Spatial variability of organic carbon within surface soils of an ombrotrophic bog in

Western Washington

by

Joshua Carter

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Joshua Carter

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by

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Erin Martin, Ph.D
Member of the Faculty

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Date

ABSTRACT

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Bogs are exceptional long-term carbon sinks, but have not been subject to the same level of study as less quantitatively significant terrestrial carbon sinks. Although the role of *Sphagnum* mosses as major drivers of carbon storage in bogs has been well-established, the intrinsic variables that affect carbon content of surface soils within bogs tend to be highly site-specific and are not well known in the Pacific Northwest, as they have not been studied to the same extent as other peatland systems. Thus, several intra-bog variables were selected in order to determine how they affect internal C cycling within PNW bogs. Additionally, carnivorous plants were studied to determine their role in the C cycle. To our knowledge, this is the first study to examine their role in C cycling within peatland systems. Soil cores were taken and vegetative, chemical, and topographic features were studied to identify associations within a bog on the coast of Western Washington in Gray's Harbor county. Results indicate the study site shares many commonalities with bogs in other regions, particularly in *Sphagnum*'s preference for high microtopography, its positive association with soil moisture, and its relationship with higher soil carbon content. Carbon concentrations ranged from 396 mg/g to 445 mg/g by dry weight, which is comparable to worldwide peatland averages as well as those of neighboring regions. However, the C:N ratios and total nitrogen (N) content of the soils were abnormally high (17:1 and 2.39% by dry weight, respectively) compared to similar analyses in other regions of the world. This pattern appears to be driven by high organic N content. These results have implications for wetland management and also for the potential impacts of climate change as precipitation patterns shift and temperatures rise, potentially shifting the carbon balance of peatlands from being net sinks to net sources of atmospheric carbon. Further study is required to determine the causal relationships within these results as well as whether these results apply to other bogs within the region.

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1. Introduction

Bogs are a form of wetland characterized by highly acidic (pH < 5), peaty, and oligotrophic soils; hydrologic isolation from surrounding landscapes resulting in atmospheric deposition as the sole major water and nutrient input; vegetative communities dominated by mosses of the *Sphagnum* genus, graminoids, and small shrubs that tolerate poor soils well; and a high water table that is both highly acidic and anoxic. These landforms contain a number of unique taxa, including the carnivorous plants, which have evolved adaptations that allow them to live in soils with few available nutrients, as well as numerous amphibians, macroinvertebrates, and insects that can not live anywhere else (Ellison and Gotelli 2001, Matušíková et al. 2005). Despite only encompassing 3% of the world's land area, peatlands, of which bogs are the principle type, represent over 1/3 of the world's terrestrial carbon stores (Yu 2012, Gorham et al. 2012, Charman et al. 2013). Additionally, peatlands efficiently sequester carbon at an estimated rate of 24-32 g $C/m^2/yr$ over the last 1000 years, indicating that they are exceptional long-term carbon sinks (Loisel et al. 2014). However, these systems are relatively understudied compared to other terrestrial habitats due to their scarcity and relative inaccessibility, and so much is still unknown about them that they have been traditionally excluded in most climate models, despite the large carbon pool they represent (Limpens et al. 2008).

In particular, Pacific Northwest bogs have received very little attention compared to bogs in other regions of the world. Most research has been focused on experimental bogs in Eastern Canada, tropical bogs, and the vast peat bogs of Ireland and Northern

Europe (Draper et al. 2014, Sheppard et al. 2013, Ohlson & Okland 1998, Blodau et al. 2007). While bogs are less abundant in Western North America than they are in these parts of the world, Lacourse and Davies (2015) found significantly lower C deposition and higher N deposition within a bog in Western Canada compared to the aforementioned sites. Additionally, temperate bogs sequester much more carbon per unit area than do tropical bogs and are much more numerous, making their study more important in terms of understanding global carbon cycling and potential feedbacks from climate change (Page et al. 2011, Holden 2005). The near future may bring with it severe declines in wetland habitat due to rising temperatures, disturbances in precipitation regimes, development, agriculture, and other human-caused disturbances, so it is important to understand these systems and the underlying processes that control carbon flux (Charman et al. 2013, Bu et al. 2011).

The intra-wetland variables that affect carbon cycling within bogs are highly site-specific, and bogs found within the PNW have already been found to differ from those elsewhere (Loisel et al. 2014). While many factors, *Sphagnum* cover, water table depth, and precipitation are positively correlated with carbon concentrations in a predictable way across many different regions, many other variables, such as nitrogen addition, vascular plant cover, and air temperature have inconsistent relationships to carbon concentrations (Basiliko et al. 2006, Wang et al. 2014, Charman et al. 2015). As such, based on published results so far, it is hard to predict how carbon cycling is affected by these latter variables in this region. Additionally, while these factors have not been studied adequately in Pacific Northwest bogs, the role of carnivorous plants in carbon cycling has remained unexplored at the time of writing this paper. Due to their presence

in many peatland systems, and the additional mechanism of carbon capture through insectivory they represent, I hypothesize that insect capture may represent a significant carbon flux in peatland systems.

In this paper, I investigate several of these intra-wetland variables within a bog that is part of the Washington Department of Natural Resources North Bay Natural Area Preserve on the coast of Western Washington, just south of the Olympia Peninsula. Specifically, the role of bog microtopography, the presence of two plant functional groups (*Sphagnum* and carnivorous plants), and various soil components (organic and inorganic nitrogen, pH) were sampled and compared to levels of organic carbon within the surface soil (2-5 cm deep) to determine relationships between carbon content and these variables. In keeping with the literature, carbon concentrations were expected to be positively correlated with the thickness of *Sphagnum* cover, soil acidity, water depth, and the presence of high microtopography (hummocks), and negatively associated with the presence of low topography (hollows) (Ohlson and Okland 1998, Laine et al. 2006).

Sundews are a unique area of study for this paper, as their role in C cycling has not been studied. There are many species of carnivorous plants, but the most common in this region is *Drosera rotundifolia,* the round-leafed sundew. This species is one of the most widely distributed carnivorous plants, occurring in northern latitudes throughout North America, Europe, and Asia. Additionally, its physiology is well understood and has been studied for well over a century, making it a model plant for this type of study. Because bogs have such acidic and nutrient poor soils, sundews have evolved the capability to ensnare and digest insects in order to acquire the nutrients they need (mostly nitrogen, phosphorous, and calcium, but also many trace elements) (Givnish et al. 1984).

But like all plants, they photosynthesize using CO_2 taken up from the atmosphere. This means that the fate of the carbon contained within the insects they ensnare remains unknown and has not been studied at the time of writing this thesis. I hypothesize the C from such insects to be either consumed by microbes or remain in the bog itself, and thus I expect to find that soils supporting sundews will have higher concentrations of organic carbon than those without. Additionally, because sundews are not 100% efficient at extracting the nitrogen from the insects they capture, higher levels of organic nitrogen may also be found in soils where they are present.

I expect this research to elucidate the intra-wetland variables that affect carbon cycling in Pacific Northwest bogs and to also further our understanding of carbon cycling in bogs in general. If the results obtained by this study can be replicated on a larger scale and in a broader array of sites, the processes that control carbon cycling in PNW bogs may be better elucidated, allowing us to understand the unique characteristics of peatlands in this region. These results may allow wetland restoration efforts to be customized to the specific needs of the region, to create more accurate climate change models, and may increase the precision of global carbon budget models.

In the following paper I will review the current literature significant to this topic and report the findings of this study. While there were a number of challenges in collecting and analyzing the data, several interesting trends revealed themselves. Many of these results are in agreement with prior studies or are inconclusive, but some, such as the C:N ratio values reported in soil samples were surprisingly low, which has greater implications in terms of the study site.

2. Literature Review

2.1 Introduction

In the following text I briefly explain what an ombrotrophic bog is in relation to other peatlands, the relationships between bog vegetation and carbon cycling, the important carbon fluxes within bog systems and how nutrient limitation affects them, how carbon is distributed within bogs and why, how climate change may impact bogs in the future, and what gaps in the literature this research fills.

2.2 Ombrotrophic bogs

Bogs are one of the principle types of wetlands (the others being fens, marshes, and swamps), and are characterized by highly acidic soils, dominance of the vegetative community by *Sphagnum spp.,* and the accumulation of peat, which is largely composed of the partially decayed remains of *Sphagnum* mosses and vascular bog plants. There are several types of bogs, but ombrotrophic bogs are characterized by being hydrologically separate from the surrounding landscape and by being entirely precipitation fed (Vitt, 2013). While many non-bog wetlands also produce peat (primarily fens), ombrotrophic bogs make up the majority of the world's peatlands, contain the majority of its peat, and contain peat that is less labile than that of other peatlands, making them the single most important type of wetland in terms of carbon storage (Bridgham et al. 2006, Corbett et al. 2009).

Ombrotrophic bogs are also distinct from other wetlands in their water and soil chemistry. Rain is typically more acidic and contains fewer nutrients than surface or

groundwater, and because these bogs receive all of their moisture from precipitation, this results in very low nutrient inputs and highly acidic conditions. The lack of water movement also tends to create anoxic conditions, as microbial activity quickly depletes the water column of its available oxygen. Because of these factors, ombrotrophic bogs are inhospitable to most plants, as there is very little nitrogen or phosphorous available, and the acidic soil makes nutrients, even when present, difficult to absorb by a plant's roots due to a much decreased cation exchange capacity (Vitt, 2013). Additionally, *Sphagnum* mosses produce a number of phenolic compounds that have been shown to inhibit microbial and fungal growth and their ability to decompose organic matter (Bragazza et al. 2006, Turetsky et al. 2008). These properties of bogs are what allow ancient bodies, wood, and other organic material to remain largely preserved after being submerged for thousands of years (Purdy 2002). Ancient peoples even used bogs to preserve substances such as butter and tallow which are still recognizable to archaeologists after thousands of years (Ball, 2004)!

  Sphagnum mosses are ecosystem engineers and arguably the most important biotic component of an ombrotrophic bog. Their presence facilitates the formation of peat, contributes to the water and soil chemical properties that prevent decomposition, and prevents most vascular plants, which are typically more labile sources of carbon, from growing within the bog (Nichols et al. 2014). When *Sphagnum* cover declines, it is often the first indication that a bog is shifting from a net carbon sink and is becoming a net carbon source, as microbial respiration rates and vascular plant cover both increase as *Sphagnum* cover decreases (Larmola et al. 2013).

2.3. Relationship between the vegetative community and the carbon cycle

2.3.1 Sphagnum moss

Unlike most ecosystems, bogs are dominated by bryophytes, specifically the

Sphagnum mosses. Because bogs typically have a high water table year-round,

Sphagnum's lack of vascular tissue is advantageous compared to vascular plants, as it

absorbs water and nutrients directly without the need to grow roots, enabling it to quickly

spread across the surface of the soil (Adkinson and Humphreys 2011). These mosses

typically blanket the surface of a bog, which prevents most other plants from growing.

Sphagnum mosses are characterized by having alternating layers of living green

cells and large, dead hyaline cells within their leaves (Fig. 1) (Vitt 2013).
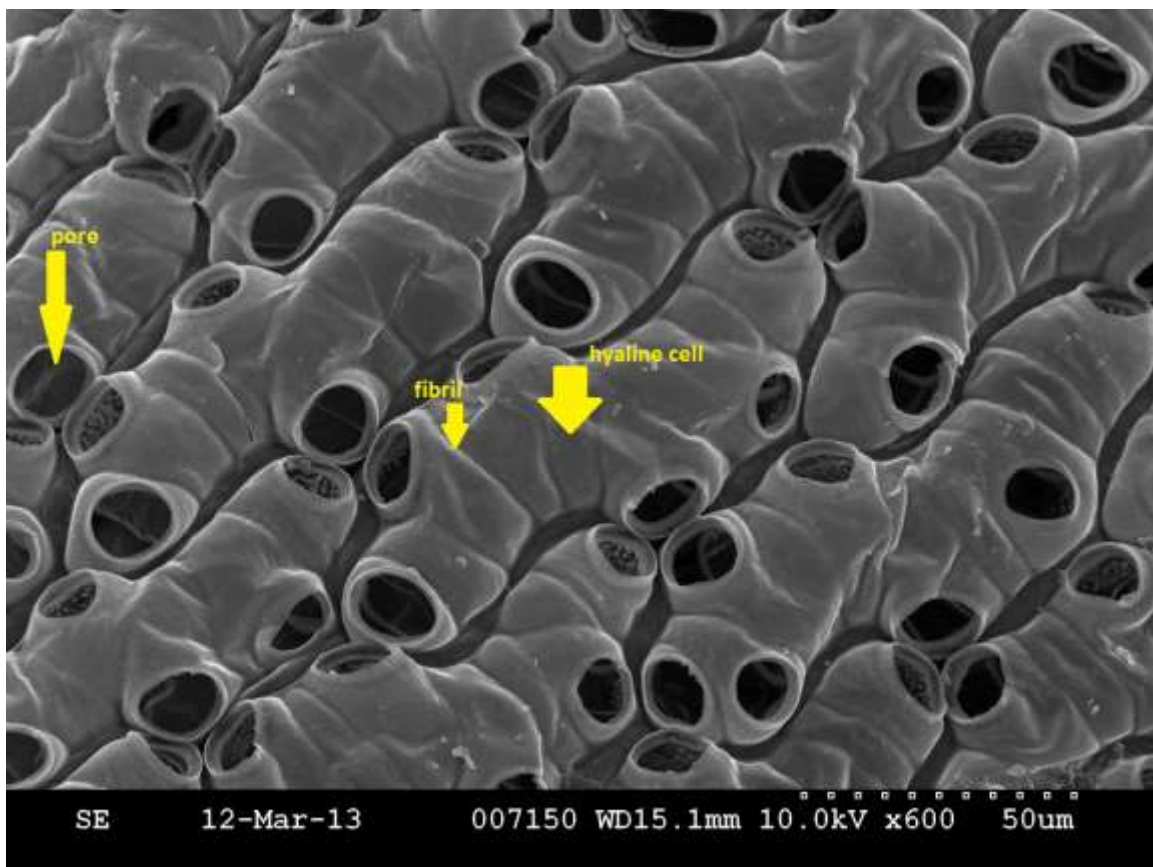
Figure 1: a scanning electron microscope image of hyaline cell structures within a Sphagnum leaf cell. The pores in these cells allow for greater water uptake and retention in saturated soils than a vascular root system would (https://sphagnumsem.wordpress.com).

These hyaline cells are also found outside stems and branches, and are perforated throughout, providing numerous tiny reservoirs that allow for capillary transport of water well above the water table (Vitt 2013).

Additionally, *Sphagnum* produces uronic acid, which increases its cation exchange capacity when pH is low, allowing it to extract nutrients from acidic soils much more efficiently than vascular plants (Spearing 1972, Richter & Dainty 1990). When combined with its hyaline structure, *Sphagnum* is exceptionally efficient at taking up nutrients, essentially acting as a sponge for water and the nutrients contained within it (Fritz et al. 2014). This also prevents other plants from encroaching, as *Sphagnum* is able to take up nutrients as they become available much faster than vascular plants. However, these adaptations work against *Sphagnum* when conditions are dry or less acidic, respectively, as without vascular tissue, the plant is unable to control its water loss and is much less efficient at extracting nutrients from less acidic soils (Adkinson and Humphreys 2011).

Interestingly, *Sphagnum* also produces a unique phenolic compound, Sphagnum acid, found in no other taxa. This compound prevents predation, preserves remains within the bog site, and contributes to the ability of *Sphagnum* to act as ecosystem engineers, as Sphagnum acid contributes to the acidification of their habitat, inhibits microbial growth, is unpalatable to animals, and creates adverse growing conditions for other plants (van Breeman 1995). In turn, because vascular plant growth is reduced, less evapotranspiration occurs within the bog, resulting in higher moisture retention, which allows the *Sphagnum* to flourish while excluding plants that are less tolerant of inundation.

While *Sphagnum* is a less efficient photosynthesizer than vascular plants, its phenolic content and the resulting acidity of the peat produced from its remains means that carbon derived from *Sphagnum* has a much longer residence time than that of vascular plants or other bryophytes. Importantly, while *Sphagnum*'s capacity to act as an ecosystem engineer decreases the lability of all carbon within the peat column, carbon derived from *Sphagnum* is still up to ten times less labile than carbon from other sources (Dorrepaal et al. 2005).

2.3.2. Peat

As previously mentioned, *Sphagnum* mosses are extremely important in the formation of peat, the primary form of carbon stored within bogs. Peat is composed of the partially decayed remains of *Sphagnum* that have sunk below the living *Sphagnum* layer. As new *Sphagnum* growth occurs, this dead layer compacts and sinks deeper into the bog. After it sinks below the water table, where anoxic conditions prevail, decomposition almost comes to a stop, and only small amounts of anaerobic respiration occur, allowing this peat to remain essentially preserved for long periods of time (Vitt 2013). However, this is such a slow process that peat is not considered a renewable resource; peak peat accumulation in most bogs is less than 1 mm yr^{-1}, and it can take well over a millennium to form a layer of peat one meter deep (Holden 2005).

If components of water and soil chemistry aren't right, mossy remains will decompose rather than form peat. Acidic soils, anoxic water, and oligotrophic conditions are essential to the formation of peat, as they inhibit microbial growth and respiration and enable the preservation of mossy remains (Vitt 2013). Also important to the formation of

peat are the aforementioned phenolic compounds *Sphagnum* produces within its leaves, which, upon death of the plant, inhibit microbial and fungal decomposition, either by direct action on the organism or by inhibition of the enzymatic processes that break down organic matter (Bragazza et al. 2006, Turetsky et al. 2008).

Generally, as long as the water table is high and there is no significant disturbance, a bog will sustain the correct soil and water chemistry on its own. However, significant disturbances in the form of peat mining, development, or drainage can kill the *Sphagnum* layer, and when bare peat is exposed to the atmosphere, it undergoes accelerated decay due to increased oxygen levels and temperature, increased availability of nutrients, and decreased moisture and acidity (Leifeld 2011). Additionally, climatic changes can affect soil and water chemistry in bogs, primarily by changing temperature and precipitation patterns. Generally, colder temperatures and higher levels of precipitation contribute to a bog's ability to act as a carbon sink, while the opposite increases the rate of decomposition and may create habitat unsuitable for *Sphagnum* (Ise et al. 2008, Charman et al. 2013). Unfortunately, human disturbance on local and global scales (climate change) will likely lead to increased loss of peatlands in the foreseeable future.

The formation of peat also constitutes a positive feedback in forming more peat. Because so little decomposition occurs, peat retains most of the nutrients the living plant contained at the time of death. As a result, *Sphagnum* peat can contain up to 0.5% nitrogen, while graminoid peat can contain up to 3% nitrogen, as well as significant amounts of other macro and micronutrients, but because all of it occurs below the water table where little respiration occurs, these nutrients are essentially unavailable (Crum and

Planisk, 1992). In a seemingly contradictory fashion, oligotrophic bogs are very rich sources of nutrients, but those nutrients are virtually unavailable so long as the bog maintains a positive carbon balance, as they are stored within the anoxic peat layer where very little respiration can occur.

2.3.3. Vascular plant community

Vascular plants that exist in bog ecosystems have developed a number of novel adaptations allowing them to survive in conditions of semi-permanent inundation, chronic oligotrophic conditions, and a *Sphagnum* community that occupies a majority of the bog's substrate. These are typically small, herbaceous plants or slow-growing, oligotrophic conifers (such as *Pinus contorta,* Shore Pine). In general, they play a much smaller role in carbon cycling as their abundance is very low and their growth is very slow compared to *Sphagnum* (Ward et al. 2009). Vascular plants do represent a more labile source of carbon than *Sphagnum,* and Nichols et al. (2014) reconstructed historical carbon accumulation rates in a bog near Cordova, Alaska using hydrogen isotope ratios and found that during the periods of time in which the bog's vegetative community was dominated by *Sphagnum*, its carbon accumulation rate was 60% higher than during the periods of time in which the community was dominated by sedges. They also found that in addition to accumulating less carbon than *Sphagnum* dominated communities, sedge-dominated communities also increased the rate at which the underlying peat lost carbon.

Of special consideration are the carnivorous plants, the most common of which in the Pacific Northwest is *Drosera rotundifolia,* the Roundleaf Sundew. Sundews have evolved a unique adaptation that allows them to grow directly on beds of *Sphagnum*,

using their roots primarily for anchoring and support rather than nutrient absorption

(although their roots are still capable of absorbing nutrients if they are present within the

substrate they grow upon) (Chandler and Anderson 1976). Instead, they are covered in

trichomes (glandular protrusions) that secrete sweet, sticky mucilage which act to attract

and then ensnare insects. When an insect becomes stuck, the sundew reacts by curling its

stalk around the insect to trap it further and by secreting digestive enzymes that break

down the insect's chitinous exoskeleton and internal organs (Matušíková et al. 2005). It

then absorbs the nutrients released from these tissues (primarily nitrogen and

phosphorous, but also calcium and a number of micronutrients) (Ellison and Gotelli

2001). In this way, a sundew is able to attain the nutrients it needs without competing

with *Sphagnum* for those resources. Indeed, experiments have shown that even when

grown on a nutrient-rich substrate, sundews display inhibited growth compared to when

they get their nutrients from insects (Chandler and Anderson 1976). Additionally, while

sundews have vascular tissue and grow taller than mosses, they do not shade out the

Sphagnum they grow upon, implying at least a commensal relationship between the two

taxa (Svensson 1995). Given that sundews don't appear to stifle photosynthesis in

Sphagnum and that they capture insects to acquire the nutrients they need, one might

expect carbon concentrations to be higher in areas where sundews occur, as they do not

utilize the carbon contained within their prey. Conversely, it is also possible that insect-

derived carbon is decomposed or otherwise removed via abiotic/biotic processes prior to

being preserved within the peat column. However, while Millett et al. (2003) attempted to

determine if insect-derived C was taken up by sundews, they were unable to determine

the isotopic carbon signature of the insects they were utilizing as prey and were thus

unable to analyze this aspect of sundew carnivory. No further studies have been performed that investigate the relationship between *Drosera* spp. and carbon distribution within bogs as of yet, so the fate of this carbon is unknown at this time.

Few studies have examined the effects of vascular plants in bogs on carbon cycling. Ward et al. (2009) performed a plant-removal experiment on an ombrotrophic bog in northern England and found that the presence of dwarf-shrubs actually inhibited the ability of the bog to take up carbon in the short-term by impairing photosynthesis in graminoid plants (grasses, sedges, and rushes) that were shaded by the shrubs. However, this experiment did not examine the long-term impacts of the presence of these plants, and while it established a change in *gross* carbon flux, there was no change in *net* carbon flux.

2.4. Carbon cycling in ombrotrophic bogs

Peatlands[1] contain up to one-third of the world's terrestrial soil carbon stores, between 400–600 Pg, while only representing less than 3% of its total land surface area, making them the single largest component of the terrestrial carbon sink (Gorham, 2012, Yu 2012, Charman et al. 2013). Russia currently holds the largest peatland reserves of any region (214 Pg), with North America containing the second largest (178 Pg), the majority of which is found in Canada (Botch et al. 1995, Bridgham et al. 2006). Despite this, carbon cycling in peatlands is still poorly understood.

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[1] Peatlands are peat-forming wetlands, of which there are two types: fens and bogs. If left undisturbed, fens will eventually become bogs as layers of peat form and decrease the hydrologic interaction of the wetland from its surroundings. Bogs represent the bulk of the world's peatlands (Blodau 2002).

Bogs are composed of two main layers: the acrotelm and the catotelm. The acrotelm is composed of the shallow section of the bog where living *Sphagnum* and other plants reside and typically is above the minimum depth of the water table, while the catotelm includes the partially decomposed column of peat below the acrotelm (Holden 2005). Virtually all aerobic respiration occurs within the acrotelm, as well as a significant portion of anaerobic respiration (which varies depending upon temperature and water table depth), while the catotelm is permanently saturated, anoxic, and undergoes a very slow rate of anaerobic respiration.

As a result of interactions between these two zones, carbon cycling in bogs is mainly affected by three processes: photosynthesis, aerobic decomposition within the acrotelm layer, and anaerobic processes within the catotelm layer (Vitt, 2013).

2.4.1 Carbon fluxes

In general, carbon flux and storage are driven by the flow of water in ombrotrophic bogs. Because of their anoxic environments, most carbon mineralization occurs anaerobically, producing primarily methane (CH_4), the second most important greenhouse gas as well as one of the most potent, and hydrogen sulfide (H_2S) (Keller & Bridgham, 2007). CO_2 is also produced, but mostly as a product of plant and microbial respiration within the acrotelm layer (Holden 2005). CO_2 production tends to increase when the water table drops and peat is exposed to the air, as well as during desiccation events (Adkinson and Humphreys 2011).

Ohlson and Okland (1998) found that it takes approximately 40 years for a statistically significant amount of carbon to have been released from peat by decay. This

extremely slow process of decay is the main reason why bogs are net carbon sinks.

Bridgham et al. (2006) calculated a global sequestration of 137 Tg C yr^{-1} into peatlands, although this number comes with an uncertainty of over 100% (the actual number may be >±100%). Nichols et al. also calculated a historical carbon sequestration rate of 7.5 g/m^2/yr to 27 g/m^2/yr in sedge dominated and *Sphagnum* dominated bos, respectively.

The vast majority of carbon flux to the atmosphere comes from the acrotelm. The catotelm is responsible for less than 1% of total ecosystem respiration and is not considered a significant flux, while 90-97% of all the carbon fixed by plants is respired before and during transfer to the acrotelm through plant respiration and decomposition (Blodau et al. 2007, Ohlson and Okland 1998). An experiment performed by Blodau et al. (2004) determined that microbial respiration decreases as depth increases, but that water table position can greatly influence this process. When water tables were low, photosynthesis decreased by 24–42% due to desiccation, while aerobic respiration within the catotelm and acrotelm increased significantly; in addition, while overall methane production decreased when the water table was low, CO_2 production increased by a factor of 13–103!

2.4.2 Nitrogen

Nitrogen mineralization is generally extremely limited in bog habitats due to their acidic soils, and in ombrotrophic bogs nitrogen inputs are limited entirely to atmospheric deposition (Keller and Bridgham 2007). Thus, bogs are generally nitrogen-poor habitats with plant communities that are highly adapted to these conditions.

A number of experiments have been performed in bogs to determine the relationship between nitrogen deposition and carbon accumulation. This is of special importance because peat contains large amounts of nitrogen that may become available as the climate warms. Most of these experiments confirm that inorganic nitrogen addition (whether through artificial means or by monitoring atmospheric deposition) increases vascular plant growth and decreases *Sphagnum* growth and cover, resulting in increased CO_2 efflux from bogs and a loss of carbon storage capacity (Basiliko et al. 2006, Bragazza et al. 2006, Bubier et al. 2007, Kivimäki et al. 2013, Larmola et al. 2013).

However, some studies have shown a positive correlation between nitrogen addition and carbon accumulation. Basiliko et al. (2006) found that increased nutrient inputs (nitrogen, phosphorous, and potassium) also caused the soil microbial community to become a larger, more efficient carbon sink. Charman et al. (2015) also found a slightly positive effect of nitrogen addition on carbon accumulation at one of their sites, but only at lower levels of nitrogen addition. This is in agreement with Wang et al. (2014), who reconstructed the historical records of a bog in Eastern Canada and found that carbon accumulation was positively correlated with nitrogen accumulation over the last ~8000 years, although these records only look at total nitrogen, not inorganic and organic nitrogen separately.

It thus appears that the effects of nitrogen addition to bog systems are variable, with smaller additions potentially increasing a bog's carbon uptake efficiency, while larger amounts decrease that efficiency. This is in keeping with *Sphagnum's* established role as a very efficient scavenger of nitrogen, as it can effectively prevent other plants

from taking up excess nitrogen to a certain point, after which vascular plants begin to benefit from excess nitrogen as well (Fritz et al. 2014).

It is also important to note that these experimental studies are, by necessity, short-term when compared to the length of time it takes carbon to move throughout the peat column, so it is not clear whether large amounts of N addition permanently decreases a bog's carbon sequestration or if it only does in the short-term.

2.4.3 C:N Ratios

C:N ratios generally decrease along the peat column as decomposition occurs, preferentially decomposing carbon and releasing CO_2 and CH_4 while retaining much of the N present within the vegetative tissues (Wang et al. 2014). The result is a soil column relatively high in nitrogen, albeit mostly unavailable to microbes and plants, as mentioned in section 2.2.

Wang et al. (2014) report an average C:N ratio of 47:1 in living tissues at Mer Bleue Bog, and a steady decrease of 42:1 to 31:1 down the gradient of the peat column. Kuhry and Vitt (1996) reported C:N ratios of 55:1 to 76:1 in living *Sphagnum fuscum*, with a similar decrease in C:N ratios in older, deeper peat. However, Kurhy and Vitt found preferential decomposition of nitrogen in the acrotelm resulting in C:N ratios as high as 300:1, in contrast to Wang et al.'s findings, indicating that these processes may differ from site to site depending upon variables such as community composition, soil pH, water table depth, and so forth. Loisel et al. (2014) supports this notion in a meta-analysis of the available literature, showing average regional C:N ratios of 34.2–77.2 for most of the Northern Hemisphere's temperate peatlands.

2.5. Distribution of carbon storage & efflux within a bog

The spatial relationships between carbon accumulation and bog components are highly variable from site to site, and are affected by factors such as vegetative community, water table depth, nitrogen content of soils, temperature, topography, and seasonality.

Charman et al. (2015) looked at historical carbon deposition within three different bogs on the East Coast of North America and found that while nitrogen and vegetation were weakly associated with carbon accumulation in one or two of the sites, water table depth and temperature were the only variables that were significant in all three bogs. Additionally, water table depth was always positively correlated with higher soil carbon levels, while temperature was always positively correlated with methane and CO_2 production, whereas the other variables often showed contradictory relationships with carbon accumulation and/or greenhouse gas production, likely due to individual differences in vegetation, climate, and location between the sites.

In another study, Blodau et al. (2007) found that by artificially lowering the water table in an ombrotrophic bog, the total ecosystem respiration rate increased by 61%, indicating that water table depth is perhaps one of the most important controls on total carbon efflux.

Landscape features also play a prominent role in the spatial distribution of carbon in bogs. There are three main landforms within bogs: hummocks, or elevated sections; hollows, which are the lower elevation spaces between hummocks; and lawns, which are flat expanses or plateau-like features (Laine et al. 2006). Hummocks tend to have deeper

Sphagnum cover and higher rates of photosynthesis and respiration, while hollows are closer to the water table and engage in less respiration, although Laine et al. (2006) found that even though respiration is higher in hummocks, they are still more effective carbon sinks than hollows due to their increased rate of photosynthesis (Ohlson and Okland 1998).

2.6. Climate change implications for bogs

Climate change is likely to lead to a number of changes in bogs, but those specific changes depend upon regional climatic changes. Overall, evapotranspiration is predicted to increase in most bogs, which may result in desiccation events that dry out *Sphagnum* and result in a higher carbon flux to the atmosphere (Bu et al. 2011). If evapotranspiration surpasses precipitation, the hydrology of the bog will shift, resulting in the disappearance of bog plant communities and ultimately the loss of bog function (Nichols et al. 2014).

2.6.1. Vascular plant dominance

Climate change is likely to cause a shift in the community composition of bogs towards vascular plant dominance. Increased evapotranspiration and altered precipitation patterns may decrease the water table, and as the water table decreases, vascular plants become increasingly common and *Sphagnum* disappears (Moore et al. 2002, Bubier et al. 2007). Because *Sphagnum* is instrumental in the accumulation and preservation of carbon within bogs, and because it is easily outcompeted by vascular plants in drier, warmer conditions, this will result in increased contribution of carbon to the atmosphere not just

because vascular plants represent a more labile source of carbon than *Sphagnum,* but also because the disappearance of *Sphagnum* will result in increased peat decomposition (Ise et al. 2008).

2.6.2. Disappearance and regressive succession

Ombrotrophic bogs are often an "end stage" in terms of succession; those that exist today were formed, on average, 7000 years ago (Gorham et al., 2012). Unless climate and/or precipitation patterns change, a bog will continue to form layers of peat and sequester more and more carbon (Bu et al. 2011). However, if evapotranspiration exceeds precipitation (either through higher temperatures, less precipitation, or some combination of both), the hydrology of the bog will no longer support *Sphagnum* and the bog will undergo regressive succession, meaning it will transition to a forested or grassy ecosystem (Bu et al. 2011). As this happens, stored peat undergoes increased decomposition, releasing more carbon into the atmosphere than the plant community takes up via photosynthesis.

2.6.3. Global implications

Despite being the single largest terrestrial carbon store, peatlands are often excluded from climate models and emissions scenarios, which may be problematic, as Holden (2005) estimates that carbon sequestration by peatlands over the past 10,000 years has reduced global temperatures by 1.5–2º C (Limpens et al. 2008).

Northern latitudes are also disproportionately warming compared to lower latitudes, and 80% of the world's peatlands exist in these locales, containing an estimated

547 Pg of carbon (Holden, 2005). This suggests a possible positive feedback loop as warming causes the loss of bog habitat, which then results in the decomposition and release into the atmosphere of the carbon stored within them, which will in turn cause global temperatures to rise even further. Ise et al. (2008) projects losses of 40% of the carbon in shallow peat layers and 90% losses in deep layers if the global climate warms 4º C, suggesting a catastrophic positive feedback to global warming.

Alternatively, some studies have shown that an increase in temperature may lead to negative climate feedbacks in bogs. As temperatures rise to about 27º C, the net photosynthetic rate of *Sphagnum* increases so long as sufficient water is present (Bu et al. 2011). In fact, a number of studies have shown increases in *Sphagnum* abundance as temperatures rise, even as the abundances of vascular species are reduced, although too much warming leads to the death of *Sphagnum* communities and the dominance of vascular plants (Bu et al. 2011). Additionally, high-latitude bogs may expand as the climate warms and their rate of carbon sequestration may even increase as well (Charman et al. 2013)

There are also studies showing no correlation between temperature and peat formation. Novak et al. (2008) studied five bogs in the UK and the Czech Republic and used pollen records to construct regional climate models. They found that while temperature was related to carbon storage in the short-term (<50 years) in all five sites, there was no relationship between temperature and carbon storage over the past 150 years. Wieder et al. (1994) found similar results in their study of five *Sphagnum-*dominated peatlands in North America.

2.7. Present study contributions

2.7.1. Determine topographic patterns of carbon distribution

Topographic carbon distribution has only been addressed in a handful of studies, none of which were performed in the Pacific Northwest. This research will increase our understanding of where carbon is deposited in an ombrotrophic bog by looking at various factors other than *Sphagnum* cover. In particular, it will attempt to show the relationships between carbon concentrations within surface soils and vascular plant communities, water table depth, microtopography, dissolved oxygen concentrations, and nitrogen levels (which may, in turn, be influenced by these other factors). Additionally, it will further our understanding of PNW bogs, potentially elucidating their similarities and differences from those in other regions.

2.7.2. Provide avenues of future research

This research may reveal relationships in two general categories that stimulate future research: the spatial relationships found within bogs in general, and the relationships within Pacific Northwestern bogs.

Ombrotrophic bogs are still poorly understood, and while research has been performed on spatial relationships within several bog systems, few of these studies have looked at these relationships on as fine a scale as I intend to. Additionally, all of the studies I have found have either been manipulative experiments looking at a single relationship (e.g. nitrogen input vs. carbon efflux), or have reconstructed the climatic and vegetative history of a site using proxy data, whereas I intend to look at carbon and nutrient content within the acrotelm layer and associated vegetative data.

Most research has also focused on bogs outside of the Pacific Northwest. The ecology and carbon balance of bogs is highly variable depending on regional climatic and soil conditions, and what we know about bogs in one part of the world does not necessarily apply to bogs elsewhere. By looking at a bog in the Pacific Northwest, I may find relationships unique to the region.

2.7.3. Help understand the consequences of climate change and other human activities

Bogs are currently under threat from a variety of human activities, including peat mining (for peat products and for fuel), bog drainage (for different land use), and pollution (particularly N and P). Understanding the processes in bogs may allow us to better mitigate the deleterious effects of human activities on them, inform policy relating to bogs, devise improved restoration strategies for bogs that have already been degraded, promote carbon sequestration in existing bogs, and possibly inform a strategy towards preventing a massive CO_2 flux into the atmosphere as peat trapped within permafrost at northern latitudes thaws.

2.8 Conclusion

Ombrotrophic bogs are highly variable systems that can display a range of responses in carbon flux and storage when faced with environmental changes. In general, lower temperatures, higher water tables, and nutrient limitation promote carbon sequestration, but regional processes are more important than global ones and individual bogs may deviate from these patterns depending on their specific soil chemistry, vegetative community, nutrient inputs, and landscape structure. Because of this high

variability, research on ombrotrophic bogs is needed on the regional level within the Pacific Northwest in order to predict the effects of climate change, reveal previously unknown relationships, and to determine what course of action, if any, should be taken to protect our bog systems.

3. Methods and Materials

3.1 Field collection

The study site consisted of a bog within the North Bay Natural Area Preserve wetland system, which is located in Gray's Harbor county in Washington state, west of Hoquiam. This wetland system consists of 1,215 acres of various wetland systems, including salt marshes and a *Sphagnum* bog. It is surrounded by a temperate rainforest system averaging ~70 inches of precipitation a year and is dominated by Douglas-Fir (*Pseudotsuga menziesii*), Western Hemlock (*Tsuga heterophylla*), and Western Redcedar (*Thuja plicata*). Also located nearby are a number of privately owned wetlands, including several cranberry bogs.

This site was chosen for three reasons: ease of access, the presence of vegetation of interest (*Sphagnum spp., Drosera rotundifolia,* graminoids) and relative lack of human disturbance. This particular site fit all three criteria better than other sites considered in Western Washington, although it was located adjacent to a rural road and trash was observed within a buffer of woody shrubs separating the road from the bog complex. Sampling occurred between February 6th, 2016 and February 10th, 2016.

The study site consisted of a 100 m baseline with ten transects ranging from 61– 100 m in length. Because of the trash observed within the buffer, the baseline was set 50 m away from the buffer to minimize the impact of human disturbance on the samples taken. Transects were spaced 10 m from each other and perpendicular to the baseline, with the first one being placed randomly along the baseline using a random number

generator. Each was checked to ensure heterogeneity of vegetation, microtopography, and inundation, and to ensure there were no obvious disturbances present.

There were a total of 25 sample units (SU) placed along the transects. Two random SUs were placed on each transect, while the remaining five SUs were randomly assigned a transect and a point along the transect using the same process as the first twenty SUs. A new random number was generated if an SU fell within 10 m of another SU, and if an SU was completely barren (>95% free of vegetation) or inundated, a new location for the SU was chosen. The number of sample units was agreed upon in conjunction with the State of Washington Department of Natural Resources to prevent unnecessary damage to the wetland complex.

Each SU consisted of a 0.5 m^2 quadrat placed so that the right side of the frame overlapped with the meter tape and the upper right hand corner of the frame was underneath the meter number assigned to the SU. Within these quadrats, the following measurements were made in this order so as not to disturb the SUs before data were collected: water chemistry, vegetation functional groups, microtopography, and soil cores.

Additionally, living *Sphagnum* thickness was measured using a meter stick on both sides of the quadrat, with a final value consisting of the average of both values. Water depth was also measured at the deepest point in each SU using a meter stick. All of these measurements will be elaborated upon within the following sections.

3.1.1 Water chemistry

Temperature, dissolved O_2, and pH were characterized in each SU using a Yellow Springs Instrument Pro2030 meter and an Oakton pH meter with an Oakton 35641-51 electrode, respectively. These values were taken before any other sampling so as to minimize disturbance within the SU, and they were placed either near the center of the SU or where the water was deep enough to cover the electrodes. Values were given time to equilibrate (~10 minutes) before final values were recorded as data. The electrodes were thoroughly rinsed with DI water after each measurement was taken, and the pH meter was calibrated before each sampling event with three standards: pH 3, 5, and 7.

3.1.2 Vegetative sampling

Vegetation functional groups (*Sphagnum* spp., carnivorous plants, non-carnivorous vascular plants, graminoids) were marked as either present or absent in each SU. These functional groups were chosen because *Sphagnum* is considered an ecosystem engineer and has dramatic, well-defined impacts on wetland systems, graminoids are also common wetland plants that have well-defined impacts on wetland systems, and non-graminoid vascular plants are also common, and their presence may have differing impacts than the graminoids.

If cover for a functional group within each SU was qualitatively estimated to be less than 5%, it was not counted as being present with the exception of carnivorous plants. Because *Drosera rotundifolia*, the carnivorous plant present at this site, forms a tiny, difficult to see hibernaculum in winter, it was counted as present if observed within

an SU regardless of its estimated cover, as it is impossible to estimate vegetative cover of

this plant unless it is its active stage.

Vegetation for the entire study site was also characterized using the point-

intercept method using the same functional groups, save for the carnivorous plants. Using

the same SU numbers as for the sample plots, points every 0.5 m for 10 m were recorded

as either hits or misses for each functional group, for a total of 20 points in each SU and

500 points in the entire site, following the methods of Canfield (1941). Cover estimates

for each group were then obtained via the following equation, where a "hit" and "miss"

are defined as the presence or absence of vegetation directly below the point along the

tape, respectively:

$$Cover\ of\ functional\ group\ A = \left(\frac{\#\ hits\ group\ A}{Total\ \#\ points}\right) x\ 100$$

This data was not used for actual analysis, but was taken to ensure the site contained a

heterogeneous mix of vegetative groups, to ensure the vegetative community was of the

correct type for an ombrotrophic bog, and to ensure the site chosen was representative of

the bog complex as a whole.

3.1.3 Soil cores

Soil cores were taken in each SU after all other sampling was finished. A 1.27 cm

(0.5 inch) diameter stainless steel tubular soil corer was used for each soil core. Two soil

cores were taken 2-5 cm in depth (due to difficulty in coring peaty soils with narrow

corers) from opposite sides of the quadrat in each SU, just below the litter where the

acrotelm begins. These cores were then combined in a plastic bag, and placed in a cooler

filled with ice until it could be brought back to the lab for freezing at the end of the day. The soil corer was thoroughly rinsed with DI water in between SUs.

Some inconsistency is present with the first five soil cores. First, 5 shallow soil cores were taken from each SU and combined instead of two. The method was modified due to challenges in using the soil corer within a peaty bog. Second, the samples were placed in a refrigerator/incubator upon return to the lab at the end of the day. These samples were moved to a freezer two days later and stored over the next two months, but the temperature in the refrigerator was raised to just above room temperature sometime during these two days. However, soil N and C analyses did not reveal any obvious abnormalities compared to the other 20 samples that did not undergo this inconsistency, and they were thus included in all results except where stated otherwise.

3.2 Lab analyses

Except for the first five samples collected, all of the soil samples were placed in the freezer upon being homogenized the same day they were collected. Samples were homogenized via a milkshake mixer and placed inside 500 mL HDPE bottles before being frozen. Any living plant material present within the soil samples was also removed by hand at this point. Living plant material was defined as green vegetation, as well as red in the case of *Sphagnum*.

A portion of each sample was weighed and then dried by placing it in an oven set to 110º C (±5º C) for 16 hours, weighed again, and then placed within a desiccator for future C:N ratio analysis.

Soil moisture percentage was calculated at this point via the following equation, where W_1 and W_2 equal the weights of the soil before and after drying, respectively (Delaune et al. 2013):

$$Moisture\ content\ (\%) = \frac{(W_1 - W_2)100}{W_1}$$

3.2.1 Soil pH

Soil pH was determined in duplicate for each sample using an Orion 601A Ionalyzer pH meter with an Oakton 35641-51 electrode using a method adapted from Hendershot et al. (2008). Briefly, approximately 2.00 g of dried sample was placed within a 50 mL beaker. 20 mL of deionized water was then pipetted into the beaker and it was then agitated for half an hour, left to sit for an hour, and the pH was then measured. The pH meter's calibration was checked every ten samples and recalibrated as necessary. Per Hendershot et al.'s method (2008), if duplicates registered a difference in pH by more than 0.20 new subsamples were measured. The mean of both readings was used as the final pH value for statistical purposes.

3.2.2 Nitrate

Nitrate was extracted from soil samples using DI water per EPA Method 300.0 (1993). Approximately 10 g of field wet sample was measured into a beaker, and then 50 mL of DI water was pipetted into it. Samples were mixed for 15 minutes and then filtered using a 0.45 μm filter (Whatman no. 42) into 60 mL polypropylene bottles. These

samples were then frozen until analysis, which was approximately one week. Samples

were then thawed and analyzed via ion chromatography using a Dionex 25A ion

chromatograph. A standard curve was constructed using 0.15 mg/L, 0.25 mg/L, and 0.50

mg/L NO_3^- standard solutions with an R^2 value of 0.999. Samples 3, 8, 10, and 20 were

determined to be above the range of the high standard and were diluted with a 4:1 ratio of

DI water and filtrate and re-run. NO_3^- concentrations were then standardized to mg/gdw

(gram dry weight) sample.

3.2.3 Ammonium

NH_4^+ was extracted from soil samples by weight approximately 2 g of wet sample

into an Erlenmeyer flask, pipetting 20 mL of a 2 M KCl solution, and agitating the flask

for 30 minutes (Maynard et al. 1993). The sample was then filtered using a 0.45 μm filter

(Whatman no. 42) into a 60 mL polypropylene bottle and frozen. Samples were then

thawed and analyzed by UV-visible spectroscopy using an Agilent 8453 diode array at a

wavelength of 640 nm. This analysis was adapted from a colorimetric analysis method

using sodium salicylate in place of phenate by Le and Boyd (2012), with the addition of

the EPA's extraction method. A standard curve was constructed using 0.1 mg/L, 0.5

mg/L, and 1.0 mg/L NH_4^+ standard solutions with an R^2 value of 0.997. Actual NH_4^+

concentrations were computed via the following equation, where $C = NH_4^+$ concentration

(mg/L), A = absorbance, and s and u are the standards and unknowns, respectively:

$$\frac{C_s}{C_u} = \frac{A_s}{A_u}$$

NH_4^+ concentrations were then standardized to mg/gdw of sample.

3.2.4 Organic carbon & nitrogen

Total organic carbon and nitrogen content of the soil samples were determined by dry combustion using using a Perkins Elmer Series II 2400 CHNS/O Analyzer with a Perkins Elmer AD6 Autobalance (Batjes 1996). 8x5 mm tin capsules were weighed to the nearest 0.001 mg, packed with 1.5–2.5 mg of dry sample, weighed again, and combusted within the CHN analyzer to determine the C:N ratio, total nitrogen, and total carbon of each sample. NIST SRM 1547 Peach Leaf standard was used as a conditioner, and acetanilide was used as a K-factor. Because these samples were so acidic, inorganic carbon was assumed to be absent, and thus the total carbon value reported by the instrument was assumed to be entirely organic.

Organic nitrogen content was determined by subtracting the NH_4^+ and NO_3^- from the total nitrogen content of each sample. Inorganic nitrogen content was determined by summing the NH_4^+ and NO_3^- content of each sample. NO_2^- is generally not detectable in peatlands and was thus not included in this analysis (Sheppard et al. 2013).

3.3 Statistical analyses

JMP Pro 12 and Microsoft Excel were used for all statistical analyses. Categorical variables paired with continuous variables were analyzed via one-way ANOVA, while continuous variables paired with continuous variables were analyzed via linear regression. Data were checked for normal distribution and analyzed via the non-parametric Kruskal-Wallis test and Spearman rank correlation in addition to ANOVA and

linear regression, respectively, to determine if significance differed between statistical tests. Significance was set at α = .05 for all tests.

3.3.1 Treatment of data

The ion chromatograph used to analyze NO_3^- samples was unable to differentiate rinse blanks from sample concentrations below 0.10 mg/L. Sample numbers 2 and 5 registered NO_3^- values below this concentration and were treated as if concentrations half the detection limit, or 0.05 mg/L. Per Croghan & Egeghy (2003), this method of data substitution should not introduce significant bias into the results, but statistical tests involving NO_3^- and total inorganic N were performed with and without these two samples to ensure that this was the case.

Because multiple microlandforms were present within each quadrat, microtopograhy was characterized as either low, medium, or high based on the average of the landforms. Hummocks were considered high, lawns medium, hollows low, and the single plot that was almost completely inundated was also treated as low. Qualitative observations were also used to characterize terrain, particularly when a specific microlandform made up an overwhelming majority of the plot.

While four vegetative functional groups were surveyed, only *Drosera* and *Sphagnum* were present and absent in enough plots to perform statistical analysis. All but one plot contained vascular plants, and all but three contained graminoids. Thus, they were not included in analyses.

4. Results

4.1 Vegetation

Graminoids and other vascular plants were present in nearly all plots, but qualitative estimates of cover indicated that graminoids were dominant overall and were most common in the more inundated portions of the site, while *Sphagnum* tended to be dominant near the less inundated Northern and Southern portions as well as the raised section near the Western boundary of the site. Additionally, *Sphagnum* tended to be more clumped, with a smaller overall distribution but a tendency to dominate the areas it was present in. Vascular plants, while found in the most plots, did not contribute much overall cover, as they mostly consisted of small shrubs such as Bog Cranberry (*Vaccinium oxycoccos*), Labrador Tea (*Rhododendron groenlandicum*), Bog Rosemary (*Andromeda polifolia*), etc. Overall, the plots' vegetative composition largely matched that of the site at large. Vegetative data in study plots and for the site as a whole are summarized in table 1.

Vegetation Type	Graminoids	Vascular	*Sphagnum*	*Drosera*
# Sample plots present	22	24	18	9
% of plots present	88%	96%	72%	36%
Actual site % Cover	71.6% ±16.2%	40.2% ±19.3%	35.4% ±19.1%	NA

Table 1: Summary of vegetation data. The "Vascular" column includes all vascular plants except for Drosera and graminoids. Actual site data % cover was derived from can be found in Appendix 1. _____

Graminoids and vascular plants were nearly ubiquitous to the study plots. As a result of this, their interactions with the other two functional groups and the other physical and chemical measurements were unable to be determined.

4.1.1 Physical and chemical summary data

      Sphagnum's impact on physical and chemical properties such as soil pH and soil moisture are well known, but the presence of *Drosera* also appears to vary with some of these factors (table 2). Additionally, across all plots studied, dissolved O_2 values ranged from 2.7–9.5 mg/l, water depth from 0–15 cm, *Sphagnum* depth from 0–9.5 cm, soil moisture from 90.96–95.69%, and soil pH from 4.71–5.79.

Physical/chemical Factor	Site Total	Sphagnum		Drosera	
		Absent	Present	Absent	Present
Dissolved O_2 (mg/l)	7.49±1.87	7.87±0.78	7.17±0.72	6.74±066	8.37±0.71
Water depth (cm)	5.16±4.88	8.71±1.79	3.39±1.05	4.31±1.30	5.89±1.74
Sphagnum depth (cm)	3.62±3.23	N/A	5.03±0.55	4.00±0.81	2.94±1.09
Soil moisture %	94.04±1.06	93.11±0.34	94.41±0.21	94.37±0.24	93.46±0.33
Soil pH	5.46±0.26	5.33±0.10	5.50±0.06	5.44±0.06	5.48±0.10

Table 2: Summary of physical and chemical data by the presence and absence of plant functional groups. ± values indicate standard error for each value. Note that dissolved O_2 measurements were made in plots with standing water only.

4.1.2. Sphagnum

      Even though soil moisture differences were slight, soil moisture in plots where *Sphagnum* was present was higher (94.41% ±0.69%[2]) than in plots where it was absent (93.11% ±1.30%) (Fig. 2; *t(23) = 3.27*; *p < 0.01*), with soil moisture increasing as moss depth increased (Fig. 3; *R = 0.4750*). Soil pH, by contrast, did not differ in plots where *Sphagnum* was present from those where it was absent.

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[2] ± Values within text indicate one standard deviation
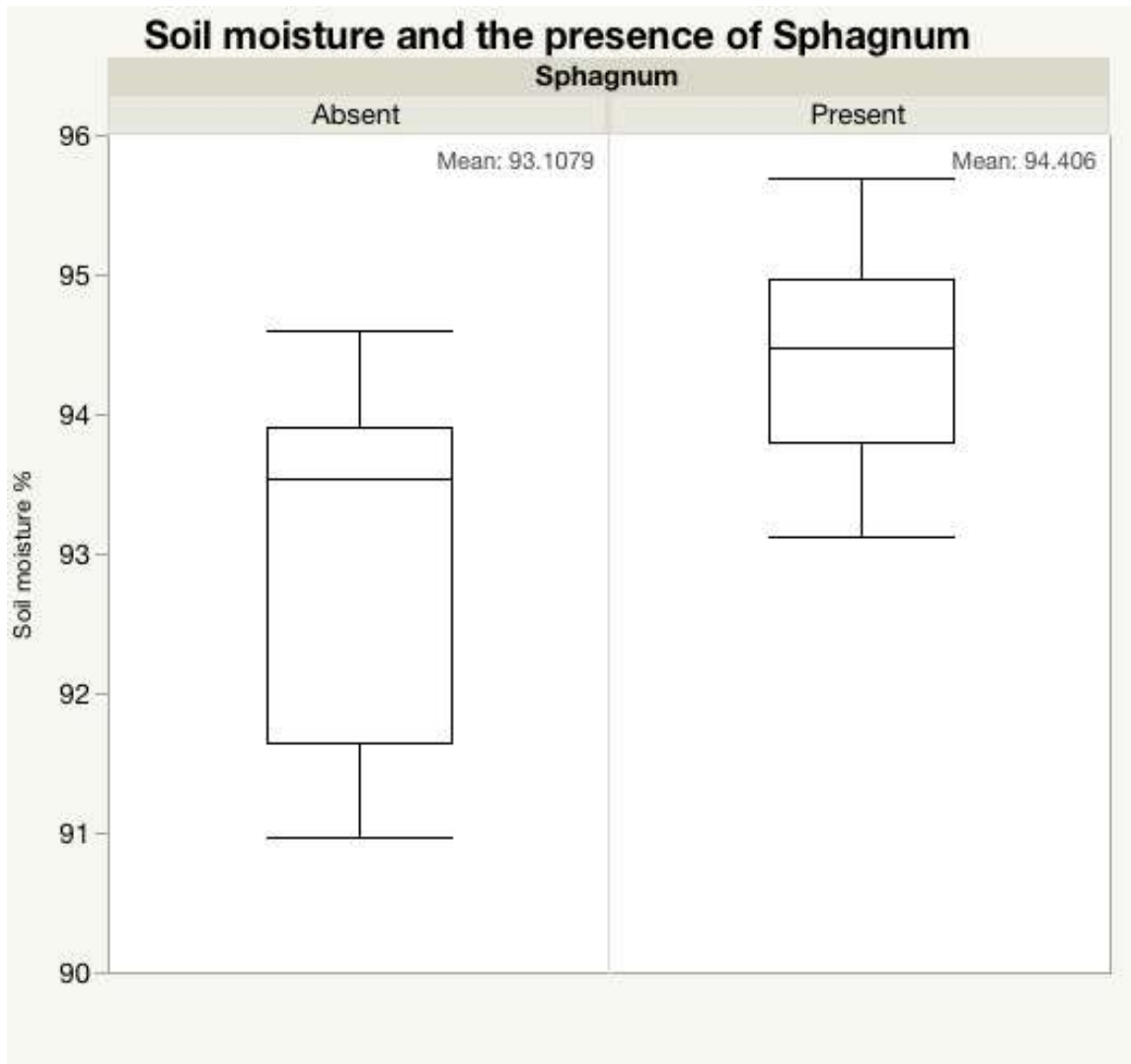
Figure 2: Soil moisture is significantly greater in the presence of Sphagnum (p < 0.01).
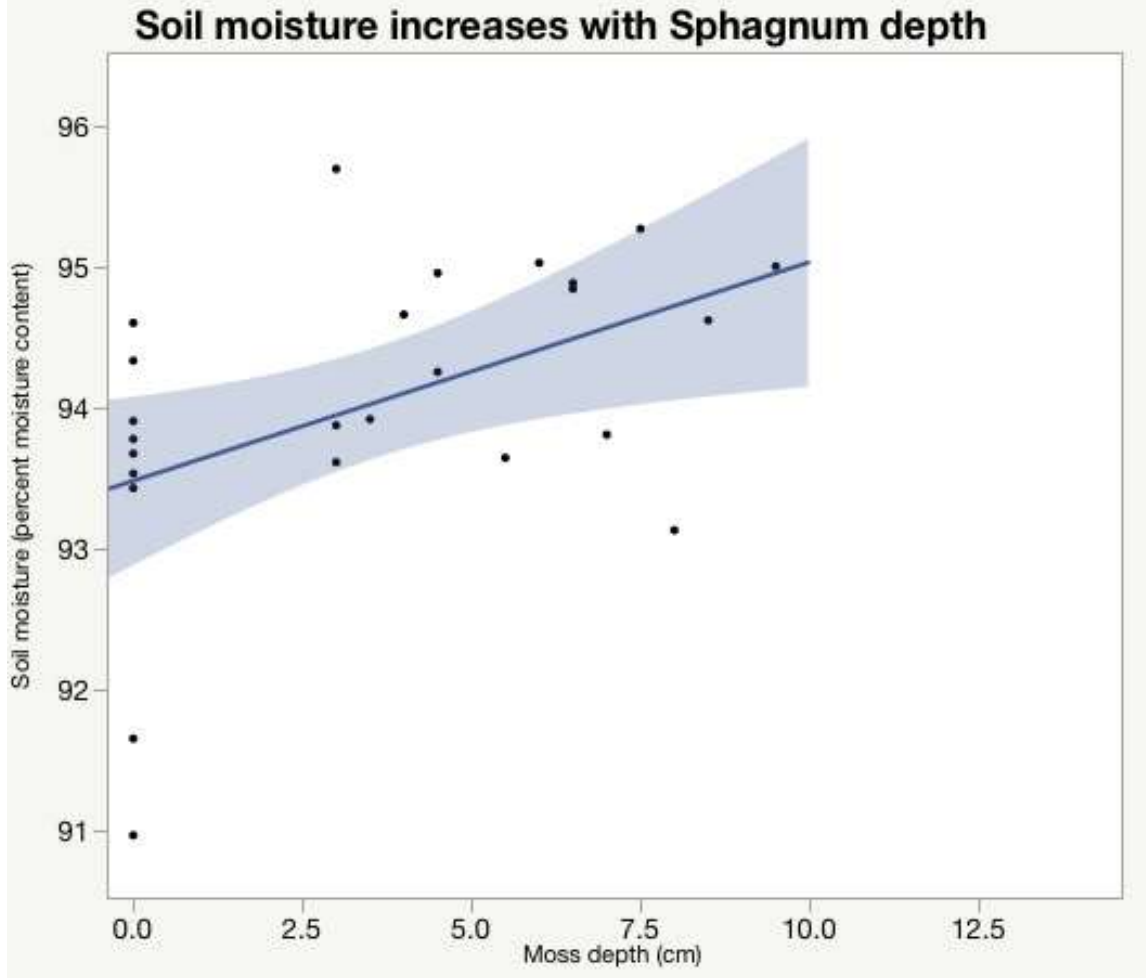
Figure 3: Soil moisture increases as Sphagnum depth increases (p < 0.05)

4.1.3. Drosera

The presence of *Drosera* was not affected by the depth of *Sphagnum* or standing water. *Drosera's* presence was affected by the presence of *Sphagnum*, with *Drosera* showing a preference for plots without *Sphagnum* (X^2 *(1, N = 25) = 5.226; p < 0.05*). Presence of *Drosera* also indicated lower soil moisture (93.46% ±1.40%) than plots without Drosera (94.37% ±0.65%) (Fig. 4; *F(1, 23) = 4.94 ;p < 0.05*)). There was no association between soil pH and the presence of *Drosera* nor was there a significant correlation between *Drosera* and dissolved O_2, although there was a modest, non-significant positive association (*t(11) = 1.67 ; p > 0.10*).
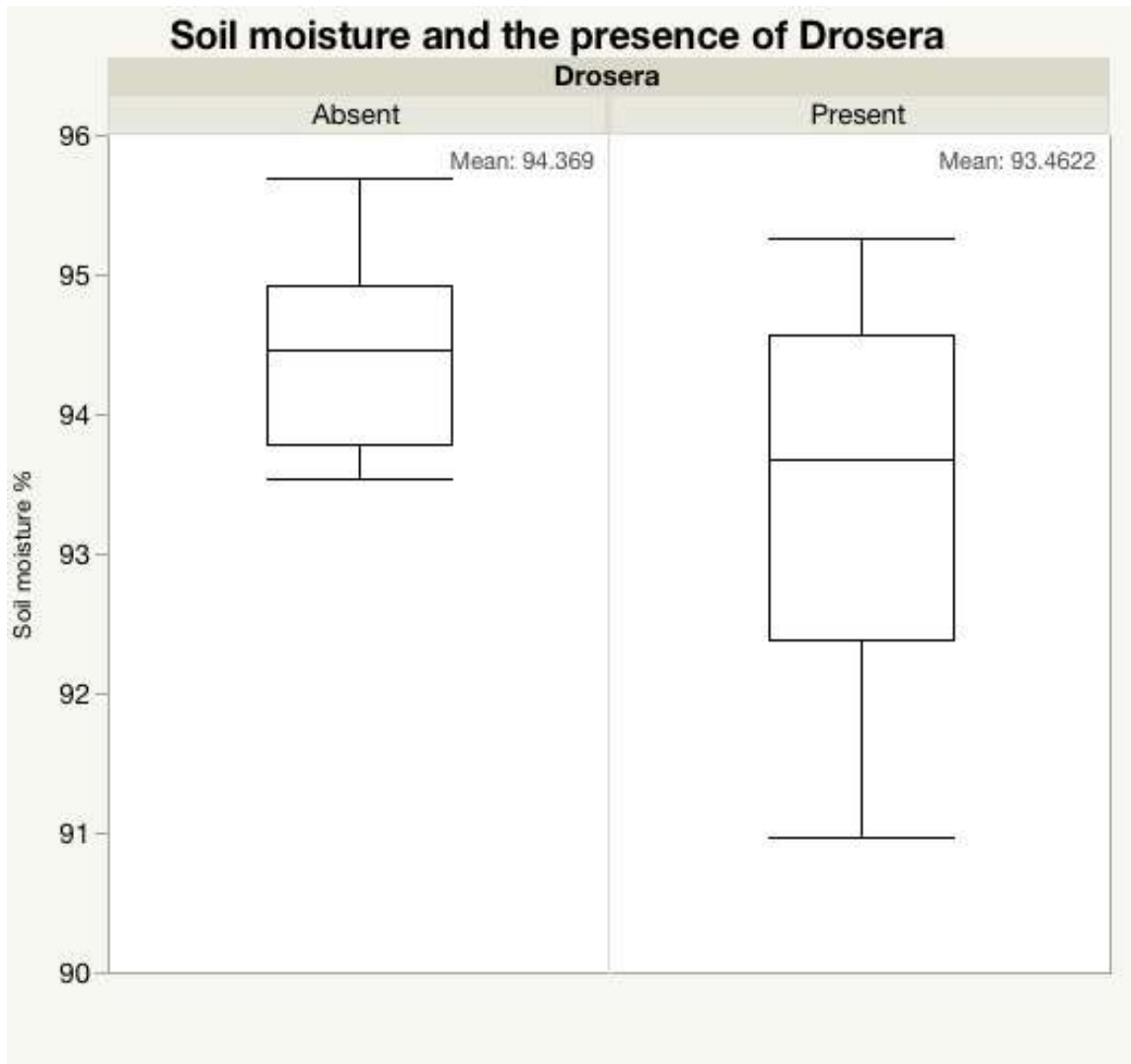
Figure 4: The presence of Drosera *is associated with lower soil moisture (p < 0.05).*

4.2 Microtopography

Most plots contained multiple microlandforms, and all plots contained at least one

of the microlandforms, except for plot #10, which was almost completely inundated and

was classed as "low" topography (table 3).

Microlandform	Hollow	Lawn	Hummock
# Plots present	11	13	14
% of plots	44%	52%	56%

Table 3: Summary microtopography data. Most plots contained more than one microlandform, while one
plot was almost completely inundated and did not contain any of the three microlandforms. Each plot was

standardized based on average landform data into one of three categories: "low," "medium," and "high." Landform data can be viewed in Appendix 2.

Sphagnum presence (Fig. 5; $p < 0.01$) and thickness (Fig. 6; $F(2, 22) = 3.62; p < 0.05$) showed a strong positive association with average microtopography height. The presence of *Drosera* showed no such association with average microtopography height ($p > 0.05$).
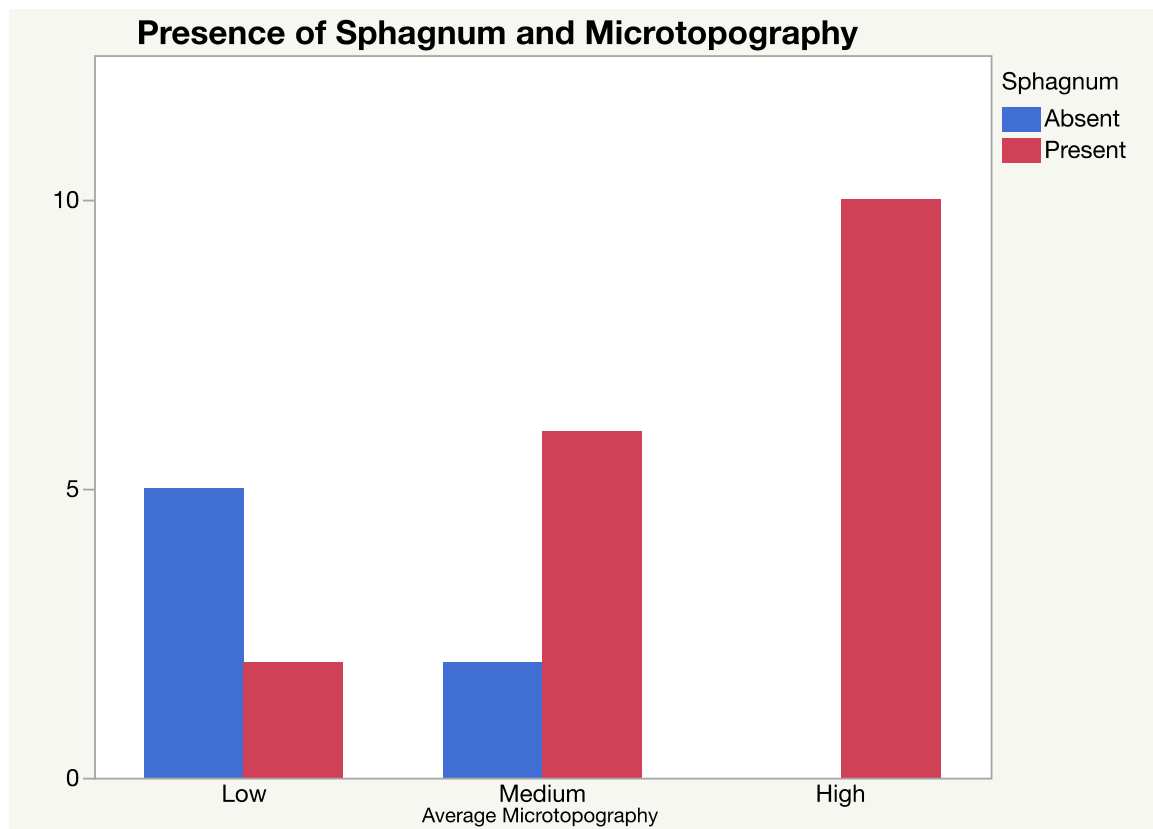
Figure 5: Sphagnum presence is strongly associated with landform height (p < 0.01). See appendix B for how average microtopography was determined.
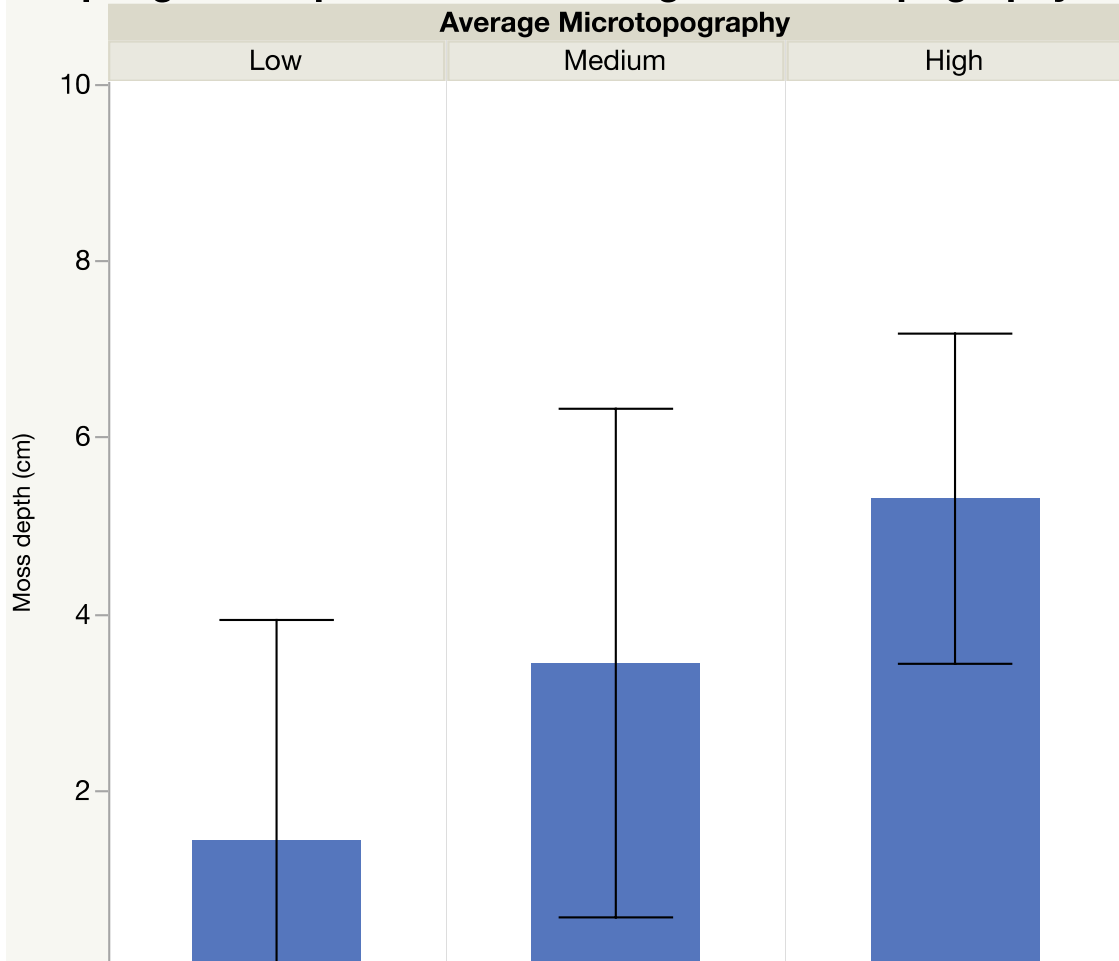
Figure 6: Sphagnum increases with landform height (p < 0.05). Graph shows 95% confidence interval for each value.

Average microtopography height was not associated with either soil pH or

dissolved O_2 in standing water.

4.3 Nitrogen

Total N content was largely dictated by organic N, which made up greater than

99% of the total N present in soils (table 4). Nitrogen results will be discussed beginning

with inorganic nitrogen content (NH_4^+ and NO_3^-) and ending with an examination of variation in organic N content.

N Type	Mean (mg/g)	Std. Deviation (mg/g)	% Total N
Total N	24.08	3.21	100.00
Organic	23.91	3.18	99.30
Inorganic ($NH_4^+ + NO_3^-$)	0.17	0.06	0.70
Ammonium	*0.127*	*0.04*	*0.53*
Nitrate	*0.043*	*0.06*	*0.17*

Table 4: Summary of N content in soil samples. Organic N makes up the vast bulk of the N present within the soil samples, with ammonium making up the majority of the inorganic N present.

4.3.1 Inorganic nitrogen

Total inorganic N ($NH_4^+ + NO_3^-$) made up less than 1% of total soil nitrogen content, with a mean of 0.17 mg/g and a range of 0.10 mg/g to 0.34 mg/g. It was not associated with soil moisture, *Sphagnum* depth, water depth, or soil pH. However, NH_4^+ concentration was negatively correlated with water depth (*R = -0.57; p < 0.01)* and NO_3^- concentration was positively correlated with water depth (*R = 0.54; p < 0.01)* (Fig. 7).
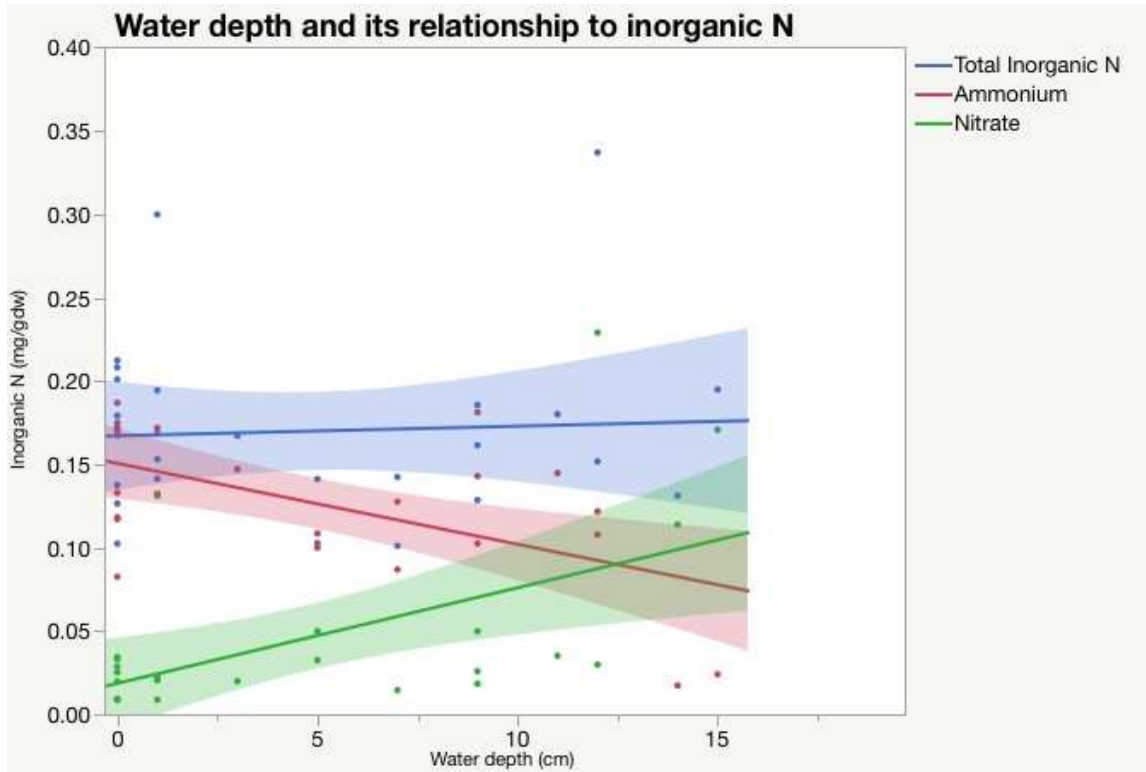
Figure 7: While total inorganic N is not significantly correlated with water depth, both NH_4^+ and NO_3^- are, but in opposite ways. NH_4^+ is negatively correlated with water depth (p < 0.01), while NO_3^- is positively correlated with water depth (p < 0.01).

Similarly, NH_4^+ and NO_3^- were both significantly correlated with soil pH, but in opposite ways. NH_4^+ appears to increase with soil pH ($R = 0.49; p < 0.05$), while NO_3^- appears to decrease as water depth increases ($R = -0.38; p = 0.0599$) (Fig. 8). Total inorganic N, however, was not significantly associated with soil pH.
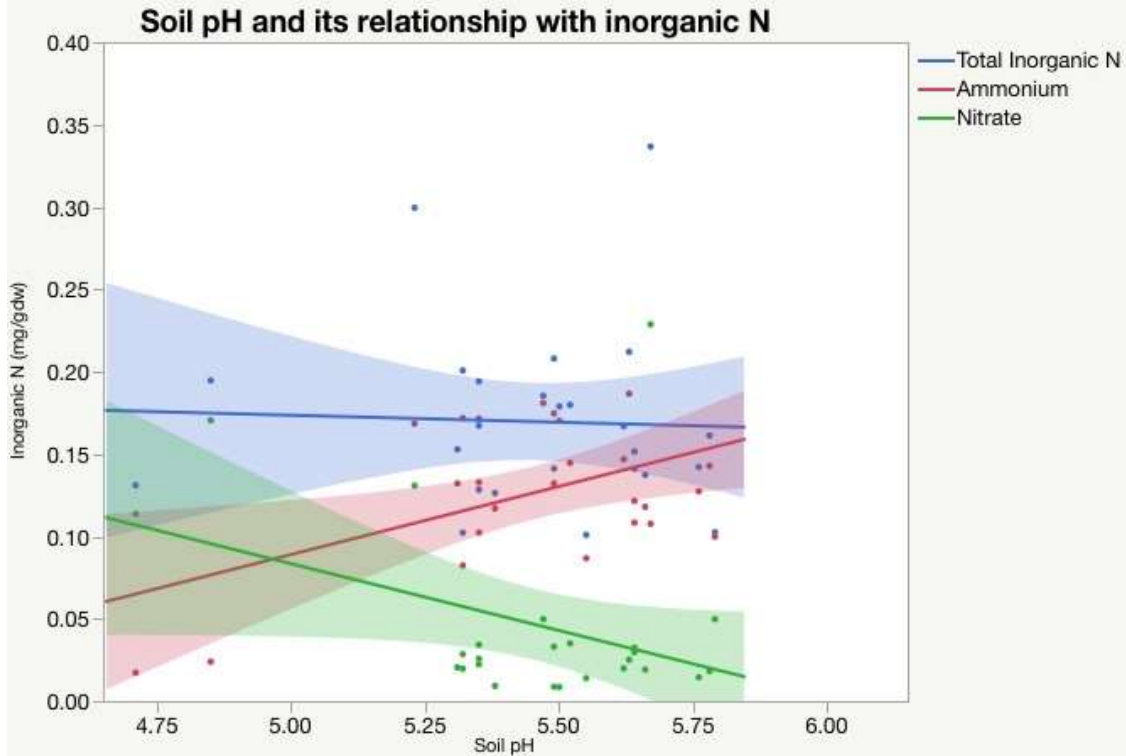
Figure 8: While total inorganic N is not significantly correlated with soil pH, NH₄⁺ is, and NO₃⁻ shows a non-significant correlation in the opposite direction. NH₄⁺ is positively correlated with soil pH (p = 0.0128), while NO₃⁻ is negatively correlated with soil pH (p = 0.0599).

Inorganic N and NO_3^- were not significantly associated with the dissolved O_2 content in plots containing standing water, but ammonium was *(R = -0.62; p < 0.05)* (Fig. 9).
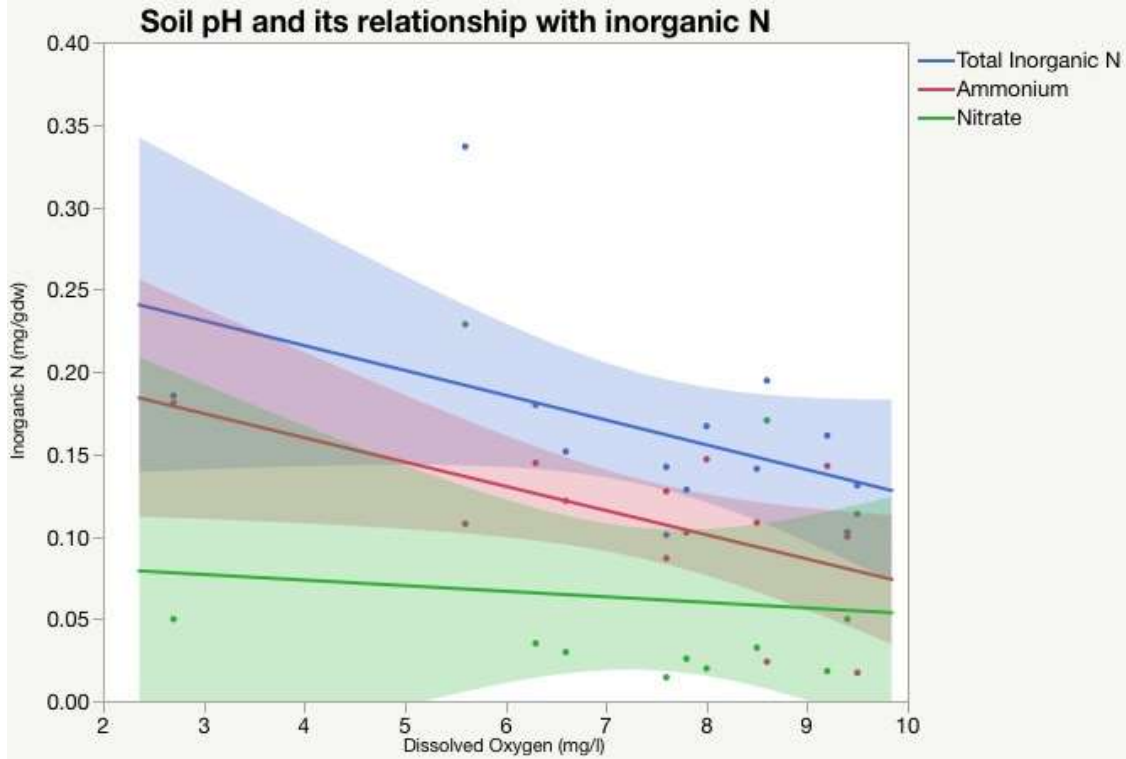
Figure 9: NO$_3^-$ is not significantly correlated with dissolved O$_2$, but NH4$^+$ is (p < 0.05), and total inorganic N shows a non-significant correlation (p = 0.1031).

The presence of *Drosera* was negatively associated with inorganic N concentrations (0.14 mg/g dry weight ± .02 mg/g in the presence of *Drosera* and 0.18 mg/g ±0.01 mg/g in its absence; (*t(23) = 2.52; p < 0.05*) (Fig. 10).
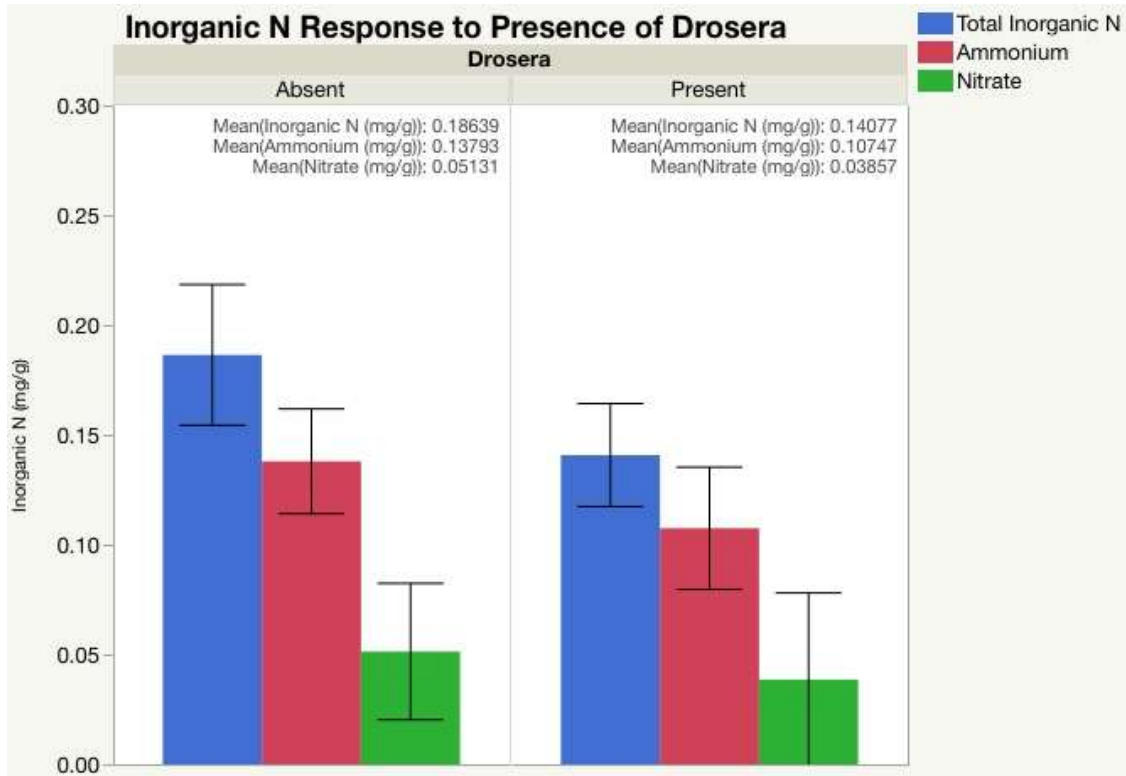
Figure 10: The presence of Drosera *indicates lower inorganic N values than in plots where it was absent ($p < 0.05$). NO_3^- and NH_4^+ alone were not significantly different between plots. Graph shows 95% confidence intervals for each value.*

Microtopography also did not show any association with total inorganic N levels, although "low" topography was associated with significantly higher concentrations of NO_3^- ($F(2, 22) = 3.69; p < 0.05$), and "high" topography was non-significantly associated with higher concentrations of NH_4^+ ($F(2, 22) = 2.71; p = 0.0884$) (Fig. 11).
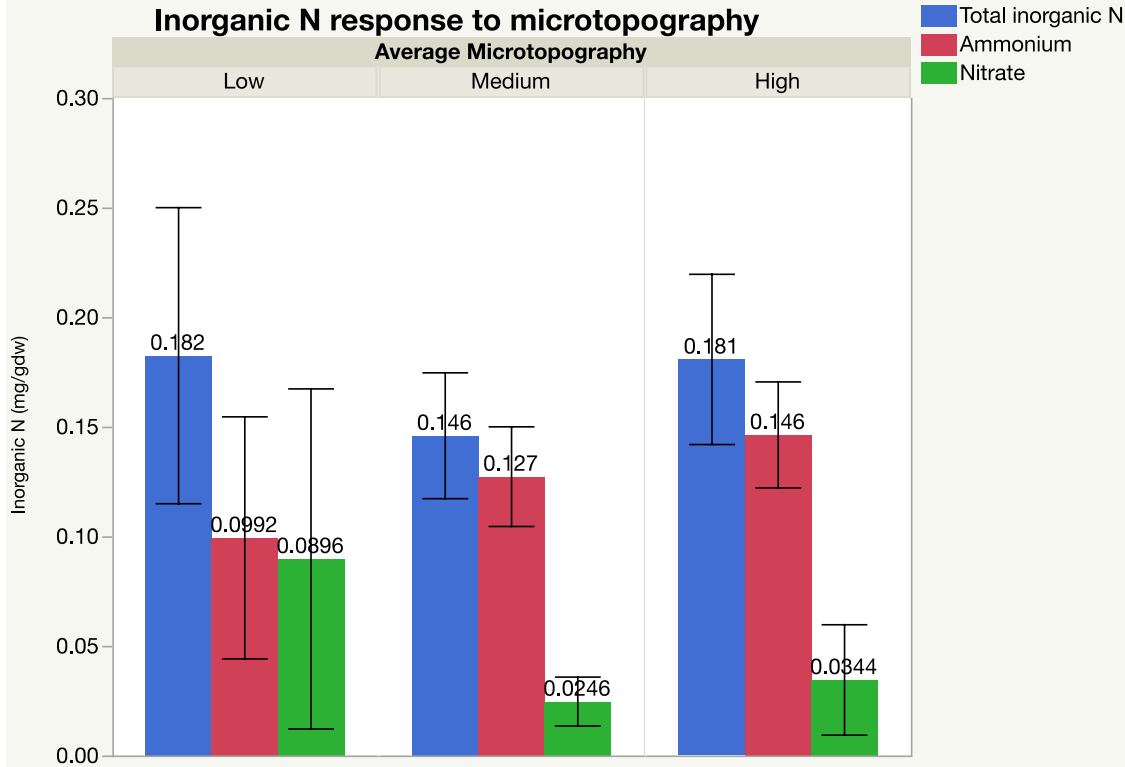
Figure 11: Total inorganic N concentrations are not affected by microtopography, but NH_4^+ concentrations were higher in "low" topography areas than in the others, although this relationship was not significacant (p = 0.0884). NO_3^- concentrations were significantly higher in "high" topography than they was in "low" topography (p < 0.05). Graph shows 95% confidence interval for each value.

Inorganic N concentrations were also higher in the presence of *Sphagnum* (0.19 mg/g dry weight ±0.02 mg/g) (*t(23) = 1.29; p = 0.2091*) than in its absence (0.14 mg/g dry weight ±0.01 mg/g) (*t(23) = 1.29; p = 0.2091*), but there was no relationship between *Sphagnum* depth and inorganic N. Further analysis showed that NH_4^+ was significantly associated with the presence of *Sphagnum* but not its depth (*t(23) = 2.23; p < 0.05*). Results are summarized in Fig. 12.
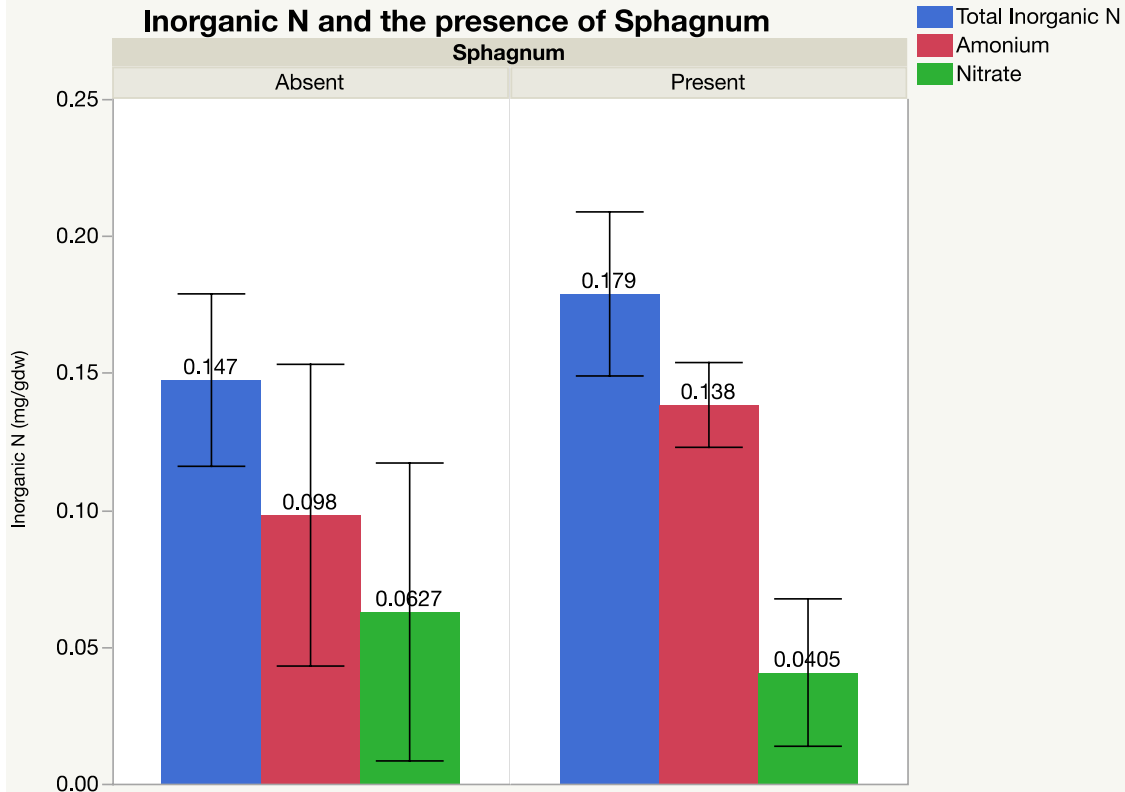
Figure 12: Inorganic N concentrations are higher where Sphagnum is present*, although not significantly so (p = 0.2091). NO3- was not significantly correlated with the presence or absence of* Sphagnum*, while NH4+ concentrations were significantly higher where* Sphagnum *was present (p < 0.05). Graph shows 95% confidence intervals for each value.*

4.3.2. Organic nitrogen

Mean organic N concentration was 2.39% of dry soil weight, with a range of 1.81% to 3.14%. Organic N was not found to be significantly associated with any chemical variables except organic C (*R = 0.79; p < 0.001*) and inorganic N (*R = 0.51; p < 0.01*), where it was positively correlated with both (Fig. 13).
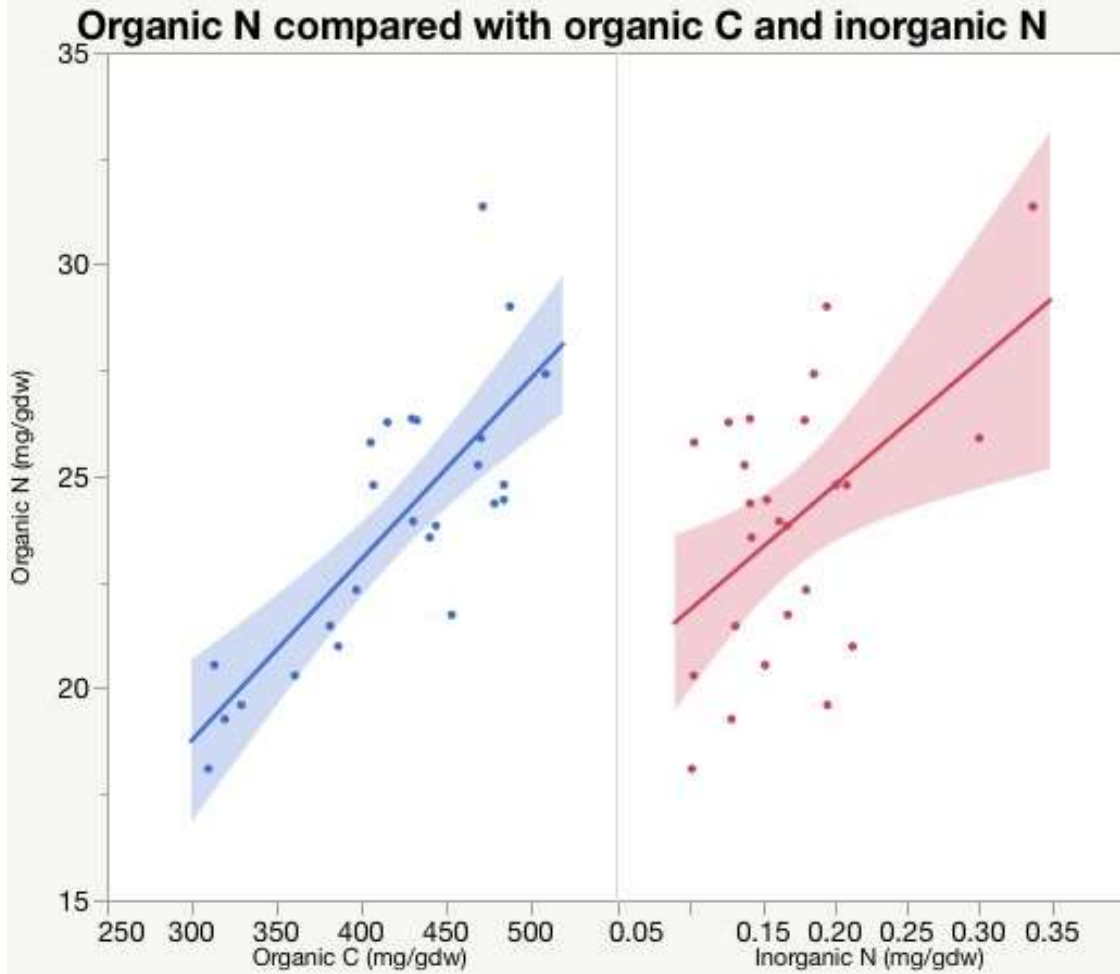
Figure 13: Organic C and N are positively correlated (p < 0.001), as are organic N and inorganic N (p < 0.01).

Though there was a modest negative association between the presence of *Drosera* and organic N levels, it was not significant ($t(23) = 1.71; p = 0.1007$).

Microtopography was not associated with organic N concentrations.

4.4 Organic Carbon Concentrations

The concentration of organic carbon averaged 420 mg/g $\pm$ 59 mg/g of dry weight, with a range of 310 mg/g to 509 mg/g. Concentrations were not significantly affected by soil pH or dissolved O_2, although a positive non-significant relationship was found

between organic C concentrations and dissolved O_2 concentrations ($R = -0.59; p = 0.1607$), as well as between organic C and soil moisture % ($R = 0.38; p = 0.0589$). Water depth was negatively correlated with organic C concentrations ($R = -0.44; p < 0.05$) (Fig. 14).
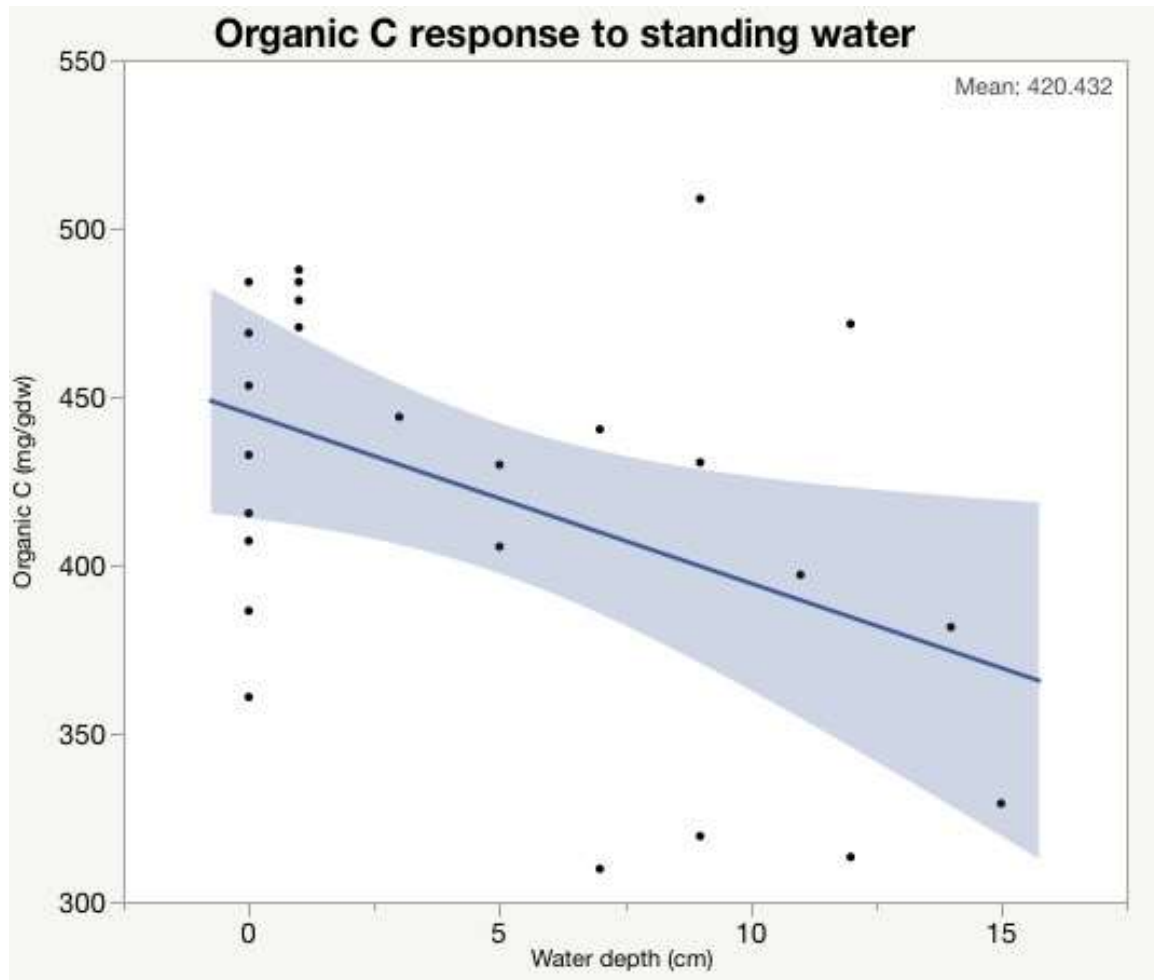
Figure 14: Organic C concentrations and water depth show a significant negative correlation (p < 0.05). "Depth" refers to the maximum depth of standing water measured within the sample plot.

The presence of *Sphagnum* as well as its depth were not significantly associated with organic C concentrations. However, when samples 1-5 were excluded from the dataset, a non-significant association between *Sphagnum*'s presence and carbon

concentration appears (*t(18) = 1.89; p = 0.0751*) (Fig. 15). These samples were excluded due to the additional incubation they underwent prior to analysis (see section 3.1.3).
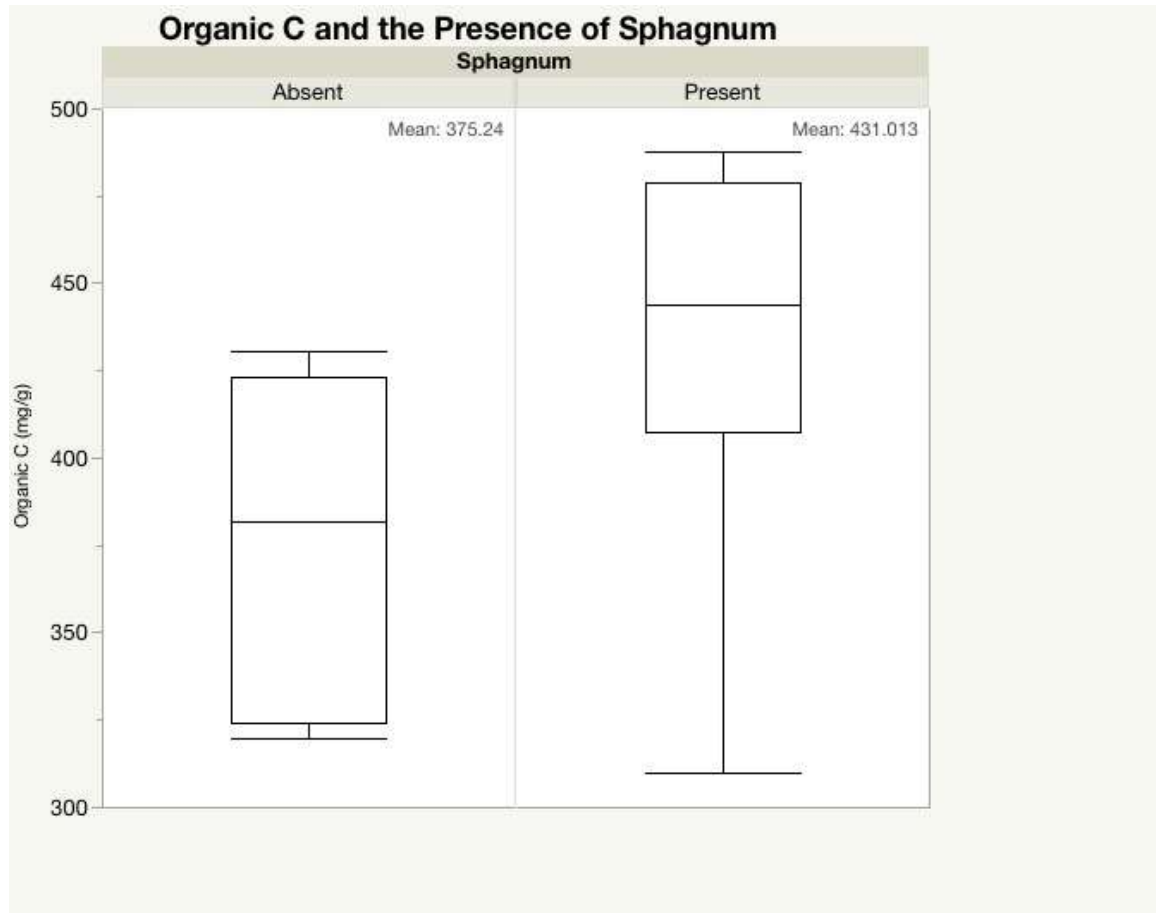
Figure 15: Soil C concentrations are non-signficiantly associated with the presence of Sphagnum when the first five samples are excluded from the dataset (p = 0.0751).

The presence of *Drosera* showed a modest negative association with organic C concentrations, but this was not significant (*t(23) = 1.46; p = 0.1572*).

Microtopography height was not significantly associated with organic C concentrations.

4.5 C:N Ratio

The mean C:N ratio was 17:1, with a range of 21:1 to 15:1. Soil moisture was positively correlated with the C:N ratios of the soil samples (*R = 0.48; p < 0.05*), while water depth (*R = 0.38; p = 0.0609*) and *Sphagnum* depth (*R = 0.34; p = 0.1012*) were negatively correlated with them, but only soil moisture significantly so (Fig. 16). There was no relationship between the presence of *Drosera* and C:N ratios.
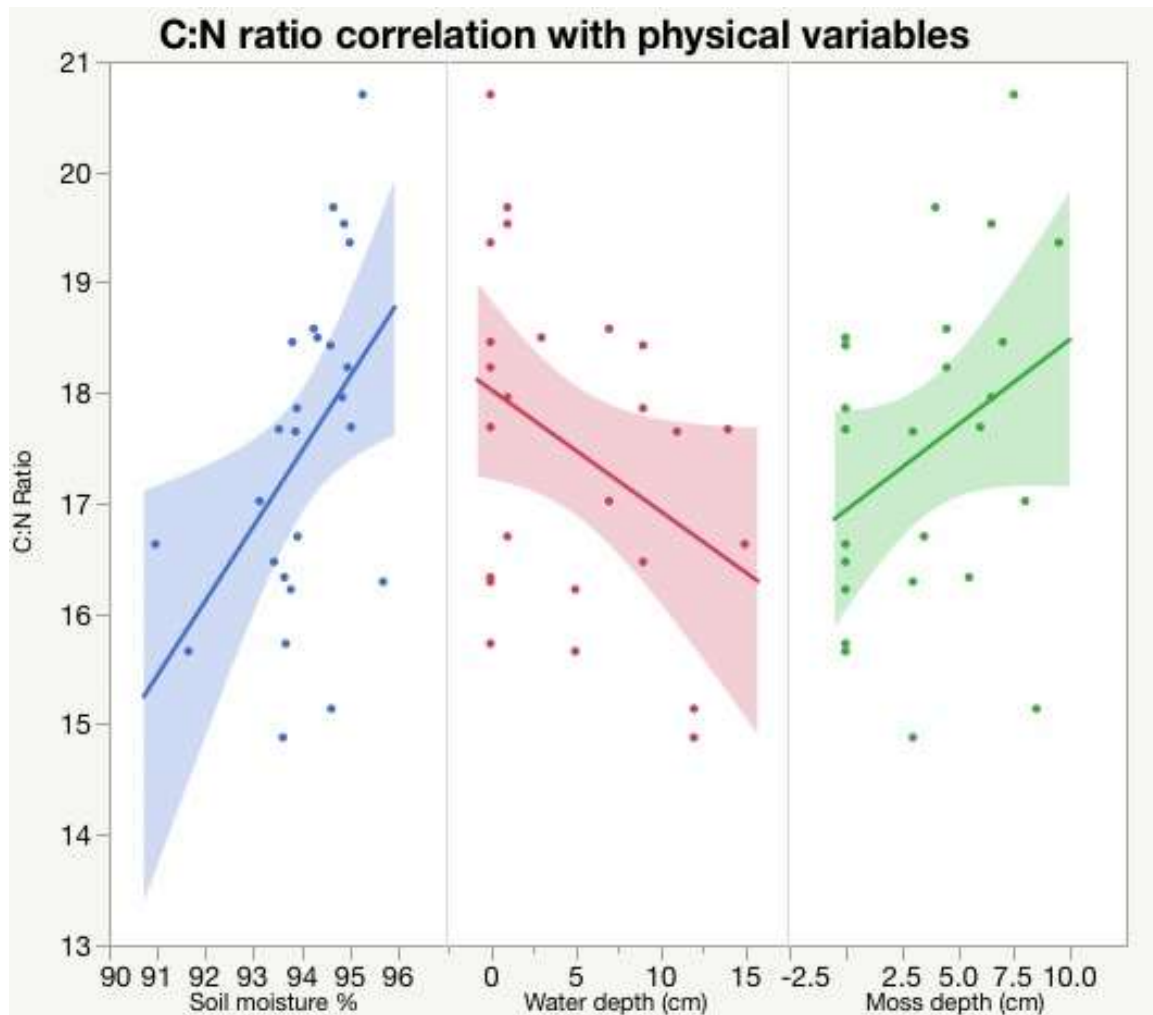
Figure 16: C:N ratios are positively correlated with soil moisture (p < 0.05) and moss depth (p = 0.1012), while they are negatively correlated with water depth (p = 0.0609). Only soil moisture shows a significant correlation.

5. Discussion

Overall, many of the relationships between internal variables found within the study site are consistent with relationships found within bogs in other regions of the world, while a few inconsistencies may be explained by unique soil chemistry or vegetative characteristics. However, the site was less acidic than is typical in bogs with most plots registering a pH above 5, where most bogs fall within a pH range of 3-5 (Vitt 2013). In addition, organic nitrogen content is abnormally high, causing the C:N ratios to be unusually low, which is possibly due to unique vegetative and/or soil characteristics of the region, as discussed further below. In aggregate these results may indicate that this site is atypical or that the soil chemistry within the region is atypical compared to sites in regions that have undergone more study.

5.1 Carbon

The average carbon concentration of the site (420 ± 59 mg C/gdw) fell within both the worldwide average for peatlands (492 ± 24 mg C/gdw)[3] and the averages of nearby regions (Loisel et al. 2014). This suggests that the study site's ability to accumulate organic carbon within the acrotelm is similar to that of peatlands in other regions, although these results do not reflect the long-term storage potential of this carbon, as only the top half of the acrotelm was sampled, and the vast bulk of decomposition ($>99\%$) occurs within this layer (Blodau et al. 2007).

Carbon concentrations decreased as dissolved O_2 concentrations increased, but this was statistically insignificant ($p > 0.15$). Significance may be achieved with a higher

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[3] Note that this value excludes tropical peatlands, which undergo very different carbon cycling regimes than do northern peatlands and are also much less efficient carbon sinks (Holden 2005)

sample size, as a lack of dissolved O_2 indicates anoxic soil conditions, which should result in less respiration and more carbon retention, although it is important to note that dissolved O_2 in soils was not actually looked at, so the dissolved O_2 values observed for standing water may be completely unrelated to O_2 concentrations within the soil column (Vitt 2013). Additionally, one of the sampling events occurred during a rain event, and one occurred just after a rain event. The physical agitation that precipitation causes and the higher dissolved O_2 content of rainwater may have temporarily elevated dissolved O_2 and water levels in plots sampled at these times, potentially reducing the ability to detect this expected relationship. Wind speeds ranged from 12 mph to 23 mph during the sampling period as well, which may have resulted in significant mixing and aeration of the waters on site.

Additionally, while not statistically significant, there was a positive correlation between percent soil moisture and organic carbon concentrations. The actual variation in carbon concentrations is probably due to the presence of *Sphagnum,* which is also associated with higher soil moisture (see Fig. 15). When the presence of *Sphagnum* was controlled for between soil moisture and organic C concentrations, a partial correlation of r = 0.6074 (*p = 0.1480*) was found between the two variables in plots where *Sphagnum* was absent, and both the strength and certainty of this correlation drops dramatically in plots where *Sphagnum* was present (r = 0.1027; *p = 0.6850*). This likely indicates that *Sphagnum* largely controls organic C concentrations, as *Sphagnum*'s positive association with soil carbon levels is well-documented (see section 2.3.1). This is in agreement with the literature, which shows *Sphagnum* reduces the decomposition of existing carbon within the soil column, represents a less labile source of carbon than other plants, and

promotes the acidic conditions required for the formation of peat (van Breeman 1995, Adkinson and Humphreys 2011, Leifeld 2011).

Interestingly, no relationship was found between microtopography and carbon concentrations. This is in contrast to the findings by Laine et al. (2006), who found that higher microtopography represented a larger net carbon sink than lower microtopography due to increased levels of photosynthesis, leading to increased carbon sequestration. This discrepancy may be attributed to differences in site-specific variables between this study site and Laine et al.'s or an inability to detect differences between microtopographic features in this study due to a small sample size.

Likewise, a negative trend between water depth and carbon content was detected. This was not expected, as standing water reduces the rate of respiration and CO_2 efflux, resulting in larger amounts of carbon retention within soils (Charman 2015, Blodau et al. 2007, Laine 2006). As previously mentioned, much of the sampling was done during and after rain events, so it is possible that water depth was temporarily increased throughout the bog or that standing water existed where it doesn't normally, potentially skewing the results. Sampling was also more difficult in inundated areas, leaving more room for researcher error. Additionally, many of the inundated areas had little or no vegetative cover, which, particularly in the case of *Sphagnum*, could lead to higher rates of peat decomposition (Ise et al. 2008). The vegetation that did exist in these areas were typically graminoids and vascular plants, which represent a much more labile source of carbon than does *Sphagnum* (Dorrepaal et al. 2005).

Carbon concentrations within the surface soils were positively correlated with both inorganic and organic N content (see Fig. 13). As reported in Basiliko et al. (2006)

and Wang et al. (2014), increases in available inorganic N tends to lead to increases in the organic C content of soils. However, Basiliko et al. attributes this increase to the soil's microbial community becoming larger but also more efficient at respiration, leading to an increase in total soil organic C, which is beyond the scope of this study. Wang et al., by contrast, looked at historical records within a bog and found that the increases in N likely led to more vegetative growth, resulting in larger C additions to the underlying peat structure.

5.2 Nitrogen

Total N content in all soil samples were high, exceeding 2% in most cases. This may indicate that a larger proportion of the peat is made up of graminoid and vascular plant matter rather than *Sphagnum,* as *Sphagnum* peat tends to contain less than 1% total N, while graminoid peat can contain up to 3% total N (Crum and Planisk 1992). This agrees with Lacourse and Davies (2015), who also found elevated N concentrations in comparison to previously studied sites, although the N values found here are even higher. This conclusion is supported by the graminoid dominance of the site, although interestingly, there was no significant difference in total N between plots where *Sphagnum* was present than in those where it was absent.

The presence of *Drosera* also showed a modest, non-significant negative correlation to organic N concentrations. This result was expected, as *Drosera* utilizes the N trapped within an insect's tissues, but it is also capable of extracting N from soils with its roots (Millett et al. 2003). Likewise, inorganic N concentrations were significantly lower in plots containing *Drosera* than in those without, suggesting that *Drosera* are

utilizing soil nutrients. However, because associations between graminoids and other vascular plants with inorganic N could not be determined, this difference may be associated with the absence of *Sphagnum* rather than the presence of other functional groups, or with the relative abundance of the functional groups, which was not studied.

5.2.1 Inorganic N

Total inorganic N did not show a significant relationship with water depth. However, when NH_4^+ and NO_3^- were looked at individually, both displayed a significant relationship with water depth, but in opposite ways (see Fig. 7). Interestingly, NH_4^+ decreased as water depth increased, while NO_3^- increased along with water depth, which is the opposite of what one would expect, as NO_3^- requires the presence of oxygen to form, the availability of which tends to be lower in inundated areas compared to those exposed to the atmosphere. This may be a result of differences in preferential uptake of NH_4^+ and NO_3^- between species, which unfortunately has not been thoroughly studied, so it is unknown whether this is the case for the species found at the study site, although Wang and Macko (2011) found that plants in wetter environments preferred NH_4^+ over NO_3^-, which is consistent with the relationship between water depth and inorganic N. NH_4^+ concentrations were significantly higher in plots containing *Sphagnum*, while NO_3^- concentrations in plots containing *Drosera* were non-significantly higher, suggesting that *Drosera* and *Sphagnum* have different N uptake preferences (see figs. 10 and 12, respectively). However, this experiment was performed hydroponically with European deciduous forest species, so it is unknown if its findings apply to Pacific Northwest

wetland species. Additionally, once again, it is important to note that the influence of other functional groups could not be established.

Similarly, total N was unrelated to soil pH, but NH_4^+ concentrations were positively correlated with higher soil pH, and NO_3^- concentrations showed a non-significant negative correlation with soil pH (see Fig. 8). Olsson and Falkengren-Grerup (2000) found that acid-tolerant plants preferentially uptake NH_4^+ and that less acid-tolerant plants preferentially uptake NO_3^-, which may possibly explain why NH_4^+ concentrations increase with pH and NO_3^- concentrations decrease. Alternatively, N mineralization has been shown to favor NH_4^+ when pH is lower and NO_3^- when pH is higher, so this relationship may largely be a result of microbial activity (Cornfield 1952).

5.3 C:N Ratios

The C:N ratios of surface soils within the site were surprisingly low. Wang et al. (2014) reported an average C:N ratio of 42:1 for peat in the acrotelm layer of their study site, while Kuhry and Vitt (1996) reported C:N ratios of up to 300:1 within the acrotelm. Lacourse and Davies (2015) reported C:N ratios as low as 20:1 in a bog in British Columbia. This latter result is closest to those found in this study, but still higher, and also falls within the low end of Loisel et al.'s (2014) meta-analysis of peatlands worldwide. Even more surprisingly, the C:N ratios gathered by this study were even lower than the most decomposed layers of peat in all of the aforementioned studies! These results are not driven by low levels of organic C, however, as the site had relatively normal concentrations of C, as discussed in section 5.1. Instead, it is being driven by high N concentrations. A low C:N ratio can indicate excessive decomposition within a bog,

but in order to determine if this is the case here, soil cores looking at both the acrotelm and catotelm would need to be taken (Clymo 1996).

Alternatively, because the bog is situated near a number of privately-owned cranberry bogs, fertilizer runoff may have contaminated the site, contributing to decomposition and/or artificially elevating N concentrations. This explanation is also troubling, as *Sphagnum* loses its competitive advantage and produces fewer decomposition-inhibiting polyphenols in the presence of elevated N concentrations, potentially increasing CO_2 efflux (Bragazza and Freeman 2007). However, this wouldn't increase organic N concentrations, which drove the high total N concentrations within the site, making this explanation unlikely. Future studies should look at C:N ratios at various depths within the peat column to determine whether the surface soils have abnormally low C:N ratios compared to deeper soils and to determine if N signatures match those of adjacent privately-owned wetlands, and whether or not these landowners apply fertilizers with high levels of organic nitrogen (such as manure).

Wang et al. (2014) did, however, differentiate between soil microbes and the peat itself, as the microbial community's C:N composition was 10:1, significantly lower than the peat itself. Because this study did not take into account soil microbe abundance, C:N ratios may have been affected by higher than normal microbial growth, either due to environmental factors or due to the period of unexpected thawing the samples were exposed to prior to analysis. All of the samples were thawed and exposed to room temperature conditions for up to five days due to a freezer power failure, so it is possible that a significant level of decomposition and/or increase in soil microbes may have occurred during this time. However, samples 1-5 were accidentally incubated for several

days prior to being frozen, and there was no statistical difference in C:N ratios between these samples and the 20 that were not incubated.

Additionally, Loisel et al.'s 2014 meta-analysis, while not including this region, reported average C:N values of 62:1 (±38) and 44:1 (±33) in Western Canada and Alaska, respectively. All values were highly variable, but the results presented in this study fall outside the range of the former and within the latter, suggesting that bogs in coastal Washington may have more in common with Alaskan bogs than Western Canadian bogs. It is worth noting that the study site's total N content were well above the ranges reported for both regions. However, these results may also simply be a result of PNW soil variability as a whole. Carpenter et al. (2014) reports mean C:N ratios of 20:1 to 22:1 in temperate rainforest systems within Gray's Harbor County, WA, the same area as this study's research site. As this study site was surrounded by temperate rainforest typical for the area (Douglas-Fir and Western Hemlock dominant), the nitrogen values for the soils may, in fact, be driven by processes outside of the bog itself.

5.4 Vegetation

Carbon concentrations were not associated with the presence or depth of *Sphagnum* cover, which was not expected (see Fig. 15). However, samples 1-5 had been accidentally incubated for several days, which may have artificially lowered their carbon concentrations. When excluded, *Sphagnum* presence was positively associated with carbon concentrations, albeit non-significantly. This is interesting, because *Sphagnum* is the most important biotic component that influences carbon retention in bogs, but in this study, it is not as strongly associated with carbon concentrations as one would expect

(Nichols et al. 2014). This may be due to small sample size, or it may indicate that other plants (such as the graminoids) are the overarching control of carbon concentrations at this site.

The presence of *Drosera* was not significantly associated with soil carbon concentrations, and in fact showed a modest non-significant negative association. This was unexpected as *Drosera* doesn't utilize the carbon contained within the insects it captures, as its digestive enzymes function solely to release the nutrients (largely N and P, but also Ca, K, and other micronutrients) contained within the insect's tissues (Ellison and Gotelli 2001, Matušíková et al. 2005). Therefore, the carbon within the insects should end up in the bog where normal bog processes would reduce the lability of that carbon. This hypothesis was not borne out by the data, but there several possibilities as to why this would be the case. First, *Drosera* was simply counted as "present" or "absent" in each plot, regardless of the actual number of plants present, so a larger number of *Drosera* may be required to detect a signal in the data. Second, *Drosera* were observed during the winter when their leaves form a small, furled hibernaculum that is very difficult to detect amongst the other foliage present, so it may be that *Drosera* were missed in several plots. Third, *Drosera* has been shown to rely less upon carnivory to attain nutrients when soil nutrients are high, and as discussed in section 5.2, N content in soils at this site was high (Millett et al. 2015). Fourth, because *Drosera* are vascular plants, it may be that the increased lability of their tissues overpowers the signal from the carbon they collect. Fifth, microbial communities, other macroinvertebrates, or small animals may consume the partially digested insect before it can be affected by the biogeochemical processes within the bog that act to preserve carbon. And sixth, it is

possible that carbon derived from insects may represent an insignificant flux relative to other carbon fluxes within the bog. Microbial community size and composition should be evaluated in future research, as was the original intent in this study. Additionally, soils should be tested for the presence and concentration of chitinase, as an absence of this substance may suggest that *Drosera* is not, in fact, capturing insects (Matušíková et al. 2005).

7. Conclusion

In this study several variables were analyzed that contribute to carbon cycling in bogs. Several of these variables were related to soil carbon concentrations in expected ways, but some were not. Particularly, the C:N ratios of the soil samples were exceptionally low when compared to the values cited in existing literature, and this is potentially troubling in that it may indicate a higher rate of decomposition than is normal for bogs in other regions, and thus it may be a weaker carbon sink or even a net carbon source. However, because organic carbon concentrations are *not* abnormally low, it is more likely that the soil chemistry at this site is simply significantly different from that of sites in other regions, or that the peat at this site is largely made up of plant matter from sedges and other vascular plants that tend to have lower C:N ratios than *Sphagnum* does.

Another surprising result was the negative correlation between soil carbon and water depth, as the literature indicates that these should be positively, although only surface soils were sampled, so this correlation may not hold up as peat depth increases. Likewise, dissolved O_2 was not significantly associated with soil carbon or inorganic nitrogen content, when, again, it should have shown a positive and negative correlation, respectively, based upon the literature. However, confounding factors may have affected the data, casting doubt on the veracity of these results. Should this study be replicated, care should be taken to sample during a year with a normal amount of precipitation and during a time when the weather is unlikely to change.

Still, the results show that the study site is unique and differs substantially from other sites that have been studied, even within the Pacific Northwest. While they can't be

generalized to other bogs, or even the entire bog that the study site was part of, they provide direction for future studies of this sort, and may provide hints at the kinds of variables that uniquely affect bogs in our region.

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Appendices

Appendix A. Site vegetation Data

Each "hit" represents a point where the vegetation was present. Each sample unit had a total of 20 possible points over a 10 m length along the transect, and multiple vegetative types could be "hit" at each point.

SU	*# hits Sphagnum*	# hits Vascular	# hits Graminoid	# hits Bare ground
1	10	5	13	2
2	11	10	11	2
3	11	8	13	2
4	13	6	13	1
5	3	11	12	4
6	7	15	16	1
7	7	14	20	0
8	1	13	18	2
9	6	10	17	2
10	2	11	15	2
11	5	12	13	5
12	5	3	17	2
13	5	2	16	4
14	13	6	11	2
15	6	8	15	2
16	8	9	14	3
17	11	8	14	0
18	13	4	17	0
19	8	3	15	4
20	1	2	6	14
21	3	2	10	10
22	2	11	19	0
23	7	10	19	1
24	8	9	12	1
25	11	9	12	3
Total # hits	177	201	358	69

Appendix B. Microlandform data

Sample plots were characterized as average "high," "medium," or "low" topography to account for the presence of multiple microlandforms within each plot.

SU	Hummock (high)	Lawn (medium)	Hollow (low)	Average topography	Notes
1	x			High	
2			x	Low	
3		x	x	Low	
4		x		Medium	
5		x		Medium	
6	x		x	Medium	
7	x		x	Medium	
8		x	x	Low	
9		x	x	Low	
10				Low	No landforms present, plot almost completely inundated
11		x	x	Low	
12	x			High	
13		x		Medium	
14	x			High	
15	x	x		High	
16	x	x		High	
17	x			High	
18	x	x		High	
19	x		x	Medium	
20	x		x	High	Hollow less than 5% of total area; hummock dominates
21	x	x		High	
22	x		x	Medium	
23		x	x	High	
24	x			Low	
25		x		Medium	