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Plant Responses to Increased Experimental Nitrogen Deposition in a Boreal Peatland

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PLANT RESPONSES TO INCREASED EXPERIMENTAL NITROGEN DEPOSITION IN A BOREAL PEATLAND

by

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A Thesis
Submitted in Partial Fulfillment of the Requirements for the
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in the field of Plant Biology

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Increased nitrogen (N) deposition onto boreal peatlands and forests is anticipated with further expansion of Alberta's oil sands industry and consequently, an increase in sources of nitrogen oxide emissions. Increased N deposition has the potential to affect peatland flora and alter N cycling patterns in peatlands, therefore it is imperative to investigate at what level of excess N deposition these effects take place. This thesis discusses results from the first two years of a five year N fertilization study being conducted at a peatland complex near the hamlet of Mariana Lake in northeastern Alberta, Canada aimed at quantifying the N "critical load" for these peatland ecosystems. At the study site there are forty-two experimental plots – half in an ombrotrophic bog, the other half in the poor fen – with varying N fertilization treatments ranging from 0 kg/ha/year to 25 kg/ha/year. To investigate nitrogen uptake by plants at the Mariana Lake study site, I measured nitrogen (N) and carbon (C) concentrations of *Sphagnum* capitulum tissue and vascular plant foliar tissue. For *Sphagnum* species, I also analyzed C:N ratios and capitulum N storage. To investigate potential growth response of the target *Sphagnum* species, measurements were taken for linear growth (the vertical elongation of the *Sphagnum* shoots), stem mass density (the weight of *Sphagnum* stems occupying a volume after capitula were removed), and ultimately, net primary production (the product of the prior two measurements). Capitulum mass density (biomass) was measured as well to investigate

possible changes in *Sphagnum* capitulum growth. Also, during the height of the growing season (mid-July, 2011 and 2012), the plant communities in each treatment plot were sampled to provide “baseline” data necessary for documenting any shifts in plant distribution or community composition that may occur after N additions.

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CHAPTER I

INTRODUCTION TO PEATLANDS AND N CYCLING IN PEATLANDS

Overview of Peatlands

Peatlands are wetland ecosystems where over the long term, net primary production exceeds organic matter decomposition, resulting in substantial accumulation of peat, or incompletely decomposed organic matter. These ecosystems are carbon (C) sinks since net C fixation outweighs C output. Even though peatland ecosystems cover only 2-3% of the earth's land surface, they currently store one third of the world's organic soil carbon, and thus their importance is not proportional to their land surface area. These ecosystems are found in arctic, temperate, and tropical climates, but boreal climates have the majority with 80% of the world's peatlands being found in this region (Wieder et al. 2006). Peatlands are a very important component of the boreal landscape and comprise nearly a third of the Central Mixedwood Sub-region of northeastern Alberta (Vitt et al. 1996).

Bogs are peatlands whose sole source of water and nutrients is precipitation. Fens are peatlands whose water and nutrient supplies come from precipitation as well as water that has been in contact with upland soils. Bog ecosystems, then, are oligotrophic (nutrient poor) with ombrotrophic vegetation and fen ecosystems are either oligotrophic or mesotrophic with a dominance of minerotrophic vegetation (Vitt and Wieder 2008).

Sphagnum Mosses

The ground layer of peatlands is dominated by mosses, with a typical cover of 90 – 100%. Bogs and poor fens are *Sphagnum*-dominated while rich fens are brown moss-dominated (Vitt

and Wieder 2008). The presence of peat mosses (*Sphagnum* spp.) has been shown to be strongly linked with the capacity for peat formation (Van Breemen 1995), partly because their litter decays much slower than that of other plants (Clymo and Hayward 1982). Further slowing the decomposition process is the fairly high acidity of many peatlands, particularly bogs and poor fens. Various *Sphagnum* species have the ability to actually acidify their surroundings, through cation exchange (Clymo 1967) and sulfate production by *Sphagnum* (Gorham 1961, 1967), and production of weak organic acids from humified *Sphagnum* (Hemond 1980; Andrus 1986). The acidification properties of *Sphagnum* allow it to be a driver of succession under some conditions. Also relevant to its role in driving succession is the immense water-holding capacity of *Sphagnum*, which can result in a raising of a local water table that facilitates lateral expansion of peatlands into nearby upland areas (Andrus 1986; Vitt and Kuhry 1992). *Sphagnum* plants can hold up to 10 – 25 times their dry weight in water, which is due to a distinct morphology of leaves that consist of a single layer of alternating small, living green cells with large, dead hyaline cells, which are specialized to retain high quantities of water (Vitt et al. 1975; Andrus 1986).

Sphagnum species typically occur along a microtopographic gradient from hummock to hollow, or high to low distance from water table (Vitt et al. 1975; Andrus et al. 1983). Competition may affect the composition of *Sphagnum* assemblages, but probably only in hollow environments, whereas tolerance to the physical environment seems more important in hummocks (Rydin 1986). Throughout the western boreal region, a sequence of species from *S. angustifolium* in the hollows to *S. magellanicum* at mid-hummock to *S. fuscum* on the hummock top is normally present (Vitt et al. 1988).

The moss layer of peatlands influences ecosystem functioning in various ways, including nutrient uptake. *Sphagnum* acts as a "gatekeeper" for accessibility of nitrogen into peatlands, scavenging nearly all atmospherically deposited nitrogen when its tissues are un-saturated with nitrogen (Vitt and Wieder 2008). The efficient capture of nitrate in rainwater by *Sphagnum* deprives higher plants rooted in the peat column of this nutrient supply (Woodin et al. 1985). Thus, the living *Sphagnum* layer can effectively control subsequent nutrient availability, and hence plant production. The ground layer typically produces about 41% of the total annual plant production, with trees, shrubs, and herbaceous plants making up the rest (Vitt and Wieder 2008).

Nitrogen Cycling in Peatlands

Peatlands contain 9-16% of the world's soil nitrogen (N) (8-15 Pg of N), retaining a high percentage of the N they receive, and thus are generally regarded as effective N sinks (Limpens et al. 2006). When discussing N cycling in peatlands, it is important to remember the different types of peatlands (bogs and fens) and their differing nutrient sources. The main N inputs to peatlands are N deposition from the atmosphere, N_2-fixation by bacteria/algae, and N inflow through upland runoff or discharge, with the latter only being a considerable input in fens or raised bogs with a lagg zone. Intrasystem N cycling in peatlands primarily includes N uptake by vegetation, N retention and retranslocation in *Sphagnum*, and decomposition/N mineralization. N losses in peatlands are fairly minimal – there are negligible gaseous N losses via denitrification or volatilization and low N losses by hydrologic export (Limpens et al. 2006).

❖ *N Inputs*

In ombrotrophic bogs, atmospheric N deposition is considered the main N input, providing 13-80% of the nutrient requirements of plants (Limpens et al. 2006). However, several studies propose that other N inputs to peatlands have been underestimated (eg. Damman 1978; Moore et al. 2004; Vile et al. *in review*). Moore et al. (2004) found that N accumulation in bog cores taken from study sites across eastern Canada was about four times the N that could be accounted for by wet deposition. Other sources of N for an ombrotrophic bog include organic N depostion, dry deposition, and N_2-fixation. Total N deposition consists of both wet and dry deposition; it is fairly plausible that estimates of N contributions to peatlands via dry deposition have historically been underestimated since measuring dry deposition is very difficult (Limpens et al. 2006). Dry deposition may be smaller in bog systems than in forests since there is a small vascular leaf surface area (Moore et al. 2002, 2004), however, *Sphagnum* has a large moist leaf surface, and may be a very effective absorber of dry N deposition (Limpens et al. 2006). Thus, the N input via dry deposition could potentially be even larger than wet N deposition and *Sphagnum* may have access to more atmospheric deposition than previously assumed (Limpens et al. 2006). Overall deposition may increase by roughly 50% above the wet deposition if organic N deposition is taken into account as well, since DON (dissolved organic nitrogen) forms a variable proportion of atmospheric N deposition (Moore et al. 2004).

In addition to dry deposition and inorganic N deposition, N_2-fixation also has been a much overlooked contribution to N in peatlands. Biological N_2-fixation is the process by which specialized prokaryotic microorganisms containing the enzyme nitrogenase convert atmospheric N_2 to NH_3, thereby taking a non-reactive N form and transforming it into a

reactive, organic form that is biologically useful (Schlesinger 1997). A wide array of prokaryotes carry out biological N_2-fixation in peatlands including cyanobacteria, symbiotic actinomycetes, and free-living bacteria (Limpens et al. 2006). Reported amounts of N input attributable to N_2-fixation have ranged from 0.03 to 11.5 g N m^{-2} yr^{-1}, showing a great deal of spatio-temporal variability (Limpens et al. 2006). Consequently, it has been difficult to quantify N_2-fixation in peatlands and determine its importance as an N input. Since the process of N_2-fixation is energetically costly (16 ATP for every mole of N fixed) and environmental conditions typical of peatlands (e.g. low pH and low mean annual temperatures of 1°C) may be constraining for nitrogen-fixing organisms, contributions from N_2-fixation often have been assumed to be insignificant (Vile et al. *in review*). However, recently it has been shown that in boreal peatlands in Alberta, N_2-fixation is an extremely significant process, providing a substantial amount of newly fixed N (with mean rates ranging from 7.2-26.4 kg N ha^{-1} yr^{-1}) that can account for the aforementioned discrepancies in the amount of N deposition and the measured N accumulation at various peatland sites (Vile et al*. in review*).

- *Intrasystem N Cycling*

As mentioned earlier, *Sphagnum* is a critical component in within-ecosystem N cycling. Although there is considerable variation among sites, *Sphagnum* is generally very effective at capturing N inputs and retaining N (retention rates range from 11 to almost 100%) (Limpens et al. 2006). When un-saturated, *Sphagnum* can scavenge nearly all atmospherically deposited N, thus restricting the nutrient supply to vascular plants (Aldous 2002a; Vitt and Wieder 2008; Woodin et al. 1985). *Sphagnum* also limits nutrient availability to vascular plants by slowing down decomposition through its recalcitrant litter (Limpens et al. 2006). Following N uptake,

Sphagnum is able to assimilate NO_3^- almost immediately due to its ability to quickly activate nitrate reductase (Woodin et al. 1985). Despite *Sphagnum* lacking vascular conducting tissues, 10-50% of the N in *Sphagnum* stems can be retranslocated upwardly to support new growth (Bragazza et al. 2004).

Since *Sphagnum* does not uptake and retain 100% of atmospherically deposited N, there is some amount that makes it past the moss layer (Aldous 2002a). However, since this is a limited amount of N that makes it downward to the lower peat column, vascular plants and microbes must also rely on the mineralization of peat (Damman 1988; Malmer et al. 1994). In peatlands, both decomposition and N mineralization rates are low, owing to abiotic factors such as low temperature soils, poor aeration, high water tables, and low pH, as well as factors associated with the presence of *Sphagnum*, including poor litter quality and anti-microbial chemicals produced by *Sphagnum* (Clymo 1984; Regina et al. 1996; Aerts et al. 1999; Vitt 2006; Bragazza and Freeman 2007). It has been proposed that the organic material in *Sphagnum* dominated peatlands, which is predominantly composed of litter and peat formed by *Sphagnum*, consists of a labile cell protoplasm component with a high N:C ratio and a recalcitrant cell wall component with a very low N:C ratio (Verhoeven et al. 1988; Koerselman and Verhoeven 1992). Therefore, microbes may mineralize labile N forms rapidly (high N:C ratio of litter exceeds the ratio required for the growth of microbes) and then may take longer to mineralize N within recalcitrant compounds (very low N:C ratio of litter results in net immobilization rather than net mineralization) (Limpens et al. 2006). This hypothesis has been supported by several studies, including Brock and Bregman (1989) who found that *Sphagnum recurvum* litter lost only 18 % of its dry weight after one year of decomposition, but nearly 45 % of its N.

❖ *N Outputs*

The main N losses from undisturbed peatlands are gaseous losses from denitrification and losses from hydrolic export (runoff or streamflow). As discussed earlier, *Sphagnum* is efficient at retaining N, and therefore, concentrations of inorganic N in pore water are typically low (Limpens et al. 2006). Thus, N losses via hydrolic export are relatively small (1.5-6.3 kg ha^{-1} yr^{-1}) and mainly take place in organic forms (dissolved organic nitrogen). Denitrifcation is the microbial reduction of NO_3^- to N_2O and N_2, taking place under anaerobic conditions (Limpens et al. 2006). Denitrification requires the presence of NO_3^-, and denitrifying bacetria prefer wet soils rich in organic matter that express a neutal pH (Schlesinger 1997). In peatlands, the supply of NO_3^- is generally low since the peatland flora, *Sphagnum* especially, usually take up nitrate inputs (from atmospheric deposition and nitrification of NH_4^+) before they reach anaerobic zones where denitrification takes place. Thus, N losses via denitrification are fairly minimal as well, though fens, which have a greater supply of inorganic N and a higher pH that does not inhibit nitrification of NH_4^+, may have substantial losses (Limpens et al. 2006). N losses via volatilization are even smaller than hydrolic export or denitrification; Hemond (1983) found that only trace amounts of NH_3-N were lost directly as ammonia gas at his study site. Under anaerobic conditions, facultative anaerobes are able to use NO_3^- as a terminal electron acceptor in place of oxygen to meet their energy demands, and NH_4^+ is released as an end product. Volatilization can also occur under aerobic conditions, whereby NH_3 is released as a byproduct of bacteria breaking down amino acids (Limpens et al. 2006).

Peatland Response to Increased Nitrogen Deposition

Investigations concerning peatland response to increased N deposition began with studies examining the effects of increased N deposition associated with acid precipitation. Research on this topic arose in Europe, where many regions were experiencing acid precipitation and greatly increased levels of atmospheric N deposition since the last century. An initial finding in these investigations was that increased atmospheric N deposition can have deleterious effects on bogs through negative impacts on *Sphagnum* (Press and Lee 1982). Poor growth of *Sphagnum* was observed in bogs that were in regions of high atmospheric N deposition and was found to be associated with increases in tissue N concentrations. Evidence strongly suggested that higher N supplies in polluted regions were supra-optimal for *Sphagnum* growth (Press et al. 1986).

These early investigations established the importance of taking ambient atmospheric N deposition into account when interpreting results. The study by Press et al. (1986) had study plots at differing proximity to major pollution sources, and thus with differing levels of atmospheric N deposition. Later studies conducted in unpolluted areas of western Canada and northern Sweden investigated the effect of increased N deposition where prior ambient atmospheric N deposition was low. Aerts et al. (1992) found that *Sphagnum* responded quickly to increased N deposition at a low-N site, increasing its productivity almost fourfold upon the initial N addition. Vitt et al. (2003) revealed similar results, finding that 34 years after oil sands mining startup, sites where N deposition had increased (from initially low levels) showed enhanced *Sphagnum* production.

The N required for this observed increase in production came partially from atmospheric N deposition, but also internal N cycling processes, such as mineralization and N_2-fixation, and N translocation (Aldous 2002a, 2002b). Contrary to expectations, Aldous (2002a, 2002b) found that greater amounts of N were translocated from older to younger parts of *Sphagnum* at a high-N deposition site than at a low-N deposition site. Not only does this lend further evidence that peatlands with varying levels of ambient atmospheric N deposition may respond differently to N additions, it also suggests that internal nutrient cycling must be investigated when examining the effects of N additions as well.

The Triphasic Response

In central Canada, a four-year experimental acidification study by Rochefort et al. (1990) found stimulated growth in two of the three dominant *Sphagnum* species for the initial two years of acidification, but then a decline or complete cease in the luxurious growth after the fourth year. In this study, the effect of the acid treatment changed over the years, from a short-term fertilizer effect to a possibly deleterious effect (Rochefort et al. 1990). Later investigations supported this idea of a "multi-phasic" peatland response pattern. In a three-year experiment, Gunnarsson and Rydin (2000) found that *Sphagnum* at a low N deposition site showed an increased growth in length with their intermediate N treatment after the first season. However, in the second and third seasons, the control treatment had the highest growth in length. To explain this observed inconsistency in *Sphagnum* response, a hypothesis was formed for a "triphasic" N cycling pattern in *Sphagnum* spp. subjected to increased N deposition (Lamers et al. 2000; Limpens et al. 2003).

A “triphasic” response to increased N deposition has been documented in N-limited peatlands. When *Sphagnum* are initially exposed to elevated N inputs they first respond by utilizing these additional nutrients and accelerating their growth (Aerts et al. 1992; Vitt et al. 2003). Accelerated growth continues until the plants are no longer N-limited; a further increase in the growth rate cannot occur because other minerals and nutrients are limiting, such as phosphorus. The second response, then, is the *Sphagnum* plants begin to store excess N to be used at later times. However, the plants are only able to store limited amounts of excess N before becoming N saturated. When the *Sphagnum* plants are N saturated, their N-filtering ability fails. Lamers et al. (2000) observed an apparent failure of *Sphagnum* mosses to intercept new N inputs in regions where N deposition rates exceeded approximately 20 kg N/ha/yr. At high levels of N deposition, *Sphagna* become super-saturated and eventually reach a limit where they cannot take in any more N. With the living *Sphagnum* layer no longer able to filter N, inorganic N leaches through the living *Sphagnum* layer to deeper peat. Additional N may leach down to the deeper peat as *Sphagnum* leaches N out of its tissues as DON (dissolved organic nitrogen) to prevent accumulating chronic concentrations of internal N content (Gerdol et al. 2006). Evidence for this has been shown by Bragazza and Limpens (2004), who found that peatlands in high N deposition regions have higher concentrations of pore water DON compared to pristine peatlands. Increased DON concentrations in the rhizosphere could provide an alternative N source for vascular plants. These additional N inputs to the organic matter profile may supply vascular plant species with the opportunity to colonize and proliferate (Lamers et al. 2000; Limpens and Berendse 2003). Increased shrub NPP can negatively affect *Sphagnum* NPP by increasing understory shade (Bonnett et al. 2010).

Oil Sands Development and the N "Critical Load" concept

Alberta has the third-largest proven crude oil reserve in the world, next to Saudi Arabia and Venezuela (Government of Alberta (1) 2012). Of the 171.3 billion barrels, 169.9 billion barrels consist of bitumen and 1.4 billion barrels consist of conventional oil. These reserves are estimated to be enough oil to meet Canada's current oil demand for almost 400 years. Oil sands (also called "tar sands") refer to bitumen, which is a viscous form of oil that is combined with sand and water. Oil sands are located in three major areas – the Athabasca Oil Sands, Peace River Oil Sands, and Cold Lake Oil Sands - in northeastern Alberta underlying 140,200 km^2. The bitumen must be removed from the sand and water prior to being upgraded into crude oil and other petroleum products. This extraction can be done in two ways: *in situ* (which means in place) recovery and surface mining. For deeper oil sands reservoirs (about 80% of reservoirs), an *in situ* recovery method is used to produce bitumen through wells that look like those used for conventional oil and gas production. *In situ* operations result in much less land disturbance and are able to reclaim areas much sooner than surface mines. *In situ* projects also eliminate the need for tailings ponds. The majority of *in situ* operations use steam-assisted gravity drainage (SAGD), which involves pumping steam underground through a horizontal well to liquefy the bitumen, which is then pumped to the surface through a second well. The other extraction method, surface mining, requires an open-pit mine operation, similar to many coal, iron ore, copper and diamond mine operations. Oil sands are dug up and moved by diesel trucks to a cleaning facility where the material is mixed with hot water to separate the recoverable oil from sand. The majority of this resource can only be developed using *in situ* (or in place) recovery; as of June 2010, there were 91 active oil sands projects in Alberta and of

these, four were mining projects and the remaining projects used various *in situ* recovery methods (Government of Alberta (1) 2012; Oil Sands Truth 2012).

Unprocessed oil sands contain 3–18% bitumen by weight, along with 2–10% water and 80–85% mineral matter (such as sand and clay). Bitumen is composed chiefly of polycyclic aromatic hydrocarbons (PAHs), sulfur, lead, mercury, arsenic, nickel, vanadium, chromium, and selenium. Since it contains far more carbon and far less hydrogen than conventional crude oil, it has to be "upgraded" through the addition of hydrogen and the subtraction of carbon, and natural gas is added to enable the material to be pumped to a refinery for processing. Much of the controversy about oil development centers around tailings ponds, where the remaining water and solids, including a small amount of un-extracted bitumen, are discharged as waste. Tailings ponds cover more than 130 km^2 in northern Alberta. Some large tailings ponds are separated by earthen dikes from the Athabasca River, which joins the Mackenzie River to form the major watershed of northwest Canada. The water in these ponds often contains arsenic, mercury, PAHs, and other toxics found in the bitumen. Oil sands operators maintain interceptor ditches and wells to catch leakage from the tailings ponds, but despite these precautions the Environmental Defence report calculated that 11 million liters of contaminated wastewater nevertheless escapes each day (Tenenbaum 2009; Government of Alberta (3) 2012).

Emissions from oil sands development are of great concern as well, and the threat they pose to the health of peatland ecosystems is the focus of my research. Oil sands development is associated with the production of greenhouse gas emissions, nitrogen oxides (NO_x), sulphur dioxide (SO_2), hydrogen sulfide (H_2S), ozone and fine particulate matter (Government of Alberta (2) 2012). Since oil sands production and upgrading are more energy intensive than the

production of conventional oil, it creates more greenhouse gas emissions (Government of Alberta (4) 2012). Increased concentrations of the potent greenhouse gas nitrous oxide (N_2O) are particularly worrisome because not only does nitrous oxide have a tremendous ability to trap heat in the atmosphere, it also can catalyze the destruction of stratospheric ozone by reacting with excited oxygen atoms in the stratosphere (Vitousek et al. 1997). The presence of other nitrogen oxides (NO_x) in the atmosphere has known health and environmental effects as well. Nitrogen dioxide, which is part of the family of gases known as nitrogen oxides (NO_x), is a reddish-brown gas formed through burning at high temperatures. Exposure can cause lung irritation and lower resistance to respiratory infections, such as influenza. Nitrogen dioxide contributes to acid precipitation by reacting with moisture in the air to form nitric acid and is also one of the gases responsible for the formation of ground-level ozone (Government of Alberta (5) 2012).

It has been well documented that acid precipitation has contributed substantially to the acidification of soils, streams, and lakes in many regions around the world (Schindler 1994; Likens et al. 1996; Vitousek et al. 1997). Acidification of soils can lead to significant losses of soil nutrients, such as calcium and potassium, which are essential for the long-term maintenance of soil fertility. Increased nitrogen additions associated with acid precipitation can lead to increased nitrate mobility, which induces nitrate loss – as nitrate (an anion) moves through soils to streams and to groundwater, it pulls cations along with it and thereby depletes the soil of nutrients such as calcium as well as increasing the soil acidity. Besides increasing the loss of nutrients from soils, acidification can disrupt the nitrogen cycle in freshwater ecosystems (acidic conditions may slow down or halt biological N_2-fixation or nitrification, and possibly

stimulate denitrification) and can decrease diversity of animal and plant species in terrestrial and aquatic ecosystems (Vitousek et al. 1997). Thus, nitrogen oxide emissions have far-reaching impacts that extend beyond just air quality issues.

Increased nitrogen oxide emissions lead to increased atmospheric nitrogen (N) deposition onto the landscape. Increased N deposition onto boreal peatlands and forests is anticipated with further expansion of Alberta's oil sands industry and consequently, an increase in sources of nitrogen oxide emissions. As discussed earlier, increased N deposition has the potential to affect peatland flora and alter N cycling patterns in peatlands. It is imperative now to investigate at what level of excess N deposition these effects take place.

A nitrogen "critical load" is defined as the quantitative estimate of the level of exposure of natural systems to N below which significant harmful effects on specified sensitive elements of the environment do not occur (UN Organization for Economic Co-operation and Development, 1997). The objective of the CEMA (Cumulative Environmental Management Association) project, which my research is within, is to set a regional nitrogen critical load (CL) for the Regional Municipality of Wood Buffalo (RMWB). To reach this objective, various activities are being undertaken by collaborating researchers from Southern Illinois University Carbondale (SIUC), Villanova University, University of Victoria, and Trent University. My component of the project is monitoring plant responses, including growth and community change, for an experimental nitrogen fertilization study at a peatland site in Alberta, Canada. To quantify the N critical load for these peatland ecosystems, both plant responses and components of the peatland N cycle (e.g. N_2 fixation, N mineralization, nitrification, denitrification, and N leaching) must be monitored for deviations from their previously

undisturbed background behavior (CEMA grant). Once a nitrogen CL value is determined, it will hopefully be utilized in setting nitrogen oxide (NO_x) emission standards for the RMWB.

Research Plan

- *Study Site*

The study site is a peatland complex located near the hamlet of Mariana Lake, Alberta, Canada, approximately 101 km south of Fort McMurray, Alberta (N 55.89, W 112.09) (FIGURE 1.1). The site includes a large poor fen ($\approx$164,000 m^2) and two ombrotrophic bogs ($\approx$43,290 m^2). Both peatland landforms are dominated in the understory by *Sphagnum angustifolium*, *S. magellanicum*, *S. fuscum,* and the bog is wooded (*Picea mariana*). Annual bulk N deposition at the site is approximately 1 kg N ha^{-1} yr^{-1} [0.5 kg NH_4^+-N ha^{-1} yr^{-1} and 0.5 kg NO_3^--N ha^{-1} yr^{-1}] (Vitt et al. 2003).

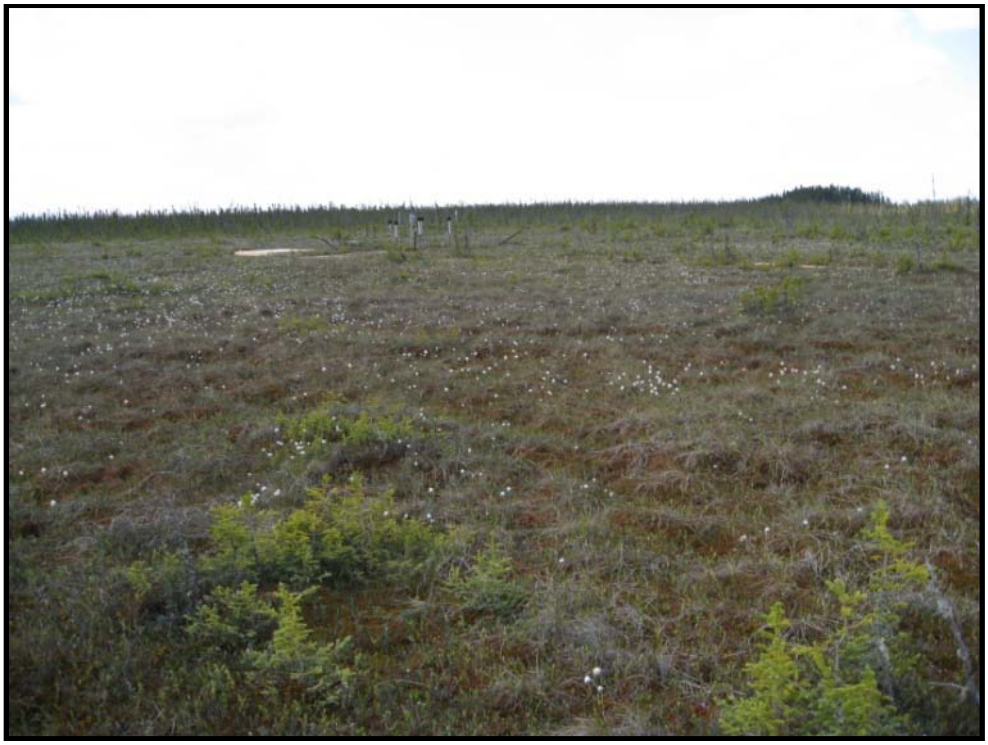

FIGURE 1.1 Photo of Mariana Lake study site, taken in poor fen looking toward wooded bog (left) and a mineral island (right).

❖ *Experimental Design*

At Mariana Lake there are forty-two experimental plots – half in an ombrotrophic bog, the other half in the poor fen – with varying N fertilization treatments ranging from 0 kg N/ha/year to 25 kg N/ha/year (FIGURE 1.2). The twenty-one plots in each area (bog and poor fen) are located on three replicate arms, with each arm having the following seven treatment plots: water control, 0, 5, 10, 15, 20, and 25 kg N ha/year. The water control plots do not receive any nitrogen or water addition. The 0 kg N/ha/year treatment plots (N treatment control plots) do not receive any nitrogen addition, but they do receive the same amount of additional water as the nitrogen addition plots to account for any benefit that the extra water may provide the plants. During each fertilization event, the water added to each plot was approximately 205 L (54 gallons); since each year there are eight fertilizations, 1642 L (432 gallons) of water is added to each plot per year (again, excluding the water control plots), which amounts to 288 mm of water over a 7.2 m^2 plot (5 x 15 feet).

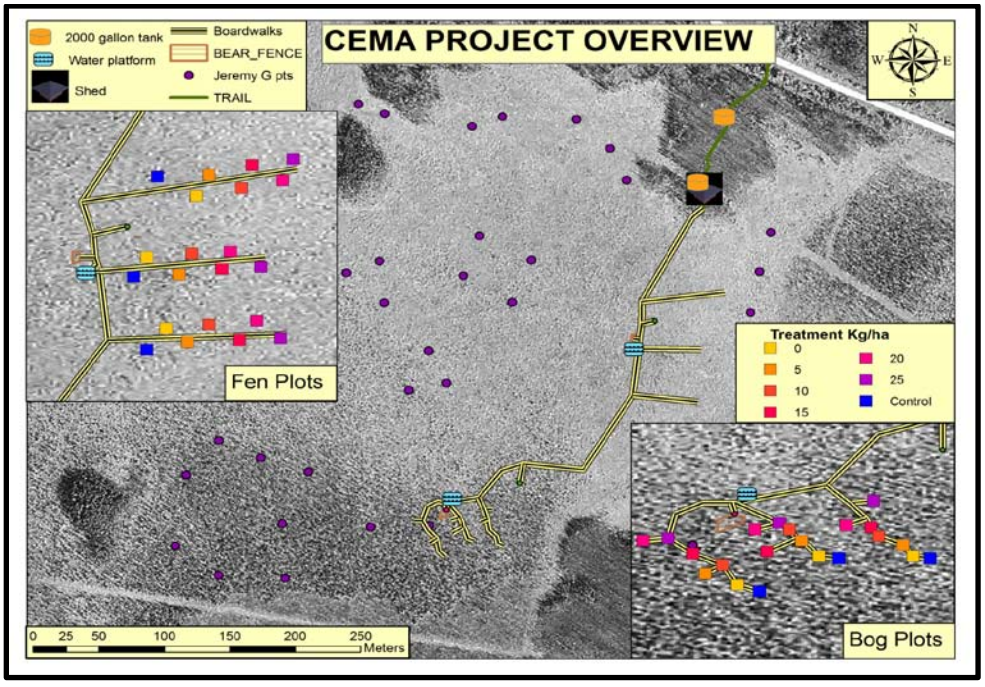

FIGURE 1.2 Mariana Lake Study Site – boardwalk and plot layout

CHAPTER II

PLANT RESPONSES TO INCREASED NITROGEN DEPOSITION – NITROGEN UPTAKE AND *SPHAGNUM* GROWTH RESPONSE

INTRODUCTION

Peatlands characteristically have high, stable water tables and greater rates of primary production than decomposition (Vitt 2006; Wieder and Lang 1983). Peatlands have low productivity (Frolking et al. 1998), thus formation of peat is attributed more to extremely low decomposition rates rather than to high rates of production (Vitt 1990; Moore and Basiliko 2006). The presence of peat mosses (*Sphagnum* spp.) has been shown to be strongly linked with the capacity for peat formation (van Breemen 1995), partly because their litter decays much more slowly than that of other plants (Clymo and Hayward 1982). *Sphagnum* is considered to be the most important plant contributing to peat accumulation, at least for bogs and poor fens (Wieder 2006).

Sphagnum growth and production is influenced by an array of factors including nutrients (especially nitrogen), atmospheric CO_2 levels, and climate and moisture (Wieder 2006). In this chapter, I investigate how *Sphagnum* growth and production are influenced by experimental nitrogen (N) fertilization treatments. Prior research has found varying impacts on *Sphagnum* growth and production with N additions due to variables including the background levels of atmospheric N deposition and the severity and duration of the N additions. In areas with low background levels of N deposition, such as northern Sweden and parts of North America, N additions sometimes enhanced *Sphagnum* production (Aerts et al. 1992; Li and Vitt

1997; Rochefort et al. 1990; Vitt et al. 2003). However, in other studies, N additions had no effect or had a detrimental effect on *Sphagnum* production (Berendse et al. 2001; Gunnarsson and Rydin 2000; Heijmans et al. 2001; Limpens et al. 2004).

Under low background N conditions and with increasing nitrogen addition, the first expected plant response should be increased nitrogen uptake and subsequently, increased growth (Lamers et al. 2000). To investigate nitrogen uptake by plants at the Mariana Lake study site, I measured nitrogen (N) and carbon (C) concentrations of *Sphagnum* capitulum tissue and vascular plant foliar tissue. For *Sphagnum* species, I also analyzed C:N ratios and capitulum N storage. To investigate potential growth response of the target *Sphagnum* species, measurements were taken for linear growth (the vertical elongation of the *Sphagnum* shoots), stem mass density (the weight of *Sphagnum* stems occupying a volume after capitula were removed), and ultimately, net primary production (the product of the prior two measurements). Capitulum mass density (biomass) was measured as well to investigate possible changes in *Sphagnum* capitulum growth.

Questions and Hypotheses

Nitrogen uptake:

***Question #1*:** How is the N concentration (%N) of *Sphagnum* capitulum affected by various supplementary N influxes (0, 5, 10, 15, 20, and 25 kg/ha/yr)?

Hypothesis #1: The N concentration (%N) of *Sphagnum* capitulum will increase with increasing N addition.

***Rationale #1*:** This result would be seen if the bog and poor fen ecosystems at Mariana Lake displayed a triphasic response to elevated N deposition, such as that observed in European peat bogs. With increased N deposition, N would no longer be a limit to *Sphagnum* growth. The

organic N concentration in living *Sphagnum* tissues would increase as more N would be taken up by the growing moss layer.

***Question #2*:** How is the N concentration (%N) of vascular plant foliar tissue affected by various supplementary N influxes (0, 5, 10, 15, 20, and 25 kg/ha/yr)?

Hypothesis #2: An increase in the N concentration (%N) of vascular plant foliar tissue will be observed following an increase in the N concentration (%N) of *Sphagnum* capitulum with increasing N addition.

***Rationale #2*:** As I discuss above, I predict that the nitrogen concentration (%N) of *Sphagnum* will increase with increasing N addition. Once *Sphagnum* becomes super-saturated with N, the excess N would then leach down to the lower peat layers where it would become available for vascular plant species. As vascular plants in peatlands are N-limited, the net primary production (NPP) of these plants would increase with an increased N supply. It has been shown for low nutrient environments that once a level is reached where the vascular plant NPP is no longer N-limited, the vascular plants exhibit luxury consumption, increasing the N concentrations in their tissues in excess of immediate growth requirements (Chapin 1980).

<u>*Sphagnum* growth response</u>:

Question #3: How is *Sphagnum* production affected by various supplementary N influxes (0, 5, 10, 15, 20, and 25 kg/ha/yr)?

Hypothesis #3: *Sphagnum* production in the 20 and 25 kg/ha/yr treatment plots will be lower than production in the 0, 5, 10, and 15 kg/ha/yr treatment plots in the second year of N fertilization applications (summer 2012).

***Rationale #3*:** Lamers et al. (2000) observed an apparent failure of *Sphagnum* mosses to intercept new N inputs in regions where N deposition rates exceeded approximately 20 kg N/ha/yr. At high levels of N deposition *Sphagnum* become super-saturated and eventually reach a limit where they cannot take in any more nitrogen. When this occurs, additional N inputs then go to the organic matter profile and may supply vascular plant species with the opportunity to colonize and proliferate. Increased vascular shrub NPP can negatively affect *Sphagnum* NPP by increasing understory shade (Bonnett et al. 2010).

Study Site

Site Description:

The study site is a peatland complex located near the hamlet of Mariana Lake, Alberta, Canada, approximately 101 km south of Fort McMurray, Alberta (N 55.89, W 112.09) (FIGURE 2.1). The site includes a large poor fen (≈164,000 m^2) and two ombrotrophic bogs (≈43,290 m^2). Both peatland landforms are dominated in the understory by *Sphagnum angustifolium*, *S. magellanicum*, *S. fuscum,* and the bog is wooded (*Picea mariana*). Annual bulk N deposition at the site is approximately 1 kg N ha^{-1} yr^{-1} [0.5 kg NH_4^+-N ha^{-1} yr^{-1} and 0.5 kg NO_3^--N ha^{-1} yr^{-1}] (Vitt et al. 2003).

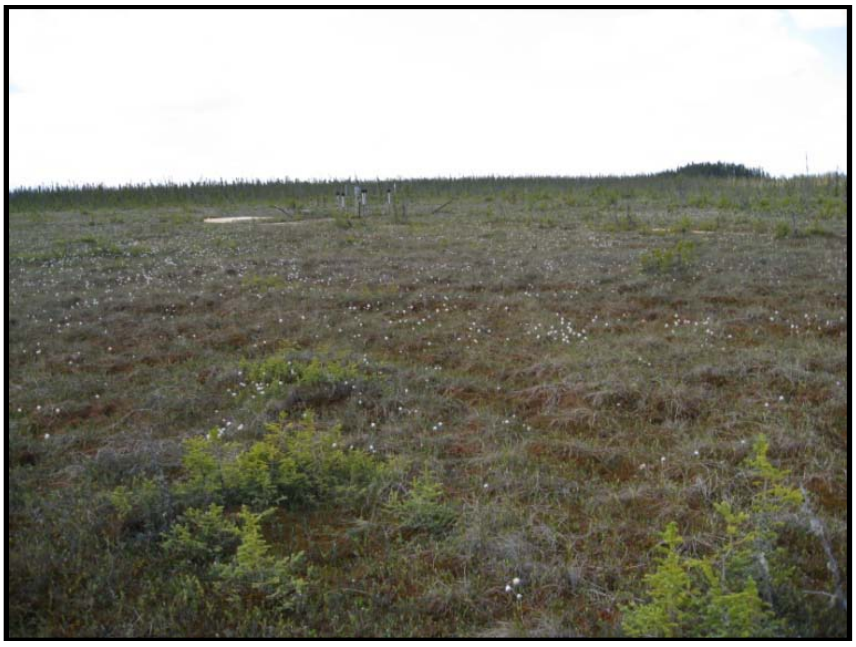

FIGURE 2.1 Photo of Mariana Lake study site, taken in poor fen looking toward wooded bog (left) and a mineral island (right).

Experimental Design:

At Mariana Lake there are forty-two experimental plots – half in an ombrotrophic bog, the other half in the poor fen – with varying N fertilization treatments ranging from 0 kg N/ha/year to 25 kg N/ha/year (FIGURE 2.2). The twenty-one plots in each area (bog and poor fen) are located on three replicate arms, with each arm having the following seven treatment plots: water control, 0, 5, 10, 15, 20, and 25 kg N/ha/year. The water control plots do not receive any nitrogen or water addition. The 0 kg N/ha/year treatment plots (N treatment control plots) do not receive any nitrogen addition, but they do receive the same amount of additional water as the nitrogen addition plots to account for any benefit that the extra water may provide the plants. During each fertilization event, the water added to each plot was approximately 205 L (54 gallons); since each year there are eight fertilizations, 1642 L (432 gallons) of water is added to each plot per year (again, excluding the water control plots), which amounts to 288 mm of water over a 7.2 m^2 plot (5 x 15 feet).

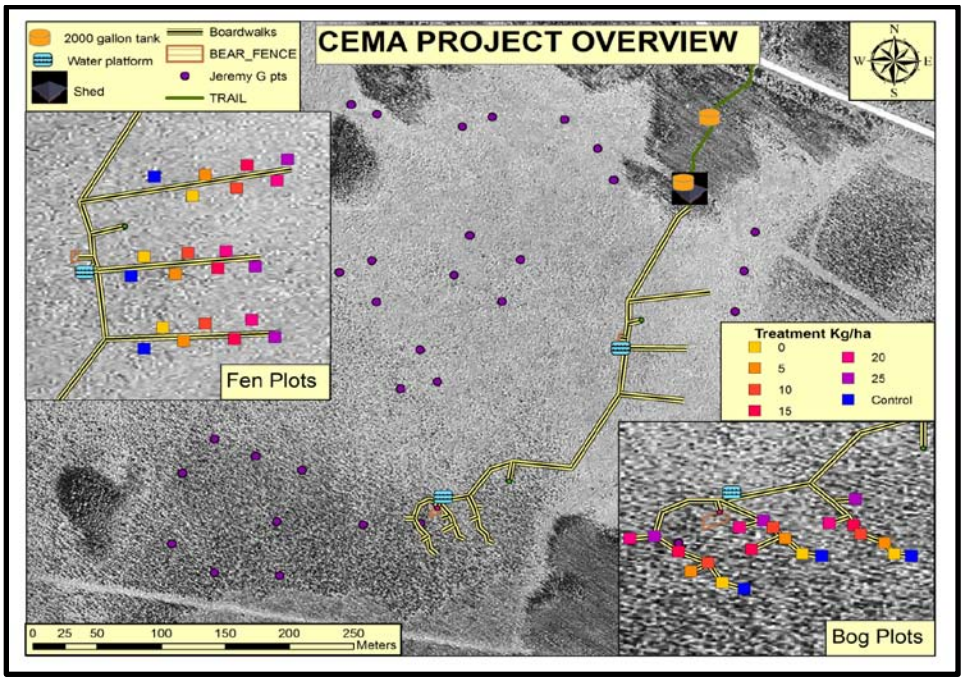

FIGURE 2.2 Mariana Lake Study Site – boardwalk and plot layout.

Atmospheric N Deposition:

Rates of bulk atmospheric deposition of ammonium (NH_4^+-N), nitrate (NO_3^--N), and sulfate (SO_4^{2-}-S) were determined using resin samplers (ion exchange beads housed in PVC) (2013 Annual CEMA Report). During the 2011 growing season (data taken from 5/31/11 to 10/9/11), the mean N deposition (NH_4^+-N and NO_3^--N) was 0.547 mg m^{-2} day^{-1} (TABLE 2.1). During the 2012 growing season (data taken from 5/24/12 to 10/18/12), the mean N deposition (NH_4^+-N and NO_3^--N) was 0.797 mg m^{-2} day^{-1} (TABLE 2.1).

TABLE 2.1 Mean ± SE, N, and Max./Min. values for daily NH_4^+, NO_3^-, and SO_4^{2-} deposition (mg m^{-2} day^{-1}) recorded at the Mariana Lake study site during three separate time intervals (Batch 1-3).
Source: K. Wieder, *personal communication*

BATCH 1 is 5/31/11 to 10/9/11
BATCH 2 is 10/9/11 to 5/24/12
BATCH 3 is 5/24/12 to 10/18/12

UNITS are $mg/m^2/day$

BATCH 1					
VARIABLE	MEAN	STD ERR	N	MAX	MIN
DAILY NH_4^+ DEP.	0.226	0.009	5	0.245	0.197
DAILY NH_3^- DEP.	0.321	0.015	5	0.353	0.278
DAILY SO_4^{2-} DEP.	1.466	0.048	5	1.584	1.329

BATCH 2					
VARIABLE	MEAN	STD ERR	N	MAX	MIN
DAILY NH_4^+ DEP.	0.062	0.004	5	0.077	0.050
DAILY NH_3^- DEP.	0.352	0.036	5	0.459	0.236
DAILY SO_4^{2-} DEP.	1.874	0.294	5	2.888	1.145

BATCH 3					
VARIABLE	MEAN	STD ERR	N	MAX	MIN
DAILY NH_4^+ DEP.	0.336	0.015	4	0.359	0.293
DAILY NH_3^- DEP.	0.461	0.020	4	0.497	0.405
DAILY SO_4^{2-} DEP.	1.800	0.049	4	1.881	1.657

Climate:

During the 2011 growing season (data taken from 6/8/11 to 10/4/11), the average daily temperature was 13.8 °C and the total precipitation was 217.4 mm (FIGURE 2.3). During the 2012 growing season (data taken from 6/8/12 to 9/12/12), the average daily temperature was 15.7 °C and the total precipitation was 355.3 mm (FIGURE 2.4). For the 2011 growing season (data taken from 6/8/11 to 9/12/11), growing degree days (GDD; summed daily mean temperatures above 0 °C) totaled 1442.5, and for the 2012 growing season (data taken from 6/8/12 to 9/12/12), GDD totaled 1520.3 (FIGURE 2.3 and 2.4).

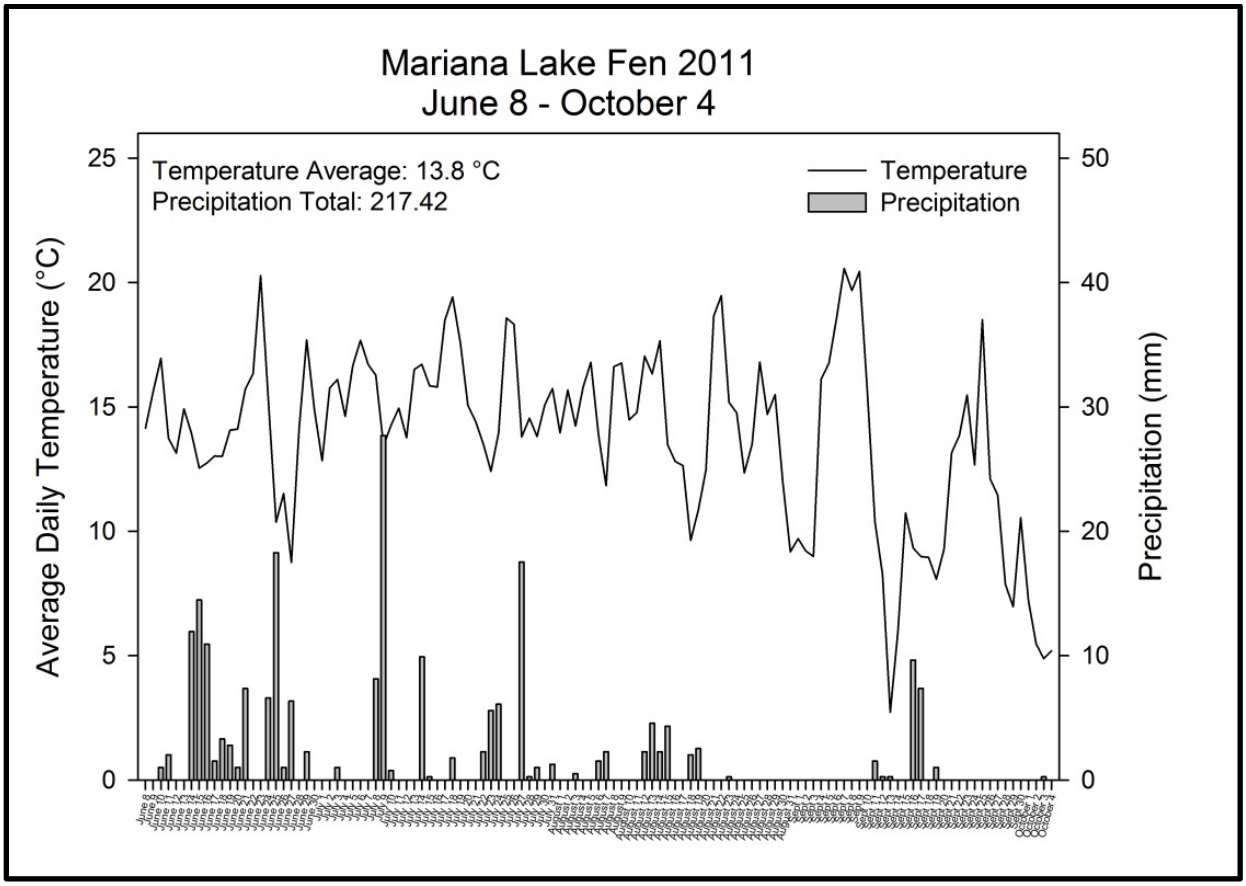

FIGURE 2.3 Average daily temperature (°C) and precipitation (mm) recorded at the Mariana Lake study site (poor fen) from 6/8/11 to 10/4/11. Source: Data from weather station at the Mariana Lake study site, operated by Dr. John Gibson, University of Victoria; figure made by Jeremy Graham, SIUC

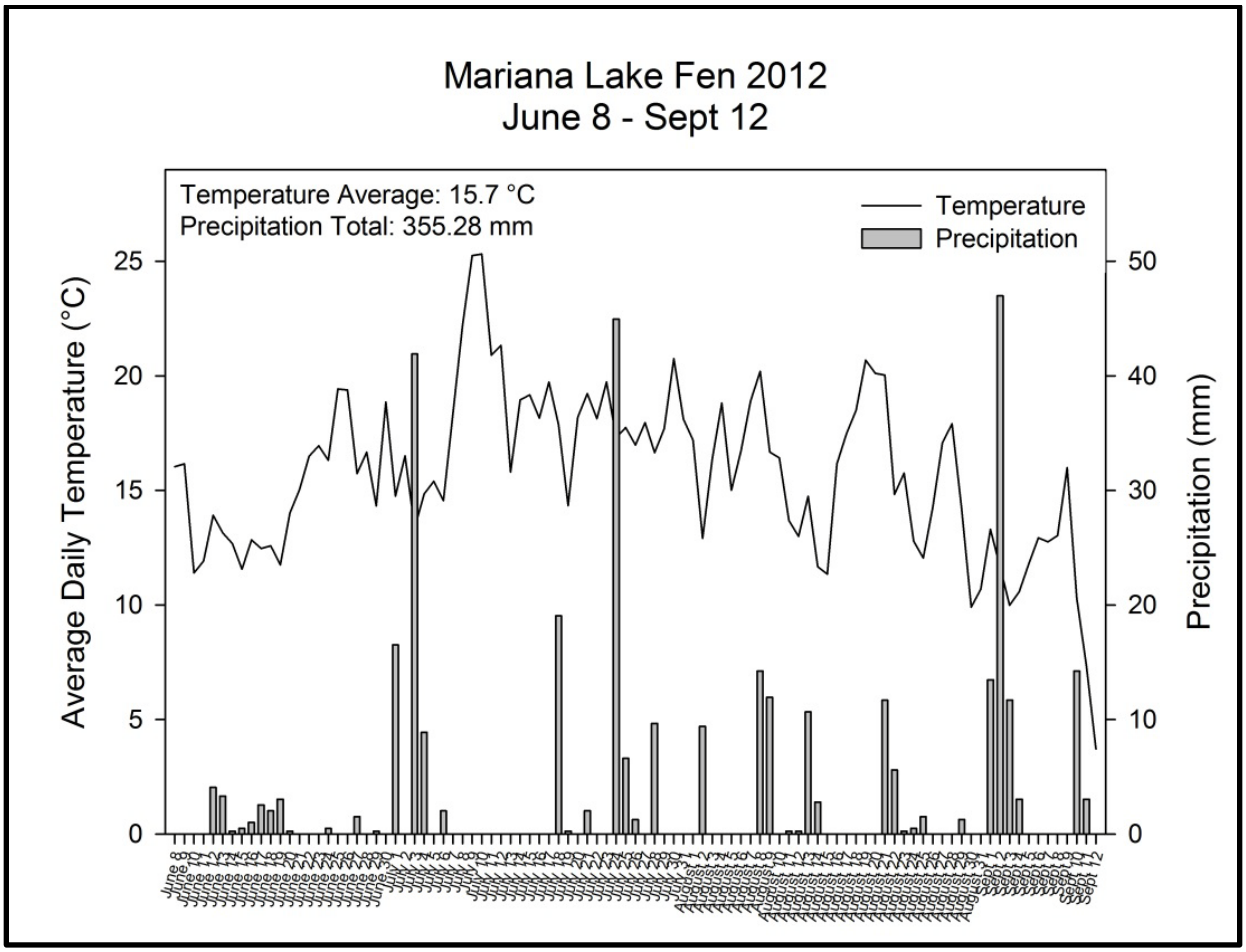

FIGURE 2.4 Average daily temperature (°C) and precipitation (mm) recorded at the Mariana Lake study site (poor fen) from 6/8/12 to 9/12/12. Source: Data from weather station at the Mariana Lake study site, operated by Dr. John Gibson, University of Victoria; figure made by Jeremy Graham, SIUC

METHODS

Nitrogen uptake

Field Sampling and Lab Techniques

At the height of each growing season (July 10th – 11th 2011 and July 12th-13th 2012), I collected volumetric samples of each species of *Sphagnum* located within each of the experimental plots – i.e. *Sphagnum fuscum, Sphagnum angustifolium,* and *Sphagnum magellanicum* – as well as five replicates of each *Sphagnum* species from areas outside the plots in both the bog and poor fen. These volumetric samples were used for mass density calculations. Capitula were removed and counted, and a selection of stems (70 stems for *S. fuscum* cores and 20 stems for *S. angustifolium* and *S. magellanicum* cores) were snipped at 2 cm below the capitulum. Capitulum and stem mass density samples were dried for a minimum of 4 days at 55°C, and then weighed to obtain respective mass densities. After being weighed, all capitulum samples were then homogenized in a Thomas Wiley Mini-Mill and analyzed for carbon (C) and nitrogen (N) concentrations on a Flash EA 1112 Series NC Soil Analyzer. The error rate for N was +/- 0.028 and the error rate for C was +/- 0.118.

At the height of each growing season (July 5th – 9th 2011 and July 8th – 11th 2012), I also collected that season's new growth from several vascular plant species (bog – *Smilacina trifolia, Rubus chamaemorus, Oxycoccos microcarpus, Ledum groenlandicum, Andromeda polifolia, Chamaedaphne calyculata,* and *Picea mariana;* poor fen - *Andromeda polifolia, Chamaedaphne calyculata*, *Eriophorum vaginatum,* and *Scheuchzeria palustris*) from all 42 plots as well as 5 replicates outside the plots in both the bog and poor fen. In order to ensure that I did not re-

sample the same plants in subsequent years, I banded plants that I collected from with colored zip-ties. This process was implemented for *Ledum groenlandicum* (purple zip-ties)*, Andromeda polifolia* (pink zip-ties)*,* and *Chamaedaphne calyculata* (yellow zip-ties) as these species are perennials and individuals will remain in the plot from year to year. *Picea mariana* individuals that were sampled were marked with orange flagging tape. All vascular plant samples were collected in paper bags and brought back to the lab where they were sorted. Only foliar material was used for the analysis, so for *Oxycoccus microcarpus*, leaves were removed from the stem, and for *Picea mariana*, needles were removed from the stem. After being sorted, samples were dried for a minimum of 4 days at 55°C. All samples were then homogenized in a Thomas Wiley Mini-Mill and analyzed for carbon (C) and nitrogen (N) concentrations on a Flash EA 1112 Series NC Soil Analyzer.

Nitrogen concentrations for *Sphagnum* capitula and vascular plant samples are represented as % N in biomass (mid-July). *Sphagnum* capitulum carbon to nitrogen ratios (C:N) also were compared. To analyze for capitulum N storage, the mass of capitula was extrapolated to g m^{-2} (assuming 100% cover for the *Sphagnum* species being analyzed) and multiplied by the nitrogen concentration (mid-July).

Statistical Analyses

Differences of nitrogen concentration (%N), carbon to nitrogen ratios (C:N), and capitulum N storage were analyzed by two-way ANOVA with N treatment and year as factors. Normality of residuals were tested using the Shapiro-Wilk's normality test ($\alpha = 0.05$) along with interpretation of Q-Q residual plots. If the data failed the Shapiro-Wilk's normality test, the data were then rank transformed, and Friedman's two-way nonparametric ANOVA was performed.

When running the two-way ANOVA analyses, I interpreted the output from the Type III tests. Type III tests analyze the significance of each factor while controlling for the level of the other factors. Post-hoc multiple comparisons were done by Tukey's HSD (honestly significant difference) test. For analyses using Friedman's two-way nonparametric ANOVA, post-hoc multiple comparisons were done using the Bonferroni-Dunn test. Statistics were calculated using SAS 9.2 (SAS 2009).

***Sphagnum* growth response**

Field Sampling and Lab Techniques

To investigate potential growth response of the target *Sphagnum* species, measurements were taken for linear growth (the vertical elongation of the *Sphagnum* shoots), stem mass density (the weight of *Sphagnum* stems occupying a volume after capitula were removed), and ultimately, net primary production (NPP). On May 25th-26th 2011, 30 wires were set in each plot following the cranked wire method (Clymo 1970). In the bog, cranked wires were placed exclusively in *S. fuscum,* and in the poor fen, wires were set to measure *S. fuscum, S. angustifolium* and *S. magellanicum*. Based on the dominant *Sphagnum* species composition in the plot, one plot in the poor fen had all 30 cranked wires in *S. fuscum*, one had 15 wires in *S. fuscum* and *S. angustifolium* each, three had 15 wires in *S. fuscum* and *S. magellanicum* each, nine had 15 wires in *S. angustifolium* and *S. magellanicum* each, and seven had 10 wires in *S. fuscum*, *S. angustifolium*, and *S. magellanicum* each. The wires were re-measured on October 7th-8th 2011, when air temperatures were below freezing and it was assumed that annual growth had ceased. By subtracting the height the cranked wire was initially set to at the start of the growing season (May 2011) from the measurement taken at the end of the growing season,

I was able to calculate 2011's linear *Sphagnum* spp. growth. The same method was used to calculate 2012's linear *Sphagnum* spp. growth (with measurements taken on May 24th-25th 2012 and October 5th-6th 2012).

Stem mass density is expressed as the mass of the top 1 cm of *Sphagnum* shoots excluding capitula in a meter squared with a unit of g cm^{-1} m^{-2}. Volumetric samples of *Sphagnum* were collected from each plot for mass density analysis at the height of the growing season (mid-July, 2011 and 2012) using a 6.5 cm diameter core. The core was a steel can, open on each end, with one side sharpened. Capitula were removed and counted, and a selection of stems (70 stems for *S. fuscum* cores and 20 stems for *S. angustifolium* and *S. magellanicum* cores) were snipped at 2 cm below the capitula. Capitula and stem mass density samples were dried for a minimum of 4 days at 55°C, and then weighed to obtain respective mass densities. The mass of stems was then divided by 2 to obtain the mass of 1 cm vertical growth for an area of 33 cm^2. Stem mass density was then extrapolated to g cm^{-1} m^{-2} by dividing by 33 cm^2 and then multiplying by 10,000 cm^2/m^2.

When extracting the *Sphagnum* cores, a location in the plot with full cover of the desired species was selected; however, there were often cores with *Sphagnum* plants other than the desired species. Therefore, in order to find the stem mass density of solely the desired species, the "foreigners" (the other *Sphagnum* spp. individuals) were accounted for. I measured the capitulum diameter (mm) of 20 individuals of *S. fuscum*, *S. angustifolium*, and *S. magellanicum* each, selected randomly from the study site outside of the treatment plots. I calculated the average capitulum diameter for each *Sphagnum* species and used that value in my calculations. For example, the average capitula diameter for *S. angustifolium* (based on

measurements from the sample of 20 individuals) was 8.6 mm (0.86 cm). I then calculated the area of one *S. angustifolium* individual using this value ($A = \pi \times (0.8563/2)^2 = 0.576$ cm^2). To account for the presence of "foreigners" in a core, I subtracted the estimated area of those "foreigners" from the total area of the core. Since capitula sometimes overlap each other when individuals are compacted, a correction factor (0.80) was multiplied to the area being subtracted so the estimated area more accurately expressed how much of the core those "foreigners" were occupying. For the "Bog – Arm 1 – 0 kg/ha" plot, there were 8 *S. angustifolium* individuals in the *S. fuscum* core that was taken in 2012. Thus, the area of 8 *S. angustifolium* individuals (= 8 x (0.576 cm^2) x 0.80) was subtracted from the total area of the core, and I was left with the area that only *S. fuscum* (the desired species for this core) occupied. I scaled this area back up to m^2 and I was able to calculate stem mass density (g cm^{-1} m^{-2}) for just *S. fuscum*.

Net primary production (NPP) was calculated as the product of the previous two measurements: Linear Growth (cm) x Stem Mass Density (g cm^{-1} m^{-2}) = NPP (g m^{-2} year^{-1}).

Sphagnum Community Response

The previous section addressed my investigation into how specific *Sphagnum* spp. (*S. fuscum*, *S. angustifolium*, and *S. magellanicum*) each responded to the N additions; however, I also investigated how the *Sphagnum* community as a whole responded to the N additions in the treatment plots. The estimated percent cover of each *Sphagnum* species utilized in this analysis was derived from the number of cranked wires placed in each *Sphagnum* species in each treatment plot. As detailed earlier, 30 wires were set in each plot following the cranked wire method (Clymo 1970). In the bog, cranked wires were placed exclusively in *S. fuscum,* and

in the poor fen, wires were set to measure *S. fuscum, S. angustifolium* and *S. magellanicum*. Based on the dominant *Sphagnum* species composition in the plot, one plot in the poor fen had all 30 cranked wires in *S. fuscum*, one had 15 wires in *S. fuscum* and *S. angustifolium* each, three had 15 wires in *S. fuscum* and *S. magellanicum* each, nine had 15 wires in *S. angustifolium* and *S. magellanicum* each, and seven had 10 wires in *S. fuscum*, *S. angustifolium*, and *S. magellanicum* each. Therefore, the twenty-one plots in the bog were assumed to have 100% *S. fuscum* cover for these analyses. In the poor fen, the plots that had 15 wires in two different *Sphagnum* sp. had 50% cover for each of those species and the plots that had 10 wires in three different *Sphagnum sp.* had 33.3 % cover for each of those species. Since data were collected on the specific *Sphagnum* sp. individually, to look at the *Sphagnum* community in each plot, I took the data values for each different *Sphagnum* sp. and multiplied them by the fraction of the plot they represented. For example, in the "Fen – Arm 1 – Control" plot, there were 15 cranked wires in *S. fuscum* (50% cover) and 15 cranked wires in *S. magellanicum* (50% cover); to look at the linear growth response of the *Sphagnum* community in this plot, I took the average linear growth value from the 15 wires in *S. fuscum* (for 2012, 3.64 cm) and multiplied it by 0.50, and then added the average linear growth value from the 15 wires in *S. magellanicum* (for 2012, 4.13 cm) multiplied by 0.50. This calculation [[(3.64 cm)(0.50) + (4.13 cm)(0.50)] = 3.9 cm] determines that the linear growth response of the *Sphagnum* community in the "Fen – Arm 1 – Control" plot is 3.9 cm (for the 2012 growing season). The linear growth response of the *Sphagnum* community in each treatment plot was determined in this manner, as well as stem mass density and net primary production (NPP).

Statistical Analyses

Differences of linear growth, stem and capitulum mass densities, production, and capitula weight were analyzed by two-way ANOVA with N treatment and year as factors. Normality of residuals were tested using the Shapiro-Wilk's normality test ($\alpha = 0.05$) along with interpretation of Q-Q residual plots. If the data failed the Shapiro-Wilk's normality test, the data were then rank transformed, and Friedman's two-way nonparametric ANOVA was performed. When running the two-way ANOVA analyses, I interpreted the output from the Type III tests. Type III tests analyze the significance of each factor while controlling for the level of the other factors. Post-hoc multiple comparisons were done by Tukey's HSD (honestly significant difference) test. For analyses using Friedman's two-way nonparametric ANOVA, post-hoc multiple comparisons were done using the Bonferroni-Dunn test. Statistics were calculated using SAS 9.2 (SAS 2009).

RESULTS

Nitrogen uptake

Sphagnum Capitulum N Concentration (%N)

N Treatment and Year Effects - Differences in capitulum N concentration (%N) were detected for year and N treatment for *S. fuscum* in the poor fen (year: $F = 71.01$, $p < 0.0001$; N: $F = 6.45$, $p = 0.003$) and *S. angustifolium* in the bog (year: $F = 47.65$, $p < 0.0001$; N: $F = 3.24$, $p = 0.022$), although for *S. fuscum* in the poor fen there was also a significant interaction ($F = 4.13$; $p = 0.022$) (FIGURE 2.6 and 2.7; TABLE 2.3)

Year Effects - For *S. angustifolium* in the poor fen there was only a significant difference in year ($F = 37.48$; $p < 0.0001$) (FIGURE 2.8; TABLE 2.3). %N values for *S. fuscum* in the bog and *S. magellanicum* in the poor fen both failed to meet normality assumptions (Shapiro-Wilk's test: $W = 0.869$, $p = 0.0002$; $W = 0.828$, $p = 0.0086$), and were examined using Friedman's two-way nonparametric ANOVA based on ranks (FIGURE 2.5 and 2.9; TABLE 2.3). For *S. fuscum* in the bog, there was a significant difference in year ($F = 48.51$; $p < 0.0001$) (FIGURE 2.5; TABLE 2.3).

No Effects - For *S. magellanicum* in the poor fen, there was a non-significant year ($F = 3.09$; $p = 0.113$) and N treatment ($F = 2.61$; $p = 0.107$) effect (FIGURE 2.9; TABLE 2.3)

Summary of Data - Capitulum N concentrations (%N) were, on average, higher in 2012 than in 2011 for all species, in both site types (bog and poor fen) (TABLE 2.2). In 2011, the mean *S. fuscum* %N in the bog was 1.1 and in 2012, the mean %N was 1.4 (TABLE 2.2). In 2011, the mean *S. fuscum* %N in the poor fen was 1.1 and in 2012, the mean %N was 1.3 (TABLE 2.2). In 2011, the mean *S. angustifolium* %N in the bog was 1.0 and in 2012, the mean %N was 1.2

(TABLE 2.2). In 2011, the mean *S. angustifolium* %N in the poor fen was 0.8 and in 2012, the mean %N was 1.2 (TABLE 2.2). In 2011, the mean *S. magellanicum* %N in the poor fen was 1.0 and in 2012, the mean %N was 1.3 (TABLE 2.2).

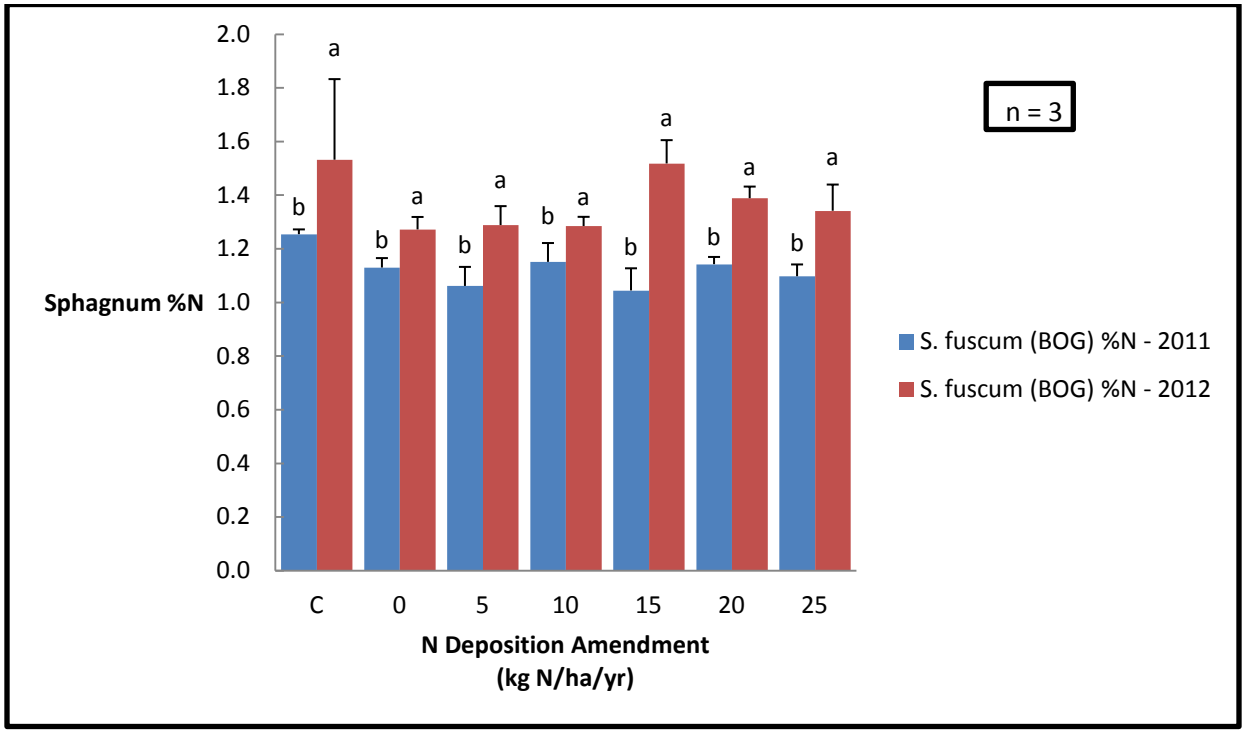

FIGURE 2.5 Mean %N values for *S. fuscum* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using the Bonferroni-Dunn post-hoc test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

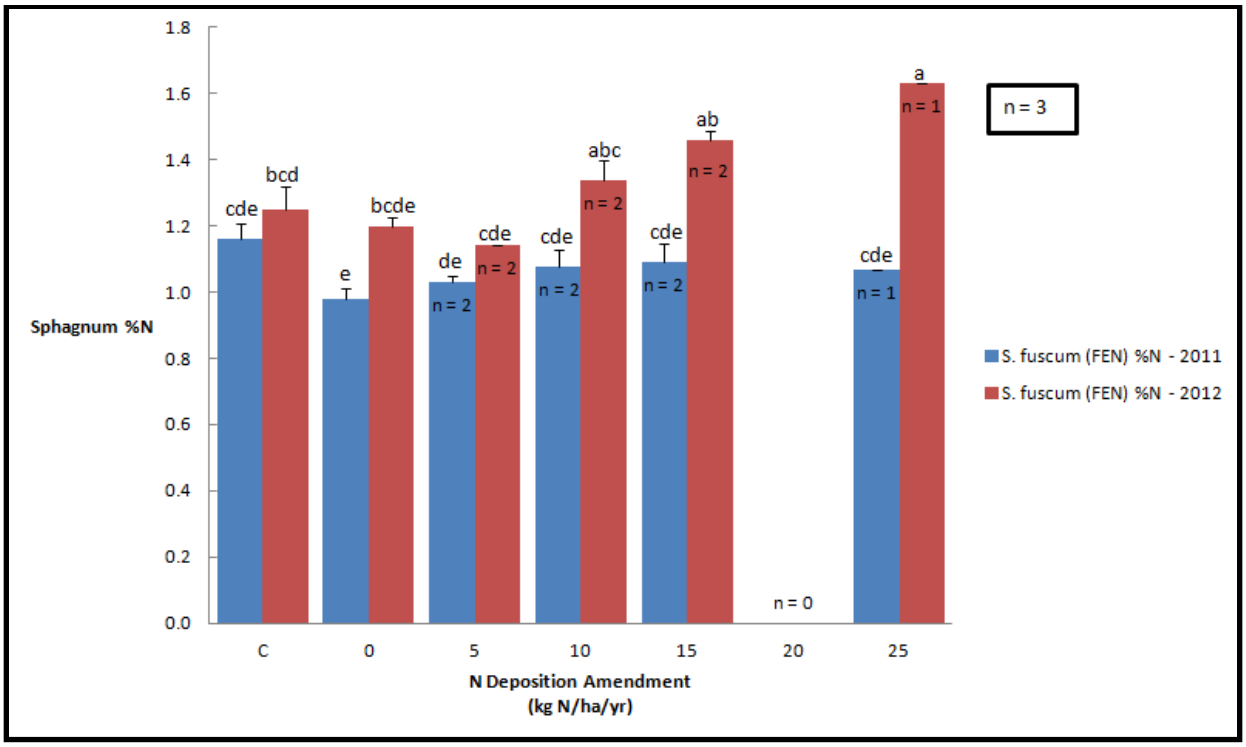

FIGURE 2.6 Mean %N values for *S. fuscum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

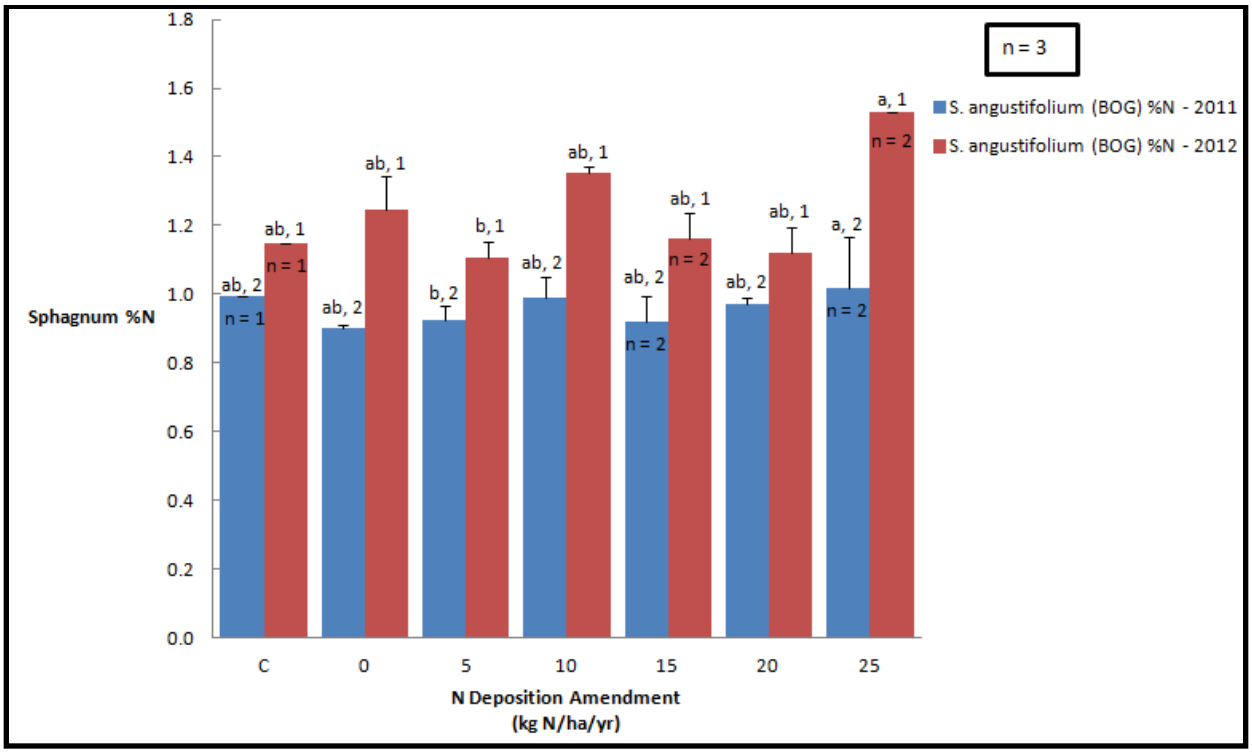

FIGURE 2.7 Mean %N values for *S. angustifolium* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters (N treatment) and numbers (year) above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

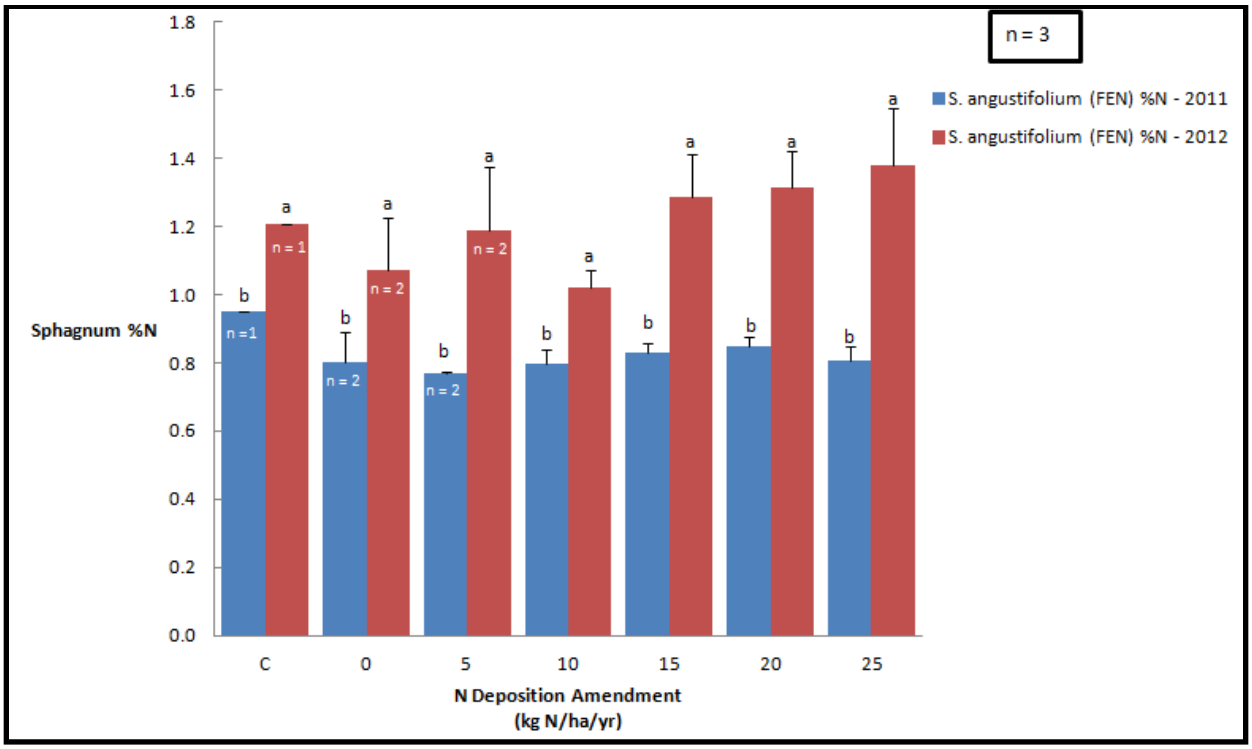

FIGURE 2.8 Mean %N values for *S. angustifolium* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

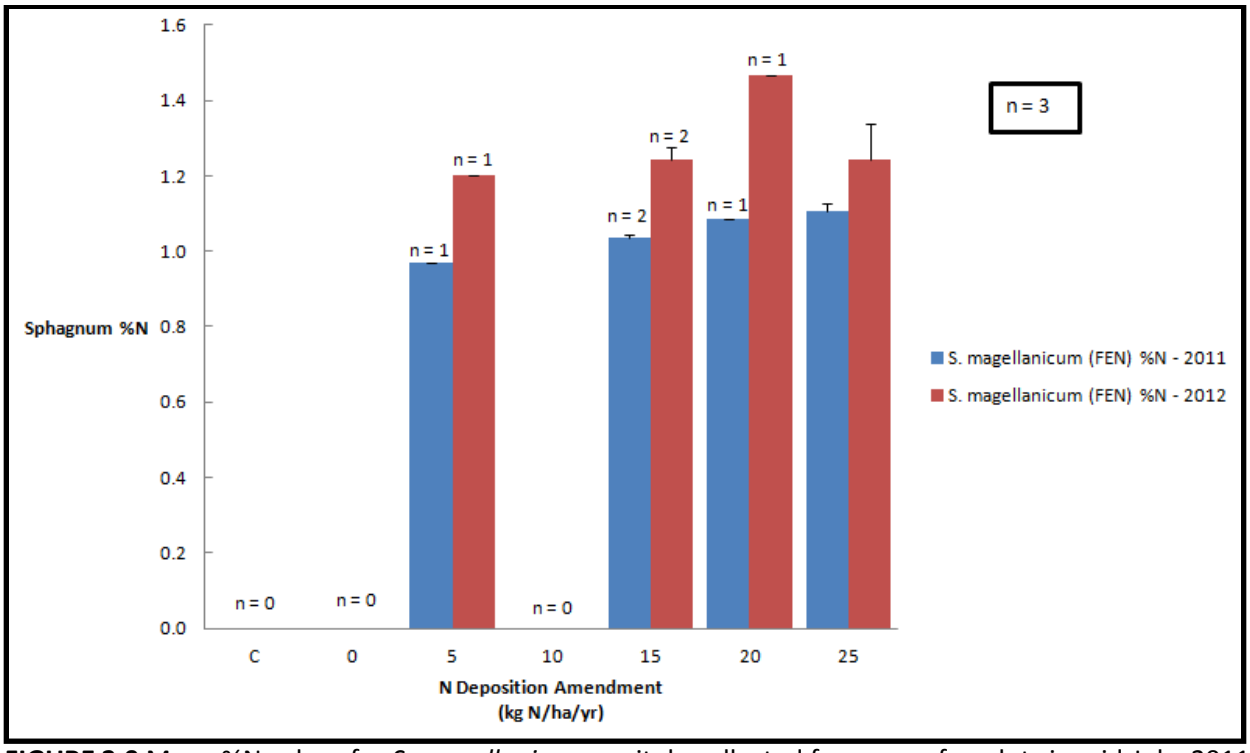

FIGURE 2.9 Mean %N values for *S. magellanicum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

TABLE 2.2 Mean N concentration (%N) values for *Sphagnum fuscum* (bog and poor fen), *S. angustifolium* (bog and poor fen), and *S. magellanicum* (poor fen) capitula collected from the treatment plots in mid-July, 2011 and 2012. Values represent means ± SE. When no standard error is noted, then n=1.

2011	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**% N**	**% N**	**% N**	**% N**	**% N**
Control	1.3 (± 0.02)	1.2 (± 0.05)	1.0	1.0	N/A
0 kg/ha	1.1 (± 0.04)	1.0 (± 0.03)	0.9 (± 0.01)	0.8 (± 0.09)	N/A
5 kg/ha	1.1 (± 0.07)	1.0 (± 0.02)	0.9 (± 0.04)	0.8 (± 0.008)	1.0
10 kg/ha	1.2 (± 0.07)	1.1 (± 0.05)	1.0 (± 0.06)	0.8 (± 0.04)	N/A
15 kg/ha	1.0 (± 0.08)	1.1 (± 0.05)	0.9 (± 0.08)	0.8 (± 0.03)	1.0 (± 0.01)
20 kg/ha	1.1 (± 0.03)	N/A	1.0 (± 0.02)	0.8 (± 0.03)	1.1
25 kg/ha	1.1 (± 0.04)	1.1	1.0 (± 0.2)	0.8 (± 0.04)	1.1 (± 0.02)
MEAN	1.1 (± 0.04)	1.1 (± 0.03)	1.0 (± 0.03)	0.8 (± 0.03)	1.0 (± 0.04)

2012	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**% N**	**% N**	**% N**	**% N**	**% N**
Control	1.5 (± 0.3)	1.2 (± 0.07)	1.1	1.2	N/A
0 kg/ha	1.3 (± 0.05)	1.2 (± 0.03)	1.2 (± 1.0)	1.1 (± 0.2)	N/A
5 kg/ha	1.3 (± 0.07)	1.1 (± 0.002)	1.1 (± 0.05)	1.2 (± 0.2)	1.2
10 kg/ha	1.3 (± 0.03)	1.3 (± 0.06)	1.4 (± 0.02)	1.0 (± 0.05)	N/A
15 kg/ha	1.5 (± 0.09)	1.5 (± 0.03)	1.2 (± 0.08)	1.3 (± 0.1)	1.2 (± 0.04)
20 kg/ha	1.4 (± 0.04)	N/A	1.1 (± 0.07)	1.3 (± 0.1)	1.5
25 kg/ha	1.3 (± 0.09)	1.6	1.5 (± 0.002)	1.4 (± 0.2)	1.2 (± 0.09)
MEAN	1.4 (± 0.06)	1.3 (± 0.11)	1.2 (± 0.09)	1.2 (± 0.07)	1.3 (± 0.07)

TABLE 2.3 Two-Way ANOVA results of N concentration (%N) for *Sphagnum fuscum*, *S. angustifolium*, and *S. magellanicum* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison.

	Sphagnum capitulum - %N									
	BOG - *S. fuscum*		FEN - *S. fuscum*		BOG - *S. angustifolium*		FEN - *S. angustifolium*		FEN - *S. magellanicum*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	0.96	0.467	6.45	**0.003**	3.24	**0.022**	1.03	0.434	2.61	0.107
YEAR	48.51	**< 0.0001**	71.01	**< 0.0001**	47.65	**< 0.0001**	37.48	**< 0.0001**	3.09	0.113
TREATMENT*YEAR	N/A	N/A	4.13	**0.016**	1.69	0.175	0.77	0.603	N/A	N/A

Vascular Plant Tissue N Concentration (%N):

BOG

N Treatment Effects - Differences in N concentration (%N) were detected for N treatment for *Oxycoccos microcarpus* in the bog (F = 4.01; *p* = 0.005) (FIGURE 2.10; TABLE 2.5).

Year Effects - For *Picea mariana* and *Chamaedaphne calyculata* in the bog there was a significant difference in year (F = 13.23, *p* = 0.001; F = 18.59, *p* = 0.0002) (FIGURE 2.13 and 2.15; TABLE 2.5).

No Effects - No differences in %N were detected for N treatment or year for *Rubus chamaemorus*, *Smilacina trifolia*, *Ledum groenlandicum*, and *Andromeda polifolia* in the bog (FIGURE 2.11, 2.12, 2.14, and 2.16; TABLE 2.5).

Summary of Data - In 2011, the mean *Oxycoccos microcarpus* %N in the bog was 1.6 and in 2012, the mean %N was 1.6 (TABLE 2.4). In 2011, the mean *Rubus chamaemorus* %N in the bog was 2.8 and in 2012, the mean %N was 2.8 (TABLE 2.4). In 2011, the mean *Smilacina trifolia* %N in the bog was 3.3 and in 2012, the mean %N was 3.2 (TABLE 2.4). In 2011, the mean *Picea mariana* %N in the bog was 0.8 and in 2012, the mean %N was 0.9 (TABLE 2.4). In 2011, the mean *Ledum groenlandicum* %N in the bog was 1.9 and in 2012, the mean %N was 1.8 (TABLE 2.4). In 2011, the mean *Chamaedaphne calyculata* %N in the bog was 2.0 and in 2012, the mean

%N was 1.8 (TABLE 2.4). In 2011, the mean *Andromeda polifolia* %N in the bog was 1.7 and in 2012, the mean %N was 1.6 (TABLE 2.4).

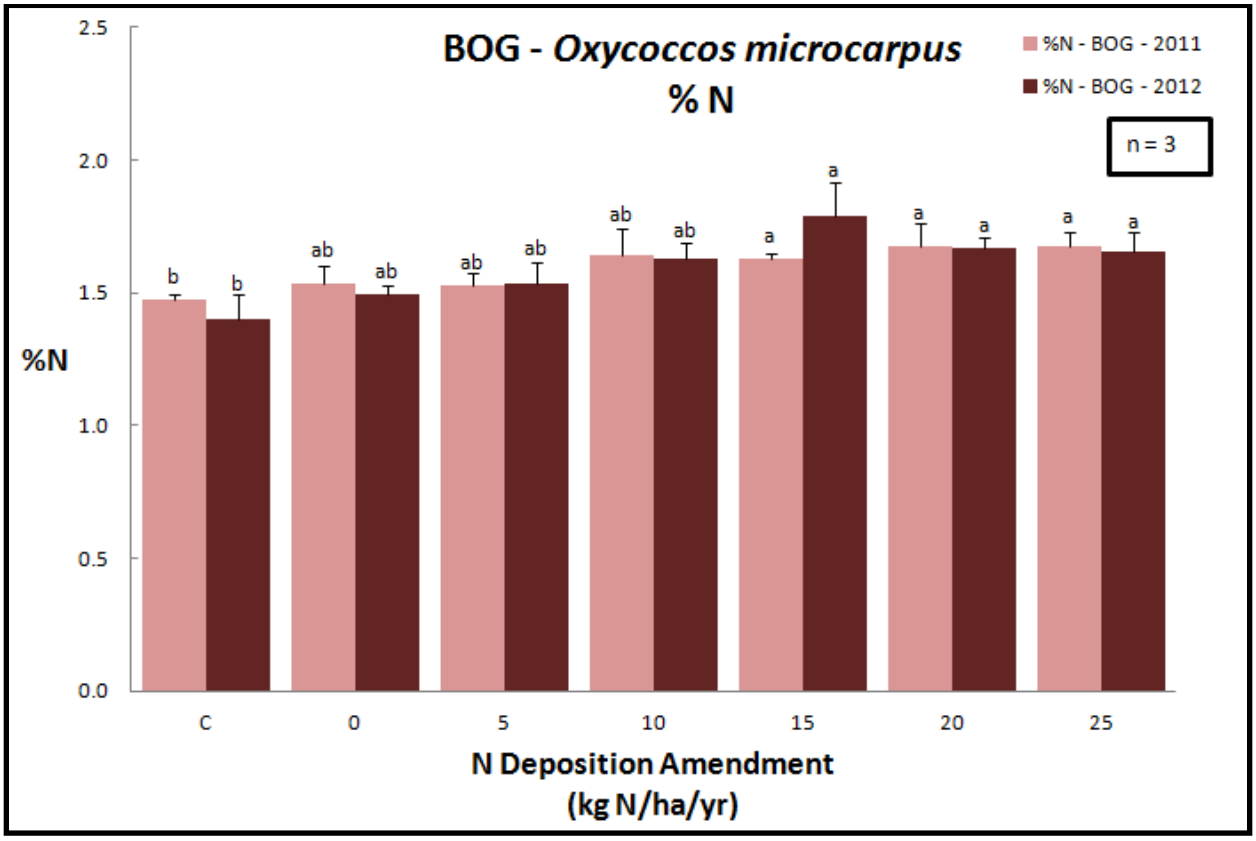

FIGURE 2.10 Mean %N values for *Oxycoccos microcarpus* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

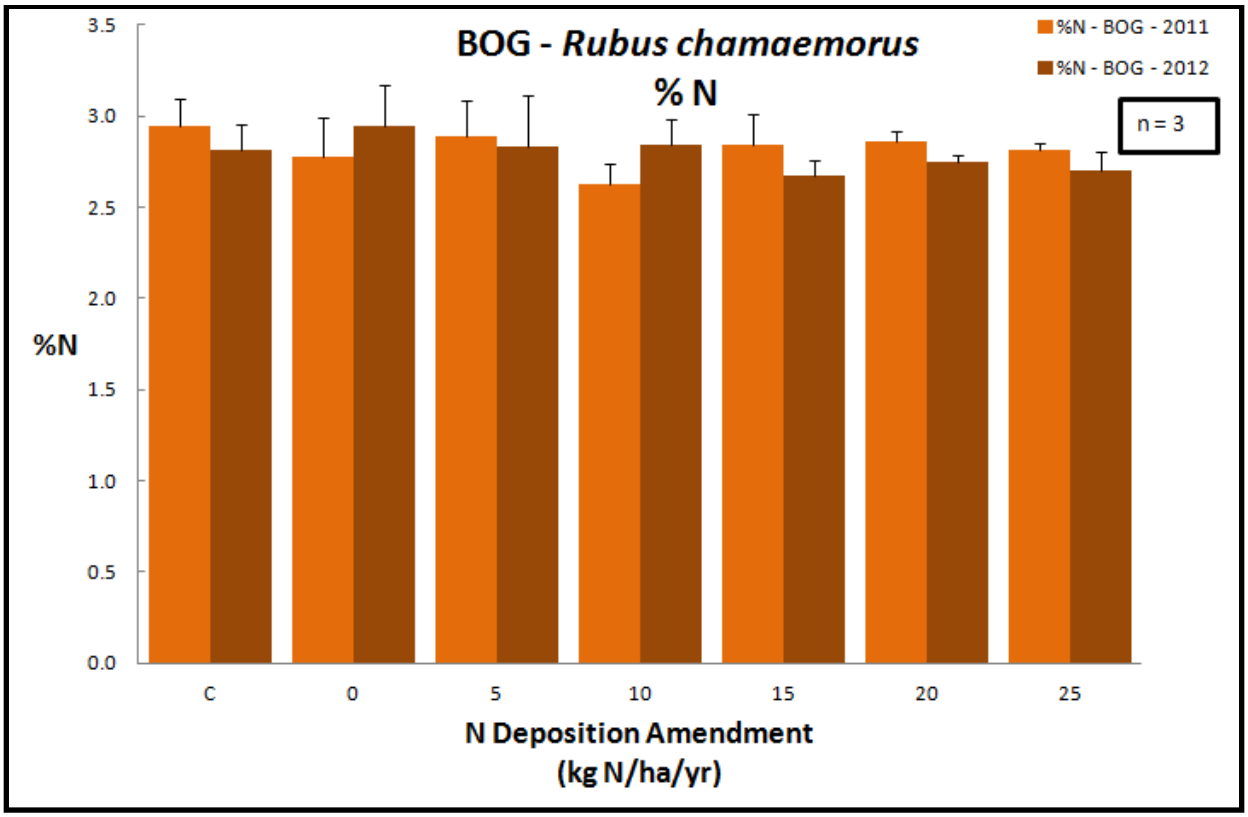

FIGURE 2.11 Mean %N values for *Rubus chamaemorus* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

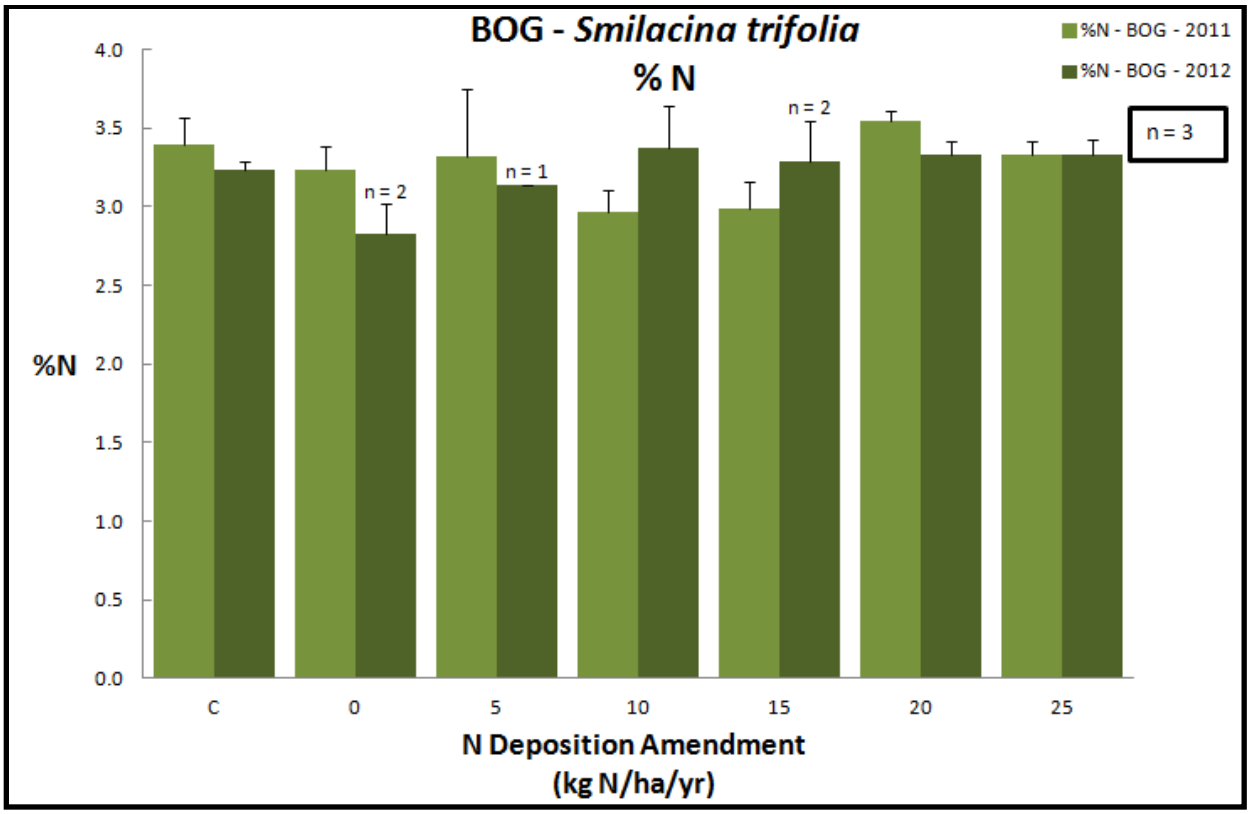

FIGURE 2.12 Mean %N values for *Smilacina trifolia* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

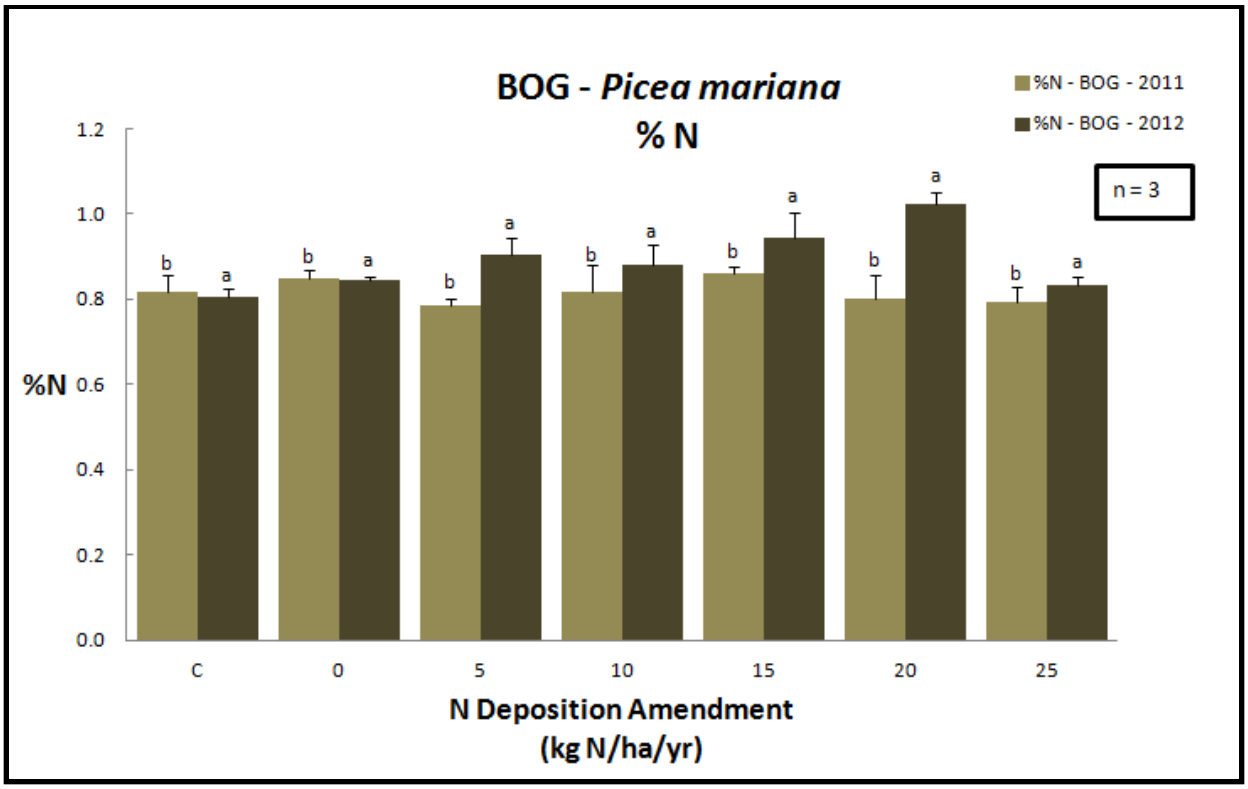

FIGURE 2.13 Mean %N values for *Picea mariana* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

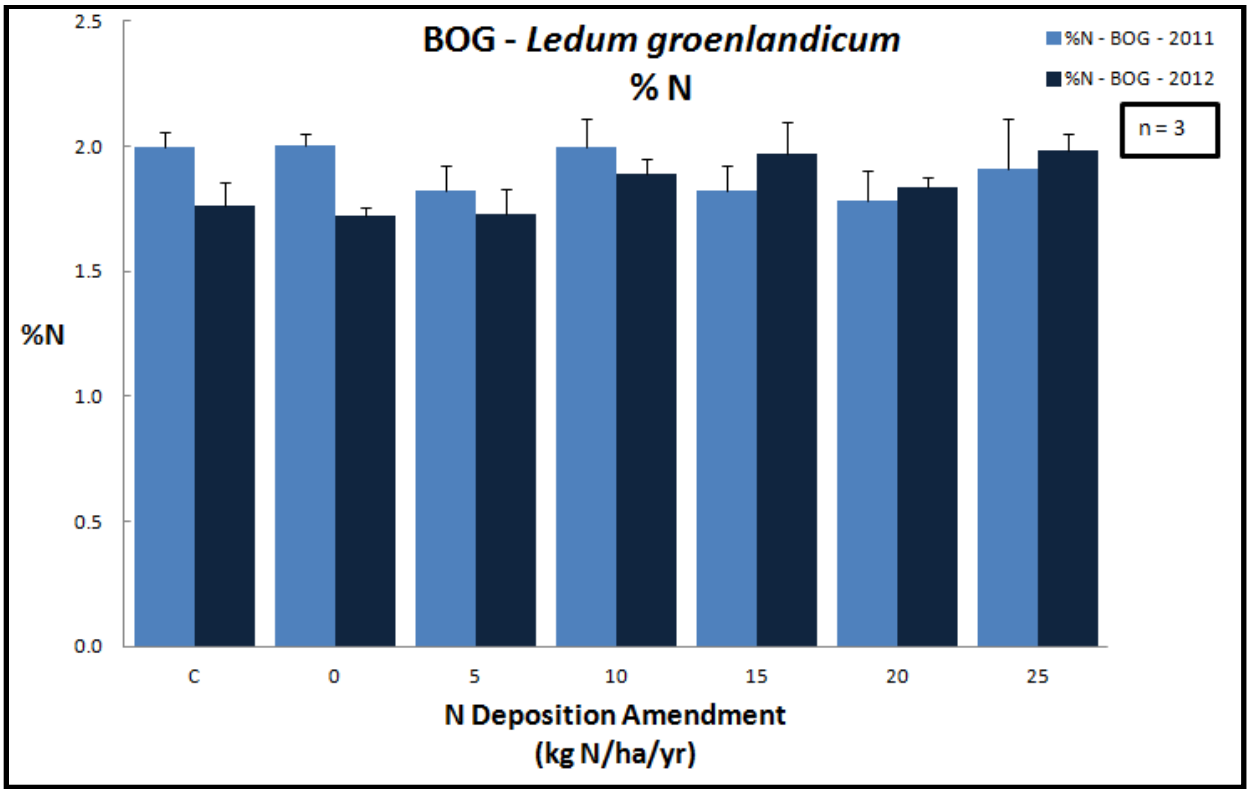

FIGURE 2.14 Mean %N values for *Ledum groenlandicum* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

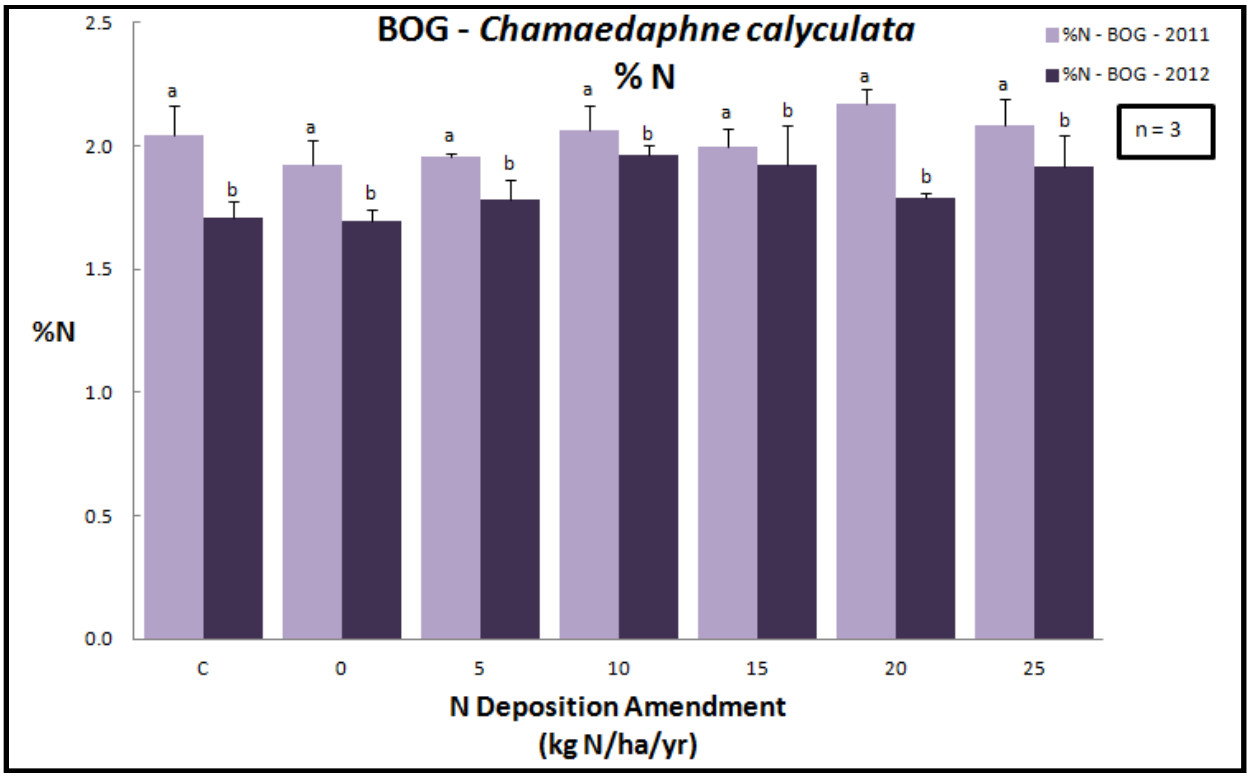

FIGURE 2.15 Mean %N values for *Chamaedaphne calyculata* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

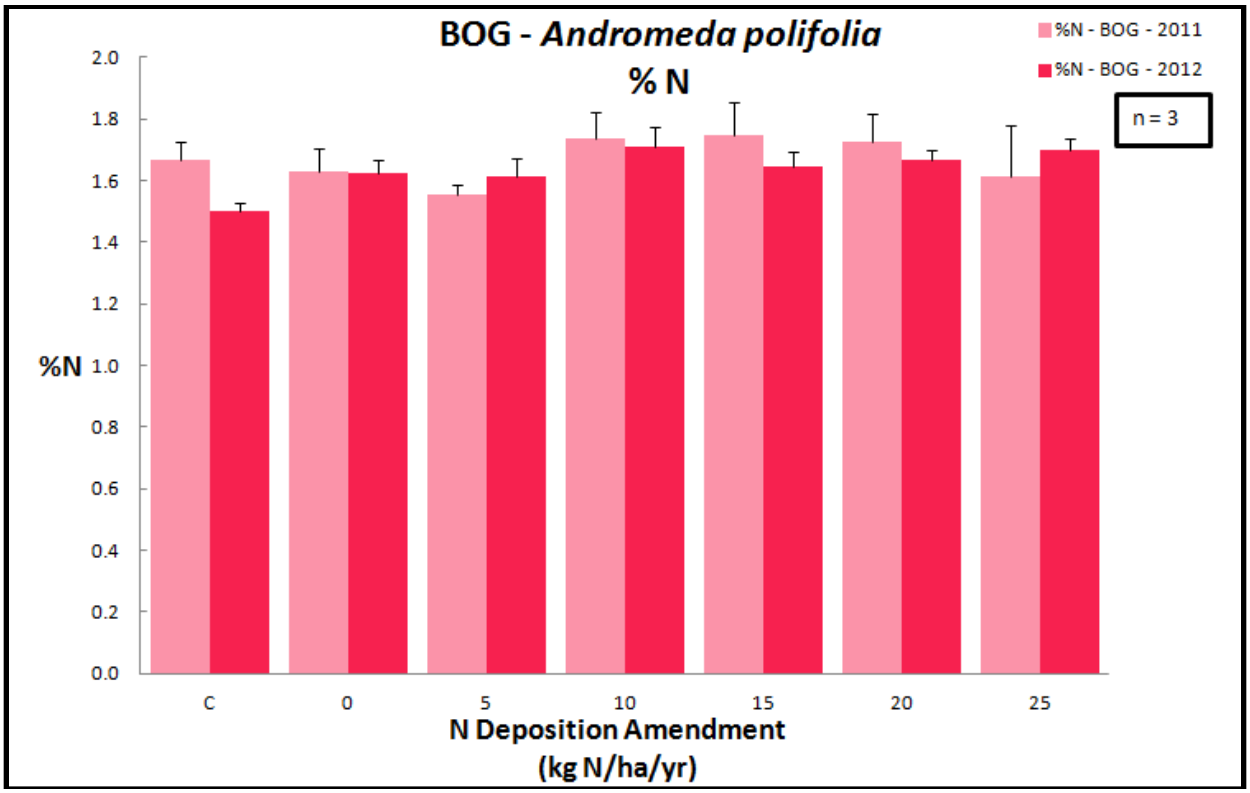

FIGURE 2.16 Mean %N values for *Andromeda polifolia* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

TABLE 2.4 Mean N concentration (%N) values for *Oxycoccos microcarpus, Rubus chamaemorus*, *Smilacina trifolia, Picea mariana*, *Ledum groenlandicum, Chamaedaphne calyculata,* and *Andromeda polifolia* samples collected from the bog treatment plots in mid-July, 2011 and 2012. Values represent means ± SE. When no standard error is noted, then n=1.

2011	*Oxycoccos microcarpus*	*Rubus chamaemorus*	*Smilacina trifolia*	*Picea mariana*	*Ledum groenlandicum*	*Chamaedaphne calyculata*	*Andromeda polifolia*
Treatment	**% N**	**% N**	**% N**	**% N**	**% N**	**% N**	**% N**
Control	1.5 (± 0.02)	2.9 (± 0.15)	3.4 (± 0.18)	0.8 (± 0.04)	2.0 (± 0.06)	2.0 (± 0.12)	1.7 (± 0.06)
0 kg/ha	1.5 (± 0.07)	2.8 (± 0.21)	3.2 (± 0.15)	0.8 (± 0.02)	2.0 (± 0.05)	1.9 (± 0.10)	1.6 (± 0.07)
5 kg/ha	1.5 (± 0.05)	2.9 (± 0.20)	3.3 (± 0.43)	0.8 (± 0.01)	1.8 (± 0.10)	2.0 (± 0.02)	1.6 (± 0.03)
10 kg/ha	1.6 (± 0.10)	2.6 (± 0.11)	3.0 (± 0.14)	0.8 (± 0.06)	2.0 (± 0.11)	2.1 (± 0.10)	1.7 (± 0.09)
15 kg/ha	1.6 (± 0.02)	2.8 (± 0.17)	3.0 (± 0.17)	0.9 (± 0.02)	1.8 (± 0.10)	2.0 (± 0.07)	1.7 (± 0.11)
20 kg/ha	1.7 (± 0.09)	2.9 (± 0.06)	3.5 (± 0.07)	0.8 (± 0.06)	1.8 (± 0.12)	2.2 (± 0.06)	1.7 (± 0.09)
25 kg/ha	1.7 (± 0.06)	2.8 (± 0.04)	3.3 (± 0.09)	0.8 (± 0.04)	1.9 (± 0.20)	2.1 (± 0.11)	1.6 (± 0.17)
MEAN	1.6 (± 0.05)	2.8 (± 0.06)	3.3 (± 0.12)	0.8 (± 0.02)	1.9 (± 0.06)	2.0 (± 0.05)	1.7 (± 0.04)

2012	*Oxycoccos microcarpus*	*Rubus chamaemorus*	*Smilacina trifolia*	*Picea mariana*	*Ledum groenlandicum*	*Chamaedaphne calyculata*	*Andromeda polifolia*
Treatment	**% N**	**% N**	**% N**	**% N**	**% N**	**% N**	**% N**
Control	1.4 (± 0.09)	2.8 (± 0.13)	3.2 (± 0.05)	0.8 (± 0.02)	1.8 (± 0.10)	1.7 (± 0.06)	1.5 (± 0.02)
0 kg/ha	1.5 (± 0.03)	2.9 (± 0.23)	2.8 (± 0.20)	0.8 (± 0.01)	1.7 (± 0.03)	1.7 (± 0.05)	1.6 (± 0.04)
5 kg/ha	1.5 (± 0.08)	2.8 (± 0.28)	3.1	0.9 (± 0.04)	1.7 (± 0.10)	1.8 (± 0.08)	1.6 (± 0.06)
10 kg/ha	1.6 (± 0.06)	2.8 (± 0.13)	3.4 (± 0.27)	0.9 (± 0.05)	1.9 (± 0.07)	2.0 (± 0.04)	1.7 (± 0.06)
15 kg/ha	1.8 (± 0.12)	2.7 (± 0.08)	3.3 (± 0.25)	0.9 (± 0.06)	2.0 (± 0.13)	1.9 (± 0.16)	1.6 (± 0.05)
20 kg/ha	1.7 (± 0.04)	2.7 (± 0.05)	3.3 (± 0.08)	1.0 (± 0.03)	1.8 (± 0.04)	1.8 (± 0.03)	1.7 (± 0.03)
25 kg/ha	1.7 (± 0.08)	2.7 (± 0.10)	3.3 (± 0.10)	0.8 (± 0.02)	2.0 (± 0.07)	1.9 (± 0.13)	1.7 (± 0.04)
MEAN	1.6 (± 0.07)	2.8 (± 0.05)	3.2 (± 0.11)	0.9 (± 0.04)	1.8 (± 0.06)	1.8 (± 0.06)	1.6 (± 0.04)

TABLE 2.5 Two-Way ANOVA results of N concentration (%N) for *Oxycoccos microcarpus, Rubus chamaemorus*, *Smilacina trifolia, Picea mariana*, *Ledum groenlandicum, Chamaedaphne calyculata,* and *Andromeda polifolia* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison.

	Vascular (BOG) - %N													
	Oxycoccos microcarpus		*Rubus chamaemorus*		*Smilacina trifolia*		*Picea mariana*		*Ledum groenlandicum*		*Chamaedaphne calyculata*		*Andromeda polifolia*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	4.01	**0.005**	0.29	0.939	0.91	0.502	2.22	0.070	0.79	0.582	1.47	0.224	1.11	0.383
YEAR	0.00	0.967	0.11	0.746	0.10	0.760	13.23	**0.001**	1.40	0.246	18.59	**0.0002**	0.58	0.454
TREATMENT*YEAR	0.56	0.756	0.48	0.818	1.01	0.441	2.19	0.074	1.30	0.290	0.79	0.585	0.67	0.672

POOR FEN

Year Effects - Differences in N concentration (%N) were detected for year for *Eriophorum vaginatum* (F = 7.49; *p* = 0.011) and *Chamaedaphne calyculata* (F = 14.05; *p* = 0.0008) in the poor fen (FIGURE 2.17 and 2.19; TABLE 2.7). %N values for *Scheuchzeria palustris* in the poor fen failed to meet normality assumptions (Shapiro-Wilk's test: W = 0.906; *p* = 0.0033), and were examined using Friedman's two-way nonparametric ANOVA based on ranks (FIGURE 2.18; TABLE 2.7). For *Scheuchzeria palustris* in the poor fen, there was a significant difference in year (F = 8.51; *p* = 0.007) (FIGURE 2.18; TABLE 2.7).

No Effects - No differences in %N were detected for N treatment or year for *Andromeda polifolia* in the poor fen (FIGURE 2.20; TABLE 2.7).

Summary of Data - In 2011, the mean *Eriophorum vaginatum* %N in the poor fen was 1.7 and in 2012, the mean %N was 1.9 (TABLE 2.6). In 2011, the mean *Scheuchzeria palustris* %N in the poor fen was 3.3 and in 2012, the mean %N was 3.1 (TABLE 2.6). In 2011, the mean *Chamaedaphne calyculata* %N in the poor fen was 2.1 and in 2012, the mean %N was 1.8 (TABLE 2.6). In 2011, the mean *Andromeda polifolia* %N in the poor fen was 1.7 and in 2012, the mean %N was 1.7 (TABLE 2.6).

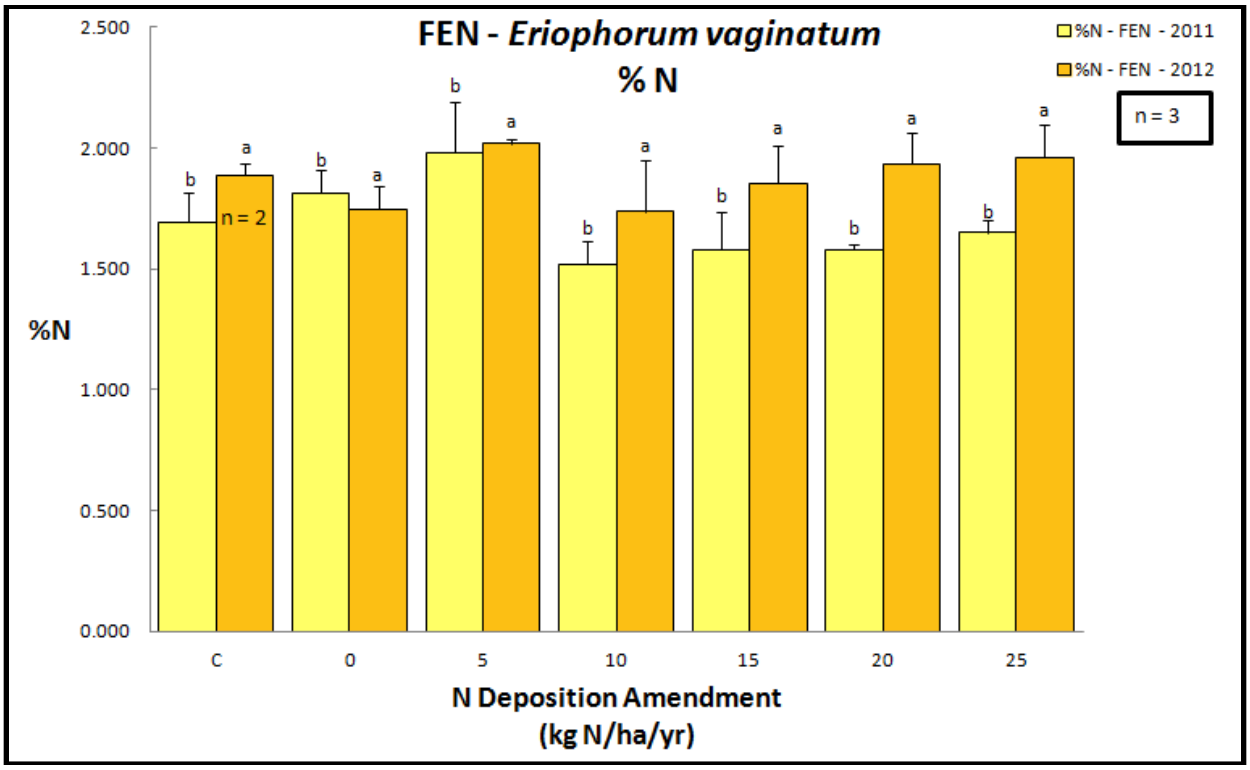

FIGURE 2.17 Mean %N values for *Eriophorum vaginatum* collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

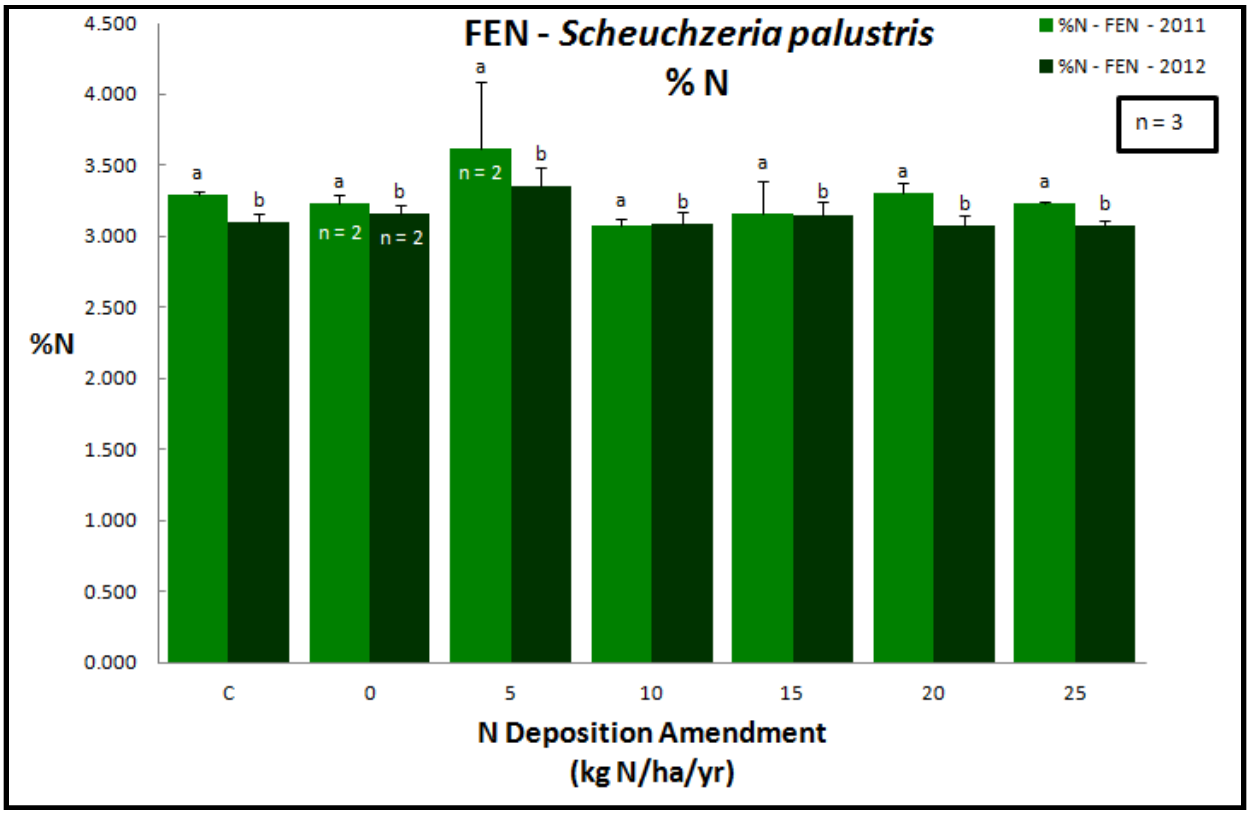

FIGURE 2.18 Mean %N values for *Scheuchzeria palustris* collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using the Bonferroni-Dunn post-hoc test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

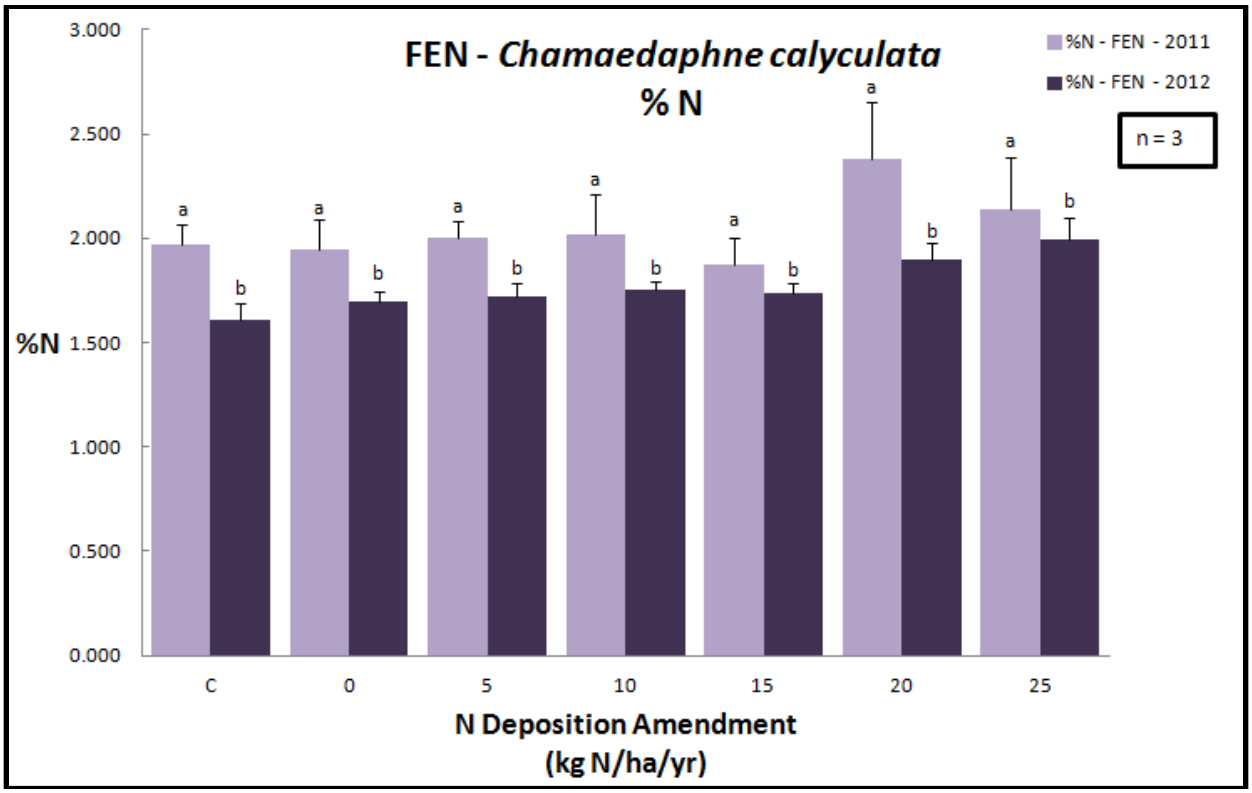

FIGURE 2.19 Mean %N values for *Chamaedaphne calyculata* collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

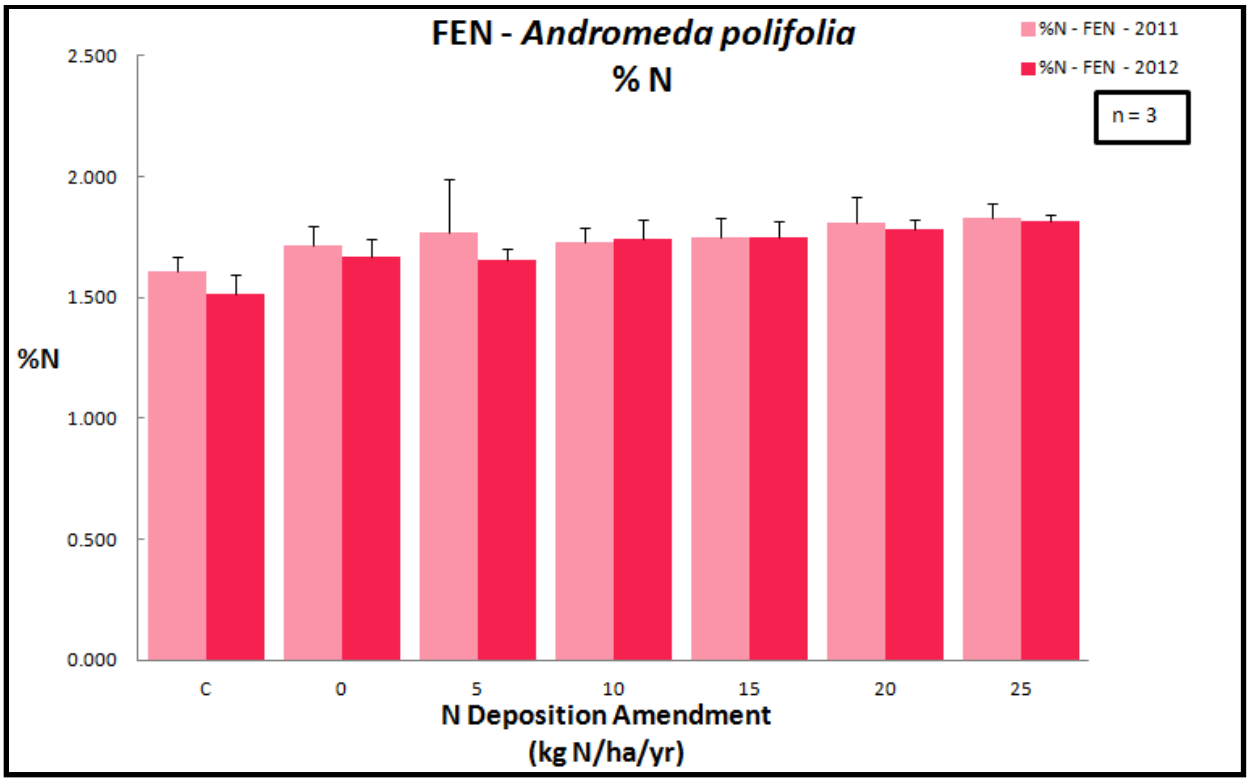

FIGURE 2.20 Mean %N values for *Andromeda polifolia* collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

TABLE 2.6 Mean N concentration (%N) values for *Eriophorum vaginatum*, *Scheuchzeria palustris, Chamaedaphne calyculata,* and *Andromeda polifolia* samples collected from the poor fen treatment plots in mid-July, 2011 and 2012. Values represent means ± SE.

2011	*Eriophorum vaginatum*	*Scheuchzeria palustris*	*Chamaedaphne calyculata*	*Andromeda polifolia*
Treatment	**% N**	**% N**	**% N**	**% N**
Control	1.7 (± 0.12)	3.3 (± 0.03)	2.0 (± 0.10)	1.6 (± 0.07)
0 kg/ha	1.8 (± 0.10)	3.2 (± 0.06)	1.9 (± 0.15)	1.7 (± 0.08)
5 kg/ha	2.0 (± 0.21)	3.6 (± 0.47)	2.0 (± 0.08)	1.8 (± 0.22)
10 kg/ha	1.5 (± 0.09)	3.1 (± 0.05)	2.0 (± 0.19)	1.7 (± 0.06)
15 kg/ha	1.6 (± 0.16)	3.2 (± 0.22)	1.9 (± 0.12)	1.7 (± 0.08)
20 kg/ha	1.6 (± 0.02)	3.3 (± 0.07)	2.4 (± 0.27)	1.8 (± 0.11)
25 kg/ha	1.6 (± 0.05)	3.2 (± 0.02)	2.1 (± 0.25)	1.8 (± 0.06)
MEAN	1.7 (± 0.09)	3.3 (± 0.10)	2.1 (± 0.10)	1.7 (± 0.04)

2012	*Eriophorum vaginatum*	*Scheuchzeria palustris*	*Chamaedaphne calyculata*	*Andromeda polifolia*
Treatment	**% N**	**% N**	**% N**	**% N**
Control	1.9 (± 0.05)	3.1 (± 0.06)	1.6 (± 0.08)	1.5 (± 0.08)
0 kg/ha	1.7 (± 0.10)	3.2 (± 0.06)	1.7 (± 0.05)	1.7 (± 0.08)
5 kg/ha	2.0 (± 0.02)	3.4 (± 0.13)	1.7 (± 0.06)	1.7 (± 0.05)
10 kg/ha	1.7 (± 0.21)	3.1 (± 0.09)	1.8 (± 0.04)	1.7 (± 0.08)
15 kg/ha	1.9 (± 0.15)	3.2 (± 0.09)	1.7 (± 0.05)	1.7 (± 0.07)
20 kg/ha	1.9 (± 0.13)	3.1 (± 0.07)	1.9 (± 0.08)	1.8 (± 0.04)
25 kg/ha	2.0 (± 0.13)	3.1 (± 0.03)	2.0 (± 0.10)	1.8 (± 0.03)
MEAN	1.9 (± 0.06)	3.1 (± 0.06)	1.8 (± 0.08)	1.7 (± 0.06)

TABLE 2.7 Two-Way ANOVA results of N concentration (%N) for *Eriophorum vaginatum*, *Scheuchzeria palustris, Chamaedaphne calyculata,* and *Andromeda polifolia* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison. %N values for *Scheuchzeria palustris* in the poor fen failed to meet normality assumptions (Shapiro-Wilk's test: W = 0.906; p = 0.0033), and were examined using Friedman's two-way nonparametric ANOVA based on ranks.

	Vascular (FEN) - %N							
	Eriophorum vaginatum		*Scheuchzeria palustris*		*Chamaedaphne calyculata*		*Andromeda polifolia*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	1.59	0.189	1.00	0.442	2.03	0.094	1.79	0.137
YEAR	7.49	**0.011**	8.51	**0.007**	14.05	**0.0008**	0.66	0.422
TREATMENT*YEAR	0.72	0.639	N/A	N/A	0.40	0.873	0.14	0.989

Sphagnum Capitulum C:N Ratios

N Treatment and Year Effects - Differences in C:N ratios were detected for year and N treatment for *S. fuscum* in the poor fen (year: $F = 75.27$, $p < 0.0001$; N: $F = 3.52$, $p = 0.029$) and *S. angustifolium* in the bog (year: $F = 52.70$, $p < 0.0001$; N: $F = 2.60$, $p = 0.049$) (FIGURE 2.22 and 2.23; TABLE 2.9).

Year Effects - For *S. fuscum* in the bog and *S. angustifolium* in the poor fen there was only a significant difference in year ($F = 50.36$, $p < 0.0001$; $F = 70.88$, $p < 0.0001$) (FIGURE 2.21 and 2.24; TABLE 2.9). C:N values for *S. magellanicum* in the poor fen failed to meet normality assumptions (Shapiro-Wilk's test: $W = 0.871$; $p = 0.043$), and were examined using Friedman's two-way nonparametric ANOVA based on ranks (FIGURE 2.25; TABLE 2.9). For *S. magellanicum* in the poor fen, there was a significant difference in year ($F = 5.24$; $p = 0.048$) (FIGURE 2.25; TABLE 2.9).

Summary of Data - C:N ratios were, on average, lower in 2012 than in 2011 for all species, in both site types (bog and poor fen) (TABLE 2.8). In 2011, the mean *S. fuscum* C:N ratio in the bog was 41.4 and in 2012, the mean C:N was 34.3 (TABLE 2.8). In 2011, the mean *S. fuscum* C:N ratio in the poor fen was 44.8 and in 2012, the mean C:N was 35.0 (TABLE 2.8). In 2011, the mean *S. angustifolium* C:N ratio in the bog was 47.7 and in 2012, the mean C:N was 37.3 (TABLE 2.8). In 2011, the mean *S. angustifolium* C:N ratio in the poor fen was 55.7 and in 2012, the mean C:N was 38.4 (TABLE 2.8). In 2011, the mean *S. magellanicum* C:N ratio in the poor fen was 43.1 and in 2012, the mean C:N was 34.9 (TABLE 2.8).

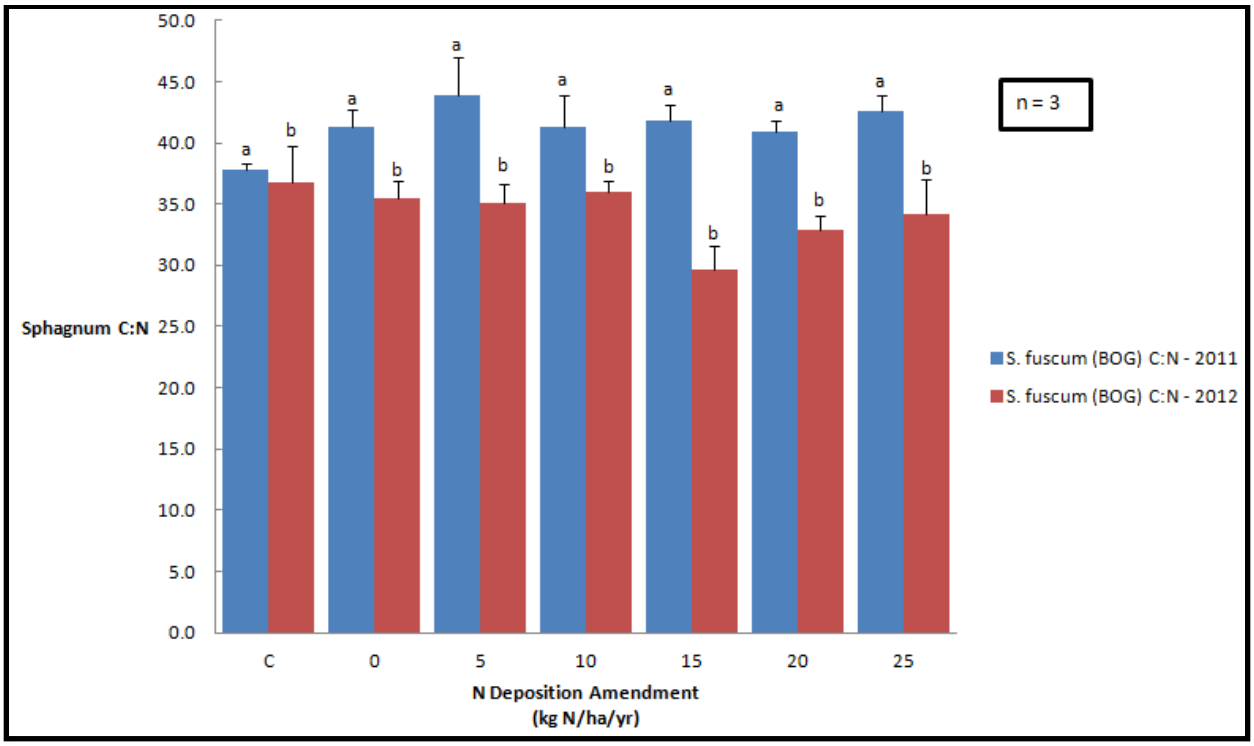

FIGURE 2.21 Mean C:N values for *S. fuscum* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

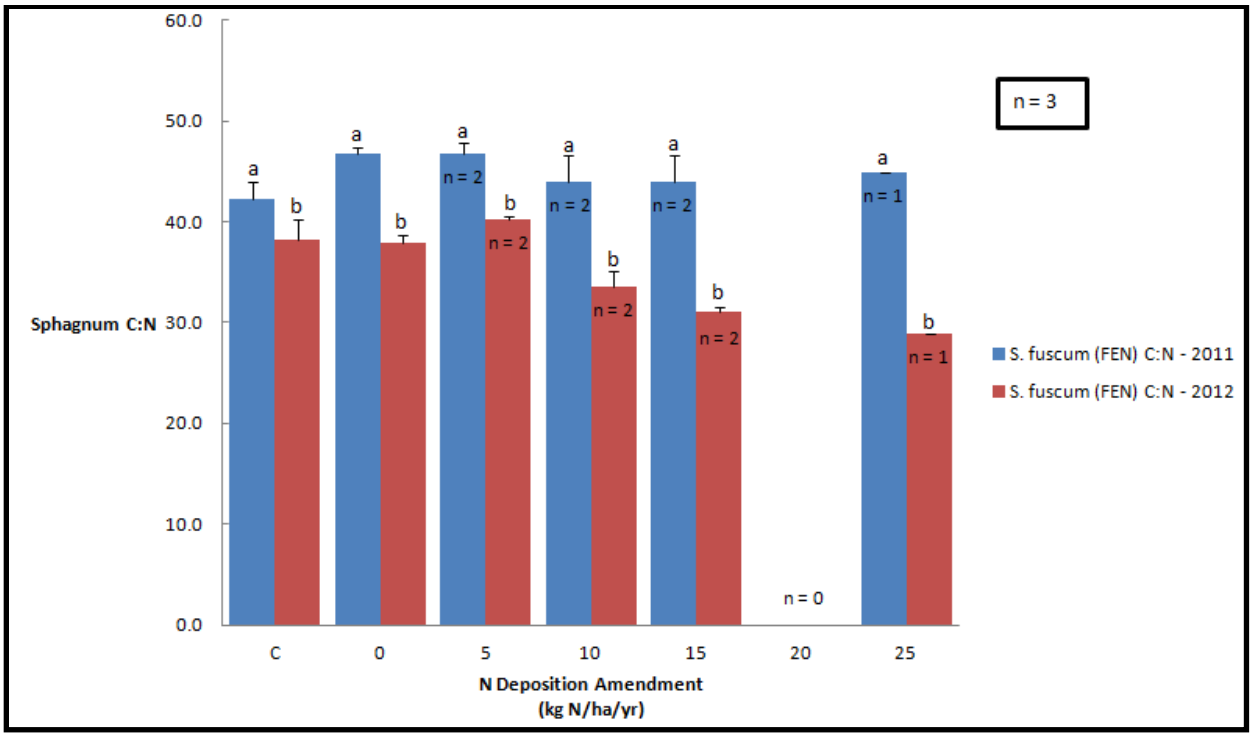

FIGURE 2.22 Mean C:N values for *S. fuscum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

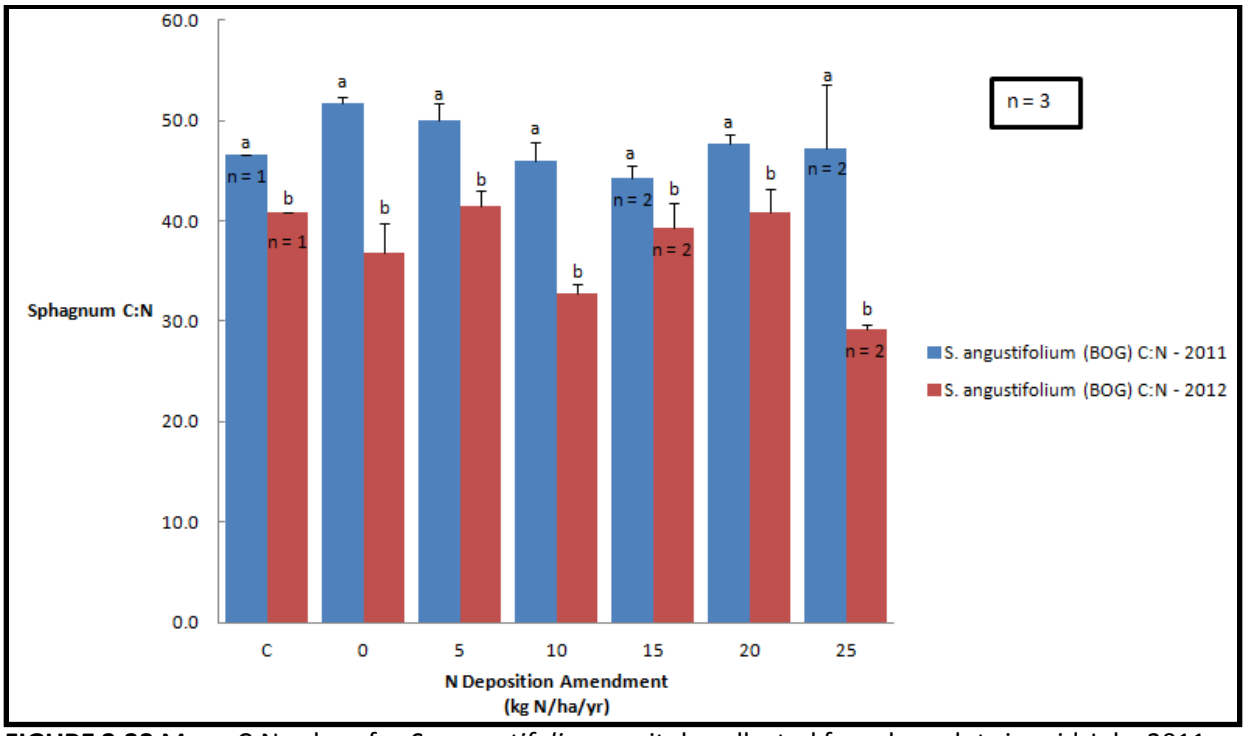

FIGURE 2.23 Mean C:N values for *S. angustifolium* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

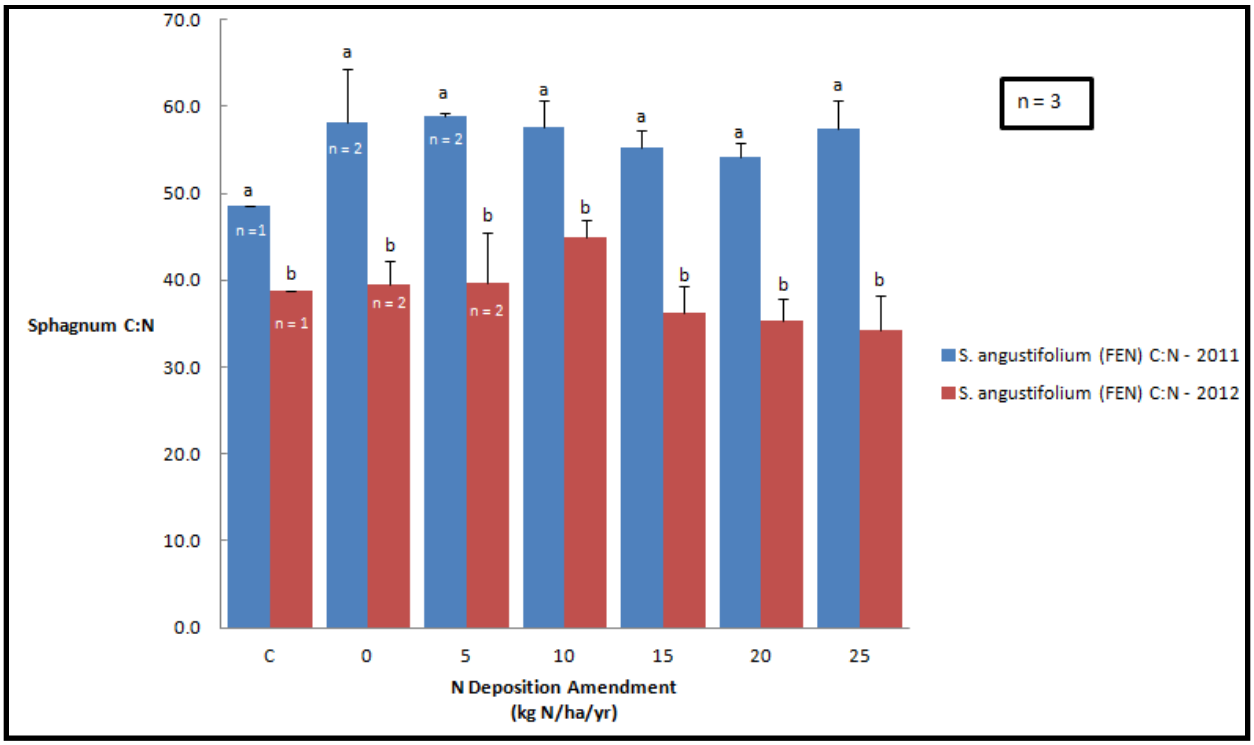

FIGURE 2.24 Mean C:N values for *S. angustifolium* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

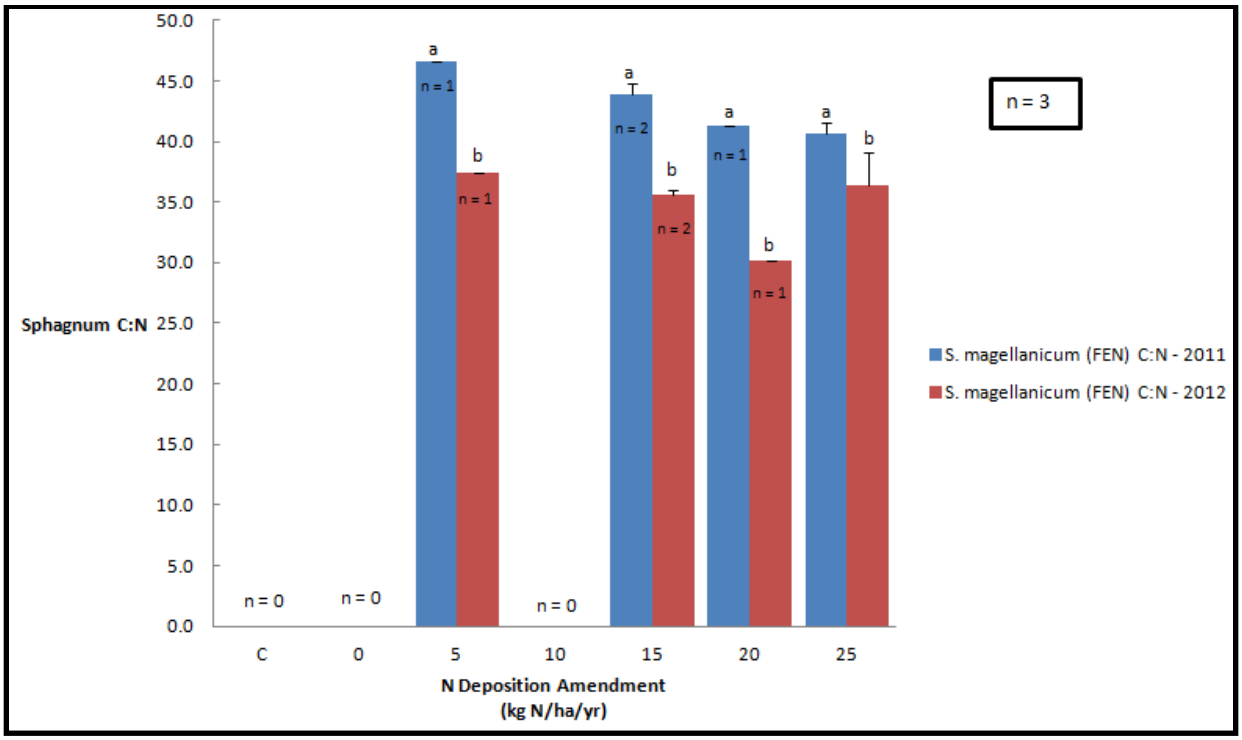

FIGURE 2.25 Mean C:N values for *S. magellanicum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

TABLE 2.8 Mean C:N values for *Sphagnum fuscum* (bog and poor fen), *S. angustifolium* (bog and poor fen), and *S. magellanicum* (poor fen) capitula collected from the treatment plots in mid-July, 2011 and 2012. Values represent means ± SE. When no standard error is noted, then n=1.

2011	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**C:N**	**C:N**	**C:N**	**C:N**	**C:N**
Control	37.8 (± 0.6)	42.2 (± 1.8)	46.6	48.6	N/A
0 kg/ha	41.3 (± 1.3)	46.8 (± 0.6)	51.8 (± 0.6)	58.2 (± 6.1)	N/A
5 kg/ha	44.0 (± 3.1)	46.8 (± 1.1)	50.0 (± 1.7)	58.9 (± 0.4)	46.6
10 kg/ha	41.3 (± 2.5)	44.0 (± 2.6)	46.0 (± 1.8)	57.6 (± 3.1)	N/A
15 kg/ha	41.8 (± 1.3)	44.0 (± 2.6)	44.3 (± 1.2)	55.3 (± 2.0)	43.9 (± 0.9)
20 kg/ha	40.9 (± 1.0)	N/A	47.7 (± 0.9)	54.2 (± 1.6)	41.3
25 kg/ha	42.6 (± 1.3)	44.9	47.2 (± 6.4)	57.4 (± 3.3)	40.7 (± 0.8)
MEAN	41.4 (± 1.1)	44.8 (± 1.0)	47.7 (± 1.5)	55.7 (± 2.1)	43.1 (± 1.6)

2012	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**C:N**	**C:N**	**C:N**	**C:N**	**C:N**
Control	36.8 (± 3.0)	38.2 (± 2.0)	40.8	38.9	N/A
0 kg/ha	35.5 (± 1.4)	37.9 (± 0.9)	36.8 (± 3.0)	39.4 (± 2.8)	N/A
5 kg/ha	35.1 (± 1.6)	40.2 (± 0.4)	41.4 (± 1.6)	39.7 (± 5.8)	37.4
10 kg/ha	36.1 (± 0.9)	33.6 (± 1.5)	32.8 (± 0.8)	44.9 (± 2.0)	N/A
15 kg/ha	29.7 (± 1.9)	31.1 (± 0.5)	39.3 (± 2.6)	36.2 (± 3.1)	35.6 (± 0.36)
20 kg/ha	32.8 (± 1.2)	N/A	40.8 (± 2.4)	35.3 (± 2.6)	30.2
25 kg/ha	34.1 (± 2.9)	29.0	29.2 (± 0.4)	34.2 (± 4.0)	36.3 (± 2.8)
MEAN	34.3 (± 1.4)	35.0 (± 2.6)	37.3 (± 2.7)	38.4 (± 2.1)	34.9 (± 1.9)

TABLE 2.9 Two-Way ANOVA results of C:N ratios for *Sphagnum fuscum*, *S. angustifolium*, and *S. magellanicum* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison. C:N values for *Sphagnum magellanicum* in the poor fen failed to meet normality assumptions (Shapiro-Wilk's test: W = 0.871; *p* = 0.043), and were examined using Friedman's two-way nonparametric ANOVA based on ranks.

	***Sphagnum* Capitula C:N**									
	BOG - *S. fuscum*		FEN - *S. fuscum*		BOG - *S. angustifolium*		FEN - *S. angustifolium*		FEN - *S. magellanicum*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	0.93	0.491	3.52	**0.029**	2.60	**0.049**	1.13	0.380	2.09	0.172
YEAR	50.36	**< 0.0001**	75.27	**< 0.0001**	52.70	**< 0.0001**	70.88	**< 0.0001**	5.24	**0.048**
TREATMENT*YEAR	1.73	0.15	2.32	0.099	1.80	0.151	0.65	0.693	N/A	N/A

Capitulum N Storage (CNS)

N Treatment and Year Effects - Differences in capitulum N storage were detected for year and N treatment for *S. fuscum* in the bog (year: F = 5.92, *p* = 0.022; N: F = 3.43, *p* = 0.012) and poor fen (year: F = 17.77, *p* = 0.0009; N: F = 7.82, *p* = 0.001) and *S. angustifolium* in the bog (year: F = 52.62, *p* < 0.0001; N: F = 2.80, *p* = 0.038; interaction: F = 3.65, *p* = 0.013) (FIGURE 2.26, 2.27, and 2.28; TABLE 2.11).

Year Effects - For *S. angustifolium* in the poor fen, there was only a significant difference in year (F = 86.27; *p* < 0.0001) (FIGURE 2.29; TABLE 2.11).

No Effects - For *S. magellanicum* in the poor fen, there was a non-significant year (F = 4.34; *p* = 0.083), N treatment (F = 0.40; *p* = 0.803), and interaction (F = 0.48; *p* = 0.709) effect (FIGURE 2.30; TABLE 2.11).

Summary of Data - Capitulum N storage was, on average, higher in 2012 than in 2011 for all species, in both site types (bog and poor fen), although *S. angustifolium* had the most drastic increases (TABLE 2.10). In 2011, the mean *S. fuscum* CNS in the bog was 1.2 g m^{-2} and in 2012, the mean CNS was 1.4 g m^{-2} (TABLE 2.10). In 2011, the mean *S. fuscum* CNS in the poor fen was 1.0 g m^{-2} and in 2012, the mean CNS was 1.5 g m^{-2} (TABLE 2.10). In 2011, the mean *S.*

angustifolium CNS in the bog was 0.9 g m^{-2} and in 2012, the mean CNS was 1.5 g m^{-2} (almost 2 times greater than the previous year) (TABLE 2.10). In 2011, the mean *S. angustifolium* CNS in the poor fen was 0.5 g m^{-2} and in 2012, the mean CNS was 1.6 g m^{-2} (over 3 times greater than the previous year) (TABLE 2.10). In 2011, the mean *S. magellanicum* CNS in the poor fen was 0.6 g m^{-2} and in 2012, the mean CNS was 1.0 g m^{-2} (TABLE 2.10).

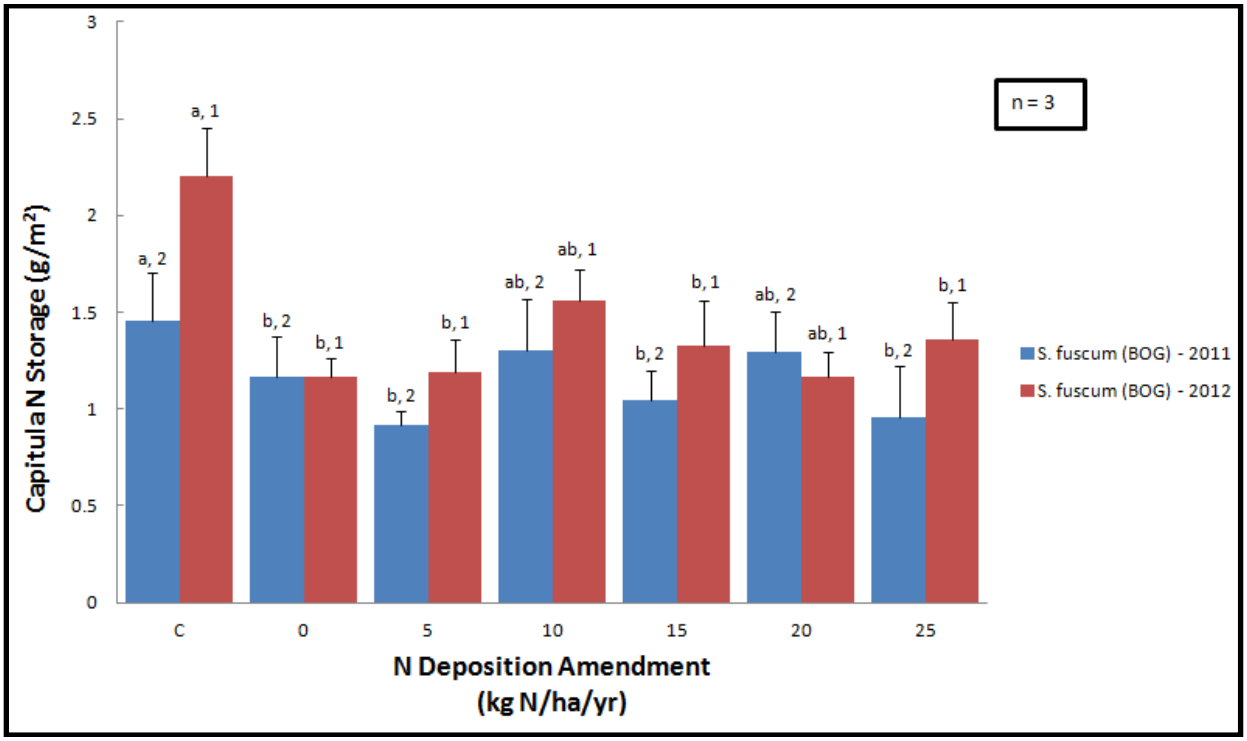

FIGURE 2.26 Mean capitulum N storage (CNS) values for *S. fuscum* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters (N treatment) and numbers (year) above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

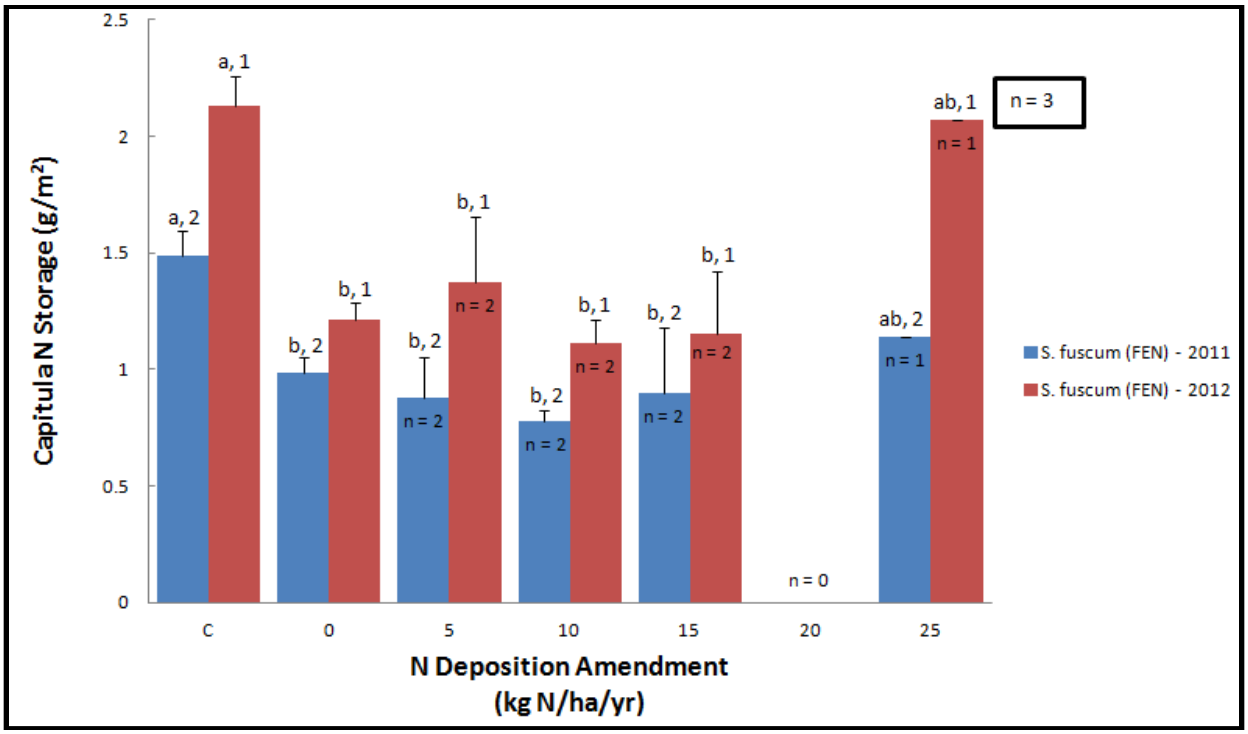

FIGURE 2.27 Mean capitulum N storage (CNS) values for *S. fuscum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters (N treatment) and numbers (year) above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

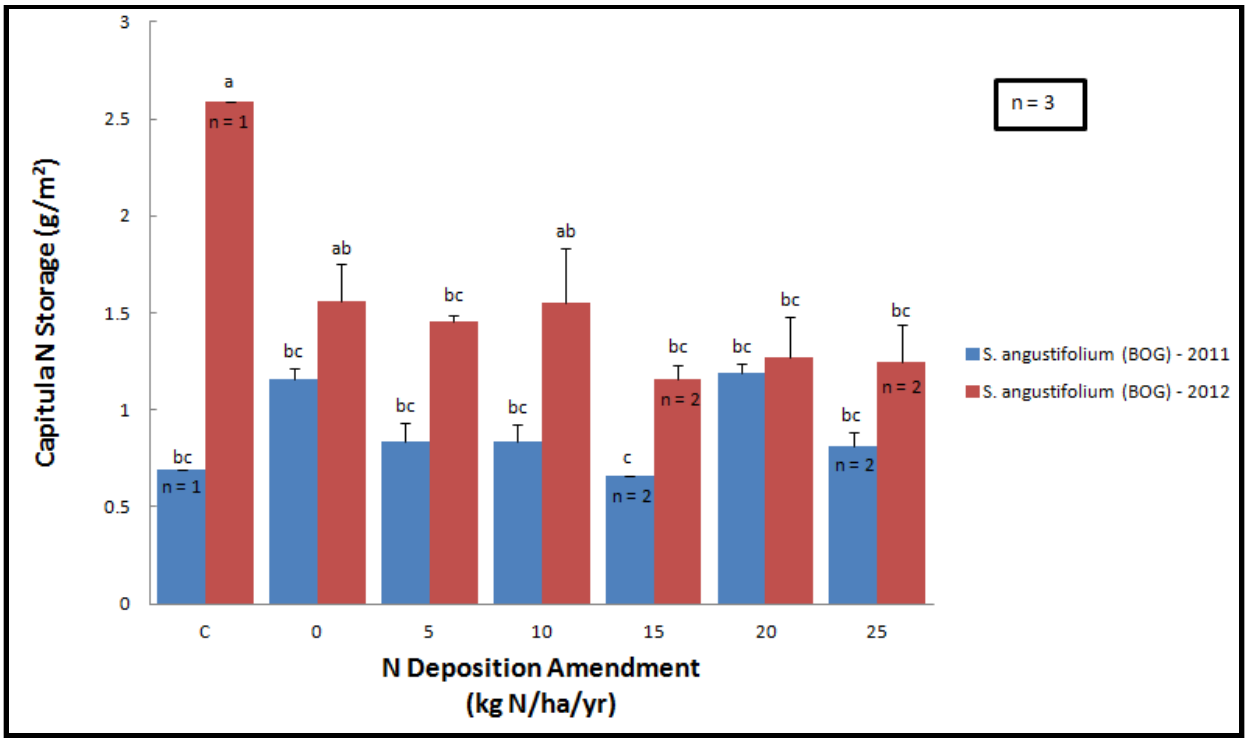

FIGURE 2.28 Mean capitulum N storage (CNS) values for *S. angustifolium* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

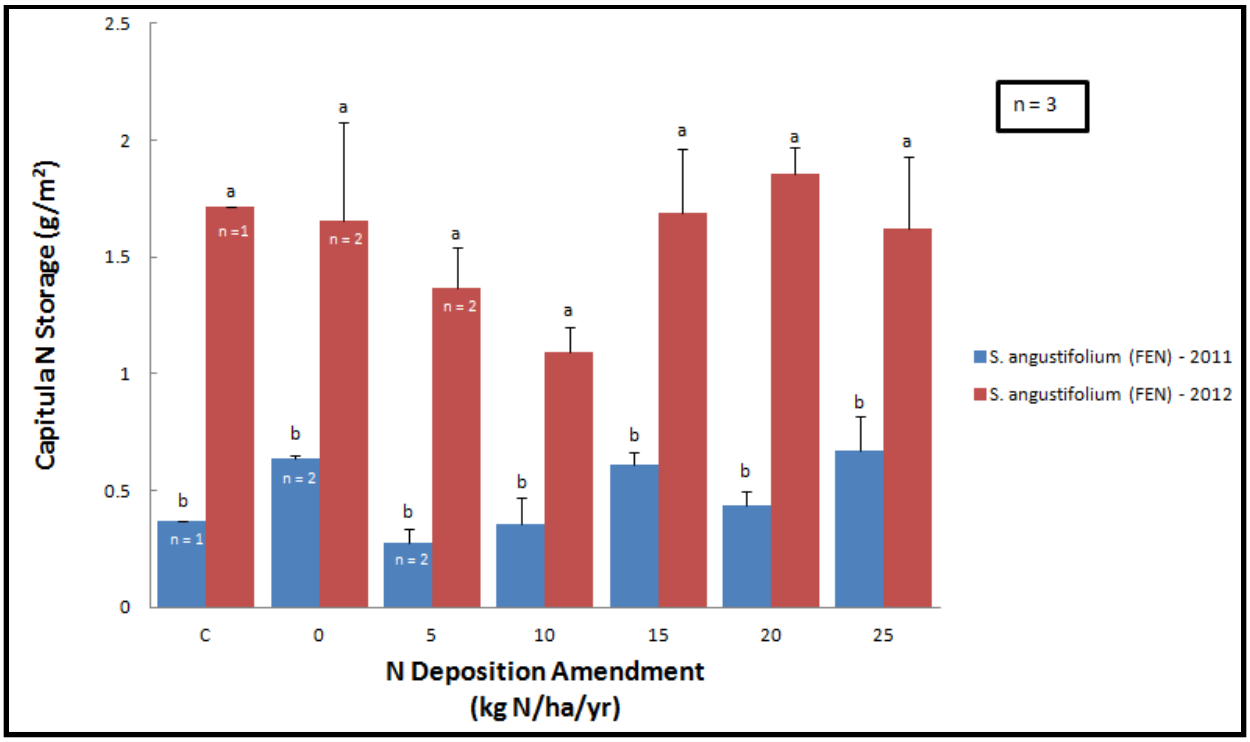

FIGURE 2.29 Mean capitulum N storage (CNS) values for *S. angustifolium* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

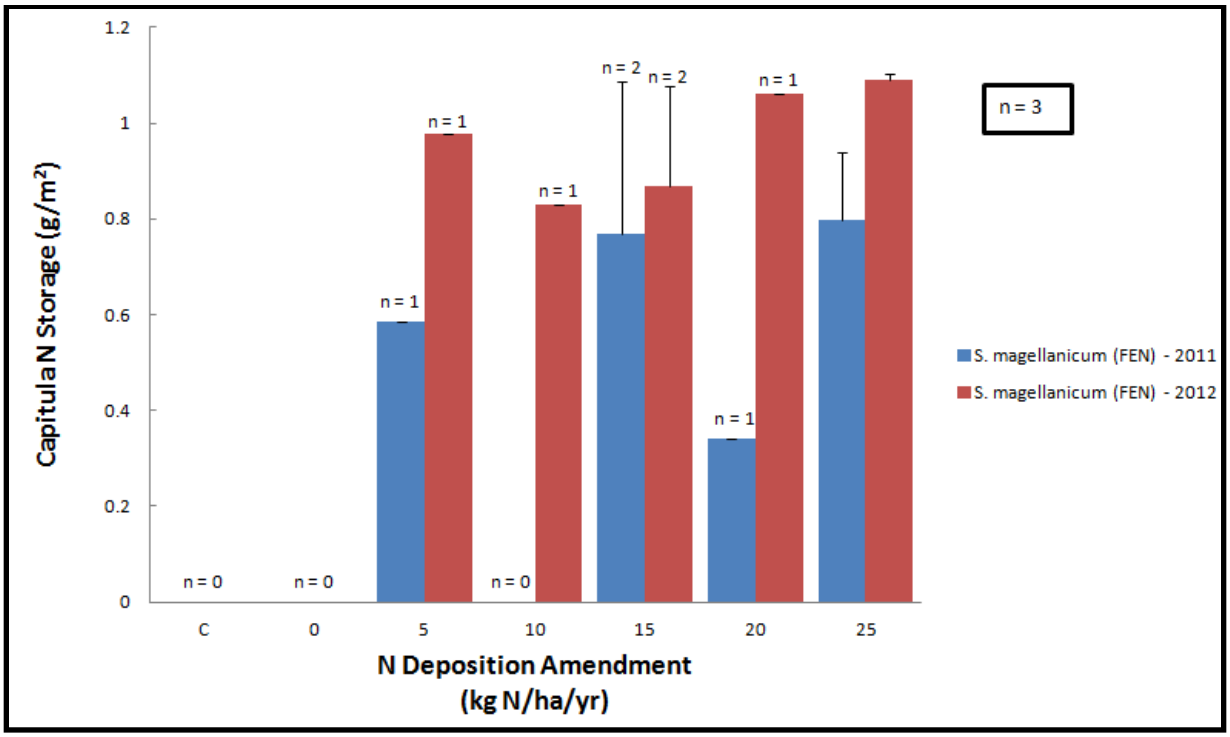

FIGURE 2.30 Mean capitulum N storage (CNS) values for *S. magellanicum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

TABLE 2.10 Mean capitulum N storage values for *Sphagnum fuscum* (bog and poor fen), *S. angustifolium* (bog and poor fen), and *S. magellanicum* (poor fen) capitula collected from the treatment plots in mid-July, 2011 and 2012. Values represent means ± SE. When no standard error is noted, then n=1.

2011	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	N storage (g m^{-2})	N storage (g m^{-2})	N storage (g m^{-2})	N storage (g m^{-2})	N storage (g m^{-2})
Control	1.5 (± 0.25)	1.5 (± 0.11)	0.7	0.4	N/A
0 kg/ha	1.2 (± 0.21)	1.0 (± 0.06)	1.2 (± 0.06)	0.6 (± 0.02)	N/A
5 kg/ha	0.9 (± 0.07)	0.9 (± 0.18)	0.8 (± 0.09)	0.3 (± 0.06)	0.6
10 kg/ha	1.3 (± 0.27)	0.8 (± 0.05)	0.8 (± 0.10)	0.4 (± 0.11)	N/A
15 kg/ha	1.0 (± 0.15)	0.9 (± 0.28)	0.7 (± 0.002)	0.6 (± 0.05)	0.8 (± 0.32)
20 kg/ha	1.3 (± 0.21)	N/A	1.2 (± 0.05)	0.4 (0.07)	0.3
25 kg/ha	1.0 (± 0.26)	1.1	0.8 (± 0.07)	0.7 (± 0.15)	0.8 (± 0.14)
MEAN	1.2 (± 0.12)	1.0 (± 0.15)	0.9 (± 0.12)	0.5 (± 0.91)	0.6 (± 0.12)

2012	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	N storage (g m^{-2})	N storage (g m^{-2})	N storage (g m^{-2})	N storage (g m^{-2})	N storage (g m^{-2})
Control	2.2 (± 0.26)	2.1 (± 0.12)	2.6	1.7	N/A
0 kg/ha	1.2 (± 0.09)	1.2 (± 0.07)	1.6 (± 0.19)	1.7 (± 0.42)	N/A
5 kg/ha	1.2 (± 0.17)	1.4 (± 0.28)	1.5 (± 0.03)	1.4 (± 0.17)	1.0
10 kg/ha	1.6 (± 0.16)	1.1 (± 0.10)	1.6 (± 0.28)	1.1 (± 0.11)	0.8
15 kg/ha	1.3 (± 0.24)	1.2 (± 0.27)	1.2 (± 0.08)	1.7 (± 0.27)	0.9 (± 0.21)
20 kg/ha	1.2 (± 0.13)	N/A	1.3 (± 0.21)	1.9 (± 0.12)	1.1
25 kg/ha	1.4 (± 0.19)	2.1	1.2 (± 0.19)	1.6 (± 0.31)	1.1 (± 0.02)
MEAN	1.4 (± 0.21)	1.5 (± 0.27)	1.5 (± 0.28)	1.6 (± 0.15)	1.0 (± 0.07)

TABLE 2.11 Two-Way ANOVA results of capitulum N storage for *Sphagnum fuscum*, *S. angustifolium*, and *S. magellanicum* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison.

	Capitula N Storage ($g\ m^{-2}$)									
	BOG - *S. fuscum*		FEN - *S. fuscum*		BOG - *S. angustifolium*		FEN - *S. angustifolium*		FEN - *S. magellanicum*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	3.43	**0.012**	7.82	**0.001**	2.80	**0.038**	1.70	0.173	0.40	0.803
YEAR	5.92	**0.022**	17.77	**0.0009**	52.62	**< 0.0001**	86.27	**< 0.0001**	4.34	0.083
TREATMENT*YEAR	0.99	0.45	0.81	0.56	3.65	**0.013**	0.69	0.661	0.48	0.709

***Sphagnum* growth response**

Linear Growth (LG)

N Treatment and Year Effects - Differences in linear growth were detected for year and N treatment for *S. fuscum* in the bog (year: F = 113.82, $p < 0.0001$; N: F = 54.06, $p < 0.0001$) and poor fen (year: F = 58.79, $p < 0.0001$; N: F = 4.78, $p = 0.0003$), although there was also a significant interaction for both (F = 14.15, $p < 0.0001$; F = 9.22, $p < 0.0001$) (FIGURE 2.31 and 2.32; TABLE 2.13). Differences in linear growth were detected for year and N treatment for *S. angustifolium* in the poor fen (year: F = 83.67, $p < 0.0001$; N: F = 12.34, $p < 0.0001$) and *S. magellanicum* in the poor fen (year: F = 323.58, $p < 0.0001$; N: F = 8.59, $p < 0.0001$), although there was also a significant interaction (F = 2.99, $p = 0.007$; F = 9.04, $p < 0.0001$) (FIGURE 2.33 and 2.34; TABLE 2.13).

Summary of Data – In 2011, the mean *S. fuscum* LG in the bog was 2.0 cm and in 2012, the mean LG was 2.6 cm (TABLE 2.12). In 2011, the mean *S. fuscum* LG in the poor fen was 2.8 cm and in 2012, the mean LG was 3.7 cm (TABLE 2.12). In 2011, the mean *S. angustifolium* LG in the poor fen was 3.7 cm and in 2012, the mean LG was 5.0 cm (TABLE 2.12). In 2011, the mean *S. magellanicum* LG in the poor fen was 2.5 cm and in 2012, the mean LG was 4.4 cm (TABLE 2.12).

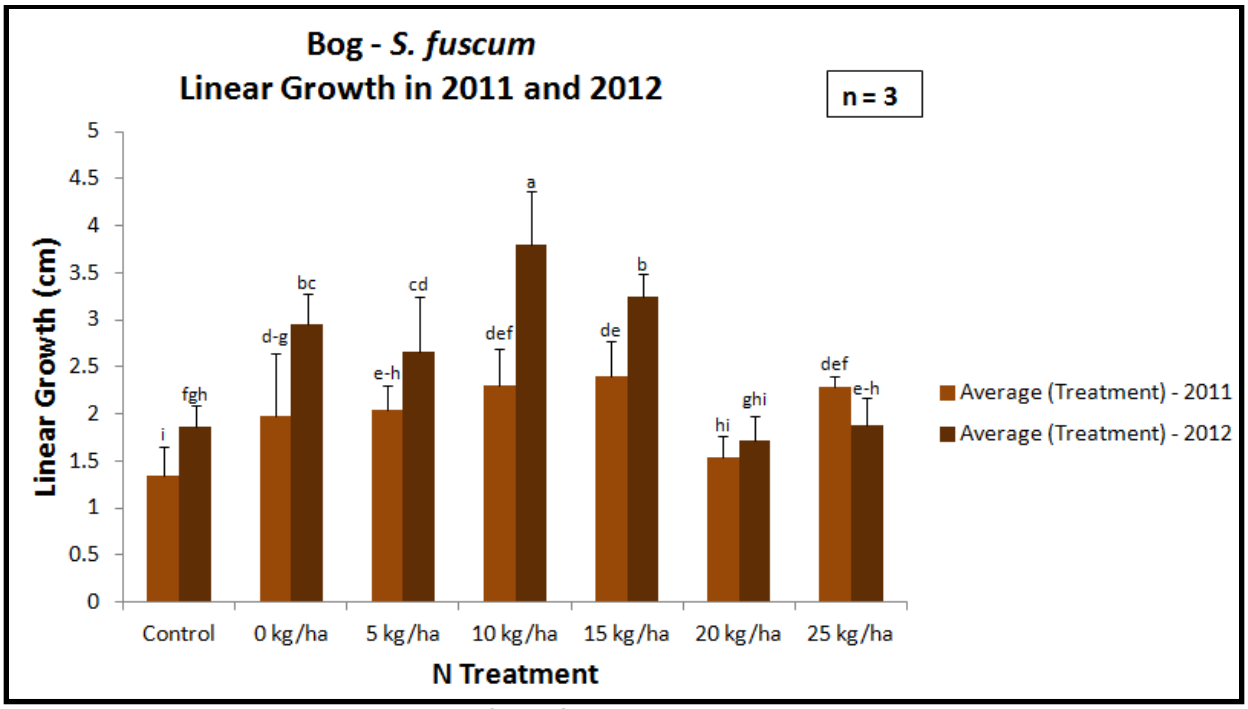

FIGURE 2.31 Mean linear growth values for *S. fuscum* measured in bog plots in 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

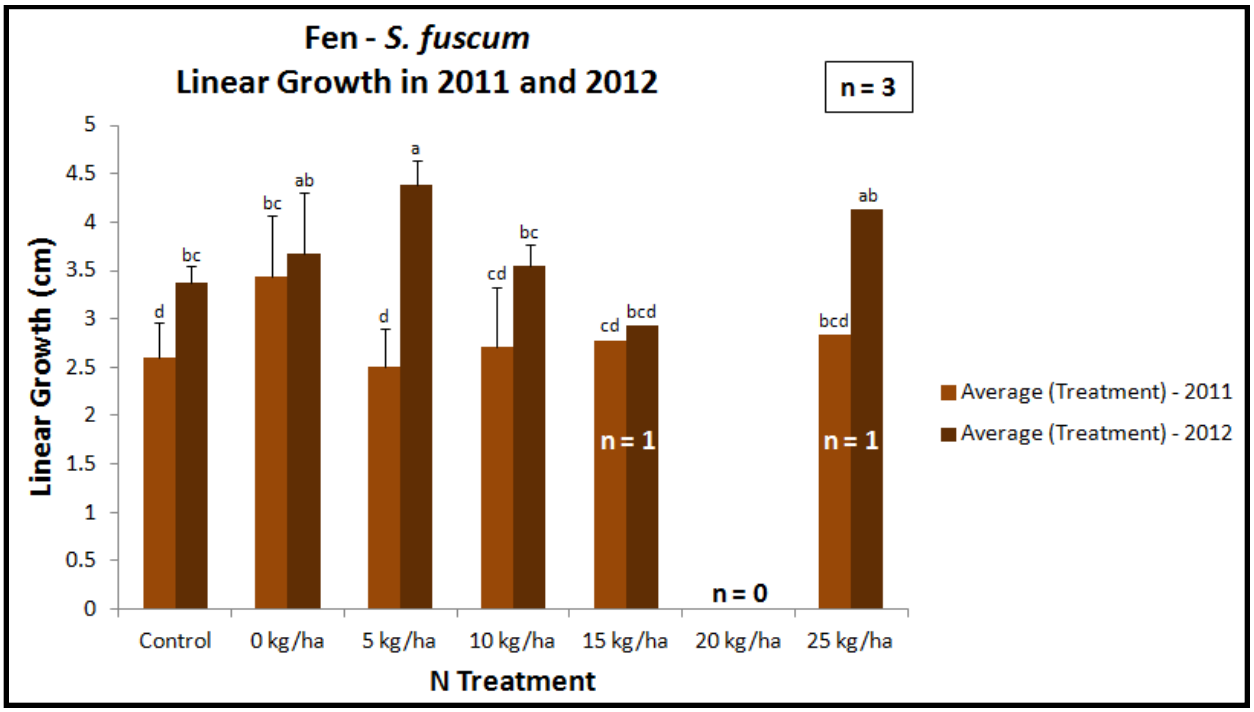

FIGURE 2.32 Mean linear growth values for *S. fuscum* measured in poor fen plots in 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

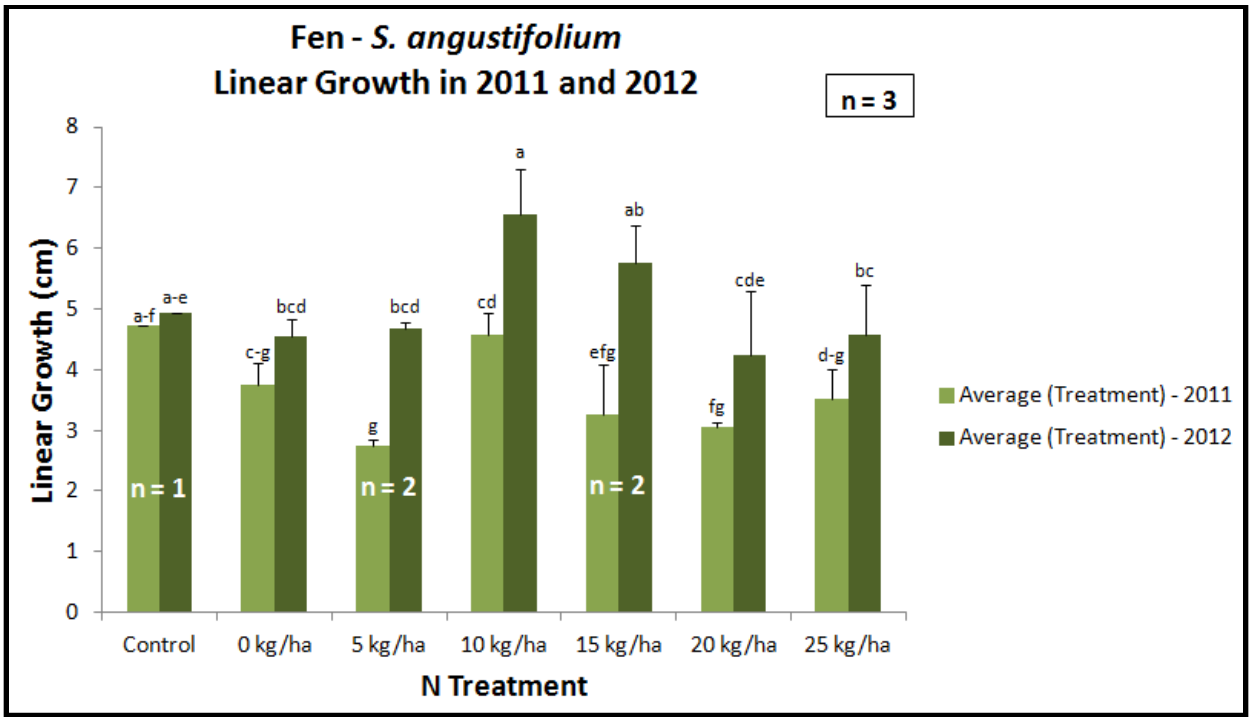

FIGURE 2.33 Mean linear growth values for *S. angustifolium* measured in poor fen plots in 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

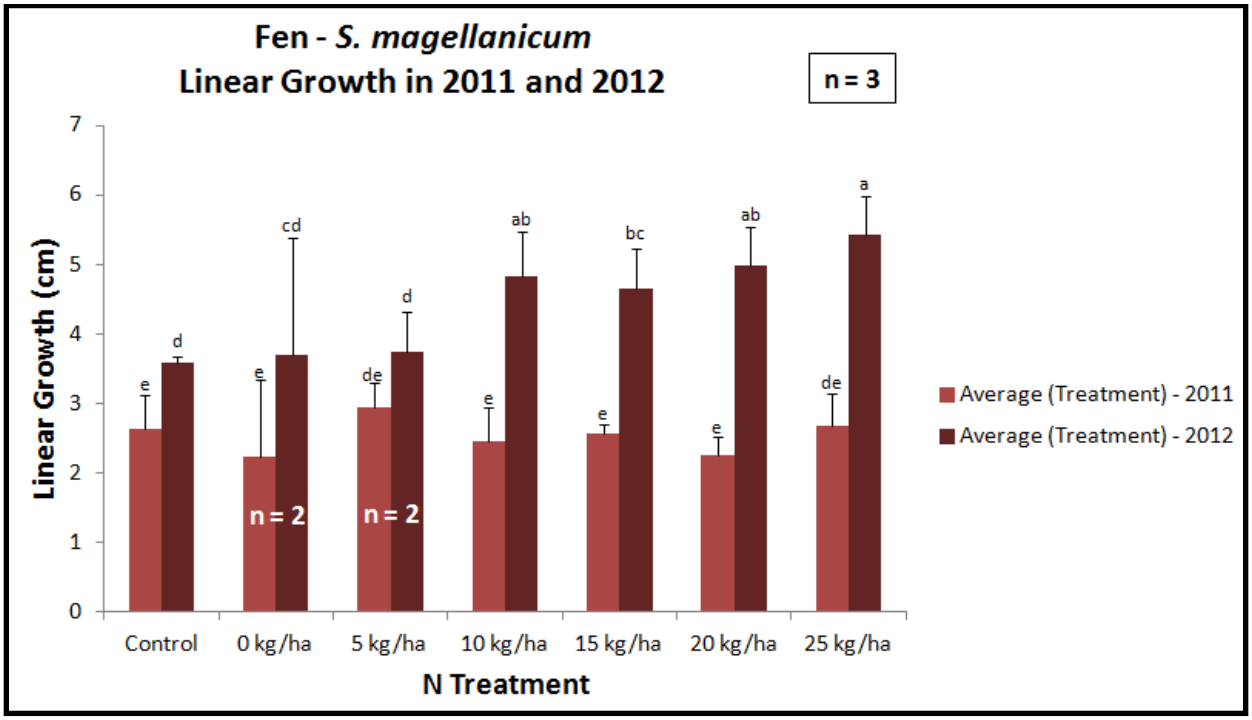

FIGURE 2.34 Mean linear growth values for *S. magellanicum* measured in poor fen plots in 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

TABLE 2.12 Mean linear growth values for *Sphagnum fuscum* (bog and poor fen), *S. angustifolium* (poor fen), and *S. magellanicum* (poor fen) in 2011 and 2012. Values represent means ± SE. When no standard error is noted, then n=1.

2011	BOG - *S. fuscum*	FEN - *S. fuscum*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**Linear Growth (cm)**	**Linear Growth (cm)**	**Linear Growth (cm)**	**Linear Growth (cm)**
Control	1.3 (± 0.3)	2.6 (± 0.4)	4.7	2.6 (± 0.5)
0 kg/ha	2.0 (± 0.7)	3.4 (± 0.6)	3.7 (± 0.4)	2.2 (± 1.1)
5 kg/ha	2.0 (± 0.3)	2.5 (± 0.4)	2.7 (± 0.1)	2.9 (± 0.3)
10 kg/ha	2.3 (± 0.4)	2.7 (± 0.6)	4.6 (± 0.4)	2.4 (± 0.5)
15 kg/ha	2.4 (± 0.4)	2.8	3.3 (± 0.8)	2.6 (± 0.1)
20 kg/ha	1.5 (± 0.2)	N/A	3.1 (± 0.1)	2.3 (± 0.3)
25 kg/ha	2.3 (± 0.1)	2.8	3.5 (± 0.5)	2.7 (± 0.5)
MEAN	2.0 (± 0.2)	2.8 (± 0.2)	3.7 (± 0.4)	2.5 (± 0.1)

2012	BOG - *S. fuscum*	FEN - *S. fuscum*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**Linear Growth (cm)**	**Linear Growth (cm)**	**Linear Growth (cm)**	**Linear Growth (cm)**
Control	1.9 (± 0.2)	3.4 (± 0.2)	4.9	3.6 (± 0.1)
0 kg/ha	3.0 (± 0.3)	3.7 (± 0.6)	4.6 (± 0.3)	3.7 (± 1.7)
5 kg/ha	2.7 (± 0.6)	4.4 (± 0.3)	4.7 (± 0.1)	3.7 (± 0.6)
10 kg/ha	3.8 (± 0.6)	3.6 (± 0.2)	6.6 (± 0.7)	4.8 (± 0.7)
15 kg/ha	3.2 (± 0.2)	2.9	5.8 (± 0.6)	4.6 (± 0.6)
20 kg/ha	1.7 (± 0.3)	N/A	4.2 (± 1.1)	5.0 (± 0.6)
25 kg/ha	1.9 (± 0.3)	4.1	4.6 (± 0.8)	5.4 (± 0.5)
MEAN	2.6 (± 0.5)	3.7 (± 0.3)	5.0 (± 0.5)	4.4 (± 0.4)

TABLE 2.13 Two-Way ANOVA results of linear growth for *Sphagnum fuscum*, *S. angustifolium*, and *S. magellanicum* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison.

	Linear Growth (cm)							
	BOG - *S. fuscum*		FEN - *S. fuscum*		FEN - *S. angustifolium*		FEN - *S. magellanicum*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	54.06	< 0.0001	4.78	0.0003	12.34	< 0.0001	8.59	< 0.0001
YEAR	113.82	< 0.0001	58.79	< 0.0001	83.67	< 0.0001	323.58	< 0.0001
TREATMENT*YEAR	14.15	< 0.0001	9.22	< 0.0001	2.99	0.007	9.04	< 0.0001

Stem Mass Density (SMD)

Year Effects – For *S. angustifolium* SMD in the bog, there was a significant year effect (F = 5.96; $p = 0.024$), but no N treatment (F = 1.02; $p = 0.438$) or interaction (F = 1.14; $p = 0.377$) effect (FIGURE 2.37; TABLE 2.15). For *S. angustifolium* SMD in the poor fen, there was a significant

year effect (F = 56.87; $p < 0.0001$) and significant interaction (F = 3.81; $p = 0.012$), but no N treatment (F = 0.50; $p = 0.802$) effect (FIGURE 2.38; TABLE 2.15).

No Effects – Stem mass density (SMD) values for *Sphagnum fuscum* in the bog failed to meet normality assumptions (Shapiro-Wilk's test: W = 0.937; $p = 0.022$), and were examined using Friedman's two-way nonparametric ANOVA based on ranks (FIGURE 2.35; TABLE 2.15). For *Sphagnum fuscum* SMD in the bog, there was a non-significant year (F = 1.15; $p = 0.290$) and N treatment (F = 1.07; $p = 0.399$) effect (FIGURE 2.35; TABLE 2.15). For *S. fuscum* SMD in the poor fen, there was a non-significant year (F = 1.09; $p = 0.314$), N treatment (F = 0.59; $p = 0.705$), and interaction (F = 0.34; $p = 0.88$) effect (FIGURE 2.36; TABLE 2.15). For *S. magellanicum* SMD in the poor fen, there was a non-significant year (F = 0.05; $p = 0.825$), N treatment (F = 0.72; $p = 0.609$), and interaction (F = 0.08; $p = 0.970$) effect (FIGURE 2.39; TABLE 2.15).

Summary of Data – In 2011, the mean *S. fuscum* SMD in the bog was 113.6 g m^{-2} cm^{-1} and in 2012, the mean SMD was 130.4 g m^{-2} cm^{-1} (TABLE 2.14). In 2011, the mean *S. fuscum* SMD in the poor fen was 108.2 g m^{-2} cm^{-1} and in 2012, the mean SMD was 131.7 g m^{-2} cm^{-1} (TABLE 2.14). In 2011, the mean *S. angustifolium* SMD in the bog was 44.7 g m^{-2} cm^{-1} and in 2012, the mean SMD was 69.5 g m^{-2} cm^{-1} (over 1½ times greater than the previous year) (TABLE 2.14). In 2011, the mean *S. angustifolium* SMD in the poor fen was 47.7 g m^{-2} cm^{-1} and in 2012, the mean SMD was 99.6 g m^{-2} cm^{-1} (over 2 times greater than the previous year) (TABLE 2.14). In 2011, the mean *S. magellanicum* SMD in the poor fen was 77.1 g m^{-2} cm^{-1} and in 2012, the mean SMD was 75.5 g m^{-2} cm^{-1} (TABLE 2.14).

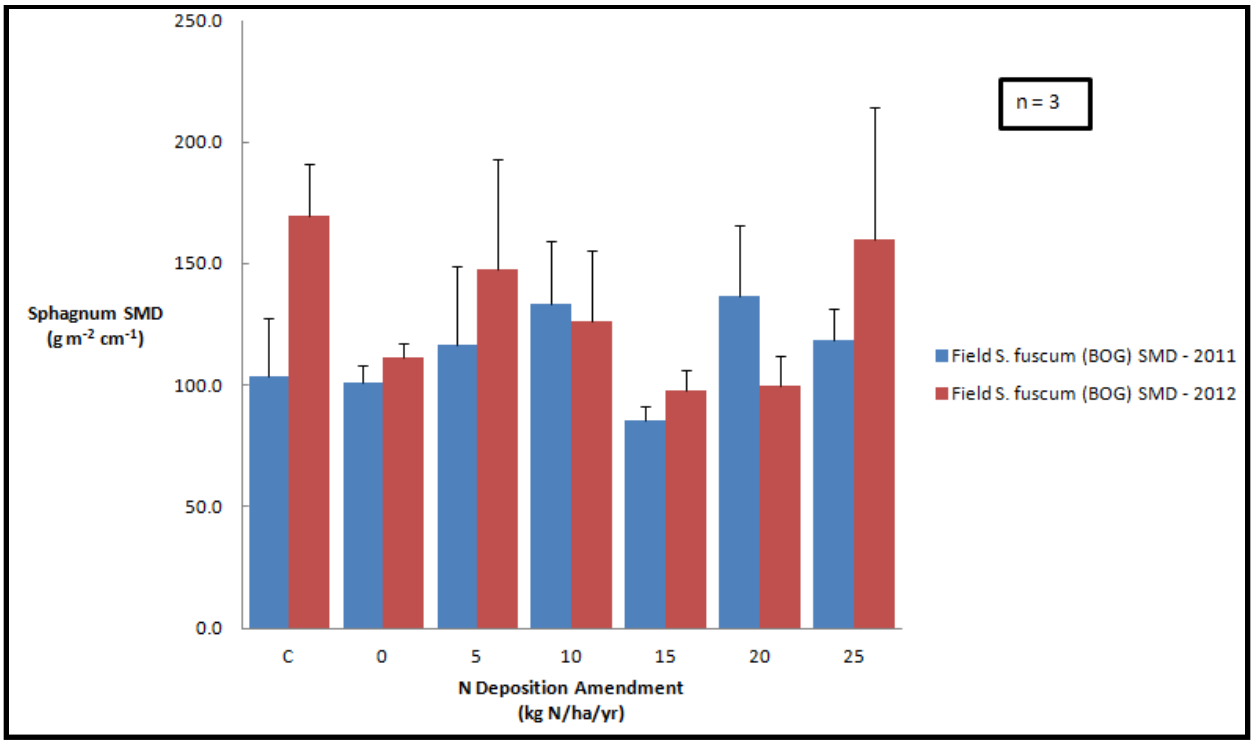

FIGURE 2.35 Mean stem mass density (SMD) values for *S. fuscum* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Sample size is n=3 unless otherwise noted.

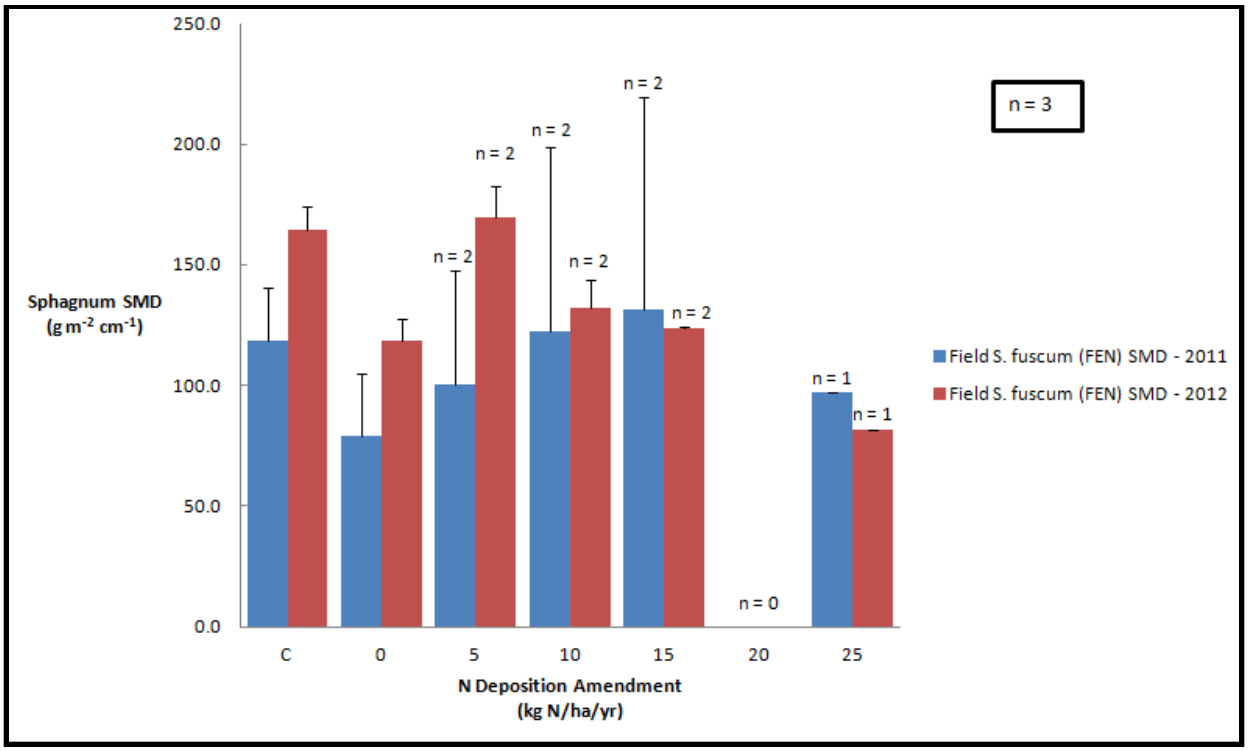

FIGURE 2.36 Mean stem mass density (SMD) values for *S. fuscum* collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

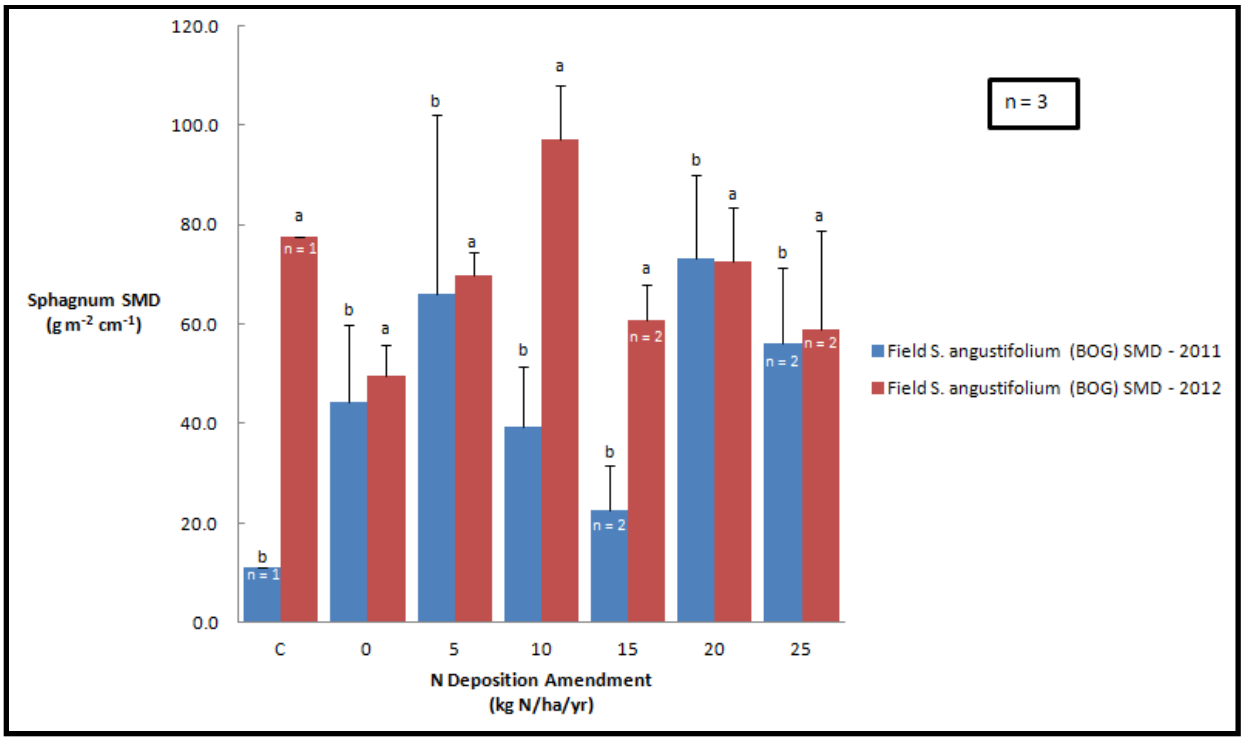

FIGURE 2.37 Mean stem mass density (SMD) values for *S. angustifolium* collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

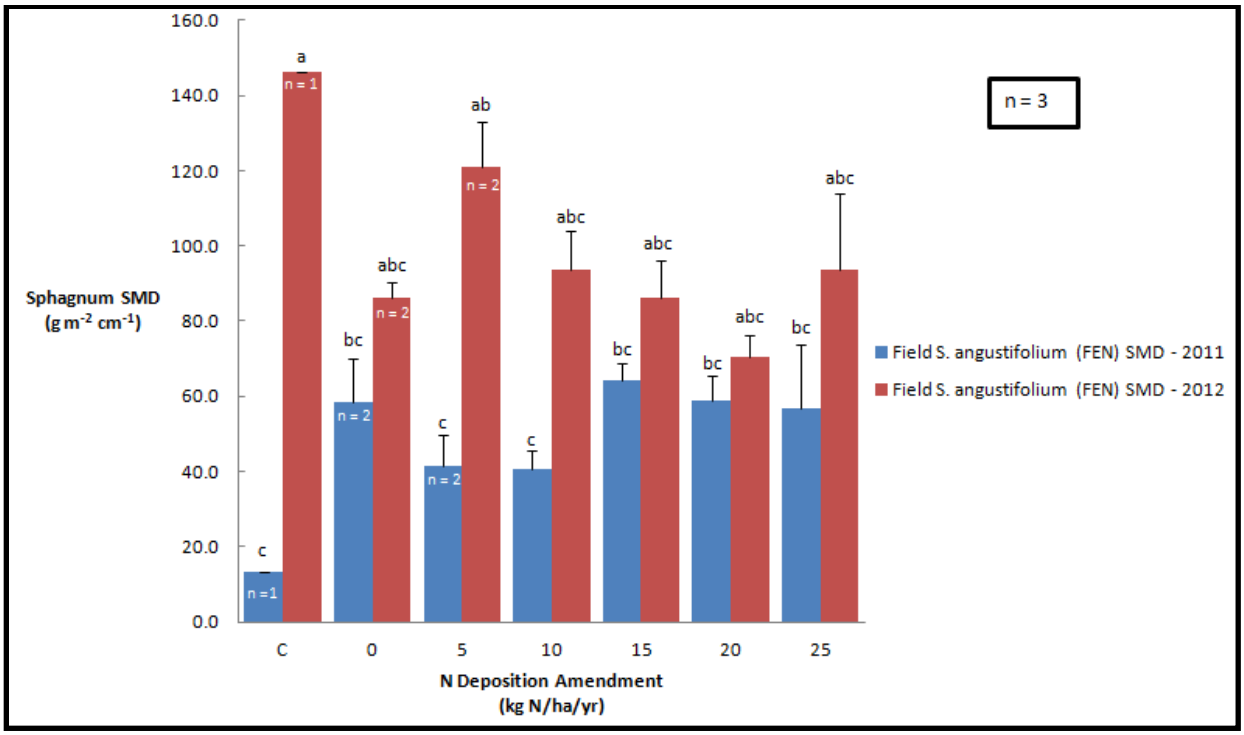

FIGURE 2.38 Mean stem mass density (SMD) values for *S. angustifolium* collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

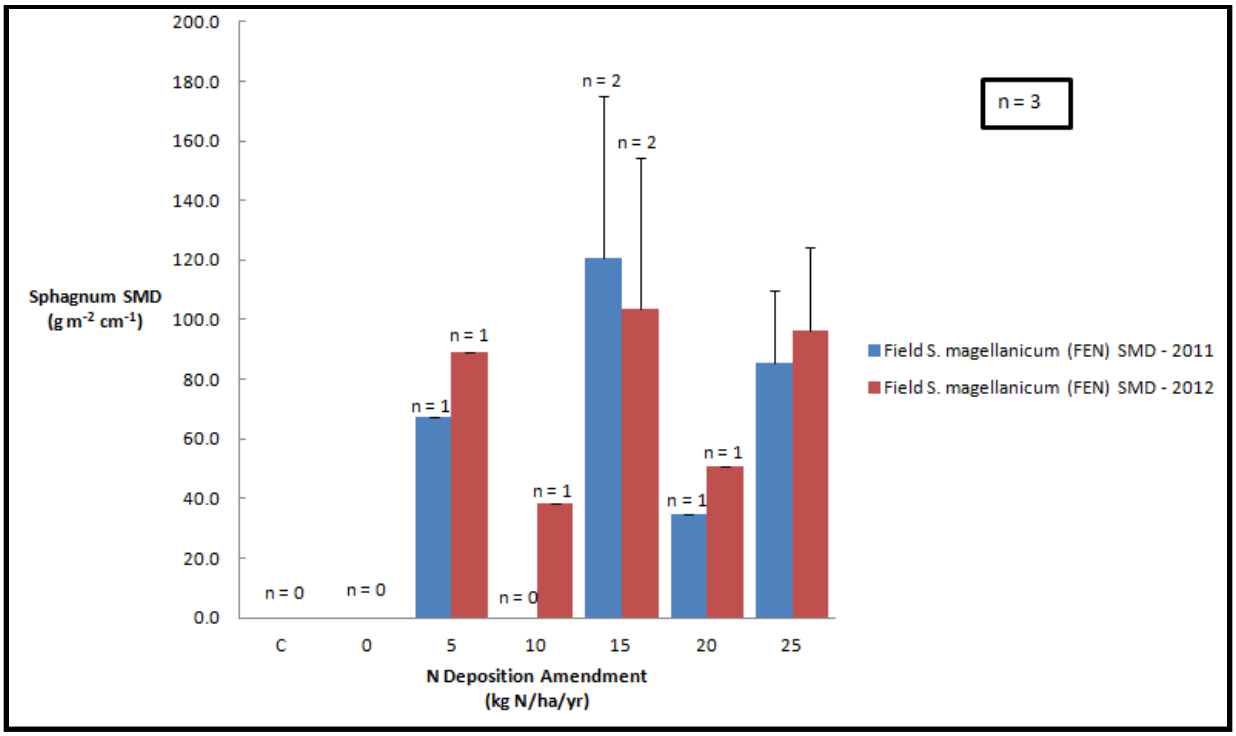

FIGURE 2.39 Mean stem mass density (SMD) values for *S. magellanicum* collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

TABLE 2.14 Mean stem mass density (SMD) values for *S. fuscum* (bog and poor fen), *S. angustifolium* (bog and poor fen), and *S. magellanicum* (poor fen) samples collected from the treatment plots in mid-July, 2011 and 2012. Values represent means ± SE. When no standard error is noted, then n=1.

2011	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**
Control	103.8 (± 23.8)	118.4 (± 22.2)	11.2	13.4	N/A
0 kg/ha	100.9 (± 7.4)	79.2 (± 25.6)	44.2 (± 15.7)	58.3 (± 11.8)	N/A
5 kg/ha	116.5 (± 32.3)	100.6 (± 46.8)	66.0 (± 36.1)	41.3 (± 8.4)	67.1
10 kg/ha	133.5 (± 25.9)	122.5 (± 75.9)	39.5 (± 11.9)	40.8 (± 4.8)	N/A
15 kg/ha	85.7 (± 5.4)	131.6 (± 88.0)	22.5 (± 9.3)	64.2 (± 4.6)	120.8 (± 54.0)
20 kg/ha	136.8 (± 29.0)	N/A	73.2 (± 16.9)	58.9 (± 6.8)	34.9
25 kg/ha	118.2 (± 13.2)	96.8	56.3 (± 15.2)	56.9 (± 16.7)	85.6 (± 24.2)
MEAN	113.6 (± 10.5)	108.2 (± 11.2)	44.7 (± 13.0)	47.7 (± 10.2)	77.1 (± 20.7)

2012	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**	**SMD (g m^{-2} cm^{-1})**
Control	169.4 (± 21.5)	164.7 (± 9.4)	77.6	146.2	N/A
0 kg/ha	111.6 (± 5.5)	118.4 (± 9.3)	49.5 (± 6.3)	86.1 (± 4.1)	N/A
5 kg/ha	147.9 (± 45.2)	169.3 (± 13.5)	69.9 (± 4.4)	121.1 (± 12.0)	89.1
10 kg/ha	126.5 (± 29.1)	131.9 (± 11.5)	97.0 (± 10.9)	93.4 (± 10.4)	38.2
15 kg/ha	97.6 (± 8.6)	123.7 (± 0.5)	60.9 (± 7.1)	86.0 (± 10.2)	103.6 (± 50.9)
20 kg/ha	99.9 (± 12.4)	N/A	72.5 (± 11.0)	70.5 (± 5.8)	50.5
25 kg/ha	159.7 (± 54.6)	81.8	58.9 (± 20.0)	93.7 (± 20.5)	96.2 (± 27.9)
MEAN	130.4 (± 16.8)	131.7 (± 18.7)	69.5 (± 8.9)	99.6 (± 14.8)	75.5 (± 16.9)

TABLE 2.15 Two-Way ANOVA results of stem mass density (SMD) for *Sphagnum fuscum*, *S. angustifolium*, and *S. magellanicum* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison. SMD values for *Sphagnum fuscum* in the bog failed to meet normality assumptions (Shapiro-Wilk's test: W = 0.937; p = 0.022), and were examined using Friedman's two-way nonparametric ANOVA based on ranks.

	Stem Mass Density (SMD) ($g\ cm^{-1}\ m^{-2}$)									
	BOG - *S. fuscum*		FEN - *S. fuscum*		BOG - *S. angustifolium*		FEN - *S. angustifolium*		FEN - *S. magellanicum*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	1.07	0.399	0.59	0.705	1.02	0.438	0.50	0.802	0.72	0.609
YEAR	1.15	0.29	1.09	0.314	5.96	**0.024**	56.87	**< 0.0001**	0.05	0.825
TREATMENT*YEAR	N/A	N/A	0.34	0.88	1.14	0.377	3.81	**0.012**	0.08	0.97

Capitulum Mass Density (CMD)

N Treatment and Year Effects - Differences in capitulum mass density (CMD) were detected for year and N treatment for *S. angustifolium* in the bog (year: F = 17.34, p = 0.0005; N: F = 3.68, p = 0.013), although there was also a significant interaction (F = 3.89; p = 0.01) (FIGURE 2.42; TABLE 2.17).

N Treatment Effects - For *S. fuscum* in the poor fen, there was only a significant difference in N treatment (F = 6.43; p = 0.003) (FIGURE 2.41; TABLE 2.17).

Year Effects - For *S. angustifolium* in the poor fen, there was only a significant difference in year (F = 59.10; $p < 0.0001$) (FIGURE 2.43; TABLE 2.17).

No Effects - For *S. fuscum* in the bog, there was a non-significant year (F = 0.01; p = 0.925), N treatment (F = 2.02; p = 0.097), and interaction (F = 0.84; p = 0.552) effect (FIGURE 2.40; TABLE 2.17). For *S. magellanicum* in the poor fen, there was also a non-significant year (F = 1.23; p = 0.309), N treatment (F = 0.60; p = 0.675), and interaction (F = 0.34; p = 0.798) effect (FIGURE 2.44; TABLE 2.17).

Summary of Data - Capitulum mass density was, on average, higher in 2012 than in 2011 for all species, in both site types (bog and poor fen), although *S. angustifolium* in the poor fen had the most drastic increases (TABLE 2.16). In 2011, the mean *S. fuscum* CMD in the bog was 103.0 g m^{-2} and in 2012, the mean CMD was 103.8 g m^{-2} (TABLE 2.16). In 2011, the mean *S. fuscum* CMD in the poor fen was 96.3 g m^{-2} and in 2012, the mean CMD was 113.4 g m^{-2} (TABLE 2.16). In 2011, the mean *S. angustifolium* CMD in the bog was 92.9 g m^{-2} and in 2012, the mean CMD was 128.0 g m^{-2} (TABLE 2.16). In 2011, the mean *S. angustifolium* CMD in the poor fen was 58.4 g m^{-2} and in 2012, the mean CMD was 127.8 g m^{-2} (TABLE 2.16). In 2011, the mean *S. magellanicum* CMD in the poor fen was 59.6 g m^{-2} and in 2012, the mean CMD was 73.1 g m^{-2} (TABLE 2.16).

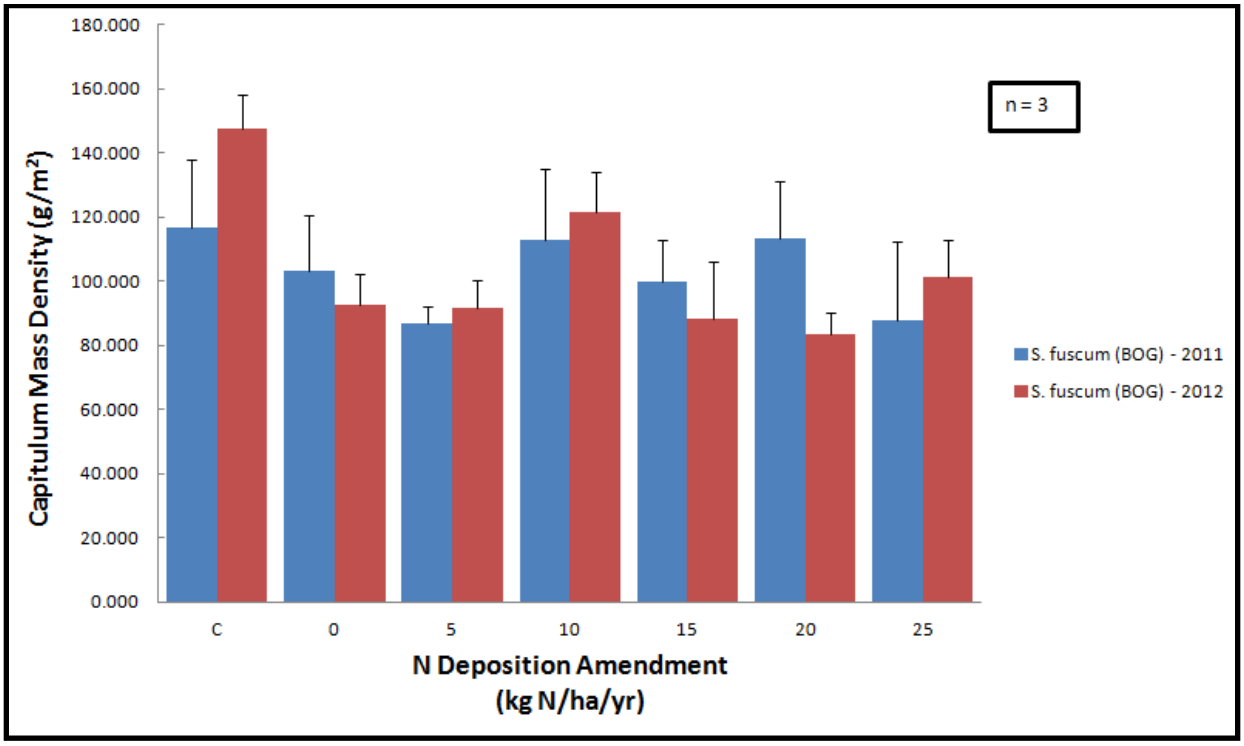

FIGURE 2.40 Mean capitulum mass density (CMD) values for *S. fuscum* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

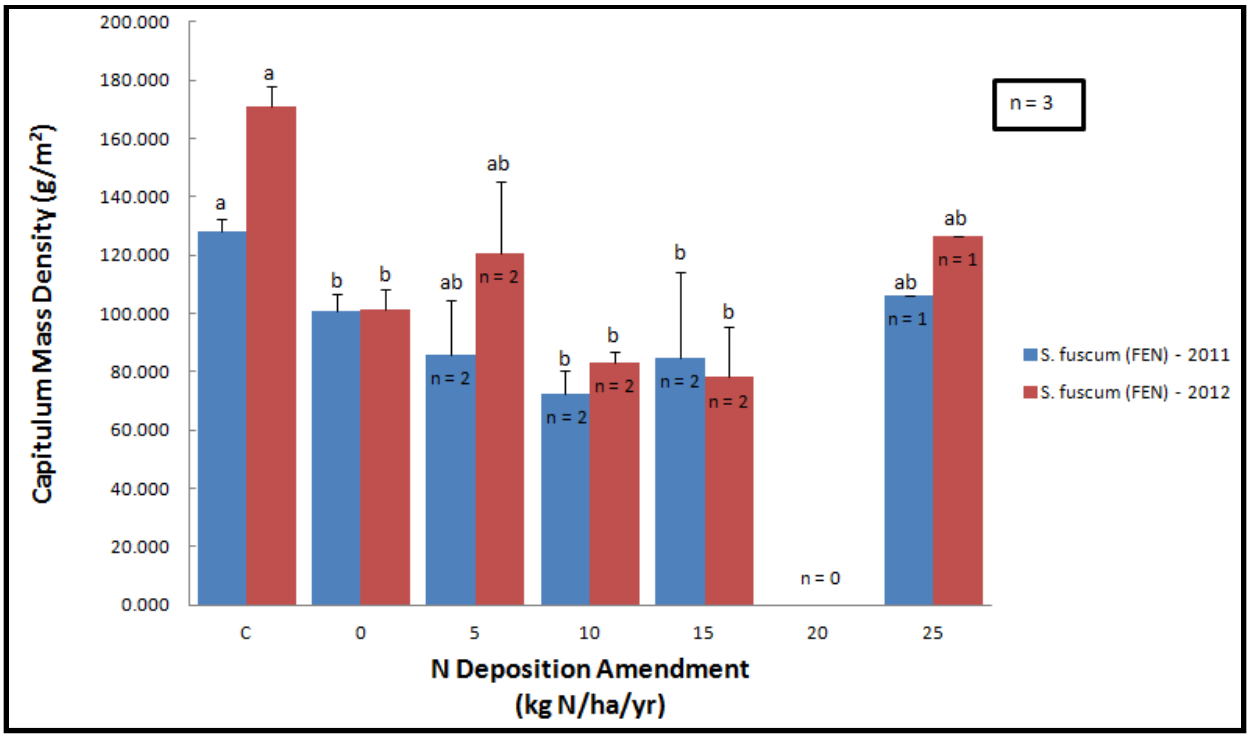

FIGURE 2.41 Mean capitulum mass density (CMD) values for *S. fuscum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

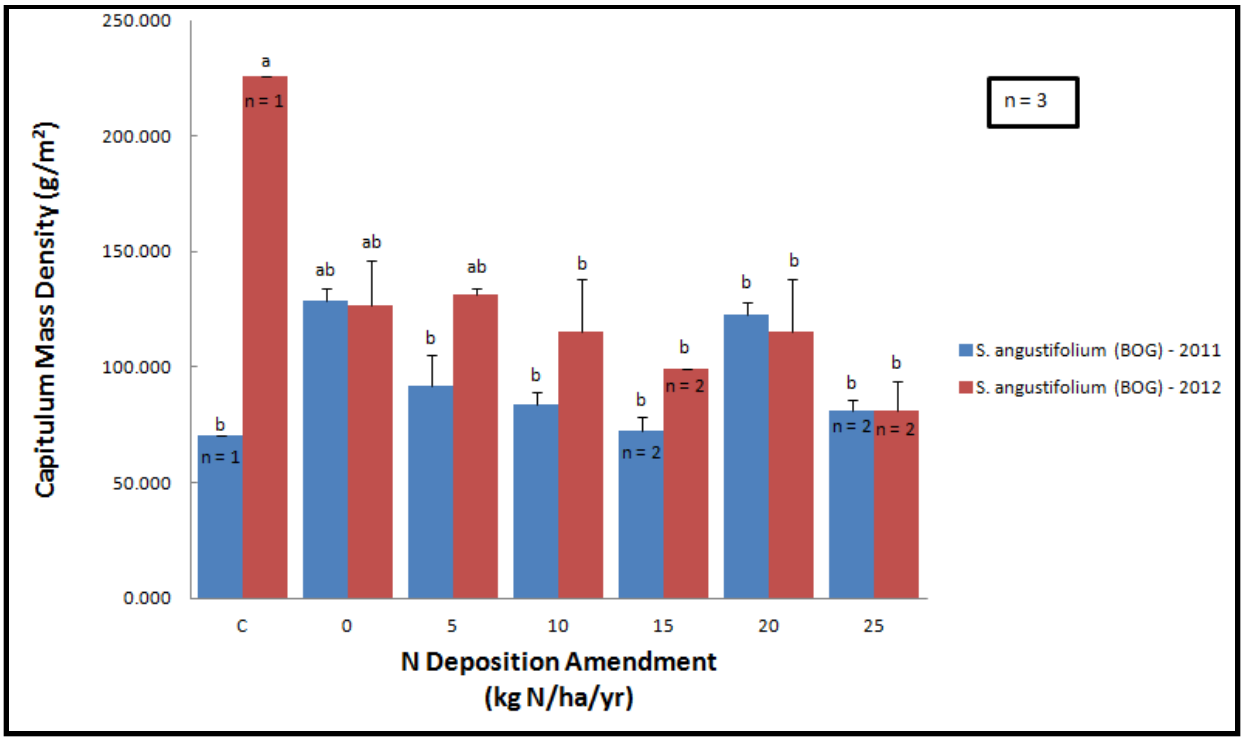

FIGURE 2.42 Mean capitulum mass density (CMD) values for *S. angustifolium* capitula collected from bog plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

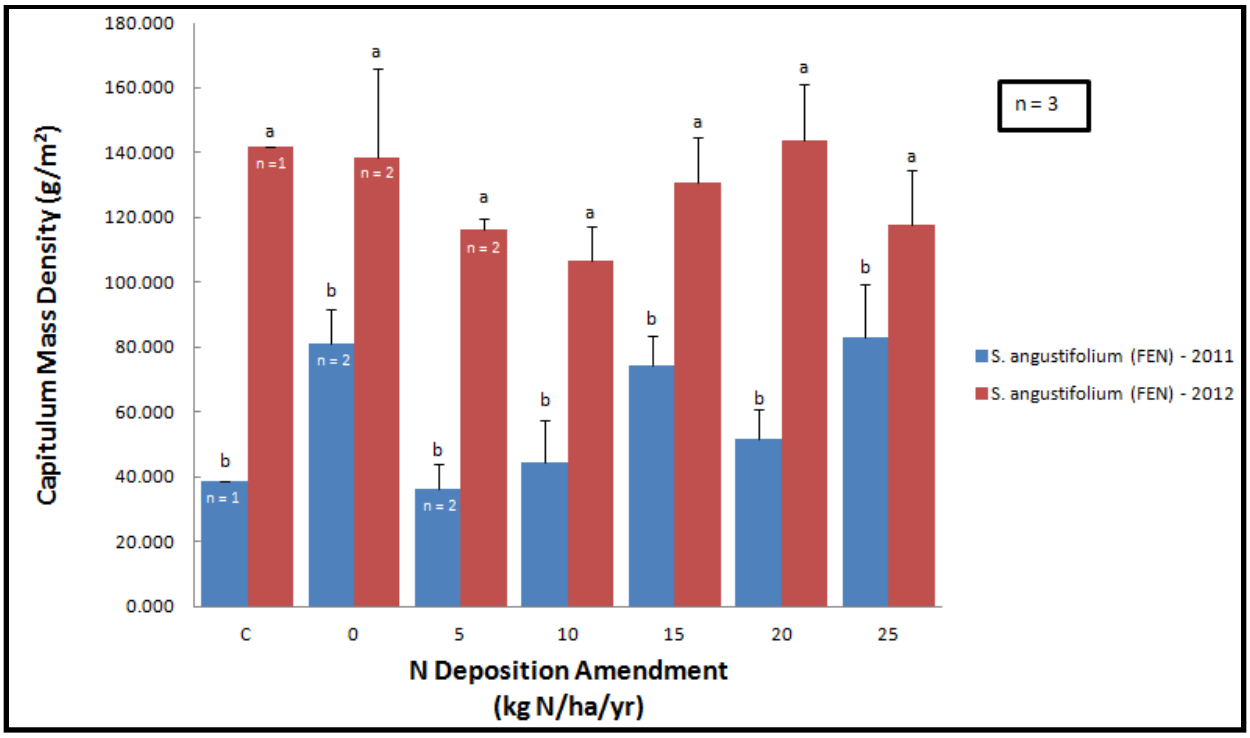

FIGURE 2.43 Mean capitulum mass density (CMD) values for *S. angustifolium* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

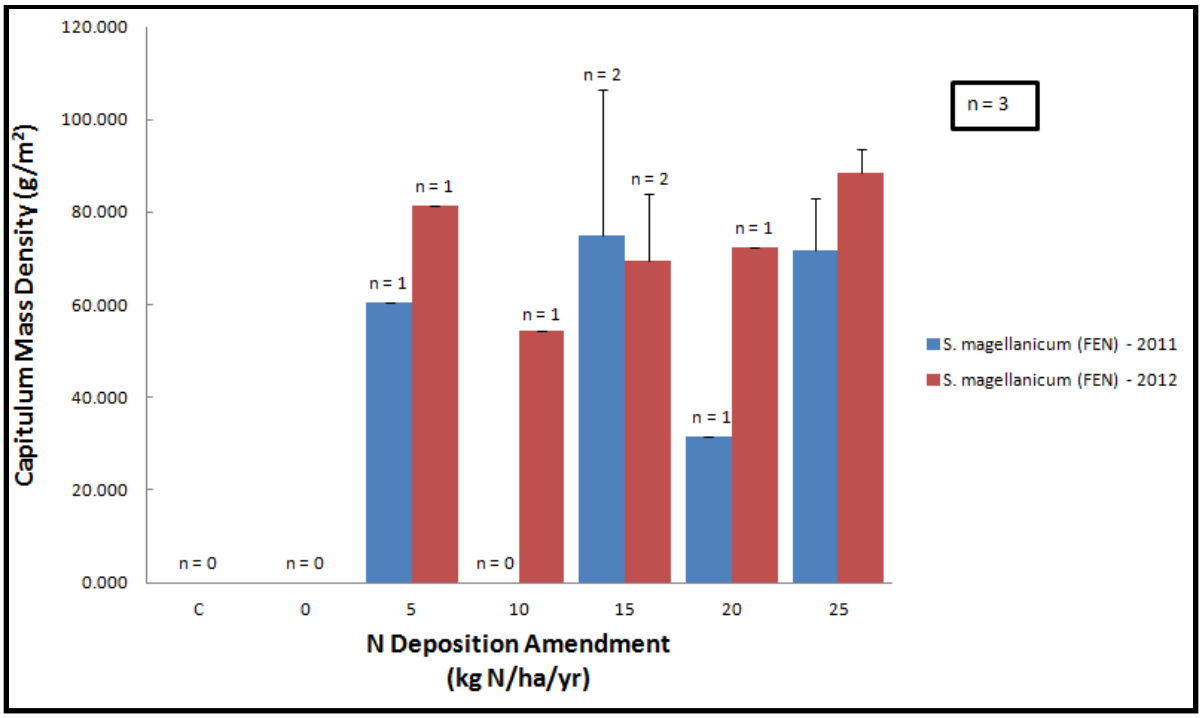

FIGURE 2.44 Mean capitulum mass density (CMD) values for *S. magellanicum* capitula collected from poor fen plots in mid-July, 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

TABLE 2.16 Mean capitulum mass density (CMD) values for *S. fuscum* (bog and poor fen), *S. angustifolium* (bog and poor fen), and *S. magellanicum* (poor fen) capitula collected from the treatment plots in mid-July, 2011 and 2012. Values represent means ± SE. When no standard error is noted, then n=1.

2011	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**CMD (g m^{-2})**	**CMD (g m^{-2})**	**CMD (g m^{-2})**	**CMD (g m^{-2})**	**CMD (g m^{-2})**
Control	116.8 (± 21.4)	128.1 (± 4.2)	70.1	38.7	N/A
0 kg/ha	103.1 (± 17.7)	100.7 (± 5.8)	128.9 (± 4.9)	80.9 (± 10.9)	N/A
5 kg/ha	87.0 (± 5.0)	85.8 (± 18.7)	91.8 (± 13.3)	36.2 (± 7.9)	60.4
10 kg/ha	112.8 (± 22.4)	72.5 (± 7.9)	83.8 (± 5.6)	44.3 (± 13.2)	N/A
15 kg/ha	99.9 (± 13.0)	84.6 (± 29.6)	72.5 (± 5.9)	74.1 (± 9.3)	74.9 (± 31.6)
20 kg/ha	113.6 (± 17.8)	N/A	122.4 (± 5.8)	51.5 (± 9.3)	31.4
25 kg/ha	87.8 (± 24.8)	106.3	80.9 (± 4.9)	83.0 (± 16.5)	71.7 (± 11.4)
MEAN	103.0 (± 7.1)	96.3 (± 11.4)	92.9 (± 13.6)	58.4 (± 11.7)	59.6 (± 11.4)

2012	BOG - *S. fuscum*	FEN - *S. fuscum*	BOG - *S. angustifolium*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**CMD (g m^{-2})**	**CMD (g m^{-2})**	**CMD (g m^{-2})**	**CMD (g m^{-2})**	**CMD (g m^{-2})**
Control	147.7 (± 10.6)	170.8 (± 7.2)	226.0	141.6	N/A
0 kg/ha	92.4 (± 10.0)	101.5 (± 7.0)	126.6 (± 19.1)	138.6 (± 27.1)	N/A
5 kg/ha	91.4 (± 8.8)	120.5 (± 24.6)	131.6 (± 2.7)	116.0 (± 3.7)	81.4
10 kg/ha	121.5 (± 12.6)	82.9 (± 3.7)	115.5 (± 22.2)	106.5 (± 10.6)	54.2
15 kg/ha	88.4 (± 17.5)	78.4 (± 17.2)	99.4 (± 8.2E-15)	130.6 (± 14.2)	69.3 (± 14.8)
20 kg/ha	83.4 (± 6.6)	N/A	115.5 (± 22.4)	143.6 (± 17.5)	72.3
25 kg/ha	101.5 (± 11.6)	126.6	81.4 (± 12.3)	117.5 (± 17.1)	88.4 (± 5.3)
MEAN	103.8 (± 13.3)	113.4 (± 19.7)	128.0 (± 26.8)	127.8 (± 8.4)	73.1 (± 7.5)

TABLE 2.17 Two-Way ANOVA results of capitulum mass density (CMD) for *Sphagnum fuscum*, *S. angustifolium*, and *S. magellanicum* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison.

	Capitulum Mass Density ($g\ m^{-2}$)									
	BOG - *S. fuscum*		FEN - *S. fuscum*		BOG - *S. angustifolium*		FEN - *S. angustifolium*		FEN - *S. magellanicum*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	2.02	0.097	6.43	**0.0027**	3.68	**0.0125**	1.42	0.256	0.60	0.675
YEAR	0.01	0.925	3.10	0.10	17.34	**0.0005**	59.10	**< 0.0001**	1.23	0.309
TREATMENT*YEAR	0.84	0.552	0.85	0.537	3.89	**0.0097**	1.00	0.451	0.34	0.798

Net Primary Production (NPP)

Year Effects - For *Sphagnum fuscum* NPP in the bog, there was a significant year effect (F = 12.80; *p* = 0.001), but no N treatment (F = 1.63; *p* = 0.176) or interaction (F = 1.48; *p* = 0.220) effect (FIGURE 2.45; TABLE 2.19). For *S. fuscum* NPP in the poor fen, there was a significant year effect (F = 6.57; *p* = 0.025), but no N treatment (F = 0.73; *p* = 0.613) or interaction (F = 1.40; *p* = 0.264) effect (FIGURE 2.46; TABLE 2.19). For *S. angustifolium* NPP in the poor fen, there was a significant year effect (F = 56.19; *p* < 0.0001), but no N treatment (F = 1.22; *p* = 0.342) or interaction (F = 2.24; *p* = 0.089) effect (FIGURE 2.47; TABLE 2.19).

No Effects - For *S. magellanicum* NPP in the poor fen, there was a non-significant year (F = 2.85; *p* = 0.142), N treatment (F = 1.02; *p* = 0.468), and interaction (F = 0.19; *p* = 0.936) effect (FIGURE 2.48; TABLE 2.19).

Summary of Data - In 2011, the mean *S. fuscum* NPP in the bog was 217.9 g m^{-2} yr^{-1} and in 2012, the mean NPP was 311.1 g m^{-2} yr^{-1} (nearly 1½ times greater than the previous year) (TABLE 2.18). In 2011, the mean *S. fuscum* NPP in the fen was 337.8 g m^{-2} yr^{-1} and in 2012, the mean NPP was 503.6 g m^{-2} yr^{-1} (also nearly 1½ times greater than the previous year) (TABLE 2.18). In 2011, the mean *S. angustifolium* NPP in the poor fen was 167.8 g m^{-2} yr^{-1} and in 2012, the mean NPP was 597.2 g m^{-2} yr^{-1} (over 3½ times greater than the previous year) (TABLE 2.18).

In 2011, the mean *S. magellanicum* NPP in the poor fen was 193.5 g m^{-2} yr^{-1} and in 2012, the mean NPP was 366.6 g m^{-2} yr^{-1} (nearly 2 times greater than the previous year) (TABLE 2.18).

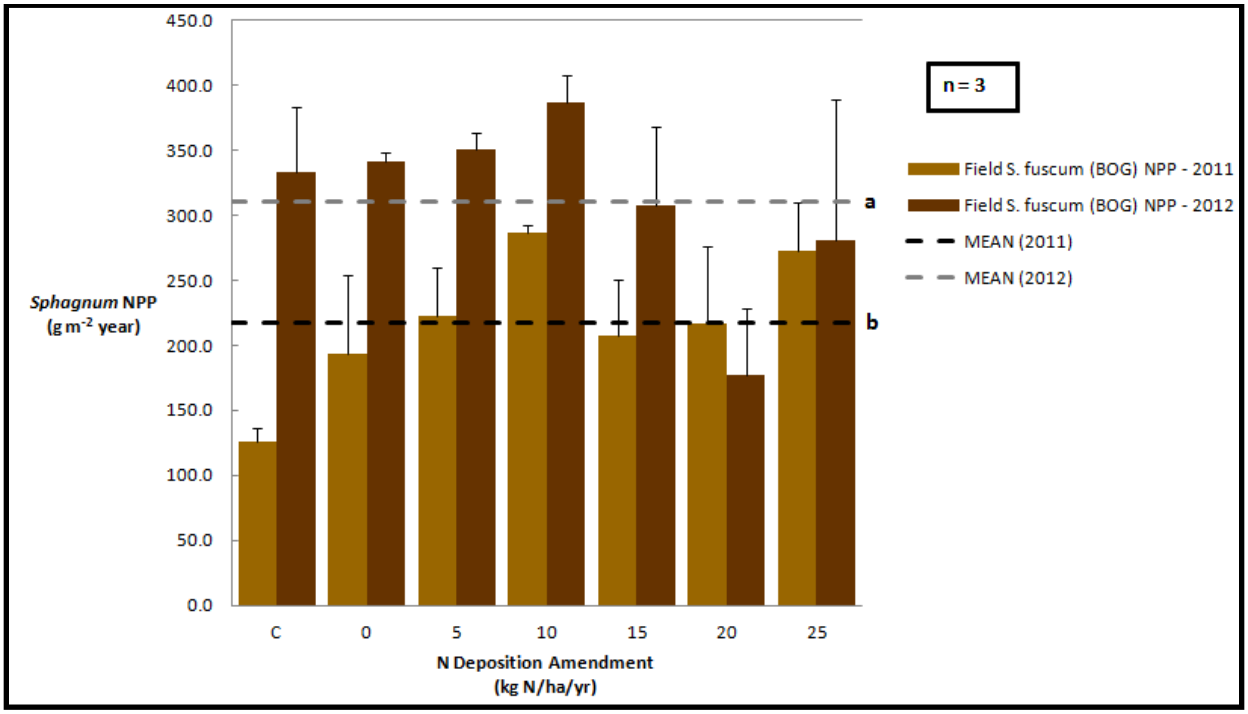

FIGURE 2.45 Mean net primary production (NPP) values for *S. fuscum* in the bog for 2011 and 2012. Bars represent means ± SE. Dashed lines represent the mean value calculated across all treatments for each year (2011 and 2012). Letters next to each dashed line represent significant differences between years using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

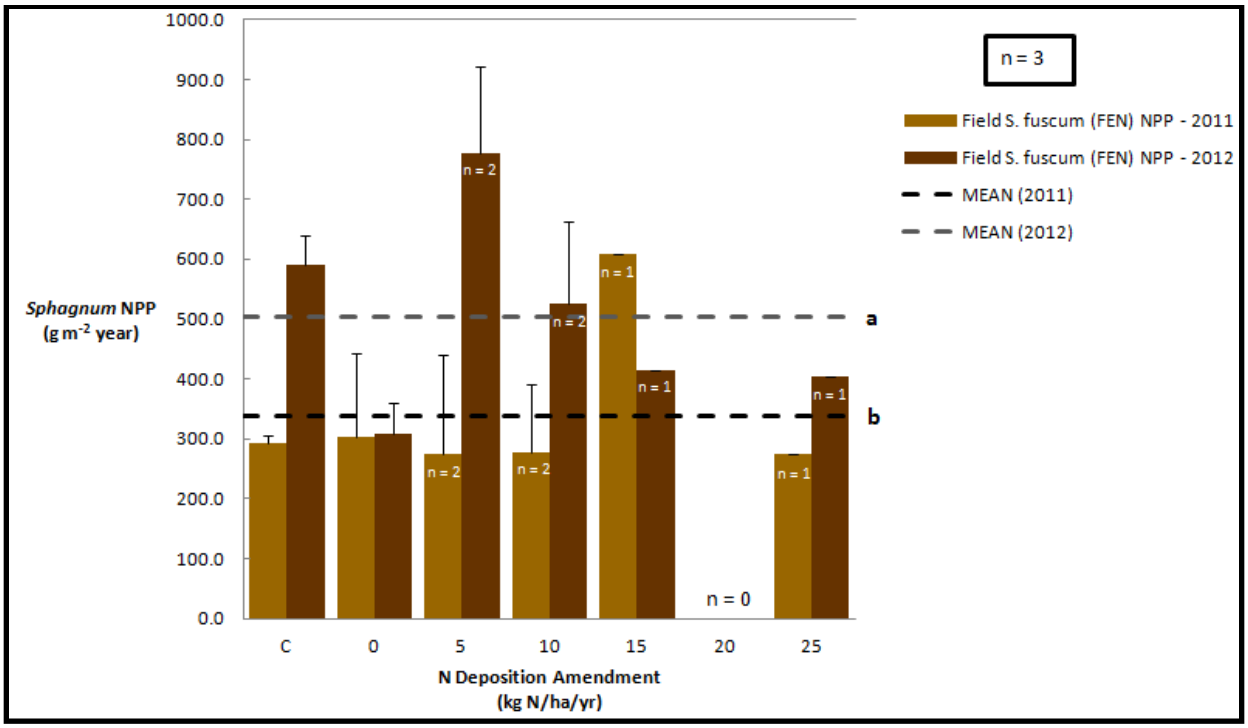

FIGURE 2.46 Mean net primary production (NPP) values for *S. fuscum* in the poor fen for 2011 and 2012. Bars represent means ± SE. Dashed lines represent the mean value calculated across all treatments for each year (2011 and 2012). Letters next to each dashed line represent significant differences between years using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

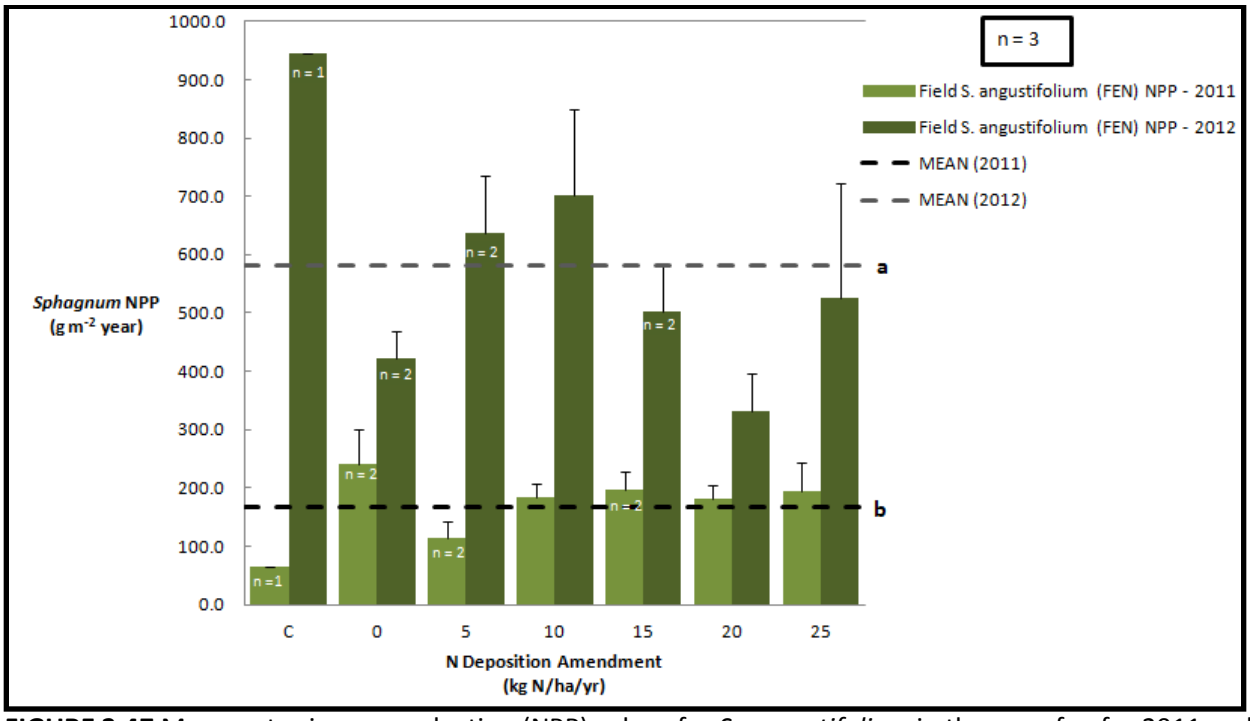

FIGURE 2.47 Mean net primary production (NPP) values for *S. angustifolium* in the poor fen for 2011 and 2012. Bars represent means ± SE. Dashed lines represent the mean value calculated across all treatments for each year (2011 and 2012). Letters next to each dashed line represent significant differences between years using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

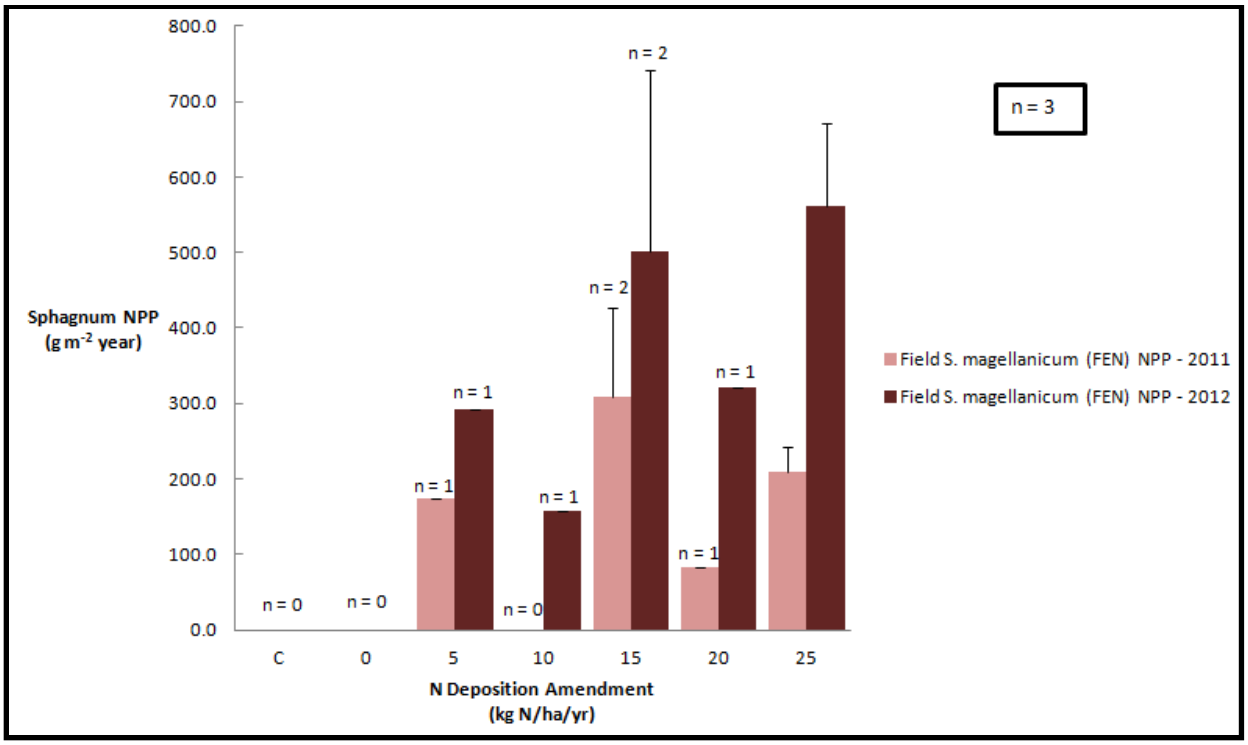

FIGURE 2.48 Mean net primary production (NPP) values for *S. magellanicum* in the poor fen for 2011 and 2012. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

TABLE 2.18 Mean NPP values for *Sphagnum fuscum* (bog and poor fen), *S. angustifolium* (bog and poor fen), and *S. magellanicum* (poor fen). Values represent means ± SE. When no standard error is noted, then n=1. Linear Growth (cm) x Stem Mass Density (g cm^{-1} m^{-2}) = NPP (g m^{-2} $year^{-1}$)

2011	BOG - *S. fuscum*	FEN - *S. fuscum*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**NPP (g m^{-2} yr^{-1})**	**NPP (g m^{-2} yr^{-1})**	**NPP (g m^{-2} yr^{-1})**	**NPP (g m^{-2} yr^{-1})**
Control	125.6 (± 11.2)	291.5 (± 13.2)	63.6	N/A
0 kg/ha	193.3 (± 60.3)	302.8 (± 140.7)	240.6 (± 59.6)	N/A
5 kg/ha	223.2 (± 37.1)	274.0 (± 165.2)	114.2 (± 29.1)	174.1
10 kg/ha	286.3 (± 6.6)	275.9 (± 115.0)	185.1 (± 20.9)	N/A
15 kg/ha	208.0 (± 42.6)	607.6	195.8 (± 32.0)	308.1 (± 118.4)
20 kg/ha	217.0 (± 59.3)	N/A	180.6 (± 24.1)	82.9
25 kg/ha	272.2 (± 38.1)	274.9	194.9 (± 48.4)	208.9 (± 33.9)
MEAN	217.9 (± 30.6)	337.8 (± 76.6)	167.8 (± 34.2)	193.5 (± 53.7)

2012	BOG - *S. fuscum*	FEN - *S. fuscum*	FEN - *S. angustifolium*	FEN - *S. magellanicum*
Treatment	**NPP (g m^{-2} yr^{-1})**	**NPP (g m^{-2} yr^{-1})**	**NPP (g m^{-2} yr^{-1})**	**NPP (g m^{-2} yr^{-1})**
Control	333.7 (± 49.9)	590.6 (± 49.2)	945.6	N/A
0 kg/ha	341.1 (± 7.4)	307.8 (± 51.1)	420.9 (± 48.4)	N/A
5 kg/ha	350.5 (± 12.8)	778.1 (± 144.0)	635.9 (± 100.4)	292.1
10 kg/ha	386.6 (± 21.1)	525.3 (± 137.8)	701.0 (± 148.6)	158.3
15 kg/ha	307.7 (± 60.1)	415.1	502.1 (± 78.3)	500.5 (± 241.7)
20 kg/ha	177.5 (± 51.3)	N/A	332.6 (± 86.1)	321.6
25 kg/ha	280.7 (± 108.9)	404.5	525.2 (± 197.1)	560.6 (± 111.3)
MEAN	311.1 (± 39.1)	503.6 (± 96.4)	580.5 (± 117.2)	366.6 (± 94.2)

TABLE 2.19 Two-Way ANOVA results of net primary production (NPP) for *Sphagnum fuscum*, *S. angustifolium*, and *S. magellanicum* as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison.

	Net Primary Production (NPP) (g m^{-2} $year^{-1}$)							
	BOG - *S. fuscum*		FEN - *S. fuscum*		FEN - *S. angustifolium*		FEN - *S. magellanicum*	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	1.63	0.1756	0.73	0.6126	0.98	0.4655	1.02	0.4682
YEAR	12.80	**0.0013**	6.57	**0.0249**	46.20	**< 0.0001**	2.85	0.1421
TREATMENT*YEAR	1.48	0.2199	1.49	0.2638	1.94	0.1296	0.19	0.9357

Sphagnum Community Response (poor fen)

N Treatment and Year Effects - Differences in stem mass density (SMD) were detected for year and N treatment for the *Sphagnum* community in the poor fen (year: F = 5.08, $p = 0.034$; N: F = 2.52, $p = 0.049$) (FIGURE 2.50; TABLE 2.21).

Year Effects - Differences in linear growth (LG) were detected for year for the *Sphagnum* community in the poor fen (F = 67.08; $p < 0.0001$) (FIGURE 2.49; TABLE 2.21). Differences in net primary production (NPP) were detected for year for the *Sphagnum* community in the poor fen (F = 39.83; $p < 0.0001$) (FIGURE 2.51; TABLE 2.21).

Summary of Data - Linear growth (cm), stem mass density (g m^{-2} cm^{-1}), and NPP (g m^{-2} yr^{-1}) values for the *Sphagnum* community in the poor fen were, on average, higher in 2012 than in 2011 (TABLE 2.20). In 2011, the mean *Sphagnum* community LG in the poor fen was 2.9 cm and in 2012, the mean LG was 5.0 cm (TABLE 2.20). In 2011, the mean *Sphagnum* community SMD in the poor fen was 73.5 g cm^{-1} m^{-2} and in 2012, the mean SMD was 98.9 g cm^{-1} m^{-2} (TABLE 2.20). In 2011, the mean *Sphagnum* community NPP in the poor fen was 207.3 g m^{-2} yr^{-1} and in 2012, the mean NPP was 487.1 g m^{-2} yr^{-1} (TABLE 2.20).

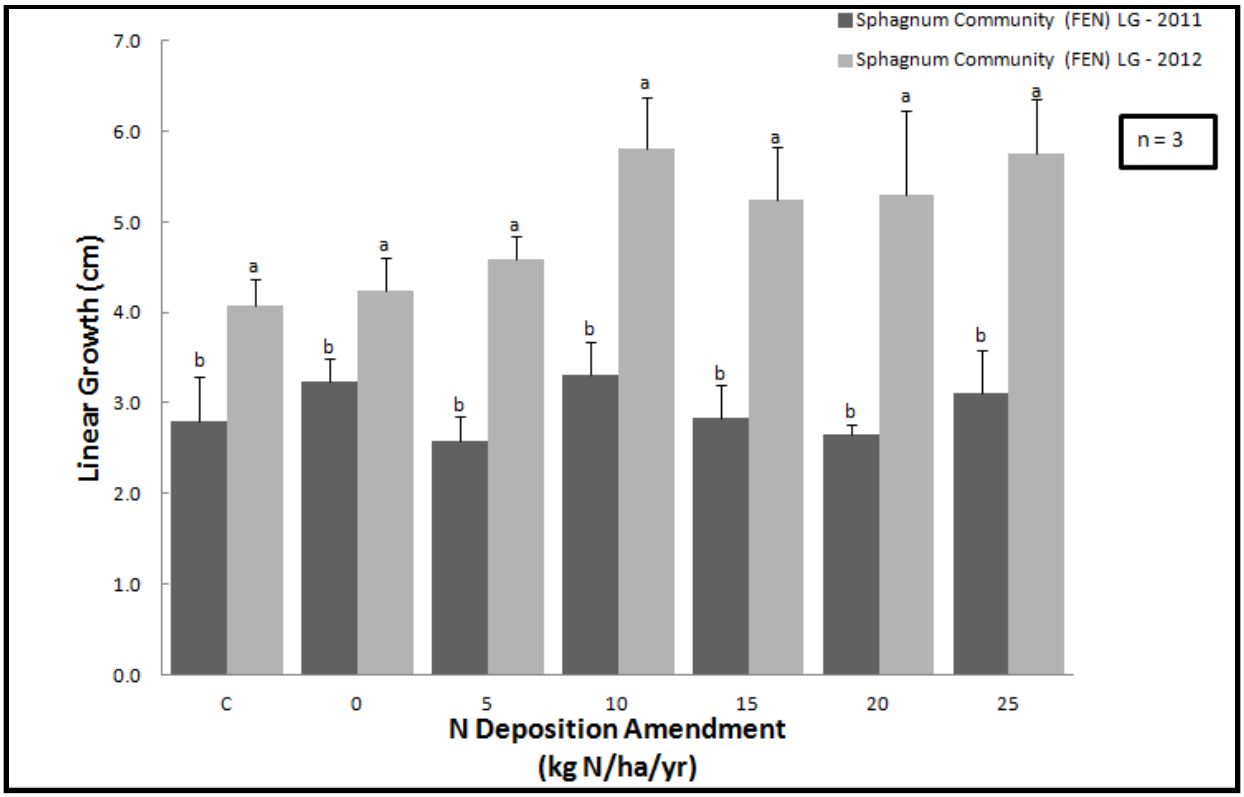

FIGURE 2.49 Mean linear growth (cm) values for the *Sphagnum* community in the poor fen treatment plots. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

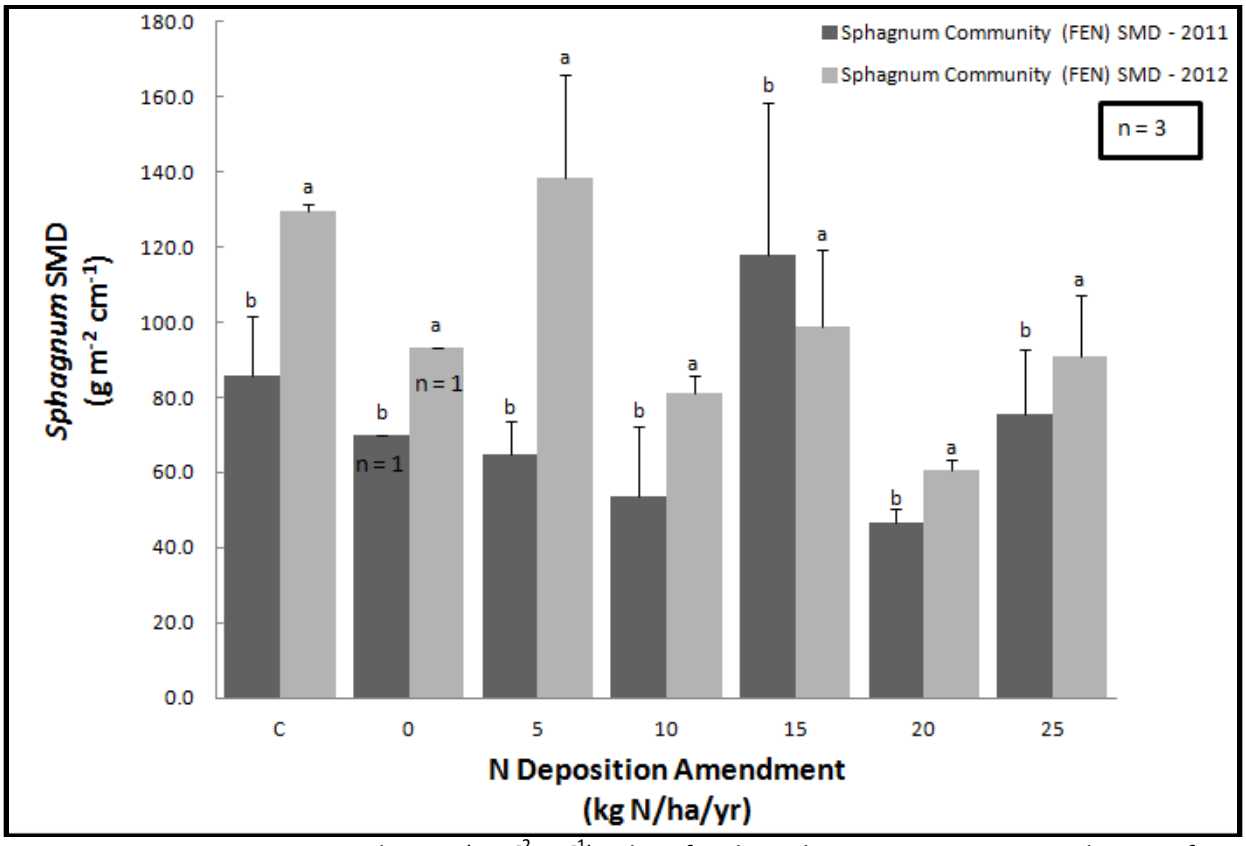

FIGURE 2.50 Mean stem mass density (g m^{-2} cm^{-1}) values for the *Sphagnum* community in the poor fen treatment plots. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

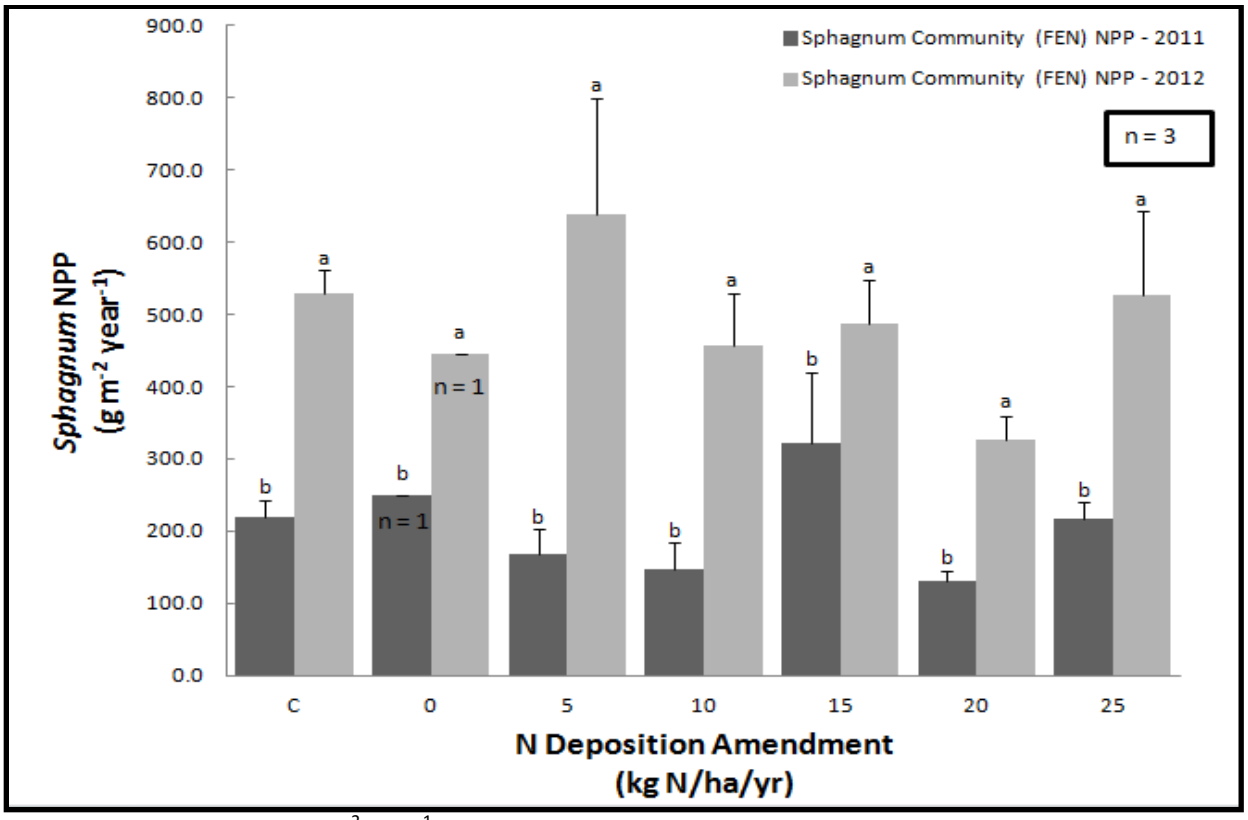

FIGURE 2.51 Mean NPP (g m^{-2} $year^{-1}$) values for the *Sphagnum* community in the poor fen treatment plots. Bars represent means ± SE. Letters above the bars represent significant differences between groups using *a posteriori* Tukey's HSD test ($p < 0.05$). Sample size is n=3 unless otherwise noted.

TABLE 2.20 Linear growth (cm), stem mass density (g m^{-2} cm^{-1}), and NPP (g m^{-2} $year^{-1}$) values for the *Sphagnum* community in the poor fen treatment plots. Values represent means ± SE. When no standard error is noted, then n=1.

2011	Linear Growth	Stem Mass Density	NPP
Treatment	(cm)	(g m^{-2} cm^{-1})	(g m^{-2} $year^{-1}$)
Control	2.8 (± 0.5)	85.8 (± 16.0)	218.9 (± 24.1)
0 kg/ha	3.2 (± 0.3)	70.0	249.6
5 kg/ha	2.6 (± 0.3)	64.9 (± 8.9)	166.7 (± 36.0)
10 kg/ha	3.3 (± 0.4)	53.4 (± 19.0)	147.5 (± 36.4)
15 kg/ha	2.8 (± 0.4)	117.7 (± 41.0)	320.6 (± 98.4)
20 kg/ha	2.7 (± 0.1)	46.8 (± 3.4)	131.8 (± 12.1)
25 kg/ha	3.1 (± 0.5)	75.5 (± 17.4)	216.0 (± 23.2)
MEAN	2.9 (± 0.2)	73.5 (± 13.6)	207.3 (± 37.8)

2012	Linear Growth	Stem Mass Density	NPP
Treatment	(cm)	(g m^{-2} cm^{-1})	(g m^{-2} $year^{-1}$)
Control	4.1 (± 0.3)	129.7 (± 1.8)	528.4 (± 32.3)
0 kg/ha	4.2 (± 0.4)	93.0	445.0
5 kg/ha	4.6 (± 0.3)	138.5 (± 27.5)	639.0 (± 160.3)
10 kg/ha	5.8 (± 0.6)	80.9 (± 5.0)	457.5 (± 71.9)
15 kg/ha	5.2 (± 0.6)	98.9 (± 20.6)	486.8 (± 61.4)
20 kg/ha	5.3 (± 0.9)	60.5 (± 2.9)	327.1 (± 31.3)
25 kg/ha	5.7 (± 0.6)	90.9 (± 16.4)	526.0 (± 118.2)
MEAN	5.0 (± 0.4)	98.9 (± 15.7)	487.1 (± 55.1)

TABLE 2.21 Two-Way ANOVA results of linear growth (cm), stem mass density (g m^{-2} cm^{-1}), and NPP (g m^{-2} $year^{-1}$) values for the *Sphagnum* community (poor fen) as a function of treatment and year. *P*-value less than 0.05 indicates significant differences among means compared using Tukey-Kramer multiple means comparison.

	Sphagnum community (poor fen)					
	Linear Growth (cm)		SMD (g m^{-2} cm^{-1})		NPP (g m^{-2} $year^{-1}$)	
EFFECT	**F VALUE**	***P***	**F VALUE**	***P***	**F VALUE**	***P***
TREATMENT	1.50	0.213	2.52	**0.049**	1.46	0.234
YEAR	67.08	**< 0.0001**	5.08	**0.034**	39.83	**< 0.0001**
TREATMENT*YEAR	0.98	0.455	1.17	0.356	0.96	0.472

DISCUSSION

Nitrogen Uptake

Changes in %N, C:N ratios, and capitulum N storage in *Sphagnum* spp. after two growing seasons

There were differences in capitulum N concentration (%N) between N treatments for *S. fuscum* in the poor fen, but only between the highest N amendment (25 kg/ha) and the lowest N amendment (5 kg/ha) and controls (water control and 0 kg/ha) in 2012, and between the 15 kg/ha and 5 kg/ha treatment plots in 2012. Unfortunately, the %N value for the 25 kg/ha treatment was measured from only one sample (n=1), so it may not accurately represent the results. The differences in %N between N treatments for *S. angustifolium* in the bog were only for 2012 as well, and were pretty sporadic; the 25 kg/ha treatment plots were different from the 20 kg/ha and 5 kg/ha treatment plots. There were no differences in %N between N treatments for *S. fuscum* in the bog or *S. angustifolium* in the poor fen. Thus, there were no clear trends for the effect of N treatments on capitulum N concentration (%N) in these first two years. *S. fuscum* and *S. angustifolium* in the bog and poor fen had differences in %N between years, with 2012 having higher %N values than 2011.

	S. angustifolium	*S. fuscum*
FEN	2012: No T ↑ 2011: No T	2012: T (high) *↑ 2011: No T
BOG	2012: Sporadic T ↑ 2011: No T	2012: No T ↑ 2011: No T

KEY
T = N Treatment effect
↑ = year effect
*↑ = year effect w/ interaction

TABLE 2.22 Visual representation of Two-Way ANOVA results of %N for *Sphagnum fuscum* and *S. angustifolium* in the bog and poor fen as a function of N treatment and year.

Although two-way ANOVA analyses indicated differences in C:N ratios between N treatments for *S. fuscum* in the poor fen ($F = 3.52$, $p = 0.029$) and *S. angustifolium* in the bog ($F = 2.60$, $p = 0.049$), post-hoc multiple comparisons done by Tukey's HSD test did not reveal any significant differences between N treatments. There were no differences in C:N ratios between N treatments for *S. fuscum* in the bog or *S. angustifolium* in the poor fen. Thus, there were also no clear trends for the effect of N treatments on C:N ratios in these first two years. *Sphagnum fuscum* and *S. angustifolium* in the bog and poor fen, as well as *S. magellanicum* in the poor fen, had differences in C:N ratios between years, with 2012 having lower C:N ratios than 2011. A decrease in the C:N ratio of *Sphagnum* could mean that nitrogen (N) concentrations increased or carbon (C) concentrations decreased. I found that *Sphagnum* capitulum N concentration (%N) values were higher in 2012 than in 2011, therefore, the lower *Sphagnum* capitulum C:N ratios in 2012 were due to increased *Sphagnum* capitulum %N.

Results for capitulum N storage (CNS) corroborate findings of increased N uptake by *Sphagnum* mosses. Capitulum N storage was, on average, higher in 2012 than in 2011 for all *Sphagnum* species, in both site types (bog and poor fen), with *S. angustifolium* having the most drastic increases. There was one notable exception where 2012 CNS values were lower than 2011 values: the 20 kg/ha N treatment for *S. fuscum* in the bog. There were sporadic differences in capitulum N storage between N treatments for *S. fuscum* in the bog and poor fen, and *S. angustifolium* in the bog. There were also differences in capitulum N storage between years for *S. fuscum* in the bog and poor fen, and *S. angustifolium* in the bog and poor fen. However, the N treatment and year effect for *S. angustifolium* in the bog could just be the result of an “outlier”, the water control (n=1).

Changes in %N in vascular plant species after two growing seasons

The results for vascular plant tissue N concentration (%N) were not as consistent as those for *Sphagnum* %N. **BOG:** In the bog, one species (*Picea mariana*) increased from 2011 to 2012, two species (*Oxycoccos microcarpus* and *Rubus chamaemorus*) remained the same, and four species (*Smilacina trifolia*, *Ledum groenlandicum*, *Chamaedaphne calyculata*, and *Andromeda polifolia*) decreased from 2011 to 2012. The only vascular plant species in the bog that actually had a significant difference in year were *Picea mariana* and *Chamaedaphne calyculata*; however, according to post-hoc multiple comparisons done by Tukey's HSD test, the only difference for *Picea mariana* was that the 20 kg/ha treatment in 2012 differed from 2011 %N values, and the only difference for *Chamaedaphne calyculata* was that the 20 kg/ha treatment in 2011 differed from the 0 kg/ha treatment in 2012. The only vascular species in the bog that had a N treatment effect was *Oxycoccos microcarpus*, but post-hoc multiple comparisons done by Tukey's HSD test revealed just the water control and 15 kg/ha treatment in 2012 were different. **FEN:** In the poor fen, one species (*Eriophorum vaginatum*) increased from 2011 to 2012, one species (*Andromeda polifolia*) remained the same, and two species (*Scheuchzeria palustris* and *Chamaedaphne calyculata*) decreased from 2011 to 2012 (TABLE). *Eriophorum vaginatum*, *Scheuchzeria palustris*, and *Chamaedaphne calyculata* in the poor fen all had a significant difference in year. However, according to post-hoc multiple comparisons done by Tukey's HSD test, there were not actually any differences between 2011 and 2012 for *Eriophorum vaginatum*, and there was only a difference between the 20 kg/ha treatment in 2011 and the control in 2012 for *Chamaedaphne calyculata*. None of the vascular species in the poor fen showed a N treatment effect.

Possible Explanations?

There were no clear trends for the effect of N treatments on N concentration (%N) for *Sphagnum* species or vascular plant species in these first two years; however, there were differences between years for %N of *Sphagnum* species and some vascular plant species, as well as *Sphagnum* C:N ratios and capitulum N storage. This year effect is potentially related to climatic factors. In 2012, the average daily temperature was 1.9 °C warmer than in 2011 and growing degree days were 5.4% higher. The total precipitation during the 2012 growing season (data taken from 6/8/12 to 9/12/12) was 137.9 mm, or about 63%, greater than the total precipitation recorded during the 2011 growing season (data taken from 6/8/11 to 10/4/11). Climate may have been a limiting factor during the 2011 growing season, thus when there were wetter conditions in 2012, climate was no longer limiting and measured %N values for *Sphagnum* species and some vascular plant species were higher. The lower C:N ratios found for *Sphagnum* capitula in 2012, as well as the increased capitulum N storages values in 2012, may also be a result of the difference in climate.

Although *Sphagnum* is extremely adept at scavenging nitrogen, it is not completely efficient at taking up all available nitrogen (Limpens et al. 2006), thus, some nitrogen inputs may have become available for vascular plant species. As vascular plants in peatlands are N-limited, the net primary production (NPP) of these plants would increase with an increased N supply (Heijmans et al. 2002; Limpens et al. 2003). It has been shown for low nutrient environments that once a level is reached where the vascular plant NPP is no longer N-limited, the vascular plants exhibit luxury consumption, increasing the N concentrations in their tissues in excess of immediate growth requirements (Chapin 1980). It is possible that the various

vascular plant species that I analyzed were in different phases of this predicted response. The only analysis I conducted for vascular plant species in the bog and poor fen was N concentration (%N) in new leaf tissue. I did not measure NPP for any of the vascular plant species. If some N not taken up by *Sphagnum* became available for vascular plant species, there would definitely be competition amongst the vascular plant species to scavenge that N. Some particular species may be more adept at scavenging N from the peat than others - for example, due to possible differences in root structure or mycorrhizal associations.

Vascular plant species with shallow roots tend to respond first to increases in N availability (Heijmans et al. 2002; Nordbakken et al. 2003). In a ^{15}N tracing experiment, Heijmans et al. (2002) retrieved 79% of the ^{15}N from living *Sphagnum*, but of the percentage that was retrieved from vascular plant species, most was recovered from *Vaccinium oxycoccos*, or bog cranberry (synonymous with *Oxycoccos microcarpus*). *Vaccinium oxycoccos* is a shallow-rooting shrub, known to have mycorrhizal associations which help with nutrient acquisition from peat (Vander Kloet 1988). At the Mariana Lake study site, *Oxycoccos microcarpus* was the only vascular plant species to have a N treatment effect (between the water control and the 15 kg/ha N treatment) for %N in 2012.

Vascular plant species that showed a decrease in %N from 2011 to 2012, didn't necessarily receive little or no additional N from leaching down the peat column, they could be in the phase where they are using the additional N for increased NPP, and are not yet at the point where NPP is no longer N-limited. Vascular plant species that showed an increase in %N from 2011 to 2012 could have been those species that were more adept at scavenging N, or they could have received a similar amount of additional N as the other species, but their growth

may be limited by some nutrient other than nitrogen (such as phosphorus). If the latter was the case, then they might begin to have a build-up of nitrogen in their tissue, as expressed by the higher %N values.

Sphagnum Growth Response

Changes in linear growth, stem mass density, capitulum mass density, and net primary production in *Sphagnum* spp. after two growing seasons

There were differences in linear growth (LG) between N treatments for *S. fuscum* in the bog and poor fen, *S. angustifolium* in the poor fen, and *S. magellanicum* in the poor fen, but there were no clear trends. For the most part, differences between N treatments were only apparent in the second growing season (2012). For *S. fuscum* in the bog, the 10 kg/ha N treatment in 2012 was different from all the other treatments. For *S. fuscum* in the poor fen, the 5 kg/ha N treatment in 2012 was different from the water control, and 10 kg/ka and 15 kg/ha N treatments. For *S. angustifolium* in the poor fen, the 10 kg/ha N treatment in 2012 was different from the 0 kg/ha, 5 kg/ha, 20 kg/ka, and 25 kg/ha N treatments. For *S. magellanicum* in the poor fen, the 25 kg/ha N treatment in 2012 was different from the water control, 0 kg/ha, 5 kg/ha, 15 kg/ha, and 20 kg/ka N treatments. There were differences in linear growth between years for *S. fuscum* in the bog and poor fen, *S. angustifolium* in the poor fen, and *S. magellanicum* in the poor fen, with 2012 having higher linear growth values than 2011.

There were no differences in stem mass density (SMD) between N treatments for *S. fuscum* in the bog and poor fen, *S. angustifolium* in the bog and poor fen, or *S. magellanicum* in the poor fen. Thus, there were no clear trends for the effect of N treatments on stem mass density in these first two years. *S. angustifolium* in the poor fen had differences in stem mass

density between years - the water control (n=1) in 2012 differed from every N treatment (the water control and 0 – 25 kg/ha N treatments) in 2011, and the 5 kg/ha N treatment in 2012 differed from the water control (n=1), 5 kg/ha N treatment, and 10 kg/ha N treatment in 2011. Although two-way ANOVA analyses indicated differences in stem mass density between years for *S. angustifolium* in the bog, post-hoc multiple comparisons done by Tukey's HSD test did not reveal any significant differences. 2012 had higher stem mass values than 2011, with a few exceptions.

There were differences in capitulum mass density (CMD) between N treatments for *S. fuscum* in the poor fen, but only between the water control and the 10 kg/ha and 15 kg/ha N treatments in 2012. There were also differences in capitulum mass density between N treatments for *S. angustifolium* in the bog, but only between the water control and the 10 kg/ha N treatment, the 15 kg/ha N treatment, the 20 kg/ha N treatment, and the 25 ka/ha N treatment in 2012. *S. angustifolium* in the bog had differences in capitulum mass density between years as well, but this year effect may just be the result of an “outlier”, the water control (n=1). There were differences in capitulum mass density between years for *S. angustifolium* in the poor fen, but just between the 5 kg/ha N treatment in 2011 and the 20 kg/ha N treatment in 2012. 2012 had higher capitulum mass values than 2011, with a few exceptions.

There were no differences in net primary production (NPP) between N treatments for *S. fuscum* in the bog and poor fen, *S. angustifolium* in the poor fen, or *S. magellanicum* in the poor fen. Thus, there were no clear trends for the effect of N treatments on net primary production in these first two years. *S. fuscum* in the bog had differences in NPP between years, but only

between the water control in 2011 and the 10 kg/ha N treatment in 2012. Although two-way ANOVA analyses indicated differences in NPP between years for *S. fuscum* in the poor fen ($F = 6.57$, $p = 0.025$), post-hoc multiple comparisons done by Tukey's HSD test did not reveal any significant differences. *S. angustifolium* in the poor fen had differences in NPP between years, but this year effect may just be the result of an "outlier", the water control (n=1). For every case, except *S. fuscum* measured in the 20 kg/ha N treatment plots in the bog (n=3) and *S. fuscum* measured in the 15 kg/ha N treatment plots in the poor fen (n=1), average NPP values were higher in 2012 than in 2011.

Looking at how the *Sphagnum* community as a whole responded to the N additions, results were similar to those presented for each *Sphagnum* species separately. Differences in stem mass density (SMD) were detected for year and N treatment for the *Sphagnum* community in the poor fen; however, post-hoc multiple comparisons done by Tukey's HSD test did not reveal any significant differences. Differences in linear growth (LG) and net primary production (NPP) were detected for year for the *Sphagnum* community in the poor fen. Linear growth (cm), stem mass density (g m^{-2} cm^{-1}), and NPP (g m^{-2} $year^{-1}$) values for the *Sphagnum* community in the poor fen were, on average, higher in 2012 than in 2011. The 15 kg/ha N treatment was the only exception where the 2012 mean stem mass density value was lower than the 2011 mean stem mass density value.

Possible Explanations?

Differences of Sphagnum fuscum, S. angustifolium, and S. magellanicum

Due to differences in morphology and growth form, I anticipated the various *Sphagnum* species I was investigating to have differing growth responses to increased nitrogen. Since

Sphagnum angustifolium grows more rapidly than either of the other two *Sphagnum* species (*Sphagnum fuscum* and *Sphagnum magellanicum*), I predicted that it would have the greatest linear growth. With additional nitrogen resources, I thought it would likely invest much of it towards vertical growth of its shoots. *Sphagnum angustifolium* did have significant increases in linear growth from 2011 to 2012, but it also had significant increases in capitulum and stem mass density from 2011 to 2012, suggesting that its allocation of nitrogen was distributed throughout the whole plant. Since *S. fuscum* forms tightly packed hummocks, I predicted that it would not have much opportunity to increase its capitula biomass with additional nitrogen, and that rather it would have substantial linear growth (but still not as much as *S. angustifolium* due to the nature of its rate of growth) as well as "bulking out" of its stem and branches (i.e. increased stem mass density). Due to its compact growth pattern, I predicted that *S. fuscum* would have the highest stem mass density values. *Sphagnum fuscum* did have the highest stem mass density values, but it did not have drastic increases from 2011 to 2012; *Sphagnum angustifolium* had the greatest increases in stem mass density in these first two years, particularly in the poor fen. *Sphagnum angustifolium* and *S. magellanicum* individuals tend to be larger and more robust than *S. fuscum* individuals, so I predicted they would have larger capitulum mass density values. *Sphagnum angustifolium* had the highest capitulum mass density values in 2012, after significant increases from 2011 (CMD for *S. angustifolium* in the poor fen in 2012 was more than double the CMD in 2011), whereas capitulum mass density values for *S. fuscum* changed very little. *Sphagnum angustifolium* grows fairly loosely in lawns, which may have provided more opportunity for increases in capitula biomass with increased nitrogen availability.

After analyzing the various measures of *Sphagnum* growth, it was not surprisingly to find that *S. angustifolium* had the greatest primary production, with NPP in the poor fen exceeding NPP in the bog in 2012. *Sphagnum angustifolium* had the most drastic increases in linear growth, capitulum and stem mass density, and net primary production (NPP) from 2011 to 2012. Gunnarsson (2005) revealed that throughout various studies on peatland production, greater production is typically measured in lawns versus hummocks, possibly owing to the fact that lawn species are generally closer to the water-table than hummock species, which helps to keep the capitula moist and able to photosynthesize. As *S. angustifolium* is found mainly in lawns at the Mariana Lake study site (especially in the poor fen), this could be one explanation for its high primary production values.

Climatic Factors

Some studies have shown that climate (temperature and precipitation) can have a considerable influence on *Sphagnum* production (Gignac et al. 1998; Gunnarsson 2005; Wieder 2006). As I discuss above, the total precipitation in 2012 was greater than in 2011. The average daily temperature was slightly warmer in 2012, and the growing degree days were also higher in 2012 than in 2011. Many *Sphagnum* growth measurements that were taken in both 2011 and 2012 had significant differences in year (i.e. linear growth for *S. fuscum* (bog and poor fen), *S. angustifolium* (poor fen), and *S. magellanicum* (poor fen); stem and capitulum mass density for *S. angustifolium* (bog and poor fen); NPP for *S. fuscum* (bog and poor fen) and *S. angustifolium* (poor fen)). This year effect may be in part due to the difference in climate between these two years. Higher *Sphagnum* growth predictably occurred in 2012, which had a much wetter, and slightly warmer, growing season.

Asada et al. (2003) suggested in their study of a hypermaritime coastal peatland that *Sphagnum* growth was positively correlated with precipitation, and to a lesser degree, temperature. In their study, they found that hummock *Sphagnum* species had lower growth rates, and that their overall seasonal growth pattern was less variable than lawn *Sphagnum* species, which can possibly be explained by the difference in moisture regime between hummocks and lawns. Though the moisture content in hummocks is lower than in lawns, it is more constant due to the dense growth form of hummock *Sphagnum* species that results in superior water-holding capabilities (Rydin 1985). Asada et al. (2003) found that hummock *Sphagnum* species were able to grow during dry conditions, albeit slowly, while lawn *Sphagnum* species could not. At the Mariana Lake study site, less growth occurred for *Sphagnum angustifolium* (lawn species) than for *Sphagnum fuscum* (hummock species) during the 2011 growing season, which was drier than the 2012 growing season, especially towards the end of the season. With increased precipitation in 2012, *S. angustifolium* grew rapidly, exceeding growth of *S. fuscum*. Thus, *S. angustifolium* growth was likely limited by water during the 2011 growing season.

With substantial growth recorded for all *Sphagnum* species in 2012, it was surprising to see higher capitulum N concentration (%N) values and lower C:N values in 2012 than in 2011. With increased growth, *Sphagnum* would have greater nitrogen requirements to support that growth. Yet despite these greater nitrogen requirements to support increased growth, *Sphagnum* still had fairly high %N values for its capitulum tissue. I discussed the possibility of nutrient limitation other than N limitation earlier, in light of higher %N values for some vascular plant species in 2012. This could also be a potential explanation for higher %N values for

Sphagnum capitulum in 2012. Aerts et al. (1992) found that under conditions of high N deposition in a peatland, *Sphagnum* may shift from a nitrogen (N) limitation to a phosphorus (P) limitation. Another possible explanation for higher %N values for *Sphagnum* capitulum in 2012, could be *Sphagnum* was obtaining more nitrogen in 2012, in excess of its growth requirements.

There are a few possibilities for where *Sphagnum* could be obtaining additional nitrogen beyond that used for its growth requirements. One possibility is that there were greater N inputs in 2012 than in 2011. Atmospheric nitrogen deposition values, however, were relatively similar in 2011 and 2012 (TABLE 2.1). In 2012, N deposition (NH_4^+ and NO_3^-) values were slightly greater (0.80 versus 0.55 mg m^{-2} day^{-1}), but that would only amount to an additional 0.25 kg ha^{-1} over a 100 day period. Nitrogen mineralization measured across the Mariana Lake study site was relatively low with the exception of extremely wet areas; however, even with wetter conditions in 2012, differences in N mineralization rates were not found between 2011 and 2012 (Hartsock 2013). Nitrogen may have been translocated from older to younger parts of *Sphagnum* throughout the growing season, which Aldous et al. (2002b) found to be an important process that could contribute 0.5–11% of the annual N requirements for *Sphagnum*, but this is not being measured at the Mariana Lake study site.

Another much-overlooked N input to peatland ecosystems is N_2-fixation. In 2013, there were greater rates of N_2-fixation for the poor fen at Mariana Lake than in 2012 (N_2-fixation rates were not recorded during the 2011 growing season) (Jacqueline Popma, *personal communication*). There was a higher average daily temperature and greater total precipitation in 2013 than in 2012, which may have contributed to the higher observed rates of N_2-fixation (currently waiting for source for this data). N_2-fixation has been found to occur at greater rates

during warmer, wetter periods (Melanie Vile, *personal communication*). Although we do not have N_2-fixation rates from 2011, we can possibly guess that they were lower than N_2-fixation rates in 2012, due to the fact that it had a cooler, drier growing season. The additional N inputs from N_2-fixation in 2012 could possibly account for the higher %N values for *Sphagnum* capitulum in 2012 observed along with increased *Sphagnum* growth in 2012.

Linear Growth – "Early Spring Growth"

The linear growth values for *Sphagnum* that I have presented in my thesis are measurements of growth that took place between late May and early October (2011 and 2012 growing seasons). In 2011, cranked wires were set on May 27th, and in 2012, cranked wires were set on May 24-25th. There is a possibility that *Sphagnum* shoots started elongating prior to these dates in late May, 2011 and 2012. Once temperatures were above freezing and the upper peat layer began to thaw, *Sphagnum* shoots would have the chance to start growing, however wire placement before late May is difficult owing to the presence of late seasonal frost. On May 24th, 2012, before re-setting all the cranked wires, I first measured all the cranked wires to see if there was any "early spring growth". Since I had measured the cranked wires on October 7th, 2011 (the end of the 2011 growing season), I would be able to determine if there were any differences between those values and the values I measured on May 24th, 2012 (for our purposes, the start of the 2012 growing season) (FIGURE 2.52).

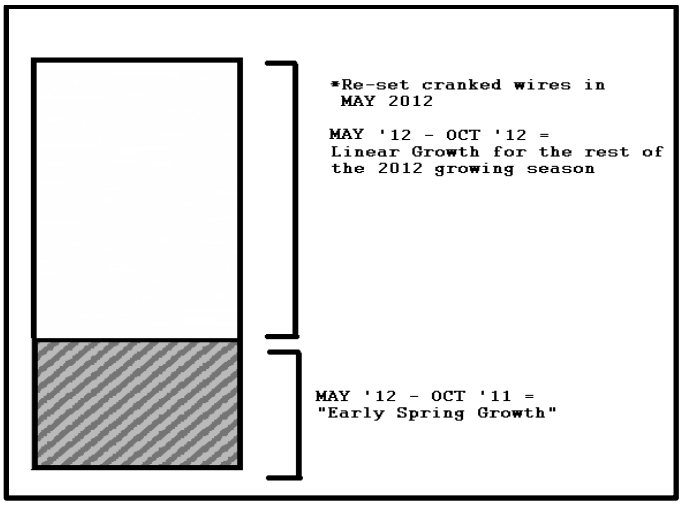

FIGURE 2.52 Visual representation of timeline and calculations used for "early spring growth".

With this technique, I did find evidence for "early spring growth" of *Sphagnum* shoots. However, I decided not to add "early spring growth" to my measurements of 2012 linear growth because there were too many factors contributing to the uncertainty of my values. For instance, there were many "negative" values, which could have been a result of wires being pushed up when lower peat layers froze during the winter months. There was very high variability among treatment plots – some plots had little to no "early spring growth", while others had up to 20% of their 2012 linear growth accounted for by "early spring growth" (TABLE 2.23 and 2.24). Also, there was the fact that I had not measured "early spring growth" for 2011, so comparing the two seasons having used different methods would have been impossible. Despite my decision not to utilize these "early spring growth" values in my results and analyses for this thesis, I do believe that my findings are relevant and suggest that studies may be underestimating annual *Sphagnum* linear growth and net primary production depending on when they set their cranked wires.

TABLE 2.23 % LG accounted for by "early spring growth" for *S. fuscum* (LEFT, bog; RIGHT, poor fen), where COL. 2 = Mean Linear Growth (cm) per Treatment Plot [2012 values] and COL. 3 = ["Early Spring Growth" (ESG) / Linear Growth '12 (COLUMN 2)] x 100. Color ramp is low to high values : yellow to orange.

BOG	Mean LG (cm)	[ESG/LG]*100
Arm 1 - Control	2.11	15.03%
Arm 1 - 0 kg/ha	2.68	13.27%
Arm 1 - 5 kg/ha	1.55	3.02%
Arm 1 - 10 kg/ha	3.57	0.47%
Arm 1 - 15 kg/ha	3.73	4.91%
Arm 1 - 20 kg/ha	2.14	11.08%
Arm 1 - 25 kg/ha	2.48	1.88%
Arm 2 - Control	2.25	1.33%
Arm 2 - 0 kg/ha	3.32	1.08%
Arm 2 - 5 kg/ha	3.26	1.84%
Arm 2 - 10 kg/ha	4.85	5.95%
Arm 2 - 15 kg/ha	2.21	2.71%
Arm 2 - 20 kg/ha	0.94	6.78%
Arm 2 - 25 kg/ha	1.80	14.71%
Arm 3 - Control	1.59	4.19%
Arm 3 - 0 kg/ha	3.22	0.21%
Arm 3 - 5 kg/ha	3.38	2.67%
Arm 3 - 10 kg/ha	1.92	2.43%
Arm 3 - 15 kg/ha	3.39	0.51%
Arm 3 - 20 kg/ha	2.21	17.32%
Arm 3 - 25 kg/ha	1.00	2.33%

FEN	Mean LG (cm)	[ESG/LG]*100
Arm 1 - Control	3.64	13.92%
Arm 1 - 0 kg/ha	4.69	0.40%
Arm 1 - 5 kg/ha	4.96	5.31%
Arm 1 - 10 kg/ha	3.29	1.21%
Arm 1 - 15 kg/ha	N/A	N/A
Arm 1 - 20 kg/ha	N/A	N/A
Arm 1 - 25 kg/ha	N/A	N/A
Arm 2 - Control	3.73	1.43%
Arm 2 - 0 kg/ha	2.54	0.00%
Arm 2 - 5 kg/ha	4.15	1.69%
Arm 2 - 10 kg/ha	4.54	15.86%
Arm 2 - 15 kg/ha	3.34	12.38%
Arm 2 - 20 kg/ha	N/A	N/A
Arm 2 - 25 kg/ha	4.94	16.40%
Arm 3 - Control	3.35	0.66%
Arm 3 - 0 kg/ha	3.90	2.05%
Arm 3 - 5 kg/ha	N/A	N/A
Arm 3 - 10 kg/ha	N/A	N/A
Arm 3 - 15 kg/ha	N/A	N/A
Arm 3 - 20 kg/ha	N/A	N/A
Arm 3 - 25 kg/ha	N/A	N/A

TABLE 2.24 % LG accounted for by "early spring growth" for *S. angustifolium* (LEFT, poor fen) and *S. magellanicum* (RIGHT, poor fen), where COL. 2 = Mean Linear Growth (cm) per Treatment Plot [2012 values] and COL. 3 = ["Early Spring Growth" (ESG) / Linear Growth '12 (COLUMN 2)] x 100. Color ramp is low to high values : yellow to orange.

FEN	Mean LG (cm)	[ESG/LG]*100
Arm 1 - Control	N/A	N/A
Arm 1 - 0 kg/ha	4.92	1.36%
Arm 1 - 5 kg/ha	N/A	N/A
Arm 1 - 10 kg/ha	5.33	0.94%
Arm 1 - 15 kg/ha	6.52	0.10%
Arm 1 - 20 kg/ha	2.67	14.97%
Arm 1 - 25 kg/ha	4.75	8.15%
Arm 2 - Control	N/A	N/A
Arm 2 - 0 kg/ha	5.72	16.08%
Arm 2 - 5 kg/ha	5.53	13.20%
Arm 2 - 10 kg/ha	9.00	19.05%
Arm 2 - 15 kg/ha	N/A	N/A
Arm 2 - 20 kg/ha	7.09	16.46%
Arm 2 - 25 kg/ha	4.17	21.58%
Arm 3 - Control	6.47	23.79%
Arm 3 - 0 kg/ha	4.13	2.91%
Arm 3 - 5 kg/ha	4.91	6.79%
Arm 3 - 10 kg/ha	7.74	15.59%
Arm 3 - 15 kg/ha	6.13	18.50%
Arm 3 - 20 kg/ha	5.02	12.38%
Arm 3 - 25 kg/ha	6.97	12.43%

FEN	Mean LG (cm)	[ESG/LG]*100
Arm 1 - Control	4.13	10.82%
Arm 1 - 0 kg/ha	N/A	N/A
Arm 1 - 5 kg/ha	N/A	N/A
Arm 1 - 10 kg/ha	5.78	1.44%
Arm 1 - 15 kg/ha	3.88	0.86%
Arm 1 - 20 kg/ha	4.42	12.82%
Arm 1 - 25 kg/ha	6.67	9.10%
Arm 2 - Control	3.62	5.16%
Arm 2 - 0 kg/ha	5.49	2.00%
Arm 2 - 5 kg/ha	4.46	3.14%
Arm 2 - 10 kg/ha	4.15	14.70%
Arm 2 - 15 kg/ha	5.15	16.30%
Arm 2 - 20 kg/ha	6.37	11.94%
Arm 2 - 25 kg/ha	5.04	13.89%
Arm 3 - Control	4.13	11.14%
Arm 3 - 0 kg/ha	2.04	1.35%
Arm 3 - 5 kg/ha	3.28	4.07%
Arm 3 - 10 kg/ha	5.76	9.37%
Arm 3 - 15 kg/ha	6.42	9.97%
Arm 3 - 20 kg/ha	6.23	11.98%
Arm 3 - 25 kg/ha	6.68	12.62%

CONCLUSIONS

In this chapter I set out to answer three questions in order to complete the objective of determining how plants respond to experimentally increased nitrogen deposition after two growing seasons. In particular, I asked how might the nitrogen concentration (%N) of *Sphagnum* capitulum and vascular plant foliar tissue be impacted by N fertilization treatments? How might *Sphagnum* production be affected by N fertilization treatments?

I found that neither nitrogen concentrations (%N) of *Sphagnum* capitulum and vascular plant species, nor *Sphagnum* production were affected by N fertilization treatments after two growing seasons. However, %N of *Sphagnum* capitulum and some vascular plants species, *Sphagnum* C:N ratios and capitulum N storage, and several growth measurements of *Sphagnum* species differed between years (2011 and 2012), and were possibly affected by climatic factors. Wetter conditions in 2012 led to increased *Sphagnum* growth and production, as well as increased %N. Thus, it appears that climatic differences between years may have an over-arching affect on plant responses and these inter-annual climate-driven responses will need to be carefully considered as N-treatments continue over the next three years.

CHAPTER III

PLANT RESPONSES TO INCREASED NITROGEN DEPOSITION – SHIFTS IN COMMUNITY COMPOSITION AFTER TWO GROWING SEASONS

INTRODUCTION

Increased nitrogen (N) deposition onto boreal peatlands and forests is anticipated with further expansion of Alberta's oil sands industry and consequently, an increase in sources of nitrogen oxide emissions. Increased N deposition has the potential to affect peatland flora and alter N cycling patterns, therefore it is imperative to investigate at what level of excess N deposition these effects take place. This chapter discusses results from the first two years of a five year N fertilization study being conducted at a peatland complex near the hamlet of Mariana Lake in northeastern Alberta, Canada aimed at quantifying the N "critical load" for these peatland ecosystems. At the study site there are forty-two experimental plots – half in an ombrotrophic bog, the other half in a poor fen – with varying N fertilization treatments ranging from 0 kg/ha/year to 25 kg/ha/year, with a water control as well.

During the height of the growing season (mid-July, 2011), the plant communities in each treatment plot were sampled to provide "baseline" data necessary for documenting any shifts in plant distribution or species composition that may occur after N additions. Sampling took place the following season (mid-July, 2012) as well, and data from the two years were analyzed for differences in species composition and species richness. With increasing N addition, it is expected that plants will respond differently depending on the severity of the N addition and the amount of time being submitted to the N addition. The first expected plant response should

be increased N uptake and subsequently, increased growth followed by changes in plant frequency, and then with further N additions over time, changes in plant occurrence.

Previous studies have observed shifts in species composition with high ambient levels of atmospheric N deposition or experimentally increased N deposition. In Europe, studies in polluted regions with high levels of atmospheric N deposition (UK and the Netherlands) found declines in *Sphagnum* mosses (Greven 1992; Press et al. 1986; Woodin et al. 1985). Additionally, in eastern Canada, a N fertilization study found declines in *Sphagnum* mosses with increased N addition (Bubier et al. 2007). *Sphagnum* decline was attributed to indirect effects of changes in shrub cover and direct effects of the fertilizer addition (Bubier et al. 2007). *Sphagnum* mosses are a key component for carbon storage in peatland ecosystems because they slow down decomposition with their unique water-holding capabilities and recalcitrant tissues. If increased N deposition leads to changes in species composition, particularly declines in *Sphagnum* mosses, there could be a decrease in the ability of peatlands to sequester carbon (Bubier et al. 2007; Juutinen et al. 2010).

Questions and Hypotheses

Question #1*:* How are plant distributions impacted by the N fertilization treatments?

Hypothesis #1**:** There will not be a significant change in the distributions of plant species during the first two years of this study.

Rationale #1**:** Shifts in species composition have been observed at sites in Europe that have high ambient levels of atmospheric N deposition. At a Dutch ombrotrophic bog, the composition of the moss layer in the small remnants of formerly large bog areas showed considerable change over the years as N loads increased up to 20-40 kg N/ha/year; the most characteristic *Sphagnum* species have been replaced by more nitrophilous moss species (Greven 1992; Bobbink et al. 2003). High atmospheric N deposition has been linked to *Sphagnum* decline in bogs in polluted areas of the United Kingdom as well (Press et al. 1986;

Woodin et al. 1985). However, these studies worked in areas where atmospheric N deposition had increased upwards to 30 kg N/ha/year. In the peatland complex we are investigating, there are historically low levels of N deposition, and prior research conducted at high-N sites may not be a very accurate predictor for plant responses that we may find. I am predicting no significant changes in the distributions of plant species during the first two years of this study because I think changes at the plant community level will not occur until there have been several seasons of N fertilizations.

Question #2: Is there a difference in plant community composition in a bog compared to a poor fen after N addition?

***Hypothesis #2*:** There will not be a significant change in plant community composition during the first two years of this study.

Rationale #3*:* As I discuss above, I am predicting no significant changes in the distributions of plant species during the first two years of this study because I think changes at the plant community level will not occur until there have been several seasons of N fertilizations.

METHODS

Field Sampling Techniques

During the 2011 summer field season I developed a point sampling procedure for obtaining a record of plant species occurrences at thirty random points along a transect in each plot. The apparatus that I constructed was a point sampling frame that was set over the vegetation in each plot with thirty 1/8" diameter steel pins lowered through the plant canopy (Bonham 1989) (FIGURE 3.1). I sampled at the height of the growing season (mid-July). The record of what plant species were present at the sampling points in 2011 (the first year of N-additions) provided "baseline" data to use for comparison in later years with what plant species are present then. Each year the same points will be sampled and an analysis will be done for any changes in species distribution. I sampled the plots on July 17-20, 2011 and July 19-21, 2012.

To ensure that the same points were sampled, several measures were taken. Permanent PVC posts were hammered into each plot so that the sampling frame could be easily attached each year and remain in the same location. At the mid-point of the frame (the fifteenth wire), a thick steel wire was placed in the peat so that when the frame is re-attached in subsequent years it can be aligned properly. The point sampling frame was constructed from sturdy materials (PVC piping and aluminum v-channel) so the apparatus would not sway in the wind and move around while sampling occurred. Thirty holes were drilled through the aluminum v-channel at a size just slightly wider (9/64" diameter drill bit) than the wires that were placed down through the holes so that the wires would go straight down without shifting. Throughout the sampling process, the wires were clipped in place to the apparatus with binder clips to reduce shifting as well.

FIGURE 3.1 Point frame sampling apparatus being used in the FEN – Arm 1 – Control plot.

Statistical Methods

My sampling technique also gave a measure of estimated plant frequency within each plot (i.e. by counting how many times each plant species was "hit" by a pin along the transect). I calculated both the relative and absolute frequency of each plant species sampled in each plot. Relative frequency is the number of hits for an individual species divided by the total number of hits for all species in the plot times 100. For example, if a plant species was sampled 16 times (out of 30 sampling points), I would divide that value by the total number of hits for all plant species in that plot (ex. 60) X 100, = 26.7% as the relative frequency for that species within that plot. Absolute frequency is the number of hits for an individual species divided by the total number of possible hits (the total number of sampling points, or pins along the transect) times 100. For example, if a plant species was sampled 16 times (out of 30 sampling points), I would divide that value by 30 (the total number of sampling points, or pins along the transect) X 100, = 53.3% as the absolute frequency for that species within that plot. I recorded a hit or miss for each plant per pin regardless of the number of times the pin hit the plant, so my data cannot be accurately used to estimate percent cover; however, since the set up of the point sampling frame is in an area of each plot that seemed representative of the dominant vegetative community assemblage within that plot, my point sampling data can potentially be used as an estimated measure of the species composition of each plot.

NMDS and PERMANOVA:

To examine patterns of community composition, I utilized a Non-metric Multidimensional Scaling (NMDS) technique to ordinate plots (the sample units in the analysis) based on relative frequency values. NMDS searches for an ordination where the distances

between pairs of sample units are in rank-order agreement with their dissimilarities to the highest degree, thus providing the strongest structure (McCune and Grace 2002). The NMDS ordination used the PRIMERv6 software package from Plymouth Marine Laboratory, UK, standardizing the data by maximum for variables (i.e. the plant species) and using Bray-Curtis as the dissimilarity measures. Along with an NMDS ordination, I ran PERMANOVA (permutational multivariate analysis of variance) to test for differences in community composition among groups of sample units. PERMANOVA was run using PRIMERv6 with the PERMANONA+ package added on. The PERMANOVA main test was run for three factors – site type (bog and fen; n = 2), N treatment designation (n=7), and year (2011 and 2012; n = 2). I selected NMDS for the exploratory analyses and PERMANOVA for my explanatory analyses because they were appropriate methods to examine patterns of community composition.

Indicator Species Analysis (ISA):

Indicator Species Analysis (ISA) was used to identify plant species that were good "indicators" of groups of sample units (SUs). The ISA was conducted using PC-ORDv4.34, with indicator values being calculated using the method of Dufrêne and Legendre (1997). For the ISA, I selected site type (bog and fen) as the group; therefore, I examined whether there were plant species that were good "indicators" of the two site types. I chose to do an Indicator Species Analysis (ISA) after I discovered the two site types differed in their community composition in order to identify species that typified the two site types.

Species Richness:

To investigate the plant species richness of the treatments plots I calculated species richness (S) for each plot. Species richness is the number of species present in a sample unit (i.e.

the treatment plots). I then calculated alpha, beta, and gamma diversity for all plots, and then for plots in the bog and fen separately. Alpha diversity is the number of species in individual sample units, calculated as a mean of the plot species richness; beta diversity is the amount of compositional variation among a collection of sample units, calculated as gamma diversity divided by alpha diversity; and gamma diversity is the overall species richness in a collection of sample units, calculated as the total number of species in the entire data matrix (McCune and Grace 2002).

RESULTS

NMDS and PERMANOVA

Species Differences: The relative frequencies of all plant species (both vascular and non-vascular) for all plots are shown in APPENDIX A and APPENDIX B. Mean relative frequency percentages for each species averaged from all the treatment plots were used as a measure of how abundant each plant species was throughout the bog and fen plots (TABLE 3.1). In both 2011 and 2012, *S. fuscum* was the most abundant species. In 2011, *Dicranum undulatum* was the least abundant species (sampled at only one plot), and in 2012 it was not found.

TABLE 3.1 Mean relative frequency percentages for bog and poor fen species (LEFT, 2011 and RIGHT, 2012), ranked from highest to lowest. Values are mean ± standard error.

2011	Abundance
Species	REL. FREQ. (%)
Sphagnum fuscum	22.9 ± 0.035
Sphagnum angustifolium	19.0 ± 0.021
Oxycoccos microcarpus	14.3 ± 0.012
Sphagnum magellanicum	10.2 ± 0.018
Andromeda polifolia	7.4 ± 0.011
Chamaedaphne calyculata	4.9 ± 0.010
Rubus chamaemorus	4.2 ± 0.011
Kalmia polifolia	3.7 ± 0.007
Ledum groenlandicum	3.3 ± 0.009
Eriophorum vaginatum	2.7 ± 0.005
Vaccinium vitis-idaea	2.1 ± 0.006
Smilacina trifolia	1.8 ± 0.005
Scheuchzeria palustris	1.2 ± 0.003
Drosera rotundifolia	0.9 ± 0.002
Picea mariana	0.8 ± 0.004
Mylia anomala	0.3 ± 0.002
Pleurozium schreberi	0.1 ± 0.0008
Pohlia nutans	0.1 ± 0.0009
Dicranum undulatum	0.04 ± 0.0003

2012	Abundance
Species	REL. FREQ. (%)
Sphagnum fuscum	17.6 ± 0.028
Oxycoccos microcarpus	16.7 ± 0.013
Sphagnum angustifolium	16.1 ± 0.018
Sphagnum magellanicum	9.5 ± 0.016
Andromeda polifolia	8.2 ± 0.012
Chamaedaphne calyculata	5.3 ± 0.010
Eriophorum vaginatum	4.5 ± 0.009
Kalmia polifolia	4.4 ± 0.009
Rubus chamaemorus	4.1 ± 0.010
Ledum groenlandicum	3.8 ± 0.009
Smilacina trifolia	2.7 ± 0.007
Vaccinium vitis-idaea	2.6 ± 0.007
Scheuchzeria palustris	2.2 ± 0.005
Drosera rotundifolia	1.1 ± 0.003
Picea mariana	0.7 ± 0.004
Mylia anomala	0.4 ± 0.003
Pohlia nutans	0.08 ± 0.0005
Pleurozium schreberi	0.06 ± 0.0006

The mean absolute frequencies of plant species (both vascular and non-vascular) from the bog and poor fen in 2011 and 2012 are shown in TABLE 3.2. In general, the ranked order and percent frequencies changed little between the two years; however, two changes are noteworthy. Shrubs in the poor fen (*Andromeda polifolia*, *Chamaedaphne calyculata*, *Oxycoccos microcarpus*, and *Kalmia polifolia*) increased by 21% in absolute frequency from 2011 to 2012; shrubs in the bog (*Andromeda polifolia*, *Chamaedaphne calyculata*, *Oxycoccos microcarpus*, *Kalmia polifolia*, *Vaccinium vitis-idaea*, and *Ledum groenlandicum*) increased by 33%. Herbaceous plant species in the poor fen (*Eriophorum vaginatum* and *Scheuchzeria palustris*) increased by 11% in absolute frequency from 2011 to 2012; herbaceous plant species in the bog (*Smilacina trifolia*, *Rubus chamaemorus*, and *Eriophorum vaginatum*) increased by 17%.

TABLE 3.2 Mean absolute frequency percentages for poor fen (LEFT) and bog (RIGHT) species in 2011 and 2012. Values are mean (standard error).

FEN	Abundance ABS. FREQ. (%)	
Species	2011	2012
Andromeda polifolia	0.23 (0.11)	0.29 (0.16)
Chamaedaphne calyculata	0.06 (0.14)	0.07 (0.15)
Eriophorum vaginatum	0.06 (0.06)	0.11 (0.10)
Scheuchzeria palustris	0.04 (0.04)	0.09 (0.07)
Oxycoccos microcarpus	0.32 (0.17)	0.45 (0.21)
Kalmia polifolia	0.02 (0.04)	0.03 (0.05)
Vaccinium vitis-idaea	N/A	N/A
Drosera rotundifolia	0.02 (0.03)	0.03 (0.04)
Smilacina trifolia	0.01 (0.03)	0.01 (0.02)
Picea mariana	0 (0.02)	0.01 (0.03)
Rubus chamaemorus	0 (0.02)	0.01 (0.04)
Sphagnum fuscum	0.36 (0.41)	0.32 (0.38)
Sphagnum angustifolium	0.34 (0.24)	0.36 (0.21)
Sphagnum magellanicum	0.29 (0.22)	0.30 (0.24)
Mylia anomala	0 (0)	0.01 (0.05)
Pohlia nutans	N/A	N/A

BOG	Abundance ABS. FREQ. (%)	
Species	2011	2012
Andromeda polifolia	0.05 (0.07)	0.07 (0.11)
Chamaedaphne calyculata	0.16 (0.09)	0.20 (0.12)
Smilacina trifolia	0.06 (0.08)	0.14 (0.14)
Rubus chamaemorus	0.18 (0.17)	0.22 (0.23)
Oxycoccos microcarpus	0.24 (0.12)	0.33 (0.17)
Kalmia polifolia	0.12 (0.10)	0.19 (0.16)
Vaccinium vitis-idaea	0.09 (0.11)	0.14 (0.14)
Drosera rotundifolia	0.02 (0.03)	0.02 (0.03)
Ledum groenlandicum	0.13 (0.15)	0.21 (0.19)
Eriophorum vaginatum	0.05 (0.07)	0.10 (0.19)
Picea mariana	0.05 (0.11)	0.03 (0.08)
Sphagnum fuscum	0.47 (0.38)	0.47 (0.38)
Sphagnum angustifolium	0.44 (0.35)	0.39 (0.32)
Sphagnum magellanicum	0.08 (0.09)	0.13 (0.13)
Mylia anomala	0.0 (0.01)	0.01 (0.02)
Pleurozium schreberi	0.0 (0.02)	0.0 (0.02)

Community Differences: The relative frequency data for 2011 and 2012 was compiled into a single data matrix, and utilized to ordinate the forty-two plots. The NMDS ordination chosen was two-dimensional (2-D) with a computed Kruskal's stress value of 0.18 (FIGURE 3.2). The reported stress value (0.18) allows for a fair ecological interpretation of the plots in ordination space (FIGURE 3.3) (Kruskal 1964). The plots formed discrete clusters in the 2-D NMDS ordination space. The bog plots (plots #1 – 21, 2011; #43-63, 2012) formed a distinct cluster from the fen plots (plots #22-42, 2011; #64-84, 2012) on the ordination space, with one exception, the FEN – Arm 1 – 0 kg/ha treatment plot (#23, 2011 and #65, 2012) clustered along with the bog plots. Fen plots formed a tighter cluster than bog plots, indicating less dissimilarity in species composition between these plots.

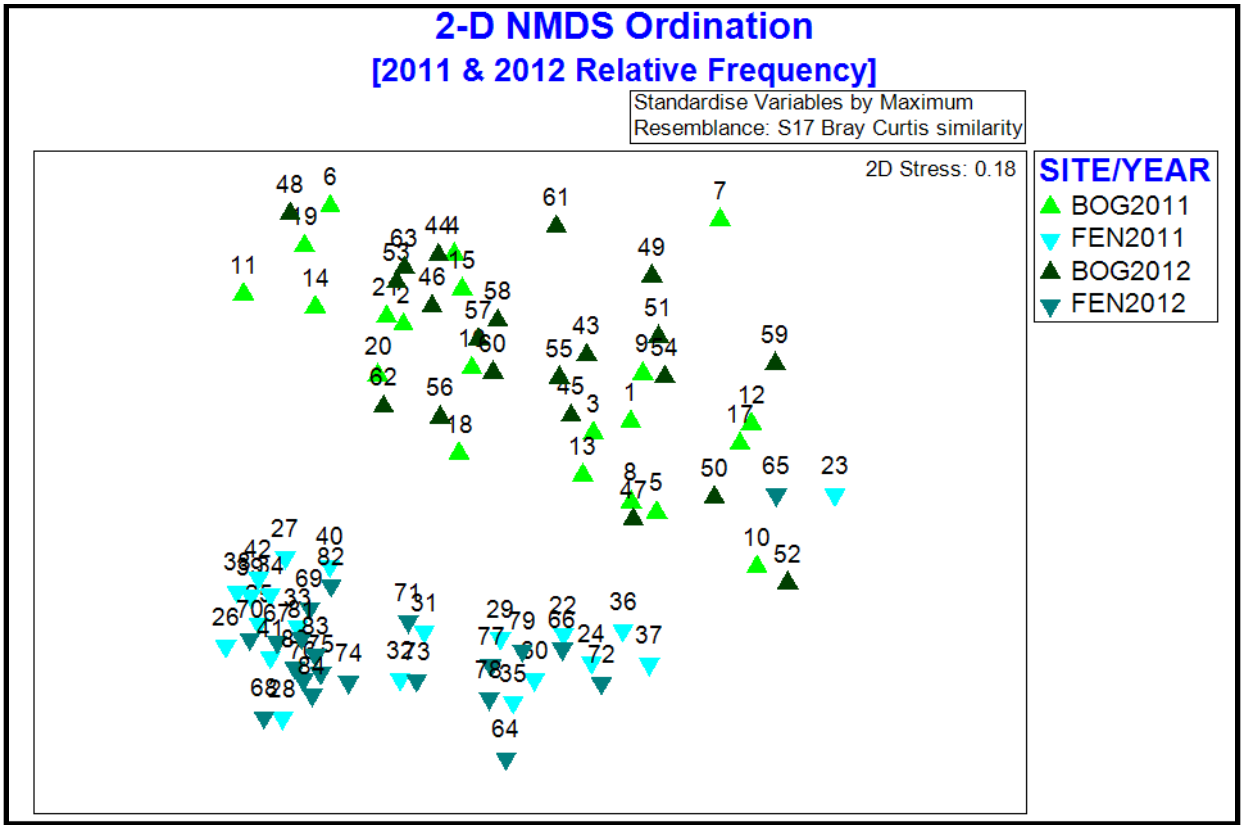

FIGURE 3.2 2-D NMDS ordination of treatments plots in the bog and fen at Mariana Lake (sampled in mid-July, 2011 and 2012) based on relative frequency values. The bog plots are #1 – 21, 2011 and #43-63, 2012, and the fen plots are #22-42, 2011 and #64-84, 2012.

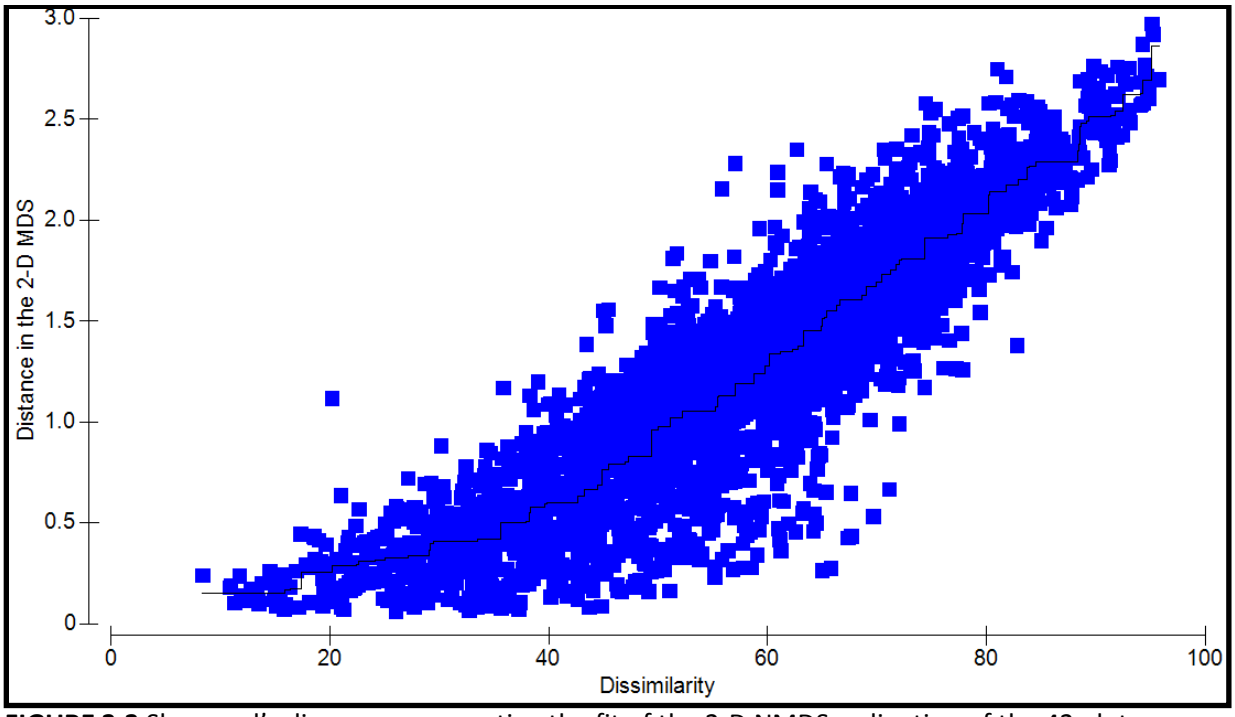

FIGURE 3.3 Sheppard's diagram representing the fit of the 2-D NMDS ordination of the 42 plots (sampled in both 2011 and 2012, for a total of 84 ordination points) based on Bray-Curtis dissimilarities.

The NMDS ordination was based on a Bray-Curtis dissimilarity matrix, which was examined to compare the two sampling years (2011 and 2012) for treatment plots (TABLE 3.3). According to two-way ANOVA, there was no difference between dissimilarity values for either site type or N treatment (site type: F = 0.21, p = 0.650; N treatment: F = 0.62, p = 0.712). In the bog, the plot with the highest dissimilarity value between 2011 and 2012 was the Arm 3 – 5 kg/ha treatment plot. In the fen, the plot with the highest dissimilarity value between 2011 and 2012 was the Arm 2 – 10 kg/ha treatment plot. In the bog, the plot with the lowest dissimilarity value was Arm 3 – 0 kg/ha. In the fen, the plot with the lowest dissimilarity value was Arm 1 – 5 kg/ha.

TABLE 3.3 Dissimilarity values between 2011 and 2012 for each treatment plot in the bog (LEFT) and poor fen (RIGHT). Color ramp expresses values orange to yellow : highest to lowest.

BOG	2011	2012	DISSIMILARITY
ARM 1 - CONTROL	1	43	28.533
ARM 1 - 0 kg/ha	2	44	38.987
ARM 1 - 5 kg/ha	3	45	19.685
ARM 1 - 10 kg/ha	4	46	19.702
ARM 1 - 15 kg/ha	5	47	19.829
ARM 1 - 20 kg/ha	6	48	21.813
ARM 1 - 25 kg/ha	7	49	25.957
ARM 2 - CONTROL	8	50	23.389
ARM 2 - 0 kg/ha	9	51	10.933
ARM 2 - 5 kg/ha	10	52	29.028
ARM 2 - 10 kg/ha	11	53	30.438
ARM 2 - 15 kg/ha	12	54	24.838
ARM 2 - 20 kg/ha	13	55	17.383
ARM 2 - 25 kg/ha	14	56	36.168
ARM 3 - CONTROL	15	57	11.813
ARM 3 - 0 kg/ha	16	58	8.416
ARM 3 - 5 kg/ha	17	59	40.290
ARM 3 - 10 kg/ha	18	60	22.662
ARM 3 - 15 kg/ha	19	61	20.261
ARM 3 - 20 kg/ha	20	62	15.088
ARM 3 - 25 kg/ha	21	63	25.067

FEN	2011	2012	DISSIMILARITY
ARM 1 - CONTROL	22	64	29.516
ARM 1 - 0 kg/ha	23	65	16.968
ARM 1 - 5 kg/ha	24	66	13.353
ARM 1 - 10 kg/ha	25	67	13.435
ARM 1 - 15 kg/ha	26	68	30.726
ARM 1 - 20 kg/ha	27	69	23.369
ARM 1 - 25 kg/ha	28	70	26.182
ARM 2 - CONTROL	29	71	19.034
ARM 2 - 0 kg/ha	30	72	20.033
ARM 2 - 5 kg/ha	31	73	19.416
ARM 2 - 10 kg/ha	32	74	36.879
ARM 2 - 15 kg/ha	33	75	23.909
ARM 2 - 20 kg/ha	34	76	23.401
ARM 2 - 25 kg/ha	35	77	22.654
ARM 3 - CONTROL	36	78	29.535
ARM 3 - 0 kg/ha	37	79	26.660
ARM 3 - 5 kg/ha	38	80	18.645
ARM 3 - 10 kg/ha	39	81	17.819
ARM 3 - 15 kg/ha	40	82	15.180
ARM 3 - 20 kg/ha	41	83	13.855
ARM 3 - 25 kg/ha	42	84	26.178

The output for the PERMANOVA main-test (TABLE 3.4) revealed a highly significant p-value for site type (p = 0.001; alpha value = 0.05), N treatment (p = 0.007), and year (p = 0.001). There was also a significant interaction - site type crossed with year (p = 0.04). Since there was a non-significant interaction for site type crossed with N treatment (p = 0.43) as well as N treatment crossed with year (p = 0.45), this means that differences between N treatments were not significant within the levels of site type (bog and poor fen) or year (2011 and 2012).

TABLE 3.4 Output for PERMANOVA main test from PRIMERv6 with PERMANOVA+; significant p-value for site type (p = 0.001), N treatment (p = 0.007), year (p = 0.001) and SITExYEAR (p = 0.04).

PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
SI	1	44385	44385	20.711	0.001	999
TR	6	24045	4007.6	1.87	0.007	998
YE	1	1500.4	1500.4	6.2116	0.001	999
SIxTR	6	13310	2218.4	1.0351	0.429	995
SIxYE	1	623.7	623.7	2.5821	0.04	999
TRxYE	6	1484.4	247.4	1.0242	0.451	997
ob(SIxTR)	28	60007	2143.1	8.8725	0.001	997
SIxTRxYE	6	1684.1	280.68	1.162	0.3	998
Res	28	6763.2	241.54			
Total	83	1.538E5				

Since there was a significant interaction for site type crossed with year (p = 0.04), I decided to investigate further by performing a PERMANOVA pair-wise test for the term "SITExYEAR" for pairs of levels of factor "YEAR". This test examined pairs of years within the two site types, bog and fen, separately. The two sampling years, 2011 and 2012, differed for the poor fen (p = 0.001), but not for the bog (p = 0.162).

TABLE 3.5 Output for PERMANOVA pair-wise test from PRIMERv6 with PERMANOVA+; results compare pairs of years (2011 and 2012) for plots within the bog and poor fen site types.

PAIR-WISE TESTS

Term 'SIxYE' for pairs of levels of factor 'YEAR'

Within level 'BOG' of factor 'SITE'

Groups	t	P(perm)	Unique perms
2011, 2012	1.3034	0.162	998

Denominators

Groups	Denominator	Den.df
2011, 2012	1*Res	14

Average Dissimilarity between/within groups

	2011	2012
2011	54.515	
2012	52.038	52.14

Within level 'FEN' of factor 'SITE'

Groups	t	P(perm)	Unique perms
2011, 2012	2.8418	0.001	999

Denominators

Groups	Denominator	Den.df
2011, 2012	1*Res	14

Average Dissimilarity between/within groups

	2011	2012
2011	47.398	
2012	46.284	43.926

Indicator Species Analysis (ISA) – The Indicator Species Analysis (ISA) identified species that were good "indicators" of the two site types (TABLE 3.6). The bog had more significant indicator species than the fen, suggesting more species with high fidelity. For the bog, significant indicator species included *Chamaedaphne calyculata* (shrub), *Kalmia polifolia* (shrub), *Ledum*

groenlandicum (shrub), *Rubus chamaemorus* (herbaceous), *Smilacina trifolia* (herbaceous), and *Vaccinium vitis-idaea* (shrub). For the fen, significant indicator species included *Andromeda polifolia* (shrub), *Scheuchzeria palustris* (herbaceous), and *Sphagnum magellanicum* (moss).

MONTE CARLO test of significance of observed maximum indicator value for Species
9999 permutations.
Random number seed: 120

	Column	Maxgrp	Observed Indicator Value (IV)	IV from randomized groups Mean	S.Dev	p *
1	ANDR	2	82.6	43.7	5.41	0.0001
2	CHAM	1	69.1	39.6	5.96	0.0003
3	DICR	1	4.8	4.8	0.05	1.0000
4	DROS	2	20.0	23.9	5.94	0.6702
5	ERIO	2	35.9	36.0	5.95	0.4285
6	KALM	1	72.4	37.3	5.99	0.0001
7	LEDU	1	81.0	28.1	6.44	0.0001
8	MYLI	2	2.7	6.0	3.40	1.0000
9	OXYC	2	57.4	52.5	2.84	0.0647
10	PICE	1	21.7	12.8	4.84	0.0975
11	PLEU	1	9.5	6.4	3.17	0.5020
12	POHL	2	9.5	6.3	3.17	0.4850
13	RUBU	1	74.2	27.7	6.13	0.0001
14	SCHE	2	85.7	28.9	6.06	0.0001
15	SANG	1	48.0	49.6	4.32	0.5713
16	SFUS	1	46.0	38.9	5.43	0.1099
17	SMAG	2	63.7	42.9	5.75	0.0038
18	SMIL	1	44.6	23.8	5.91	0.0070
19	VACC	1	61.9	22.5	5.77	0.0001

* proportion of randomized trials with indicator value equal to or exceeding the observed indicator value.
p = (1 + number of runs >= observed)/(1 + number of randomized runs)
Maxgrp = Group identifier for group with maximum observed IV

TABLE 3.6 Output for ISA from PC-ORD (calculated from 2011 data); significant indicator species are highlighted. Abbreviations are defined as followed: ANDR = *Andromeda polifolia*, CHAM = *Chamaedaphne calyculata*, DICR = *Dicranum undulatum*, DROS = *Drosera rotundifolia*, ERIO = *Eriophorum vaginatum*, KALM = *Kalmia polifolia*, LEDU = *Ledum groenlandicum*, MYLI = *Mylia anomala*, OXYC = *Oxycoccos microcarpus*, PICE = *Picea mariana*, PLEU = *Pleurozium schreberi*, POHL = *Pohlia nutans*, RUBU = *Rubus chamaemorus*, SCHE = *Scheuchzeria palustris*, SANG = *Sphagnum angustifolium*, SFUS = *Sphagnum fuscum*, SMAG = *Sphagnum magellanicum*, SMIL = *Smilacina trifolia*, and VACC = *Vaccinium vitis-idaea*.

Species Richness – Calculations of species richness confirmed that richness of the bog site type (2011: alpha diversity = 9.4; beta diversity = 1.8; gamma diversity = 17) was higher than species richness of the fen site type (2011: alpha diversity = 7.1; beta diversity = 2.1; gamma diversity = 15) (TABLE 3.7). Overall richness (bog and fen together) in 2011 was: alpha diversity = 8.3, beta diversity = 2.3, and gamma diversity = 19 (TABLE 3.7).

In 2012, species diversity indices were similar to those calculated in 2011. Species richness (S, or α diversity) values for 2011 and 2012 failed to meet normality assumptions (Shapiro-Wilk's test: $p < 0.05$), and were examined using a Mann-Whitney Rank Sum test. According to the Mann-Whitney Rank Sum test, species richness was not different between sampling years ($p = 0.58$) (TABLE 3.8). Overall alpha diversity increased slightly, but beta and gamma diversity decreased: alpha diversity = 8.64, beta diversity = 2.08, and gamma diversity = 18 (TABLE 3.7). Species richness of the bog site type (2012: alpha diversity = 10.05; beta diversity = 1.59; gamma diversity = 16) was again higher than species richness of the fen site type (2012: alpha diversity = 7.24; beta diversity = 2.07; gamma diversity = 15) (TABLE 3.7). Gamma diversity for the bog plots decreased in 2012 (γ = 16 vs. 17) because *Dicranum undulatum* (moss) was not sampled – in 2011, it was sampled in the BOG – Arm 2 – 25 kg/ha treatment plot.

TABLE 3.7 Species diversity indices (α, β, and γ) calculated in 2011 and 2012 for treatment plots in the bog and poor fen, as well as overall richness.

Diversity Indices

2011			2012	
OVERALL		α ↑	OVERALL	
ALPHA	8.29	β ↓	ALPHA	8.64
BETA	2.29	γ ↓	BETA	2.08
GAMMA	19		GAMMA	18
BOG			BOG	
ALPHA	9.43		ALPHA	10.05
BETA	1.80		BETA	1.59
GAMMA	17		GAMMA	16
FEN			FEN	
ALPHA	7.14		ALPHA	7.24
BETA	2.10		BETA	2.07
GAMMA	15		GAMMA	15

TABLE 3.8 Species richness (S, or α diversity) values for 2011 and 2012 failed to meet normality assumptions (Shapiro-Wilk's test: $p < 0.05$), and were examined using a Mann-Whitney Rank Sum test. According to the Mann-Whitney Rank Sum test, species richness was not different between sampling years ($p = 0.58$).

SU	S (2011)	S (2012)
1	11	12
2	11	9
3	10	11
4	9	10
5	9	8
6	8	9
7	8	10
8	8	8
9	7	8
10	5	6
11	12	14
12	10	9
13	12	13
14	14	12
15	10	12
16	10	9
17	7	9
18	9	11
19	8	9
20	10	9
21	10	13
22	9	9
23	7	7
24	5	6
25	5	6
26	6	8
27	8	9
28	8	6
29	8	9
30	9	7
31	9	8
32	9	7
33	6	7
34	6	6
35	7	8
36	8	7
37	7	8
38	6	7
39	7	7
40	7	6
41	7	7
42	6	7

Normality Test (Shapiro-Wilk) Failed (P < 0.050)

Test execution ended by user request, Rank Sum Test begun

Mann-Whitney Rank Sum Test Thursday, February 21, 2013, 11:09:47 AM

Data source: Data 1 in Notebook1

Group	N	Missing	Median	25%	75%
Col 1	42	0	8.000	7.000	10.000
Col 2	42	0	8.000	7.000	9.250

Mann-Whitney U Statistic= 820.500

T = 1723.500 n(small)= 42 n(big)= 42 (P = 0.580)

The difference in the median values between the two groups is not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.580)

DISCUSSION

Shifts in community composition after two growing seasons?

The "baseline" data collected from the point sampling frame in the first year of this study (summer 2011) indicate that there are two distinct site types – bog and poor fen - with clear indicator species. Work done previously (Graham 2012) in the summer of 2010 found similar differences when the entire bog/fen peatland complex was sampled. Thus, the bog and poor fen treatment plots are representative of the bog and fen expanse site types in the peatland complex overall.

There were no differences in species composition of the treatment plots between years. Also, there was no difference between dissimilarity values for N treatments. These results signify that the species composition of the treatments plots in 2012 had little or no change from their "baseline" record in 2011.

There were some changes in plant frequency that were observed between sampling years. The ground cover remained relatively the same, with *Sphagnum* spp. at nearly 100% absolute frequency for each plot. However, shrubs had noticeable increases in absolute frequency from 2011 to 2012, as well as herbaceous plant species, although to a lesser degree. There was no difference in species richness of the treatment plots between sampling years. As this was only the first two years of N additions, I did not predict any changes in species richness (quantified as the number of species present in a sample unit, i.e. the treatment plots). For there to be a change in species richness, that would mean an addition or loss of plant species in the treatment plots. With increasing N addition, the first expected plant response should be increased N uptake and subsequently, increased growth. The next response should be changes

in plant frequency, and then with further N additions over time there should be changes in plant occurrence. When there are changes in plant occurrence, one way in which this will be revealed is through differences in species richness.

Shifts in community composition after further increased N deposition?

Shifts in species composition have been observed at sites in Europe that have high ambient levels of atmospheric N deposition. At an ombrotrophic bog in the Netherlands, the composition of the moss layer in the small bog areas still intact showed considerable change over the years as nitrogen loads increased up to 20-40 kg N/ha/year; nitrophilous moss species replaced *Sphagnum* species that were once predominant at the site (Greven 1992; Bobbink et al. 2003). High atmospheric N deposition has been linked to *Sphagnum* decline in bogs in polluted areas of the United Kingdom as well (Press et al. 1986; Woodin et al. 1985); however, these studies were in areas where atmospheric N deposition had increased upwards to 30 kg N/ha/year.

At Mer Bleue bog, an ombrotrophic bog near Ottawa, Ontario (eastern Canada), Bubier et al. (2007) also found shifts in species composition with increasing N additions. Vascular shrub biomass increased, as did leaf area (leaf area index, or LAI), which increased vascular plant shading and led to greater litter accumulation, both of which contributed to declines in moss photosynthesis and moss abundance. The declines in moss photosynthesis and moss abundance were also attributable to the direct effect of fertilizer addition, which caused nutrient toxicity. An imbalance between N uptake and assimilation can lead to toxic levels of NH_4^+ in *Sphagnum* cells (Limpens and Berendse 2003; Bragazza et al. 2005); however, this study

had plots that were treated with phosphorus (P) and potassium (K) as well as N, and there's the possibility that these nutrients were even more toxic to *Sphagnum* than N (Bubier et al. 2007). Also, this study was conducted in the zone with the highest atmospheric nitrogen deposition for Canada, estimated at 8 – 12 kg N/ha/year (Bubier et al. 2007). Furthermore, N fertilization treatments ranged from 16 – 64 kg N/ha/year, with the two highest N additions (32 and 64 kg N/ha/year) being much higher than our highest N addition at the Mariana Lake study site (25 kg N/ha/year). In the peatland complex we are investigating, there are historically low levels of N deposition, and prior research conducted at high-N sites may not be a very accurate predictor for plant responses in pristine western Canada.

Regardless of effects of N addition, there are possibilities for *Sphagnum* spp. to change their distributions along the hummock-lawn gradient. Individuals of *Sphagnum* species characteristic of lawns, such as *S. angustifolium*, can grow higher above the water table by exploiting the greater capillary conduction and reduced water loss characteristics of *Sphagnum* species on hummock tops, such as *S. fuscum,* but this greater height above the water table is only marginally suitable for them (Titus and Wagner 1984). It is unlikely that hummock tops dominated by *S. fuscum* will be invaded by more than just a few *S. angustifolium* individuals or small clusters of plants. The ability of *Sphagnum* species typical of hummocks to spread downward to lawns is also limited. There is typically a low frequency of *S. fuscum* at sites close to the water table since the fast-growing *S. angustifolium* can out-compete *S. fuscum* in wetter locations where it has a superior water balance (Titus and Wagner 1984; Andrus 1986). However, Andrus et al. (1983) found that hummock species did have a fairly large vertical range, greater than that of lawn species, indicating it may have a considerable ability to tolerate

the full range of conditions along the hummock-lawn gradient. Thus, competition rather than physical tolerance to the environment, is likely excluding *S. fuscum* from establishing in lawns (Rydin 1986). These literature findings suggest that when *Sphagnum* is positively affected by N-additions, the faster growing lawn species, *S. angustifolium*, may expand at the expense of *S. fuscum*, whereas when the growth of lawn species is negatively impacted by the N-additions, this may provide an opportunity for hummock species to compete for space more effectively in lawn environments. Since I did not predict that N-additions would negatively impact *Sphagnum* growth initially (in the first two years of this study), I did not expect to see any significant shifts of *S. fuscum* into lawns, or consequently a significant increase in its distribution, when I sampled again in mid-July, 2012.

CONCLUSIONS

In this chapter I set out to answer two questions in order to complete the objective of determining how plants respond to experimentally increased nitrogen deposition after two growing seasons. In particular, I asked how might plant distributions be impacted by N fertilization treatments? Is there a difference in plant community composition in a bog compared to a poor fen after N addition?

As I hypothesized, there were not any significant changes in the distributions of plant species or community composition during the first two years of this study. My data indicated that there are two distinct site types – bog and poor fen - with clear indicator species; however, both the bog and poor fen had no yearly changes in species composition or species richness. As discussed earlier, it appears that both the growth response and sequestration of nitrogen in

Sphagnum is tri-phasic. There is no certain time frame for these phases to move from one to the next, but I predicted that *Sphagnum* would remain in the first phase even into our second season of fertilizations, maintaining its "gatekeeper" function. This would mean that most of the N deposited would be taken up by *Sphagnum,* with only a small fraction making its way to the vascular plants (Li and Vitt 1997). Since the vascular plants are likely not yet receiving much of the additional N, I did not expect that their distributions would shift much either. In the coming growing seasons, however, this may change. When *Sphagnum* becomes super-saturated with N (third phase), N leaches down through the living moss layer and these additional N inputs to the organic matter profile may supply vascular plant species with the opportunity to colonize and proliferate (Lamers et al. 2000; Limpens and Berendse 2003). Increased vascular shrub net primary production (NPP) can negatively affect *Sphagnum* NPP by increasing understory shade and increasing litter accumulation (Bonnett et al. 2010; Bubier et al. 2007). Thus, there is potential for significant change in species composition as we continue our N fertilizations. One looming fear is that if increased N deposition leads to changes in species composition, there could be a decrease in the ability of peatlands to sequester CO_2 from the atmosphere (Bubier et al. 2007; Juutinen et al. 2010).

CHAPTER IV

SYNTHESIS OF THESIS RESEARCH

The aims of this thesis were to monitor and analyze peatland plant responses, including plant nitrogen uptake and growth as well as vegetative community change, for an experimental nitrogen fertilization study at a peatland site in Alberta, Canada. This research is part of a five-year study funded by CEMA (Cumulative Environmental Management Association; Fort McMurray, AB) aimed at setting a regional nitrogen critical load for the Regional Municipality of Wood Buffalo (RMWB). A nitrogen "critical load" is defined as the quantitative estimate of the level of exposure of natural systems to N below which significant harmful effects on specified sensitive elements of the environment do not occur (UN Organization for Economic Co-operation and Development 1997). To reach this objective, various activities are being undertaken by collaborating researchers from Southern Illinois University Carbondale (SIUC), Villanova University, University of Victoria, and Trent University.

In order to monitor peatland plant responses, I worked on two levels: individual plant species responses (Chapter II) and plant community responses (Chapter III). The individual plant species level of Chapter II focused on nitrogen uptake responses by *Sphagnum* species and vascular plant species, as well as growth responses of *Sphagnum* species after two growing seasons. The plant community level of Chapter III focused on changes in plant distribution and shifts in plant community composition after two growing seasons.

In Chapter II it was found that experimental nitrogen fertilizations did not have any clear effects on nitrogen uptake by *Sphagnum* species and vascular plant species or growth of *Sphagnum* species after two growing seasons. However, there was a year effect for many

measurements, which can likely be attributed to climatic differences between the two sampling years (2011 and 2012). There were increased nitrogen concentrations (%N) in *Sphagnum* capitulum tissue and increased growth for *Sphagnum* species in 2012, which had a wetter, and slightly warmer, growing season. Possible sources of increased nitrogen inputs in 2012 included atmospheric nitrogen deposition, nitrogen mineralization, nitrogen translocation within *Sphagnum* tissue, and N_2-fixation. Evidence suggests that N_2-fixation may be a very significant contributor of nitrogen to *Sphagnum* mosses at the Mariana Lake study site, and with more precipitation in 2012, there were likely greater rates of N_2-fixation and thus, more available nitrogen for *Sphagnum* mosses. Not only is N_2-fixation affected by climate, it has also responded to experimental nitrogen fertilizations at the Mariana Lake study site (Jacqueline Popma, *personal communication*). In the face of increased atmospheric nitrogen deposition with continued Oil Sands industry expansion, N_2-fixation will likely be one of the most important processes that we must try to understand.

In Chapter III it was found that experimental nitrogen fertilizations did not have any effects on plant distributions or plant community composition in the first two years of this study. There were some changes in plant frequency that were observed between sampling years. The ground cover remained relatively the same, with *Sphagnum* spp. at nearly 100% absolute frequency for each plot. However, shrubs had noticeable increases in absolute frequency from 2011 to 2012, as well as herbaceous plant species, although to a lesser degree. There was no difference in species richness of the treatment plots between sampling years. As this was only the first two years of N additions, I did not predict any changes in species richness. For there to be a change in species richness, that would mean an addition or loss of plant

species in the treatment plots. With increasing N addition, the first expected plant response should be increased N uptake and subsequently, increased growth. The next response should be changes in plant frequency, and then with further N additions over time there should be changes in plant occurrence. There is certainly potential for significant changes in plant community composition with increased atmospheric nitrogen deposition as the Oil Sands industry expands, with consequences for the health of *Sphagnum* mosses and the ability of peatlands to store carbon.

These results emphasize the over-riding affect that annual variation in climate has on peatland plant communities and suggests that at least in the short term, increased N deposition does not have an effect on plant responses. The increased growth of *Sphagnum*, along with an increase in N tissue concentrations, suggests that in wet years, factors other than nitrogen may be limiting - these factors could include other nutrients (P, K, etc), while in dry years, wetness or temperature may have limiting affects. These results, however, do not rule out that over a longer period increases in N may have associated treatment responses on plant growth and function.

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APPENDICES

APPENDIX A. Relative frequency matrix for point frame sampling data (2011); #1-21 are bog plots and #22-42 are poor fen plots. Species names are given in full in TABLE 3.3.

	Andromeda	Chamaedaphne	Dicranum	Drosera	Eriophorum	Kalmia	Ledum	Mylia anomala	Oxycoccos	Picea mariana	Pleurozium	Pohlia	Rubus	Scheuchzeria	S. angustifolium	S. fuscum	S. magellanicum	Smilacina	Vaccinium
1	0.031746032	0.063492063	0	0.01587	0	0.04762	0	0	0.1269841	0	0	0	0.14286	0	0.031746032	0.396825	0.047619048	0.015873	0.0793651
2	0.018181818	0	0	0	0.03636364	0	0.0727	0	0.1090909	0	0.01818182	0	0.03636	0	0.254545455	0.181818	0.090909091	0.054545	0.1272727
3	0	0.076923077	0	0.01538	0.03076923	0.07692	0.0615	0	0.1692308	0	0	0	0	0	0.107692308	0.353846	0	0.061538	0.0461538
4	0	0.1	0	0	0.05714286	0.04286	0.1	0	0.1	0	0	0	0.02857	0	0.428571429	0	0	0.128571	0.0142857
5	0.021276596	0.14893617	0	0	0.0212766	0.02128	0	0	0.0851064	0	0	0	0	0	0.14893617	0.468085	0.021276596	0.06383	0
6	0.017241379	0.017241379	0	0	0	0.18966	0.1379	0	0.0172414	0	0	0	0.10345	0	0.431034483	0	0.086206897	0	0
7	0	0.028571429	0	0	0.01428571	0	0.1714	0	0.0428571	0	0	0	0.04286	0	0	0.428571	0	0.085714	0.1857143
8	0	0.070175439	0	0	0	0.14035	0	0	0.1929825	0.035087719	0	0	0	0	0.122807018	0.385965	0.01754386	0.035088	0
9	0	0.097222222	0	0	0	0.08333	0.1389	0	0.1527778	0	0	0	0.11111	0	0.083333333	0.333333	0	0	0
10	0	0.104166667	0	0	0.10416667	0.0625	0	0	0.1041667	0	0	0	0	0	0	0.625	0	0	0
11	0.055555556	0.055555556	0	0.01389	0	0	0.0278	0.041666667	0.0972222	0.027777778	0.02777778	0	0.26389	0	0.319444444	0.027778	0	0	0.0416667
12	0	0.185185185	0	0	0.01851852	0.03704	0.0185	0	0.0740741	0	0	0	0.09259	0	0.018518519	0.518519	0.018518519	0	0.0185185
13	0.030769231	0.092307692	0	0.01538	0.12307692	0.12308	0.0154	0	0.0769231	0	0	0	0.04615	0	0.046153846	0.261538	0.153846154	0.015385	0
14	0.043478261	0.057971014	0.0144928	0.05797	0.02898551	0.05797	0.029	0	0.057971	0.072463768	0	0	0.08696	0	0.246376812	0.130435	0.043478261	0	0.0724638
15	0	0.092105263	0	0	0	0.05263	0.0263	0	0.1578947	0.144736842	0	0	0.07895	0	0.302631579	0.065789	0.026315789	0	0.0526316
16	0	0	0	0	0	0.11667	0.1	0	0.15	0	0	0	0.05	0	0.183333333	0.166667	0.15	0.016667	0.0666667
17	0	0.136363636	0	0.0303	0	0.01515	0.0303	0	0.1363636	0	0	0	0.19697	0	0	0.454545	0	0	0
18	0	0.017857143	0	0	0.07142857	0.03571	0.1071	0	0.1785714	0	0	0	0	0	0.232142857	0.196429	0.107142857	0.053571	0
19	0.115942029	0.057971014	0	0	0	0.01449	0.2464	0	0	0	0	0	0.02899	0	0.347826087	0.086957	0	0	0.1014493
20	0.057142857	0.028571429	0	0	0	0.07143	0.0143	0	0.1428571	0	0	0	0.15714	0	0.357142857	0	0.071428571	0.057143	0.0428571
21	0.043956044	0	0	0.01099	0	0.0989	0.0879	0	0.0989011	0	0	0	0.23077	0	0.252747253	0	0.076923077	0.065934	0.032967
22	0.117647059	0.039215686	0	0.01961	0	0	0	0.078431373	0.1568627	0	0	0	0	0.019607843	0.098039216	0.411765	0	0.058824	0
23	0.017857143	0.321428571	0	0	0	0.01786	0	0	0.0535714	0	0	0	0.05357	0	0	0.517857	0.017857143	0	0
24	0.130434783	0.02173913	0	0	0	0	0	0	0.1956522	0	0	0	0	0	0.086956522	0.565217	0	0	0
25	0.170212766	0	0	0	0	0	0	0	0.1489362	0	0	0	0	0.042553191	0.361702128	0	0.276595745	0	0
26	0.195652174	0	0	0.02174	0.04347826	0	0	0	0.0869565	0	0	0	0	0	0.195652174	0	0.456521739	0	0
27	0.203703704	0.018518519	0	0	0.05555556	0.05556	0	0	0.0925926	0	0	0	0	0.018518519	0.37037037	0	0.185185185	0	0
28	0.142857143	0	0	0.03571	0.01785714	0	0	0	0.25	0	0	0.0357	0	0.017857143	0.178571429	0	0.321428571	0	0
29	0.117647059	0	0	0	0	0.05882	0	0	0.2647059	0.044117647	0	0	0	0.029411765	0	0.308824	0.132352941	0.044118	0
30	0.18	0	0	0.02	0	0.02	0	0	0.12	0	0	0	0	0.04	0.06	0.5	0.04	0.02	0
31	0.196428571	0	0	0.01786	0.10714286	0.01786	0	0	0.1071429	0	0	0	0	0.017857143	0.178571429	0.25	0.107142857	0	0
32	0.220338983	0	0	0.01695	0.03389831	0	0	0	0.2033898	0	0	0.0169	0	0.016949153	0.118644068	0.220339	0.152542373	0	0
33	0.172413793	0	0	0	0.06896552	0	0	0	0.2068966	0	0	0	0	0.034482759	0.310344828	0	0.206896552	0	0
34	0.18	0	0	0	0.02	0	0	0	0.18	0	0	0	0	0.02	0.4	0	0.2	0	0
35	0.119047619	0	0	0.02381	0	0	0	0	0.0952381	0	0	0	0	0.047619048	0.119047619	0.547619	0.047619048	0	0
36	0.02	0.04	0	0	0.08	0.02	0	0	0.22	0	0	0	0	0.02	0.06	0.54	0	0	0
37	0.071428571	0	0	0	0.02380952	0.07143	0	0	0.0952381	0	0	0	0	0.023809524	0.047619048	0.666667	0	0	0
38	0.038461538	0	0	0	0.03846154	0	0	0	0.3269231	0	0	0	0	0.019230769	0.269230769	0	0.307692308	0	0
39	0.054545455	0	0	0.05455	0.03636364	0	0	0	0.2909091	0	0	0	0	0.018181818	0.309090909	0	0.236363636	0	0
40	0.088235294	0.117647059	0	0	0.05882353	0	0	0	0.2794118	0	0	0	0	0.014705882	0.294117647	0	0.147058824	0	0
41	0.178571429	0.089285714	0	0	0.01785714	0	0	0	0.0892857	0	0	0	0	0.089285714	0.232142857	0	0.303571429	0	0
42	0.06	0	0	0	0.04	0	0	0	0.26	0	0	0	0	0.02	0.38	0	0.24	0	0
TOTAL	3.110772886	2.078451059	0.0144928	0.37002	1.14822723	1.54911	1.3855	0.120098039	5.9949286	0.324183754	0.0459596	0.0527	1.75119	0.51007027	7.985084824	9.610388	4.290037069	0.776801	0.8820123
MEAN	0.074	0.049	0.0004	0.009	0.027	0.037	0.033	0.003	0.143	0.008	0.001	0.001	0.042	0.012	0.190	0.229	0.102	0.018	0.021
STD ERR	0.011	0.010	0.0003	0.002	0.005	0.007	0.009	0.002	0.012	0.004	0.001	0.001	0.011	0.003	0.021	0.035	0.018	0.005	0.006

APPENDIX B. Relative frequency matrix for point frame sampling data (2012); #1-21 are bog plots and #22-42 are poor fen plots. Species names are given in full in TABLE 3.3.

	Andromeda	Chamaedaphne	Dicranum	Drosera	Eriophorum	Kalmia	Ledum	Mylia anomala	Oxycoccos	Picea mariana	Pleurozium	Pohlia	Rubus	Scheuchzeria	S. angustifolium	S. fuscum	S. magellanicum	Smilacina	Vaccinium
1	0.02325581	0.093023256	0	0.03488	0	0.03488	0	0.011627907	0.1395349	0	0	0	0.093	0	0.058139535	0.22093	0.058139535	0.116279	0.1162791
2	0	0.1	0	0	0	0.01667	0.1	0	0.1	0	0	0	0.0333	0	0.45	0	0.05	0.083333	0.0666667
3	0	0.070588235	0	0.01176	0.058823529	0.05882	0.03529	0	0.2	0	0	0	0	0	0.094117647	0.235294	0.023529412	0.070588	0.1411765
4	0.01428571	0.071428571	0	0	0.028571429	0.11429	0.08571	0	0.0857143	0	0	0	0.0714	0	0.371428571	0	0.057142857	0.1	0
5	0.01923077	0.076923077	0	0	0	0.05769	0	0	0.1923077	0	0	0	0	0	0.096153846	0.461538	0.019230769	0.076923	0
6	0.07142857	0	0	0	0	0.24286	0.15714	0	0.0142857	0.014285714	0	0	0.0286	0	0.414285714	0	0.014285714	0.042857	0
7	0	0.051020408	0	0.0102	0.030612245	0.02041	0.15306	0	0.122449	0	0	0	0.0408	0	0	0.306122	0	0.163265	0.1020408
8	0	0.025	0	0	0	0.2	0	0	0.2375	0.0375	0	0	0	0	0.025	0.35	0	0.1125	0.0125
9	0	0.096385542	0	0	0	0.10843	0.14458	0	0.1325301	0	0	0	0.1566	0	0.024096386	0.301205	0.036144578	0	0
10	0	0.063492063	0	0	0.301587302	0.01587	0	0	0.1111111	0	0	0	0.0317	0	0	0.47619	0	0	0
11	0.048780049	0.048780488	0	0.0122	0	0.0122	0.07317	0.024390244	0.0731707	0.048780488	0	0	0.2195	0	0.231707317	0.060976	0.048780488	0.02439	0.0731707
12	0	0.142857143	0	0	0	0.08571	0.1	0	0.1285714	0	0	0	0.1	0	0.057142857	0.357143	0.014285714	0	0.0142857
13	0.01052632	0.094736842	0	0.02105	0.189473684	0.13684	0.01053	0	0.0842105	0	0	0	0.0842	0	0.052631579	0.105263	0.157894737	0.031579	0.0210526
14	0.08045977	0.068965517	0	0.03448	0.103448276	0.03448	0.05747	0	0.091954	0	0	0	0.0805	0	0.172413793	0.091954	0.08045977	0	0.1034483
15	0	0.093023256	0	0	0.011627907	0.06977	0.01163	0	0.2093023	0.127906977	0	0	0.0581	0	0.244186047	0.093023	0.011627907	0.011628	0.0581395
16	0	0	0	0	0	0.11765	0.10294	0	0.1323529	0	0	0	0.1029	0	0.176470588	0.147059	0.117647059	0.014706	0.0882353
17	0	0.25	0	0	0.016666667	0.01667	0.08333	0	0.05	0	0	0	0.05	0	0.016666667	0.483333	0	0	0.0333333
18	0	0.033707865	0	0	0.056179775	0.07865	0.1236	0	0.1910112	0	0	0	0.0449	0	0.146067416	0.089888	0.101123596	0.101124	0.0337079
19	0.11956522	0.130434783	0	0	0	0	0.22826	0	0.0326087	0	0	0	0.0217	0	0.141304348	0.173913	0.010869565	0	0.1413043
20	0.11235955	0.078651685	0	0	0	0.04494	0	0	0.1348315	0	0	0	0.2022	0	0.269662921	0	0.06741573	0.05618	0.0337079
21	0.03603604	0.036036036	0	0.01802	0	0.07207	0.11712	0.009009009	0.1351351	0.02702703	0	0	0.2342	0	0.144144144	0	0.09009009	0.045045	0.036036
22	0.07843137	0.058823529	0	0.05882	0	0	0	0.137254902	0.0980392	0	0	0	0	0.058823529	0.196078431	0.254902	0	0.058824	0
23	0	0.294117647	0	0	0.073529412	0.01471	0	0	0.1029412	0	0	0	0.0735	0	0	0.411765	0.029411765	0	0
24	0.14035088	0.035087719	0	0	0.070175439	0	0	0	0.2280702	0	0	0	0	0	0.070175439	0.45614	0	0	0
25	0.13461538	0	0	0	0.038461538	0	0	0	0.1730769	0	0	0	0	0.076923077	0.307692308	0	0.269230769	0	0
26	0.10204082	0	0	0.06122	0.020408163	0.02041	0	0	0.1020408	0	0	0	0	0.081632653	0.183673469	0	0.428571429	0	0
27	0.15254237	0.016949153	0	0	0.050847458	0.0339	0	0	0.2033898	0	0	0.0169	0	0.033898305	0.288135593	0	0.203389831	0	0
28	0.15625	0	0	0	0.0625	0	0	0	0.3125	0	0	0.0156	0	0	0.203125	0	0.25	0	0
29	0.10606061	0	0	0	0	0.06061	0	0	0.2424242	0.060606061	0	0	0	0.060606061	0.121212121	0.181818	0.151515152	0.015152	0
30	0.15555556	0.022222222	0	0.02222	0	0	0	0	0.1333333	0	0	0	0	0	0.044444444	0.6	0.022222222	0	0
31	0.27118644	0	0	0.0339	0.101694915	0.0339	0	0	0.0508475	0	0	0	0	0	0.220338983	0.20339	0.084745763	0	0
32	0.15068493	0	0	0	0.054794521	0	0	0	0.2876712	0	0	0	0	0.095890411	0.178082192	0.109589	0.123287671	0	0
33	0.26582278	0	0	0.02532	0.126582278	0	0	0	0.1518987	0	0	0	0	0.050632911	0.291139241	0	0.088607595	0	0
34	0.25	0	0	0	0.138888889	0	0	0	0.1527778	0	0	0	0	0.041666667	0.208333333	0	0.208333333	0	0
35	0.12903226	0	0	0.03226	0	0.08065	0	0	0.2096774	0	0	0	0	0.064516129	0.064516129	0.370968	0.048387097	0	0
36	0.15	0	0	0.01667	0.05	0	0	0	0.2333333	0	0	0	0	0.05	0.066666667	0.433333	0	0	0
37	0.11290323	0.016129032	0	0	0.032258065	0.06452	0	0	0.2419355	0	0	0	0	0.048387097	0.064516129	0.419355	0	0	0
38	0.07936508	0	0	0.01587	0.031746032	0	0	0	0.3333333	0	0	0	0	0.063492063	0.206349206	0	0.26984127	0	0
39	0.06349206	0	0	0.03175	0.063492063	0	0	0	0.3015873	0	0	0	0	0.063492063	0.333333333	0	0.142857143	0	0
40	0.12820513	0.102564103	0	0	0.051282051	0	0	0	0.3333333	0	0	0	0	0	0.192307692	0	0.192307692	0	0
41	0.16901408	0.056338028	0	0	0.014084507	0	0	0	0.2535211	0	0	0	0	0.084507042	0.211267606	0	0.211267606	0	0
42	0.09230769	0.015384615	0	0	0.092307692	0	0	0	0.2769231	0	0	0	0	0.061538462	0.138461538	0	0.323076923	0	0
TOTAL	3.42378892	2.242670817	0	0.44063	1.870043837	1.84759	1.58384	0.182282062	7.0212366	0.289079239	0.02702703	0.0326	1.7275	0.936006471	6.775468231	7.395092	4.005720781	1.124373	1.0750847
MEAN	0.082	0.053	0	0.011	0.045	0.044	0.038	0.004	0.167	0.007	0.0006	0.0008	0.041	0.022	0.161	0.176	0.095	0.027	0.026
STD ERR	0.012	0.01	0	0.003	0.009	0.009	0.009	0.003	0.013	0.004	0.0006	0.0005	0.01	0.005	0.018	0.028	0.016	0.007	0.007

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Major Professor: Dale H. Vitt