Deeper Burning Increases Available Phosphorus, Promotes Moss Growth, and Carbon Dioxide Uptake in a Fen Peatland One-Year Post-Wildfire in Fort McMurray, AB

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Carbon storage in northern peatlands is estimated to be ~795 Tg, equivalent to ~40% of atmospheric CO_2. Peatlands are dominant features of the Western Boreal Plains (WBP), which are experiencing a regime shift to a warmer and drier climate, as well as an increase in forest fire disturbance. Burning of the upper layers of rich organic matter peat releases enormous quantities of C to the atmosphere. The projected response of peatlands to forest fire is concerning, but widely understudied and could be of the utmost importance for the biogeochemical function and future net C balance of peatland. Impacts of climate change driven drying on peatland nutrient dynamics have been explored previously, however, the impacts of wildfire on nutrient dynamics have not been examined. This study assessed the impact of wildfire on N and P bioavailability and nutrient mineralization, plant nutrients balance, and the C and macronutrient stoichiometry and stock in a fen one-year post-wildfire by comparing a Burned and Unburned area. The results show that bioavailable P increased up to 200 times in surface water leachate, 125 times in groundwater and 5 times in peat. Surface ash leachate had increased concentrations in ammonium (NH_4^+) and nitrate (NO_3^-), and through groundwater mobility, the entire fen experienced increased bioavailable N. Mineralization of N and P were minimal at the Burned sites, relative to Unburned sites. Fire affected plant nutrient limitation patterns, switching from dominantly N-limited to NP co-limited in moss and P-limitation in vascular species. Burned site C stock (~14000 kg/ha) was higher relative to the Unburned site, which also increased CN and CP ratios. These findings suggest that long-term effects of elevated C, N, and P concentrations on plant productivity and decomposition must be re-evaluated for fire disturbance to understand the resiliency of peatland biogeochemistry post-wildfire.

Environmental controls, including hydrologic, biologic, and edaphic variables modified by the fire and their effect on CO_2 fluxes have not been studied holistically. In this thesis, I studied a treed fen burned during the Horse River wildfire in Fort McMurray, AB, comparing CO_2 fluxes between a Burned and Unburned area of the fen. We see that both gross ecosystem productivity (GEP) and total respiration (R_{tot}) were reduced in magnitude at the Burned sites in comparison to the Unburned site, with peak fluxes in the Unburned site occurring in late June, whereas the Burned site CO_2 fluxes peaked later in the growing season. GEP and net ecosystem exchange (NEE) increased in carbon uptake in the Burned sites along a depth of burn (DOB) gradient, with the deepest burned areas having an increased potential to uptake more CO_2 than the Unburned site. The data also showed that both bioavailable P and moss recolonization were highest in the deepest burned areas. Unburned environmental controls on CO_2 fluxes were dominated by soil temperature, whereas the Burned sites CO_2 fluxes were controlled by leaf area index. One-year post-wildfire, the deepest burned areas had between 5-200 times greater concentration of P than the Unburned site, the most moss recolonization, and the greatest CO_2 uptake, showing that deeper burning could potentially increase the recovery trajectory and resiliency of northern peatlands after fire disturbance.

Dedication

To the most loving, supportive, parents;

Mardy and Dirk van Beest were the first teachers I ever had, and my love of learning and knowledge could not have truly been discovered without both of you by my side every step of the way.

I love you both!

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With increasing DOB in peatlands there is evidence that increased P and moss regrowth results in greater CO_2 uptake and C sink potential, which over time has a faster trajectory to sequestering C lost to the atmosphere from the initial wildfire.

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1.0 Introduction

1.1 Background

Peatlands cover approximately 12% of Canada's land mass and are an important feature in the western boreal forest (WBF) of Canada (Bridgham et al. 2006). Fens cover 63% of boreal peatlands and store over half of the C stock (Vitt et al. 2000; Vitt et al. 2009). The ability of fens to remain a store of C and other macronutrients, as well as improve water quality, is currently under threat due to anthropogenic climate change, leading to warmer and drier conditions (IPCC 2007). Many of the predicted changes that will affect boreal peatlands involve not just a warming effect but also increased evapotranspiration (ET) rates that will result in lower water table (WT) positions in peatlands (Roulet et al. 1992; Brown et al. 2010; Solondz et al. 2008). This change in hydrologic dynamics increases the vulnerability of boreal peatlands to burning during boreal wildfire season, which leads to changes in ecological function, microbial activity, and nutrient cycling that are in a delicate equilibrium due to the dominant anoxic environment in peatlands (Strack and Waddington 2007; Macrae et al. 2012). Thus, a climate regime shift creates significant uncertainty around the ability of boreal peatlands to continue as C sinks due to increased aerobic mineralization of organic material and increased nutrient export (Blodau 2002; Holden et al. 2004; De Mars et al. 1996). However, a changing climate is not the only impact on peatland function, especially in the WBF zone of North America. Boreal wildfire is increasing in magnitude and frequency, resulting in the burning of the organic-rich upper layers of these peatlands, which will become more vulnerable with further drying and lowering of WT (Kettridge et

al. 2015). The effect of these changes on peatland ecosystem functions are uncertain, and require more research attention.

1.2 Literature Review

The WBF is 270 million hectares of the Canadian landscape, where wildfire is the primary natural disturbance due to the continental climate and low rates of human fire suppression (Stocks et al. 2002). Wildfire is a naturally occurring phenomenon that is essential for a healthy life cycle of forests, acting as a renewing agent (Flannigan et al., 2000). There is a correlated increase in area burned and rising summer temperatures and drying, due to ET rates exceeding precipitation and decreasing surface soil moisture (Flannigan et al., 2006; Gillet et al. 2004; Roulet et al. 1992). The seasonal severity rating (SSR) for the WBF has increased ~10-30%, causing an increase in area burned and fire severity (Flannigan et al., 2000). The length of the fire season has also been affected by the warmer drier climates, with the fire season starting earlier in spring and ending later in autumn (Wotton and Flannigan, 1993).

Northern peatlands have demonstrated their resilience to large-scale disturbance, including wildfire, over the last thousands of years by ultimately returning to a pre-fire function of carbon sequestration (Kettridge et al., 2015). However, shortened fire cycles in the WBF are likely to increase peatland fire frequency, changing the biogeochemical function of peatlands (Wieder et al. 2009). A major concern in this region is a drop in WT that will increase the aerobic zone for decomposition and allow upper layers of the peat to be vulnerable to burning (Kettridge et al., 2015). The burning of these upper layers of rich organic matter releases enormous quantities of C to the

atmosphere and oxidizes macronutrients that were locked up in the peat (Zoltai et al., 1999). Indeed, the biogeochemical feedback of bioavailable macronutrients addition in post-wildfire peatlands has not been studied in the literature. However, it is anticipated that a large pulse of the macronutrients released by wildfire could contribute to the regeneration and productivity of the peatland post-fire, but could also become a tipping point of ecosystem change under new climate regimes. Therefore, there is need to develop a better understanding of how wildfire may contribute to the release of stored macronutrients and their effect on the internal cycling of C, nitrogen (N), and phosphorus (P), among other functional attributes to the peatland biogeochemical process.

One of the prime ecosystem services resulting from peatland biogeochemical function is their ability to uptake and store C (Gorham, 1991). It is widely acknowledged that northern peatlands store one-third of terrestrial soil C (Wang et al. 2014; Yu et al. 2010). This 'carbon stock' and other macronutrients, is estimated to be ~500 Pg since the last glaciation (Wang et al. 2015). This high accumulation of C in peatlands is mainly attributed to the higher rates of primary productivity in vegetation than the rate of litter and peat decomposition, as well as the loss of C from dissolved organic carbon (DOC) (Charman 2002; Vitt et al 2009). Treed fens, common throughout Canada's WBF have been shown to have the highest C stock of peatland types at ~223 kg C m-2 (Akumu and McLaughlin 2013). However, N, P, calcium (Ca), magnesium (Mg), and potassium (K) are also stored in peatlands, and play key roles in plant production, litter decomposition, and nutrient cycling, which in turn allows these systems to store C (Clymo 1978; Wang et al. 2015). As organic matter accumulates in the peat profile,

large quantities of N and P are sequestered along with C (Clymo 1978). However, due to low rates of nutrient recycling, most of these essential nutrients are stored in the peat and not available for plant growth (Verhoeven et al. 1990). Wang et al. (2015) examined the stoichiometry of C to N and P and found that the C:N ratio from vegetation and litter to peat declines over the soil profile, with ratios of 40:1 to ~25:1 for litter and peat, respectively. C:P, however, showed a different trend, increasing from litter to peat, from approximately 900:1 to 1750:1, respectively. This illustrates that N is accumulating at a higher rate than P as C is stored in the peat profile, indicating that during decomposition, recycling of P to the surface layers for microbial and vegetation uptake occurs (Wang et al. 2015). Therefore, it has been estimated that ~18 Pg of N and ~0.3 Pg of P has been stored since the last deglaciation (Wang et al. 2015).

Aboveground vascular plant litter, belowground vascular roots, and the bryophyte ground cover are the main C inputs into the peat profile (Wang et al. 2014). Bryophytes have phenolic compounds that slow decomposition, whereas vascular plants and true mosses have higher rates of decay (Wang et al. 2014). Saturation in peatlands is also important for slow decomposition, surface water flow remains relatively stagnant that allows organic matter to remain and not be carried away (Verhoeven 1986). The peat column can be broken up into two sections, the lower *catotelm*, which is usually water saturated and anaerobic, and the upper section *acrotelm,* which is normally unsaturated and aerobic (Ivanov 1957). Nutrient decomposition is higher in the acrotelm due to aerobic microbial breakdown and is presumed to be extremely low in the catotelm. Fens have WTs that fluctuate less and normally remain in the upper 10-20 cm of the surface, which creates an acrotelm much smaller relative to the catotelm (Vitt et al. 2009). Even

with the high WTs, Vitt et al. (2009) that support slow decomposition, the vegetation makeup of fens (true mosses and abundant vascular species) that are not resistant to decomposition, which results in a poorly developed acrotelm and lower rates of peat accumulation. Moderate to rich fens still accumulate peat even though they have higher decomposition rates, more neutral pH, and more decomposable vegetation (Vitt et al., 2009). However, organic matter is still stored due to the rapid production of inputs exceeding the rapid decomposition in the acrotelm (Vitt et al. 2014). It follows then, that disturbance that affects acrotelm-catotelm dynamics, such as wildfires, could impact C sequestration in fens (Vitt et al. 2009).

Fens are more productive and have faster decomposition rates than bogs (Frolking et al. 2001), due to their vegetation and water sources, and it is therefore widely accepted that fens are more effective in the mineralization of nutrients (Bridgham et al. 1996). The soil in peatlands contains large amounts of N and P, however, only 3 % of these nutrients are in bioavailable form for microbial and plant use (Verhoeven 1986). The bio-accessible pools of N and P are dependent on the mineralization of organic matter from microbial activity and the water supply coming into the system through precipitation and groundwater (Verhoeven 1986). Microbial activity is the bacterial breakdown of organic matter by microbial decomposition or the transformation of nutrients from bacteria (i.e. nitrification, denitrification, or N fixation), both processes result in the mineralization or immobilization of inorganic macronutrients stored in the peat and litter (Verhoeven 1986). N and P recycling rates are low as well, and their concentration in the plant litter often results in the needs of microbial decomposers exceeding available nutrient concentrations (Manzoni et al. 2010). This imbalance of

nutrient needs for decomposers at the beginning of the growing season leads to immobilization (Nwaishi et al. 2015). However, once microbes break down enough litter to meet their needs, net mineralization will occur and nutrients will be available for vegetation productivity (Moore et al. 2006; Manzoni et al. 2010).

Nutrient cycling responds to hydrological and microbial functions within peatlands and are essential for plant productivity, which leads to C storage (Blodau, 2002; Chivers et al. 2009; Wood et al. 2015). Hydrologic conditions, such as WT and soil moisture, affect the cycling of N and P in the peat through many factors including flow transport, redox conditions and soil temperature (Plach et al. 2017). It is predicted that WT within fens will decrease, affecting nutrient cycling and bioavailable pools by increasing the aerobic zone. This will cause warmer temperatures in the peat substrate, and increased decomposition rates, all of which leads to increased release of C and mineralization of N and P with the peat (Clymo, 1965; Plach et al 2017).

In peatlands, N and P are usually at much lower concentrations than K, and P tends to have the lowest concentrations of all macronutrients (Vitt, 2006). Due to the saturated nature of these ecosystems, ammonium (NH_4^+) is the dominant form of inorganic N (Verhoeven 1986). High organic matter in the soil of peatlands increases the cation exchange capacity in comparison to other types of soils, which increases the binding of P in the system, in turn locking up P and reducing bioavailability (Verhoeven 1986). Inorganic P becomes bound to organic matter through bridges formed commonly by calcium (Ca), iron (Fe), aluminum (Al), or other cations (Gerke, 1992). This binding of P predominates in peatlands due to the high organic matter content and the high cation levels (Gerke and Hermann 1992; Bedrock et al. 1997).

Within peatlands, there are different vegetation microforms (hummocks and hollows) that have different moisture, oxidation, and vegetation dynamics influencing the cycling of nutrients at the local scale (Rydin and Jeglum 2006; Strack et al. 2006). These microforms have vegetation differences, which can result in different storage rates of C and nutrients due to differences in productivity and decomposition rates (Strack et al. 2006). There is a distinct vegetation difference between hummocks and hollows that leads to changes in nutrient demands, altering the available nutrient pools (Turetsky 2003; Aerts et al. 1999). In drier, aerobic hummocks, organic matter is sequestered at a larger rate than hollows, and extractable pools of nutrients are higher, and N mineralization increases available N pools, while P concentrations in hollows are normally higher due to saturation increasing P solubility (Moser et al. 2009; Macrae et al. 2013).

Under low available nutrient concentrations, understanding N and P limitations for vegetation is important to the rate of productivity in peatlands, in turn affecting C uptake and sequestration. N-limited or P-limited is regarded as when the plant's N:P ratio is smaller than 14:1 or larger than 16:1, respectively (Koerselman and Meuleman 1996). Vegetation productivity then increases with N and P availability with some studies showing that aboveground productivity with increased N mineralization (Alerts et al. 1995), whereas others suggest that organic-rich soils need both N and P supply to be elevated to increase productivity due to co-limitation (Bedford et al. 1999; Plach et al. 2017). Wang et al. (2014) suggest that N and P are co-limiting for most species in peatlands and that even though nutrient source concentrations change over the growing season, usually due to microbial activity, plant uptake and environmental conditions, the

stoichiometric balance does not change. The C:N and C:P ratios of fresh plant litter can be used to predict if mineralization or immobilization of N and P will take place due to the microbial demands. During decomposition of plant litter, nutrients will be utilized by microbes to meet their stoichiometry demands, and until these needs are met the immobilization of N or P will occur (Güsewell and Koerselman 2002). The release of P during decomposition is, in general, faster than the release of N (Verhoeven 1986) and will only be mineralized if C:P is below a critical level (Brinson, 1977).

Disturbances to peatlands lead to changes in nutrient release due to increased peat oxidation (Shenker et al. 2005). Examples of such disturbances include lowering of the WT from drainage or burning of upper soil layers from wildfire (Shenker et al. 2005). Peatlands act as efficient nutrient sinks, that can reduce downstream eutrophication and water quality issues, but after a fire, little is known about the release and potential effects of increased nutrient loading. Nwaishi et al (submitted) show that N:P ratios of soil and groundwater do not reflect the ratios and limitation patterns observed in vegetation; however, it was shown that disturbance in these peatlands can cause a reversal in both the source and vegetation N:P ratios. This reversal of N:P ratios also reflects a change to the C:N:P stoichiometric balance when a disturbance happens affecting the decomposition, microbial activity, plant uptake, and overall nutrient cycling, that could shift long-term C and macronutrient storage. Shifts in C storage due to C:N:P ratios are projected to affect the minerotrophic gradient of fens differently, where mineral-poor fens will increase and mineral-rich fens will decrease in C storage. This mainly contributes to increased P availability and decreased WT levels that shift the vegetation communities from moss to vascular dominated communities (Nwaishi et al.

submitted). A shift in the nutrient stoichiometry of peatland soil will change the C cycling within the system as a function of peatland and disturbance type; however, it is unknown whether that shift will result in a net loss or gain of C (Bragazza et al. 2004; Jiroušek et al. 2011). With wildfire, there is the potential to 'unlock' the P that is organically bound within the peat, however little is known about the effect elevated P, and potentially N will have on peatland C cycling as the peatland recovers from disturbance.

Future climate warming, anthropogenic activities and natural disturbances are likely to increase the nutrient availability in peatlands (Keller et al. 2006). Along with disturbance, a warming summer climate will affect nutrient recycling and concentrations due to nutrient mineralization being highest when peat experiences drier and warmer temperatures (Wood et al. 2015; Bridgham et al. 1995; Updegraff et al. 1995; Keller et al. 2004). Thus, the increase in concentrations of N and P will change the C cycling and become important controls for vegetation productivity and microbial activities (Lukenbach et al. 2015).

1.3 Research Objectives

The frequency and spatial extent of wildfire disturbance are increasing in the peatland dominated WBF of North America affecting the nutrient cycling of these wetlands (Flannigan et al. 2000). After a wildfire, depending on the pre-fire moisture levels in the peatland, the vegetation, and upper peat layers are lost, and the remaining peat left oxidized. This has the potential to unlock stored nutrients (N and P), changing both the nutrient concentrations and availability for the regrowth of plants. However, it is

unknown how a fire will change the nutrient storage and concentrations in fen peatlands. It is especially important to determine how this cycling is influenced by disturbance such as wildfire. The resistance to combustion from different microtopographical species, along with an increase in nutrient availability from peat combustion, will affect vegetation regrowth post-fire and the rate of C uptake. However, it is unknown how the regrowth of plants and the degree of burning will change the CO_2 fluxes post-fire. Therefore, this study aims to:

i) explore the temporal and spatial dynamics of nutrient concentrations between Burned and Unburned sites in a fen peatland one-year post-wildfire

ii) Understand the role of nutrients in vegetation recovery of a burned fen peatland

iii) Compare nutrient storage in the upper layers of peat pre- and post-fire to quantify the loss of nutrients due to wildfire.

iv) Understand the temporal and/or spatial variability observed in the CO_2 fluxes of a fen peatland one-year post-wildfire relative to an unburned area

v) Determine which environmental factors (ie. hydrologic, biologic and edaphic) explain this temporal and/or spatial variability observed in CO_2 fluxes.

These five objectives are addressed in two chapters that form the basis of two manuscripts to be submitted to journals upon completion of this thesis.

1.4 Study Site

1.4.1 Study Site Pre-Fire

Our research was carried out in the Poplar Creek Fen (hereafter referred to as Poplar) located approximately 20 km north of Fort McMurray, Alberta (56°22′N, 111°14′W) in the Athabasca Oil Sands Region (AOSR). Poplar is classified as a moderate-rich treed fen surrounded by a mosaic of upland coniferous forest (Figure 1) (Nwaishi et al. 2015). Peat depths at Poplar range between 0.4 to 1.6 m, underlain by fluvial sand and fractured bedrock from the McMurray lowland formation (Nwaishi et al. 2015). While Poplar has experienced some indirect industrial disturbance including increased atmospheric deposition of NO_3^- and NH_4^+ (Proemse et al. 2013) and the development of cutlines in the surrounding landscape, the peatland is used as a reference study site relative to the many, much more directly impacted sites in the AOSR. As such, there is an extensive (pre-fire) data history of the site, including vegetation, nutrients, carbon, and hydrology data (Nwaishi et al. 2015; Wood et al. 2015; Borkenhagen, 2013; Elmes et al. 2018). The pH ranges between 6.5 to 6.8, soil organic matter between 81 to 88% and a relatively low EC between 150 and 300 (Nwaishi et al. 2015; Wood et al. 2015). Poplar fen is an intermediary between a drier bog and wet fen, containing traditional peatland micro-topographic features with dry hummocks and wet hollows (Wood et al, 2015).

The surrounding uplands are a mixture of *Populus tremuloides* (trembling aspen), *Picea mariana* (black spruce) and *Pinus banksiana* (Jack Pine), with groundcover dominated by *Ledum groenlandicum* (Labrador Tea), *Equisetum sylvaticum* (Wood Horsetail) and *Tomenthypnum nitens* (Brown moss) (Borkenhagen, 2013). Upland vegetation extends into the peatland margin and rich fen areas and the current vegetation includes black spruce, Labrador tea, and wood horsetail, as well as *Carex*

spp., *Maianthemum Trifolium* (Three-Leaved Solomon's Seal) and a mixture of moss species (Borkenhagen, 2013). The center of the fen area has more classic peatland species including *Larix laricina* (Tamarack), stunted black spruce, *Sphagnum spp.*, *Betula pumila* (Dwarf Birch), *Vaccinium oxycoccos* (Small Cranberry), and *Carex spp.* (Borkenhagen, 2013). Concentrations of extractable forms of nitrogen, (i.e. NO_3^- and NH_4^+) have been shown to steadily decrease over the growing season, as well as processes such as ammonification rates, whereas net nitrification rates increase due to the decreasing WT and aerobically favorable conditions (Nwaishi et al. 2016). Water extractable pools of P were shown to be the lowest in the middle of the growing season, with the highest net mineralization of P also occurring in the middle of the growing season (Nwaishi et al. 2016). Nwaishi et al. (2016) looked at the carbon fluxes of the sites showing that over the growing season Poplar functions as a carbon sink.

Local recharge is the main water source for Poplar Fen, unlike many fens that are recharged from regional aquifers, leading to increased fluctuations in WT levels (Elmes et al. 2018). Water table levels during the 2015 growing season averaged 20 cm below ground surface with lower WTs found closer to the upland margins (Elmes et al. 2018). Elmes et al. (2018), also found the vertical hydraulic gradients were strongest when WTs were high and weakest when precipitation was low, resulting in less recharge. A longer record of WTs throughout the study site shows that Poplar experiences extended dry periods, with persistent low WTs due to lack of precipitation driven recharge.

1.4.2 Study Site Post-Fire

During May of 2016, the Horse River Wildfire consumed approximately 590,000 ha of the WBF surrounding Fort McMurray, Alberta. Poplar was almost entirely engulfed by the wildfire, burning both the upland mixed coniferous forest and the moderately-rich fen. Areas of the fen burned at differing depths of burn depending on vegetation, location and water levels. The center of the fen was untouched by the fire and surrounding areas were severely burned (Figure 1). In the 'Burned' site, hollows were completely burnt and the mixed moss hummocks singed with brown dead vegetation, and, all black spruce trees were completely charred and dead. The Unburned site at the center of the fen had noticeably higher water levels and an abrupt transition of the types of tree and vegetation species, with stunted Tamarack trees and *Sphagnum* moss dominating the ground cover. The Unburned site has live vegetation and little trace of any fire interactions with both hummocks and hollows. For the study, two transects were selected for the Burned sites, on either side of the Unburned site at the center of the fen (Figure 3-1). Each transect had the same sampling design, with all instrumentation focused in an approximately 20 x 20 m area.
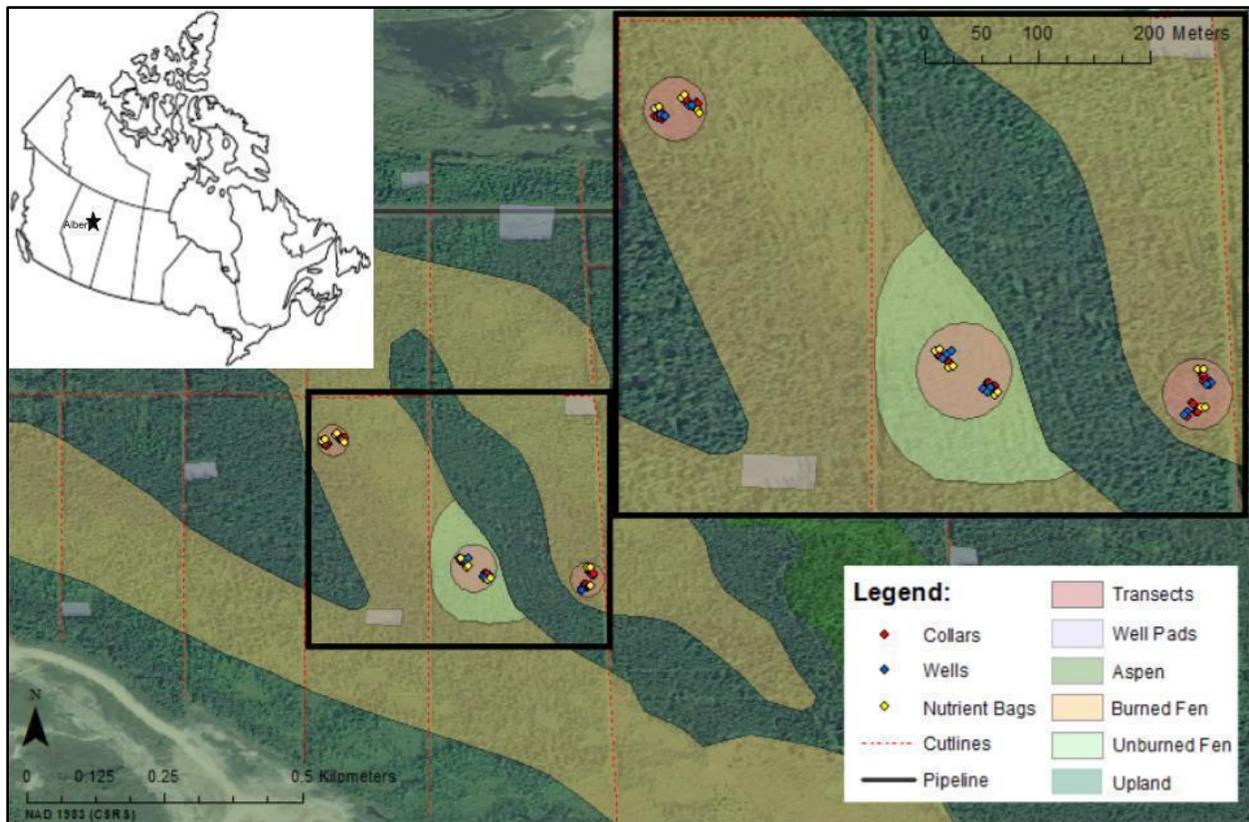
Figure 1 - 1. Map of Poplar study site denoting the Burned and Unburned sites after the wildfire and the three study transects: two burned, one un-burned area of the fen.

1.4.3 Study Site Burn Severity

Peat burn severity was quantified along each transect through depth of burn (DOB) measurements following the protocols commonly used by Lukenbach et al. (2015), Kasischke et al. (2008) and Mack et al. (2011). This protocol assumes a pre-fire flat surface between multiple reference points, including adventitious roots and/or unaltered (unburned) reference points. A string attached between two reference points was used as the assumed flat surface and 10 equally spread out measurements were taken from the string to burned ground giving a single DOB estimate. This was repeated 20 times for each transect to achieve a large sample size (n=200). An ash layer post-fire did not factor into DOB measurements as peat has a low mineral content and there was little to

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no ash layer at the surface (<2 cm) (Lukenbach et al. 2015). For the Burned sites, the adventitious roots of black spruce were used as references points for the pre-fire surface. Lukenbach et al. (2015) found that these DOB methods were conservative since adventitious roots of black spruce are on average 5 cm below peat surface, therefore when adventitious roots were used as the reference point, 5 cm was added to the DOB measurements. DOB measurements at the Burned sites ranged between 9.9 to 16.7 cm (Figure 1-2).
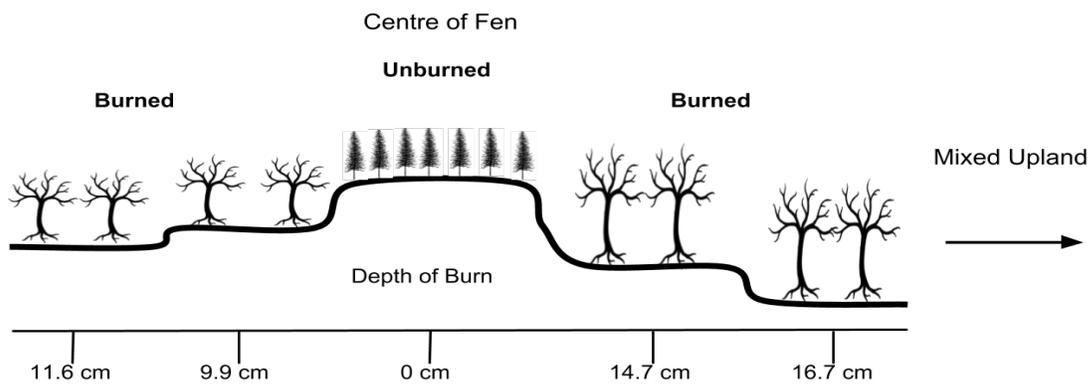
Figure 1 - 2. Illustration of the three areas for this study showing the spatial DOB measurements across Poplar.

2.0 Manuscript Chapter 1. Increased peatland nutrient availability following the Fort McMurray Horse River wildfire

2.1 Introduction

Peatlands cover approximately 12% of Canada's land surface and are an important feature in the western boreal forest (WBF) of Canada (Bridgham et al., 2006). Fens cover 63% of boreal peatlands and store over half of the carbon (C) stock (Vitt et al., 2000; Vitt et al., 2009). The ability of fens to retain C and other macronutrients, as well as improve water quality, are currently threatened due to anthropogenic climate change leading to warmer and drier conditions (Roulet et al., 1992). Many of the predicted changes that will affect boreal peatlands involve not just a warming effect but also increased evapotranspiration (ET) rates, which will result in lower water table (WT) position in peatlands (Roulet et al., 1992; Brown et al., 2010; Solondz et al., 2008) and cause an overall drying effect. This drying can change peatland ecological function, microbial activity, and nutrient cycling, which are in a delicate equilibrium due to the anoxic peatland environment (Strack and Waddington, 2007; Macrae et al., 2013). This drying effect can also increase the vulnerability of boreal peatlands to smoldering combustion carbon losses, which can lead to accelerated post-fire peat oxidation with further drying and lowering of the WT (Kettridge et al., 2015). To better understand the response and resilience of northern peatlands to climate disturbance and wildfire, knowledge is needed on the roles of N and P cycling in the primary production process that allows C to be sequestered by peatlands, and, if and how these relationships are changed by wildfire.

It is unclear how climate disturbance and wildfire will affect peatland biogeochemical function. The primary ecosystem service provided by natural peatlands is an ability to sequester atmospheric C and accumulate peat reserves, representing a stable and resilient long-term C store (Gorham, 1991). Northern peatlands store approximately 500 Pg (Wang et al., 2015) or about one-third of terrestrial soil C (Wang et al., 2014). Peatland ecosystems also store N, P, calcium (Ca), magnesium (Mg), and potassium (K); these macronutrients play key roles in plant production, litter decomposition, and nutrient cycling, which in turn allows these systems to store C (Clymo, 1978; Wang et al., 2015). Natural disturbances are likely to increase the nutrient availability in peatlands (Keller et al., 2006) by increasing nutrient mineralization rates under drier and warmer temperatures (Wood et al., 2015; Bridgham et al., 1998; Updegraff et al., 1995; Keller et al., 2004). Although the impacts of climate change on peatland nutrient dynamics have been explored previously (Wood et al., 2015; Bridgham et al., 1998; Updegraff et al., 1995; Keller et al., 2004), the combined impacts of both climate drivers and wildfire on nutrient dynamics have not been examined.

Northern peatlands have historically demonstrated their resilience to large-scale disturbance including wildfire over the past several thousand years by ultimately returning to a pre-fire carbon sequestration function (Kettridge et al., 2015). However, increased fire frequency and severity may change the biogeochemical function of peatlands (Wieder et al., 2009) and their overall resilience. The burning of these upper layers of rich organic matter releases enormous quantities of C to the atmosphere but also oxidizes macronutrients previously locked up in the peat (Zoltai et al., 1999). The biogeochemical feedback of the increased supply of bioavailable macronutrients in post-

wildfire peatlands has not been studied. Little is known about the effect that elevated P and potentially N will have on the nutrient limitation patterns of peatland plant communities and stoichiometric balance of CNP in plant nutrient sources (i.e. peat and groundwater). While a large post-fire pulse of macronutrients released by wildfire combustion of trees, shrubs, moss, and peat may enhance post-fire moss and shrub regeneration and productivity, it is anticipated that too much nutrient release could push the peatland towards a regime shift (e.g. Kettridge et al., 2015) as peatland form and function are strongly linked to nutrient availability (Rydin and Jeglum, 2013). As such, there is an urgent need to develop a better understanding of how wildfire may contribute to the release of stored macronutrients and their effect on the internal cycling of C, N, and P among other functional attributes to the peatland biogeochemical process.

The goals of this study are to: i) quantify the differences in temporal and spatial dynamics of available nutrients (N and P) concentrations and mineralization rates in peat between Burned and Unburned sites from multiple sources in a fen peatland one-year post-wildfire; ii) compare the C, N, and P stoichiometric balance from pre- and post-fire to understand how disturbance changes nutrient limitation patterns and the feedback on vegetation recovery and decomposition ; and iii) quantify the net loss of C, N, and P from the fire by comparing nutrient storage in the upper layers of peat pre- and post-fire.

2.2 Material and Methods

2.2.1 Soil Properties, Nutrient Dynamics and Stock Calculations

Extractable (bio-available pools) and net mineralization rates of nitrogen (N) and phosphorus (P) were determined in all three transects during the full growing season, and soil moisture and soil temperature were taken over an integrated 10 cm depth (Delta-T Devices, UK, WET Sensor) on a weekly basis. To fully understand both the difference in nutrient cycling due to peat burning and seasonal changes, buried-bag nutrient mineralization incubation experiments (after Hart et al., 1994 and Macrae et al., 2013) were conducted three times during the growing season: Early (May), Middle (mid-June to mid-July), and Late (mid-August to mid-September), with each incubation period lasting for 28 days. Briefly, two adjacent "paired" peat cores, approximately 10 cm deep, were taken from all three transects (4 hummock and 4 hollows), using a "dutch corer" and live vegetation was removed from both cores. One of the paired cores, the "pre-incubation" core, was taken to the lab, homogenized, put on ice in a cooler, and processed within 24 hours for KCl-extractable concentrations of ammonium (NH_4^+) and nitrate (NO_3^-), and water extractable phosphorus (WEP). The second core, "post-incubation" core, was used , for in-situ net mineralization and was loosely wrapped in polyethylene and placed back in the hole from which it had been removed for an incubation period of 28 days, then subsequently analyzed following the same procedure as the first core. All filtered extractants were analyzed using colorimetric analysis at the Biogeochemistry Lab at University of Waterloo (Bran Luebbe AA3, Seal Analytical, Seattle, U.S.A., Methods G-102-93 (NH_4^+), G-109-94 (NO_3^- + NO_2), and G-103-93 (SRP)). According to Nwaishi et al. (2015) and Pote et al. (1996) the drying of samples can enhance extractable nutrient pools, therefore, field moist samples were used for all nutrient extractions. Moisture content, using a drying oven for 24 hours at 80 ^{o}C, with a

sub-sample of each core was determined so that extractable nutrient pools and net mineralization rates could be expressed in per unit dry weight. Net nitrification, net ammonification, and net P mineralization rates (mg g^{-1} dry peat day^{-1}) were estimated for all three incubation periods by taking an average of the difference between the post-incubation and pre-incubation extractable pools to quantify the difference in NO_3^-, NH_4^+, and SRP. Negative values for the net mineralization of NO_3^-, NH_4^+, and SRP indicates net immobilization, whereas positive values rates indicate net nutrient release (net mineralization) into pore water.

Peat cores (20 cm length, 5 cm diameter) were extracted at peak growing season to measure the C:N:P ratios in the upper layers of the peat and to characterize the soil properties used in estimating changes in C and nutrient storage in peat. Four cores were taken at each transect (2 hollow cores, 2 hummock cores) and frozen until transported to the University of Waterloo for analyses of percent organic matter by loss on ignition, bulk density, and porosity (after Plach et al., 2017). Total C and N in peat was determined using EA-IRMS at the Environmental Isotope Laboratory, University of Waterloo, and total P, Fe, and K concentrations were measured after digestions procedures (after Parkinson and Allen, 1975) using ICP analysis at the Centre for Cold Regions and Water Science, Wilfrid Laurier University. Using the C and macronutrient concentrations from peat nutrient stocks were calculated using the bulk density of peat layers for potential C storage within the Unburned and Burned sites.

2.2.2 Ground and Surface Water Dynamics

Surface water infiltration (shallow leachate) was measured by installing a 500m^3 plastic lysimeter buried 5 cm below the surface of the peat with a mesh screening to allow only water to be collected. Water samples were collected within 24 h of rainfall events. Groundwater levels were measured weekly from shallow wells (5 cm ID, ~ 1m depth, screened through the entire well length). Water samples were collected monthly from these wells between May and September, and wells were purged 24 hours prior to sampling. Each transect had 4 infiltration lysimeters and 4 wells, split evenly between hollows and hummocks. All collected water samples were split into 3 sub-samples. The first sub-sample was gravity filtered into a specimen cup using 1 mm porosity ashless filter paper (Whatman no. 42) and frozen to test for anions, cations and bioavailable N and P. The second sub-sample was gravity filtered into a specimen cup using 1 mm porosity ashless filter paper (Whatman no. 42) for the analysis of total dissolved N and P. A third sub-sample was left unfiltered for the analysis of total Kjeldahl N and P, including particulate matter. Both the second and third subsamples were preserved with acid (0.2% final H_2SO_4 final concentration) for storage and subsequently digested (after Parkinson and Allen, 1975). The N and P species were analyzed using colorimetric analysis (described above). Major ions were analyzed using a Dionex ICS3000. Lab analyses were completed in the Biogeochemistry Lab at the University of Waterloo.

2.2.3 Vegetation Sampling and Nutrient Analysis

A tree survey at all three transects was conducted in a 400 m^2 area to better understand how tree density and species could have affected burn patterns during the 2016 fire. The vegetation survey was conducted at the peak of vegetation growth at the end of

June (Brown et al., 2010; Solondz et al., 2008). Each transect has 12 collars (6 hummocks and 6 hollows) that were installed for CO_2 measurements. Vegetation cover was assessed within the area of these collars (approximately 300 cm^2) installed in the untouched Unburned site and regrowth in the Burned sites, between microtopographic gradients. Both ground cover and stem count were used to study both moss cover and vascular plant density. Ground cover portions of the surface were either burned bare soil or burnt remnants of vegetation; therefore, ground cover was classified either as bare", "burned vegetation, or "live vegetation". Vegetation samples were collected at peak growing season for the analyses of foliar C and nutrients chemistry. Samples were measured for C:N and P as described above.

2.2.4 Statistical Analysis

All statistical analyses were performed with R (R Development Core Team, 2013). All data for this paper were analyzed and tested for normality, however even with log transformations data set was not normal and nonparametric testing was used. To analyze for temporal, wildfire, and microtopographic effects on surface water and groundwater nutrient concentrations, peat nutrient concentrations and mineralization, and peak season peat and soil stoichiometry ratios the Kruskal-Wallis ANOVA function for analysis of variance was run on all datasets (Chambers and Hastie, 1992) using the function "aov", were considered significant if $p < 0.05$. All data was analyzed for the effects of three main reasons for potential variable differences: 1) the effect of wildfire, 2) differences between microforms, and 3) temporal change over the growing season.

2.3.0 Results

2.3.1 Nutrient Availability and Dynamics in Surface Water, Groundwater and Peat

There were significant differences in water chemistry between the Burned and Unburned sites, and between microforms over the growing season. The concentrations of major forms of bioavailable nutrients (NH_4^+, NO_3^-, TDN, TN, and SRP) in surface water were significantly ($p < 0.05$) greater at the Burned sites relative to the Unburned site. Differences in surface water chemistry were also observed between microforms. For example, within the Burned site, hollows (with deeper depth of burn) had greater concentrations of total N than hummocks ($p < 0.01$). Indeed, Burned hollows had concentrations in excess of 60 mg/L N, more than 10 times greater than the largest concentration observed in the Unburned site. Although there was no significant difference in total P between Burned and Unburned sites, it appears that the Burned still had an effect, as it reversed trends between microforms (Figure 2-2), where higher TP concentrations were observed in the Unburned hummocks, but in the Burned sites, hollows had higher concentrations. No significant temporal trends were observed for the inorganic N forms; however, TDN and SRP increased toward the end of the season although this was apparent at both the Burned and Unburned sites.
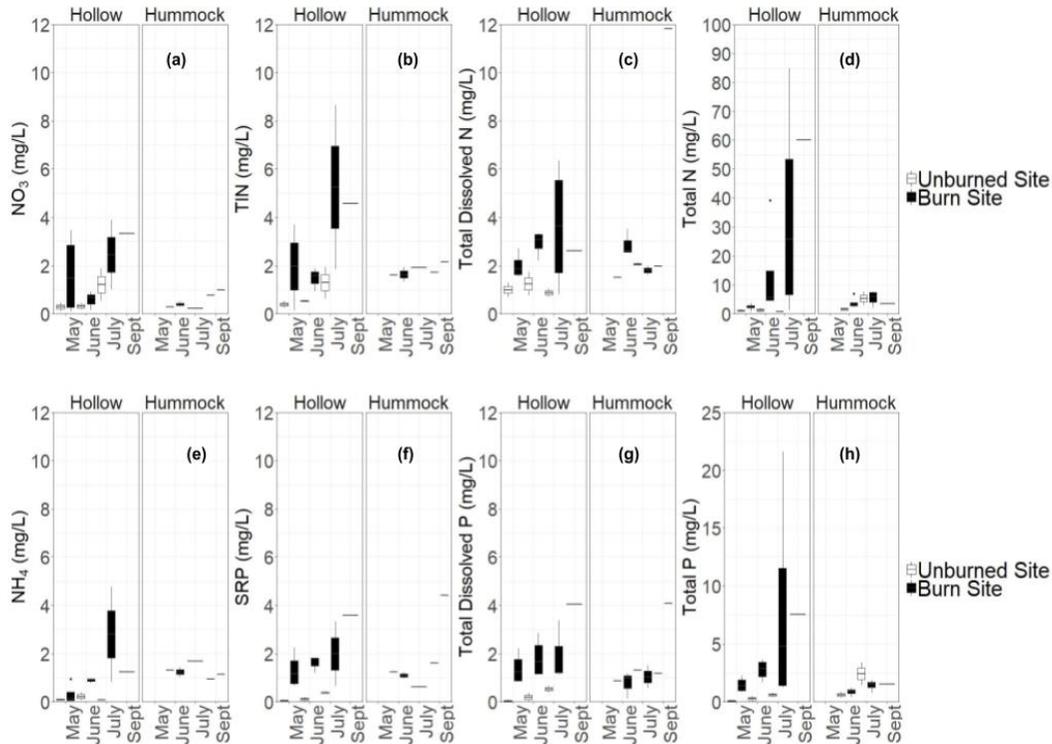
Figure 2 - 1. Surface leachate concentrations for (e) ammonium (NH_4^+), (a) nitrate (NO_3^-), (b) total inorganic nitrogen (TIN), (f) phosphorus (SRP), (c) and (g) total dissolved N and P respectively, (d) and (h) and total N and P concentrations respectively over the growing season, comparing the Unburned (white) and Burned (black) sites and the microtopographical difference observed.

Water table position at the study sites showed a typical difference ($p < 0.01$) between microforms due to differences in elevation, where it was closer to the surface in hollows than in hummocks. The water table decreased steadily throughout the study period and was deeper in the Burned sites due to their proximity to the uplands. Unlike the surface water leachate, differences in groundwater nutrients between sites were only observed for inorganic forms of P. All the P forms (SRP, TDP, and TP) were significantly greater ($p < 0.01$) at the Burned sites in comparison to the Unburned site (Figure 2-3). Differences in groundwater chemistry were also observed between microforms, with significantly ($p < 0.05$) higher concentrations of SRP in hummocks than hollows for the Burned sites, but the reverse was found for the Unburned sites. For TP and TN there was also a significant difference ($p < 0.05$) between microforms and

concentration changes were similar to surface leachate, where higher concentrations were observed in Burned hollows, but at the Unburned site, hummocks had higher concentrations of TP and TN. Temporally, NH_4^+ in groundwater increased significantly ($p < 0.05$) towards the end of the season, while SRP, TN, and TP decreased significantly ($p < 0.05$) towards the end season. This temporal trend was consistent in both sites and between microforms (Figure 2-3).
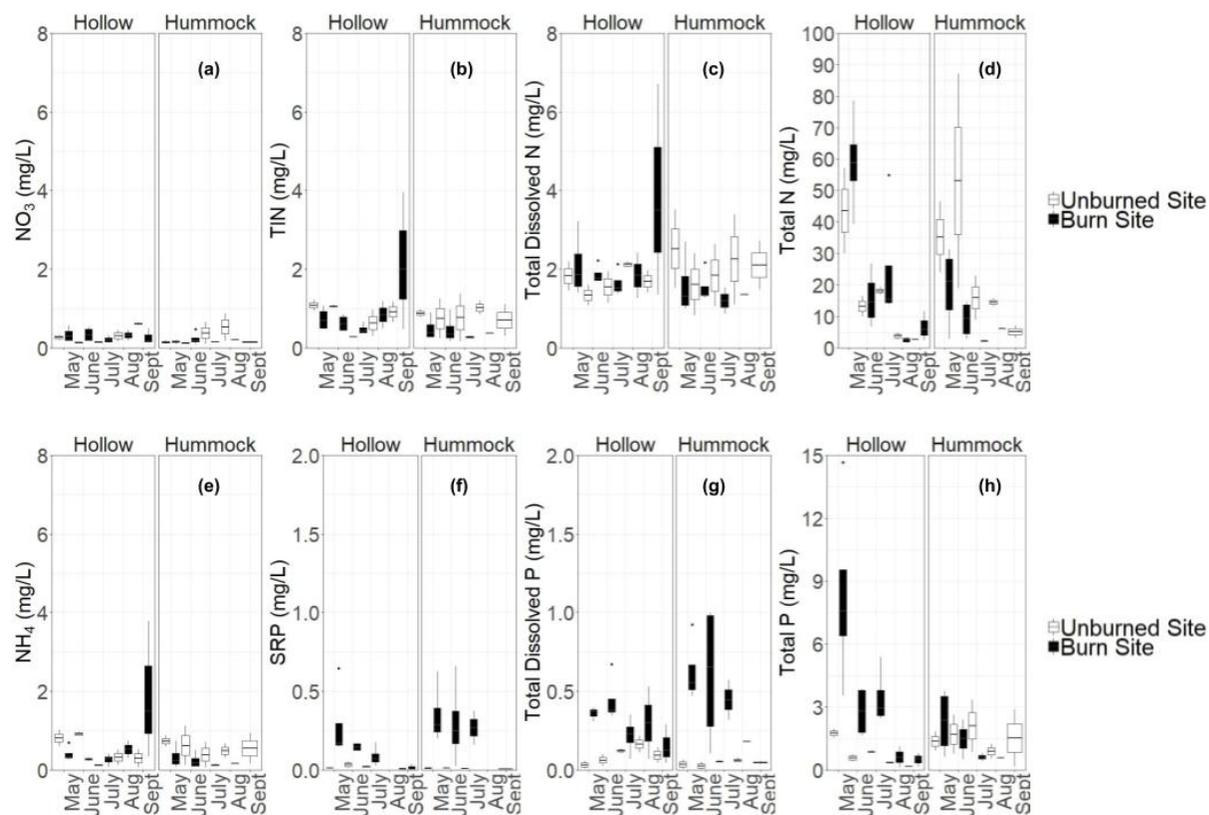
Figure 2 - 2. Groundwater concentrations for (e) ammonium (NH_4^+), (a) nitrate (NO_3^-), (b) total inorganic nitrogen (TIN), (f) phosphorus (SRP), (c) and (g) total dissolved N and P respectively, (d) and (h) and total N and P concentrations respectively   over the growing season, comparing the Unburned (white) and Burned (black) sites and the microtopographical difference observed.

Extractable NH_4^+ concentrations decreased significantly ($p < 0.01$) over the season in peat. Net ammonification did not differ over the growing season but was significantly reduced ($p < 0.05$) in the Burned site, at varying rates between microforms, with lower rates ($p < 0.001$) in the hummocks (Figure 2-4). Similar patterns with

microtopography were observed for net NO_3^- mineralization, but unlike ammonification, the rate significantly varied ($p < 0.001$) over the growing season. Nitrate was immobilized early in the season, whereas net mineralization occurred in the late season ($p < 0.001$), with Burned sites experiencing less immobilization and more mineralization ($p < 0.05$). Although concentrations of extractable forms of inorganic N varied temporally, this pattern was consistent across sites, where NH_4^+ concentrations did not vary between sites and NO_3^- concentrations were higher in the Burned site.

Concentrations of SRP followed a similar seasonal trend as NH_4^+ in peat, decreasing significantly ($p < 0.001$) over the season (Figure 2-4). However, there is a clear and significant ($p < 0.05$) contrast in SRP concentrations between sites, with concentrations 5 times greater in the Burned sites, especially in hollows. In the Burned site, deeper burning, with DOB ranging from 9.9 to 16.7 cm, resulted in increased availability of P. Mineralization of P varied significantly ($p < 0.001$) across the DOB range within microforms, with net immobilization observed in deeper burned hollows and increased mineralization in the shallow burned hummocks.
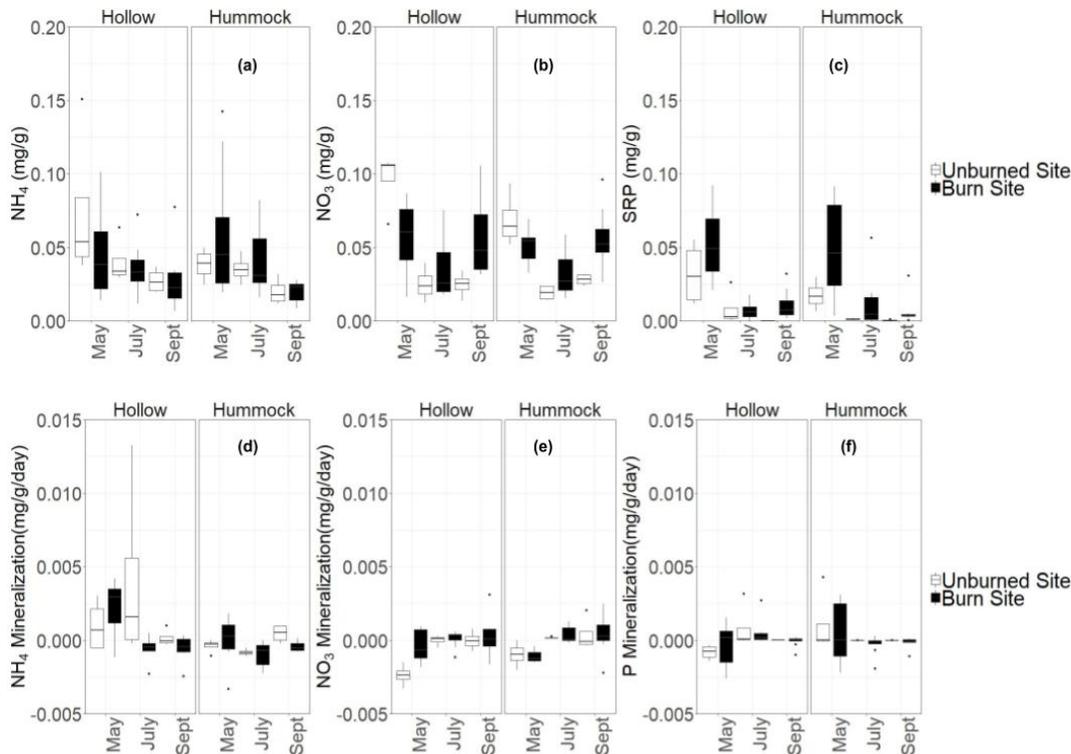
Figure 2 - 3. Extractable and mineralization rates for ammonia (NH_4^+) (a) and (d), respectively, nitrate (NO_3^-) (b) and (e), respectively, and phosphorus (SRP) (c) and (e), respectively, over the growing season (May to September) with 3 study periods (early, middle, and late). Mean (95% confidence intervals shown with error bars) for all observed variables. Burned sites (black) and Unburned sites (white) are differentiated, with microtopography shown in different panels for hollow and hummocks.

2.3.2 Carbon and Nutrients Stoichiometric Balance of Peat and Vegetation

Total N and P concentrations and N:P ratios were significantly higher ($p < 0.05$) in the upper peat layers of the Unburned site in comparison to the Burned sites (Figure 2-5). However, concentrations of total C, K, and the C:N and C:P ratios in peat were significantly ($p < 0.05$) higher in Burned sites (Table 2-1). Total N concentrations and C:P ratios showed significant ($p < 0.01$) increase with depth in the peat column, whereas C:N ratios decreased with depth ($p < 0.01$) at both the Unburned and Burned sites. There was a significant ($p < 0.001$) difference in Fe concentrations and Fe:P ratios

in peat between microforms, with higher concentrations and ratios found in hollows at both sites.

Concentrations and stoichiometric analysis of macronutrients in vegetation were categorized as mosses or vascular plants (Table 2-2) with the N:P ratio for nutrient limitation shown in Figure 2-5. Total C and K in vegetation significantly ($p < 0.05$) differed between sites, with lower concentrations of total C and higher concentrations of K at the Burned sites. Total C and N concentrations were significantly higher ($p < 0.01$) in vascular plants than mosses for both the Burned and Unburned sites (Table 2-2). Stoichiometric balance within the vegetation did not differ between sites, but both C:N and N:P ratios differed significantly ($p < 0.05$) with vegetation type, with mosses having a larger C:N ratio (Table 2-2) and vascular plants a larger N:P ratio (Figure 2-5) at all sites.
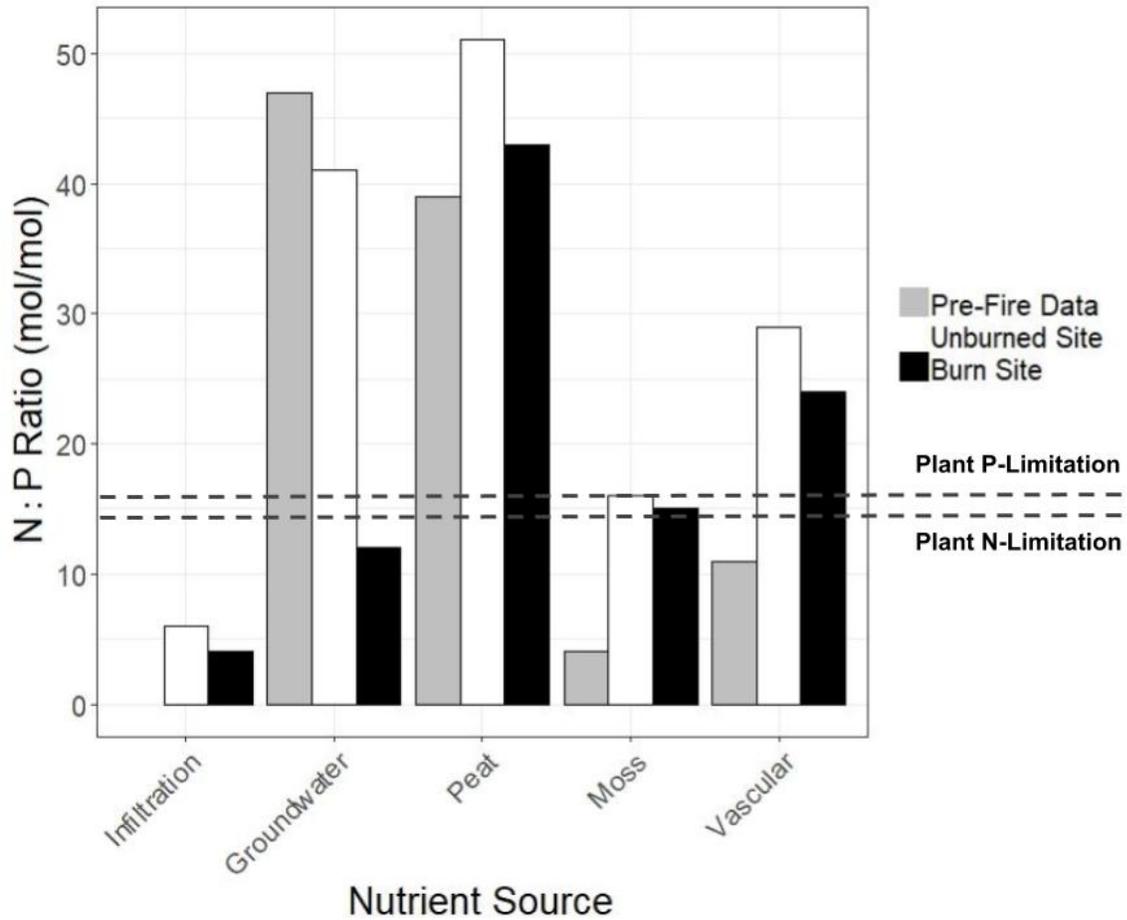
Figure 2 - 4. N:P ratios comparing Pre-Fire (grey), Unburned (white), and Burned (black) sites with the potential sources imbalance (groundwater, surface infiltration, and peat) to moss and vascular vegetation illustrating the shifting nutrient limitations after wildfire disturbance.

Table 2 - 1. Carbon and macronutrient concentrations and nutrient ratios are shown from peak season period, comparing the Unburned and Burned sites and the microtopographical differences. Standard deviation of samples are provided in parentheses. N/d is the result of samples being below the detection limit of the ICP analysis.

| Transect | Microform | Depth (cm) | Macronutrient Concentrations | | | | | Nutrient Ratios | | | |
| | | | C | N | P | Fe | K | C:N | C:P | N:P | Fe:P |
			(mg/g)					ratio			
Unburned	Hollow	0-5	415.8 (20.6)	17.2 (5.2)	1.8 (1.6)	2.7 (1.1)	1.6 (0.9)	27 (10.4)	393 (364.5)	12 (6)	3 (3.2)
		5-10	415 (13.4)	19.2 (4.4)	0.9 (0)	3.2 (2.7)	17.3 (3.7)	23 (6.1)	475 (29.9)	24 (0.1)	4 (3.1)
		10-15	434.9 (24.3)	18.1 (5.3)	0.7 (0.1)	2.3 (1.4)	14.8 (19.5)	25 (5.6)	597 (5.1)	27 (7.6)	3 (1.7)
		15-20	404.6 (40.9)	16.6 (7.1)	0.7 (0)	2.9 (2.3)	20.2 (26.3)	27 (8.7)	609 (38.1)	26 (15.2)	4 (3)
Unburned	Hummock	0-5	445.5 (41.1)	14.3 (4.9)	0.6 (0.2)	1.2 (0.3)	18.6 (12)	35 (13.9)	722 (217.3)	20 (5.2)	2 (0)
		5-10	438.2 (10.8)	17.7 (5.5)	0.7 (0.2)	1.3 (0.6)	n/d	27 (11.5)	653 (176.1)	22 (6.6)	2 (0.3)
		10-15	405.6 (88.2)	19.8 (8.5)	0.6 (0.2)	1.4 (0.1)	n/d	24 (10)	586 (3.7)	23 (11.5)	2 (0.6)
		15-20	422.5 (17.7)	21.7 (2.8)	0.8 (0.1)	1.2 (0.2)	n/d	20 (2.5)	539 (96.9)	31 (7)	2 (0.4)
Burned	Hollow	0-5	457.4 (26.9)	10.3 (1.3)	0.8 (0.2)	2.9 (1.7)	80.5 (66.4)	45 (8)	673 (306.4)	16 (6.1)	4 (1.3)
		5-10	479.2 (31.4)	12.2 (2.5)	0.6 (0.2)	1.4 (0.7)	34.7 (20)	42 (14.1)	903 (397.1)	20 (1.4)	2 (0.7)
		10-15	461.7 (55.1)	12.8 (3.1)	0.5 (0.2)	1.7 (1.7)	25.5 (20.7)	40 (18.6)	977 (580.1)	20 (4.2)	3 (2.8)
		15-20	460.7 (10.5)	14.3 (2.8)	0.8 (0.3)	2 (1.8)	19.6 (18.3)	34 (8.2)	688 (275.9)	20 (7)	2 (1.3)
Burned	Hummock	0-5	477 (17.7)	9.5 (1.9)	0.5 (0)	0.6 (0.4)	40.4 (15.4)	52 (11.2)	975 (79.7)	17 (0.8)	1 (0.9)
		5-10	478.3 (14)	11 (3.8)	0.6 (0.2)	0.8 (0.5)	24.3 (35)	49 (20.3)	812 (249.9)	19 (2.3)	1 (0.4)
		10-15	471.5 (14.3)	13.4 (2.8)	0.7 (0.3)	0.8 (0.6)	3.4 (4.1)	38 (12.8)	849 (460)	20 (4.5)	1 (0.4)
		15-20	462.4 (24.1)	14.6 (2.5)	0.7 (0.2)	1.3 (1.3)	12.8 (15.7)	33 (8.8)	715 (281.9)	21 (3.3)	2 (1.8)

Table 2 - 2. Macronutrient concentrations and nutrient ratios are shown for both moss and vascular vegetation from peak season, comparing the Unburned and Burned sites and the microtopographical difference observed. Standard deviation of samples are provided in parentheses.

Transect	Vegetation Type	Macronutrient Concentrations					Nutrient Ratios		
		C	N	P	Fe	K	C:N	C:P	N:P
		(mg/g)					ratio		
Unburned	Moss	443 (3.2)	8.8 (1.4)	1.1 (1.3)	341.9 (333.5)	1.4 (0.9)	51.3 (8.5)	380 (230.4)	7.1 (3.3)
Unburned	Vascular	512.9 (31.5)	17.8 (5.4)	0.8 (0.9)	232 (280.5)	1.7 (1.1)	31.9 (12.4)	445.9 (336.8)	13.2 (7.1)
Burned	Moss	449 (38.5)	8.7 (2.4)	0.9 (0.7)	52.8 (101)	2 (1.2)	54.6 (12.7)	345.1 (241.3)	6.3 (4.4)
Burned	Vascular	476.5 (47.2)	17.4 (5.6)	1.1 (0.8)	12.1 (10.7)	1.6 (0.4)	30.9 (12.5)	314.4 (78.8)	11.7 (5.6)

2.3.3 Carbon and Macronutrient Stocks in Upper Peat Column

Percentage organic matter content in peat (OM %) showed a significant ($p < 0.01$) decreases in the Burned sites relative to the Unburned site. Organic matter was higher ($p < 0.05$) in hummocks than hollows in both Unburned and Burned sites, and decreased ($p < 0.01$) with depth at both sites. Bulk density was significantly ($p < 0.05$) lower on average at the Burned sites in comparison to the Unburned. Bulk density also increased with depth significantly ($p < 0.01$) at both sites for both microforms, however this trend was much more pronounced in the Burned sites. The estimated C stores (kg/ha) were significantly ($p < 0.001$) higher in the Burned site, while N was lower relative to Unburned site. (Table 2-4). The N stock in peat was significantly lower ($p < 0.001$) in the surface peat, relative to peat layers at 20 cm depth. The total P stock was not significantly different between the Unburned and Burned sites, or by microtopographic changes.

Table 2 - 3. C and nutrient stock calculations using bulk density and macronutrient concentrations from Table 2. Standard deviation of samples is provided in parentheses. N/d is the result of samples being below the detection limit of the ICP analysis.

Transect	Microform	Depth (cm)	Peat Properties		Calculated Nutrient Stock		
			Organic Matter	Bulk Density	C Stock	N Stock	P Stock
			%	g/cm3	(kg/ha)		
Unburned	Hollow	0-5	88.3 (1.4)	0.145 (0.07)	32852 (1628)	2747.2 (1979)	345.1 (413)
		5-10	89.8 (3.1)	0.186 (0.03)	32786.6 (1056)	3572.2 (1123)	151.1 (44)
		10-15	89 (3.6)	0.147 (0.03)	34353.8 (1922)	2707.2 (1143)	100.5 (41)
		15-20	87.8 (5)	0.154 (0.09)	31964.4 (3233)	2742 (1940)	87.5 (51)
Unburned	Hummock	0-5	88.8 (1)	0.104 (0.03)	35196.1 (3246)	1536.4 (835)	77.8 (51)
		5-10	90.7 (0.4)	0.141 (0.04)	34620.7 (854)	2626.3 (1323)	91.1 (56)
		10-15	90.4 (4)	0.197 (0.04)	32043.5 (6971)	3643.1 (1236)	128.4 (9)
		15-20	88.9 (2.4)	0.175 (0.04)	33379.4 (1398)	3801.8 (958)	153 (34)
Burned	Hollow	0-5	82.4 (4.7)	0.078 (0.02)	36134.5 (2122)	808.3 (276)	59.4 (23)
		5-10	87.5 (5)	0.094 (0.03)	37854.8 (2482)	1186.8 (550)	58.7 (36)
		10-15	86.1 (5.3)	0.168 (0.09)	36473.1 (4355)	2151 (1215)	102.1 (69)
		15-20	81.5 (5.6)	0.177 (0.07)	36399.2 (831)	2596.4 (1050)	140.5 (85)
Burned	Hummock	0-5	89.2 (4.9)	0.07 (0.03)	37681.3 (1398)	719.9 (544)	39.7 (24)
		5-10	87.9 (4.3)	0.109 (0.06)	37782.1 (1105)	1335.5 (945)	73.9 (57)
		10-15	86 (5.5)	0.18 (0.07)	37245.4 (1132)	2526 (1145)	145 (110)
		15-20	82.8 (4.4)	0.206 (0.05)	36526.4 (1904)	3056.7 (999)	152.7 (69)

2.4.0 Discussion

2.4.1 Increased Nutrient Availability Following Burning

This study has shown that burning had no effect on NH_4^+, and led to increases in both

NO_3^- and P in the WBF. This concurs with previous findings on P, but contrasts previous

findings on N in other peatland studies that have generally shown a decrease in total

amounts of N, and an increase in the availability of P (Sulwiński et al. 2017; Ketterings

and Bridgham 2000; Laubhan 1995; Bååth and Arnebrant 1994; Baldock and Smernik

2002; Neff et al. 2005). In a previous study (Nwaishi et al. submitted) at the same fen (Poplar), pre-fire NH_4^+ comprised 80-90% of TIN concentrations in peat. However, at Poplar post-fire, the average make-up for both the Burned and Unburned sites was on average 48-57% NO_3^- in peat, which can be attributed to the oxidation of NH_4^+ to NO_3^- from peat burning. Previous studies at Poplar (Nwaishi et al. 2015; Nwaishi et al. submitted; Wood et al. 2015) provided evidence on the potential for large oxidation of N following lowering of the WT over the growing season. However, the magnitude of increase in NO_3^- concentration observed in the Burned site was never observed in this site, even under dry conditions. Indeed this increase in NO_3^- concentration led to a dramatic shift in the ratio of dominant forms of inorganic N, and this has important implications on post-fire N mobility and off-site exports given the high mobility of NO_3^- relative to NH_4^+. The excess NO_3^- observed in the Burned site may have been supplied to the Unburned sites through groundwater-surface connectivity or wind erosion of ash. Our result supports this proposition, given that NO_3^- was considerably greater in surface leachate at the Burned sites, which is hydrologically connected to the Unburned site.

At the study fen, little mineralization occurred in the Burned sites, especially when compared to pre-fire studies that show high levels of nitrification and P mineralization for peatlands in the WBF (Nwaishi et al. 2015; Nwaishi et al. submitted; Wood et al. 2015). The lower rates of mineralization observed in the Burned site could be attributed to the loss of microbial biomass, through the burning of upper peat layer, which a represent a critical niche for microbial communities that mediate nutrient mineralization processes in peatlands (Mandic-Mulec et al., 2014; Elliot et al., 2015). These findings suggest that peatland fire could indirectly modify the cycling of N and P

through the direct effect of fire on the surface peat layer and microbial communities that dominate this critical niche.

Another significant finding of this study was the increase in available P after a fire. Similar to the work of Sulwiński et al. (2017), where a peatland 11-year post-fire had 6 times larger concentrations of available P. Our results show that available P was 5 times larger in the Burned sites compared to the Unburned site. The median seasonal value in the Burned site was 0.0093 mg/g and 0.0017 mg/g of peat for hollows and hummocks respectively, however, we see that this concentration of P in the Burned area is highest in the early season and decreases steadily over the growing season. In peatlands, P is geochemically reactive, especially in mineral-rich fens, where availability of P is limited by mineral control. Thus, the elevated P concentration in burned peat is likely due to the oxidation of peat resulting in the unbinding of organically locked P, which is usually bound to cations such as Ca^{2+}, Mg^{2+}, and/or Fe^{3+} in fens (Manzoni et al. 2010; Sulwiński et al. 2017). The observed increase in concentrations of available P in the Burned sites was consistent across all potential plant nutrient sources (i.e. peat, groundwater, and surface water). Notably, available P was highest in the Burned hollows, which could be a result greater burn severity in hollows than hummocks (Benscoter and Wieder 2003; Benscoter et al. 2005). Disturbance has been shown to cause increased nutrient input in groundwater due to the oxidation of peat (Wood et al. 2015; Plach et al. 2017; Nwaishi et al. submitted). Surface water infiltration through the ash layer at the Burned site allows for significantly larger concentrations of available P to be added to the groundwater, which remains apparent in groundwater where P concentrations are significantly higher than concentrations observed in the Unburned

sites. Surface infiltration of available P actually increased over the growing season, but groundwater concentrations decrease, which could be the result of a decreasing WT with a larger portion of the peat column being aerobic for surface water to infiltrate through. This infiltration over greater aerobic depths could potentially cause P binding to occur at lower depths where the peat layers were unaffected by the fire. The significant increase of P in these low nutrient peatlands can potentially lead pooled or standinf water in the fen becoming eutrophication, P loading in adjacent downstream aquatic ecosystems and vegetation shifts (Grygoruk et al. 2015). Further, vegetation shifts from post-fire regrowth can lead to the development of highly productive species, which have the ability to out-compete typical fen species, especially mosses that are critical for slow decomposition rates and net carbon sequestration function (Verhoeven et al. 1996; Sulwiński et al. 2017). The effects of increased P availability can be long-lasting (Zak et al. 2014) and when coupled with a warmer and drier climate, the resiliency of both the regrowth of fen species and the persistence of P effects has the potential to change fens like Poplar into a carbon source, changing its pre-fire ecosystem function (Schrautzer et al. 2013; Sulwiński et al. 2017).

2.4.2 Wildfire Disturbance on the Nutrient Stoichiometry Balance

Burned site N and P concentrations were higher than the Unburned site which will likely affect vegetation, litter quality and the oxidation and turnover of C (Moore et al. 2005; Güsewell and Gessner 2009; Manzoni et al. 2010). Elevated levels of N and P in the peat could affect microbial breakdown as the mismatch in the stoichiometry of peat and microbes could accelerate decomposition and change C sequestration functionality

(Wang et al. 2014; Nwaishi et al. submitted). The N:P ratio for vegetation was examined to assess potential alteration in nutrient limitation patterns for plant growth, relative to N:P imbalances of peat and groundwater nutrient reservoirs for the Unburned and Burned sites (Figure 2-3).

Based on the Redfield Ratio, plant growth is commonly classified as N or P-limited, when the N:P is smaller than 14 or larger than 16, respectively, with the possibility of co-limitation when the ratio falls between 14 and 16 (Koerselman and Meuleman 1996; Wang et al. 2014). In most peatlands, N is the limiting nutrient (Walker and Syers 1976; LeBauer and Treseder 2008) due to low mineralization rates and limited exogenous nutrient inputs in often isolated peatlands (Aerts and others 1992; Gunnarsson and Rydin 2000). However, this is probably not the case in our study site because as Poplar is located within the vicinity of active industrial development in the Alberta Oil Sands Region (Nwaishi et al. submitted). A previous study at Poplar (where it is denoted as the "Rich Fen") by Nwaishi et al. (submitted) found that both mosses and vascular vegetation were N-limited, while the peat and groundwater nutrient balance was dominated by N. This is consistent with other findings, which show that N:P ratios in plants do not reflect the N and P concentrations in peat or other potential nutrient sources (Güsewell and Koerselman 2002). Nwaishi et al. (submitted) also showed that an industry impacted peatland produced a reversal in N:P limitations, where vegetation shifted to P-limitations and nutrient balance in potential sources became dominated by P. Even though this was a different type of anthropogenic disturbance compared to Poplar's natural disturbance, we see that the oxidation of organic peat material, whether it is from drying or from fire, support the theory that

peatland disturbance results in a shift in N:P ratios in plants and potential nutrient sources. The main cause for the shift in N and P concentrations seems to be the result of increase P in the system due to peat oxidation and reduce P binding.

In this study, the N:P ratio of moss at the Unburned and Burned sites was 16 and 15 respectively, while vascular species was 29 and 24, respectively (Figure 2-5). This suggests the mosses were co-limited and vascular plants were P-limited at both sites. This is a shift in comparison to Nwaishi et al. (submitted) at this site where all plants were N-limited. We suggest that the resultant change in nutrient limitation is very likely due to the wildfire disturbance, increasing both N and P concentrations. At Poplar post-fire potential sources of nutrients include surface water, groundwater, and peat. For surface waters at both the Burned and Unburned sites, there was an imbalance of high P concentrations with an average N:P ratios of 4 and 6 respectively and peat had a higher N imbalance with an average N:P ratio of 43 and 51, respectively (Figure 2-5). Groundwater has higher P concentrations relative to N at the Burned site and the reverse at the Unburned site. This is indicative of the higher P concentrations at the Burned sites. In Nwaishi et al. (submitted) vegetation was N-limited and any potential nutrient sources (peat and groundwater) were P-limited. This comparison shows that across the entire site post-fire there was a shift in nutrient limitation, where vegetation shifted to co- or P-limitation. Peat remained similar to pre-fire values while groundwater in the Unburned site also remained P-limited and the Burned sites dramatically shifted from Nwaishi et al. (submitted) pre-fire values, shifting to N-limitation post-fire (Figure 2-5).

Clear differences in nutrient stoichiometry due to the fire were observed, with both C:N and C:P higher in the Burned sites. The C:N ratios ranging between 20 to 35 and 34 to 52 and C:P ratio between 393 to 522 and 673 to 975 for the Unburned and Burned sites respectively (Table 2-3). The amount of increased P at the Burned site is evident, however, there was also a significant increase in C levels as well, which possibly affected the C:P ratio. The imbalance between biomass production and decomposition is controlled by availability of P, moisture, and soil temperature, therefore the increase in P could lead to carbon storage post-fire if water level and soil moisture stay constant and high (Nwaishi et al. submitted; Bradford et al. 2008; Lavoie et al. 2011; Limpens et al. 2011). The fire also impacted the N stock, decreasing N stock by as much as 33% and changing the C:N ratio (Neff et al. 2005). As well, the Burned sites exceeded both critical threshold ratios (> 40 and > 200 for C:N and C:P respecively, meaning there is a microbial substrate limitation (Verhoeven 1986). Therefore is there is future aeration of the burned peat it will not lead to microbial peat mineralization (Verhoeven 1986; Nwaishi et al. submitted), further increasing the ability of recalcitrant C accumulation post-fire.

2.4.3 Carbon and Macronutrient Stock Post-Wildfire

The storage of carbon and nutrients is one of the primary functions of pristine peatlands (Vitt et al. 2009), therefore it is essential to understand the impact of fire on peatland C and nutrient storage. Turetsky et al. (2002) estimated that approximately 6500 Gt of C per year was released to the atmosphere just from peatland fires. Peatlands were also shown to have ~85% decrease in carbon uptake under post-fire conditions, with treed

fens, like Poplar, at higher risk of fire disturbance, which raises major concerns about the resiliency of peatlands to remain a C sink after wildfire (Turetsky et al. 2002). In a study of boreal forest 1-year post-wildfire, Neff et al. (2005) found that burned soil contained ~1100 to 1400 g/m^2 less C then the adjacent unburned areas. However, changes in nutrient stoichiometry in this study show an opposite effect in C stock where average C stock in the top 20 cm of peat was ~129000 and ~143000 kg/ha for the Unburned and Burned sites, respectively (Table 2-4). The C stock findings here were not expected, with C levels in peat being significantly higher in the Burned areas. The Burned site contained large amounts of ash in the new peat surface, as well as a difference in pre-fire peat substrate quality and vegetation difference in the peat margins could have resulted in a higher C stock in comparison to the Unburned site is observed. Depth of burn at the Burned Site ranged from 9.9 to 16.7 cm of peat loss, therefore if we conservatively say 10 cm of peat was lost overall for the burned areas, the peat surface of the Burned site is comparable to the 10 cm depth at the Unburned site. When the 0-10 cm C stock at the Burned site is compared to the 10-20 cm depth at the Unburned site, there is a difference of ~26272 kg/ha of C stock increase at the Burned site that is not explained and is outside of the acceptable standard deviation range. However, differences in peat quality and increased tree density and vegetation in the fen margins pre-fire could contribute to higher C stock after fire combustion in the Burned sites. Peatland margins are typically higher in vascular woody shrub density (Borkenhagen, 2013), and the Burn site had a lower tree density than the Unburned site (0.53 m^2 and 1.36 m^2 respectively), a higher average DBH (19.7 cm and 5.9 cm respectively) and a much taller trees (5.35 m and 1.5 m respectively) where all trees burned completely

during the fire and along with other vegetation could have added to the total C concentration through ash addition post-fire. Potentially "extra" C at the Burned site could also be the result of incomplete combustion of peat layers during the fire. Overall, the peatland margins where the Burned sites are located has increased input of C stock in the upper layers of peat which was unexpected and has never been observed in previous literature and could be potentially mitigate continued C loss from the Burned sites post-fire.

2.5.0 Conclusions and Implications for Post-Fire Fen Recovery

This study demonstrates the increased availability of P in peat post-fire, with only a slight elevation of NO_3^- across the entire sight. The increase in available P supports findings in other post-fire studies. However, the longevity of the effect of elevated P on plant productivity and C storage is still in question. Due to the isolated contamination of high P concentrations to the Burned sites, unlike NO_3^- post-fire shows higher concentrations at all sites, it is possible eutrophication due to high nutrient loading will be contained within the Burned sites due to an unburned buffer of peat. Peatland disturbance is proven to switch N- and P-limitation in vegetation, which can be used as functional biometric for assessing the potential nutrient limitations that can retard the recovery of pre-fire peatland vegetation assemblage. Poplar with increased P has the potential to increase biomass production, intaking CO_2 from the atmosphere, and reduce CO_2 respiration from microbial activity due to increase C:macronutrient ratios caused by the wildfire. Increased vegetation and tree biomass pre-fire in the Burned sites most likely lead to increased ash addition and a higher C stock (~14000 kg/ha) in

comparison to the Unburned site. Due to the increase P, vegetation productivity will increase in these Burned areas, and higher C stock and C:macronutrient ratios, coupled with decreased microbial activity will reduce microbial respiration. There is an overall likelihood that the Burned sites nutrient cycling will lead to C storage, however, the trajectory of recovery is unknown but the severity of burn may play a key role in increased nutrient availability and plant regrowth in the timeline for a return to the fen becoming a C sink post-fire.

3.0 Manuscript Chapter 2. Deeper Burning in a Boreal Fen Peatland One-Year Post-Wildfire Accelerates Recovery Trajectory of Carbon Dioxide Uptake

3.1 Introduction

Peatlands play a significant role in the global carbon (C) budget (Turetsky et al. 2002). C storage in northern peatlands is estimated to be ~795 Tg, equivalent to ~40% of atmospheric CO_2 (Wu and Roulet, 2014; Bridgham et al., 2006). Northern peatlands cover 3% of the Earth's terrestrial surface but contain approximately 30% of the global soil C (Gorham 1991; Blodeau, 2002). However, this C stock in Boreal peatlands could be vulnerable to oxidation as global temperatures continue to rise due to anthropogenic climate change (Blodeau, 2002; Wu and Roulet, 2014). However, climate change is not the only disturbance that may affect this function. Peatlands, especially in the Western Boreal Plains (WBP) are threatened by several l natural resource exploration activities (e.g. oil sands mining and development) as well as the spreading of forest fire into peatlands from upland forest areas. Fire ignition rates and area burned are predicted to increase under all global climate models, which will affect key elements of peatlands (e.g. vegetation, hydrology and nutrient dynamics), which regulates the C cycling processes (Flannigan et al. 2005; Krawchuk et al. 2009). The post-fire recovery, coupled with increased warming, will influence the resiliency of these ecosystems, affecting their critical C storage function.

The WBP covers 270 million ha, where wildfire is the primary natural disturbance due to the sub-humid climate and low rates of human fire suppression (Stocks et al. 2002). Wildfire is a naturally occurring phenomenon that is essential for a healthy life cycle of forests and surrounding areas (Flannigan et al. 2000). There is a correlated

increase in area burned and rising summer temperatures, and drying due to evapotranspiration (ET) rates exceeding precipitation (P) (Flannigan et al. 2006; Gillet et al. 2004; Roulet et al. 1992). Peatlands in the WBF are experiencing a regime shift to a warmer and drier climate, as well as an increase in forest fire disturbance (Tarnocai, 2006).. Shortened fire cycles are likely to increase peatland fire frequency, changing the function of peatlands from net C sinks to net C sources (Wieder et al. 2009). Northern peatlands have demonstrated their resilience to large-scale disturbance, including wildfire, over the past thousands of years by ultimately returning to a pre-fire function of C sequestration (Kettridge et al. 2015).

A major concern when peatlands experience drying is the drop in WT that increases the aerobic zone for decomposition and allows the upper layers of the peat to be vulnerable to burning (Belyea et al. 2009; Waddington et al. 2014). Limited fluctuations in the WT and the *Sphagnum* moss species that dominate most boreal peatlands allow for resistance to burning by retaining high surface moisture content (Waddington et al. 2014; Kettridge et al. 2015). However, shortened fire cycles in the WBP are likely to increase peatland fire frequency, changing the biogeochemical function of low-lying peatlands (Wieder et al. 2009). The burning of these upper layers of rich organic matter releases enormous quantities of C to the atmosphere and oxidizes locked up macronutrients in the peat (Zoltai et al. 1995). This release of C during the fire is coupled with a post-fire reduction in C uptake and growth of invasive species (Turetsky et al 2002; Benscoter et al. 2005).

Rapidly changing climate and temperature increases are putting the C sink function of peatlands in jeopardy, raising concerns about the net impact on the global

carbon balance (Charman 2002; Frokling et al., 2011). Peatlands are located in high latitudes, which are projected to be the most at risk regions to temperature increases (Wu and Roulet, 2014). There are many uncertainties that exist when trying to understand the role of C cycling in peatlands and how the delicate balance of net C storage will be impacted by these temperature changes (Moore et al., 1998; Wu and Roulet, 2014). The largest of the uncertainties is whether or not peatlands will continue to function as C sinks, or how this strength might be weakened, or even switched to a C source (Wu and Roulet, 2014). As noted earlier, wildfire rates and area burned are projected to increase, where fire from uplands may spread into adjacent peatlands accounting for an estimated annual 3.1 Tg C released due to combustion to the atmosphere (Turetsky et al. 2004). The projected response of peatlands to forest fire is concerning, but widely understudied and could be of the utmost importance for the future net C balance of peatlands. Post-fire emissions strongly depend on the response of hydrology and vegetation to wildfire (Wu and Roulet 2014).

Peatland fire in the WBP is estimated to release 6460 ± 930 Gt C yr^{-1} to the atmosphere (Turetsky et al. 2002). Disturbance from wildfire reduces the ability of WBP peatlands to uptake carbon by ~85% when compared to a non-disturbed scenario (Turetsky et al., 2002). An increase in forested area burned in Alberta, including thousands of low-lying peatlands dispersed throughout, calls for a re-evaluation of how these ecosystems will contribute to the Canadian C budget (Tymstra et al., 2007; Turetsky et al., 2002). Fire disturbances in the boreal forest resulting in a decreased C storage focus on damages to uplands but are not evaluated in the peat-accumulating lowlands (Turetsky et al., 2002). With increased fire ignitions, shortened fire interval and

a drying of wooded peatlands, a warming climate regime will increase peatland fires and the amount of combustible C, shortening the recovery time for peatlands to transition back to C sinks (Krawchuk et al., 2009; Kettridge et al., 2015; Turetsky et al., 2002). A chronosequence post-fire study of ombrotrophic treed bogs in Alberta by Wielder et al. (2009) using multiple sites between 1-102 years of post-fire recovery found that sites were a C source for approximately 13 years after fire.

Nutrient dynamics are essential for plant productivity and decomposition rates; hence, nutrient cycling is an important factor for C uptake in peatlands (Blodau, 2002; Wood et al., 2015). This suggest that the effect of fire on nutrient availability (Ref) will affect peatlands C cycling processes.

Microtopography in peatlands is unique as the system is a mosaic of high, drier hummocks and lower, wetter hollows, which can be separated vertically by up to 0.5 m (Benscoter et al., 2005). Post-fire environmental and nutrient conditions play an important role in the recolonization of peatland species after fire disturbance that affects this microtopography (Benscoter et al. 2005). Combustion and vegetation loss post-fire is highly variable and differs between microforms. Moss dominated hummocks resist extensive combustion while hollow vegetation burns to a much greater degree due to the greater moisture retention in hummock species (Benscoter and Wieder 2003; Benscoter et al. 2005). The post-fire succession of peatland vegetation will further modify the C-cycling and sequestration (Benscoter 2006), with pre-fire microtopographic gradient being a dominant influence on vegetation recolonization (Zoltai et al. 1995; Benscoter et al. 2005). The reestablishment of ground cover species, mainly moss species, is critical for returning a peatland to a C sink post-fire because of the high C

sequestration and low decomposition rates of mosses (Vitt et al., 2000; Benscoter 2006). Post-fire there are differing edaphic conditions due to peat combustion (Benscoter & Wieder 2003), including soil, moisture, the position from the WT, and surface deposition of charcoal that will affect recolonization of vegetation (Vitt 1990; Benscoter et al. 2005).

After wildfire, the resistance to combustion from different microtopographical species, along with an increase in nutrient availability from peat combustion, will affect vegetation regrowth and the rate of C uptake. However, it is unknown how the regrowth of plants and the degree of burning will change the CO_2 fluxes post-fire. Therefore, the goals of this study is: i) to characterize the temporal and/or spatial variability of CO_2 fluxes observed in the burned area of a fen peatland one-year post-wildfire relative to an unburned area; ii) determine the ecohydrological and edaphic factors that explain temporal and/or spatial variability.

3.2.0 Material and Methods

3.2.1 Carbon Flux Measurements

Instantaneous CO_2 fluxes from the peat surface were measured on a weekly basis along each transect, 12 chambers per site, over the growing season. A clear acrylic cylindrical chamber, with dimensions of 40 cm height and 20 cm in diameter, was placed over a plastic collar, 20 cm in height, placed permanently 15 cm into the ground for measurement. Instantaneous CO_2 concentrations in the chamber were measured with a portable infrared gas analyzer (EGM-4, PP Systems, Maryland, USA) with an integrated temperature/PAR sensor (TRP-2, PP Systems, Maryland, USA). Total

ecosystem respiration (R_{tot}) and net ecosystem exchange (NEE) was measured using the standard light/dark chamber approach (Solondz et al. 2008; Petrone et al. 2011) and gross primary productivity (GEP) was calculated as the difference between NEE and R_{tot}.

$$GEP = NEE - R_{tot} \qquad\qquad (1)$$

The chamber was lifted off a collar and inverted between 3 min runs, to avoid the build of gas between sample runs. Further, the top of the chamber contained a battery-operated fan to continuously circulate air inside of the chamber during measurements (CO_2 concentration, chamber air temperature, relative humidity and photosynthetic active radiation (PAR)), which were taken at 20-second intervals for 3 minutes. Measurements were taken between 9:00 and 16:00 in random in order to ensure a wide spectrum of PAR conditions during sampling over the season. CO_2 uptake by vegetation is represented by negative values, whereas release to the atmosphere is represented by positive values.

3.2.2 Vegetation Survey

A tree survey at all three transects was conducted in a 400 m^2 area to better understand how tree density and species could have affected burn patterns during the 2016 fire. The vegetation survey was conducted at the peak of vegetation growth at the end of June (Brown et al. 2010; Solonda et al. 2008) in each 300 cm^2 collar to assess vegetation cover between the Unburned and regrowth in the Burned sites. Both %

ground cover and stem count were used to study both moss cover and vascular plant density. Leaf area index (LAI) was calculated using samples from the field without destructive sampling from collars and taken back to the lab where an average LAI for each species was calculated using a Li-Cor LI-3100C Area Meter.

3.2.3 Available Nutrient Dynamics

Extractable pools of nitrogen (N) and phosphorus (P) were measured in all three transects during the growing season. Nutrient measurements captured three time periods during the growing season to understand the difference in nutrient availability after peat burning: Early (May), Middle (mid-June to mid-July), and Late (mid-August to mid-September). Extractable nutrient sampling techniques were used as described by Nwaishi et al. (2015), Hart et al. (1994) and Macrae et al. (2013) and are summarized below. For extractable nutrient availability, peat cores, approximately 10 cm deep, were taken from all three transects (4 hummock and 4 hollows), using a "dutch corer" with live vegetation removed from both cores. Cores were taken to the lab, on ice to be processed within 24 hours, for extractable levels of ammonium (NH_4^+), nitrate (NO_3^-) and soluble reactive phosphorus (SRP). Peat cores were hand homogenized before lab processing for extractable N and P, and involved the removal of two core sub-samples (10 g wet weight) from each sample and placed in a specimen cup. One sub-sample, processed for NH_4^+ and NO_3^-, was extracted with 50 ml of 2 M KCl. The second sub-sample, processed for SRP, was extracted with 50 ml of double deionized water. Both sub-samples with solution were shaken for 1 hour to fully dissociate the peat and nutrients, after which extractants were gravity filtered into another specimen cup using 1

mm porosity ashless filter paper (Whatman no. 42). All filtered extractants were frozen after filtering until they could be analyzed using colorimetric analysis at the Biogeochemistry Lab at University of Waterloo (Bran Luebbe AA3, Seal Analytical, Seattle, U.S.A., Methods G-102-93 (NH_4^+), G-109-94 (NO_3^- + NO_2), and G-103-93 (SRP)). According to Nwaishi et al. (2015) and Pote et al. (1996) the drying of samples can enhance extractable nutrient pools, therefore, field moist samples were used for all nutrient extractions. Moisture content, using a drying oven for 24 hours at 80 ^{o}C, with a sub-sample of each core was determined so that extractable nutrient pools could be expressed in per unit dry weight (Macrae et al. 2013).

3.2.4 Ground and Surface Water Dynamics

Surface water infiltration (shallow leachate) was measured by installing a 500 m^3 plastic lysimeter buried 5 cm below the surface of the peat with a mesh screening to allow only water to be collected. Water samples were collected within 24 h of rainfall events. Groundwater levels were measured weekly from shallow wells (5 cm ID, ~ 1m depth, screened through the entire well length). Water samples were collected monthly from these wells between May and September, and wells were purged 24 hours prior to sampling. Each transect had 4 infiltration lysimeters and 4 wells, split evenly between hollows and hummocks. All collected water samples were split into 3 sub-samples. The first sub-sample was gravity filtered into a specimen cup using 1 mm porosity ashless filter paper (Whatman no. 42) and frozen to test for anions, cations and bioavailable N and P. The second sub-sample was gravity filtered into a specimen cup using 1 mm porosity ashless filter paper (Whatman no. 42) for the analysis of total dissolved N and

P. A third sub-sample was left unfiltered for the analysis of total Kjeldahl N and P, including particulate matter. Both the second and third subsamples were preserved with acid (0.2% final H_2SO_4 final concentration) for storage and subsequently digested (after Parkinson and Allen 1975). The N and P species were analyzed using colorimetric analysis (described above). Major ions were analyzed using a Dionex ICS300. Lab analyses were completed in the Biogeochemistry Lab at the University of Waterloo.

3.2.5 Statistical Analysis

All statistical analyses were performed with R (R Development Core Team, 2013). All data for this paper were analyzed and tested for normality, however even with log transformations data set was not normal and nonparametric testing was used. To analyze for temporal and spatial effects, as well as environmental variables (vegetation regrowth, nutrient availability, WT, soil moisture and temperature) that may influence CO_2 fluxes (GEP, R_{tot}, and NEE) a Kruskal-Wallis Anova function for analysis of variance was run on all datasets (Chambers et al., 1992) for the effects of four potential variable differences: 1) temporal change over the growing season; 2) spatial differences based on DOB measurements; 3) the effect of wildfire; and 4) differences between microforms. To further our understanding of the effect of environmental variables on CO_2 fluxes, a hierarchical analysis using the R package "rpart" was used to make regression trees (Breiman et al. 1984). The "rpart" function was performed for GEP, R_{tot}, and NEE for both the Burned sites and the Unburned site to see if the environmental variables affecting CO_2 fluxes varied post-fire.

3.3.0 Results

3.3.1 Carbon Fluxes

Carbon dynamics varied throughout the season and among sites. In the early season, exchange rates were relatively small (Figure 3-2), but there was a noticeable peak at the end of July in both GEP and R_{tot} at the Unburned site In contrast at the Burned site there was a plateau where CO_2 uptake and output were maintained at a relatively similar levels from the beginning of July to the end of August (Figure 3-2). The uptake of CO_2 by vegetation photosynthesis (GEP) and output through combined soil and plant respiration (R_{tot}) both changed significantly ($p<0.001$) over the course of the growing season. At both the Burned and Unburned site there were no notable differences in CO_2 fluxes for hollows and hummocks. GEP and R_{tot} were also significantly reduced ($p<0.001$) by the wildfire in the Burned sites. NEE did not change significantly over the growing season or between the Burned and Unburned sites. However, when the CO_2 fluxes are broken down into Early (DOY 130-166), Middle (DOY 167-219), and Late (DOY 220-265) growing season, distinct trends in NEE can be seen (Table 3-1). NEE in the Unburned site for both microforms demonstrates a net uptake of CO_2 in the Early and Middle growing season, but a net release to the atmosphere later in the season. In comparison, hollows in the Burned site in the Early growing season have a net release and net CO_2 uptake in the Middle and Late season. The Burned site hummocks was a slight net uptake in the Early period, a slight average net release in the Middle and an average net uptake of CO_2 in the late growing season (Table 3-1).
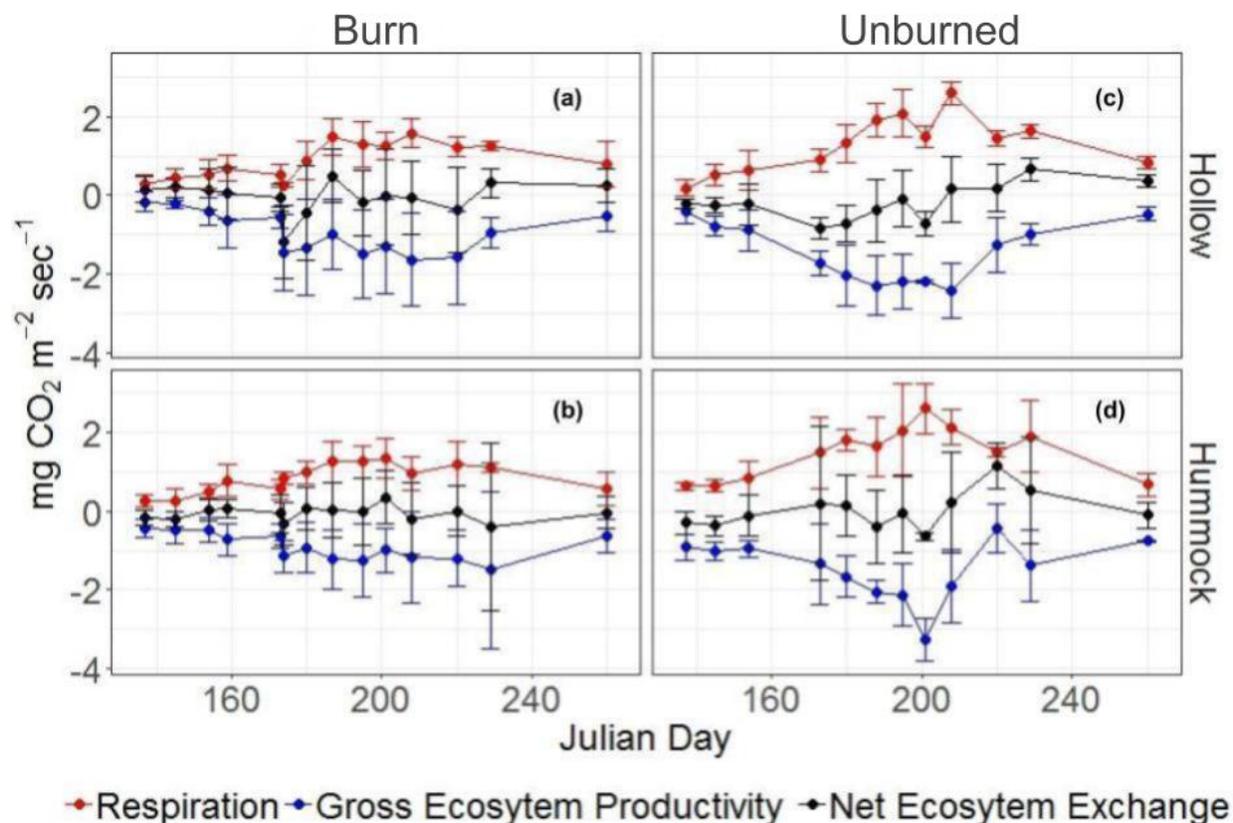
Figure 3 - 1. CO_2 fluxes over the growing season (May to September) at the Poplar fen showing the Burned sites, (a) and (b) for hollows and hummocks, respectively, and for the Unburned site with (c) and (d) for hollows and hummocks, respectively. CO_2 fluxes are shown as R_{tot} (red), GEP (blue), and NEE (black).

Table 3 - 1. Poplar fen CO_2 fluxes from the Unburned and Burned sites split by microtopography. Fluxes are shown as an average with the standard deviation in parentheses over the growing season in three periods: Early (DOY 130-166), Middle (DOY 167-219), and Late (DOY 220-265).

Site	Microform	GEP			Resp			NEE		
		Early	Middle	Late	Early	Middle	Late	Early	Middle	Late
Unburned Site	Hollow	-0.717 (0.4)	-2.138 (0.6)	-0.943 (0.5)	0.481 (0.4)	1.743 (0.7)	1.349 (0.4)	-0.235 (0.3)	-0.395 (0.7)	0.406 (0.4)
	Hummock	-0.959 (0.2)	-1.946 (0.8)	-1.701 (0.9)	0.706 (0.3)	1.898 (0.8)	1.787 (0.8)	-0.253 (0.4)	-0.038 (1.1)	0.098 (1.1)
Burned Site	Hollow	-0.395 (0.5)	-1.258 (1.1)	-1.102 (1)	0.519 (0.3)	1.137 (0.6)	1.081 (0.4)	0.127 (0.5)	-0.121 (1)	-0.022 (0.8)
	Hummock	-0.53 (0.3)	-1.065 (0.8)	-1.008 (0.8)	0.48 (0.3)	1.077 (0.5)	0.935 (0.5)	-0.05 (0.3)	0.011 (0.7)	-0.067 (0.8)

The burning of Poplar caused notable differences in the CO_2 fluxes between the Unburned and Burned sites, and along the burn severity (DOB) gradient (Figure 3-3). GEP varied significantly ($p < 0.01$) with the depth of combusted peat ranging from 9.9 to 16.7 cm at the Burned sites. With the deepest burned area, we see that average uptake of CO_2 is highest for the Burned sites and the most similar to the Unburned area (denoted by 0 cm DOB). For R_{tot}, there is a similar trend; however, there is no significant variation with DOB. R_{tot} for the Burned site was highest with a 16.7 cm DOB, which was still substantially less than the Unburned site (Figure 3-3). NEE also varied along a DOB gradient with a significant difference ($p < 0.01$), where the deepest burned area the range in NEE was more negative (increase in net uptake of CO_2) than even the Unburned site.
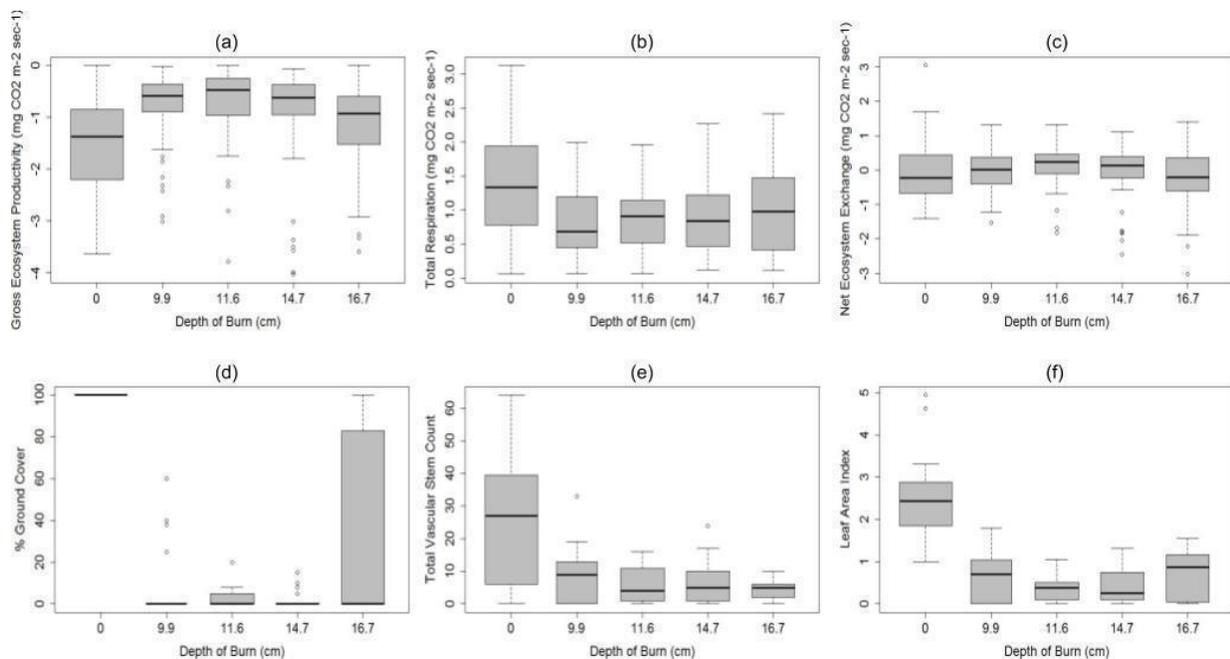
Figure 3 - 2. CO_2 fluxes and vegetation characteristics over a depth of burn (DOB) gradient, where 0 cm represents the Unburned site, and the Burned sites range between 9.9 to 16.7 cm of peat lost to combustion.

3.3.2 Environmental and Vegetation Patterns and Controls on CO_2 Fluxes

Both WT and soil moisture decreased significantly towards the end of the growing season ($p < 0.001$). Soil temperature and WT varied significantly between microforms ($p < 0.001$) (Table 3-2), where hollows had higher water tables, higher soil moisture and lower soil temperature than hummocks (Table 3-2). Only WT varied significantly ($p<0.0001$) between the Burned and Unburned sites (Table 3-2). Photosynthetically active radiation (PAR) did not vary between sites, however, it did significantly decrease ($p<0.05$) with increasing DOB, with the deepest burned hollows receiving more shade from surrounding hummocks. Soil moisture, temperature, and WT were significantly ($p<0.001$) affected by DOB, where the deepest burned areas had lower soil temperatures, a higher WT, and increased soil moisture.

Table 3 - 2. Average environmental conditions, with standard deviation in parentheses, over the growing season for the Unburned and Burned sites, partitioned by microtopography.

		Unburned Site		Burned Site	
Environmental Variable		Hollow	Hummock	Hollow	Hummock
Water Table	(cm)	-9 (12.5)	-27.2 (18)	-17.3 (16.1)	-50.4 (22)
Soil Moisture	(% VWC)	28 (22.2)	7.5 (4.8)	28 (16.7)	7.5 (5.2)
Soil Temperature	(°C)	17.4 (5.3)	18.1 (4.7)	16 (5.3)	17.3 (5.2)
PAR	(μmoles m^{-2} s^{-1})	945.9 (491)	976.3 (536.6)	827.4 (457.3)	928.8 (466.6)

In general, the concentration of all nutrient forms increased or decreased significantly over the growing season ($p <0.05$), however growing season trends for NO_3^-, NH_4^+ and P all differed. NO_3^- was lowest in the middle of the growing season, NH_4^+ was highest at the end of the growing season, and P concentrations were highest early in May and June in peat and groundwater, but lowest in the surface water leachate. Available nutrients and nutrient sources varied with microtopography;

however, available nutrients were generally higher in hummocks in the Unburned site but higher concentration were generally seen in hollows at Burned sites (Table 3-3). P was always higher (p < 0.001) at the Burned site (Table 3-3), and increased DOB resulted in higher concentrations of available P in both peat and surface water P (p < 0.01).

Table 3 - 3. Average available N and P from peat, groundwater and surface water infiltration, with standard deviation in parantheses, over the growing season from the Unburned and Burned sites partitioned by microtopography.

	Available Nutrients		Unburned Site		Burned Site	
			Hollow	Hummock	Hollow	Hummock
Peat	NH_4^+	(mg/g)	0.045 (0.017)	0.033 (0.006)	0.039 (0.015)	0.045 (0.019)
	NO_3^-	(mg/g)	0.042 (0.031)	0.035 (0.022)	0.045 (0.012)	0.042 (0.013)
	P	(mg/g)	0.012 (0.012)	0.006 (0.008)	0.024 (0.024)	0.041 (0.052)
Groundwater	NH_4^+	(mg/L)	0.504 (0.367)	0.535 (0.384)	0.368 (0.492)	0.235 (0.187)
	NO_3^-	(mg/L)	0.222 (0.14)	0.244 (0.24)	0.277 (0.147)	0.288 (0.359)
	P	(mg/L)	0.041 (0.057)	0.018 (0.019)	0.131 (0.087)	0.306 (0.204)
Surface Water	NH_4^+	(mg/L)	0.118 (0.108)	1.537 (0.192)	1.415 (1.542)	1.263 (0.194)
	NO_3^-	(mg/L)	0.807 (0.685)	0.255 (0.03)	1.391 (1.383)	0.472 (0.192)
	P	(mg/L)	0.246 (0.158)	0.87 (0.309)	1.727 (0.941)	1.372 (0.99)

The ground surface in the Unburned site was entirely covered by moss species, whereas the Burned sites had on average less than 20% moss regrowth, with the rest of the surface being charred bare peat (Table 3-4). Further, vascular plant growth was significantly reduced in (p<0.001) in the Burned sites in comparison to the Unburned site. A large portion of the vascular plant regrowth was *Equisetum sylvaticum* (Wood Horsetail), which is typically an upland species; however, all other vascular species in

the Burned sites were also found in the Unburned site (Figure 3-4). Due to the minimal regrowth in both ground cover and vascular plants, the LAI at the Burned site was significantly ($p<0.001$) less than the fully-grown Unburned site. There was also a significant ($p<0.001$) difference in the regrowth of vegetation in the Burned site along the DOB gradient. The deepest burned areas (16.7 cm) had the highest average moss regrowth, typically *Polytrichum spp.* (Figure 3-4), the lowest vascular plant cover, and highest average LAI in the Burned sites (Figure 3-3).
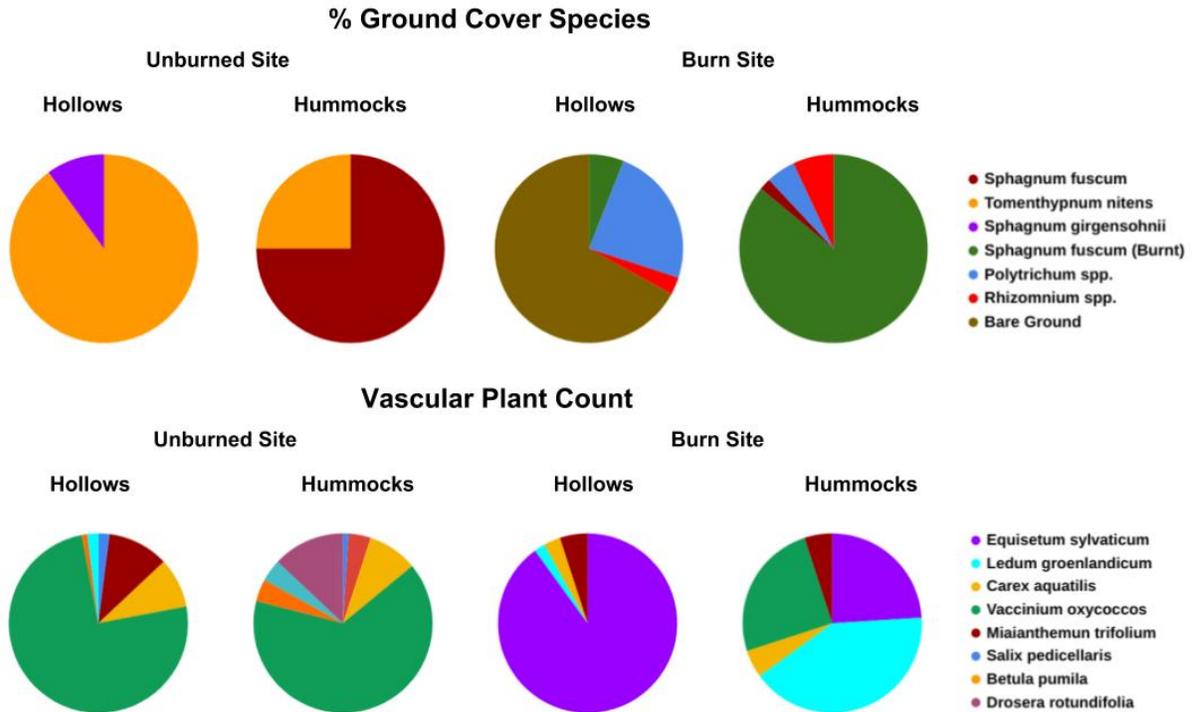

Figure 3 - 3. Pie charts indicating the % cover of ground species (top) and the average number of vascular stems (bottom) from the vegetation survey at peak growing season at the Unburned and Burned sites, with microtopographic (hollow and hummock) differences.

Table 3 - 4. Average vegetation characteristic with the standard deviation in parentheses over the growing season from the Unburned and Burned sites, partitioned by microtopography.

		Unburned Site		Burned Site	
Environmental Variable		Hollow	Hummock	Hollow	Hummock
Moss Cover	(% ground cover)	100 (0)	100 (0)	16 (31)	5 (11)
Vascular Plants	(stem count)	24 (18)	26 (22)	5 (7)	9 (7)
LAI	(dimensionless)	2.23 (0.77)	2.84 (1.16)	0.62 (0.58)	0.53 (0.43)

To better understand the different controls on CO_2 dynamics among the sites, a hierarchical regression tree was used to determine the primary environmental controls on CO_2 fluxes (Figure 3-5). For the Unburned sites, soil temperature was the primary control for all CO_2 fluxes, with the exception of WT being the primary control on NEE in hollows. In the Burned site, the main environmental variable controlling post-fire CO_2 fluxes was LAI, with the exception of R_{tot} and NEE in the Burned hollows being more influenced by WT (Figure 3-5). Due to the dominance of LAI control on post-burn CO_2 fluxes the regression tree for the primary controls on vegetation regrowth were analyzed. Available peat nutrients were the primary control affecting LAI at both sites. However, NO_3^- was the primary control in the Unburned site and P in the Burned site (Figure 3-5).
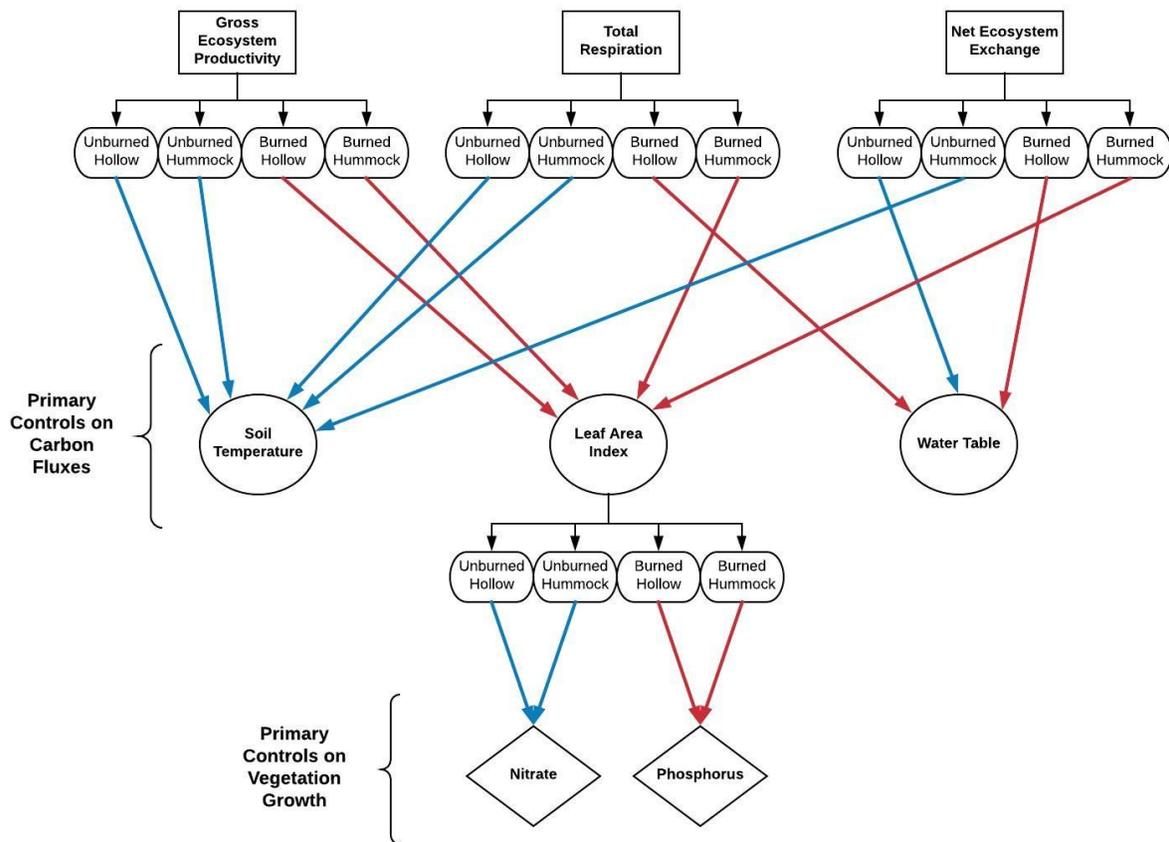
Figure 3 - 4. Regression tree hierarchical analysis of the primary controls on CO_2 fluxes and LAI for the Unburned and Burned sites, along with microtopographic differences. Red lines denote the Burned site, and blue lines the Unburned site.

3.4.0 Discussion

3.4.1 CO₂ Fluxes Post-Wildfire

The increase in fire frequency (Flannigan et al. 2005) has the potential to increase severity and quantity of organic matter and vegetation removal in peatlands (Maltby et al. 1990; Lukenbach et al. 2017) resulting in favorable conditions for peat decomposition and CO_2 release (Hogg et al. 1992). Peatlands post-fire are commonly thought of as C sources to the atmosphere from ~13 to 20 years after burning (Wielder et al., 2009). However, the magnitude to which peatlands become a source and how DOB variability affects C fluxes is often overlooked. This study shows that GEP was reduced in

magnitude at the Burned sites overall, however at the Unburned site peak C uptake was similar to typical peak growing season (Brown et al. 2010; Solonda et al. 2008), while the Burned site peaked later in the growing season (early August). The later peak in C uptake at the Burned site is likely from late vegetation recolonization due to partial or complete vegetation removal from the fire (Figure 3-2). Further, deeper burning increases the uptake of C than moderately burned areas (Figure 3-3).

In the Burned sites, the R_{tot} decreased in magnitude during the peak season (late June and July) when soil temperature is highest and WT was low, causing favorable conditions for microbial respiration (Figure 3-2). Ash addition has been shown (Hogg et al. 1992) to inhibit respiration in peat soil due to increased resistance to decay, reducing carbon loss over the entire peat column, which is observed here (Figure 3-2). However, when deeper peat burning is examined (pre-fire surface layers of 10 to 20 cm peat) deeper burning (16.7 cm) had higher rates of R_{tot} relative to more moderately burned peat (Figure 3-3). This increase in R_{tot} in deeper burned areas can be attributed to the increase in LAI observed, due to the increased vegetation. This is considered a "priming effect", where there is an increase in both above and belowground biomass that becomes a source of labile C for microbial activity, which is an indicator for recovery (Kuzyakov et al. 2000). Further, the increase in vegetation causes both R_{tot} and GEP increases due to increased autotrophic respiration and vegetation productivity, respectively (Waddington et al 2010).

Due to a decrease in both GEP and R_{tot}, NEE at the Burned sites was similar to the Unburned site. However, there is a difference in timing when NEE becomes a C sink (Figure 3-2). For the Unburned site, NEE is greatest (most negative) in mid-June,

whereas the Burned areas peak in early August, demonstrating that post-disturbance there is a temporal shift in the peak CO_2 uptake. It has been found that in terms of atmospheric emissions most burned natural peatlands become CO_2 neutral because limited surface peat burning and released carbon being rapidly re-sequestered by recovering vegetation; however, this neutrality of C can take decades (Frolking et al. 2011; Turetsky et al. 2014). In this study, spatial differences in NEE are observed, where the deepest burned areas have the greatest CO_2 sink potential, sometimes exceeding CO_2 uptake in the Unburned areas (Figure 3-3). With the deepest burned areas having a greater CO_2 sink potential, the carbon budget for Poplar could return to a C sink function quicker. However, even with CO_2 being relatively neutral, both methane (CH_4) and dissolved organic carbon (DOC) research is required to fully understand whether Poplar post-fire is a C sink or source on an ecosystem scale.

3.4.2 Environmental Variables and Vegetation Effects on Post-fire CO_2 Fluxes

Peat combustion differs between microtopographic features (hummocks and hollows), with hummock mosses having a greater water-holding capacity and a reduced burning vulnerability (Shetler et al. 2008; Benscoter et al. 2001; Turetsky et al. 2014; Benscoter et al 2011). At Poplar, similar to other peatlands (Benscoter and Wieder 2003; Shetler et al. 2008), there was extensive combustion in the low-lying hollows and slight combustion in hummocks where *Sphagnum* moss had the photosynthetic capitula burned off with the rest of the moss slightly singed (McCarter and Price, 2014). If the climate change induced drying that causes peatlands to be more vulnerable to burning persists post-fire, warming could stimulate vascular and tree growth while reducing

moss productivity, resulting in a diminished C sink function and more frequent and severe peatlands fires (Turetsky et al 2014). However, there is the potential for initial deep burning to allow more surface water-groundwater connectivity, increased P availability and moss recolonization that can cause a negative feedback (Figure 3-6) leading to the peatland to be more resilient when the next fire occurs.
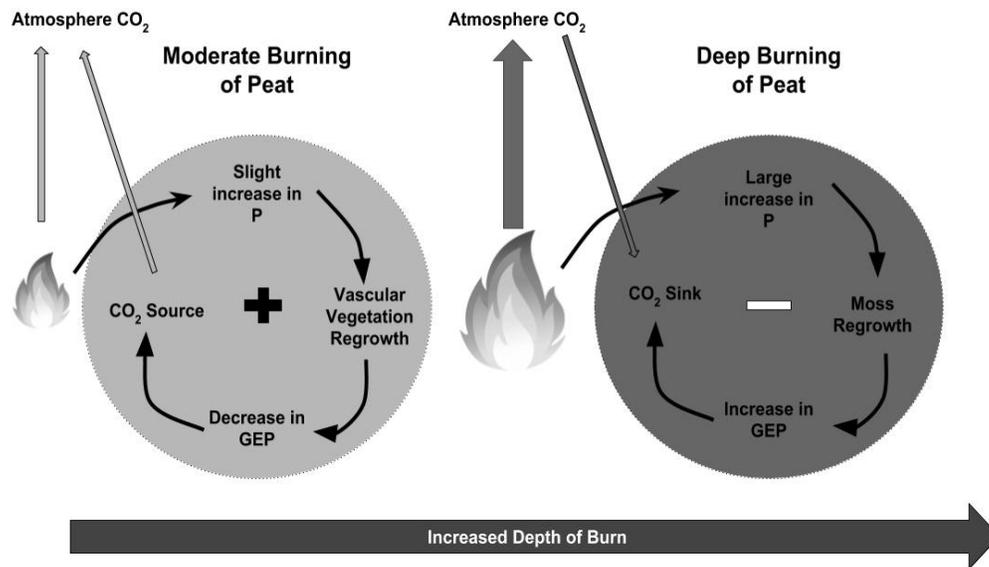
Figure 3 - 5. With increasing DOB in peatlands, there is evidence that increased P and moss regrowth results in greater CO_2 uptake and C sink potential, which over time has a faster trajectory to sequestering C lost to the atmosphere from the initial wildfire.

Bare peat after industrial disturbance has been shown to be a persistent source of CO_2 (Petrone et al. 2003; Waddington and Warner 2001) and *Sphagnum* moss species reestablishment is integral to the return of C sink functionality (Waddington et al. 2010). In most industry-disturbed peatlands P fertilizer is often applied to promote rapid vascular species recolonization, which are companion species to *Sphagnum* mosses (Rochefort et al. 2003; Waddington et al. 2010). This is similar to the natural increase in available P that is found in the Burned sites caused by peat burning. P availability increases with deeper burning, along with the recolonization of mosses, but vascular plants growth is lowest in the deepest burned areas, therefore potentially moss

recolonization is able to out-compete vascular plant for the increase in P (Figure 3-3). Wildfire in boreal peatlands can cause successional change promoting the recolonization of pioneer species (Benscoter and Vitt 2008; Waddington et al. 2010). The moss growing back at the Burned sites in the hollows where all the vegetation was removed by the fire is dominated by *Polytrichum spp.* moss (Figure 3-4). *Polytrichum spp.* has been found to be a pioneer species in peatlands undergoing restoration and due to its high tolerance to desiccation and aid in the reestablishment of Sphagnum species (Groeneveld and Rochefort, 2005; Waddington et al. 2010). Having *Polytrichum spp.* growing post-fire is a good indicator of recovery of pre-fire C functioning. Other disturbed peatlands have had *Polytrichum spp.* dominate in the early stages of recovery, which when combined with a WT increase, produced over a 200% increase in C sink function within 3 years (Waddington et al. 2010).

Deeper burned hollows saw the highest moss recolonization but had, on average, a lower water table over the growing season (Table 3-2), which could be due to the Burned sites being located in peatland margins where increased water table fluctuations are common (Lukenbach et al. 2017). Precipitation in 2017 was highest in late-May and June, with the rest of the growing season experiencing below average precipitation, therefore high water tables early in the season when moss recolonization was beginning could be the key to higher moss regrowth, regardless of the moisture regime in the later season.

The Burned sites are located closer to the uplands in the peatland margins where nutrients from groundwater are regulated (Dimitrov et al., 2014a; Hartshorn et al., 2003), and since these areas experience deeper rates of burning (Lukenbach et al. 2017) the

increase in available P in burned areas is a significant control on the regrowth of vegetation (Figure 3-5). Lukenbach et al. (2017) found that post-fire recolonization rates were highest in peatland margins with low connectivity to sandy adjacent uplands typical of boreal forest, resulting in a nutrient-poor environment. However, this study finds that the high levels of P in the burned margins are the primary control of vegetation growth in burned areas.

Hydrologic conditions post-fire can be altered by DOB due to hydrophobicity in peat reducing water availability to vegetation regrowth (Lukenbach et al. 2015; Kettridge et al. 2015) However, Lukenbach et al. (2015) found that deeper burning in peatland margins had high water availability and, in this study, there was a significant increase in the available nutrients to plants. If the overall function of concern for peatlands is C sequestration, nutrient availability, mainly P, could be more important than the hydrologic conditions in establishing pioneer mosses and Sphagnum species regrowth (Figure 3-5).

3.5.0 Conclusions and Implications for Post-fire Peatland Carbon Function

In the Unburned site, soil temperature is the dominant environmental control on CO_2 fluxes (Figure 3-5), which is common in peatland literature (McKenzie et al. 1998; Waddington and Warren 2001) and could be used as a recovery indicator. The peatland margins where the Burned sites are located represent a small portion of the peatland, but can account for over 50% of the total carbon lost during the fire (Hokanson et al. 2016). However, we see that deeper burning in the peatland margins increases P availability due to more peat oxidation from fire, which leads to an increase in moss

regrowth (Figure 3-3). Peatland disturbance and climate warming have been shown to shift plant communities to more shrub and tree dominated systems, increasing CO_2 emissions to the atmosphere (Weltzin et al., 2000; Camill, 1999; Lohila et al., 2011; Blodau and Siems, 2012). The deepest burned areas, which were the most vulnerable to disturbance pre-fire, have increased moss growth and reduced vascular plants post-fire compared to more moderately burned areas. This increased moss growth is a key indicator of more rapid recovery and a shortened trajectory to a return in C sink function (Figure 3-6). Previous literature has shown that recolonization of key species to peatland C sequestration (*Sphagnum* mosses) post-fire rely on hydrologic conditions post-fire (Lukenbach et al., 2015; Lukenbach et al., 2017; Kettridge et al. 2015), but the environmental controls on moss recolonization may be more dynamic. Increased burning results in increased P availability and in-turn is a more dominant control on moss recolonization, resulting in a greater uptake of CO_2 from the Burned sites and may be a key to C sequestration and long-term resilience creating a negative feedback to fire disturbance (Figure 3-6) (Tilman et al., 2006; Salonen, 1994; Lukenbach et al. 2017).

4.0 Summary and Recommendations

This study overall demonstrates that bioavailable P becomes unbound to organic material in peat due to oxidation from the fire and the concentration of P increases with deeper burning. New moss vegetation, especially in the deepest burned areas, outcompete vascular vegetation and rely on the increased bioavailable P to regenerated post-fire. The deepest burnt hollows are shown to have the highest amount of moss regrowth post-fire and the greatest capacity to uptake CO_2 (GEP) and function more similar to the Unburned sites. Overall the deepest burnt hollows have a slight negative NEE, meaning CO_2 is being stored, in comparison to the burned areas of the fen when NEE is positive and carbon is being released to the atmosphere.

The increase in available P supports findings in other post-fire studies. However, the longevity of the effect of elevated P on plant productivity and C storage is still in question. Peatland disturbance is proven to switch N- and P-limitation in vegetation, which can be used as functional biometric for assessing the potential nutrient limitations that can retard the recovery of pre-fire peatland vegetation assemblage. Poplar with increased P has the potential to increase biomass production, intaking CO_2 from the atmosphere, and reduce CO_2 respiration from microbial activity due to increase C:macronutrient ratios caused by the wildfire. Increased vegetation and tree biomass pre-fire in the Burned sites most likely led to increased ash addition and a higher C stock (~14000 kg/ha) in comparison to the Unburned site.

There is also a clear dichotomy in the environmental control on CO_2 fluxes (Figure 3 - 5), where soil temperature is the dominate control on the Unburned site and LAI (vegetation cover) is the dominant control in the Burned sites. Peatland disturbance

and climate warming have been shown to shift plant communities to more shrub and tree dominated systems, increasing CO_2 emissions to the atmosphere (Weltzin et al., 2000; Camill, 1999; Lohila et al., 2011; Blodau and Siems, 2012). The deepest burned areas, that were the most vulnerable to disturbance pre-fire, have increased moss growth and reduced vascular plants post-fire compared to more moderately burned areas. This increased moss growth is a key indicator of more rapid recovery and a shortened trajectory to a return in C sink function (Figure 3 - 6).

Due to the increase P, vegetation productivity will increase in these Burned areas, and higher C stock and C:macronutrient ratios, coupled with decreased microbial activity will reduce microbial respiration. There is an overall likelihood that the Burned sites nutrient cycling will lead to C storage, however, the trajectory of recovery is unknown but the severity of burn may play a key role in increased nutrient availability and plant regrowth in the timeline for a return to the fen becoming a C sink post-fire. Environmental controls on moss recolonization may be more dynamic than once thought. Increased P availability is the dominant control on moss recolonization post-fire and results in a greater uptake of CO_2 from the Burned sites and may be a key to C sequestration and long-term resilience creating a negative feedback to fire disturbance (Figure 6) (Tilman et al., 2006; Salonen, 1994; Lukenbach et al. 2017).

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