nitrogen concentrations in the capitula throughout the growing season.

During the spring months there is a surge of available nitrogen released to the system via the melting of accumulated snow. For a Minnesota bog, Urban et al. (1988) identified that over 50% of annually exported nitrogen from a bog occurs before June. The high N concentrations found here in May are likely the result of high nitrogen retention by capitula of *Sphagnum* mosses (Li and Vitt 1997; Lamers et al. 2000). Estimates for N retention in North America range from 50-90 % in Maine (Aldous 2002a) and 98-99 % for a bog in Alberta, Canada (Li and Vitt 1997). If indeed there is an excess amount of N released into the system it is expected, according the triphasic response, that there would be some luxury consumption by the *Sphagnum* layer before nitrogen passes through the moss layer (Lamers et al. 2000). Based on literature data the triphasic model predicts that 12 mg g^{-1} N is the limit of N concentration at which *Sphagnum* can no longer take in nitrogen (Lamers et al. 2000). Converting to percentage gives 1.2 %N, nearly identical to the concentrations found in May capitula, suggesting that capitula have experienced luxury uptake of excess nitrogen during the pulse from snow melt. After this pulse of N, bulk inputs for the remainder of the season ultimately rely on precipitation, which at the site is <1 kg ha^{-1} yr^{-1}, N-fixation, and in the fen through-flow. As the growing season progresses much of this luxury N is most likely used to propel growth while the water conditions are suitable for growth. Ultimately, at the end of the growing season in October much of the N in the capitula has been put into the linear elongation of the stem, resulting in the low %N and high C:N ratios found in the fall capitula.

Interestingly enough, as luxury N in the capitula is put into newly formed stems, the capitula increase in size, adding new leaves and branches before stem elongation occurs. Despite a 32% increase in biomass the total amount of N in capitula decreases by 23% as a result of the relocation of capitula N into growth. An explanation for the increase of capitula size over the season may reveal a seasonal pattern in *S. angustifolium* growth strategy. Capitula in October are more carbon saturated than those in May, with C:N ratios 68% higher in October. As nitrogen, and perhaps water, become limiting to stem elongation, the capitula continue to build up carbon rich branches and leaves, awaiting the next surge of nitrogen to fuel growth, resulting in the bulky N-poor capitula tissue found here in October.

This finding of seasonal pattern for capitulum N has several implications. As mentioned, the triphasic model (Lamers et al. 2000) demonstrated that at high N deposition regimes (>12 kg ha^{-1} yr^{-1}) capitula N concentrations top out at 1.2% N, and at lower deposition capitula are lower - 0.6-0.8 %N. However, the values used for the low deposition sites were collected at the end of the growing seasons (Malmer 1988; Aerts et al. 1992). Had these been collected earlier there may have been complications in the model, indicating that when drawing conclusions from N concentration data, attention should be heeded to the sampling time.

Utilizing this seasonal depletion of capitula N under natural low deposition regimes could be useful in examining N critical loads. If nitrogen concentrations increase with increasing nitrogen application then the plant has not reached its maximum organic N content (Lamers 2000; Nordbakken 2003); conversely, if the plant is nitrogen deficient concentrations can be expected to drop to a certain minimal concentration. If there is constantly sufficient nitrogen in capitula to satisfy needs for growth the capitula should not experience a decline in concentrations and may be at their saturation point, thus allowing additional N to pass through the moss horizon. Monitoring of capitula N concentrations could provide insight to this critical point.

Annual N assimilation and tissue quality – At the Mariana Lakes peatland complex, atmospheric inputs fall below 0.1 g N ha^{-1} yr^{-1}. Rounding to 0.1 g N ha^{-1} yr^{-1}, these inputs meet only a minor fraction (4.63 % ± 0.69 SD) of N required for the annual growth of *S. angustifolium,* similar findings to those of Aldous (2002a) for *S. capillifolium.* As concluded in other studies this shortcoming in N requirements must come from other sources of inputs or from internal recycling of N, such as inflow, N-fixation, mineralization, and translocation. Recently, Berg et al. (2012) demonstrated that a portion of fixed N is immediately available for growth in *Sphagnum*. Due to low N availability most mineralization in bogs and poor fens terminates in production of ammonium, with only trace nitrate (Schimel and Bennett 2004). Data from literature suggest an inflow of 0.20 g N m^{-2} yr^{-1} (Verry 1975; Verry and Timmons 1982), N fixation rates for *S. angustifolium* in Alberta of 0.8 g N m^{-2} yr^{-1}(Prsa 2012), Albertan ammonification rates in bogs and poor fens of 0.3-0.6 g N m^{-2} yr^{-1} (Bayley et al. 2005; Hartsock 2012 pers. comm.), and translocation rates from Aldous (2002a;b) of 0.03-0.79 g N m^{-2} yr^{-1}. Using the means of these estimates, and a mean N requirement of 2.50 g N m^{-2} yr^{-1}, these sources account for 8, 32, 18, and 17% of yearly N for inflow, fixation, mineralization and translocation, respectively. With the addition of atmospheric deposition this accounts for 79% of the required

N for annual *S. angustifolium* growth. An additional source was also identified from the seasonal shift of capitula stored N to stem growth. When the storage of N in the saturated capitula is seasonally transferred to the elongating stem it accounts for 0.5 g N m^{-2} annual N requirements, adding an additional 20% to the mass budget.

This simple budget for N requirements is not far off the actual required amounts, suggesting that there is good accuracy amongst the literature data. While simplified there are many caveats to this budget. This calculation combines mineralized and translocated N, when in fact much of the translocated N may be first mineralized and competed for prior to vertical movement and re-assimilation. The capacity for intracellular transport may explain gaps in a N budget (Malmer 1988; Rydin and Clymo 1989). Also the calculations from Aldous (2002b) were in a bog and translocated N was somewhat restricted due to water limitations, signifying that amounts translocated will vary along a moisture gradient. Literature for through-flow in fens is scarce and values from (Verry 1975; Verry and Timmons 1982) are based on a study from a perched bog, where inputs via flow should not occur, if truly a bog by definition (Vitt 2006). At other sites, mineralization rates were shown to be much higher than the included Albertan rates with values from Minnesota ranging from 0.8 – 7.7 g N m^{-2} (Urban and Eisenrich 1988; Grigal and Homman 1994), enough at the high end to alone support growth requirements. Including analyses of these measurements at the site of N requirement measurements is the only way to truly test accuracy and build a mass budget for a single species. While there has been documented colonization of cyanobacteria in *Sphagnum* hyaline cells (Basilier et al. 1978) there is no guarantee of N-fixation uniformly across the moss surface as not all *Sphagnum* plants have association with symbiotic N-fixers (Aldous 2002a).

The differences in production, annual net N requirement, and tissue quality along the wet dry gradient in the three site types illuminates some site type level differences in growth limitations between these sites. The higher production and thus N requirements in 2011 were the result of higher bulk density, as linear growth did not differ between the two years nor did tissue quality of each site type from year to year. Tissue quality did decline along the water gradient with the highest N% in the bog and lowest in the wet fen, yet for each year N requirement was still highest in wet fen. The lower N% in wet fen tissue growth may be the results of rapid stem elongation, thus creating a dilution effect in the tissue. Potential sources of this N compared to the other site types could be more N in throughflow and translocation of labile N. Aldous (2002b) found translocation to be important only as long as the water table is high enough to support the process. Bayley et al. (2005) found higher mineralization rates in poor fens compared to bogs.   The combination of these results offers explanation to the higher growth in the wet fen, namely that there was sufficient water to supply the N to support growth. Growth in the bog, with the highest N concentration, being more removed from the water table, may have experienced water limited growth rather than N limited growth as the water table lowered as the season progressed. The dry fen is an intermediate between the two extremes of the site types. The growth in the wet fen represents the potential growth of *S. angustifolium* under low N regimes.

N retained in previous year's biomass - On average 37.7 % of the nitrogen assimilated in 2010 growth was lost by the end of the 2011 growing season. This loss of nitrogen is either from DON leaching or N mineralization. Bayley et al. (2005) found decomposition and mineralization to be two very closely linked processes. Here we find that loss of N is occurring faster than the loss of carbon for the first year, as noted from the increasing C:N of 2010 remnants (fig 4.3). The slow decomposition and higher C:N of 2010 remnants in the dry fen compared to the bog is indicative of the similarities in N loss throughout the site, as N was steadily being removed in spite of low decomposition.

Even though the wet fen had lower tissue quality in annual growth, and the percent of N lost from biomass was similar across all site types, the most amount of N stored annually is in the wet fen, due to the high growth rates. The tissues in the wet fen will spend less time in the acrotelm compared to the bog as more growth needs to occur in the bog before tissues are depressed into the water table. It is generally assumed that once litter enters the catotelm very little biochemical changes occur. This could make sense of findings that bogs export N (Prepas et al. 2001) and that N retention in the upper layers of fens is high (Li and Vitt 1997), in that litter in fens enters the catotelm earlier while bog litter is exposed for a longer period of time. Additionally, N in the bog may not be able to be retranslocated due to water restrictions making it available for vascular plants, or exportation. Differences between peat accumulation between the bogs and poor fens may be due to a combination of differences in tissue quality and dominant species. To retain their respective trophic statuses, bogs must accumulate peat and fens to lose some. The rapid breakdown of S. *angustifolium* in bogs due to the time spent in the acrotelm would make it appear that bogs do not continuously accumulate peat. But in bogs *S. fuscum* is typically the dominant species, and has a much higher resistance to decomposition than *S. angustifolium* (Turetsky et al. 2008). It must be that *S. fuscum* in bogs provides structural support to the hollows of *S. angustifolium*, thus keeping the *Sphagnum* surface well above the water table.

The 37.7 % of N that is lost from the tissue represents 0.67 g N m^{-2} of biologically available N per year. If hypothetically this entire N pool was retranslocated via capillary movement it would be sufficient to account for another 31 % of the annual requirements for *S. angustifolium* growth at this study site. This number will be slightly less if initially liberated N is immediately immobilized by the microbial pool (Damman 1988). Additionally, this N may not be available to *Sphagnum* in drier habitats due to water limitations (Aldous 2002b). In calculating annual N requirements, Aldous (2002a) increased values by 40% to account for N leaching losses over winter. If that procedure is applied here to the 2010 N requirements, the mean of the 2010 requirements become very close (<5 %) to those of the 2011 N requirements. This application also implies that the amount retained in the 2010 growth and the amount released is also 40% higher. The new calculations would be that 0.94 g N m^{-2} or 38 % of the required N in 2011growth becomes available for uptake. If these numbers are again combined with the previously used literature data for N-fixation and inflow the source allocations for 2011 growth become 38, 32, 20, 8, and 4 % for translocation of liberated N from 2010, N-fixation, transfer of capitula N, N in flow, and atmospheric deposition (fig 4.4). These numbers represent a budget for *S. angustifolium* across the entire moisture gradient. Because of the importance of water for N movement these numbers likely vary across the gradient.

If the values from literature and this study are accurate there is enough N to satisfy growth of *S. angustifolium.* At low levels most N via atmospheric input in these ecosystems in unavailable to vascular plants (Li and Vitt 1997; Aldous 2002a; Heijmans 2002), and N for these plants must come from internal processes such as mineralization. Further studies into the annual requirements of vascular plants could lead to an improved understanding to the effects of increased N deposition. Vitt et al. (2003) suggested a critical N deposition of 15 kg ha^{-1} yr^{-1} or

$1.5\ g\ m^{-2}\ yr^{-1}$. A critical load that supplies less than the annual requirement for NPP illustrates the importance of tightly regulated internal cycling of N to the proper functioning of boreal peatlands.

CHAPTER 5: SYNTHESIS OF THESIS RESEARCH

The aims of this thesis were to accumulate knowledge pertaining to a particular peatland complex for an ongoing ecosystem manipulation project while examining a scale not oft studied in peatland ecology. While each individual ecosite is unique, the Mariana Lakes peatland complex is very representative of bog - poor fen peatland complexes of western continental Canada, thus conclusions drawn from this study are relevant to peatlands of the region.

The effects of scale in peatland ecology, and all ecology, become quite pronounced when studied. Perhaps a Pascal quote “Nature is an infinite sphere of which the center is everywhere and the circumference nowhere” sums up the problem of scale and ecology. The scale at which interactions are or aren’t relevant to the nature that surrounds us is indeterminable, yet we accept nature and study it. The local placement of a species or the rate of a microbial process are dependent on several factors both smaller in scale (substrate chemistry, redox state, etc) and larger in scale (shade, climate, etc), of which those factors are also dependent on abiotic and biotic interactions of differencing scales. Levin (1992) pointed out the feedback of which small-scale processes influence large scale factors, only to be reciprocated back to the small-scale actions, highlighting the importance of scale in ecology. Further he urges the necessity to study all scales to develop models for large scale predictions.

This project, funded by Cumulative Effects Management Association (CEMA), has several students working individually at different scales and research topics with the primary goal of setting a critical load standard for nitrogen emissions for Alberta, Canada. Additional goals of extrapolating the effects of nitrogen deposition on peatlands on a broader scale are also considered. Due to constraints such as money, extent of labor and time the CEMA project is working on a 5 year scale. The linkages between scale, both spatial and temporal, to the effects of simulated nitrogen acidification is quite dynamic (figure 5.1). Responses at the smaller end of the scale will happen immediately to changes in the surrounds environment. The continuation of these small scale responses will ultimately be reflected in by changes in larger scale creating a hierarchy of alterations. Ultimately these large scale changes, such as altered climatic or atmospheric conditions, will begin to affect the small scale processes.

In attempting to bridge a discontinuity of scale in peatland ecology the scope of this study focused on two scales; a meso-scale (Chapter 2), and a smaller scale focusing on a single species, *Sphagnum angustifolium* (Chapters 3 and 4). The meso-scale approach of Chapter two focused on the arrangement of continuous vegetation beyond the hummock hollow approach and its relation to several environmental gradients. Chapters 3 and 4 took a more intimate approach with a single species to examine its growth habits and nitrogen patterns across a wetness gradient.

In chapter two it was found that within the Mariana Lake peatland complex local environmental gradients had influence upon the species arrangement at the meso-scale. In comparison with the literature some of the ranges of measured gradients, pH, TN, and reduced conductivity, demonstrated within site variability comparable to measurements comparing site types. Additionally, within the nearly uninterrupted cover of *Sphagnum*, the species assemblages were able to be sorted into four different communities across what visually appeared to be a slow turnover in species and growth forms. Identified communities were classified as bog, two fen types and margin or edge. These different communities differed from each other not just floristically, but also chemically (pore water pH, reduced conductivity, nitrogen, carbon) and physically (water depth, shade), suggesting an assortment of underlying factors to the arrangement of communities and their functional responses.

These chemical and physical factors play influence the species arrangements found in peatlands. While pH had a significant effect on the distribution of species at the site, it was mainly focused on differentiating peatland margin communities from interior communities. While the scale of this study was larger than the microtopographic differences of the hummock-hollow relationship where water depths are quite variable on the small scale, I found a mean depth to water in larger plots encompassing hummocks and hollows that influenced species assemblages along a bog to wet poor fen gradient.

The use of a loosely based systematic spatial sampling technique revealed intricate spatial patterning of these environmental gradients. When coupled with multivariate techniques the significance of these patterns and their relation to the vegetation became more evident. Mapping of the water chemistry distinguished patterns of water movement and sources. While nitrate is an uncommon N form in bogs and poor fens the spatial mapping demonstrated that the pattern of nitrate concentrations in pore water in peatlands is associated with and influenced by runoff from adjacent upland forest. One of the key findings was the higher proportions of other nitrogen forms in the bog suggesting water limitation rather than nitrogen limitation to the growth of *Sphagnum* and possible shallow rooted vascular bog plants.

Operating on a smaller scale (hummock-hollow) or larger scale (fewer sample units, more sites or larger area) along these gradients would have not revealed the spatial complexities demonstrated by these gradients within one site. In addition to these findings on a spatial scale, this study found spatial patterns along a temporal scale, namely the accumulation of soluble organic nitrogen and carbon in the less disturbed bog, revealing functional differences with a bog near a road less than 0.5 km away. Taking into consideration both temporal and spatial scales the peatland not only exhibited a wide range of variation at a static time across a large space but also along a temporal scale. The arrangement of vegetation is a reflection of the individual species biotic and abiotic interactions, at local spatial and temporal scales. Understanding the significant drivers on community composition at this scale and site can aid in elucidating the effects of nitrogen additions within the plots, as well as predicting community shifts. The finding of these independent communities and identifying the dominant occurrence of *S. angustifolium* along the moisture gradient led to the selection of similar plots for the smaller scale analyses within the three interior communities.

Chapters 3 and 4 focused on more precise measurements of production, nitrogen usage, and seasonal patterns in growth and nitrogen storage. Main findings of chapter 3 were that varying production between site types was purely driven by differences in linear growth, and not by stem mass density. Yet yearly differences were attributed to seasonal differences in stem mass density due to collections taking place in spring and fall of the same year, rather than climate, which was similar between the two years yet both drier and warmer than long term averages. This finding of seasonal change in stem mass density may confound comparisons of production between studies if samples are taken during different seasons. Also found was a dramatic seasonal increase in capitula biomass, revealing seasonal growth strategies of *S. angustifolium* and perhaps other sphagna.

Explanations of the results found in chapter 3 were supplemented with answers to the research questions of chapter 4. Across the moisture gradient there were differences in the amount of nitrogen used for growth and how it was concentrated. In the wettest end of the gradient more N was assimilated into the yearly growth segments, but was lesser in concentration than the drier end of the gradient. The high N concentrations and lower production suggested a limitation of water rather than N moving towards a drier habitat. Across the entire moisture gradient there was an even percentage of N lost from last year's growth, meaning that more is retained in the fen because of the higher uptake. More water availability indicates that more of this leached and/or mineralized N is available for capillary translocation back to the capitula for new growth (Aldous 2002b). Another mechanism of N movement found in this study was that of early season capitula leisure uptake, resulting in a large storage of N in capitula early in the season. During the growing season this N is reallocated back into growth with an ensuing decline in capitula N concentrations. This temporal pattern could possibly be used as an indicator for assessing the point at which N is no longer limiting.

Combining key differences from chapters 2-4 there are apparent differences in community composition, growth and N usage. The differences in community composition, namely the transition from sedge-dominated wet fen to the shrub-dominated bog, with a mixture of growth forms in the fen expanse, are likely attributed to the depth of the water table and its influence on N recycling and usage. Figure 5.2 summarizes the usage and interactions of N and possible allocations in a peat profile along the moisture gradient. The increased production and N requirements at the wet end of the gradient is partially met by a lower concentration of N in the yearly growth. The wet fen has several growing advantages compared to the bog, namely the sufficient supply of water to support capillary translocation of leached N and N-fixation. The competitive environment is also less hostile as the dominant growth form, sedges have roots below the water table making them less competitive for recently recycled N and creating less shade. In the bog most of the root biomass occurs between the water table and the moss surface, and most of these ericoid species have mycorrhizal associations (Wallen 1986; Thormann et al.

1999; Moore et al. 2002), which may compete with N recently departed from *Sphagnum* tissues. However there has been very little uptake of labeled ^{15}N applied to *Sphagnum* by vascular plants, suggesting efficient retention of internal N by *Sphagnum* (Li and Vitt 1997; Aldous 2002). Even with some competition for recycled N in bogs the smaller N requirements for growth are more easily met than in the fen. The higher concentration of N in tissue and less growth suggests a limitation of water in the bog. Likewise, the high growth in the fen, with a lesser N concentration in tissue gives evidence of a dilution effect caused by higher growth and a limited N.

While peatland ecology has many unique characteristics, it is not exempt from general principles of ecology. The studying of ecology across multiple scales can provide insight into patterns and processes found at each scale. The types of measurements across the different scales also vary in their type and error. Due to numerous difficulties in large scale experiments many broad scale conclusions are based on extrapolations and models. As smaller scale results are extrapolated to larger scales there is an increasing error, creating a major dilemma for ecologists (Englund and Cooper 2003; Wiedermann 2009). At the core of this issue the small-scale effects are less important to policymakers and the general public than the large-scale implications (fig 5.1). In terms of the CEMA project, the critical emissions standards for Alberta, with an area of 661,848 km^2, will be partly set by the results from 42 plots taking up approximately 0.3 km^2 at the Mariana Lake peatland complex, thereby stressing the importance of scalar relations. If ecological results are to dictate environmental policy in the future, issues of scale must be fully understood. Studying across multiple spatial and temporal scales is paramount to accuracy in the extrapolation of results.

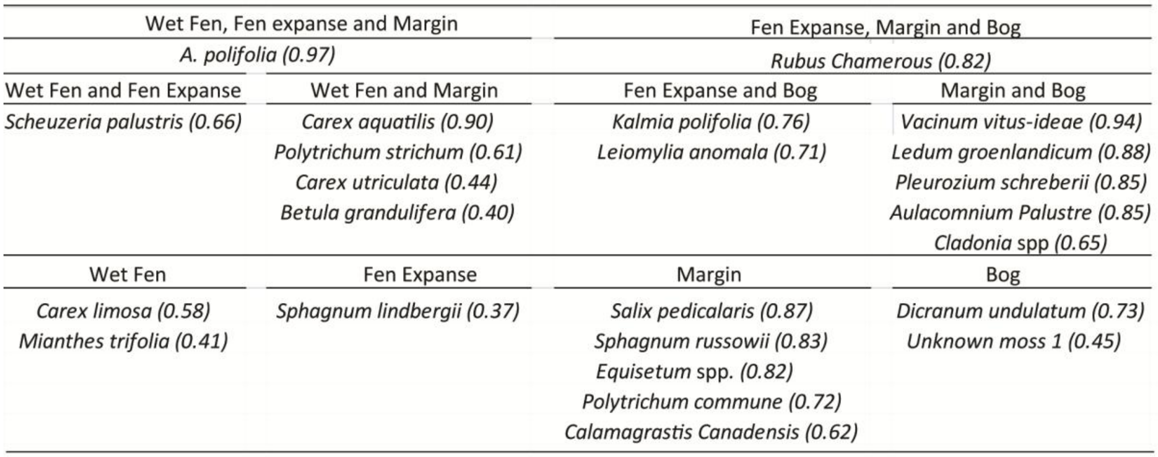
Table 2.1. Mean cover class scores based on plant abundances of Mariana Lake peatland complex for the 4 groups created by complete linkage cluster analysis. Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24. (See methods for details).

	Wet Fen	Fen Expanse	Fen Margin	Bog
Moss				
Aulacomnium palustre	0.63	0.58	2.67	1.96
Dicranum undulatum	0.00	0.61	0.24	2.00
Dicranum polysetum	0.00	0.00	0.48	0.00
Warnstorfia fluitans	0.08	0.13	0.29	0.08
Hylocomium splendens	0.00	0.00	0.48	0.17
Hypnum lindbergii	0.00	0.00	0.00	0.17
Pleurozium schreberi	0.00	0.74	2.76	2.83
Polytrichum strictum	1.21	0.35	1.43	0.29
Polytrichum commune	0.00	0.00	1.76	0.00
Pohlia nutans	3.38	2.77	2.76	2.13
Ptilium crista-castrensis	0.00	0.00	0.29	0.17
Unknown moss	0.00	0.13	0.00	0.50
Tomenthypnum falcifolium	0.13	0.00	0.00	0.08
Sphagnum angustifolium	5.13	4.58	4.38	5.29
Sphagnum magellanicum	3.75	4.06	2.14	3.96
Sphagnum fuscum	1.46	4.35	2.62	3.25
Sphagnum fallax	0.54	1.00	0.33	0.21
Sphagnum lindbergii	0.08	0.39	0.00	0.00
Sphagnum majus	0.33	0.00	0.00	0.00
Sphagnum russowii	0.29	0.13	2.57	0.00
Sphagnum capillifolium	0.00	0.00	0.10	0.00
Sphagnum riparium	0.00	0.13	0.00	0.00
Hepatic				
Calypogeia sphagnicola	0.08	0.06	0.00	0.00
Cladopodiella fluitans	0.25	1.00	0.10	0.33
Ptilidium pulcherrimum	0.00	0.00	0.52	0.08
Leiomylia anomala	0.42	1.77	0.29	1.13
Lichen				
Peltigera aphthosa	0.00	0.00	0.33	0.00
Cladonia species	0.00	0.23	0.76	1.29
Vascular				
Drosera rotundifolia	1.58	1.74	1.10	1.00
Sarracenia purpurea	0.08	0.06	0.00	0.00
Andromeda polifolia	4.29	4.42	0.57	3.92
Betula glandulosa	0.54	0.00	0.29	0.00

Table 2.1. continued

Chamaedaphne calyculata	2.88	3.97	2.52	3.88
Eriophorum angustifolium	0.29	0.06	0.48	0.00
Eriophorum vaginatum	2.25	4.00	1.76	2.83
Kalmia polifolia	0.63	2.77	0.38	1.42
Ledum groenlandicum	0.33	1.26	4.29	3.54
Oxycoccos microcarpus	4.21	3.87	3.05	4.08
Rubus chamaemorus	0.33	1.94	1.76	3.96
Salix pedicellaris	0.00	0.00	1.67	0.00
Vaccinium vitis-idaea	0.13	0.26	3.90	3.21
Vaccinium myrtilloides	0.00	0.00	1.10	0.00
Smilacina trifolia	1.63	2.48	3.86	4.17
Menyanthes trifoliata	0.58	0.00	0.00	0.00
Equisetum spp.	0.00	0.00	2.10	0.00
Empetrum nigrum	0.00	0.00	0.19	0.00
Calamagrostis canadensis	0.00	0.00	1.10	0.00
Scirpus caespitosum	0.00	0.00	0.14	0.00
Carex aquatilis	3.83	1.42	4.52	0.38
Carex paupercula	0.00	0.00	0.62	0.00
Eleocharis acicularis	0.00	0.00	0.19	0.00
Eleocharis palustris	0.00	0.00	0.14	0.00
Carex canescens	0.00	0.00	0.62	0.00
Carex disperma	0.00	0.00	1.38	0.00
Carex limosa	1.38	0.39	0.14	0.00
Carex livida	0.00	0.35	0.00	0.00
Carex media	0.13	0.00	0.00	0.00
Carex utriculata	1.00	0.00	0.52	0.04
Carex pauciflora	0.00	0.26	0.29	0.67
Scheuchzeria palustris	2.38	1.65	0.00	0.13
Picea mariana	1.25	2.68	2.67	3.33
Larix laricina	0.33	0.23	0.24	0.00
Betula papyrifera	0.00	0.00	0.05	0.00
Pinus banksiana	0.00	0.00	0.48	0.00
Alnus rugosa	0.00	0.00	0.10	0.00

Table 2.2. Multiple level indicator species analysis (see methods for details). Indicator values in parenthesis. All reported species were significant p<0.01.



Wet Fen, Fen expanse and Margin		Fen Expanse, Margin and Bog	
A. polifolia (0.97)		*Rubus Chamerous (0.82)*	
Wet Fen and Fen Expanse	Wet Fen and Margin	Fen Expanse and Bog	Margin and Bog
Scheuzeria palustris (0.66)	*Carex aquatilis (0.90)*	*Kalmia polifolia (0.76)*	*Vacinum vitus-ideae (0.94)*
	Polytrichum strichum (0.61)	*Leiomylia anomala (0.71)*	*Ledum groenlandicum (0.88)*
	Carex utriculata (0.44)		*Pleurozium schreberii (0.85)*
	Betula grandulifera (0.40)		*Aulacomnium Palustre (0.85)*
			Cladonia spp *(0.65)*
Wet Fen	Fen Expanse	Margin	Bog
Carex limosa (0.58)	*Sphagnum lindbergii (0.37)*	*Salix pedicalaris (0.87)*	*Dicranum undulatum (0.73)*
Mianthes trifolia (0.41)		*Sphagnum russowii (0.83)*	*Unknown moss 1 (0.45)*
		Equisetum spp. *(0.82)*	
		Polytrichum commune (0.72)	
		Calamagrastis Canadensis (0.62)	

Table 2.3. Summary statistics of all measured parameters throughout the peatland complex, n=100. TN, total nitrogen; DON, dissolved organic nitrogen; DIN, dissolved inorganic nitrogen; DOC, dissolved organic carbon. Asterisks indicate significance; * $p<0.05$, ** $p<0.01$, *** $p<0.001$

	r^2		μ	σ	CV100%	Min	Max	Moran's *I*	
Depth To Water (cm)	0.38	***	14.08	4.87	34.61	6.40	27.80	0.41	***
Shade (%)	0.43	***	10.11	15.94	157.74	0.00	73.50	0.29	***
TN Spring (mg L^{-1})	0.22	***	0.80	0.24	29.91	0.35	1.48	0.12	*
NO_3^- -N Spring (mg L^{-1})	0.07		0.04	0.06	160.51	0.00	0.28	0.16	**
NH_4^+-N Spring (mg L^{-1})	0.05		0.16	0.05	28.15	0.05	0.32	0.27	***
DONSpring (mg L^{-1})	0.31	***	0.60	0.20	33.19	0.21	0.94	0.16	**
DIN Spring (mg L^{-1})	0.04		0.20	0.09	43.70	0.08	0.54	0.16	**
Deuterium excess (‰)	0.20	***	3.66	1.28	35.03	0.61	6.48	0.36	***
Spring DOC (mg L^{-1})	0.10	*	56.60	13.30	23.49	29.30	98.02	0.03	
Fall DOC (mg L^{-1})	0.42	***	57.89	20.19	34.88	25.23	116.25	0.67	***
Fall TN (mg L^{-1})	0.25	***	1.01	0.25	25.23	0.58	1.86	0.36	***
NH_4^+-N Fall (mg L^{-1})	0.02		0.17	0.12	72.32	0.05	0.59	0.13	*
DON+NO_3^--N Fall (mg L^{-1})	0.38	***	0.84	0.19	22.74	0.52	1.33	0.41	***
Spring pH	0.50	***	4.09	0.30	7.22	3.72	5.27	0.24	***
Fall pH	0.56	***	3.93	0.21	5.45	3.67	4.78	0.26	***
Fall reduced conductivity (μS-cm^{-1})	0.07	*	17.92	5.88	32.79	8.31	45.36	0.17	**
Spring reduced conductivity (μS-cm^{-1})	0.14	***	17.52	8.19	46.76	6.84	42.48	0.08	
Richness	0.48	***	17.36	3.71	21.37	8.00	26.00	0.00	
H'	0.47	***	2.78	0.23	8.12	2.03	3.20	0.00	
Pielou's J	0.01		0.98	0.01	0.63	0.96	0.99	-0.01	
Simpson's D	0.44	***	0.93	0.02	1.74	0.86	0.96	0.02	
Shrubs	0.47	***	16.57	3.87	23.36	9.00	27.00	0.23	***
Sedges	0.38	***	8.50	4.82	56.71	0.00	22.00	0.36	***

Table 2.4. Results of One-way ANOVA tests between groups. Values represent means (±SD). An asterisk (*) represents non-parametric Kruskall-Wallis test. See table 2.3 for abbreviations. Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

	F, *χ2	p	Wet Fen	Dry Fen	Margin	Bog
Depth To Water (cm)*	31.25	<0.0001	10.9(3.3)	12.9(3.6)	14.7(4.1)	18.5(4.9)
Shade*	71.47	<0.0001	0.03(.15)	0.9(2.1)	27.2(19.1)	17.1(15.3)
TN Spring (mg/L)	7.25	<0.001	0.64(±.16)	0.78(±.27)	0.95(±.20)	0.83(±.20)
NO_3^- -N Spring (mg/L)*	13.15	0.004	0.02(±0.04)	0.05(±0.08)	0.06(±0.06)	0.02(±0.02)
NH_4^+-N Spring (mg/L)*	18.74	<0.001	0.16(±0.03)	0.17±(0.05)	0.18(±0.05)	0.13(±0.04)
DONSpring (mg/L)*	24.00	<0.0001	0.46(±0.13)	0.56(±0.19)	0.71(±0.17)	0.68(±0.20)
DIN Spring (mg/L)*	19.29	<0.001	0.19(±0.07)	0.22(±0.12)	0.24(±0.07)	0.15(±0.04)
D excess*	12.18	0.007	3.73(±1.39)	3.06(±1.29)	4.12(±1.38)	3.97(±0.71)
Spring TC (mg/L)	1.74	0.161	51.3(±9.8)	59.0(±12.2)	57.5(±16.1)	58.0(±14.5)
Fall TC (mg/L)*	36.90	<0.0001	41.8(±8.9)	59.5(19.2)	53.9(±13.5)	75.2(±20.6)
Fall TN (mg/L)	12.09	<0.0001	0.84(±0.19)	1.03(±0.20)	0.94(±0.17)	1.20(±0.30)
NH_4^+-N Fall (mg/L)*	14.45	0.002	0.14(±.11)	0.20(±0.14)	0.12(±0.08)	0.20(±0.13)
DON+ NO_3^- -N Fall (mg/L)	14.85	<0.0001	0.070(±0.09)	0.83(±0.15)	0.82(±0.14)	1.00(±0.22)
Spring pH*	24.85	<0.0001	4.15(±2.6)	4.00(±0.16)	4.33(±0.43)	3.94(±0.14)
Fall pH*	44.27	<0.0001	4.00(±0.16)	3.82(±0.12)	4.14(±0.28)	3.82(±0.09)
Fall reduced conductivity (µS-cm^{-1})*	3.47	0.325	18.3(±7.6)	16.7(±5.6)	17.9(±5.6)	19.1(±4.5)
Spring reduced conductivity (µS-cm^{-1})*	10.87	0.012	15.4(±6.9)	17.9(±8.5)	23.1(±9.9)	14.3(±4.4)
Richness	30.87	<0.0001	13.8(±2.6)	16.8(±3.1)	21.4(±2.4)	18.0(±2.4)
H'*	47.51	<0.0001	2.6(±0.2)	2.7(±0.2)	3.0(±0.1)	2.8(±0.1)
Pielou's J	0.59	0.621	0.98(±0.01)	0.98(±0.01)	0.98(±0.01)	0.98(±0.01)
Simpson's D*	46.66	<0.0001	0.92(±0.02)	0.93(±0.01)	0.94(±0.01)	0.94(0.01)
Shrubs	26.40	<0.0001	12.7(±2.0)	16.1(±2.9)	17.9(±3.7)	19.9(±2.9)
Sedges	20.70	<0.0001	11.0(±3.8)	8.3(±3.6)	11.5(±4.8)	3.7(±3.2)

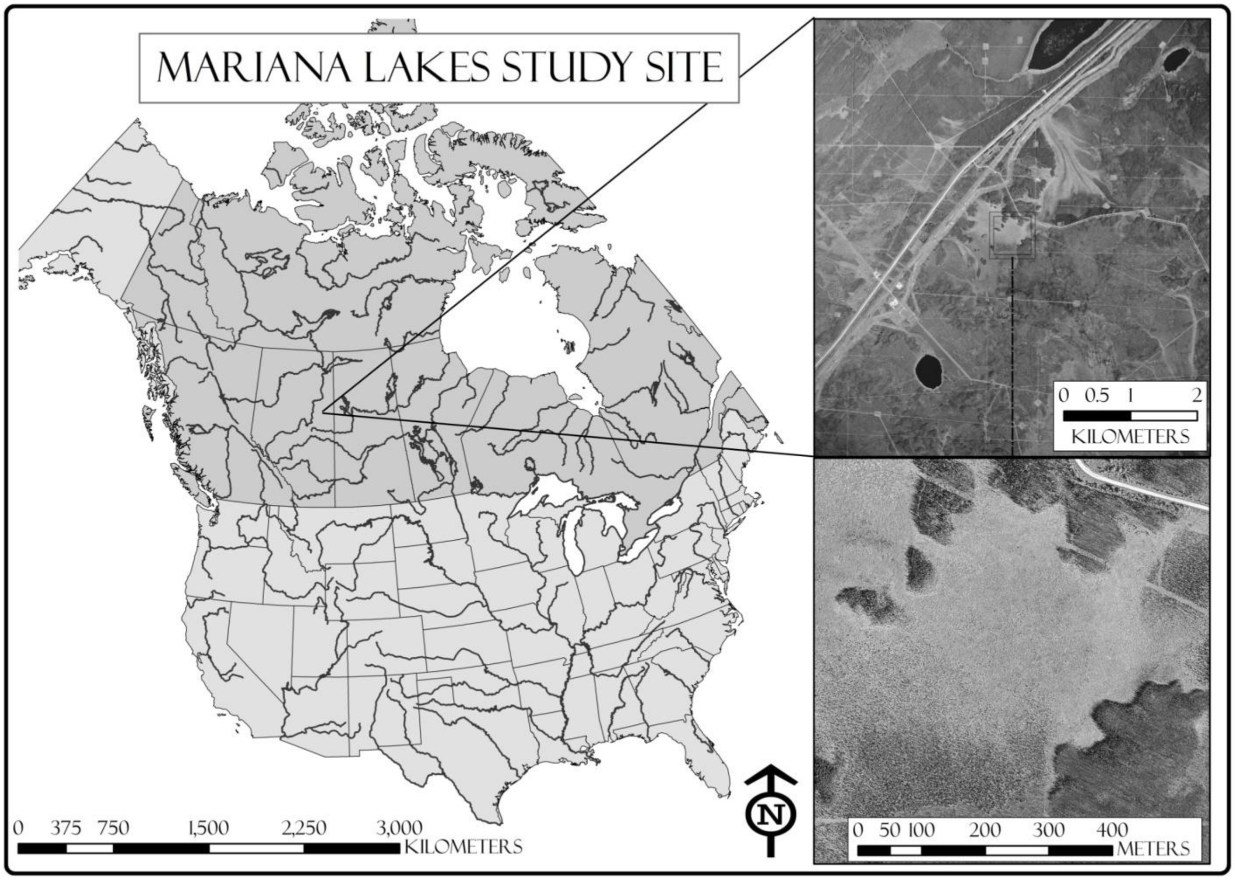


Figure 2.1. Location of study site and aerial photos of surrounding features. Screenshot used by permission. Copyright © 2012 Esri and its data providers. All rights reserved. Base map data source: ESRI ArcWorld Supplement. Aerial photos obtained from Alberta Environment and Sustainable Resource Development: Air Photo Distribution 2010. Map prepared by J. Graham.

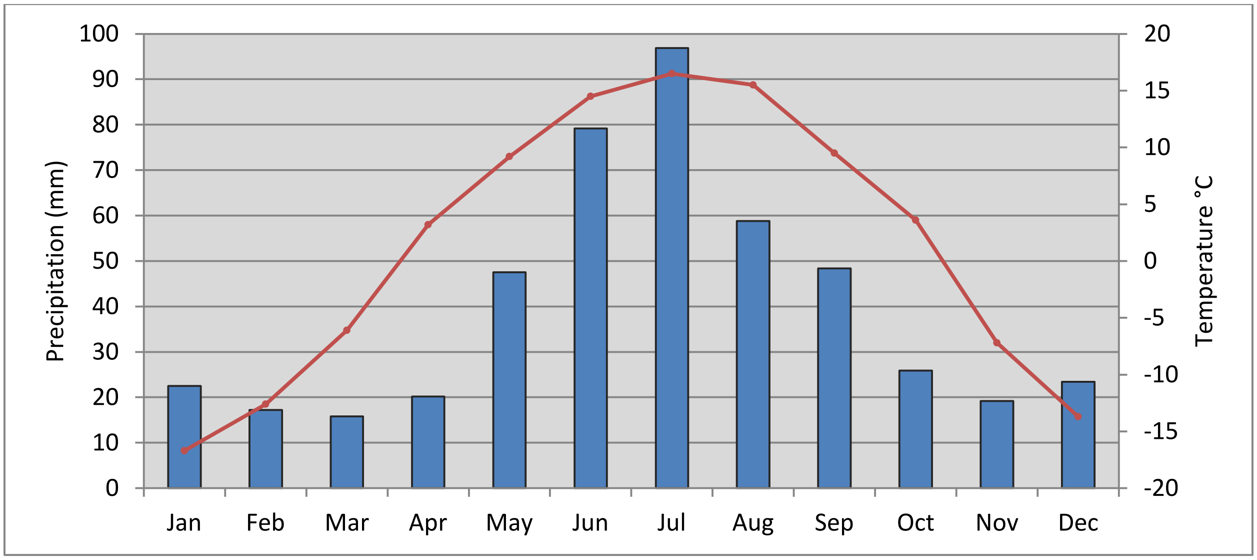


Figure 2.2. Monthly climate normals from Wabasca AB, 1971-2000. Data obtained from Canada National Climate Data and Information Archive.

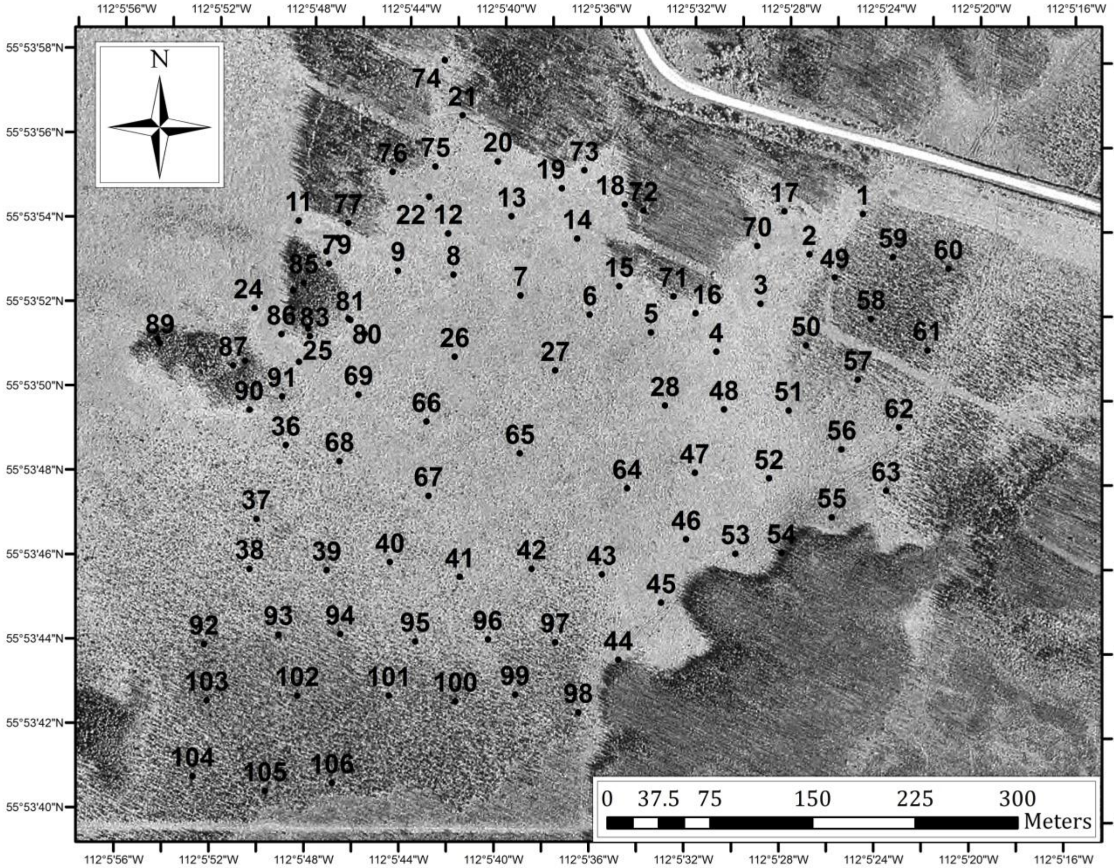


Figure 2.3. 100 point sampling scheme at the Mariana Lake peatland complex. Points 29-31 and 33-35 were initially placed on upland islands and later excluded from all analysis, hence the last point ID is 106. Lightly textured area in center of map is fen, darker textures bog, and heavily textured areas in SE and N of photo are burnt upland. Access road found in the NE of photo. Aerial photo obtained from Alberta Environment and Sustainable resource division: Air Photo Distribution.

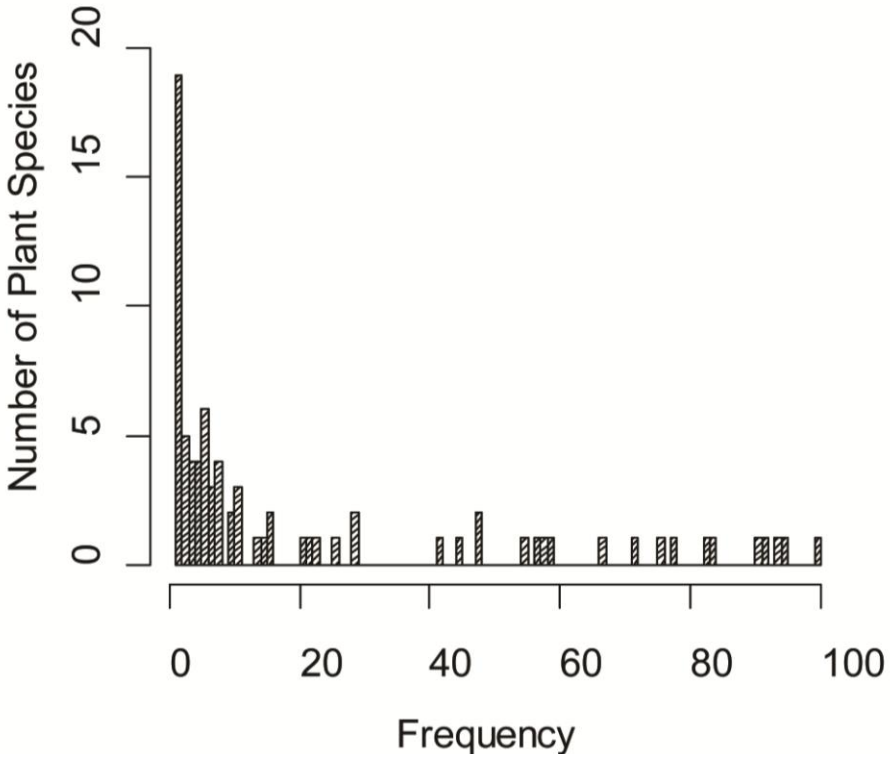


Figure 2.4. Histogram of plant frequencies found in the 100 plots in the Mariana Lake peatland complex.

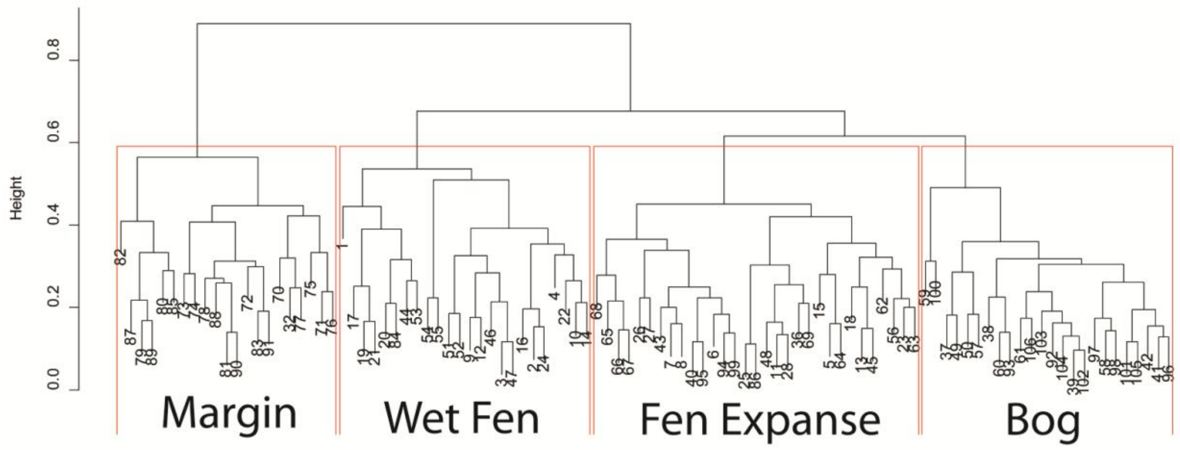


Figure 2.5. Dendrogram of the 100 plots in the Mariana Lake peatland complex based on Bray-Curtis dissimilarities. Overlain with cluster groups created at 0.6 dissimilarity by complete linkage cluster analysis. (See methods for details).

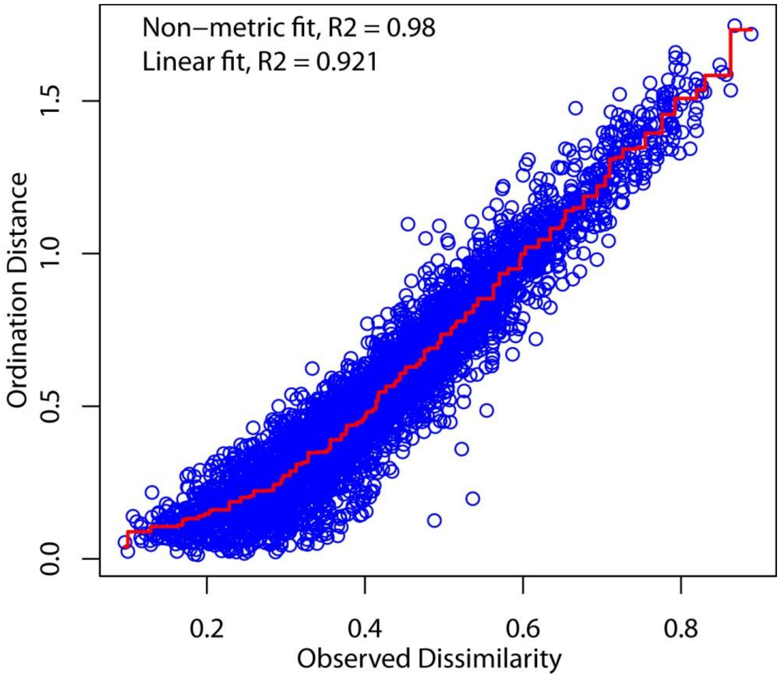


Figure 2.6. Sheppard’s diagram representing the fit of the NMDS ordination of the 100 plots based on Bray-Curtis dissimilarities in the Mariana Lake peatland complex.

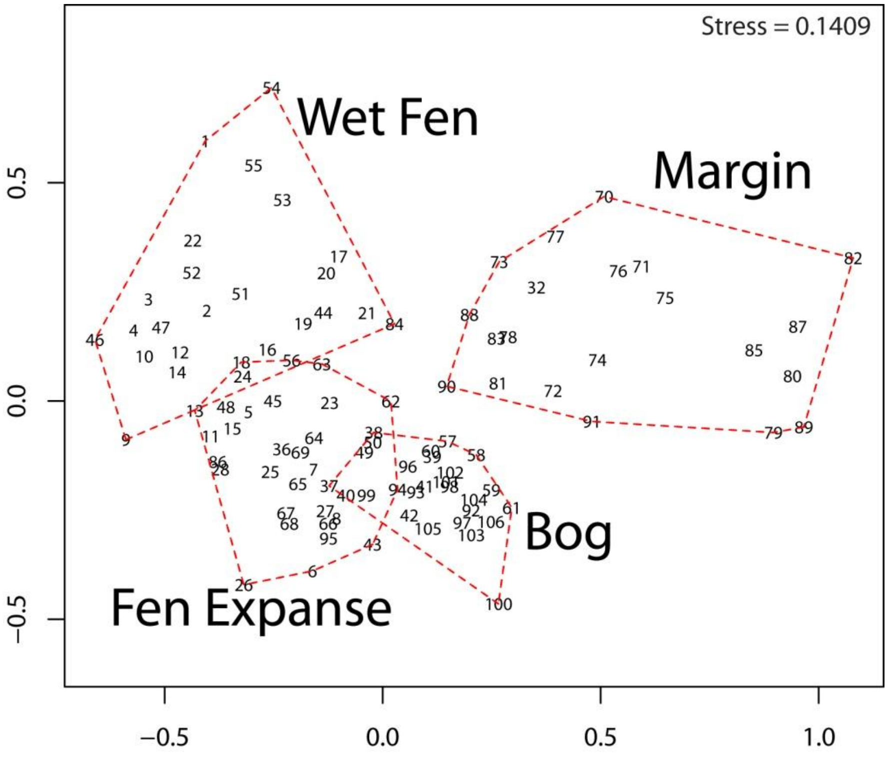


Figure 2.7. NMDS ordination of the 100 plots in the Mariana Lake peatland complex, with points labeled as plot IDs. Ordination based on Bray-Curtis dissimilarity. Data was not standardized. Groups defined by complete linkage cluster analysis bordered by dashed red lines.

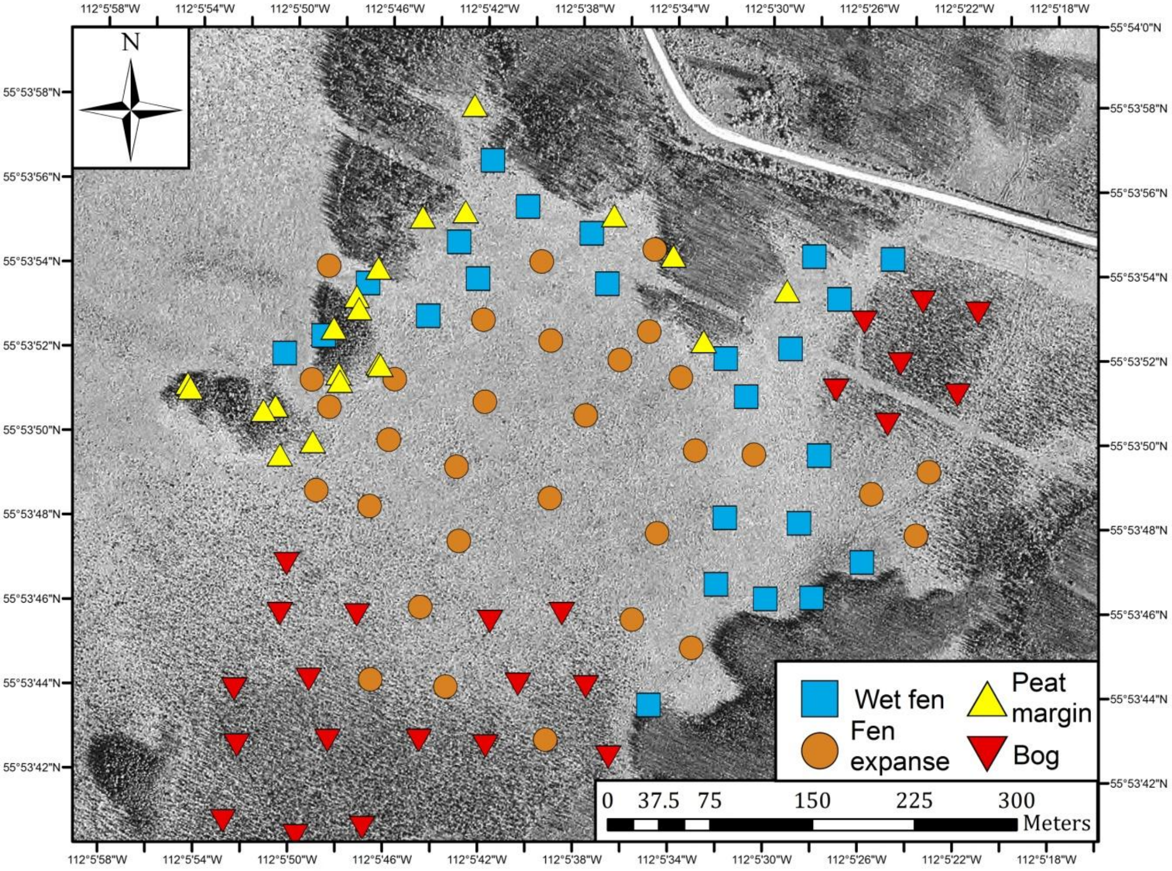


Figure 2.8. Spatial arrangement of the four communities created by complete linkage cluster analysis of the 100 plots in the Mariana Lake peatland complex.

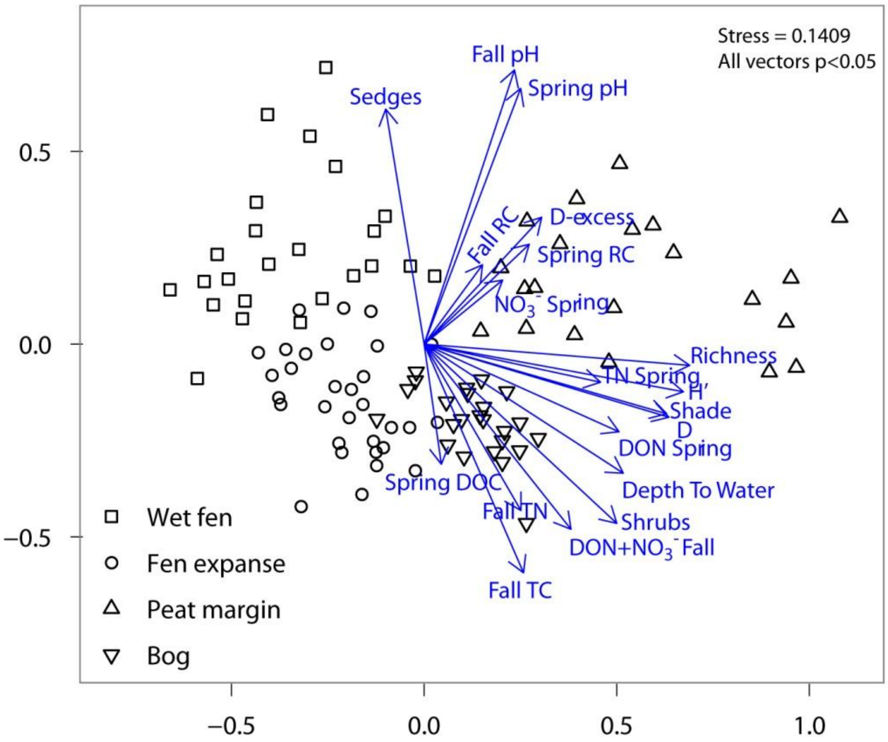


Figure 2.9. NMDS ordination of the 100 plots in the peatland complex, with symbols representing the groups defined by complete linkage cluster analysis. Ordination based on Bray-Curtis dissimilarity. Overlain by significant environmental vectored fit to the ordination. Data were not standardized. Abbreviations are; D, Simpson's Diversity; DOC, dissolved organic carbon; TN, total dissolved nitrogen; DON, dissolved organic nitrogen; NO_3^-, nitrate; H', Shannon-Wiener diversity; RC, reduced conductivity.

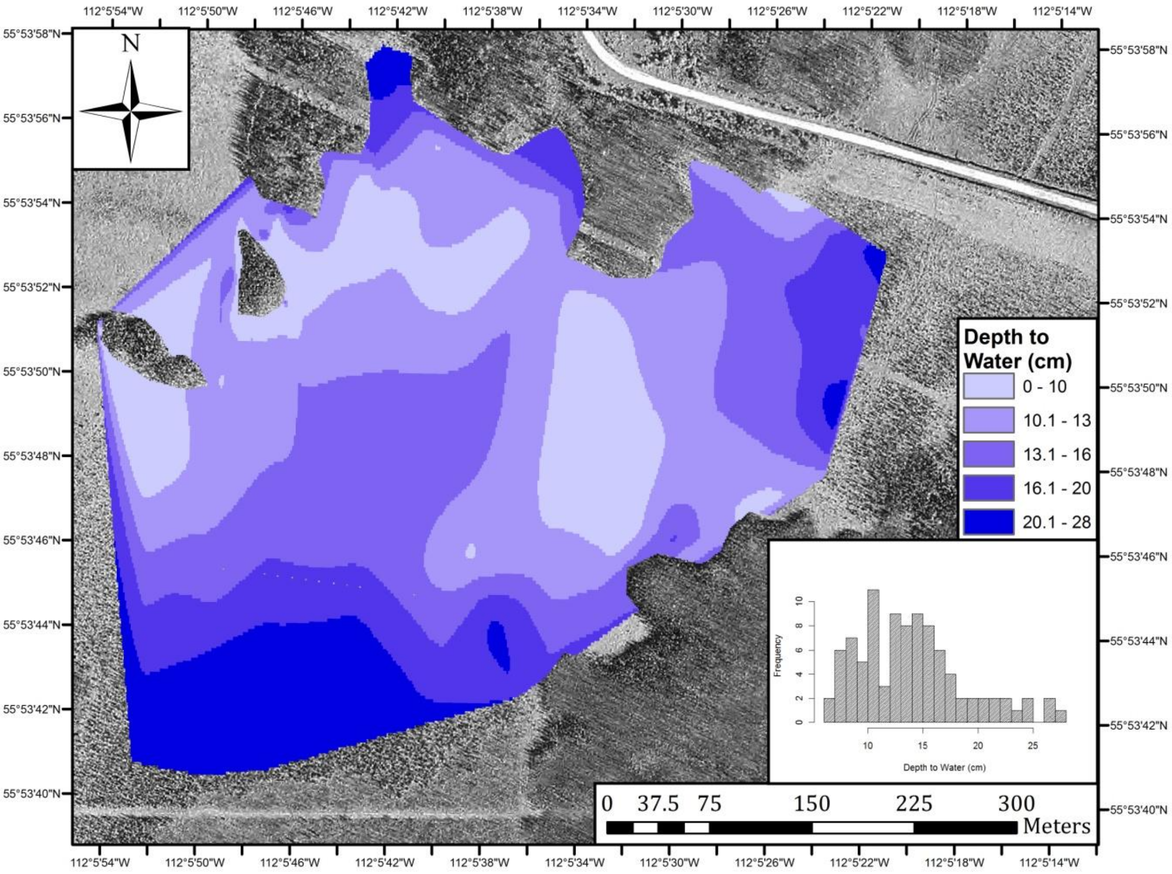


Figure 2.10. Map of mean depth to water measurements from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

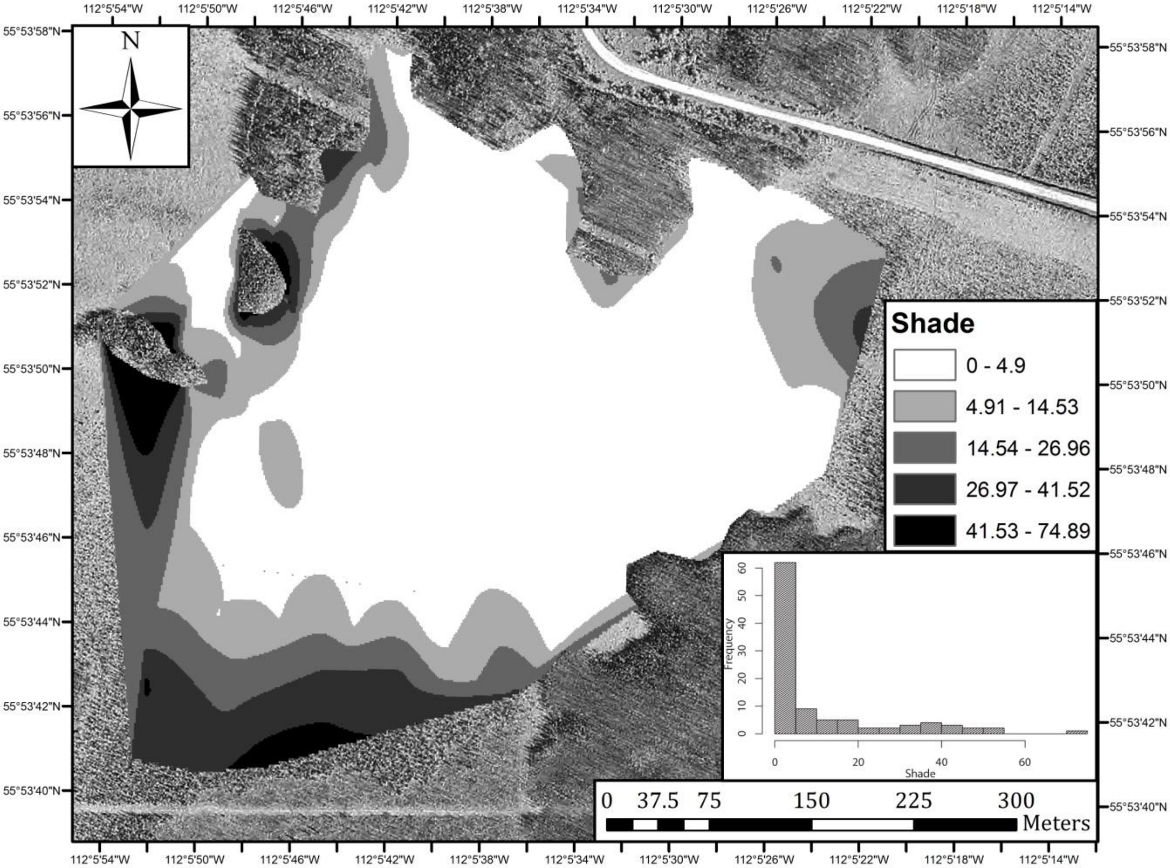


Figure 2.11. Map of shade (%) measurements from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

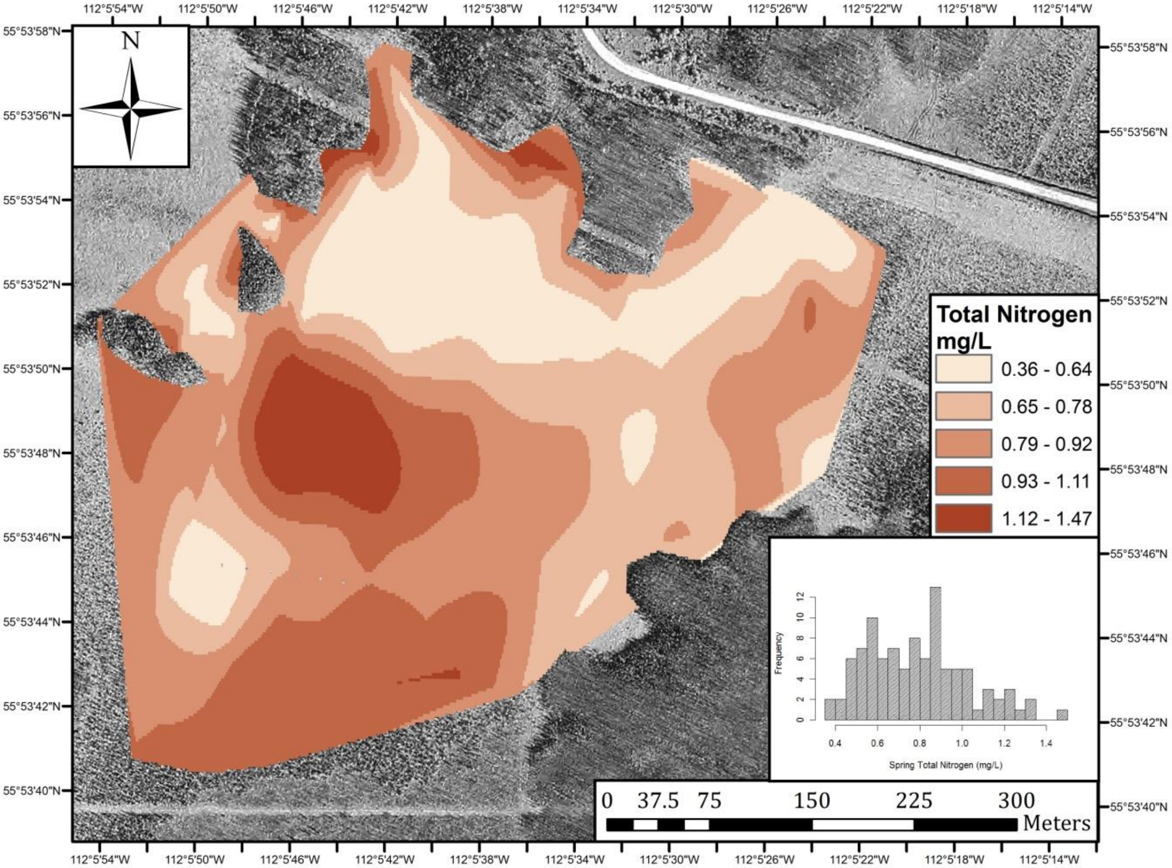


Figure 2.12. Map of pore water total dissolved nitrogen (mg L^{-1}) in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

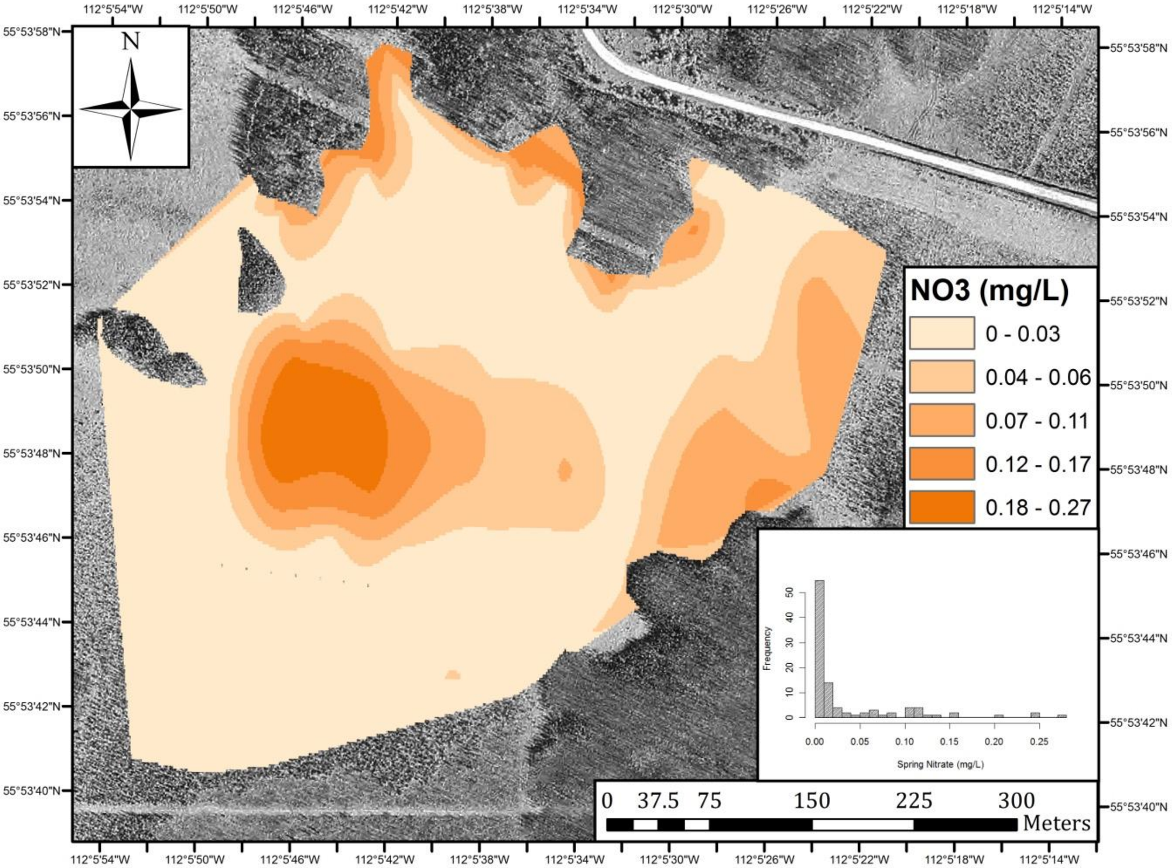


Figure 2.13. Map of pore water NO_3^--N (mg L^{-1}) in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

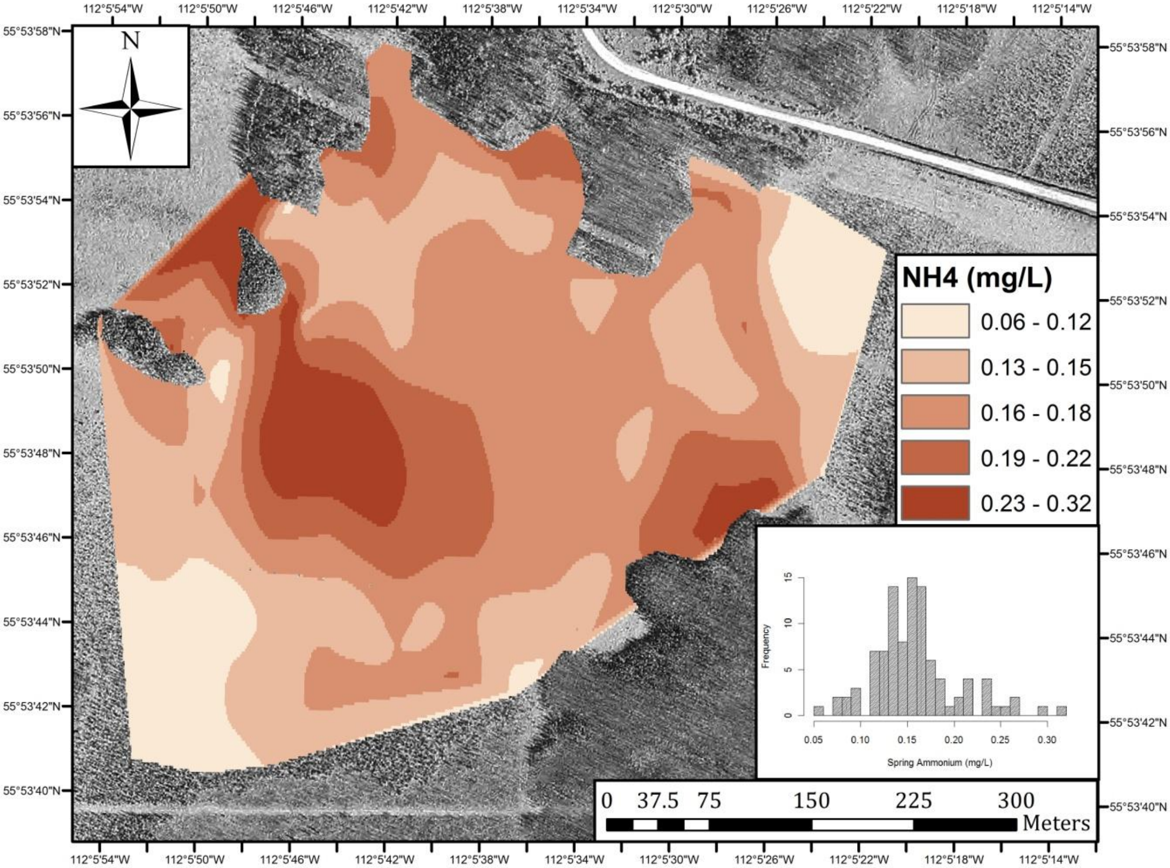


Figure 2.14. Map of pore water NH_4^+-N (mg L^{-1}) in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

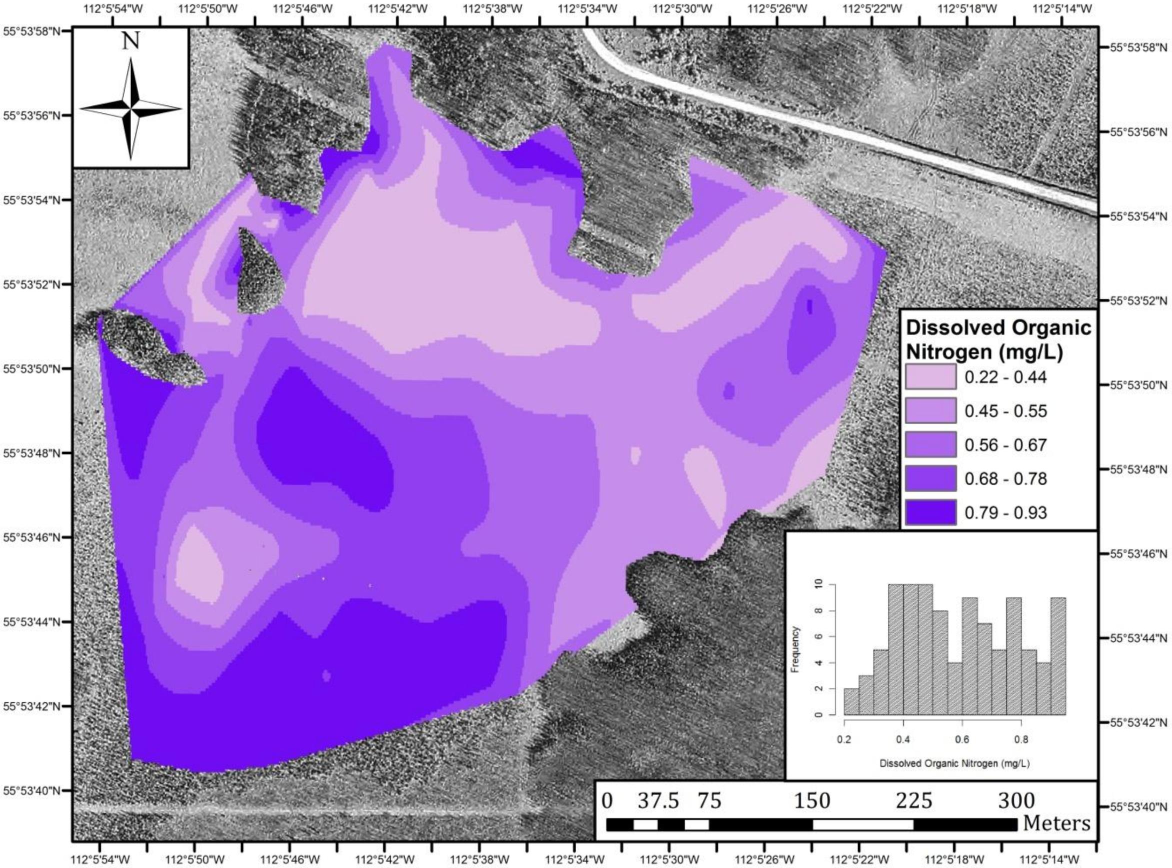


Figure 2.15. Map of pore water dissolved organic nitrogen (mg L^{-1}) in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

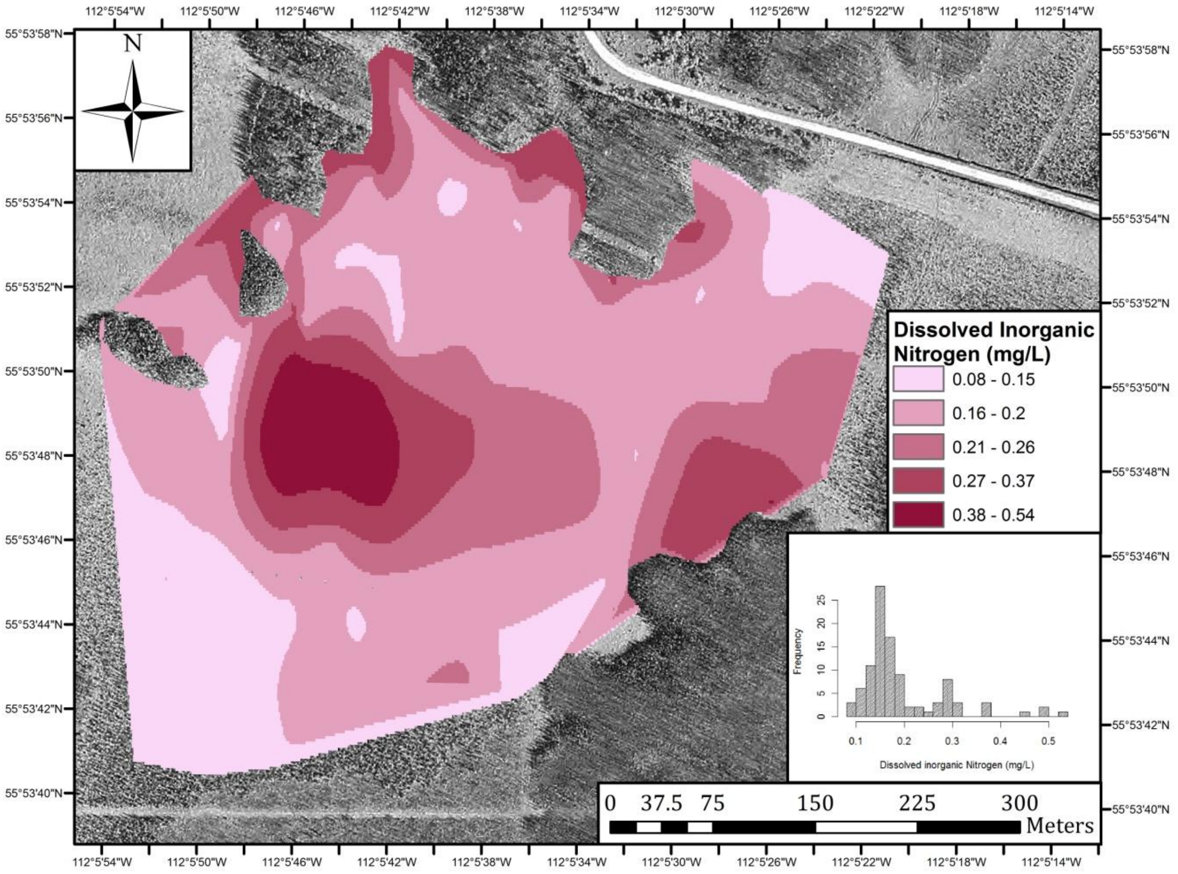


Figure 2.16. Map of pore water dissolved inorganic nitrogen (mg L^{-1}) in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

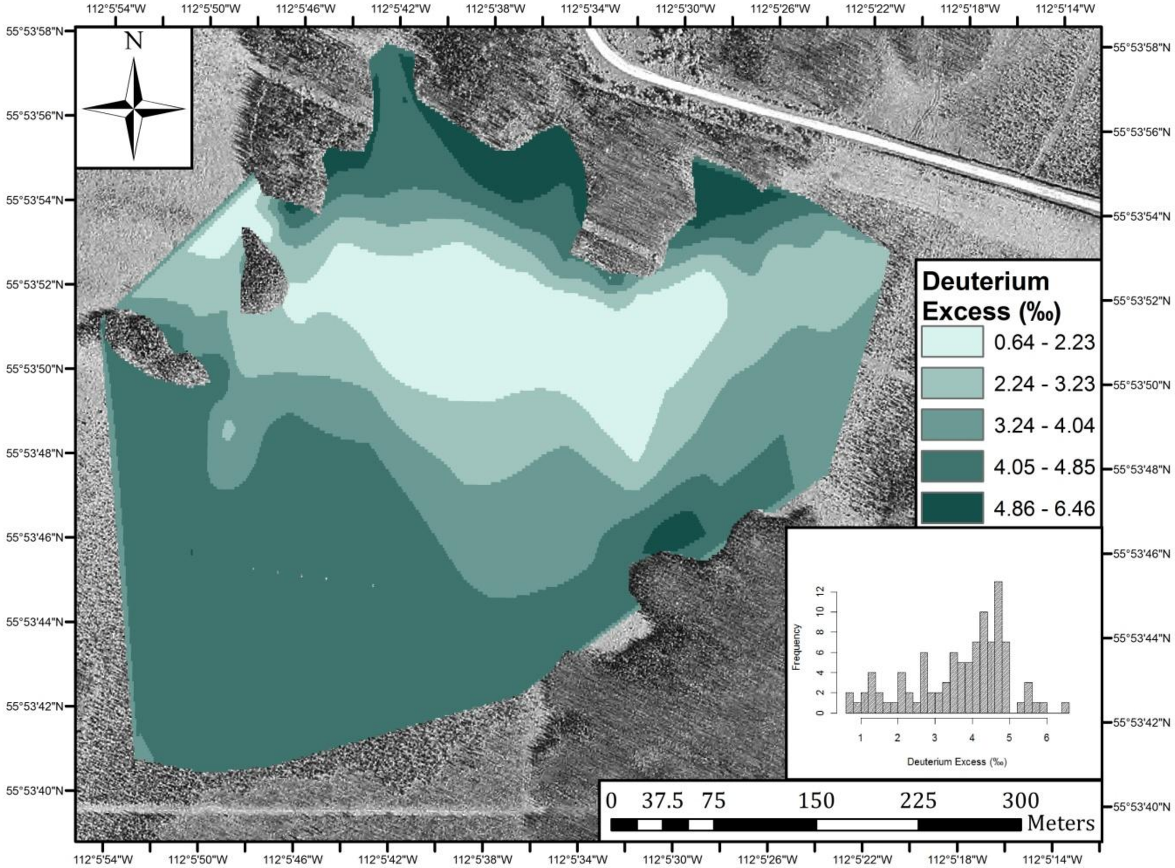


Figure 2.17. Map of pore water deuterium excess (‰) in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

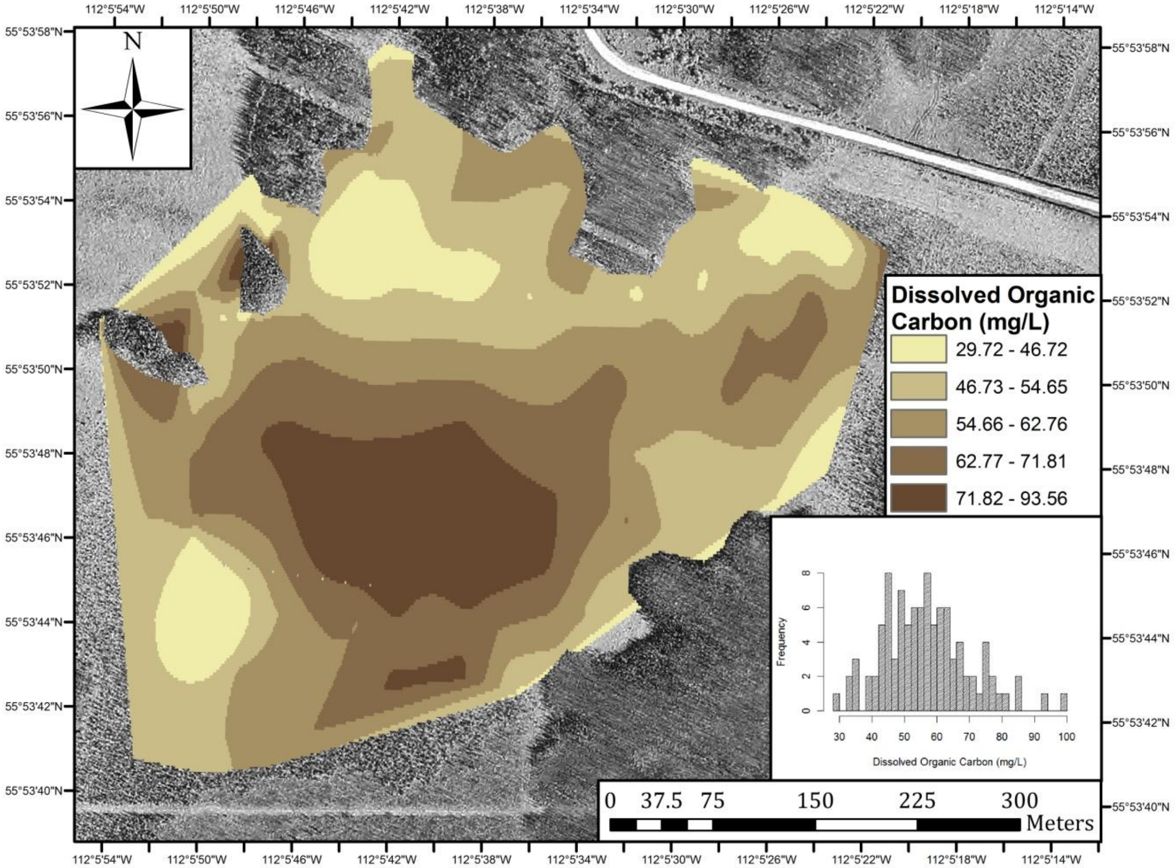


Figure 2.18. Map of pore water dissolved organic carbon (mg L^{-1}) in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

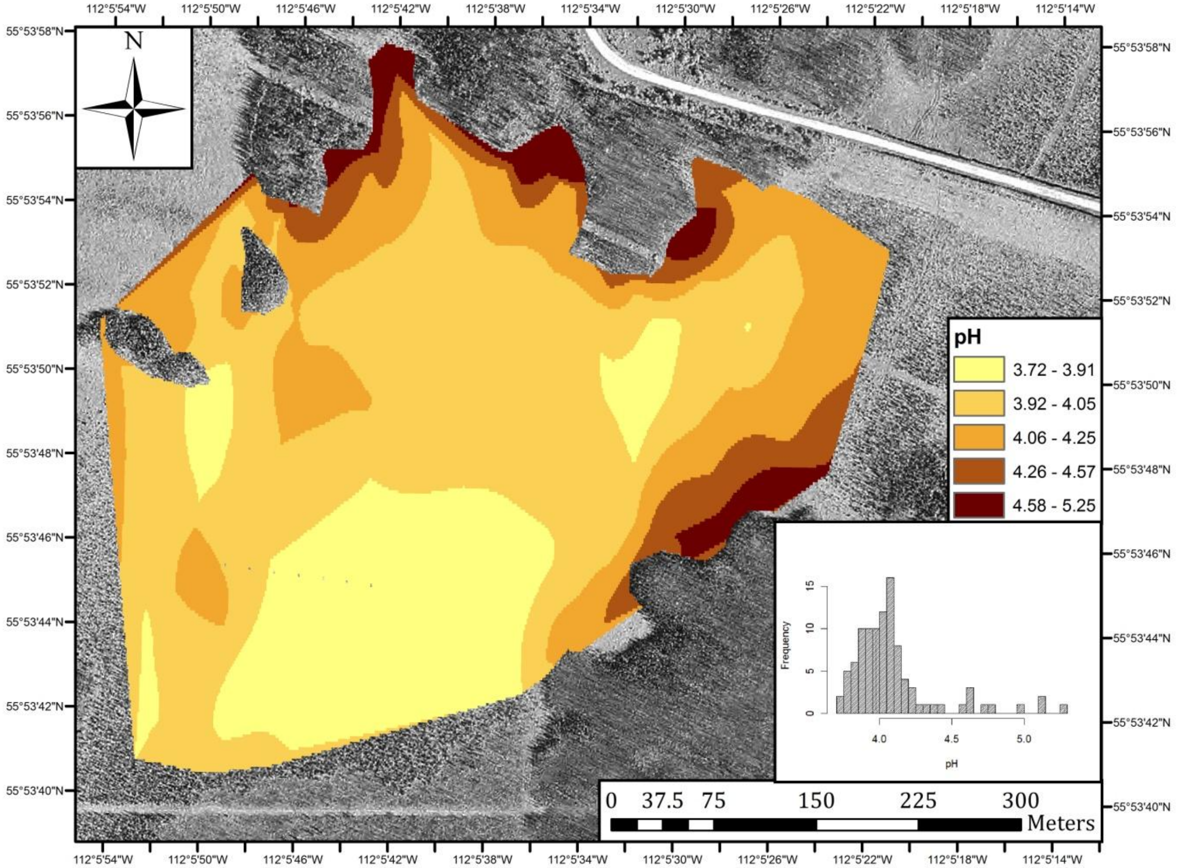


Figure 2.19. Map of pH in spring 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

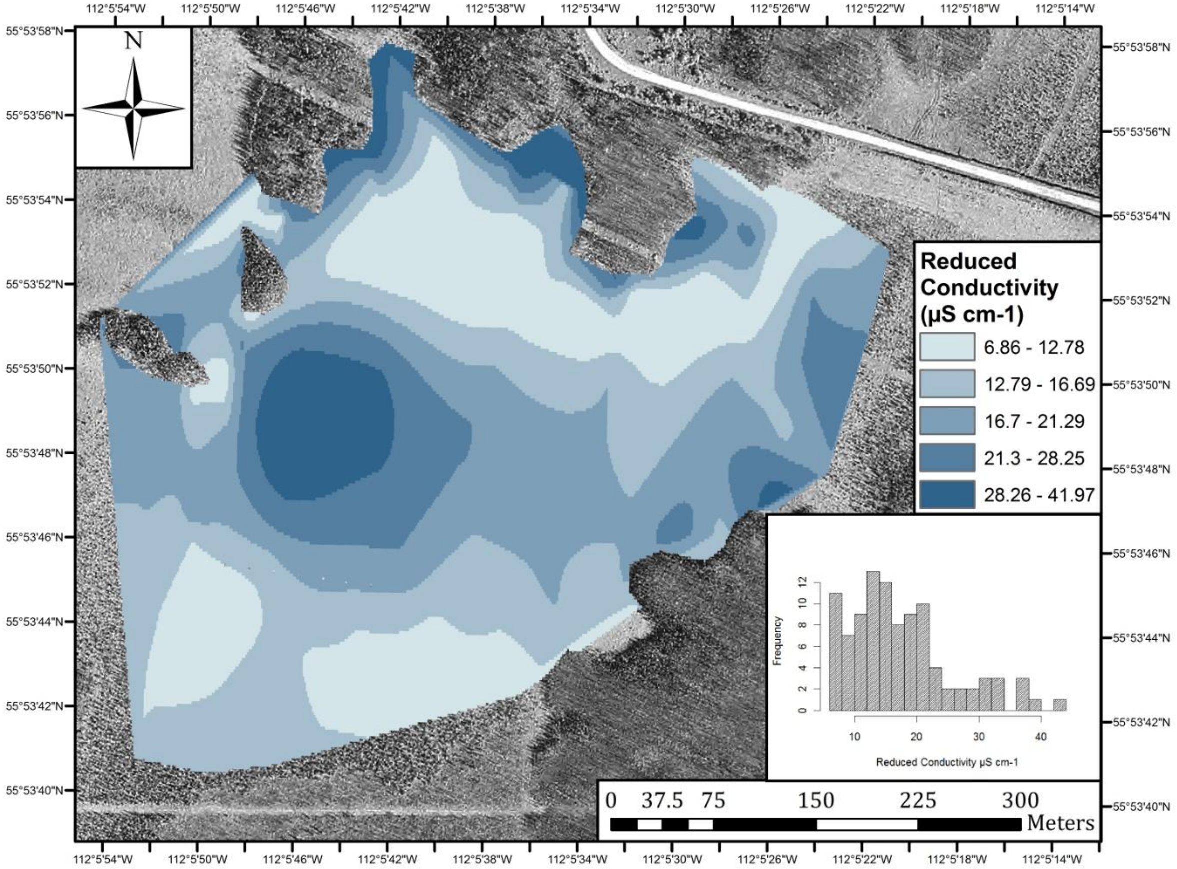


Figure 2.20. Map of pore water reduced conductivity (µS cm^{-1}) in spring from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

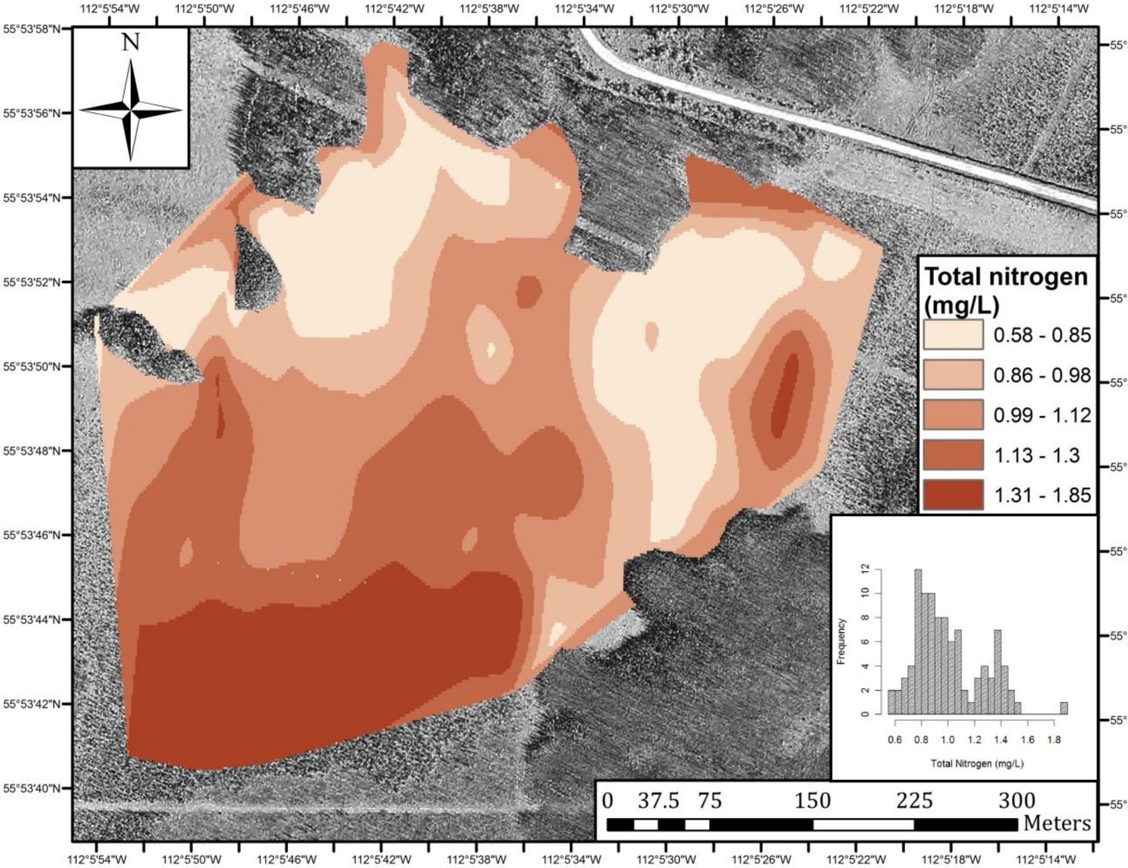


Figure 2.21. Map of pore water total dissolved nitrogen (mg L^{-1}) in fall 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

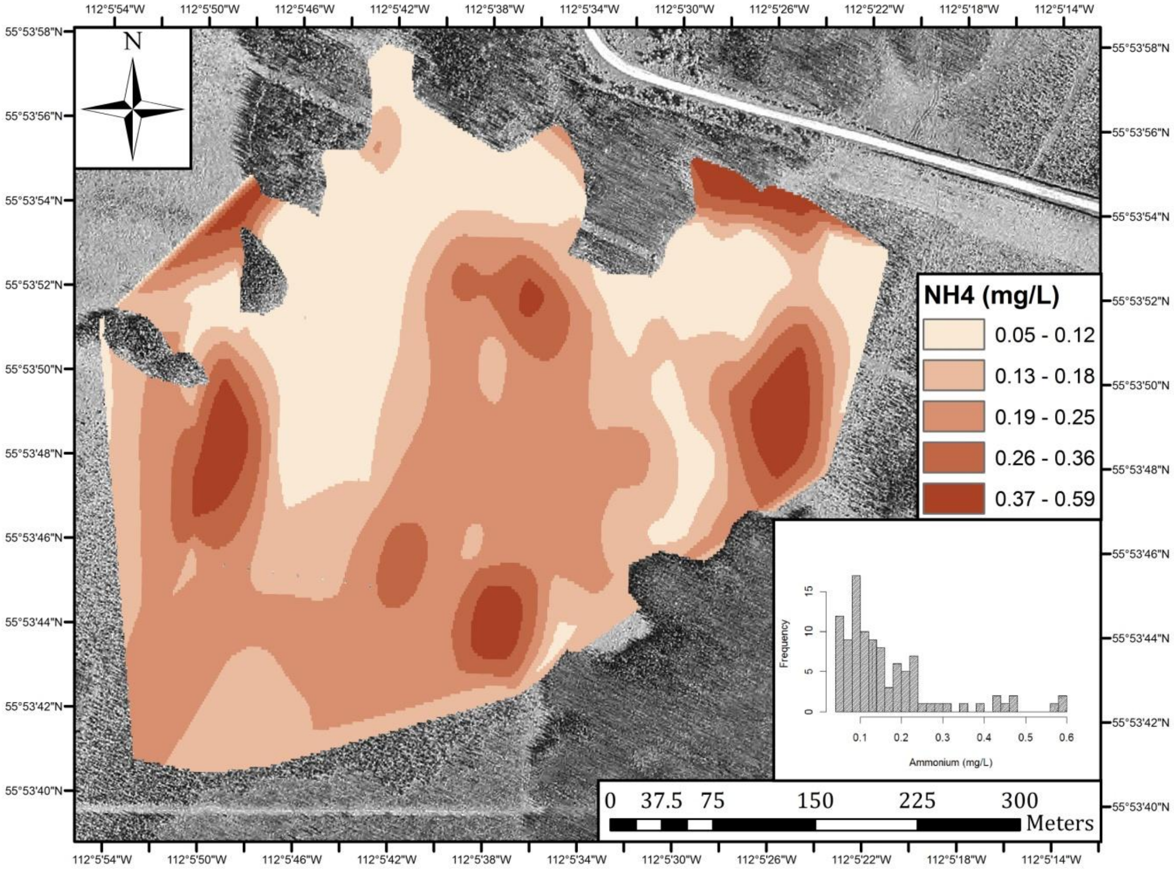


Figure 2.22. Map of pore water NH_4^+-N (mg L^{-1}) in fall 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

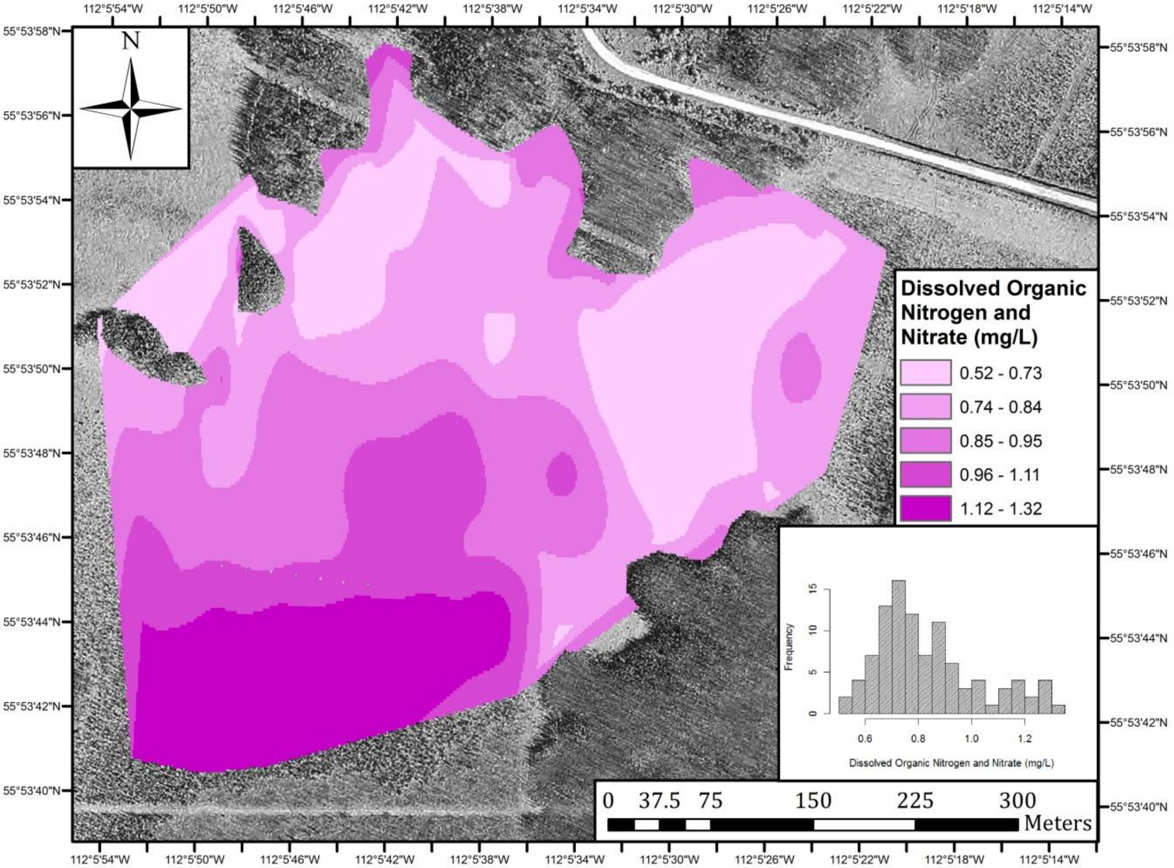


Figure 2.23. Map of pore water dissolved organic nitrogen, plus trace amounts of NO_3^--N (see methods) (mg L^{-1}) in fall 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

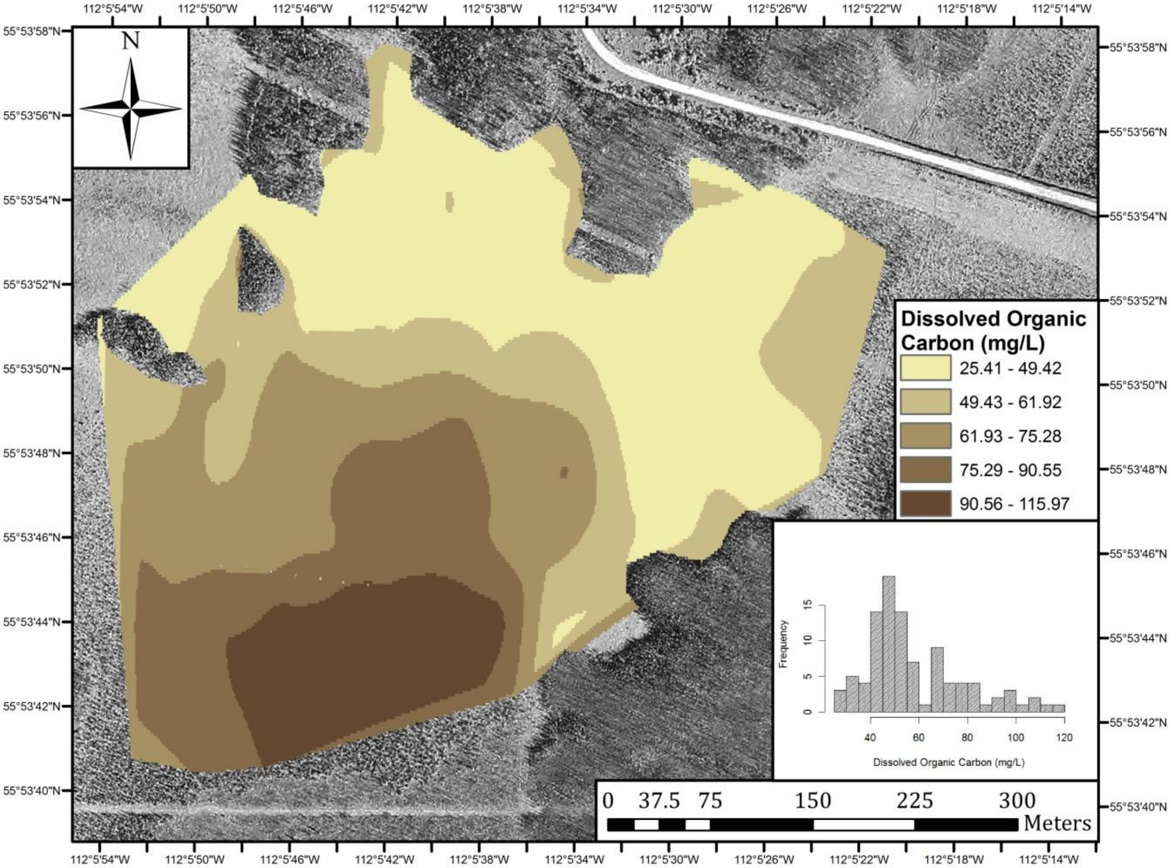


Figure 2.24. Map of pore water dissolved organic carbon (mg L^{-1}) in fall 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

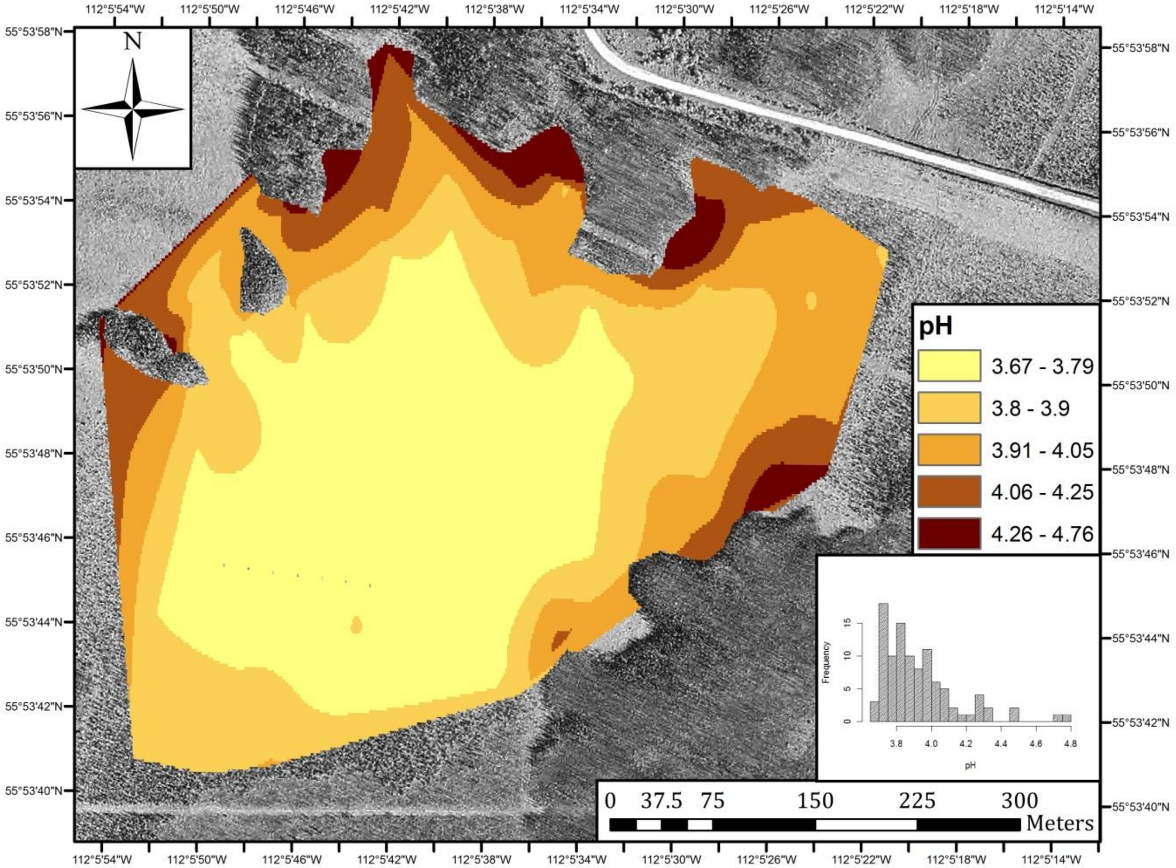


Figure 2.25. Map of pore water pH in fall 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

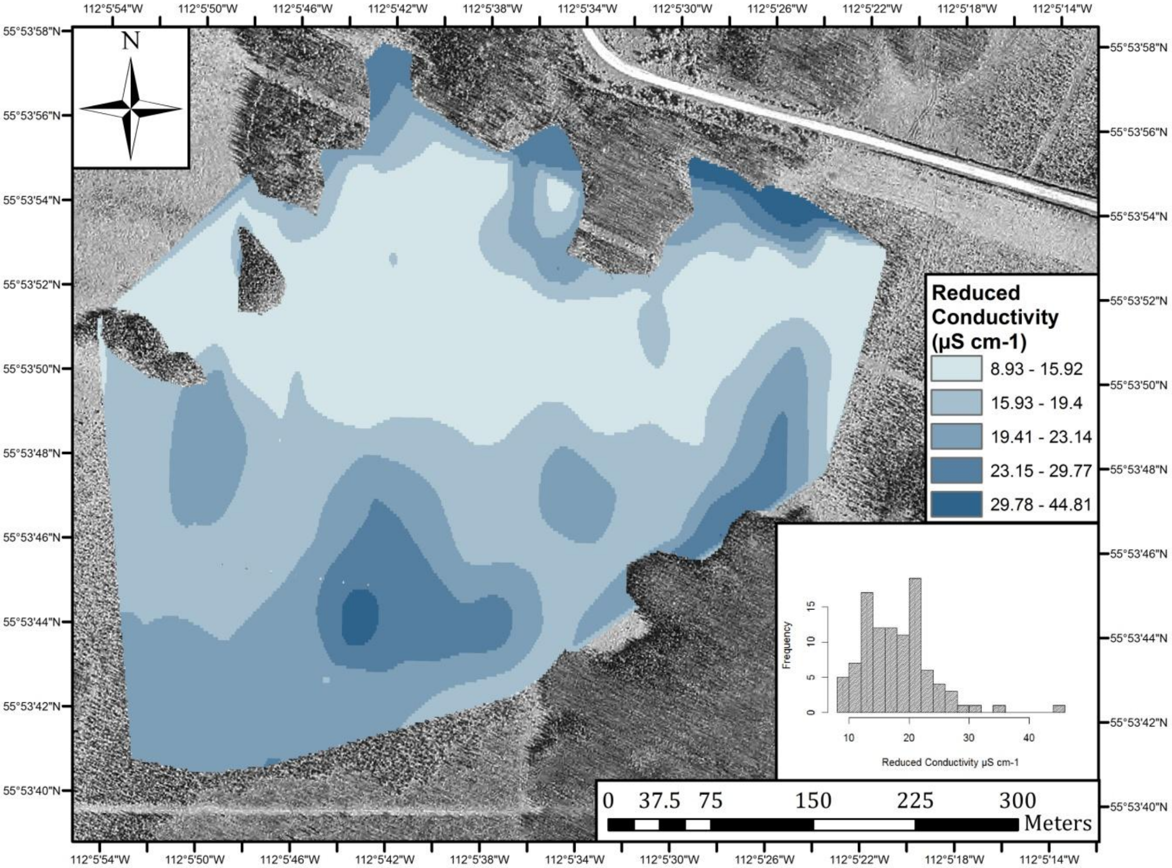


Figure 2.26. Map of pore water reduced conductivity (µS cm^{-1}) in fall 2010 from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

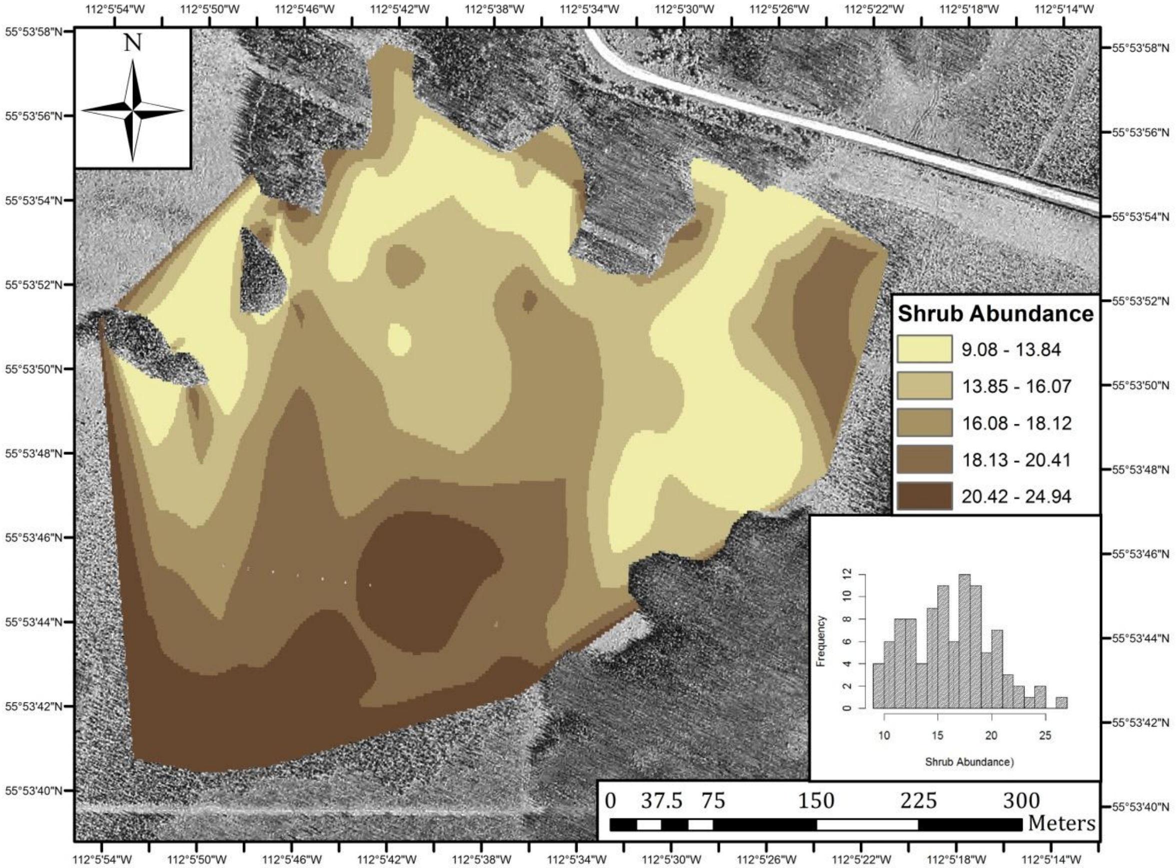


Figure 2.27. Map of shrub abundance from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

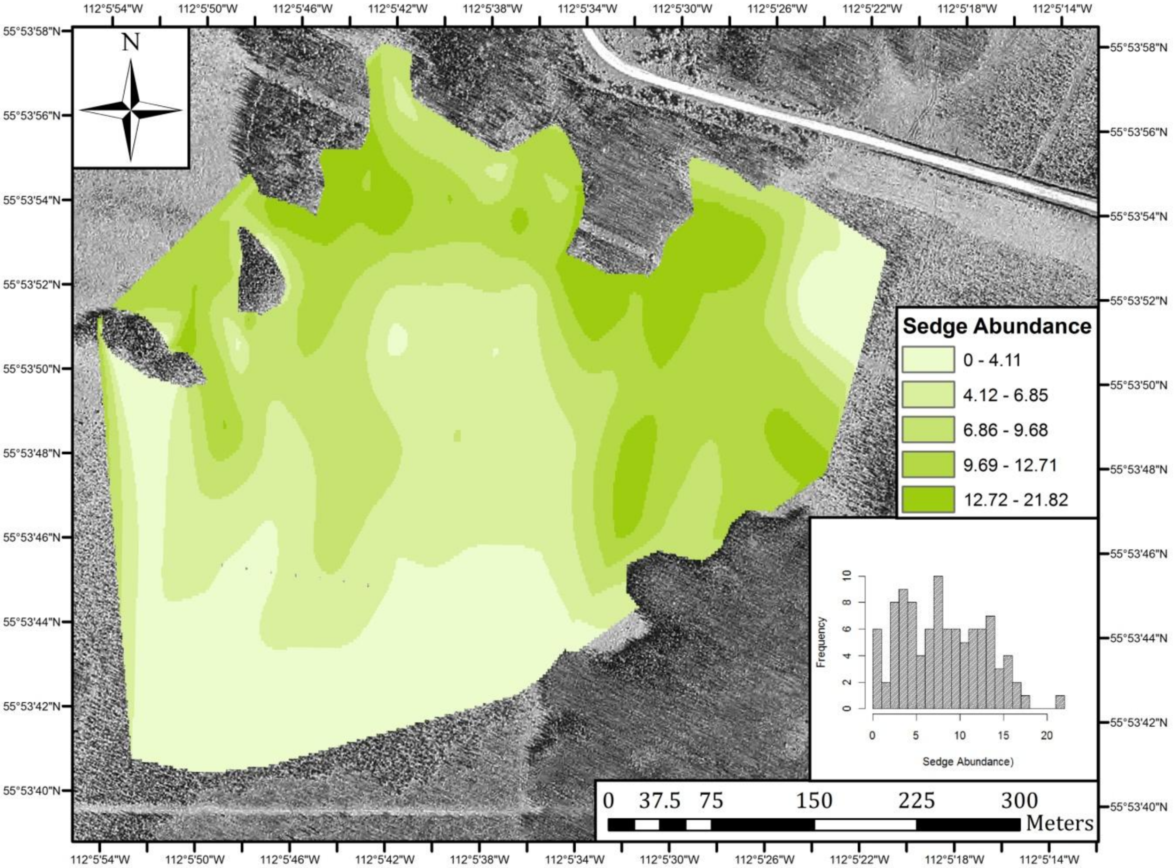


Figure 2.28. Map of sedge abundance from the 100 sample plots from the Mariana Lake peatland complex. Continuous surface created by nearest neighbor interpolation and classified into five classes using Jenks' natural breaks. Imbedded is frequency histogram of the 100 measurements.

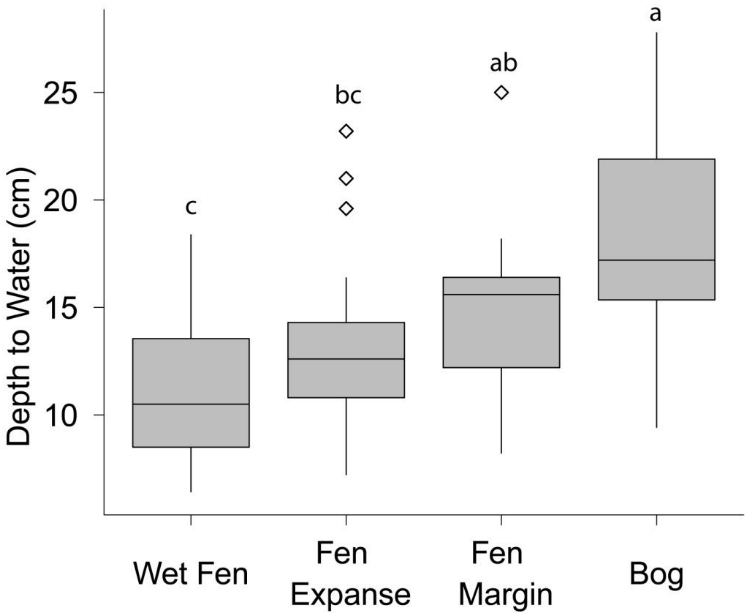


Figure 2.29. Mean depth to water (cm) for the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups ($p<0.05$). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

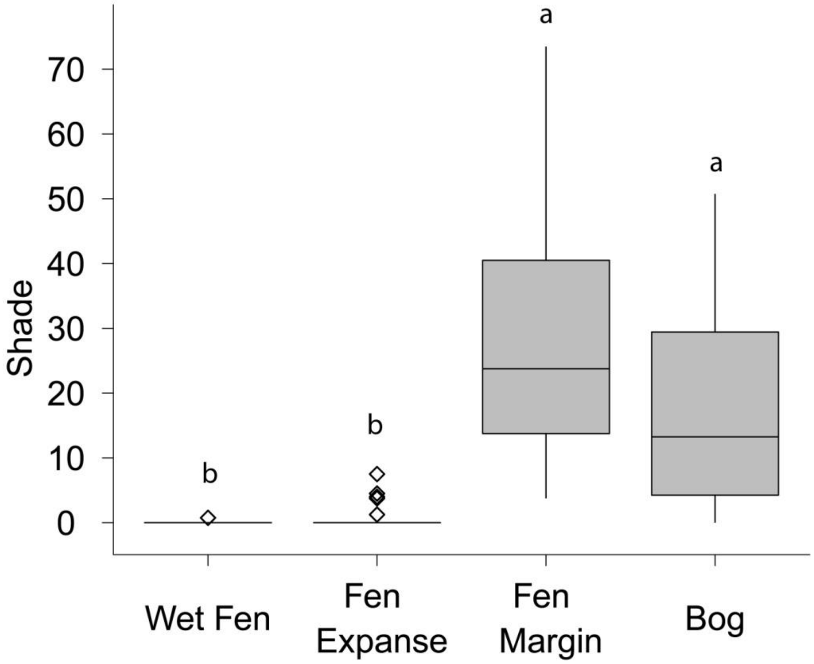


Figure 2.30. Shade measurements (%) for the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups ($p<0.05$). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

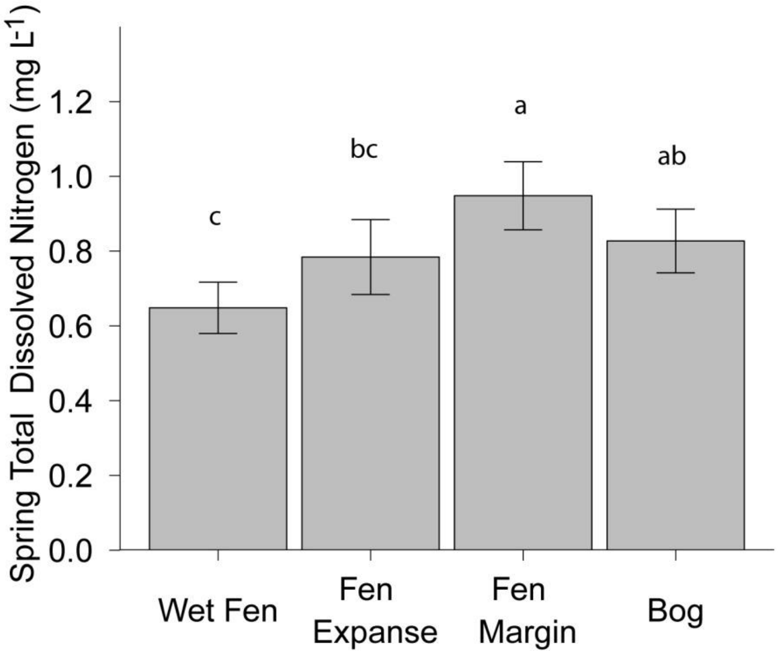


Figure 2.31. Spring 2010 total nitrogen (mg L^{-1}) from the pore water in the plots from the four groups derived from cluster analysis. Bars represent means ± SE. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

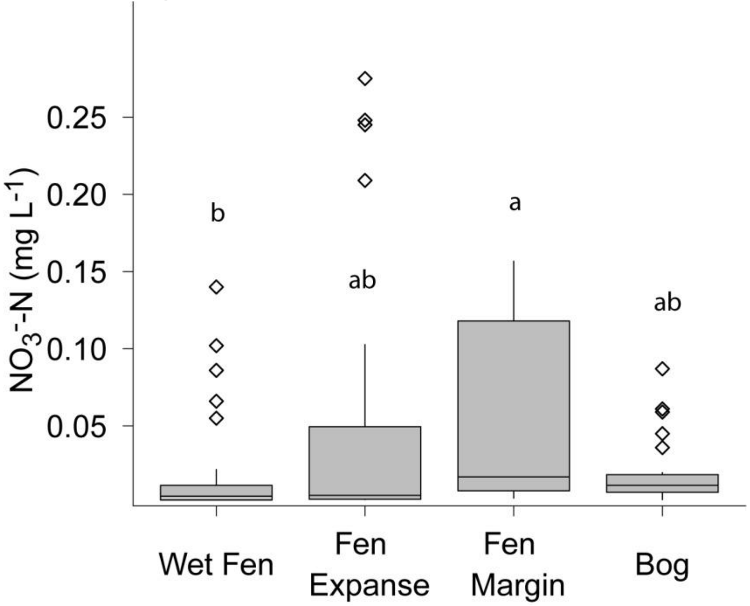


Figure 2.32. Spring 2010 NO_3^--N (mg L^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

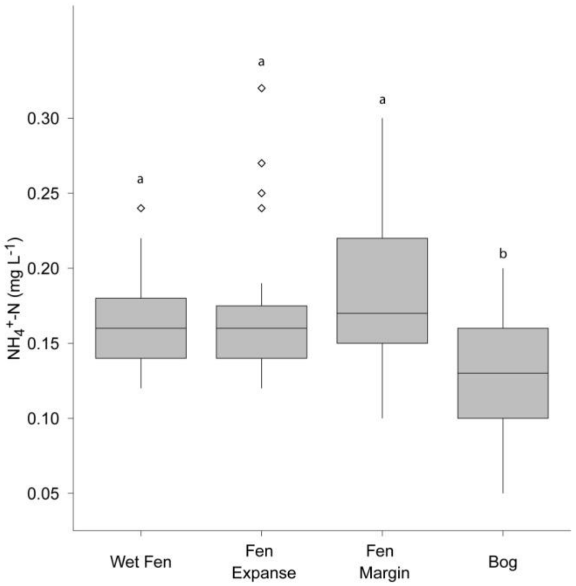


Figure 2.33. Spring 2010 NH_4^+-N (mg L^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is Q_3 - Q_1. Different letters indicate significant differences between groups (*p*<0.05) Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

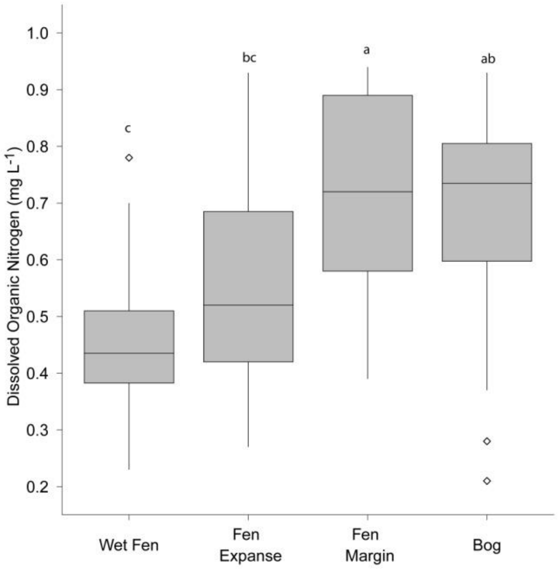


Figure 2.34. Spring 2010 dissolved organic nitrogen (mg L^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is Q_3 - Q_1. Different letters indicate significant differences between groups (*p*<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

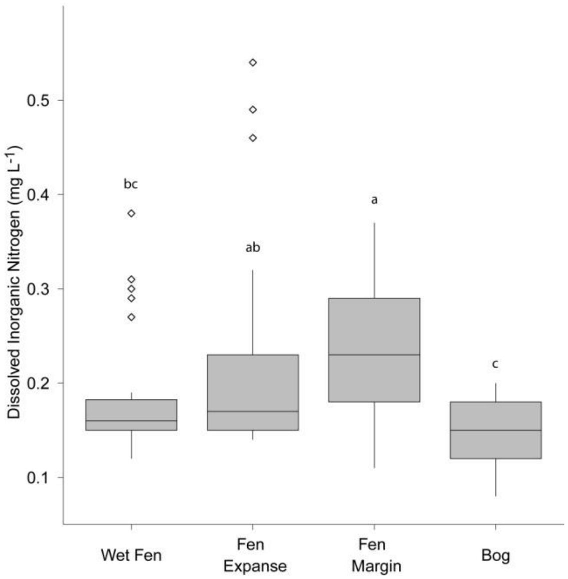


Figure 2.35. Spring 2010 dissolved inorganic nitrogen (mg L^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

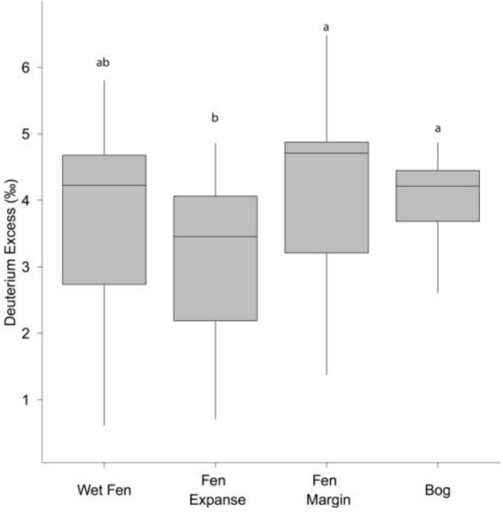


Figure 2.36. Spring 2010 deuterium excess (‰) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

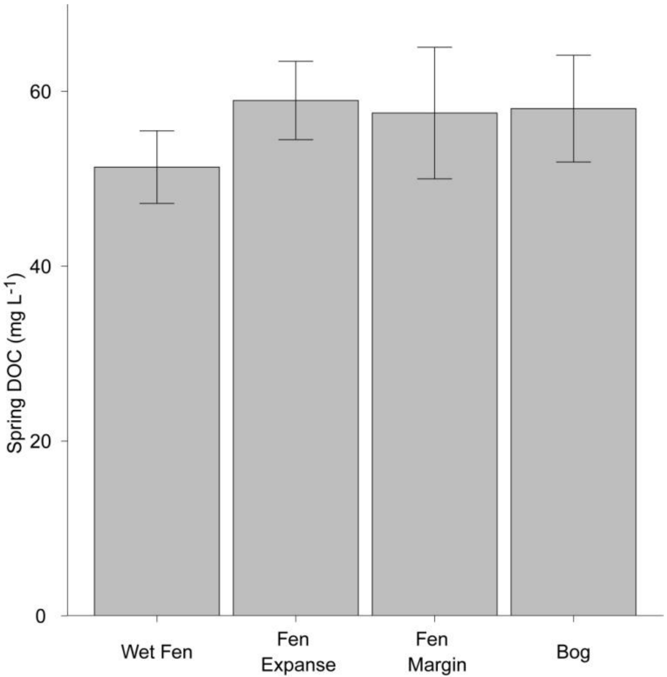


Figure 2.37. Spring 2010 total carbon (mg L^{-1}) from the pore water in the plots from the four groups derived from cluster analysis. Bars represent means ± SE. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

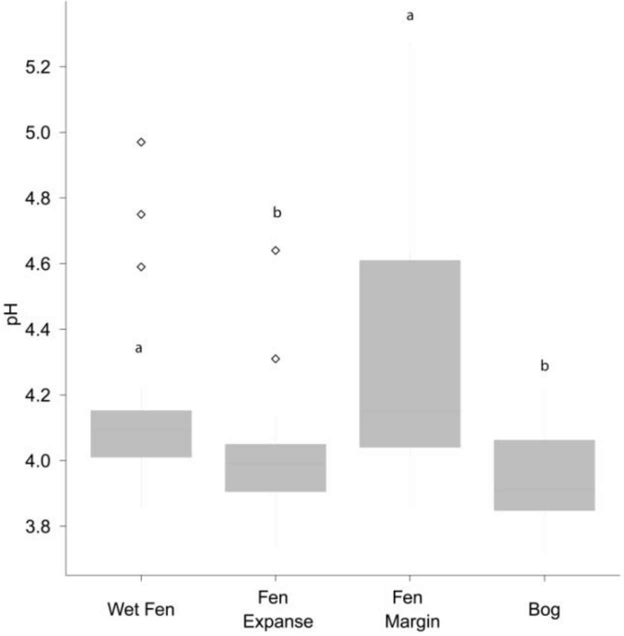


Figure 2.38. Spring 2010 pH from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

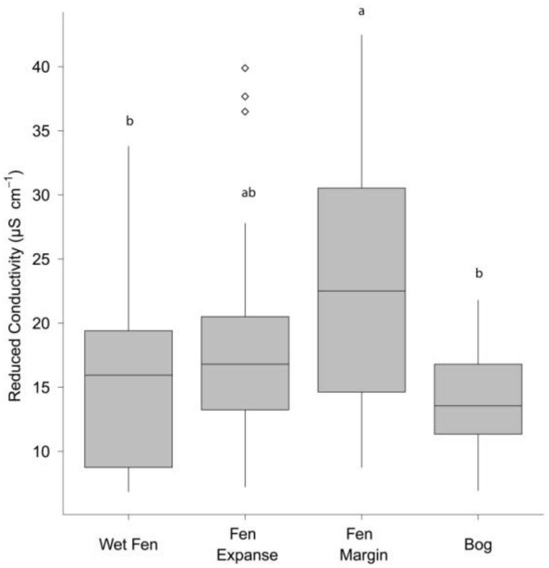


Figure 2.39. Spring 2010 reduced conductivity (µS cm^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

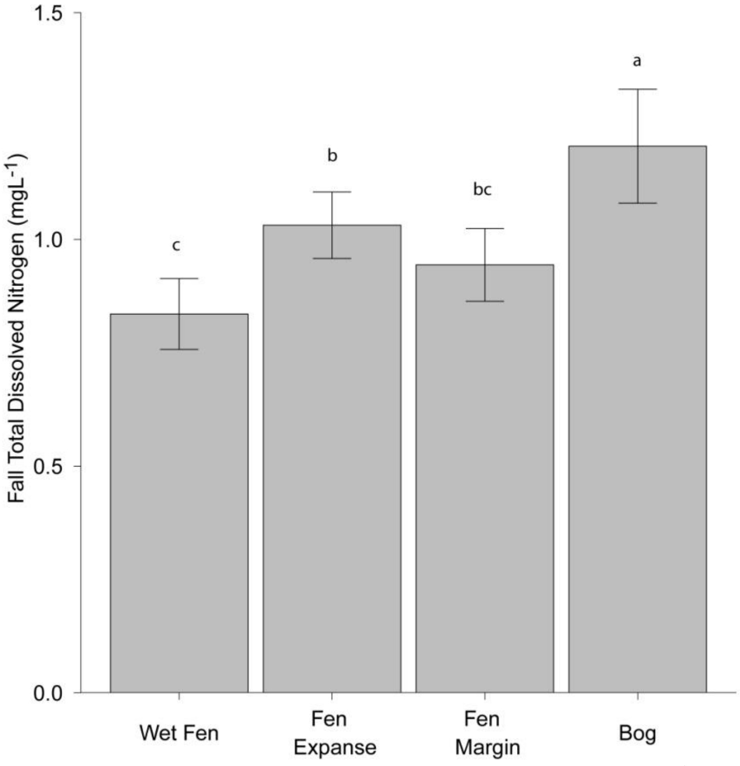


Figure 2.40. Fall 2010 total dissolved nitrogen (mg L^{-1}) from the pore water in the plots from the four groups derived from cluster analysis. Bars represent means ± SE. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24..

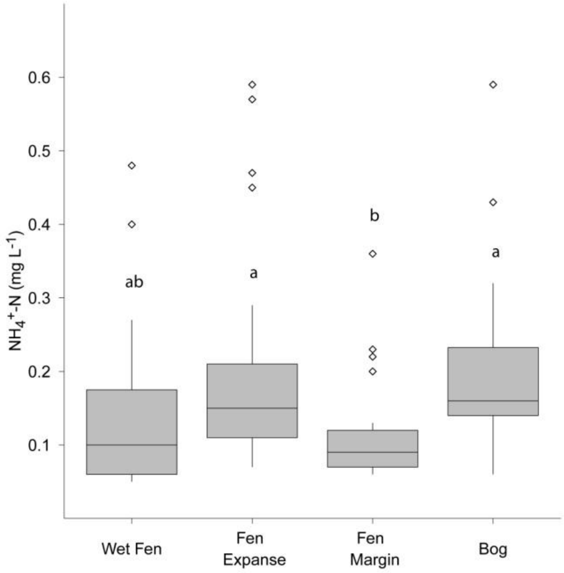


Figure 2.41. Fall 2010 NH_4^+-N (mg L^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

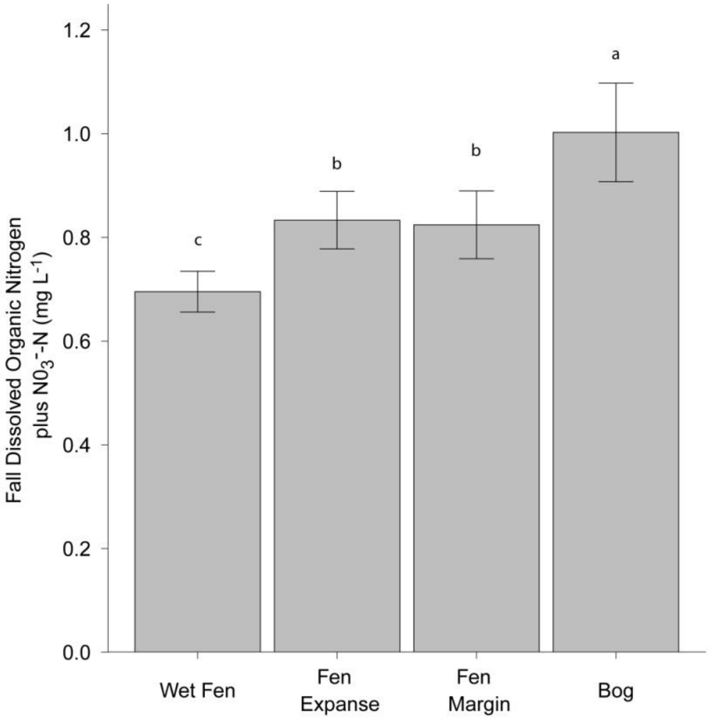


Figure 2.42. Fall 2010 dissolved organic nitrogen, plus trace amounts of nitrate (see methods) (mg L^{-1}) from the pore water in the plots from the four groups derived from cluster analysis. Bars represent means ± SE. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

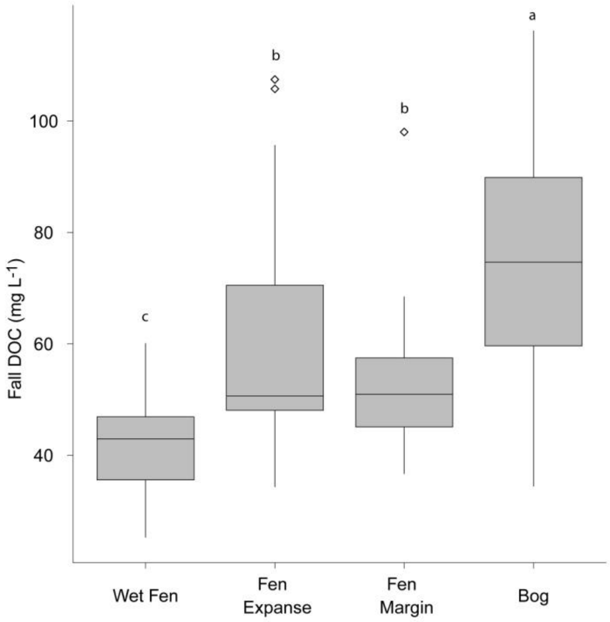


Figure 2.43. Spring 2010 dissolved organic nitrogen (mg L^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

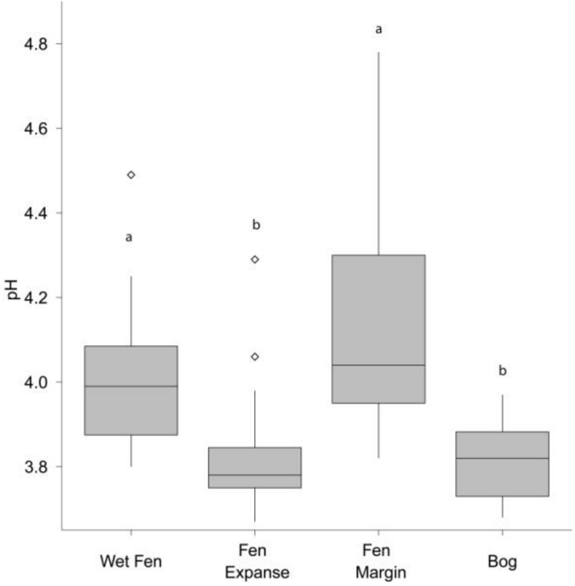


Figure 2.44. Fall 2010 pore water pH in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

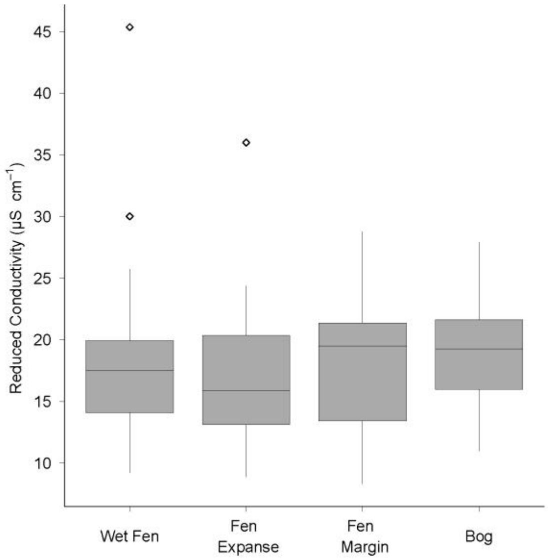


Figure 2.45. Fall 2010 reduced conductivity (µS cm^{-1}) from the pore water in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1.$ Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

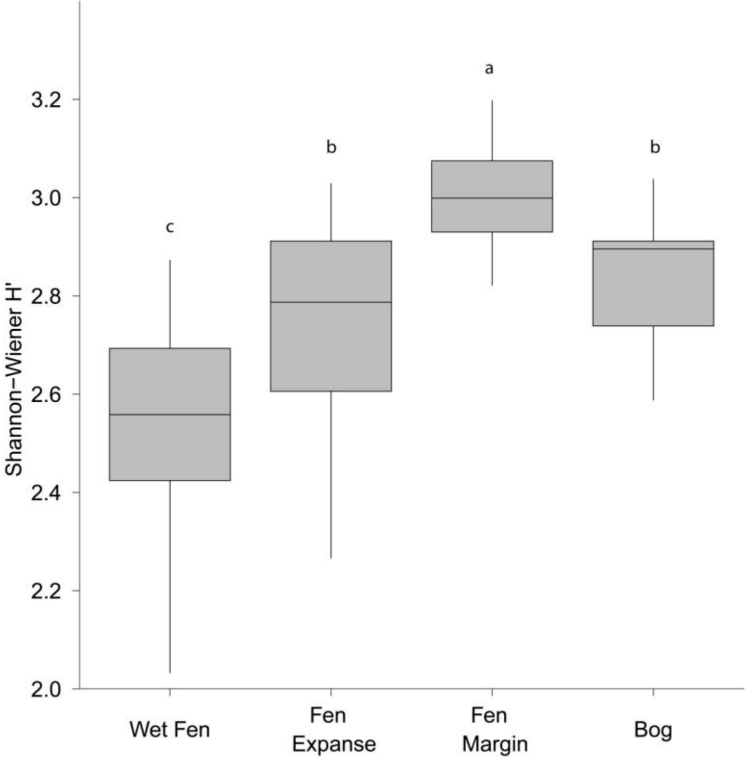


Figure 2.46. Shannon-Wiener diversity in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1.$ Different letters indicate significant differences between groups (p<0.05). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

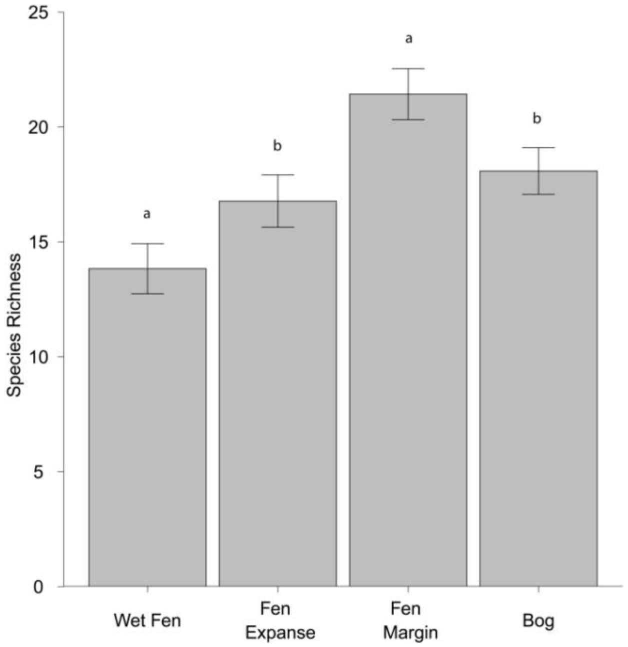


Figure 2.47. Species richness in the plots from the four groups derived from cluster analysis. Bars represent means ± SE. Different letters indicate significant differences between groups ($p<0.05$). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

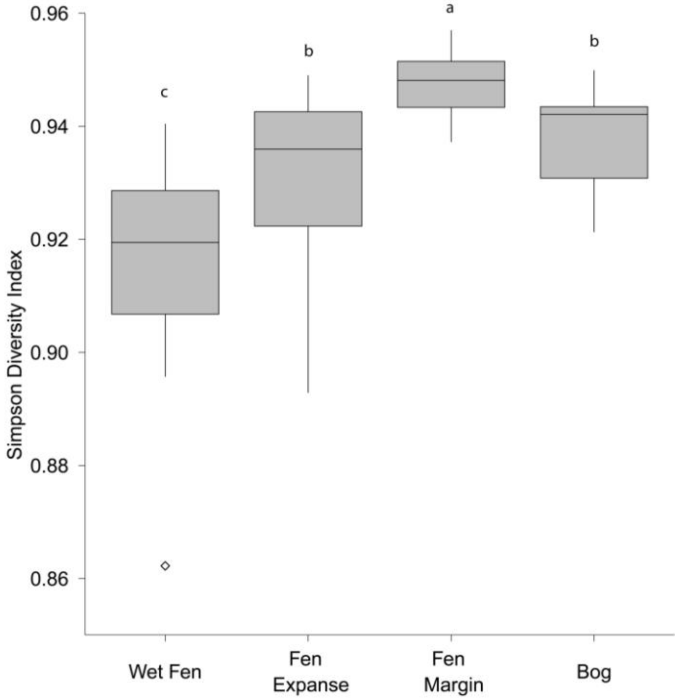


Figure 2.48. Simpson's diversity in the plots of the four groups derived from cluster analysis. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups ($p<0.05$). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

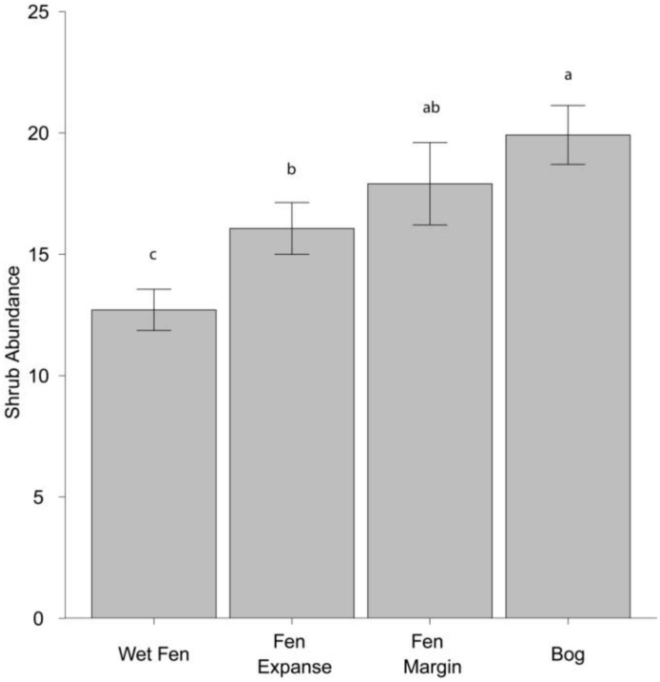


Figure 2.49. Shrub abundance in the plots from the four groups derived from cluster analysis. Shrub abundance is calculated as the sum of cover scores for shrub species. Bars represent means ± SE. Different letters indicate significant differences between groups ($p<0.05$). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

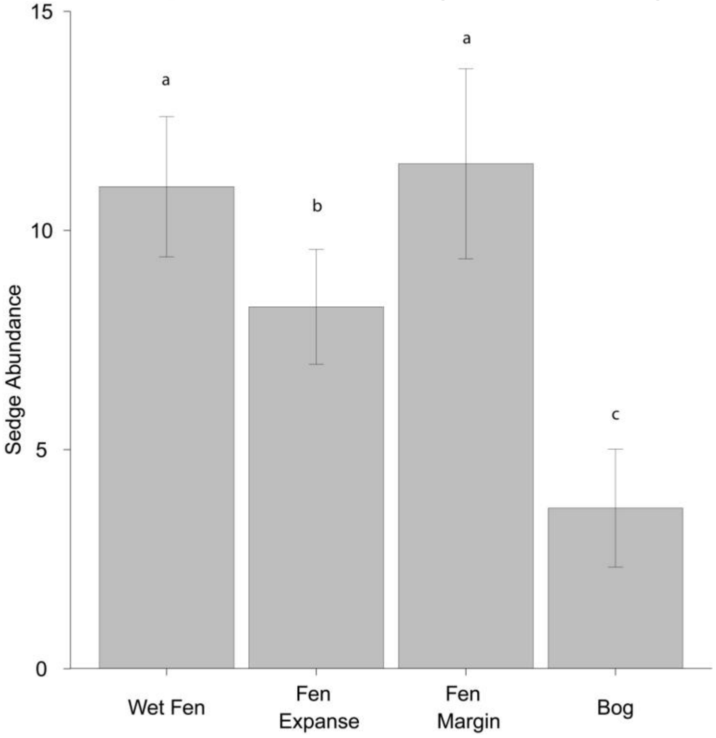


Figure 2.50. Sedge abundance in the plots from the four groups derived from cluster analysis. Sedge abundance is calculated as the sum of cover scores for shrub species Bars represent means ± SE. Different letters indicate significant differences between groups ($p<0.05$). Wet fen n=24, Fen expanse n=32, Fen margin n=20 and Bog n=24.

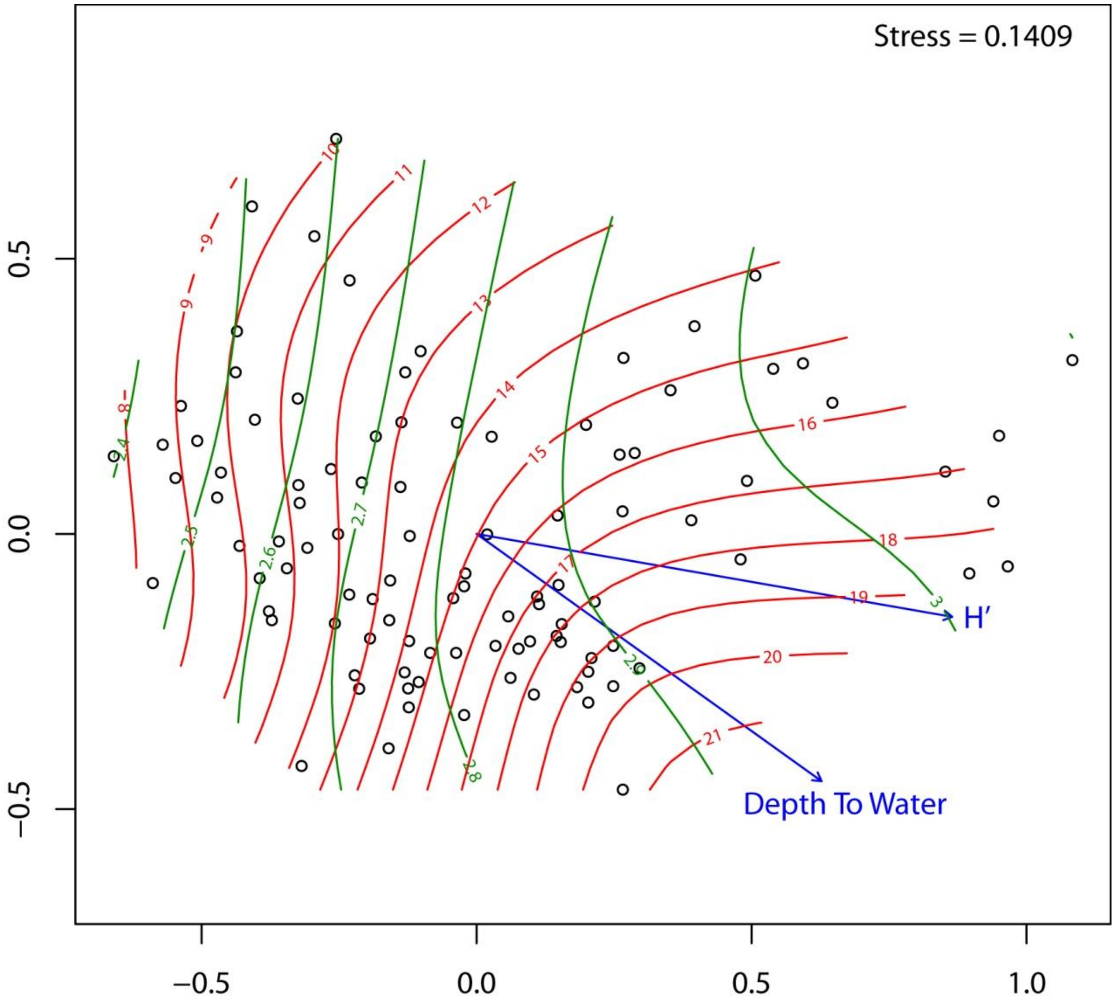


Figure 2.51. NMDS ordination of the 100 plots in the Mariana Lake peatland complex. Overlain with mean depth to water and Shannon diversity vectors, along with contour fits of both vectors. Shannon diversity in green and mean depth to water in red.

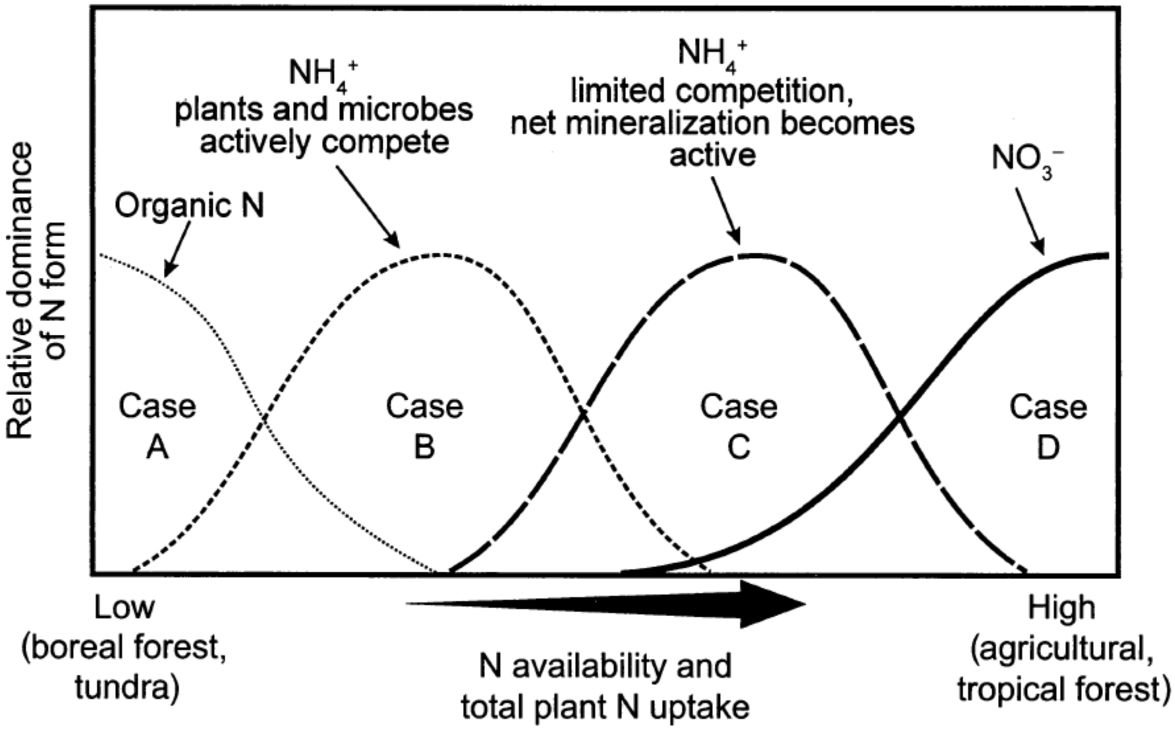


Figure 2.52. Different scenarios explaining dominance of N form. Taken from Schimel and Bennet 2004.

Table 3.1. Site characteristics for the three plot types at the Mariana Lake peatland complex. Values represent mean ± SD. Letters are significant differences from post-hoc Tukey's multiple comparisons (*p*<0.05). Bog n=10, Dry fen n=10, and wet fen n=9.

	Bog	Dry Fen	Wet Fen
May Depth to Water (cm)	18.5(±2.5)^{a}	10.2(±2.7)^{b}	5.6(±2.0)^{c}
Oct Depth to Water (cm)	27.7(±4.6)^{a}	23.8(±1.9)^{b}	14.95(±2.5)^{c}
June Reduced Conductivity (µS cm-1)	27.8(±6.8)^{a}	20.9(±4.2)^{b}	21.1(±3.7)^{b}
July Reduced Conductivity (µS cm-1)	39.9(±7.5)^{a}	31.0(±3.9)^{b}	29.2(±4.3)^{b}
June pH	4.1^{a}	3.9^{b}	4.1^{a}
July pH	4.0^{a}	3.9^{b}	4.1^{a}

Table 3.2. Results of Student's t tests comparing innate time markers and cranked wires. Values represent means ± SD. Bog n=10, Dry fen n=10, and wet fen n=9.

	Marker (cm)	Wire (cm)	Difference (cm)	% missing	|t|	p
All types	3.8(±1.26)	2.08(±0.90)	1.77(±1.51)	45.4	5.77	<0.0001
Bog	3.08(±0.49)	2.57(±1.07)	0.51(±0.62)	16.5	1.37	0.19
Dry fen	3.04(±0.65)	1.74(±0.46)	1.29(±0.61)	42.5	5.14	<0.0001
Wet fen	5.3(±0.84)	1.92(±0.91)	3.38(±1.29)	63.8	8.38	<0.0001

Table 3.3. Results of Student's t tests comparing seasonal stem and capitula weights, and stem (SMD) and capitula mass density (CMD). Values represent means ± SD. Bog n=10, Dry fen n=10, and wet fen n=9.

	May	October	|t|	p		May	October	|t|	p
Ave Stem wt					*SMD*				
All types	2.10(±0.67)	2.5(±0.51)	2.83	<0.01	All types	63.1(±12.0)	79.6(±11.8)	6.39	<0.0001
Bog	2.15(±0.60)	2.52(±0.36)	1.54	0.16	Bog	65.3(±11.1)	73.4(±9.6)	3.1	0.01
Dry fen	2.29(±0.84)	2.51(±0.71)	0.72	0.49	Dry fen	67.8(±12.4)	87.7(±14.1)	3.36	0.008
Wet fen	1.84(0.52)	2.48(±0.44)	3.87	<0.01	Wet fen	55.4(±9.4)	77.6(±5.1)	7.87	<0.0001
Ave Cap wt					*CMD*				
All types	6.02(±1.53)	7.58(±1.38)	4.11	<0.001	All types	183.0(±33.0)	242.1(±32.5)	7.39	<0.0001
Bog	6.1(±1.63)	8.02(±0.97)	2.72	0.02	Bog	186.1(±30.7)	235.2(±36.9)	3.47	<0.01
Dry fen	5.76(±1.30)	6.48(±1.07)	1.2	0.26	Dry fen	175.5(±38.4)	231.0(±26.2)	3.65	<0.01
Wet fen	6.24(±1.76)	8.32(±1.40)	3.35	0.01	Wet fen	187.9(±31.4)	261.6(±27.3)	6.34	<0.001

Table 3.4. Results of two-way ANOVAs for production measurements of *Sphagnum angustifolium*. Asterisk (*) indicated non-parametric ANOVA. SMD, stem mass density.

	df	*F*	*P*		*df*	*F*	*P*
Stems				*Linear Growth**			
Type	2	1.27	0.33	Type	2	34.71	<0.0001
Year	1	0.27	0.61	Year	1	0.53	0.47
T x Y	2	1.44	0.25	T x Y	2	0.23	0.8
SMD				*Production*			
Type	2	5.75	<0.01	Type	2	31.93	<0.0001
Year	1	35.01	<0.0001	Year	1	24.57	<0.0001
T x Y	2	2.37	0.1	T x Y	2	3.61	0.03

Table 3.5. Production and associated measurements for two years of the 3 site types within the Mariana Lake peatland complex. Values represent mean ± SE. Letters are significant differences from post-hoc Tukey's multiple comparisons (*p*<0.05). Bog n=10, Dry fen n=10, and wet fen n=9. SMD, stem mass density.

	Bog 2010	Bog 2011	Dry Fen 2010	Dry Fen 2011	Wet Fen 2010	Wet Fen 2011
Stems (m^{-2})	32,201(±2,526)	29,517(±1404)	31,718(±2,400)	36,513(±2292)	31,591(±2,326)	32,328(±2,333)
Linear growth (cm)	2.8(±0.2)^{b}	3.1(±0.2)^{b}	3.2(±0.3)^{b}	3.0(±0.2)^{b}	5.11(±0.5)^{a}	5.32(±0.3)^{a}
SMD (cm^{-1} m^{-2})	65.3(±3.5)^{bc}	73.4(±3.0)^{b}	67.8(±3.9)^{bc}	87.7(±4.5)^{a}	55.4(±3.1)^{c}	77.6(±1.7)^{ab}
Production (g m^{-2} yr^{-1})	184.8(±18.8)^{c}	224.4(±11.2)^{bc}	209.1(±14.7)^{b}	261.3(±13.1)^{b}	280.9(±25.3)^{b}	413.7(±25.7)^{a}

Table 3.6. Compilation of literature data for *S. angustifolium* linear growth (LG) and net primary production (NPP). LG = linear growth, MAT = mean annual temperature, MAP = mean annual precipitation.

LG (cm)	NPP (g m-2 yr-1)	Locale	Latitude	MAT (°C)	MAP (mm)	Reference
0.4-1.7	29.2-127.4	Quebec	54°48	-4.9	791	Moore 1989
na	19.2-57.9	Quebec	54°48	-4.9	791	Bartsch and Moore 1985
2.8-3.9	150-225	Manitoba	55°00	-3.7	NA	Camill et al. 2001
2.8-5.3	184-413	Alberta	55°89	0.3	455	This study
5	190-250	Alberta	56°40	1.3	479	Malhotra 2010
na	95-166	Alberta	54°28	1.7	500	Szumigalski 1995
2.0-3.9	97-198	NW Ontario	49°40	2.6	714	Rochefort et al. 1990
2.0-6.0	160-400	S. Finland	60°59	3.1	600	Lindholm and Vassander 1990
9.1-13.1	370-520	Minnesota	47°30	3.3	780	Grigal 1985
1.5	500	S. Norway	59°50	5.9	1250	Pedersen 1975
2.8-3.4	110-240	England	54°46	7.4	1980	Clymo and Reddaway 1971
na	240-330	England	54°46	7.4	1980	Forrest and Smith 1975
3.8-4.3	110-440	England	54°46	7.4	1980	Clymo 1970
12.0-16.0	488-1656	N Germany	54°20	8.4	714	Overbeck and Happach 1957
na	200	Global				Gunnarson 2005

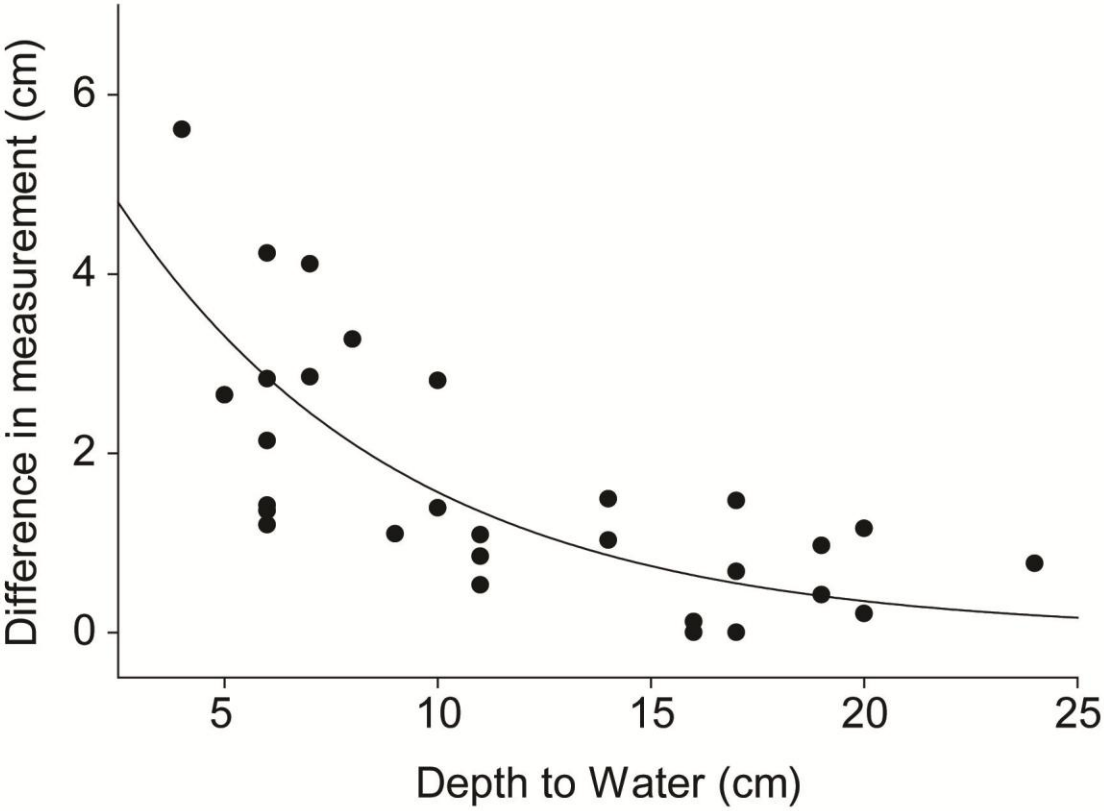


Figure 3.1. Relationship of depth to water (cm) and difference in measurements (Innate markers minus cranked wires). Non-linear regression following an exponential decay model was significant ($F_{1,27} = 54.19$; $R^2=0.54$; $p<0.0001$) with and a fit line following the formula $f(x)=6.976^{-0.149x}$.

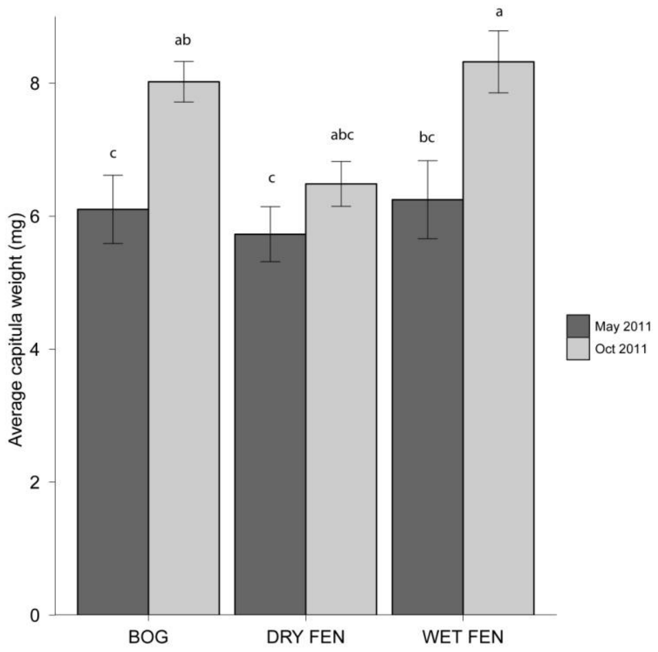


Figure 3.2. *Sphagnum angustifolium* average capitula weight (mg) for the three site types in May and 2011. Bars represent means ± SE. Different letters indicate significant differences between group and month (p<0.05).

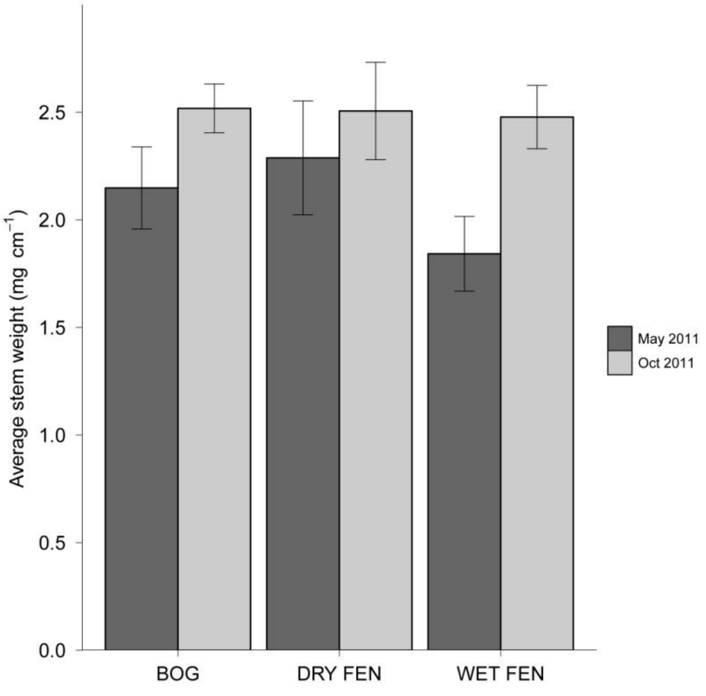


Fig 3.3. *Sphagnum angustifolium* average stem weight (mg) for the three site types in May and 2011. Bars represent means ± SE.

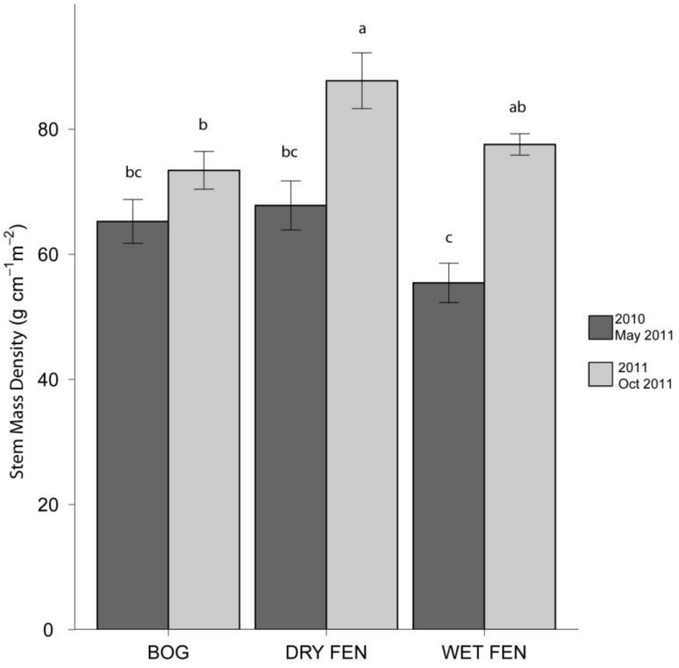


Figure 3.4. *Sphagnum angustifolium* stem mass density (g cm^{-1} m^{-2}) for the three site types in May 2011 and October 2011. Bars represent means ± SE. Different letters indicate significant differences between group and season ($p<0.05$).

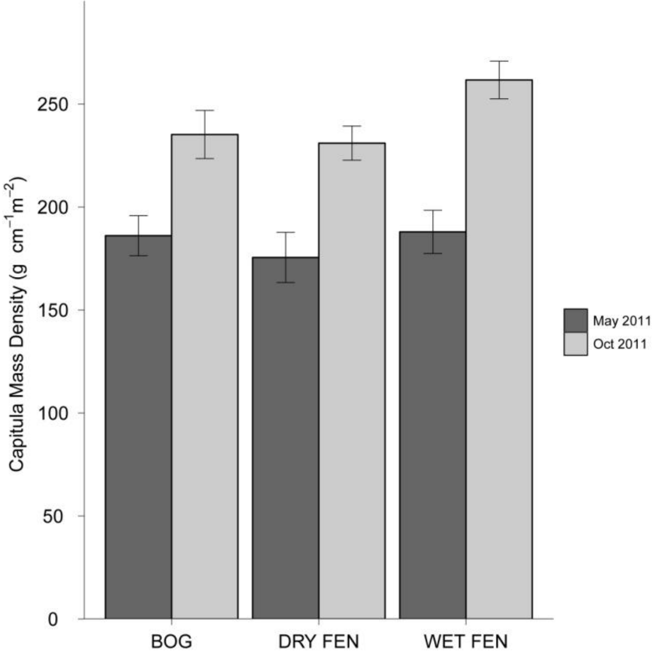


Figure 3.5. *Sphagnum angustifolium* capitula mass density (g cm^{-1} m^{-2}) for the three site types in May 2011 and October 2011. Bars represent means ± SE.

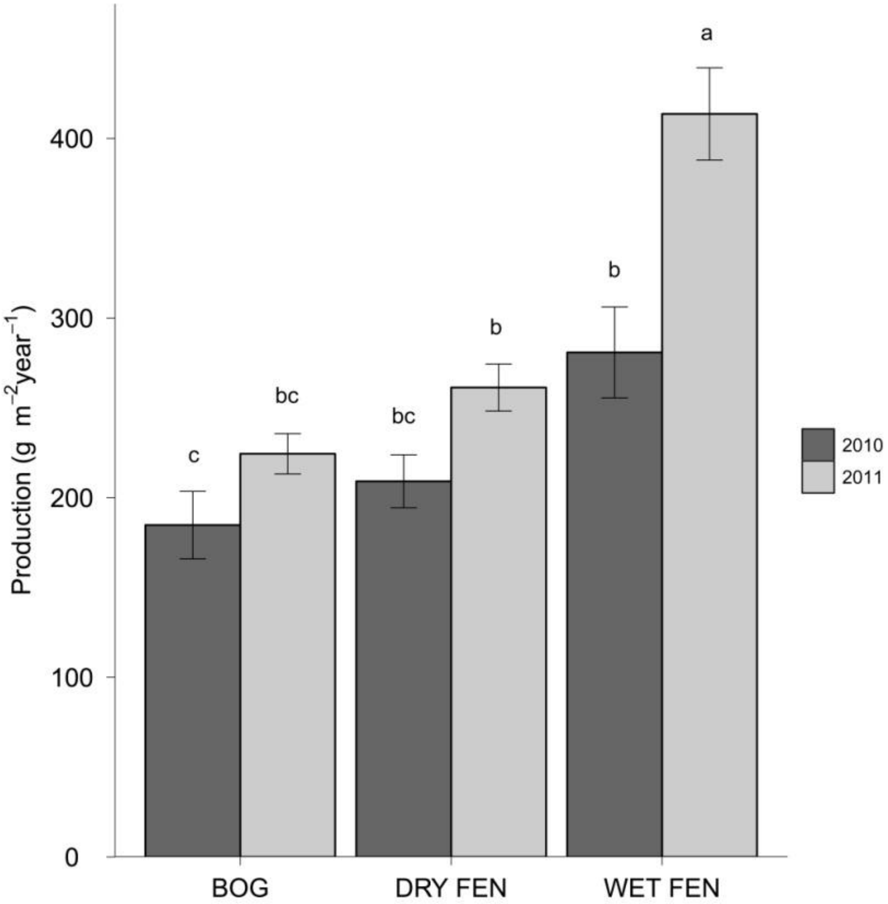


Figure 3.6. *Sphagnum angustifolium* production (g m^{-2} yr^{-1}) for the three site types in 2010 and 2011. Bars represent means ± SE. Different letters indicate significant differences between group and year (p<0.05).

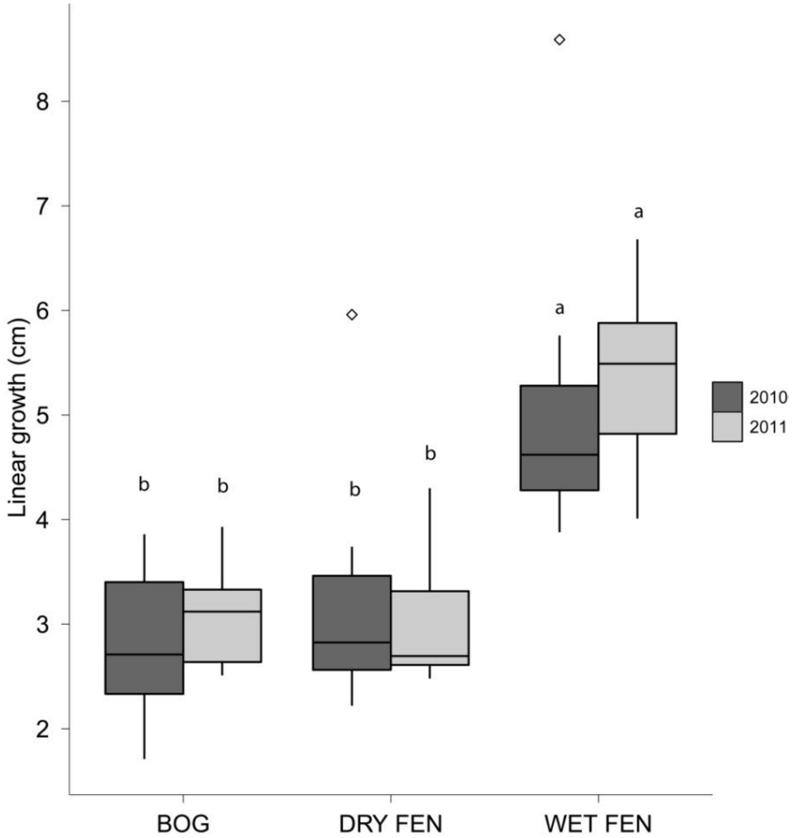


Figure 3.7. *Sphagnum angustifolium* linear growth (cm) for the three site types in 2010 and 2011. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between group and year ($p<0.05$).

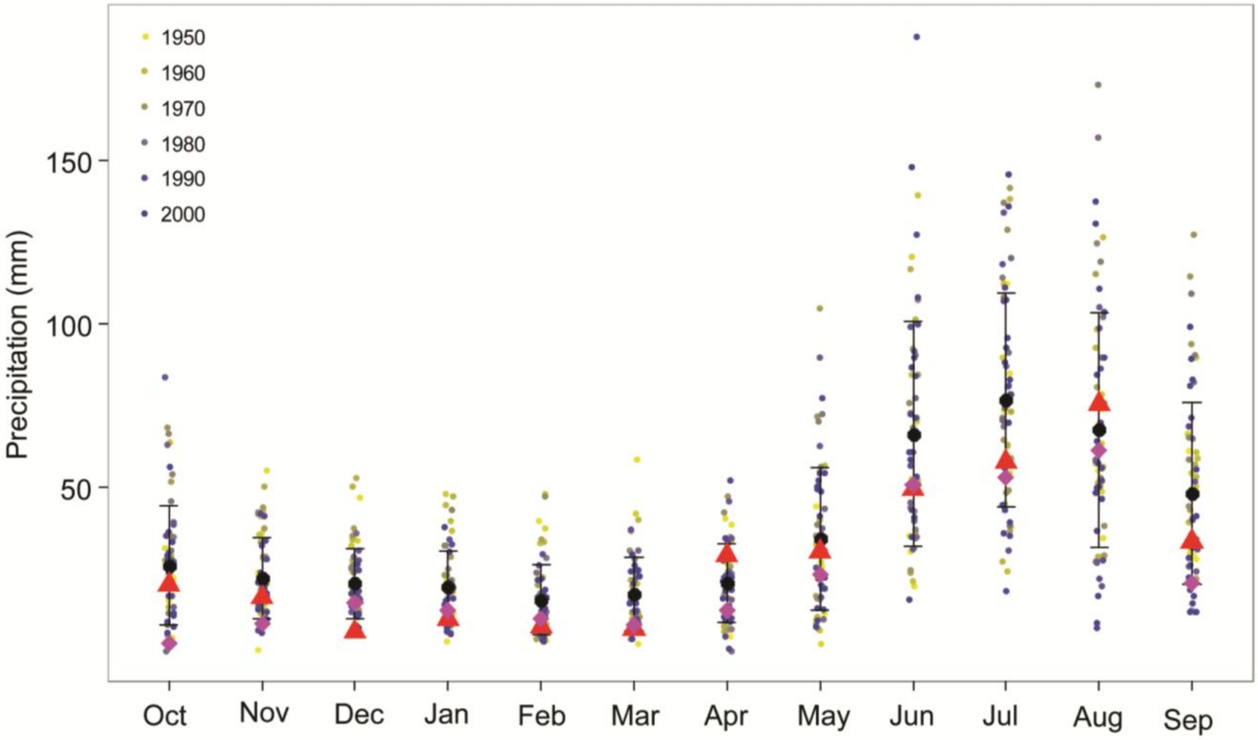


Fig 3.8. Monthly precipitation data from the Fort McMurray A weather station (56.65 N, -111.22 W, elevation 369 m) from 1944-2009, with 2010 (red triangles) and 2011 (magenta diamonds) overlain. Black circle represents mean (1944-2009) and bars represent ±1 standard deviation. Points representing total monthly precipitation are on a color gradient from yellow (oldest) to blue (most recent).

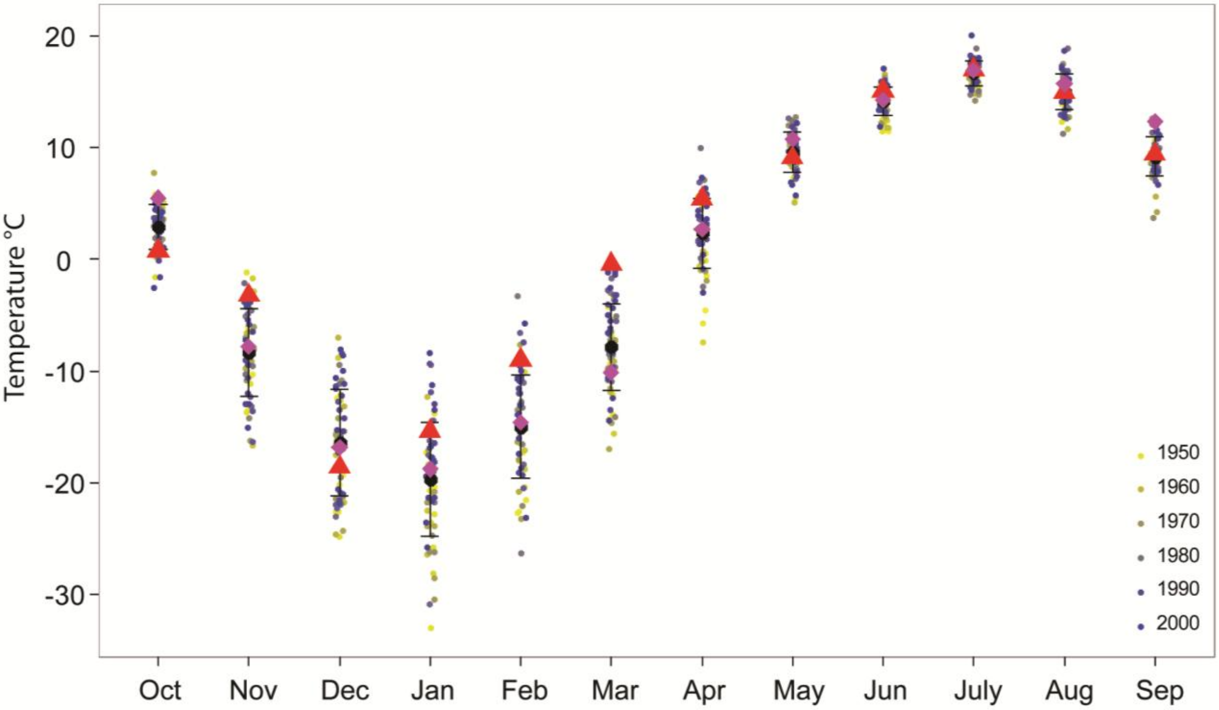


Fig 3.9. Monthly temperature means from the Fort McMurray A weather station (56.65 N, -111.22 W, elevation 369 m) from 1944-2009, with 2010 (red triangles) and 2011 (magenta diamonds) overlain. Black circle represents mean (1944-2009) and bars represent ±1 standard deviation. Points representing monthly mean temp are on a color gradient from yellow (oldest) to blue (most recent).

Table 4.1. Site characteristics for the three plot types at the Mariana Lake peatland complex. Values represent mean ± SD. Letters are significant differences from post-hoc Tukey's multiple comparisons (p<0.05). Bog n=10, Dry fen n=10, and wet fen n=9.

	Bog	Dry Fen	Wet Fen
May Depth to Water (cm)	18.5(±2.5)^{a}	10.2(±2.7)^{b}	5.6(±2.0)^{c}
Oct Depth to Water (cm)	27.7(±4.6)^{a}	23.8(±1.9)^{b}	14.95(±2.5)^{c}
June Reduced Conductivity (µS cm-1)	27.8(±6.8)^{a}	20.9(±4.2)^{b}	21.1(±3.7)^{b}
July Reduced Conductivity (µS cm-1)	39.9(±7.5)^{a}	31.0(±3.9)^{b}	29.2(±4.3)^{b}
June pH	4.1^{a}	3.9^{b}	4.1^{a}
July pH	4.0^{a}	3.9^{b}	4.1^{a}

Table 4.2. Seasonal differences of capitula biomass, N storage and C:N ratios of *Sphagnum angustifolium* from the Mariana Lake peatland complex. Letters signify significant differences (p<0.05) between months from Student's t tests.

	May	October
Biomass (g m^{-2})	182.9(±6.1)^{b}	241.9(±6.0)^{a}
N (g m^{-2})	2.2(±0.1)^{a}	1.7(±0.1)^{b}
C:N	38.1(±0.8)^{b}	64.1(±1.5)^{a}

Table 4.3. Production, tissue N concentrations and N stored in growth for 2010 and 2011. Letters signify significant differences (p<0.05) from Tukey HSD post-hoc comparisons between site types and years.

	Production (g m-2 yr-1)	Tissue % N	N (g m-2 yr-1)
Bog 2010	184.751(±18.8)^{c}	0.93 (±0.04)^{ab}	1.71 (±0.1)^{b}
Bog 2011	224.43(±11.2)^{bc}	0.97(±0.03)^{a}	2.17(±0.1)^{b}
Dry Fen 2010	209.14(±14.7)^{bc}	0.80(±0.04)^{bc}	1.66(±0.1)^{b}
Dry Fen 2011	261.32 (±13.1)^{b}	0.86(±0.03)^{abc}	2.25(±0.2)^{b}
Wet Fen 2010	280.88(±25.3)^{b}	0.76(±0.02)^{c}	2.12(±0.2)^{b}
Wet Fen 2011	413.65(±25.6)^{a}	0.77(±0.02)^{c}	3.16(±0.2)^{a}

Figure 4.4. Decomposition (%mass lost), the amount 2010 biomass left after decomposition during 2011, the N concentration in the remaining biomass and N retained in the 2010 biomass at end of 2011 growing season. (See methods for details). Letters signify significant differences (p<0.05) from Tukey's HSD post-hoc comparisons between site types.

	Bog	Dry Fen	Wet Fen
% Mass Lost	20.7(±2.4)^{a}	13.1(±1.7)^{b}	20.2(±1.9)^{ab}
2010 Biomass Remaining (g m^{-2})	145.8(±14.8)^{b}	181.9(±13.8)^{ab}	223.7(±18.9)^{a}
% N 2010 remains	0.68(±0.04)^{a}	0.56(±0.03)^{b}	0.64(±0.03)^{ab}
N left in biomass (g N m^{-2})	0.99(±0.07)	1.02(±0.05)	1.46(±0.11)

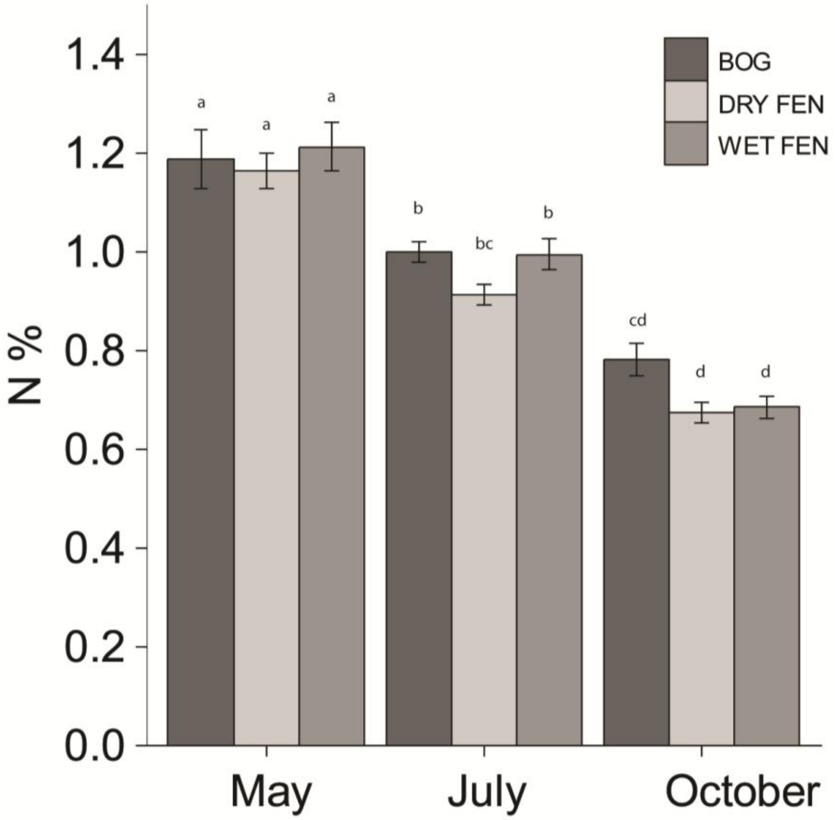


Figure 4.1. *Sphagnum angustifolium* capitula N concentration (%) for the three site types in May, July and October 2011. Bars represent means ± SE. Different letters indicate significant differences between groups (p<0.05).

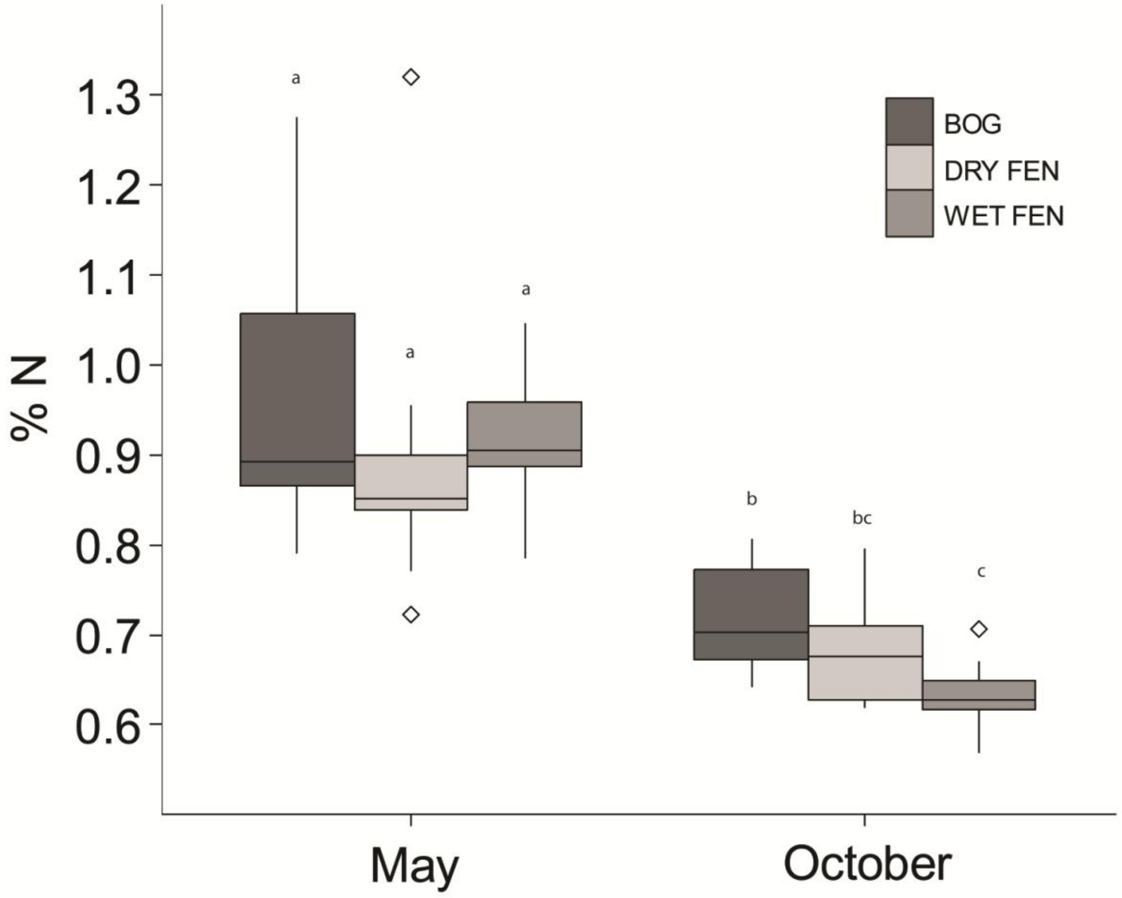


Figure 4.2. *Sphagnum angustifolium* 0-2 cm stem N concentration (%) for the three site types in May and October 2011. Middle line equal to median, upper and lower box equal to Q_1(25%) and Q_3(75%) quartiles. Whiskers are ±1.5 * IQR and diamonds are outliers > ±1.5 * IQR. IQR (Interquartile Range) is $Q_3 - Q_1$. Different letters indicate significant differences between groups (p<0.05).

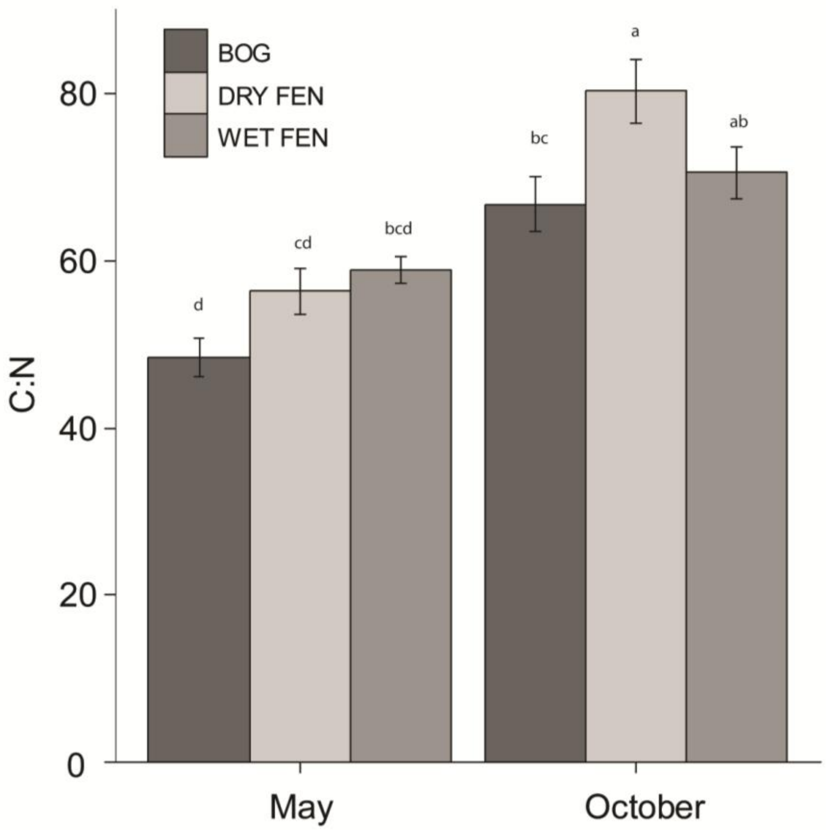


Figure 4.3. *Sphagnum angustifolium* carbon to nitrogen ratios (C:N) of 2010 growth segments in the three site types in May and October 2011. Bars represent means ± SE. Different letters indicate significant differences between groups ($p<0.05$).

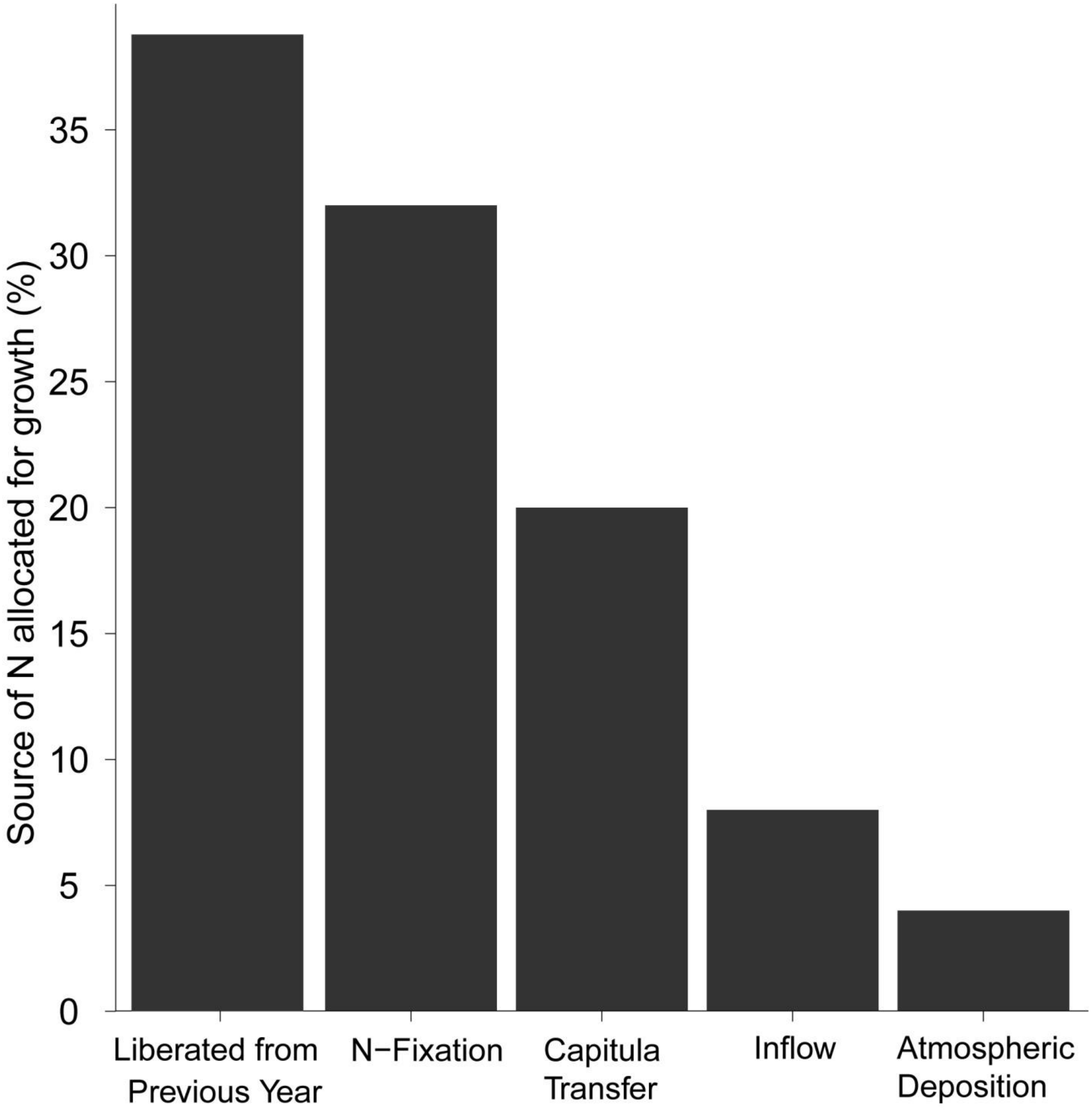


Figure 4.4. Potential source allocations (%) of N for yearly growth for *Sphagnum angustifolium* at the Mariana Lake peatland complex. These values are hypothesized for across the moisture gradient at the site. (See methods for details.) Values for N-fixation from (Prsa 2012) and inflow from (Verry 1975; Verry and Timmons 1982).

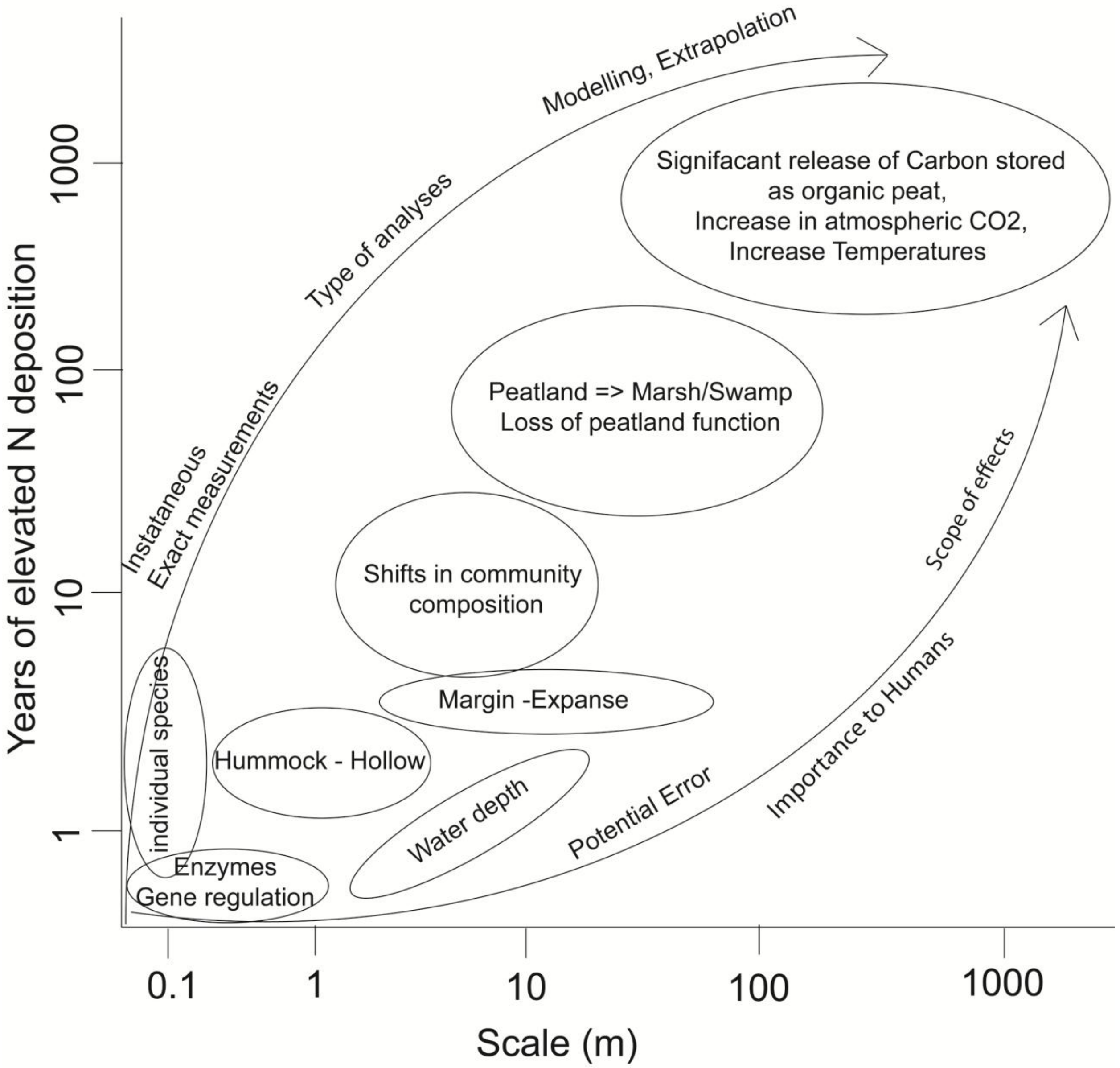


Figure 5.1. Conceptual diagram illustrating the relationships between scale and longevity of elevated nitrogen deposition.

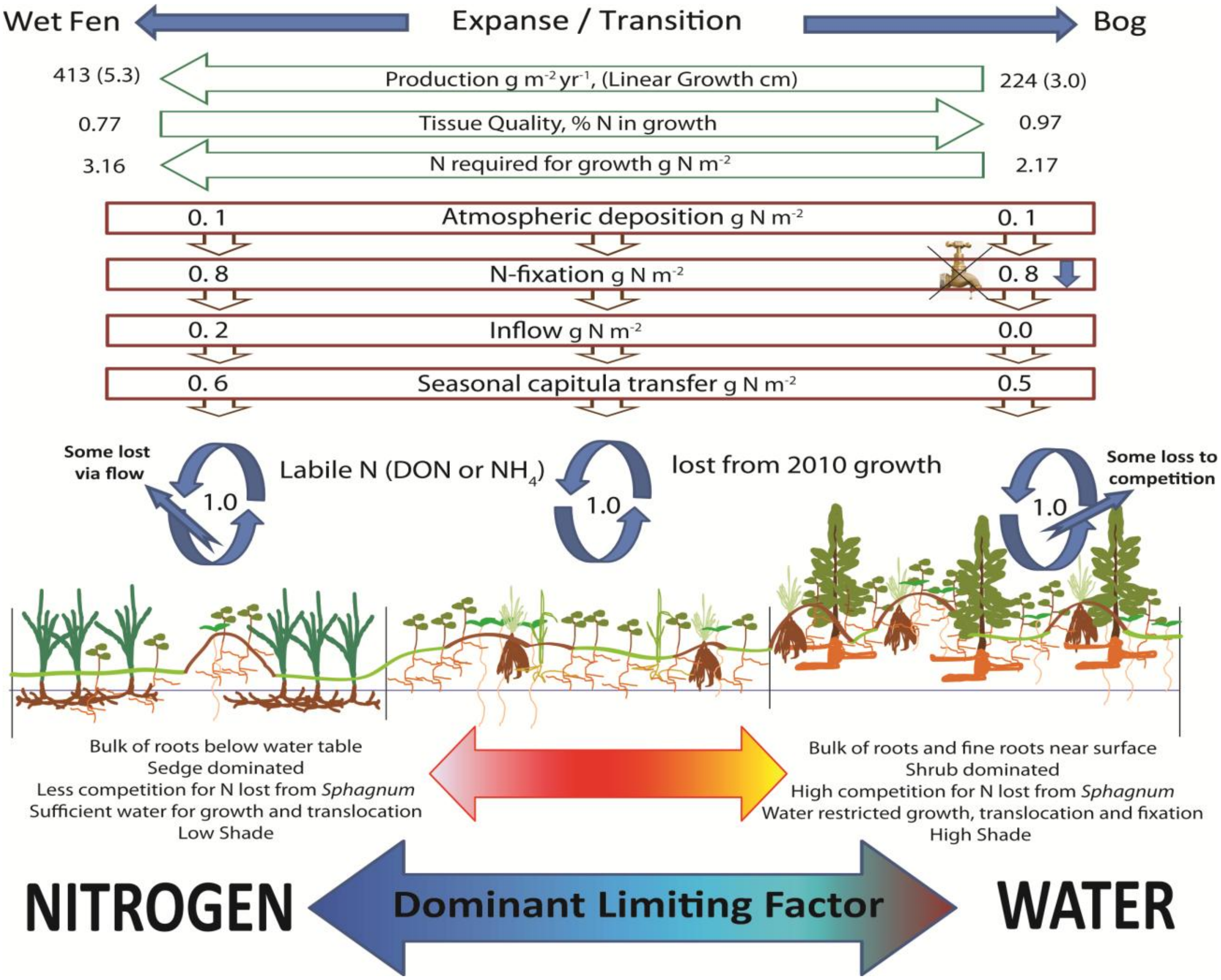


Figure 5.2. Summary of *Sphagnum angustifolium* net primary production, nitrogen requirements, potential sources and factors regarding growth limitations across the moisture gradient in bogs and poor fens. Values for production, tissue quality, nitrogen requirements, capitula transfer and labile nitrogen from previous year from this study. Values for N-fixation from (Prsa 2012), atmospheric deposition estimated from (Vitt et al. 2003), and inflow from (Verry 1975; Verry and Timmons 1982).

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APPENDICES

APPENDIX A

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Patterns in Environmental Drivers of Wetland Functioning and Species Composition in a Complex Peatland

Major Professor: Dale H. Vitt