Nutrient and Hydrologic Conditions Post-Fire: Influences on Western Boreal Plain Aspen (*Populus tremuloides* Michx.) Re-establishment and Succession

by

Midori Depante

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Master of Science
in
Geography

Waterloo, Ontario, Canada, 2016

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

The Western Boreal Plains of Alberta (WBP) contains a mixture of peatlands and forests, with the latter dominated by trembling aspen (*Populus tremuloides* Michx.). Given the sub-humid climate of the WBP, where evapotranspiration (ET) often exceeds precipitation (P), uplands are usually dependent on peatlands for water supply. The process of hydraulic redistribution (HR), the transfer of water from one area to another through roots, is a mechanism by which aspen obtain moisture from peatlands. However, the effects of disturbances such as fire on this process remain unknown, and it is uncertain if connectivity between land units through HR continues post-fire. During May 2011, a wildfire affected 90 000 ha of north central Alberta including the Utikuma Region Study Area (URSA). Portions of a glacio-fluval outwash lake catchment was burned which included forests and a ~0.5 ha peatland. Within one year after the fire, aspen were detected in peatlands and at peatland margins.

The purpose of this study was to monitor aspen recovery across a burned hillslope, and determine if nutrients, soil moisture conditions, or both were sufficient to permit regeneration in peatlands. The role of aspen in peatlands in forest recovery was also investigated. Across recovering land units in 2013 and 2014, plot transpiration (E_{plot}) measurements were taken to evaluate stress levels where on average midslope (0.42 mm hr^{-1}) > hilltops (0.29 mm hr^{-1}) > riparian (0.23 mm hr^{-1}) > peatlands (0.095 mm hr^{-1}); similar trends were observed with leaf area and stem heights. To determine if aspen required excess nutrients for regeneration, plant available nitrate (NO_3^-), ammonium (NH_4^+), and water extractable phosphorus (Ext-P) were measured in both growing seasons. While Ext-P remained elevated with the highest levels in burned peatlands, aspen stem height and leaf area were not greatly dependent on P. Similarly, negative relationships with growth were observed with increasing soil moisture content (VWC). Although VWC was below field capacity (<25%) in forests, *P. tremuloides* were sustained through roots present, likely before fire, in peatland margins through hydraulic redistribution. Evidence for this was observed in oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) isotopes (‰) where upland xylem and peat core signatures were -10.0 ‰, -117.8 ‰ and -9.2 ‰, -114.0 ‰, respectively, highlighting their importance in hydrologically connecting forests to water sources.

This study showed that while peatlands were resource rich post-fire, aspen was able to regenerate in nutrient and moisture-poor forests and that peatlands are unsuitable areas for further re-establishment. This research also highlighted the significance of hydraulic redistribution to forest recovery. The continuation of HR and water table fluctuations however, may result in soil moisture changes and the encroachment of aspen. Therefore, peat margins post-disturbance may be at risk during succession resulting in margin loss.

Acknowledgements

First and foremost, I thank my supervisor, Dr. Rich Petrone, for providing me with this opportunity to work on this research. I am especially grateful for your unending calm, patience, and support that have helped carry me through these last two years.

I also thank Dr. Kevin Devito for your guidance in the field, willingness to always talk science and data, and for asking challenging, yet thought rendering questions. Many thanks to Drs. Merrin Macrae and Janina Plach for your advice, enthusiasm, and encouragement throughout my graduate studies.

Thank you to George Sutherland, Scott Brown, Corey Wells, and the members of the UW EIL group for your technical support, and always being one phone call or step away to answer any questions.

This research would not have been completed without my army of field assistants: Aryn Cain, Sarah Irvine, Hillary McDougall, Patrick Pow, and Greg Carron. I couldn't have imagined a harder working group of students, and without your help, would still be at URSA taking porometry measurements. Thank you to the McMaster, UofA, and U of Birmingham field crews, along with the UW Hydromet group for your comradery and insightful discussions.

Thanks to Maren Pauly and Tatianna Lozier: I wouldn't have chosen better friends to share grad school, laughs, and nachos with.

I thank my family for being my biggest fans, and for your well thoughts and prayers. Finally, Jordan Rebelo, thanks for your love and free therapy.

Table of Contents

List of Figures

List of Tables

1.0 Introduction

The Western Boreal Plains (WBP) of Canada covers approximately 650,000 km^2, and contains a mixture of forests and peatlands. Within this area, the WBP has been highly subjected to natural and anthropogenic disturbances, with the latter encompassing mining, harvesting, oil exploration, and fire (Rooney *et al.*, 2012). While the former serve as economical importance through resource extraction, controlled burns and wildfires are of ecological significance.

Evapotranspiration often exceeds precipitation in the WBP (Devito *et al.*, 2005; Brown *et al.*, 2010), which makes this ecozone more susceptible to fire. Periodic fires however, are needed to maintain system heterogeneity through the destruction of current stands, which creates conditions suitable for regeneration (Weber and Stock, 1998). In recent studies in the WBP in Alberta, pre-fire conditions have been used to determine burn severities, the amount of organic matter lost, including vegetation cover type and age, soil moisture, hydrologic connectivity, and organic matter content (Lukenbach *et al.*, 2015a; Hokanson *et al.*, 2015). Further, positive correlations with burn severity typically exist with changes in soil properties including hydrophobicity, chemistry, erosion, and runoff (DeBano, 1973; Huffman *et al.*, 2001). Thus, within a landscape, as seen in Boreal forests, burn severities can vary spatially between low, moderate, and high resulting in differences in plant re-establishment (Ryan and Noste, 1983; Turner *et al.*, 1994; Smith *et al.*, 2003). For example, the consumption of fire removes canopy cover and surface organic matter allowing for sunlight, nutrient mineralization, and increased soil temperatures (Weber and Stock, 1998). Depending on the severity of the fire, post-fire conditions often favour the regeneration of species previously suppressed before disturbance (Weber and Stock, 1998). For example, most coniferous trees depend on fire for the release of seeds from cones at temperatures above 50 °C, whereas poplar species, such as balsam poplar, initiation is best on mineral seedbeds and when sunlight is not limited which occur at high severity fires (Mutch, 1970; Weber and Stock, 1998). Therefore, fires often initiate the immediate succession of species that thrive in resource rich environments, such as trembling aspen (*Populus tremuloides* Michx). Aspen are widely distributed across Canada; they are present in all provinces and territories (Peterson and Peterson, 1992). Although aspen have large resources stores in their extensive rooting zone and often require fire for regeneration, increased fire return frequencies may inhibit clone regeneration through the exhaustion of reserves (Schier and Campbell, 1978; Schier *et al.*, 1985). This may affect the hydraulic redistribution of water and nutrients to surrounding forested areas and upper soil layers facilitated by their rooting system (Lazerjan, 2014). While most of these findings have been recorded in forested areas in Western Canada, there has been limited research on immediate and longer-term succession peatland tree species post-fire.

Wetlands cover 50% of WBP; of these, peatlands make up approximately 40% of Alberta's landscape (Vitt *et al.*, 1996; Turetsky *et al.*, 2004). With over 500 km^2 of peatlands loss through fire every year in Western Canada, they have received increasing attention due to the release of stored carbon (Turetsky *et al.*, 2003; Lukenbach *et al.*, 2015a; Kettridge *et al.*, 2015; Hokanson *et al.*, 2015). Although the fire return interval of Boreal forests ranges from less than 100 to 500 years (Stocks *et al.*, 1996), peatland fires occur approximately every 120 years (Turetsky *et al.*, 2011). Given the amount of time required for peat accumulation and formation increased fire frequencies may affect their succession trajectories. They are often resilient to burning in part due to the ability of sphagnum to retain moisture and water availability reducing the extent of combustion (Shetler *et al.*, 2008; Waddington *et al.*, 2015). Recent findings, however, have found that differences in peat properties, such as bulk density and moisture, increase the vulnerability of peatland margins to fire especially under dry climate cycles (Dimitrov *et al.*, 2014; Lukenbach *et al.*, 2015a; Kettridge *et al.*, 2015; Hokanson *et al.*, 2015).

Water limitation is often linked to fluctuations in water table depths and soil moisture, thus increasing the vulnerability of the region to high severity fires through the extensive loss of organic matter (Dimitrov *et al.*, 2014; Lukenbach *et al.*, 2015a; Kettridge *et al.*, 2015; Hokanson *et al.*, 2015). Such observations were recorded in drained peatlands and peatland margins post-fire, whereas centres experienced lower severity burns (Lukenbach *et al.*, 2015a; Kettridge *et al.*, 2015; Hokanson *et al.*, 2015). Although there has been increasing research in vegetation recovery in the WBP, recent literature has focused on peatland microclimates and the return of *Sphagnum*-dominated hummocks and hollows species (Lukenbach *et al.*, 2015b; Lukenbach *et al.*, 2015c) with limited attention to tree regeneration. A study by Kettridge *et al.*, (2015) reported incoming willow and birch at margins in dry peat suggesting peatland shifts into shrub-dominated systems indicating peat margin vulnerability.

The encroachment of surrounding vegetation to peatlands has been linked to differences in soil moisture post-fire (Kettridge *et al.*, 2015), though there is a gap in understanding if changes in nutrient availability across land units also facilitate the movement of vegetation. This also aligns with the lack of studies that report the nutrient statuses of peatland-upland complexes after fire. Nutrient gradients, if they exist post-fire, could be significant for the vegetation that have a high demand for resources during re-establishment. These questions would allow for the investigation of the interactive controls that may shift peatlands into other land units with projected differences in fire frequencies. This may be significant as some species, including aspen, are often dependent on fire for regeneration (Schier and Campbell, 1978; Schier *et al.*, 1985), and if detected in peatlands, may result in peatland loss in the WBP of Alberta.

1.1 Research Objectives

The primary objective of this study is to examine aspen recovery in the Western Boreal Plains post-fire, infer if conditions in peatlands post-fire are conducive to aspen regeneration, and investigate if peatlands are susceptible to becoming upland stands. To address this, the specific objectives of this research are:

1) Determine if aspen existence and growth can be linked to nutrient availability in soil and water across a recovering upland-peatland hillslope.
2) Determine aspen water usage and stress through transpiration across varying soil moisture gradients, and the role of rooting systems in the transport of water between forests and peatlands.
3) Determine the largest control, that is, nutrients or moisture, in aspen regeneration and predict how this may affect peatland regeneration in burned and reclaimed sites.

It is hypothesized that the destruction of organic matter limits plant available nutrients in forests, whereas deep peat deposits allow for high mineral N and P. It is also predicted that possible changes in soil texture and moisture, such as ash deposition, create favourable growing conditions for seedlings. Further, extensive aspen rooting systems may allow for the transport of water from peatland to uplands through hydraulic redistribution. Aspen suckers, especially those at peatland margins may be more likely responsible for this process because of their connectivity to parent trees and their rooting zones' proximity to peat water. Overall it is hypothesized predicted that both nutrients and soil properties contribute to regeneration in peatlands, and are also significant to upland recovery.

1.2 Thesis Structure

This thesis has been divided into two manuscripts. The first manuscript determined if fire and land unit position affected nitrate, ammonium, and plant available phosphorus, in turn affecting aspen growth and the suitable of wetlands for regeneration. Traditional field methods of soil and water nutrient determination, such as mineralization bags and monitoring well sample collection were used. The second manuscript determined if aspen aided in the hydrological connectivity between uplands and peatlands, and quantify aspen success and controls across a recovering hillslope. Here, isotopic analysis of plant matter and isotopes distinguished water sources, and point measurements of aspen stomatal conductance were taken.

2.0 Manuscript 1: Nutrient Availability Post-Fire: Influences on Aspen Re-establishment

2.1 Introduction and Literature Review

The Western Boreal Plains (WBP) of Alberta have been subjected to increasing disturbance from anthropogenic and natural causes, such as forestry, conventional oil and gas, oil sands development, and fires. The effects of wildfire can range from local to regional in scale. Wildfires decrease land stability, increase erosion, and temporarily change runoff regimes through the creation of hydrophobic soil layers (Huffman *et al.*, 2001). Prescribed burns are practiced for land management including pest removal and vegetation regeneration. Contrary to wildfires, prescribed burns are generally less intense in terms of duration, areal extent, and temperature (Certini *et al.*, 2005). The WBP further contains a mixture of forests, riparian areas, and peatlands each of which contain distinct vegetation and soils (see Devito *et al.*, 2012 for more detail), and will herein be referred to as land units that can all be impacted by fire. The position of these land units can vary topographically where for example, forests can be found on topographic lows and wetlands in high elevations (Devito *et al.*, 2012). Such physical differences across land units also create changes in soil chemistry and directly affect the recovery of vegetation as result of fire (Milberg and Lamont, 1995).

Previous fire research has looked at the influence of peat fires in a range of climates and in different wetland types, including macrophyte dominated marshes, chaparrals, and northern forests (e.g., Dyrness *et al.*, 1989; Wu *et al.*, 2012; Wang *et al.*, 2014). Most studies have attributed nutrient differences across land units to hydrological exchanges through runoff, particularly from uplands to peatlands and in climates where there are no large precipitation deficits (e.g. Lamontagne *et al.*, 2000). Due to the sub-humid environment in the WBP, where potential evapotranspiration (PET) exceeds precipitation (P) in most years, the main source of water to forests is wetlands; it is only when storage is exceeded that forests feed surrounding areas (Devito *et al.*, 2005a; Devito *et al.*, 2005b; Redding and Devito, 2008; Redding and Devito, 2010; Petrone *et al.*, 2015). This indicates that nutrient transport between land units is indirectly affected by climate and may have implications for areas that are nutrient deficient (Devito *et al.*, 2005). Macrae *et al.* (2005) and Macrae *et al.* (2006) demonstrated that extractable phosphorus, NH_4^+ and NO_3^- were spatially distributed based on the topographic position of land units. However, when subjected to harvesting, there were no differences in soil extractable P and inorganic N (Macrae *et al.*, 2005; Macrae *et al.*, 2006).

Trembling aspen (*Populus tremuloides* Michx.) is a dominant tree species found in uplands that can quickly regenerate due to resource reserves in its expansive rooting systems (Schier and Campbell, 1978; Schier, 1985; DesRochers and Lieffers, 2001; Calder *et al.*, 2011). When elevated nutrient availability is temporary, high nutrient demand of aspen (Van Cleve and Noonan, 1975; Paré and Bergeron, 1996) may indicate potential dependencies on other sources and areas to fulfill recovery and growth. With areas that are limited in resources, such as nutrients and water, broadleaf trees have been shown to extract nutrients and water from adjacent areas (e.g. Dawson, 1993). Thus, similar resource extractions may be important for the succession of aspen forests, though these have yet to be recorded in the WBP

2.1.1 Nutrient cycling and transport among landscape units in the WBP

Upland forest canopies in the WBP are composed of coniferous, mixed deciduous, and aspen stands underlain by gray luvisols and brunisols, whereas low-lying areas containing riparian areas and peatlands are underlain by gleysols rich in organic matter (Devito *et al.* 2000; Whitson *et al.* 2005). Varying land units and associated soils further result in differences of nutrient availability.

The LFH of the forest floor is defined as an organic layer of soil that contains plant matter at different decomposition stages (Soil Classification Working Group 1998). This layer makes up a small portion of inorganic N, primarily ammonium (NH_4^+) and nitrate (NO_3^-), available for used for plant uptake (Huang and Schoenau, 1998). Specifically, the amount of NH_4^+ release is often based on C/N ratios (Côté *et al.* 2000; Vance and Chapin, 2001; Jerabkova and Prescott, 2006). Low C/N ratios typically describe highly decomposable and nutrient-rich litter to meet plant nutrient requirements (Van Cleve and Noonan, 1975; Longpre´ *et al.*, 1994; Pare´ and Bergeron, 1996). This further explains NH_4^+ availability and uptake patterns of upland stands in northwestern Alberta where deciduous > mixed > conifers (Jerabkova and Prescott, 2006). While N rapidly transforms into NH_4^+ in deciduous stands, nitrate (NO_3^-), through NH_4^+ oxidation, is the preferred inorganic N form for uptake as seen in aspen (Min *et al.*, 1998; DesRochers *et al.*, 2003). NO_3^- however, is prone to leaching and is usually unavailable (Schlesinger 1997) further corroborating N limitations in WBP forests. Conversely, low-lying areas, such as riparian zones can experience water table fluctuations resulting in the oxygenation of anaerobic soils and the enhancement of OM decomposition (Hill, 1996; Vidon *et al.*, 2010). Under these conditions and with NO_3^- as a by-product, riparian zones can act as nitrate hotspots (Hill, 1996; Vidon *et al.*, 2010), though have yet to be reported in the WBP. Like forests, N is generally in the organic form in peatlands with NH_4^+ primarily making up the inorganic fraction. Instead of high decomposition, inundated soils slow OM breakdown resulting in high NH_4^+ accumulation and low NO_3^- release (Huang and Schoneau, 1998). Furthermore, coniferous trees, such as black spruce (*P. mariana*) and *Sphagnum* that dominate in WBP bogs do not require high amounts of N for productivity (Aerts, 1990; Aerts, 1999; Bragazza *et al.*, 2005; Fritz, 2014). Overall, this highlights that low-lying areas may be important nutrient sources.

Similar to N, most P cycling occurs in surface layers through litter deposition, and decreases into deeper soil horizons (Moore and Basiliko, 2006). As seen in aspen uplands, organic P makes up most of the TP pool, where inorganic P in mineral soils in their non-labile form bound to minerals such as Ca (Huang and Schoenau, 1998; Whitson *et al.*, 2005). Due to varying redox conditions and high organic matter (OM) content, wetlands and low-lying areas have been shown to export P to surrounding areas based on their connectivity suggesting that wetlands in the WBP are rich in P (Devito *et al.*, 2000). These studies however, attribute the lack of differences in NO_3^- primarily to vegetative controls rather than soil moisture and trophic status of the land unit. It is difficult to compare the magnitude at which nutrient cycling/ mineralization occurs across topographic gradients as there is limited literature that compares N and P between land unit types.

Connectivity and runoff often depends on the timing of the climate cycle—wet vs. dry years and the ratio between P and (ET)—soil storage capacity, and antecedent soil moisture (Devito *et al.*, 2005a). Flow is less dependent on immediate precipitation events and is generated when soil storage capacity is exceeded. Since the storage capacity of wetlands is less than uplands, they are often able to generate flow to uplands (Ferone and Devito, 2004; Devito *et al.*, 2005a). With the ability of wetlands to generate subsurface flow to adjacent uplands, N and P also have the potential to transfer between land units (Macrae *et al.* 2005, Macrae *et al.*, 2006; Devito *et al.*, 2005a; Devito *et al.*, 2012). Conversely, the low probability of high intensity precipitation events allowing preferential flow in upper soil layers, and high storage capacity of forested soils limits the ability of lateral surface, subsurface, and overland flow to peatlands (Redding and Devito 2008, 2010). The decreased probability is also due to deep water table depths in forests (Ferone and Devito, 2004). During instances where lateral flow occurs in uplands, preferential flow paths in mineral soils typically occur along rooting channels (Redding and Devito, 2010). The role of vegetation in water transport can also occur through hydraulic redistribution. Observed in moisture-limited areas, deep tree roots can tap into water sources, such as groundwater and the water table and redistribute to drier soil depths (e.g. Dawson *et al.*, 1993; Hultine *et al.*, 2006). Overall, the lack of hydrological connectivity between uplands and wetlands indicate the importance of nutrient transport between land units.

2.1.2 Fire in the WBP

Fire intensity, the amount of energy released during fire, is often expressed as a temperature whereas burn severity measures biomass losses (Keeley, 2008). These two parameters can affect the transformations and the amount of N and P remaining in the soil. Organic matter content also determines severity. When comparing fires under black spruce and aspen stands in Alaska, Dyrness *et al.* (1989) found that burn severity was correlated with stand cover where crowned areas with high root density resulted in higher OM accumulation compared to areas that have gaps in the tree crown. The stand type along with underlying litter may also play a role in determining the burn severity. For example, mixedwood stands in Manitoba showed that areas dominated by white spruce and balsam fir had more OM consumed by fire than aspen stands due to the differences in litter moisture (Wang, 2003). Associated with OM losses in peat and LFH is lower bulk density compared to mineral soils. More recently, Lukenbach *et al.* (2015a) and Hokanson *et al.* (2015) showed that burn severity is greatest when bulk density is high and soil moisture is lowered; this was demonstrated in a peat fire in the WBP. Compared to wetlands, particularly peatlands, forests generally burn to the mineral layer due to thinner LFH or organic soils, although burn patterns in peat vary (Rein *et al.*, 2008; Thompson *et al.*, 2013; Lukenbach *et al.*, 2015b). While the presence of logs allow smouldering in forests (Rabelo *et al.*, 2004) findings have been consistent in that peatlands experience prolonged smouldering, which could contribute to increased fire duration and OM losses. If organic matter is completely destroyed in forests, uplands may need to depend on connections between riparian zones and peatlands for nutrients. Water and nutrient sources may also be limited to uplands if roots typically found in water rich areas that participate in hydraulic redistribution are severed.

Along with OM losses, soil hydrophpbicity has been shown to change after disturbance. The magnitude of hydrophobicity has been linked to OM properties and thickness where coniferous stands often exhibit greater water repellency than deciduous stands (Huffman *et al.*, 2001; Mataix-Solera and Doerr, 2004). Additional changes in soil structure and physical properties include stability or instability and erosion (Mataix-Solera and Doerr, 2004).

2.1.3 Nutrient Availability Post-fire

With changes in soil properties, such as hydrophobicity, there is potential for increases in surface runoff (Huffman *et al.*, 2001). This can be attributed to the loss of vegetation, which usually intercepts precipitation, the loss of ground cover and decreased stabilization, and hydrophobicity of the soil surface. After precipitation events in chaparral systems, the Boreal Shield of Eastern Canada, and WBP, export of TN, Mg^{2+}, SO_4^{3-}, NO_3^-, and TP into lakes increased (Lamontagne *et al.*, 2000; McEachern *et al.*, 2000; Burke *et al.*, 2005). Notably, Burke *et al.* (2005) in north-central Alberta attributed high particulate and dissolved P export to increased runoff and erosion of P-rich soil and peat in burned areas. This is surprising as runoff generation is the WBP is typically minimal (Devito *et al.*, 2005a). These findings show the potential of nutrient export into surrounding drainage areas and bodies of water such as lakes and streams (Lamontagne *et al.* 2000; McEachern *et al.*, 2000; Burke *et al.*, 2005). The amount of nutrients entering water however could be dependent on burn severity where Elliot and Vose (2005) showed that NH_4^+, NO_3^- or PO_4^{3-} in stream water did not differ between moderately burned and control sites. The lack of ground cover and less vegetation uptake can also contribute to the leaching of nutrients (Mast and Clow, 2008). There are limited studies that look at changes in water table chemistry post-fire especially in the WBP. While most of these have been recorded in forested areas, the lack of frequent lateral surface and subsurface flow originating from forests may indicate that wetlands and riparian zones may act as sources to uplands that are nutrient limited post-fire.

Immediately after fire, plant available nutrients generally increase (Certini, 2005). During the burning of soils, N bound in organic matter may undergo transformations. Along with the creation of simpler organic N compounds, heightened inorganic N and P availability, through the mineralization of organic matter, often occurs post-fire (Dunn *et al.*, 1979; Hobbs and Schimel, 1984; Galang *et al.*, 2010). In general, increases in inorganic N and P occur immediately with eventual decreases as the system recovers through leaching, erosion, wind, adsorption onto soil particles, or immobilized by microbes (Dunn *et al.*, 1979; Wilbur and Christensen, 1983; Hobbs and Schimel, 1984). For example, NH_4^+, extractable P, and NO_3^- remained elevated in a mixed white spruce, tamarack and aspen in north-central Alberta six weeks after fire (Kishchuk *et al.*, 2014). After a decade however, Kishchuk *et al.* (2014) reported lowered NH_4^+ and Ext-P while NO_3^- levels remained high.

The amount of plant available nutrients immediately after disturbance often depends on the properties of the fire. It is well understood that increases in fire intensity often alter the forms of N, which is often dependent on the temperatures at which the soil is heated (Knicker *et al.*, 2005). While organic N initially breaks down into simpler N-containing compounds, volatilization begins around 200-400 °C (DeBano and Condrad, 1978; Knicker *et al.*, 2005). If volatilization is the dominant process during disturbance, soil TN may be lower, though there still may be heightened NH_4^+ and NO_3^- (Dyrness *et al.*, 1989; Neff *et al.*, 2005). The abundance of inorganic P often exceeds N during recovery as the temperature needed for volatilization must exceed 700 °C, though the bioavailable forms are more often sorbed onto soil. Resultant ash formed through the combustion of organic matter, has also been shown to adsorb nutrients and increase NO_3^- availability due to the adsorption of hydrophobic compounds that usually inhibit nitrification (Wilbur and Christensen, 1983; Ball *et al.*, 2010). Ash has shown to increase soil pH through the deposition of calcium, potassium, and sodium carbonates and oxides formed during burning and dissociations after fire (Bodí *et al.*, 2014). Furthermore, the porosity of charcoal, also a by-product of burning, allows for the adsorption of phenols, which often bind to N (Keech *et al.*, 2005). Similar to mineralization, N and P content in litter also influences nutrient availability post-fire (Gray and Dighton, 2006). When comparing pitch pine (*Pinus rigida*) and white oak (*Quercus alba*), the latter species had greater nitrate in refractory litter due to greater organic N measured in intact leaves (Gray and Dighton, 2006).

Most of the processes discussed have been reported in forested soils with few studies looking at nutrients post-fire in peatland systems. Nutrient cycling in marshes in the everglades have consistently shown elevated inorganic P post-fire (Wu *et al.* 2012; Wang *et al.*, 2014). On the other hand, ombrotrophic peatlands showed higher NO_3^-, NH_4^+ than PO_4^{3-} (Wilbur and Christensen, 1983), though the burning of *Sphagnum* mosses from an ombrotrophic bog showed high P in different fractionated forms (Wang *et al.*, 2014). This suggests the magnitude of heightened availability varied due to differences from the time of burn and its severity, and the nutrient status of the wetland pre-fire where mineralization has consistently been linked to high organic N and P. If mineralized N and P is greater in wetlands and riparian areas than forests, low-lying areas may act as a potential source of nutrients. This may be important for upland species that require abundant nutrients for regeneration.

Much nutrient fire literature has focused on temperate wetlands that are at least mesotrophic with respect to their nutrient status. Current fire studies conducted in northern and boreal climates have focused on carbon release due to increased drying and subsequent fires in the context climate change (Turetsky *et al.*, 2011). While studies fire research in boreal forests exist, most nutrient studies have looked at forests rather than peatlands. Importantly, there is a gap in understanding if nutrient availability varies along land units.

2.1.4 Aspen Succession

Aspen in boreal forests often recolonize after disturbance and this is usually attributed to rooting system reserve (Schier and Campbell, 1978; Schier, 1985; DesRochers and Lieffers, 2001; Landhäusser *et al.*, 2003; Calder *et al.*, 2011). Although fire destroys the aboveground portions of aspen, increased temperatures stimulate sucker initiation (Schier and Campbell, 1978; Schier, 1985). Upon canopy destruction, regenerating aspen thrive in conditions where light is abundant allowing photosynthesis and growth (e.g. Kneeshaw and Bergeron, 1998; Hemming and Lindroth, 1999; St. Clair *et al., 2013*). Changes in soil physical properties, such as increases in pH and nutrient availability, are also favourable for aspen recolonization due to their high nutrient demand (Van Cleve and Noonan, 1975; Paré and Bergeron, 1996). For example, decreases in soil acidity as a result of ash deposition and calcium increases NO_3^- which has been linked to aspen sucker growth (Wilbur and Christensen, 1983; Ländhausser *et al.*, 2010). A severe fire in Alaska showed that aspen had higher aboveground and root biomass than black spruce due to higher uptake amounts of NH_4^+ and NO_3^- (Shenoy *et al.*, 2013). Accelerated growth after fire however, is often restricted to exposed mineral soils (Kay, 1993; Romme *et al.*, 1997; Johnstone and Chapin, 2006a) which may be depleted in nutrients indicating the need for additional N and P for regenerating aspen.

2.2 Study Objectives

The main goal of this study was to determine if aspen (*Populus tremulodies* Michx.), a dominant tree species in the WBP, could be linked to nutrient availability in recovering forest - peatland gradients after fire. To answer this, the following objectives were addressed:

1) Determine if fire and landscape unit influence soil and water nitrate (NO_3^-), ammonium (NH_4^+) and water extractable phosphorus (Ext-P) availability across a peatland-upland gradient during recovery after fire, and identify processes driving nutrient availability.

2) Determine aspen growth patterns, specifically leaf area (LA), stem height, and density across the same topographic hillslopes as (1) and if these are correlated with nutrient availability

These objectives were addressed by measuring the mineral (plant available) forms of nutrients in soil and surface water during the growing seasons of 2013 and 2014, two and three years after disturbance by wildfire. Leaf area and stem height were used as proxies to investigate aspen growth across burned hillslopes. It was hypothesized that NO_3^-, NH_4^+ and Ext-P were greatest in burned peatlands and decreased into aspen uplands. It was also hypothesized that the presence and growth of aspen was strongly related to elevated N and P concentrations, and that these concentrations explained their presence in peatlands during recovery. This study was used to understand if nutrients were a dominant control on aspen succession—especially in areas where they are typically not found—and potential long-term implications for succession trajectories.

2.3 Study Area

The Utikuma Region Study Area (URSA) is located in north central Alberta within the Boreal Plains of Western Canada (56°6’N, 116°32’W) (Figure 2.1). Due to glaciation, glacial deposits compose the surficial geology of the URSA resulting in uplands on rolling moraines and low-lying areas that have developed on lacustrine deposits (Finklestein, 1990; Smith *et al.*, 2003). Landforms across the URSA include moraines, clay rich tills, and glacio-lacustrine and coarse textured glacio-outwash plains. In May 2011, approximately 90 000 ha of the URSA, including the study site, was affected by the Utikuma complex fire.

The catchment area selected for this study was located on a coarse-textured outwash plain and contained a 39 ha pond (Pond 16) (Figure 2.1). Further, the lake interacts with regional groundwater creating a flow-through system (see Smerdon *et al.*, 2005 for more detail; (Lukenbach *et al.*, 2015c). Surrounding Pond 16 are riparian areas and peatlands with transitions into mineral uplands. The southwest portion of the lake was affected by the fire, which destroyed upland canopies and peatlands. The severe fire also affected adjacent peatlands that experienced smouldering, especially at the margins and in hollows (Lukenbach *et al.*, 2015a). Riparian zones and margins will be used interchangeably and are classified as transition areas between uplands and forests; instead, organic matter depths vary and the ground surface does not follow hummock-hollow microtoporaphy (Dimitrov *et al.*, 2014; Hokanson *et al.*, 2015). The nature of the crown fire sustained some peatlands and forested areas within the burned portion of the catchment.

The overstory of burned and unburned uplands was dominated by trembling aspen (*Populus tremulodies* Michx.) and spruce. Primary successional species in riparian zones included polytrichum mosses, common horsetail (*Equisetum arvense*), fire moss (*Ceratodon purpureus*), and willow (*Salix* spp.). These vascular species were also detected in recovering peatlands and further contained *Sphagnum fuscum* and feathermoss in hummocks and hollows also at reference sites with Black spruce (*Picea mariana*) at the overstory (Lukenbach *et al.*, 2015a).

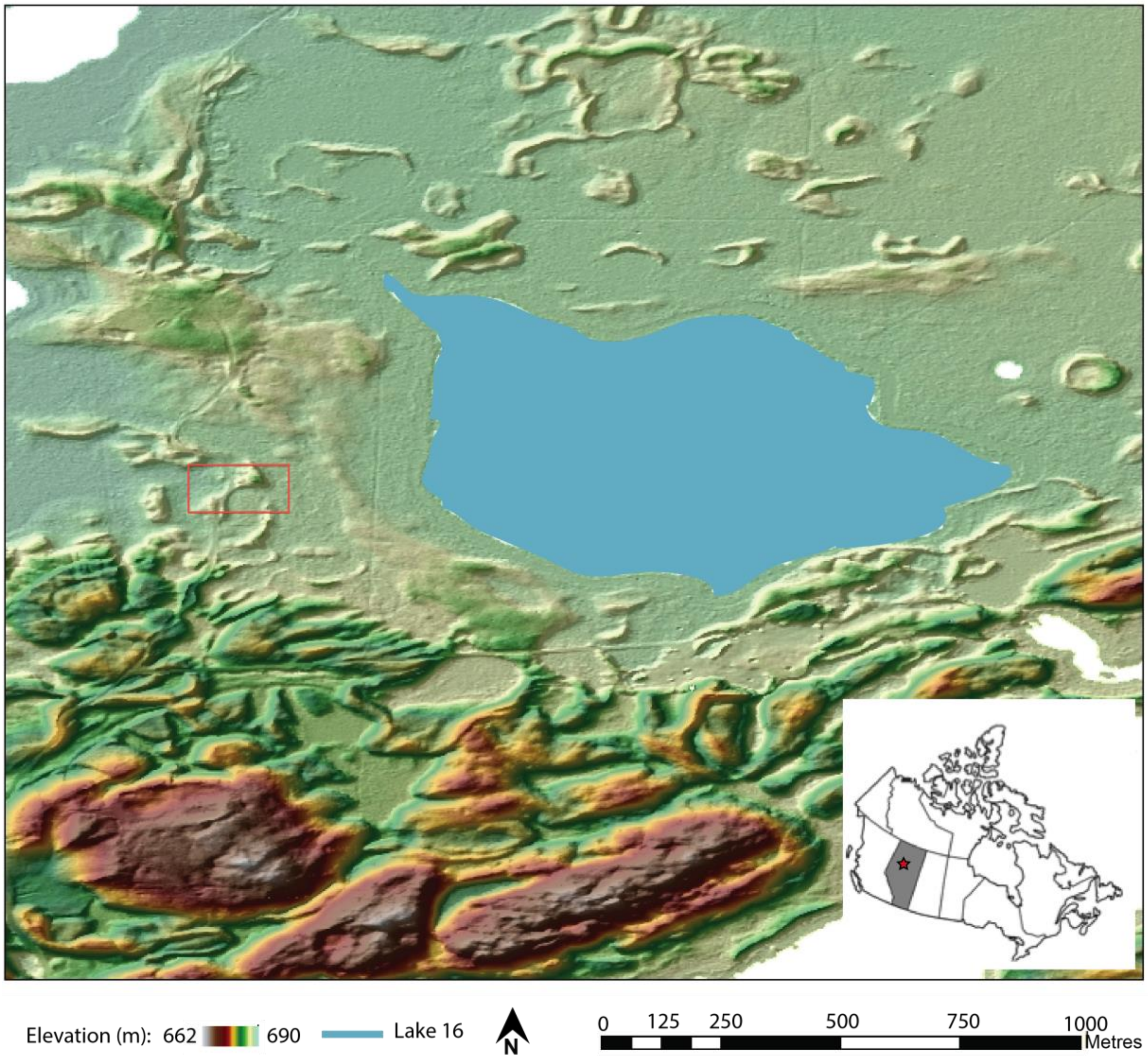
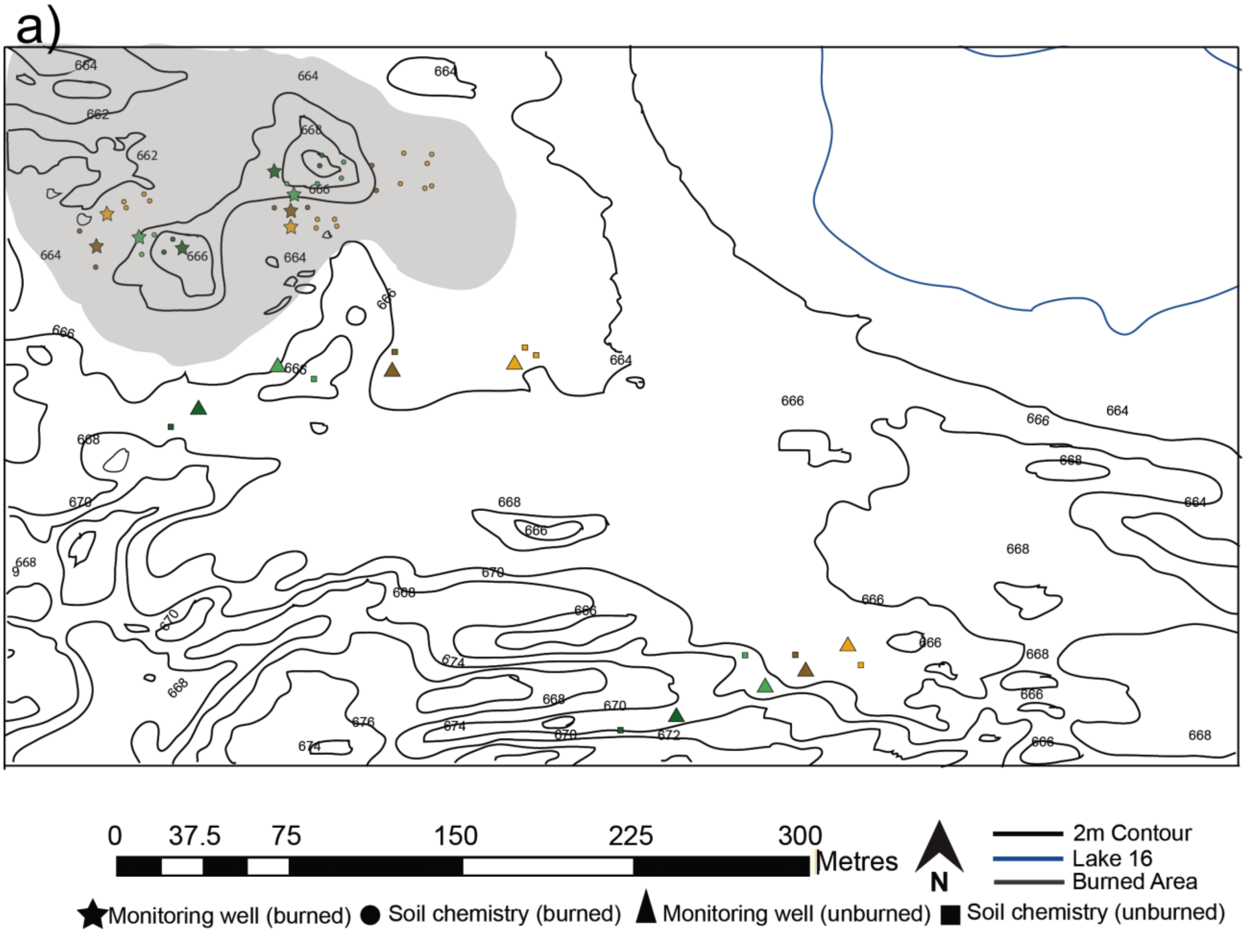


Figure 2.1: A digital elevation model (DEM) outlining the location and elevation of the main study catchment, Pond 16 with the map of the Alberta with an asterisk indicating the Utikuma Research Study Area (URSA). The portion enclosed in red indicates the general location of the burned peatland-upland complex.

2.4 Methods

2.4.1 Plant Available Nutrients

A total of six transects were sampled in this study, where three transects were located in a burned area and the remaining three were unburned; herein, the unburned areas will be also be referred to as the reference areas (Figure 2.2). Each transect contained an aspen hilltop, an aspen midslope, a riparian zone and a peatland with hummocks and hollows as the dominant microforms. An additional reference study catchment, Pond 19, also had one transect containing PRS probes (see Riddell, 2008 for more details on site description) and a separate transect containing an ephemeral draw.



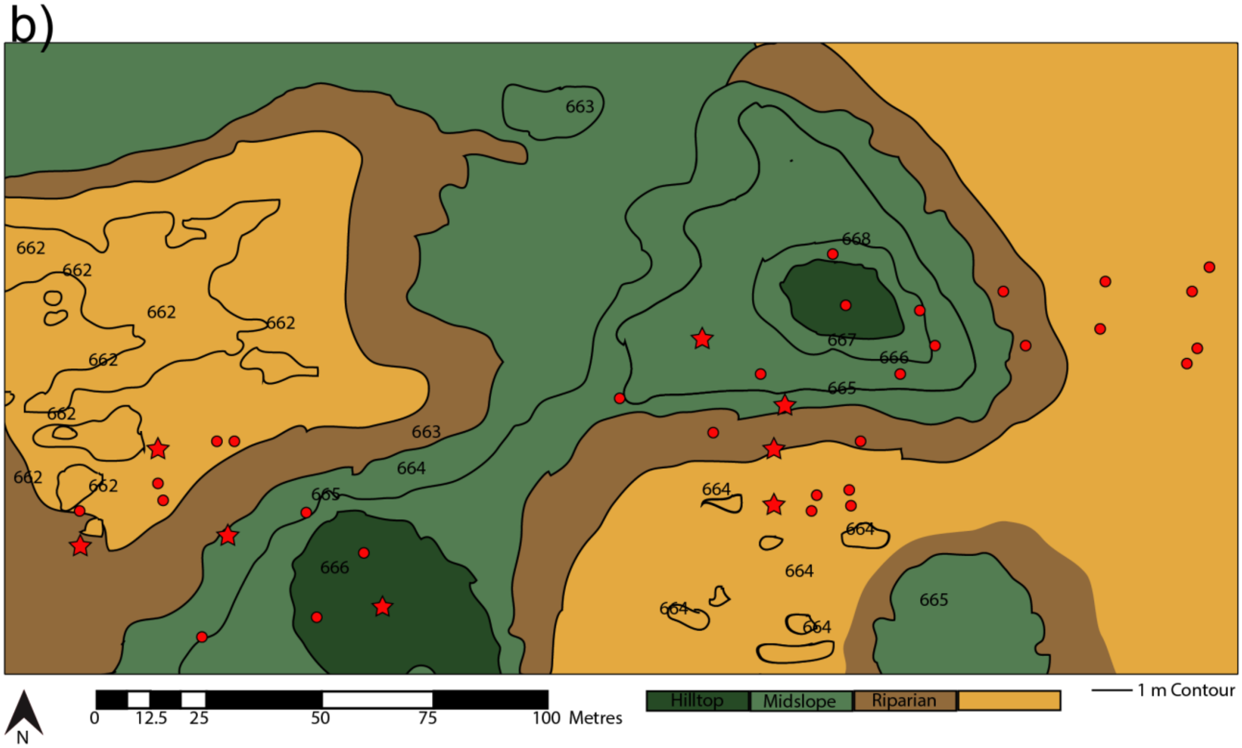


Figure 2.2: a) Soil chemistry and monitoring well location sites of the catchment that were burned (shaded) and heavily studied, and unburned. Symbols in dark green indicate hilltops, medium green indicate midslopes, brown indicate riparian areas, and yellow indicate peatlands. b) Soil chemistry and monitoring well locations for the burned areas in the study catchment.

Plant root simulator (PRS) probes (Western Ag. Innovations, Saskatoon), which contain a resin that allow for the adsorption of cations and anions, were inserted and incubated from July to August to capture the peak-growing season in both 2013 and 2014. The probes were inserted in the LFH layer in forested areas, and the top layer of peat in riparian areas and peatlands. This soil layer will be referred to as the surface soil layer. Second sets of PRS probes were inserted in the mineral soils of the forested area, along with riparian zone and peatland probes approximately 10-20 cm from the surface. The probes at depth will be referred to as the subsurface soils, though it is important to note that it only captures the maximum rooting depth of recovering vegetation in the peatland and riparian zone. In the aspen hillslope and hilltop, and riparian zone, 18 probes were randomly inserted in the burned surface soils with another 18 at the maximum rooting zone depth. The same was done at the references sites. 36 PRS probes were inserted in each peatland: half of those were placed into burned surface hummocks and with the other half in surface hollows. This distribution of PRS probes was consistent with the peatland microtopographic units at depth. PRS probes unburned sites followed the same distribution. Figure 2.2 shows a detailed map of each sampling site at the burned locations. Hummock and hollow properties were also recorded as followed by Lukenbach *et al.* (2015b): burn severity, canopy cover i.e., if the probe was inserted below a tree, and the type of cover, i.e., *S. fuscum*, *S.angustifolium*, etc. After a month of incubation, the probes were triple rinsed with distilled water with 24 hours of collection. Probes were then shipped to Western Ag. Innovations, Saskatoon, where they further were washed with HCl and analyzed colormetrically with a Technicon Autoanalyzer (Hangs *et al.*, 2004).

Compared to traditional mineralization bags (Eno, 1960), PRS probes output nutrient values that are in the soil solution over a period of time rather than an absolute value of N or P per mass of dry soil expressed as a concentration (µg of N or P/g). Results are expressed as µg N or P/ 10cm^2/ month in NO_3^- and NH_4^+; plant available phosphorus is expressed as P supply rates, or Ext-P that includes eluted organic and inorganic P forms, and orthophosphates. Herein, nitrate, ammonium, and plant available P values are expressed as a flux.

Additional parameters were also quantified at each probe site during removal and installation. Approximate redox status (oxic, suboxic, anoxic) was determined using iron rods inserted to a depth of approximately 30 cm. The depth to water table and ice, if present, were also recorded, along with the depth of the LFH layer.

2.4.2 Net Mineralization Rates

Net mineralization rates of N and P were also measured along the same transects described above (Figure 2.2), land units, and the minimum and maximum rooting zone depths as PRS probes during July 2014. In the uplands, riparian zones, and hummocks and hollows, 9 surface soils and 9 soil samples at depth were collected. For each soil sample, two cores were taken, divided by minimum and maximum rooting zone depths, and sealed into polyethylene bags. In the case of the peatland and riparian areas with greater than 20 cm of organics, minimum rooting zone cores were 0-10 cm and maximum rooting zone cores were taken from 10-20 cm depth. One core was placed into the soil layer from where it was retrieved, incubated and removed after four weeks for extraction (Eno, 1960). The other bag was immediately extracted to determine gross NO_3^-, NH_4^+, and SRP availability at the time of the collection (Eno, 1960). 5 g of organic, or 10 g of mineral soil were weighed into a sterile cup (Binkley and Hart, 1989). To extract NO_3^- and NH_4^+, 50 mL of 2 M KCl was added to the sample, whereas 50mL of distilled water was used for SRP (Binkley and Hart, 1989). The samples were shaken for two hours, filtered with 0.45 µm Whatman filter paper, and kept cold (4 °C) until analysis. Soil extracts were run on a Bran-Luebbe Autoanalyzer III, (Seal Analytical) in the Biogeochemistry Lab at the University of Waterloo using standard colourimetric methods.

To calculate net mineralization rates, the difference in concentration between the incubated soil sample and the initial soil sample were taken where values greater zero indicate net mineralization and differences less than zero indicate net immobilization (Hart *et al.*, 1994). Nutrient concentrations are expressed as µg N or P/g of dry soil. The same equation was used to determine net nitrification rates (using NO_3^-).

2.4.3 Additional Soil Properties

Carbon to nitrogen ratios (C/N) for the July 2014 mineralization soils were prepared based on Land *et al.* (1977) and Irwin *et al.* (1977). Soils were frozen dry and ground with a ball mill (Retsch, MM220). 10% HCl was added to the ground samples for carbonate removal and heated to ~80 ºC for 1 hour. The acidic supernatant was aspirated and the soils were tripled rinsed with distilled water and dried. Dried samples were combusted by an elemental analyzer (4010 Elemental Analyzer, Costech Instruments, Italy) coupled to a continuous flow isotope mass spectrometer (Delta Plus XL, Thermo-Finnigan, Germany) and yielded percent composition of carbon and nitrogen (University of Waterloo, Environmental Isotope Laboratory) for summer 2014 soils. Soil samples were also dried to calculate gravimetric water content, bulk density, and organic carbon content through loss on ignition. The pH of remaining soil samples from the mineralization experiment was also tested for pH with a pH electrode.

During the PRS and mineralization incubation period during 2014, weekly volumetric soil moisture content (VWC, m^3m^{-3}) was taken with an ML2x Theta Probe (Delta-T, Cambridge) for every PRS probe location.

2.4.4 Water Levels and Chemistry

Nests of piezometers and wells were present in each land unit, which also corresponded to soil chemistry transects (Figure 2.2). In aspen uplands and hilltops, slotted wells were inserted to approximately 2.5-3.0 m below the surface. Riparian areas and peatland nests contained shallow wells to measure the water table position. Water table levels were calculated relative to ground surface (m).

During the peak-growing season of 2013 and 2014, bailers were inserted into monitoring wells and sterilized Nalgene bottles stored water samples, after being triple rinsed with well water, filled with the water sample, and were stored chilled. Nutrient analyses on water samples were preformed at the University of Alberta, Biogeochemical Analytical Service Laboratory, and yielded concentrations of NO_2^- $+NO_3^-$, NH_4^+, SRP, and additional trace anions, cations, and trace metals in µg L^{-1}.

2.4.5 Aspen Growth Patterns

8 plots (8 m^2) in each of the three burned transects and topographic position were marked (Figure 2.2) During the 2013 growing season, the stem height (m), and number of each aspen was recorded. The aspen were further classified based on size (small, medium, or large) relative to other individuals in the plot. Average stem height was calculated for both years.

Aspen leaf area of each plot was found through destructive sampling. At the end of 2013 and 2014, one small, one medium, and one large aspen similar in height to those similar in the 8m^2 plots were cut at its base. Along with a height measurement, the leaves of the aspen were stripped, and run through a leaf area scanner (LI 3600, Li-Cor, Nebraska), which yielded cumulative leaf area of each aspen plot.

2.4.6 Statistical Analysis

PRS probe, N and P mineralization, and water chemistry data were first tested for normality using the Kolmogorov-Smirnov test; since $p<0.05$, the data was considered non-normal. All fluxes, mineralization rates, and water chemistry concentrations will be expressed as medians to determine if there were combined effects of land unit and disturbance on nutrient values. The Scheirer-Ray-Hare test was used, a non-parametric equivalent to the two-way ANOVA (Dytham, 2011). This is based on the Wilcoxon signed ranks test was preformed (Dytham, 2011). Mann-Whitney U tests compared if differences existed between soil layers and if nutrient fluxes and concentrations differed between years. Additional Scheirer-Ray-Hare tests were preformed to determine if disturbance and topographic position affected soil moisture, C/N ratios, Fe, Mn, and Ca.

Kruskal-Wallis tests, the equivalent to a non-parametric one-way ANOVA, were done to determine if topographic position influenced LAI and stem height. Further, average Spearman's rank-order correlations (r_s) were done to link aspen stem heights to nutrient fluxes, mineralization rates and physical properties of soil. All statistical analysis was preformed on IBM SPSS Statistics version 20 (IBM Corporation).

2.5 Results

2.5.1 NO_3^- Fluxes and Net Nitrification Rates

Median NO_3^- supply rates did not vary spatially across land units (Figure 2.3, Table 2.1) ($p>0.05$). Figure 2.3 shows that forests were nitrate limited. The effects of fire on NO_3^- across land units were also not observed ($p>0.05$). Ranges of supply rates were greatest in burned and unburned riparian zones and hummocks. Further, NO_3^- supply rates did not differ between years (*p*>0.05), though fluxes in undisturbed margins and hummocks at both depths remained and increased in 2014. Flux patterns did not vary with depth.

Net nitrification rates likely explained the observed fluxes for both soil layers (Figure 2.3, Table 2.1). While mobilization occurred in disturbed and undisturbed land units, nitrification ranges were greatest in burned and unburned riparian areas. In riparian zones, net nitrification medians of surface soils at the reference sites (139.2 µg N/ g dry), greatly exceeded burned areas (4.8 µg N/g dry). Similar spatial trends in net nitrification were observed at depth, but at a lower magnitude. Overall, NO_3^- was most abundant in riparian zones and peatlands and may be significant areas sources for nutrients.

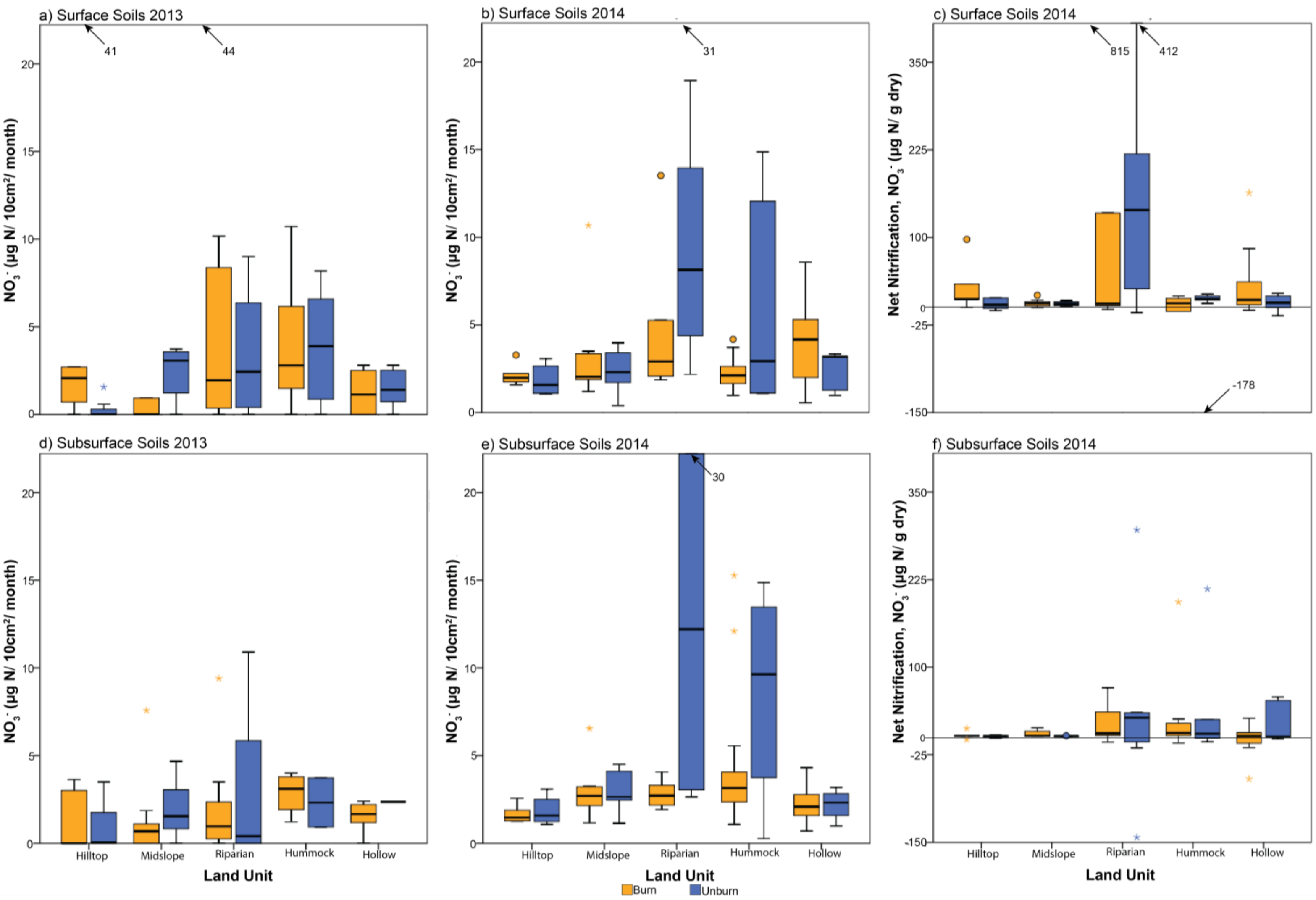


Figure 2.3 N-NO_3^- fluxes for surface soils (a, b) and subsurface soils (d,e) during 2013 and 2014. Net nitrification rates for the surface (c) and at depth (f) are also displayed.

2.5.2 Soil NH_4^+ Fluxes and Net Ammonification Rates

Plant available ammonium was greatest in peatlands and lowest in forests, thus NH_4^+ fluxes depended on land unit ($p<0.05$) (Figure 2.4, Table 2.1). The impact of fire was also insignificant ($p>0.05$) as median NH_4^+ between burned and unburned land units did not significantly vary. These trends were observed in both soil layers. Patterns with respect to the spatial distribution and the lack of fire influence did not differ in 2014, though the ranges of supply rates were significantly elevated in unburned hollows (0 – 60 µg N/ 10 cm^2/ month).

Similar to net nitification, net ammonification did not change as a result of fire, but was dependent on land unit position (Figure 2.4, Table 2.1). Ammonification was highest in peatlands at depth, which aligned with maximum rooting zone fluxes suggesting high mobilization in low-lying areas. Surface layers showed the opposite where rates were elevated in forests and decreased into peatlands. Therefore, net ammonification rates at the surface were not translated to fluxes suggesting that while forests may have a high potential for NH_4^+ transformations in uplands, ammonium may be limited due to immediate plant usage.

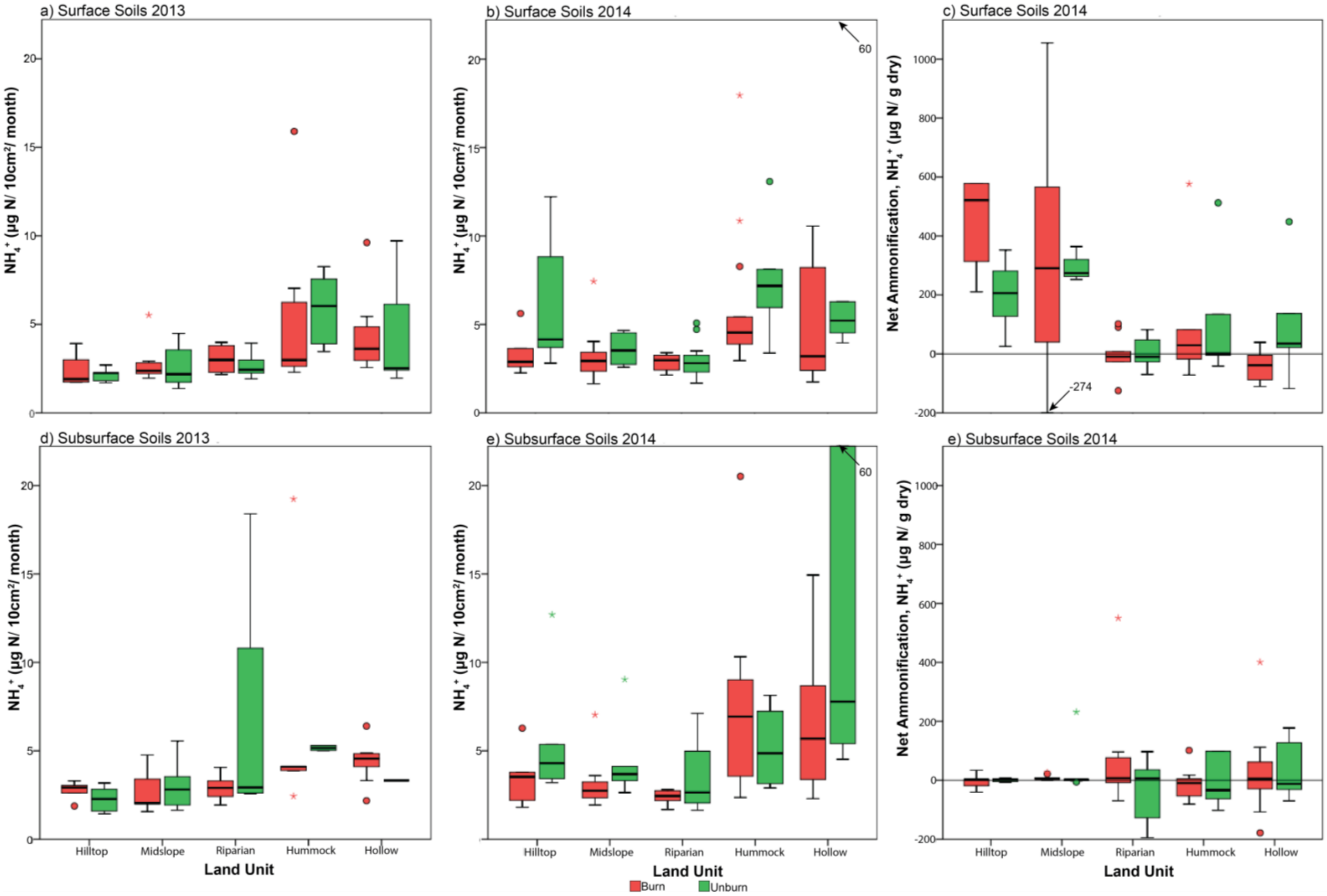


Figure 2.4: N-NH$_4^+$ fluxes for surface soils (a, b) and subsurface soils (d,e) during 2013 and 2014. Net ammonifcation rates at the surface (c) and at depth (f) are also displayed.

2.5.3 Soil Ext-P and Net SRP Mineralization Rates

Unlike NO_3^- and NH_4^+, P supply rates were dependent on land unit and fire (Figure 2.5, Table 2.1). This was evident in surface soils in 2013 where in burned areas, Ext-P medians and ranges were highest in hummocks (4.0 - 36.90 µg P/ 10 cm^2/ month) and hollows (2.2 - 171.1 µg P/ 10 cm^2/ month) and lowered into forests. Conversely, low P supply rates in unburned areas did not spatially vary. P supply rates across land units in surface soils during 2014 were consistent as those in 2013. At depth, the medians and ranges of Ext-P in burned areas approached values observed in the unburned hillslopes (Figure 2.5).

P mineralization patterns at the surface were similar to NH_4^+ trends (Figure 2.5); mineralization was dependent on land unit where greatest rates occurred in forests and the lowest in peatlands. While not reflected in surface fluxes, this shows that high immobilization dominates in peatlands though additional sources of soil Ext-P must be considered. Furthermore, while high P mobilization occurred in uplands, low supply rates showed limited P available for plant use in forests.

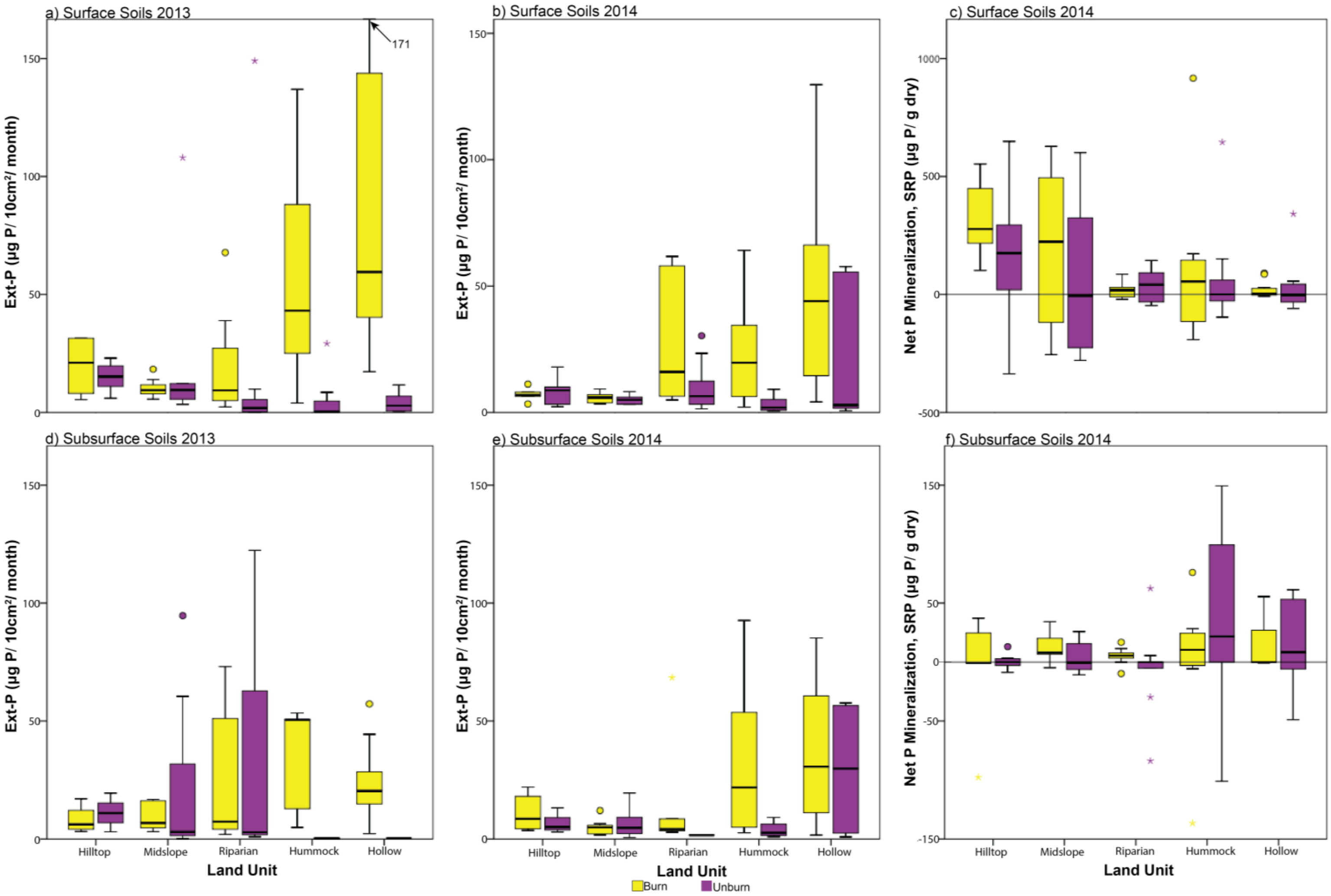


Figure 2.5: Ext-P fluxes for surface soils (a, b) and subsurface soils (d,e) during 2013 and 2014. Net P mineralization rates (SRP) for the surface (c) and at depth (f).

Depth	**Year**	**Interaction**	**NO_3^- (p-value)**	**Nitrification (p-value)**	**NH_4^+ (p-value)**	**Ammonification (p-value)**	**Ext-P (p-value)**	**P Mineralization (p-value)**
Surface	2013	Disturbance	0.97		0.49		**<0.05**	
		Land unit	0.06		**<0.05**		0.25	
		Disturbance x land unit	0.23		0.42		**<0.05**	
Surface	2014	Disturbance	0.53	0.91	**0.02**	0.42	**<0.05**	0.08
		Land unit	0.17	0.31	**0.01**	**0.05**	0.4	**0.02**
		Disturbance x land unit	0.77	0.30	0.94	0.37	0.15	0.44
Subsurface	2013	Disturbance	0.69		0.81		**<0.05**	
		Land unit	0.06		**<0.05**		0.76	
		Disturbance x land unit	0.56		0.48		**<0.05**	
Subsurface	2014	Disturbance	0.60	0.67	0.27	0.58	**<0.05**	0.74
		Land unit	**0.01**	0.60	**0.06**	0.54	0.39	0.28
		Disturbance x land unit	0.54	0.78	0.70	0.87	0.14	0.38

Table 2.1: Scheirer-Ray-Hare tests indicating if significant interactions exist between disturbance and land unit with NO_3^- flux, net nitrification rate, NH_4^+ flux, net ammonification rate, Ext-P flux, and P mineralization. Bolded values indicate significant interactions ($p<0.05$).

2.5.4 Distribution of Additional Nutrients

In both years and depths, iron fluxes were lowest in forests and highest in burned hollows and hummocks (Figure 2.6, Figure 2.7). Soils at the surface and at depth showed that Fe was dependent on topographic position and fire.

Manganese (Mn) in the disturbed transects were lowest at the forested sites with little increases into riparian zones, hummocks, and hollows in 2013. Mn did not vary across land units at the unburned areas, though the opposite was observed in 2014. Both factors affected Mn in the LFH layer during the first year, and the maximum rooting zone in 2014.

This was also seen with calcium (Ca), though the interaction term was lost at depth in 2014. Specifically, Ca was highest in riparian areas and peatlands whereas Ca at burned and unburned riparian zones with the exception of soils at depth in 2013 where the distribution across land units reversed. These trends can be found in Figure 2.6 for 2013 and Figure 2.7 for 2014. When Fe, Mn, and Ca were linked to Ext-P, positive correlated were mostly observed (Table 2.2).

Sulfur (S) medians did not greatly change throughout topographic position with the riparian area with the highest range at reference and disturbed sites. Statistically, S was only dependent on topographic position.

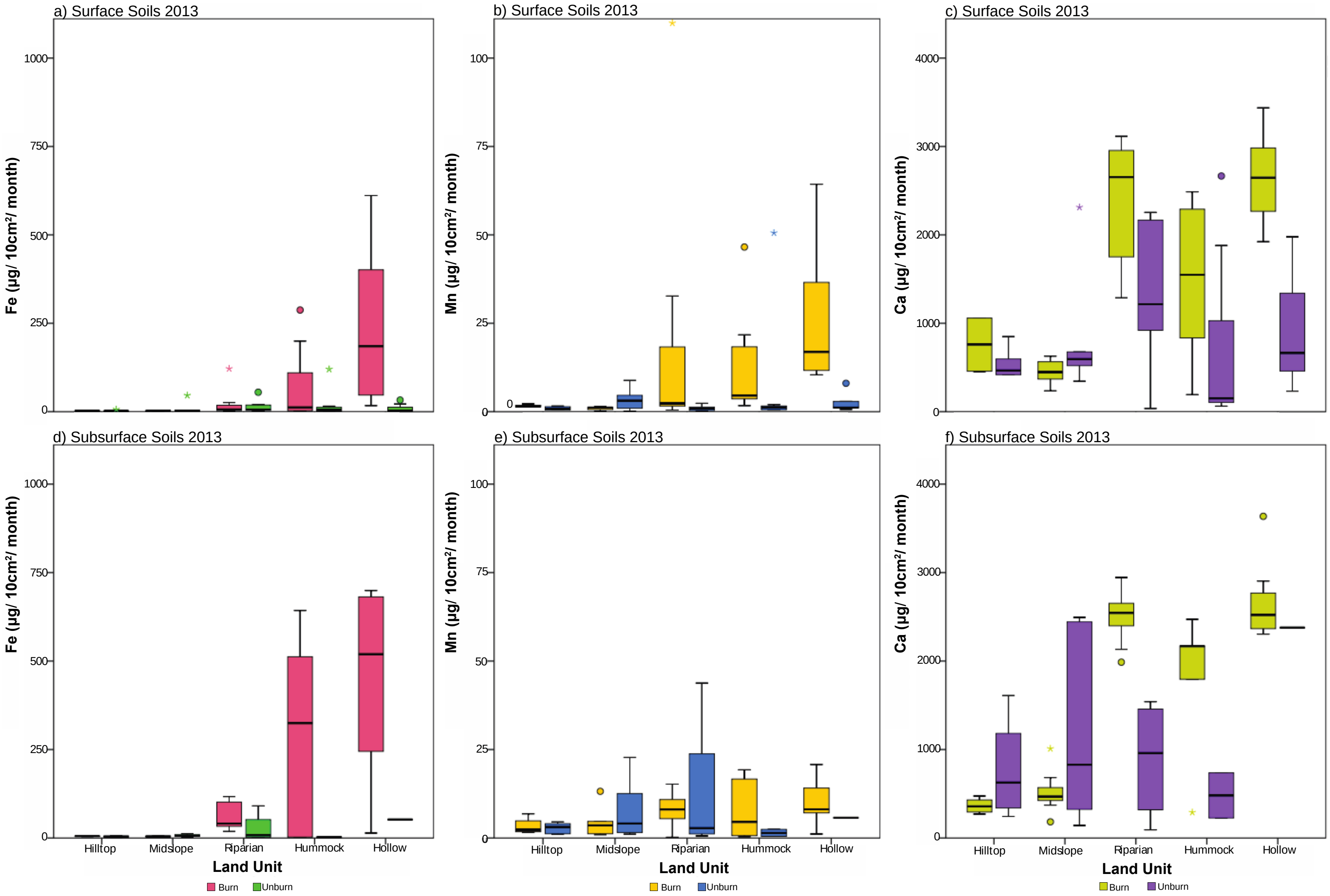


Figure 2.6: Spatial distribution of Fe, Mn, and Ca in surface and subsurface soils in 2013.

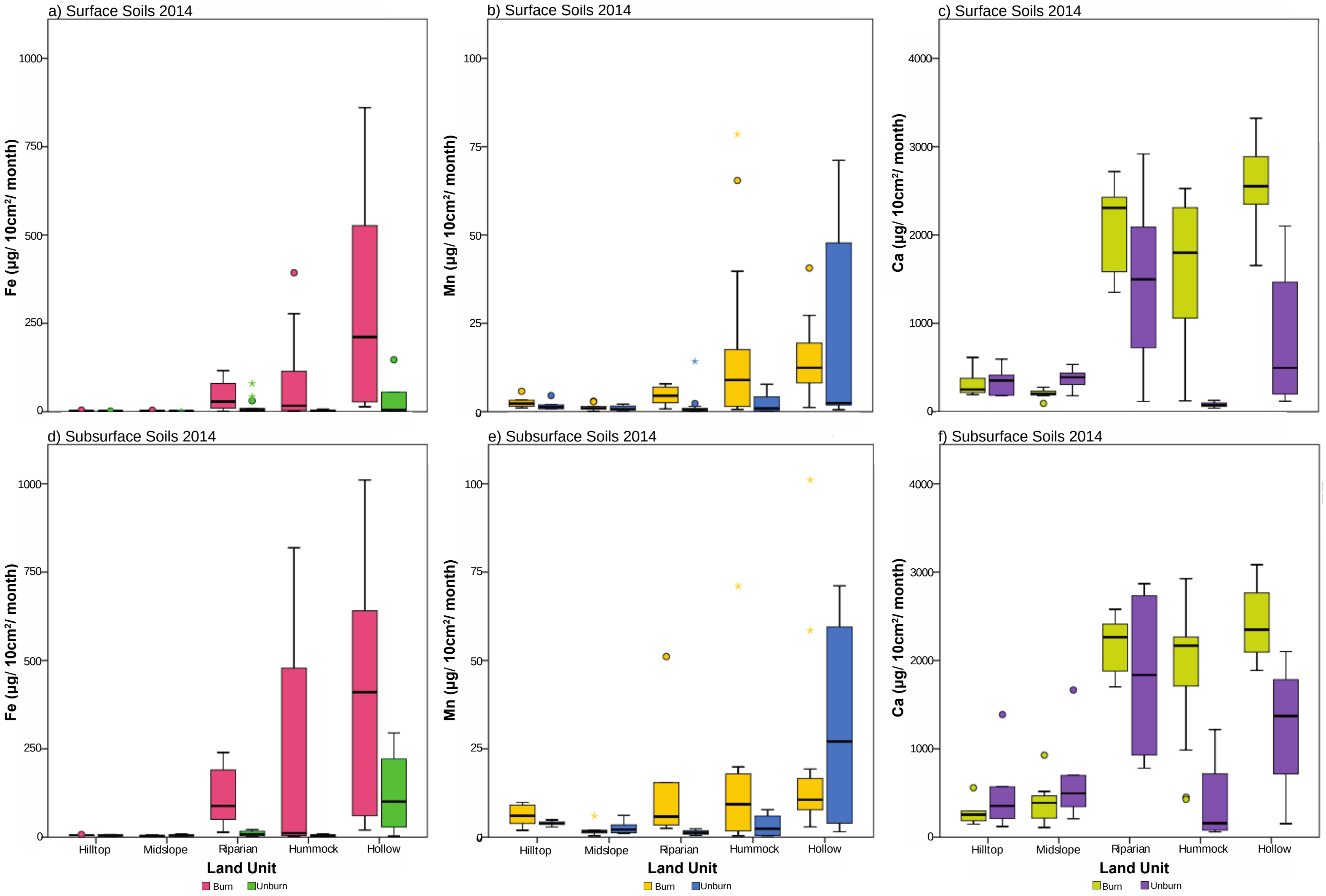


Figure 2.7: Spatial distribution of Fe, Mn, and Ca in surface and subsurface soils in 2014.

Soil layer	**Year**	**Burn/ Unburn**	**Fe × P (r_s)**	**Fe × P (r^2)**	**Mn × P (r_s)**	**Mn × P (r^2)**	**Ca × P (r_s)**	**Ca × P (r^2)**
Surface	2013	Burn	0.15	0.02	**0.38**	**0.15**	**0.36**	**0.13**
Surface	2013	Unburn	**0.49**	**0.24**	0.19	0.01	**0.30**	**0.09**
Surface	2014	Burn	**0.35**	**0.10**	0.27	0.07	**0.47**	**0.22**
Surface	2014	Unburn	**0.62**	**0.39**	**0.88**	**0.77**	0.31	0.10
Subsurface	2013	Burn	**0.49**	**0.24**	0.01	<0.01	**0.39**	**0.15**
Subsurface	2013	Unburn	**0.50**	**0.25**	**0.95**	**0.89**	0.26	0.07
Subsurface	2014	Burn	0.18	0.03	0.02	<0.01	**0.44**	**0.19**
Subsurface	2014	Unburn	0.32	0.10	**0.93**	**0.87**	0.24	0.06

Table 2.2: Spearman's rank order correlations (r_s) and r^2 between Ext-P and Fe, Mn, and Ca between years and soil layers. Bolded values indicate significant interactions ($p<0.05$).

2.5.5 Additional Soil Properties

C/N ratios were lower than 25 in upland topographic positions in comparison to the hummocks and hollows where ratios were 66 and 30, respectively. This pattern was also observed in the unburned areas and ratios did not differ between burned and unburned sites (Table 2.3) at the hilltop, midslope and riparian positions While topographic position influenced ratios ($p<0.05$), correlations existed between C/N ratios and ammonification (r_s=-0.69 and r^2=0.05 surface soils, r_s=-0.089 and r^2=0.02 at depth) and nitrification (r_s=-0.37 and r^2=0.01 surface soils, r_s=-0.049 and r^2<0.01 at depth). Similar findings were seen with organic matter content and followed the same spatial trends and correlations as C/N, although the differences in OM content across the hilltop to peatland continuum were more gradual (Table 2.3). pH at both depths were affected by fire and land unit, where pH was greatest in the forested areas and decreased into the peatland; this was especially seen at the burned surface (Table 2.3). Depths to anoxic conditions (as evidenced by the presence or absence of rust on the iron rods) were greater in the forested areas and decreased into the peatlands in both years and in the burned and unburned slopes. While initial rust measurements did not vary from the end of the incubation period in hillslopes and midslopes, rust depths generally decreased in margins and peatlands.

Depth	Land Unit	Burn/ Unburn	pH Range	OM %	C/N
Surface	Hilltop	Burn	5.59-7.00 (6.45)	37-84(46.00)	27-32 (28.0)
Surface	Hilltop	Unburn	5.43-6.62 (6.22)	37-88 (72.00)	24-45 (27.00)
Surface	Midslope	Burn	5.52-7.00 (6.56)	26-88 (45.00)	26-41 (25.00)
Surface	Midslope	Unburn	5.84-6.77 (6.35)	37-91 (78.00)	25-31 (27.00)
Surface	Riparian	Burn	5.52-7.58 (6.90)	35-87 (79.50)	19-29 (23.00)
Surface	Riparian	Unburn	4.89-6.03 (5.31)	80-91 (88.50)	2-52 (25.50)
Surface	Hummock	Burn	3.41-7.09 (3.74)	85-98 (96.50)	44-91 (66.00)
Surface	Hummock	Unburn	3.53-4.02 (3.66)	91-102 (98.00)	48-111 (78.00)
Surface	Hollow	Burn	3.70-6.98 (6.48)	33-119 (86.00)	14-42 (30.00)
Surface	Hollow	Unburn	3.49-6.82 (4.25)	87-98 (94.00)	37-77 (49.00)
Subsurface	Hilltop	Burn	4.98-6.46 (5.34)	3-5 (4.00)	20-47 (25.00)
Subsurface	Hilltop	Unburn	4.76-6.44 (6.06)	2-38 (4.00)	10-26 (18.00)
Subsurface	Midslope	Burn	4.88-6.63 (5.32)	1-79 (8.50)	22-32 (23.00)
Subsurface	Midslope	Unburn	4.95- 6.00 (5.52)	2-69 (2.00)	13-26 (19.00)
Subsurface	Riparian	Burn	6.15- 7.56 (6.86)	5-93 (83.00)	19-26 (20.50)
Subsurface	Riparian	Unburn	4.44- 6.35 (5.45)	28-94 (89.00)	19-37 (24.00)
Subsurface	Hummock	Burn	3.82- 6.07 (5.44)	85-102 (95.00)	31-77(42.00)
Subsurface	Hummock	Unburn	3.90- 6.39 (4.23)	80-100 (94.00)	23-75 (45.50)
Subsurface	Hollow	Burn	3.39- 7.05 (6.14)	18-97 (88.00)	15-72 (29.50)
Subsurface	Hollow	Unburn	3.67- 6.45 (5.14)	85-97 (94.00)	17-64 (53.00)

Table 2.3: Approximate soil pH, C/N, and OM % values for 2014 surface and subsurface soils. Brackets indicate median values.

2.5.6 Volumetric Water Content

As expected, VWC was lowest in forested areas and increased into riparian areas and peatlands in 2014. In burned areas however, soil moisture drastically increased in hilltops and midslope (Figure 2.8). This is likely due to the loss of surface organic matter and high mineral content of burned forests soils. Burning also led to higher VWC in riparian areas and hollows. These patterns were consistent at both depths.

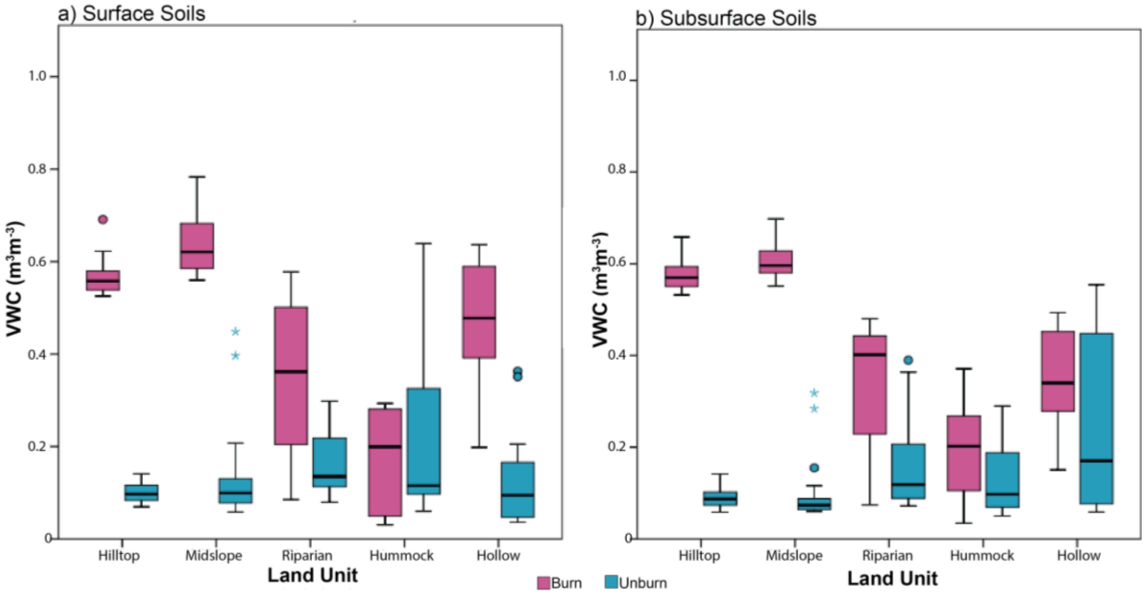


Figure 2.8: Volumetric water content (VWC) expressed in m^3m^{-3} across topographic land units in 2014 at a) surface soils (3 cm at depth) and b) subsurface soils (6 cm at depth).

2.5.7 Water table Depths

Monitoring wells in 2013 in the burned and unburned areas showed that the water table position was closet in the peatlands and increased with depth in adjacent uplands (Figure 2.9). An exception occurred at disturbed peatland along the north-south portion of the catchment where it was fed by adjacent southern riparian zone where the water table was approximately 0.53 m above ground. The same riparian area also fed an adjacent upland to its north where the water table—at the toe of the hill—was approximately 0.78 m below the surface. Smerdon *et al.* (2005) also observed mounding at this catchment and its disappearance during dry years. The reference area running along the same north-south portion of the catchment also underwent mounding.

These patterns remained in 2014 with slight decreases in water depths in the burned transects. Details of water table dynamics and site hydrology can be found through Smerdon *et al.* (2005), Lukenbach *et al.* (2015c), and Hokanson *et al.* (2015). These patterns suggest limited water availability to upland and hilltop vegetation.

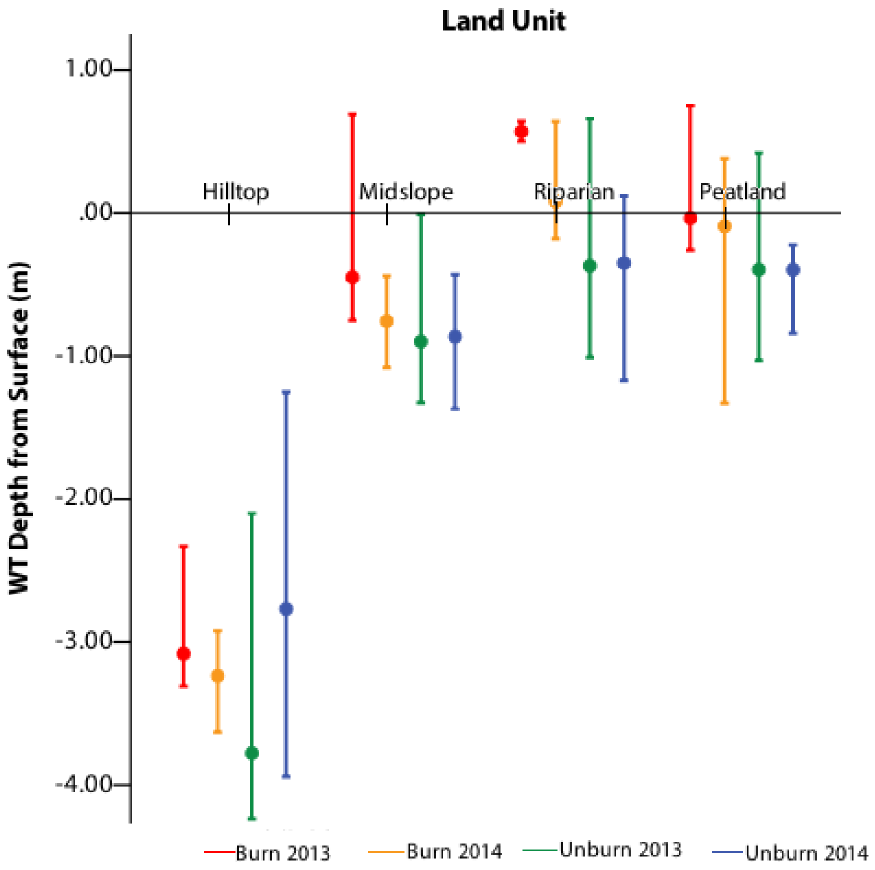


Figure 2.9: Average water table depths for 2013 and 2014 relative to ground surface (m) across all burned and unburned land units. End caps indicate minimum and maximum depths with shaded shapes showing average depths.

2.5.8 Water Chemistry

Due to the lack of standing surface water in the forested areas, only subsurface water was analyzed for chemistry in 2013 and 2014. With the exception of the hilltop in 2013 where median NO_3^- and NH_4^+ concentrations were 4.0 and 14.0 µg N/L, respectively, most land units had median concentrations that approached or were below 2 µg NO_3^- µg N/L and 3 µg NH_4^+ µg N/L the limited of detection (LOD) (Figure 2.10). Therefore, NO_3^- and NH_4^+ did not vary across land units ($p > 0.05$). Similarly, while burned hilltops had median subsurface water concentrations of 33.5µg NO_3^- µg N/L (2013) and 12.5 NO_3^- µg N/L (2014). The effects of fire were also not evident. Since these patterns were continued into 2014, fire ($p > 0.05$) and land unit ($p > 0.05$) likely did not influence NO_3^- or NH_4^+ in subsurface water (Table 2.4).

Like NO_3^- and NH_4^+, median soluble reactive phosphorus (SRP) concentrations across most land units were also near the detection limit (0.9 µg P/L), though the concentration of a well yielded 1785 µg P/L at the unburned midslope (Figure 2.10). In 2014, burned areas showed slight elevations in SRP across most land units relative to unburned sites (Table 2.4). Overall, the effects of fire and land unit position were unclear, and may be explained by the sampling period where data was reported for two and three years after fire.

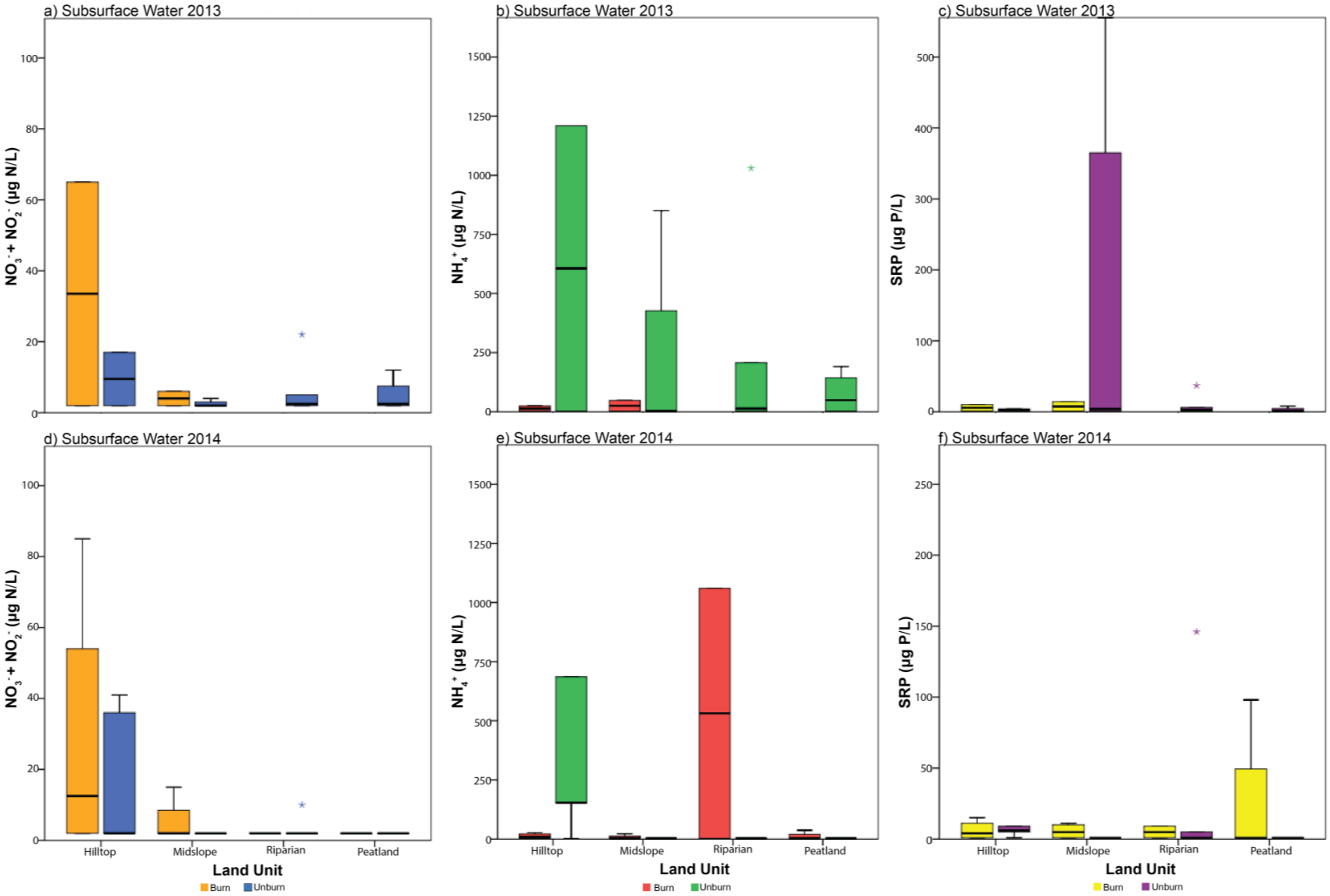


Figure 2.10: Surface water chemistry for NO_3^-, NH_4^+, and SRP graphs for 2013 and 2014.

Nutrient	**Year**	**Interaction**	***p*-value**
Nitrate	2013	Disturbance	0.58
		Land unit	0.84
		Disturbance x Land unit	0.78
Nitrate	2014	Disturbance	0.95
		Land unit	0.23
		Disturbance x Land unit	0.85
Ammonium	2013	Disturbance	0.70
		Land unit	0.97
		Disturbance x Land unit	0.51
Ammonium	2014	Disturbance	0.62
		Land unit	0.33
		Disturbance x Land unit	0.20
SRP	2013	Disturbance	0.71
		Land unit	0.96
		Disturbance x Land unit	0.76
SRP	2014	Disturbance	0.22
		Land unit	0.77
		Disturbance x Land unit	0.48

Table 2.4 Statistical trends between subsurface water nitrate, ammonium, and SRP and interactions between land unit and disturbance for 2013 and 2014.

2.5.9 Aspen Stem Height and Leaf Area and Relationships with Nutrient Fluxes and Peat Quality

Aspen stem heights in 2013 were greatest in the recovering aspen hilltops and decreased into the peatlands (Figure 2.11). During 2014 there were slight changes in median stem height patterns where riparian zones > midslopes > hilltops > peatlands (Figure 2.11). Between study periods, regenerating aspen heights in 2014 exceeded 2013. Changes between years were statistically insignificant in most topographic positions ($p>0.05$). The range of stem heights of *P. tremulodies* were greatest in peatlands (0.47 – 2.57 m) though growth was the least (0.03 m) between years; conversely, riparian zone aspen were approximately 50% taller (0.83 vs. 1.47 m) and contained suckers that grew up to 2.72 m.

Similar to stem heights, aspen leaf area was greatest in the midslope, followed by the hilltops, riparian zones, and peatlands in both years (Figure 2.11) Leaf area increased between growing seasons with aspen at the margins showing the most significant changes with medians of 393 to 968 cm^2 in 2014. This coincides with increased stem heights in the same year.

Generally, nutrient fluxes and substrate quality were not related to aspen stem heights or leaf area ($p>0.05$), with a few exceptions. Both growth parameters were significantly related ($p<0.05$) with organic matter content where $r_s=-0.75$ and $r^2=0.57$ (stem height) and $r_s=-0.77$ and $r^2=0.59$ (leaf area). Likewise, positive correlations were observed between leaf area and net ammonification rates ($r_s=0.65$ and $r^2=0.42$).

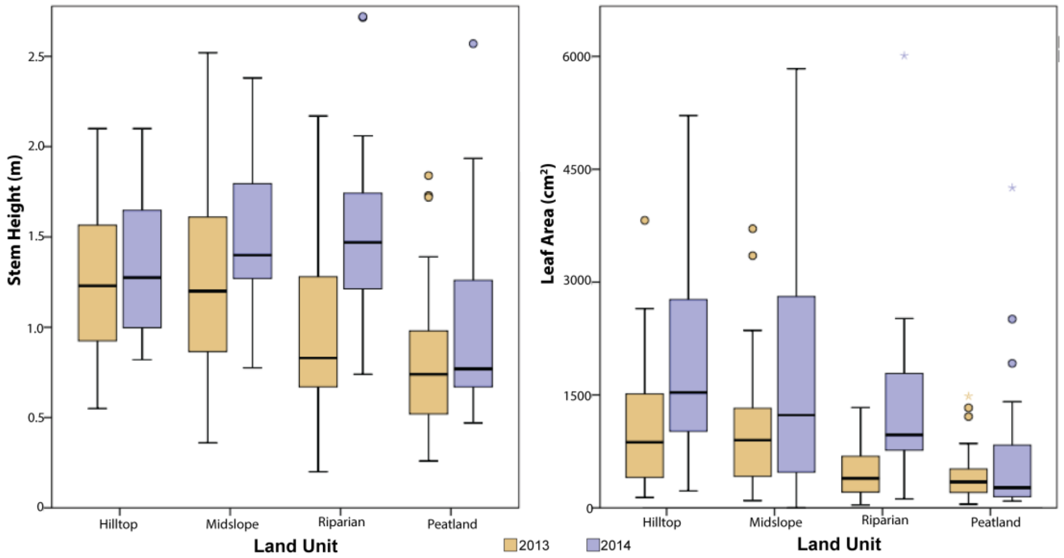


Figure 2.11 Aspen stem heights (m) and leaf area (cm^2) for 2013 and 2014.

Nutrient or Soil Property	Stem Height (r_s)	Stem Height (r_2)	Leaf Area (r_s)	Leaf Area (r^2)
NO_3^- Flux	-0.11	0.01	-0.19	0.04
NH_{4+} Flux	-0.28	0.09	-0.32	0.12
Ext-P	-0.17	0.04	-0.23	0.36
Net Ammonification	0.46	0.21	**0.65**	**0.42**
Net Nitrification	0.06	<0.01	0.12	0.02
Net P Mineralization	0.45	0.2	0.52	0.27
C/N	-0.44	0.2	-0.43	0.19
OM	**-0.75**	**0.57**	**-0.77**	**0.59**

Table 2.5 Spearman's rank order correlations (r_s) and r^2 values between soil properties and nutrients with aspen growth and leaf area. Bolded values indicate significant interactions ($p<0.05$).

2.6 Discussion

2.6.1 The Role of Fire and Land Units on Soil Nitrate and Ammonium

Results here are similar to the findings of Macrae *et al.* (2006) where NO_3^- and NH_4^+ was greatest in peatlands and nutrient availability across a landscape was dictated by land unit. This study shows that this pattern persists, irrespective of disturbance. Thus, the findings in this study reject the hypothesis that soil NO_3^- and NH_4^+ availability are governed by a combination of fire and topographic position. The lack of differences in NO_3^- and NH_4^+ after fire may be attributed to changes in resource availability during early succession.

Nitrate may have returned to its limited availability of pre-fire conditions. With the exception of riparian areas, NO_3^- availability was limited across forests and peatlands. Elevated NO_3^- fluxes in burned and unburned riparian areas is likely due to the presence of nitrate hotspots during the incubation period. This is the first study to report hotspots in the WBP where evidence is reflected in changes of rust depths suggesting that water table fluctuations lead to soil aeration and the subsequent oxidation and lowering of NH_4^+ to NO_3^- (Hill, 1996; Vidon *et al.*, 2010). Water table position and differences in soil moisture where lower VWC values in margins, compared to hummocks and hollows, are more suitable for nitrification (Venterink *et al.,* 2002). Furthermore, the translocation of NH_4^+ into burned mineral soils and elevated pH could support nitrification and NO_3^- transformations (Prieto-Fernandez *et al.*, 1998; Ste-Marie and Paré, 1999; Simard *et al.*, 2001; Shenoy *et al.*, 2013). Conversely, a reduction of nitrate in forested stands can be attributed to its uptake kinetics in aspen as NO_3^- is the preferred form of inorganic N for root suckers (Min *et al.*, 1998; DesRochers *et al.*, 2003; Landhäuser *et al.*, 2010), which explains the rapid regeneration in uplands dominated by aspen clones.

Overall, changes in NO_3^- did not occur post-fire and instead was likely dependent on processes associated with each topographic position. Furthermore, while soil NO_3^- likely returned to its limited availability similar to pre-fire conditions in forests, riparian zones may be favourable areas for aspen regeneration during nitrate deficiencies.

Similar to nitrate, the lack of fire affects could indicate the return of ammonium to pre-disturbance levels. The spatial variability is likely attributed to uptake by primary successional species including aspen in forests, and abundant OM in peatlands (Macrae *et al.*, 2006) which favours high N mineralization. The vegetation composition of each land unit may also explain differences across land units. While NH_4^+ in *Sphagnum*-dominated peatlands has shown to be the preferred form of N, uptake lowers during prolonged exposure to avoid toxicity in *Sphagnum* (Bragazza *et al.*, 2005; Fritz, 2014). This may have occurred during N burning. Continuously waterlogged soils may have further allowed NH_4^+ buildup in peatlands and the inhibition of ammonium oxidation (Macrae *et al.*, 2006), which is corroborated by small changes in rust depth as the water table in peatlands remained close to the surface. Although VWC measurements were not taken during 2013, moisture may not have varied greatly between years. Further, acidic hummocks and hollows as seen in this study and others in Western Canada (Bayley and Thormann, 2005) often inhibit nitrification and not ammonification (Dancer *et al.*, 1972). While NH_4^+ varied spatially, similar to NO_3^-, fluxes and ammonification rates between burned and unburned hillslopes did not differ. However, since the understories of forests typically do not contain *Sphagnum* due to aspen litter suppression (Startsev *et al*., 2008), and if OM is the main large supplier of ammonium (Macrae *et al.*

2006), additional sources must be considered. Net ammonification rates were highest in the uplands and may be attributed to high turnover rates of N-rich aspen litter and low C/N ratios (Lègarè *et al.*, 2005). This contrasts with lower quality litter, which often undergoes slower breakdown and immobilization (Côté *et al.*, 2000; Vance and Chapin, 2001), such as *Sphagnum* and woody debris resulting in low ammonification in peatlands. Thus, differences across land units may be attributed to the substrate quality, but may not have been detected in the flux rates because of regeneration in aspen uplands. Thus, these results show that land unit properties likely influence NH_4^+ availability post-fire and that soil NH_4^+ are at levels similar to pre-disturbance. Importantly, recovering vegetation may be dependent on their own litter to satisfy NH_4^+ demands and may not need additional ammonium from peatlands.

2.6.2 Soil Phosphorus and Lasting Fire Effects

Landscape position and the simultaneous effect of fire did seem to have an effect on soil P. In the surface layer and maximum root zone depth in 2013, Ext-P in the unburned sites did not vary spatially, whereas the burned site showed increased Ext-P into the peatland. Losses of the LFH layer may have destroyed plant available P in forests, whereas the mineralization of high organic P may explain peatlands trends. Wang *et al.* (2014) showed that differences in P fractions varied with temperature where increased temperatures led to increased P mobility. Therefore, the fire in peatlands likely mineralized high amounts of P, where temperatures may have been below those required for P volatilization. Different microforms may also explain differences in plant available P. A recent study by Lukenbach *et al.* (2015b) at the URSA found that water repellency varies with burn severity, vegetation type, and microform. For example, wettability was lowered in *S. fuscum* hummocks when burn severity was high, with similar findings in feathermoss hollows that experienced low severity burns (Lukenbach *et al.*, 2015b). Since most of the microforms in this study were severely burned, increased wettability in hollows (Lukenbach *et al.*, 2015b) may explain high Ext-P compared to hydrophobic hummocks. Further increases in soil P may also be due to additions of NH_4^+ and NO_3; heightened phosphatase activity is linked to phosphate release in *Sphagnum* (Phuyal *et al.*, 2008).

P fluxes during recovery can also be attributed to differences in vegetation demand and uptake requirements across land units. In peatlands, mineralized P post-fire may have exceeded the required amounts of orthophosphates for regenerating bog species, so the influence of disturbance may be longer lived than NH_4^+ and NO_3^- (Hauer *et al.*, 1998). Current literature reports the co-limitation of N and P, and organic and inorganic N uptake in *Sphagnum* dominated wetlands rather than the sole absorption of extractable P (Kielland, 2001; Phuyal *et al.*, 2008). This is due to the fact that the sole addition of phosphate does not enhance *Sphagnum* growth in matured sites, unless the bog is saturated with inorganic N (Aerts et al., 1992). This makes P the limiting nutrient, though this only occurs in bogs where the atmosphere is the main source of N (Aerts *et al.*, 1992). While not reported in the literature, the demand of Ext-P for *Sphagnum* may be low, which may explain it's abundance years after fire (Kellogg and Bridgham, 2003).

Relationships between iron and manganese may also play a role in the high amounts of Ext-P in peatlands. Depending on the redox conditions of the waterlogged soils, P bound to iron may have been released through the transformation of Fe^{3+} to soluble Fe^{2+} and Mn^{5+}could have also been reduced to Mn^{4+} (Sherman *et al.*, 1998; Chambers and Pederson, 2006). Increases in Fe^{2+} and Mn was observed in the peatlands indicating that anaerobic soils allowed the release of plant available P (Venterink *et al.*, 2002; Maynard *et al.*, 2011). With the exception of Smith *et al.* (2001) in the Everglades, this is the first study in the WBP that reports elevated iron in wetlands post-fire.

Opposite trends were observed in unburned sites where P supply rates did not vary across land units. As seen by P mineralization rates at the surface, immobilization may explain limited SRP in peatlands (Moore and Basiliko, 2006). Though P supply rates were limited in forests likely due to Ca, Mn, or Fe binding, net P mineralization rates show high P turnover and likely immediate uptake by aspen (Macrae *et al.*, 2005). At depth, high P supply and SRP mineralization rates may be due to high organic matter in peatlands. Notably for soils at depth, 2014 P supply measurements shows that while fire explained elevated levels; P medians did not vary across land units. This may suggest that P supply rates may be returning to pre-fire levels.

Unlike NO_3^- and NH_4^+ where fluxes and concentrations likely returned to pre-fire rates, the effect of disturbance and land unit was evident in SRP availability. Differences in soil characteristics after fire, such as organic matter content and moisture in forests compared to peatlands; changes in soil properties (e.g., hydrophobicity) and vegetation demand may explain prolonged elevated P (Kellogg and Bridgham, 2003). Importantly, these mineralization and fluxes rates show that nutrient-rich aspen litter in uplands and hilltops act as their own sources for nutrients.

2.6.3 Water Chemistry

NO_3^-. NH_4^+ and SRP did not greatly vary across land units and burned and unburned areas. While it possible that these nutrients were elevated immediately after disturbance (McEachern *et al.,* 2000), they have could been flushed into adjacent hilltops and midslopes. However, this was also observed in unaffected areas (Macrae *et al.,* 2005). While forested areas generally contained higher NO_3^- and NH_4^+

relative to lowlands, it is unlikely that aspen depended on deep-water sources for nutrients, which further supports that aspen litter act as a significant source for N and P.

2.6.4 Aspen Growth Patterns and Nutrient Relations

The results in this study show that aspen stem height and leaf area index vary across topographic positions with the largest leaf area and tallest aspen in forests in 2013, but less variability across topographic positions in 2014. This is not surprising as aspen sucker growth rates exceed those of seedlings during the first few years after disturbance (Peterson and Peterson, 1992); in this study, suckers were the dominant form of regrowth in hilltops and midslopes (see Section 3.5, Table 3.2). During the following year, 2014 riparian areas had the largest median heights (Figure 2.11). This was also observed by Roy *et al.*, (2000) who found that balsam fir growth rate was greatest at the edge of riparian swamps due to higher light availability. Though light may have been influenced growth, it is probable that suckers at the margins experienced significant growth in 2014 and drove stem heights (Peterson and Peterson, 1992).

Further differences across the gradient can be linked to aspen suckers and their rooting zones in each land unit. Rooting systems are able to store energy and use it for clone regeneration (Stadt and Lieffers, 2000; DesRochers and Lieffers, 2001; Calder *et al.*, 2011; Landhäusser *et al.*, 2003). Through wind dispersal post-fire (Kay, 1993; Romme *et al.*, 1997; Turner *et al.*, 2003), there was an increase in aspen seedlings in margins and peatlands (see Section 3.6, Figure 3.2) indicating that seedlings do not have the connectivity and resource stores for large leaf areas (Landhäusser *et al.*, 2003) unlike aspen in forested areas.

N and P mineralization rates were positively correlated with aspen growth suggesting that the high quality of aspen litter enhances N and P cycling and availability (Lègarè *et al.*, 2005). This was observed in net ammonification rates; while N transformations were greatest in recovering hilltops and midslopes, likely due to aspen litter fall, limited supply rates indicated immediate uptake. High net ammonification and resultant uptake may also control leaf area. Hemming and Lindorth (1999) and Desrochers *et al.* (2003) showed that fertilizer additions did not greatly increase *P. tremuloides* growth further supporting that foliar N is sufficient to satisfy demand. This further supports that while NH_4^+ and P supply rates were high in peatlands, they were neither required nor beneficial for aspen regeneration. Therefore, growth in peatlands could be attributed to soil properties such as organic content matter and soil moisture.

Multiple studies have shown that aspen re-establish better on mineral soils (Kay 1993; Johnstone and Chapin, 2006a; LaFleur *et al.*, 2015), whereas the burned peatlands in this study had OM content exceeding 85% at the surface. This corroborates the correlations between OM%, leaf area, and stem height (Lafleur *et al.*, 2015). Likewise, seedling germination has been found to be best when soil moisture approximates 30% (Wolken *et al.*, 2010), which is much lower than the approximate 40% VWC in peatlands in this study. Waterlogged soils have been found to reduce plant turgor and initiate wilting as a result of oxygen deficiencies in roots (Bradford and Hsaio, 1982; Ländhausser *et al.*, 2003). Notably, high mineral content, and lowered depth to water table and soil moisture between years at margins relative to peatlands suggests that riparian zones could be more favourable for regeneration and growth as indicated by increased stem heights and leaf area in 2014. Overall, while nutrients were abundant in peatlands, especially hollows where most aspen were found, excess nutrients may not be the largest and only factor in aspen recovery. The correlation analysis suggests that soil physical properties, such as organic matter and C/N (litter quality) may have a larger influence on aspen growth and recovery rather than nutrient availability post-fire.

2.6.5 Implications for WBP Succession

While the detection of aspen in saturated areas were been observed post-harvest and fire (Kay, 1993; Roy *et al.*, 2000), aspen in peatlands post-fire has not been reported in the literature. Along with wind dispersion, the burning of surface peat and aboveground vegetation likely created the deposition of mineral material at the surface (Ellery *et al.*, 1989). In combination with a high water table, the immediate post-fire enviornment may have allowed favourable conditions for early aspen establishment (Latva-Karjanmaa *et al.*, 2006).

If seedlings continue to thrive, stand replacement of coniferous species, such as black spruce, to aspen can occur after severe fires. While Johnstone and Kasischke (2005) observed stand replacement in Alaskan uplands, it is uncertain if this could occur in peatlands given differences in the physical properties of the soil and nutrient status. However, the expansive suckering rooting system of aspen and its role in hydraulic redistribution (Lazerjan, 2014; Petrone *et al.,* 2015) could aid in the potential shifts of succession patterns in peatlands and margins. A possible mechanism for this may be through the uptake of peat and riparian zone water that is subsequently redistributed (Lazerjan, 2014) and transport into surrounding hillslopes may dry out peatlands in the already sub-humid climate. While net nitrification and nitrate fluxes were not correlated with stem heights and leaf area, abundant NO_3^- in margins, as found in this study, may stimulate root suckering there. Thus, the role of aspen in peatland margins and riparian areas must be further investigated to understand their potential influences on recovery and the conditions needed to transform areas where they are usually not found.

While aspen seedlings typically grow at a slower rate than suckers (Peterson and Peterson, 1992), excess P may imply that aspen uptake is low and as reflected in stem height in leaf area. This further suggests that while nutrients are limited in uplands, the recycling of their high quality litter is sufficient during regeneration where additional sources from other areas such as peatlands are not needed. Therefore, aspen succession in peatlands cannot be attributed to nutrient availability alone, but additional variables such as light and soil moisture must also be considered together (Hemming *et al.*, 1999).

2.7 Conclusion

This study showed that nutrients and aspen distribution and growth varied across recovering topographic land units. With the exception of net ammonification, correlations between nutrient availability and *P. tremulodies* did not exist. Due to the immediate regeneration of primary succession species, such as aspen, nitrate and ammonium may have returned to pre-fire levels. Conversely, while P supply rates in burned areas remained elevated particularly in peatlands, nutrient-rich peat did not explain *P. tremuloides* existence in peatlands. This suggests that additional sources N and P were not required for re-establishment and that forest litter was sufficient for regeneration. While aspen seeds were likely blown into the surface layer of burned peat, this research showed that high OM and waterlogged soil might have inhibited further growth. When considering the fate of land units and aspen in the WBP, future studies must consider soil physical properties and nutrient status, along with the interactions between aspen roots and peat margins. Such long term monitoring would help in predicting the trajectories of forests and the potential losses of peatlands increased disturbances.

3.0 Manuscript 2: Hydrologic Controls on Trembling Aspen (*Populus tremuloides* Michx.) Regeneration and Succession Post-Fire

3.1 Introduction and Literature Review

The Western Boreal Plains (WBP) contains a mosaic of peatlands and uplands where forests are often dominated by jack pine, black spruce, paper birch, and aspen (Weber and Stock, 1998; National Forest Inventory System, 2012). Of these species, trembling aspen (*Populus tremuloides* Michx.) is the dominant upland species, and is of importance in commercial harvesting (Peterson and Peterson, 1992). While the rooting system of mature aspen forests can produce clones immediately after disturbance with densities of up 20 000 clones per hectare (Bartos and Mueggler, 1981), the presence of competing trees such as conifers in later successional stages can outcompete aspen for resources (Kneeshaw and Bergeron, 1998; Calder *et al.*, 2011; Coop *et al.*, 2014). This may result in mixed or complete stand replacement. Therefore, along with stand thinning and harvesting, controlled and wildfires are needed to sustain aspen communities (Peterson and Peterson, 1992; Romme *et al.*, 1997; Johnstone and Kasischke, 2005; Johnstone and Chapin, 2006b; Krasnow and Stephens, 2015).

The effects of fire on aspen stand succession and recovery have been well recorded in Boreal Forests (Johnstone and Chapin, 2006a; Johnstone and Chapin, 2006b), with recent studies focusing on peat fires (Kettridge *et al.*, 2014; Kettridge *et al.*, 2015; 2015; Lukenbach *et al.*, 2015a). Much of the current peat fire literature in the WBP are within the context of carbon release as a result of climate change, and has advanced the understanding of the controls and outcomes of such disturbances on peatlands (Kettridge *et al.*, 2014, Kettridge *et al.*, 2015; Hokanson *et al.*, 2015; Lukenbach *et al.*, 2015a). While the latter includes potential shifts in peatland vegetation communities (Kettridge *et al.*, 2015), little attention has been given to the influence of surrounding areas, such as forests, and how upland vegetation may affect peatland succession trajectories. While Klein *et al.* (2005) reported incoming black and white spruce, and aspen at wetland margins with less than 2 m of peat in southern Alaska, the authors attributed this to changes in soil drying rather than fire.

The hydrological connectivity of forests and wetlands in the WBP can often vary as a function of the climate cycle, soil storage, and soil texture at the hillslope scale (Devito *et al.*, 2005b). While extensive research has been conducted on the flow of water between land units in the WBP (Ferone *et al.*, 2004; Smerdon *et al.*, 2005; Devito *et al.*, 2005a), the role of vegetation and its potential role in facilitating flow across forests and wetlands have yet to be studied (Petrone *et al.*, 2015). Given that wetlands and uplands can experience hydrologic decoupling in the WBP (Devito *et al.*, 2005a), vegetation may be important in understanding the connectivity between land units. Further, there is a lack of understanding if disturbance disrupts these interactions, and the potential effects on succession.

3.1.1 Aspen Ecology and Succession

It is well understood that transpiration losses, such as those in aspen stands, play a role in determining the water budget in the WBP is often water limited (Brown *et al.,* 2013; Petrone *et al.*, 2015). In this literature review however, the importance of aspen will be highlighted with respect to their regeneration post-fire, succession patterns, and potential influence on water transport between peatlands and uplands.

Periodic fires, natural and anthropogenic, are needed to maintain system heterogeneity through creating conditions suitable for regeneration (Weber and Stock, 1998). For example, fire removes canopy cover and surface organic matter allowing for sunlight, nutrient mineralization, and increased soil temperatures (Certini, 2005). While controlled burns contribute to fires in the Boreal Plains, predicted drought conditions here has drawn attention to changes in wildfire frequencies (Weber and Stocks, 1998; Fauria and Johnson, 2008). Within a given fire, burn severities are defined by the amount of organic matter losses and are classified as low, moderate, and high (Ryan and Noste, 1983; Turner *et al.*, 1994). In recent studies in the WBP, pre-fire conditions (i.e. vegetation cover type, soil moisture, hydrologic connectivity, and organic matter content) determine burn severities (Lukenbach *et al.*, 2015a; Lukenbach *et al.*, 2015b; Lukenbach *et al.*, 2015c; Hokanson *et al.*, 2015). Further, burn severity is typically positively correlated with changes in soil properties, including hydrophobicity, chemistry, erosion and runoff (DeBano *et al.,* 1973; Huffman *et al.*, 2001). Depending on the severity of the fire, post-fire conditions often favour the regeneration of species previously suppressed before disturbance (Weber and Stock, 1998). For example, most coniferous trees depend on fire for the release of seeds from cones at temperatures above 50 °C, whereas for poplar species, such as balsam poplar and trembling aspen, initiation is best on mineral seedbeds when sunlight is not limited, which occurs with high severity fires (Mutch, 1970; Weber and Stock, 1998).

Trembling aspen (*Populus tremulodies* Michx.) are species that dominate this fire-prone region, and across Canada in part because they have large moisture and temperature regimes (Strong and LaRoi, 1983; Peterson and Peterson, 1992; Hogg *et al.*, 2008). Under water-stressed periods, aspen have also been shown to increase carbohydrate storage in rooting systems used for osmoregulation, and to increase root growth and sucker regeneration (Hogg *et al.*, 2008; Michaelian *et al.*, 2011; Galvez *et al.*, 2011).

Thus, the growth and succession of an aspen stand is often more dependent on clonal suckering than seed dispersal (Mitton, 1996; Peterson and Peterson, 1992; Romme *et al.*, 1997).

Aspen seedlings must be in moist and well-drained mineral soils, with few competitors and warm temperatures (Barnes, 1966; Kay, 1993; Romme *et al.*, 1997; Wolken *et al.*, 2010; Landhäusser *et al.*, 2010; Johnstone and Chapin, 2006b). The highest seedling amounts occurred in mineral substrates 1-5 cm thick, and rarely established on organic soils at depths deeper than 2-2.5 cm (Kay, 1993; Johnstone and Chapin, 2006a).

In areas with remnant aspen roots, clone reproduction is often high during primary succession, typically occurring at parent roots that are 2 cm in diameter (DesRochers and Lieffers, 2001). Although aspen suckers initiate structural roots, parent roots can remain incorporated in clones and are not independent of them (DesRochers and Lieffers, 2001). Clones also have the ability to graft, so connections of dead roots of live trees still allow for resource transport and the potential for high carbohydrate reserves for growth (DesRochers and Lieffers, 2001; Ländhausser and Lieffers, 2001; Landhäusser and Lieffers, 2002).

Sucker stimulation and parent clone creation are heightened as a result of disturbance (e.g. Schier and Campbell, 1978; Schier, 1985). During disturbance, such as cutting, harvesting, and fire, the hormone auxin can be destroyed or its release can be inhibited from the main stem (Schier and Campbell, 1978; Schier *et al.*, 1985; Fraser *et al.*, 2004), which acts to not limit sucker growth. Further, in the event of fire, increased temperatures allows for the production of cytokinins in root meristems, further augmenting root and sucker growth (Bartos and Mueggler, 1981; Schier *et al.*, 1985; Romme *et al.*, 1997)

Aspen seed density, germination, and aboveground biomass are often correlated with high severity fires (Romme *et al.*, 1997; Johnstone and Kasischke, 2005; Johnstone and Chapin, 2006b; Krasnow and Stephens, 2015), likely attributed to competition against shrubs and graminoids, which are only able to asexually reproduce in low severity fires (Johnstone and Kasischke, 2005). Further, high seedling mortality may occur in organic soils as a result of desiccation due to diurnal changes in soil temperature when burn severity is low (Johnstone and Chapin, 2006b; Laffleur *et al.*, 2015), and with soil hydrophobicity in high severity fires, which may draw moisture from seeds (Johnstone and Chapin, 2006b).

P. tremuloides is often observed during primary succession immediately after disturbance due to the pre-existing rooting system and resource usage of suckers (Romme *et al.*, 1997; Johnstone and Kasischke, 2005; Johnstone and Chapin, 2006b; Calder *et al.*, 2011; Krasnow and Stephens, 2015). Most studies report increased aspen photosynthesis and growth rates under abundant nutrients and light post-fire through nutrient mineralization and canopy destruction (Hemming and Lindroth, 1999; Kaelke *et al.*, 2001; Calder *et al.*, 2011). During later successional stages, the presence of other tree species, such as conifers, may lower canopy openings and thus inhibit growth (Kneeshaw and Bergeron, 1998; Calder *et al.*, 2011; Coop *et al.*, 2014). Conversely, aspen can replace stands when shade intolerant species are not present and/ or viable in the seedbank, the presence of aspen pre-fire, hetergenous canopy gaps, and low fire return intervals (Kulakowski *et al.*, 2004; Johnstone and Chapin, 2006a). Accumulation of aspen litter may also affect the seedbed needed for conifer germination (Johnstone and Kasischke, 2005; Johnstone, 2005). During early stages of regeneration, *P. tremuloides* suckers and seedlings can reach heights of 2.7 m after three years, with subsequent rates of 0.5-1.0 m/year (Horton and Maini, 1964; Bella and De Franceschi, 1980; Peterson and Peterson, 1992). Associated with aspen growth or photosynthesis and transpiration (E), the release of water from plant stomata (Farquhar and Sharkey, 1982; Jarvis and Davies, 1998; Pothier and Prevost, 2003).

3.1.2 Aspen Transpiration and Controls

Transpiration begins in the rooting zone with water uptake, sequential movement to xylem, and the release through stomatal opening (Johnson and Ferrell, 1983). If xylem water is limited, cavitation and embolism can occur as a result of high transpiration (Johnson and Ferrell, 1983), eventually leading to plant stress and death (Johnson and Ferrell, 1983). While other metrics can be used to indicate plant-stress and growth, such as water-use efficiency (see Sinclair *et al.*, 1984), relationships have also been established with E. For example, g_s and transpiration lowers during root inundation resulting in losses in plant turgor, and plant wilting, epinasty, and death (e.g. Bradford and Hsaio, 1982), though most of these studies have occurred in controlled or agricultural or humid settings. Similar reductions in transpiration have been observed in mature aspen stands in water-limited areas of Colorado (Anderegg, 2012).

Turbulent conditions within a stand as a function of stand architecture, affect humidity conditions and vapour pressure deficit (D), and as such E (Monteith, 1995; Hogg and Hurdle, 1997; Allen *et al.*, 1998; 2005; Kim *et al.*, 2014). Therefore, since aspen leaves experience high amounts of flutter—due to their light weight and petiole orientation—when exposed to wind, there is the potential for increased water loss through stomatal conductance (g_s) (Roden and Pearcy, 1993). Further losses however, are balanced by stomatal closures during high turbulence events (Rushin and Anderson, 1981; Roden and Pearcy, 1993). In addition to controlling trubulent conditions within the stand, stand architecture also controls the amount of photosynthetically active radiation (PAR; wavelengths between 400-700 nm) available to drive photosynthesis and transpiration (Ku *et al.*, 1977; Farquhar and Sharkey, 1982;

Pieruschka, 2010). Positive relationships have been observed between PAR and g_s resulting in heightened transpiration and photosynthesis, however stomatal closures may respond to reduced substrates that are able to metabolize internal CO_2 upon uptake, high internal plant CO_2, or limited atmospheric CO_2 availability (Farquhar and Sharkey, 1983; Farquhar and Wong, 1984; Jarvis and Davies, 1998). All of these drivers that lower g_s usually occur to maximize photosynthesis, while minimizing water losses to transpiration (Jarvis and Davies, 1998). Conversely, DesRochers *et al.* (2002) saw reduced aspen leaf sizes to minimize respiration effects when light is limited as a result of limited photosynthesis. Although transpiration rates have been limited to increases in PAR, temperature, and D until a given threshold, such relationships are often held true only when soil moisture is abundant (Hogg and Hurdle, 1997; MacKay *et al.*, 2012; Brown *et al.,* 2013).

In moisture deficient areas, such as the Boreal Plains, that may experience limited P and drought, E generally decreases as a response to low soil water content (MacKay *et al.*, 2012). The moisture content to achieve this depends on texture and soil storage, but often occurs below the wilting point (Bernier *et al.*, 2006; MacKay *et al.*, 2012). Brown *et al.* (2013) observed that regardless of variations in D and PAR in aspen uplands in the WBP, there was a larger response of above canopy evapotranspiration (ET) during periods of varying soil moisture. Further, a recent study by Anderegg (2012) of aspen in Colorado showed that seasonal droughts and low soil moisture reduced aspen transpiration, and that while carbohydrate stores increased, root growth decreased preventing resource allocation to suckers and recovery. Conversely, there are limited studies that have looked at aspen in inundated soils. While Landhäusser *et al.* (2003) and Wolken *et al.* (2010) studied at waterlogging on aspen seedling transpiration in controlled environments, there are currently no *in situ* studies on aspen re-establishment in wet areas. However, Petrone *et al.* (2015) highlight the importance of aspen in the WBP being able to acquire adequate moisture supplies where they are often found with very deep water tables, which is likely sourced from the adjacent peatlands (Brown *et al.*, 2013).

Hydraulic redistribution (HR) is the movement of water from saturated areas to areas of low soil moisture facilitated through roots (*Prieto et al.*, 2012). Dawson (1993) observed this process through examining diurnal changes in soil-water potentials and the isotopic analysis of plant tissue and possible water sources. While hydraulic uplift is the dominant direction of flow encompassing hydraulic redistribution and has been well cited in the literature (e.g., Prieto *et al.*, 2012), roots can also transport water from shallow soils to deeper layers (Dawson *et al.*, 1993; Hultine *et al.*, 2006), and laterally at the same depth (Smart *et al.*, 2005). HR has been well reported in a range of arid and mesic climate regions through a range of species (Dawson, 1993; Hultine *et al.*, 2006). However, limited studies have looked at this process in the sub-humid climate of the WBP (Lazerjan, 2014), though Brown *et al.* (2013) and Petrone *et al.* (2015) suggest it is the mechanism that contributes to canopy ET.

Most studies that have looked at HR used the isotopic analysis of $\delta^{18}O$ and $\delta^{2}H$ in the potential water sources (such as the water table and groundwater) and the plant matter (Dawson *et al.*, 1993; Hultine *et al.*, 2006; Burgess and Bleby, 2006). For example, Dawson *et al.* (1993) found that the isotopic composition of sinker roots were closer to those of groundwater, whereas signatures between shallow roots were closer to precipitation events and soil water. Processes that lead to enrichment include biomass production, stomatal opening and closing, and transpiration lead to isotopic enrichment (Alison *et al.*, 1983). Many studies have looked at enrichment in soil profiles as a function of evaporation (Allison *et al.*, 1983; Price *et al.*, 2009). Limited studies however, have compared the isotopic composition across peatland-upland gradients and moreover, the uptake of $\delta^{18}O$ and $\delta^{2}H$ of the surrounding vegetation, and there are no studies that have investigated this post-fire.

3.2 Study Objectives

The goal of this study was to understand the role of upland – peatland hydrological connections in meeting the moisture needs of upland aspen, and whether this changes post-fire in the WBP. The specific objectives of this chapter are to:

1) Determine if aspen, a dominant upland species, detected in burned peatlands are seedlings or suckers. Further, determining relative proportion of suckers will provide further support to understand their role in hydraulic redistribution to adjacent uplands.
2) Quantify the environmental controls (i.e. PAR, D, soil moisture, etc.) on aspen transpiration and regeneration in burned uplands, and further determine these factors are linked to their succession into peatlands.

To address the success of aspen, transpiration was used as proxy of physiological stress and productivity across land units. This was further coupled with environmental controls, such as soil moisture, to understand the factor that is allowing aspen succession into peatlands. This will help predict whether the presence of *P. tremuloides* will continue into later successional stages of peatland recovery or if the control is more tightly linked to it's regeneration in moisture limited forests. Implications of aspen detection in peatlands will also be discussed, particularly the potential loss of peatland margins to upland aspen. It is hypothesized that aspen roots existing in peatlands aid in transporting water to those in forested areas through hydraulic redistribution as observed in the isotopic signatures of soils found in peatlands and peatland margins, and aspen in forested areas. Due to dry upland soils however, it is predicted that aspen transpiration will be low in forests despite hydraulic redistribution and that waterlogged soils, such as those found in peatlands and riparian areas, are favoured for aspen re-establishment.

3.3 Study Area

The Utikuma Region Study Area (URSA) is located in north central Alberta, approximately 370 km north of Edmonton and 250 km south of Fort McMurray, Alberta within the Boreal Plains of Western Canada (56°6'N, 116°32'W) (Figure 3.1). Deep glacial deposits, as a result of glaciation, underlie the URSA where uplands are situated on rolling moraines and low-lying areas upon lacustrine deposits (Finklestein, 1990; Smith *et al.*, 2003). Landforms across the URSA include stagnant-ice moraines, and clay and sandy glacial plains (Vogwill, 1978; Ceroici, 1979). On May 3, 2011, the URSA, along with the study site was impacted by a 90 000 ha wildfire.

This study took place on a coarse-textured outwash plain and contained a 39 ha lake) (Section 2.4, Figure 2.1). The lake interacts with regional groundwater creating a flow-through system (see Smerdon *et al.*, 2005 and Lukenbach *et al.*, 2015c for more detail). Surrounding the lake are riparian areas and peatlands with transitions into mineral uplands (Smerdon *et al.*, 2005). The fire affected the southwest portion of the lake that disturbed peatlands where margins and pockets in the centre of experienced smoldering, and surrounding uplands (Lukenbach *et al.*, 2015a; Hokanson *et al.*, 2015). The nature of the crown fire however, sustained some peatlands and forested areas within the burned portion of the catchment.

The overstories of burned forested areas were dominated by trembling aspen and coniferous trees, such as pine, existed prior to disturbance in the forested areas in at the top of the hill, whereas aspen mostly existed on the slopes. It is likely that most of the recovering aspen in the forested area were clones (more to follow). In the growing seasons of June to August 2013 and May to August 2014, aspen defoliation occurred through forest tent caterpillars (*Malacosoma disstra*) during budburst. Primary successional species in riparian areas included polytrichum mosses, liverwort (*Marchantiophyta*), common horsetail (*Equisetum arvense*), fire moss (*Ceratodon purpureus*), and willow (*Salix* spp.). These vascular species, including Bog birch (*Betula pumila*), were also present in burned peatlands and further contained *Sphagnum* species and feathermoss (Lukenbach *et al.*, 2015b; Lukenbach *et al.*, 2015c). Importantly, peatland margins, riparian zones, and the centre of peatlands (hollows) also contained aspen.

3.4 Methods

3.4.1 Aspen Seedlings and Suckers

Aspen in the burned peatland were mapped with a handheld GPS (Garmin). While the accuracy of the device was ±5 m, this activity showed where aspen seedlings or suckers were most dominant. This was done by carefully removing the surface soil directly beneath the regenerating aspen until a major root was detected. If only a large vertical root was detected, the aspen was classified as a seedling. Conversely, if a large lateral root was a connected to the base of the aspen, it was classified as a sucker or clone (Kay, 1993; Romme *et al.*, 1997). This method was used to minimize destruction. The presence and distance of nearby parent aspen or other trees, if any, was also recorded.

3.4.2 Transpiration, Aspen Biometric, and Hydrologic Measurements

Three burned transects were selected for measuring aspen transpiration. The land units across a topographic gradient contained a recovering hilltop, midslope, riparian zones, and peatland. These locations on each transect contained two 2 × 4 m plots (Figure 3.1). Tree species that were killed during fire that were closest to the plot were identified as a potential parent through it's identification as a coniferous or deciduous or aspen tree (Table 3.1). All growing aspen in the plots were numbered and classified as small, medium, or large and were identified as a seedling or sucker based on the presence of a taproot (Kay, 1993; Romme *et al.*, 1997) (Table 3.2). During the summers of 2013 and 2014, daily stomatal conductance (cm s^{-1}) were taken. Transects and plots were selected at random on each sampling day to capture diurnal differences in stomatal resistance. Within each plot, nine resistance measurements were captured from three random small, three medium, and three large aspen through an AP4 Porometer (Delta-T Devices, Cambridge). Further, the resistance readings were taken from leaves at the base, middle, and top of the plant.

Ohm's analogy for transpiration was used for leaf transpiration:

$$E_{leaf} = \rho_a C_{pa} \left(\frac{D}{\gamma r_{leaf}}\right)\left(\frac{1}{\rho_w L_v}\right) \tag{1}$$

Where E is leaf transpiration (mm s^{-1}), L_v is the latent heat of vapourization (J kg^{-1}), ρ_a is air density (kg m^{-3}), ρ_w is the density of water (kg m^{-3}) $C_{\rho a}$ is the specific heat capacity (J kg^{-1} K^{-1}), D is the vapour pressure deficit (kPa), γ is the psychrometric constant (kPa K^{-1}), and $r_{\_leaf}$ is the resistance of the leaf (s mm^{-1}). Values for L_v, ρ_a, ρ_w $C_{\rho a}$, and γ were set as constants (Brunt, 1952; Monteith, 1965; Allen *et al.*, 1998).

From the leaf to plot scale:

$$E_{plot} = E_{leaf}LAI_{plot} \qquad (2)$$

Leaf area index (LAI) of aspen in each plot was measured destructively. At the end of each growing season, a plant representing each size class, small, medium, and large, outside of each plot was uprooted and had its leaves stripped. The leaves were run through a leaf scanner (LI-3100C, Li-Cor, Nebraska) and yielded the leaf area of the plant (cm^2). This was scaled to the plot level by multiplying the number of plants of each class size by their average leaf area, summed, and divided by the plot area (8m^2) to yield LAI (e.g. Chen *et al.*, 1997; Bréda, 2003). Stem lengths were also recorded.

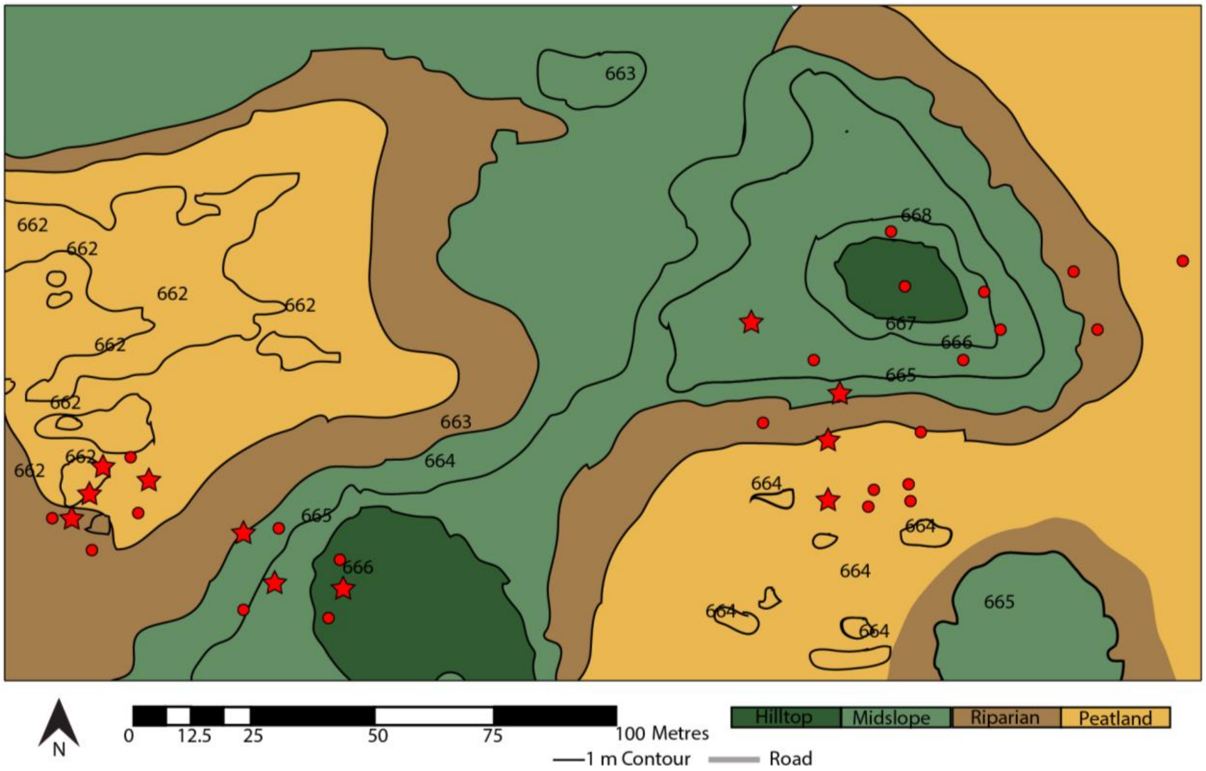


Figure 3.1: Portion of the burned study catchment where plot transpiration (circle), and soil moisture (star) measurements were taken.

Land Unit	Type of Parent	DBH	Distance from Plot
Hilltop	Deciduous	16.4	5.7
Hilltop	Conifer	5.1	3.5
Midslope	Deciduous	13.4	5.9
Midslope	Conifer	11.9	5.0
Riparian	Deciduous *	18.1	9.5
Riparian	Conifer	11.2	6.2
Peatland	Conifer	8.5	5.6

Table 3.1: Average diameter at breast height (DBH) in, and distance from plot (m) of parent trees near transpiration plots. * Indicates a single tree of a given type (conifer/deciduous).

Land Unit	Seedlings	Suckers	Total Aspen in Plot
Hilltop	4	20	28
Midslope	2	53	59
Riparian	8	25	35
Peatland	7	13	18

Table 3.2: Average number of aspen seedlings or suckers in each transpiration plot.

3.4.3 Climatic and Hydrologic Measurements

Simultaneous with resistance, point readings of vapour pressure deficit (D, kPa), and PAR (μmol m^{-2} s^{-1}) were simultaneously recorded with resistance on the porometer head. Additional instrumentation at the research site included: an incoming and reflected longwave CGR3 pyrgeometer (Kipp & Zonen, Delft, The Netherlands), an incoming shortwave PRY-PA2 pyrgeometer (Apogee Instruments Inc., Roseville, California), an anemometer (R.M. Young Wind Monitor, Transverse City, Michigan), an NR-Lite Net Radiometer (Kipp & Zonen, Delft, The Netherlands), and CS616 Water Content Reflectometer (Campbell Scientific, Edmonton, Alberta). Precipitation was collected with hand gauges.

Access tubes were installed 1.0 m from the surface in all land units for weekly volumetric water content (VWC%) with a PR2 Probe (Delta T Devices, Cambridge) in 2013 and 2014 (Figure 3.1). Though the instrument produced moisture readings depths every 0.1 m to 1.0 m, depths at 0.1, 0.2, 0. 3, and 0. 4 m from the surface will be highlighted. Further, soil moisture at these depths were also averaged to capture the most active regenerating aspen roots.

Between each transpiration plot, a monitoring well existed where water levels were recorded biweekly during both growing seasons. A total of 8 wells were measured where each transect had a well located in aspen hilltops, midslopes, riparian areas, and peatlands. For more detail on site sampling well hydrology refer to Hokanson *et al.*, (2015) and Lukenbach *et al.*, 2015c; refer to Figure 2.3 for a map of well locations.

3.4.4 Hydraulic Redistribution

Sampling took place during July 2014. To determine the recovering aspen's water source, three plants reflecting each size class, small, medium, and large were selected near transpiration plots in each transect (Figure 3.1). For each aspen, ten twigs were randomly removed throughout the top, middle, and base of the plant, and leaves stripped to avoid the enrichment of hydrogen through plant stomata (see Dawson *et al.*, 1993). The remaining twigs stored into airtight sterilized vaccutainers. With each aspen, soil cores 0.1 and 0.5 m directly beneath its rooting zone were sampled and stored into polyethylene bags. To minimize evaporation, air was ejected from the bags and tightly sealed. All plant material and soil samples were frozen until distillation. Nitrile gloves were changed between soil and aspen samples to avoid contamination.

All plant and soil cores underwent an azeotrophic distillation to determine $\delta^{18}O/\delta^{2}H$ water composition as described by USGS typically used for stable isotope-ratio methods (USGS, 2012) with modifications (Gwynne *et al.*, in prep). Approximately 50 mL of toluene was added to a round-bottom flask containing soil or plant matter for 1.5- 2.0 hours where based on boiling point, sample water separated from the solvent. To remove excess organic solvents, approximately 0.5 g of activated carbon was added to the distilled sample and filtered. The isotopic composition of soil $\delta^{2}H$ and $\delta^{18}O$ were determined by an off-axis integrated-cavity output spectroscopy laser system (Los Gatos Research, California) (Lis *et al.*, 2008; Penna *et al.*, 2012; Elena *et al.*, 2013) with precisions of ± 0.8 ‰ and ± 0.2 ‰, respectively. $\delta^{2}H$ in plant matter was prepared with a hot chromium reduction (Drimmie *et al.*, 2001; Morrison *et al.*, 2001) and analyzed with a Micromass IsoPrime Mass Spectrometer with precisions of ± 0.8‰. $\delta^{18}O$ was processed through CO_2 equilibration (Epstein and Mayeda, 1958) and analyzed on a continuous flow isotope ratio mass spectrometer (CF-IRMS) with precisions of ± 0.2‰ (Drimmie *et al.*, 2001). All isotopic analysis was conducted at the University of Waterloo. Ratios of rare isotopes, in this case, $\delta^{18}O$ and $\delta^{2}H$ are given by the equation:

$$\delta^{18}O = \left(\frac{18R_{sample}}{18R_{standard}} - 1\right) \times 1000 \tag{3}$$

Expressed in per-mille (‰), where R is the fraction between the heavy isotope compared to the abundant isotope (e.g. $\delta^{18}O$ / $\delta^{16}O$, $\delta^{2}H$ / $\delta^{1}H$), and $R_{standard}$ is the isotopic ratio of a given standard (e.g. Mook, 2001).

3.4.5 Statistical Analysis

A Kolmogorov-Smirnov test was preformed on transpiration, soil moisture, D and PAR values, though each parameter failed the test for normality (p>0.05). All of these metrics (dependent variable) were subjected to a Kruskal-Wallis H-test—a nonparametric equivalent to an ANOVA—relative to topographic position (independent variable). If p<0.05, a Mann-Whitney U test, similar to a *t*-test for data not normally distributed, was further used to determine differences amongst topographic positions. Differences between years for all parameters (E_{plot}, VWC, D, and PAR) also underwent Mann-Whitney U tests.

Plot transpiration further underwent Spearman's Rank-Order Correlation (r_s) relative to: soil moisture (median VWC from 0.1-0.4 m), D, PAR, leaf area, and stem heights. A positive r_s value indicates a positive correlation, whereas negative r_s signify inverse correlations with E_{plot}. All statistical analysis was preformed on IBM SPSS Statistics version 20 (IBM Corporation).

3.5 Results

3.5.1 Seedling and Sucker Distribution

Nearly all-recovering aspen in peatlands occurred near the margins, and were seedlings (Figure 3.2). The classification of regenerating aspen was verified by: 1) the lack of a taproot, 2) further connections with nearby aspen, and 3) excavation. Visually, however some seedlings began forming suckers as some shared lateral roots. Within the peatland, aspen appeared in severely burned hollows rather than hummocks. Further, areas where bog birch (*Betula pumila*) was present did not have nearby aspen seedlings. Nearby parent trees were not detected at the centre of the peatland.

Conversely, *P. tremulodies* closet to the peatland margins were visually larger with thick roots. Further, an increase in aspen ramets were detected along roots with larger diameters. *P.tremulodies* here also had parent trees from surrounding forested areas closer than those to the centre of peatlands.

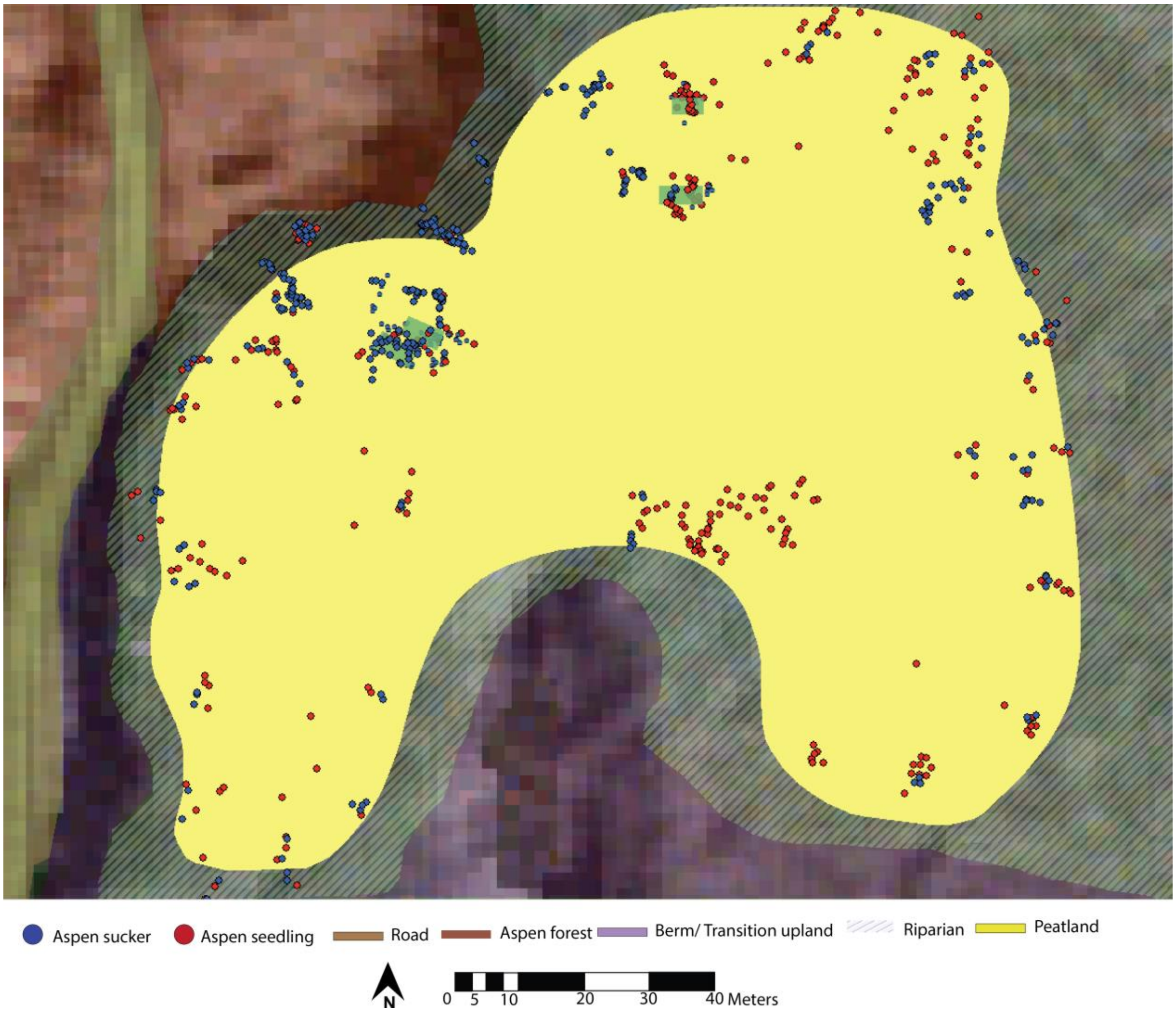


Figure 3.2: A map of the burned peatland with the location aspen seedlings (red) and suckers (blue) post-fire in 2013.

3.5.2 Aspen Growth

In 2013, leaf area of individual aspen and stem heights were greatest in the midslope, followed by the hilltops, riparian zones, and peatlands (Section 2.5, Figure 2.12) and varied statistically across land units ($p<0.05$). While patterns in leaf area did not change in 2014, the tallest aspen were found in instead found in riparian areas rather than midslopes, which were then followed by hilltops and peatlands (Section 2.5, Figure 2.12).

3.5.3 Stomatal Conductance

Trends in g_s across land units followed transpiration trends in 2013 (Table 3.3). The following year however, showed that conductance in 2014 was lower in hilltops than peatlands with rates of 0.041 $\mathrm{mms^{-1}}$ and 0.049 $\mathrm{mms^{-1}}$, respectively. Leaf stomatal conductance rates varied statistically across the hillslope ($p<0.05$) Across land units in 2013, g_s between uplands and hilltops did not vary statistically from each other ($p=0.54$), and similar observations were observed with peatlands and riparian areas ($p=0.69$). In 2014, stomatal conductance did not vary between midslopes and riparian areas ($p=0.13$) and riparian areas and peatlands. Between years, g_s lowered at all topographic positions ($p<0.05$), though it did not vary significantly in margins ($p=0.57$).

Topographic Position	**Year**	**Stomatal Conductance (mm $\mathrm{s^{-1}}$)**
Hilltop	2013	0.069 ±0.002
Hilltop	2014	0.041 ±0.002
Midslope	2013	0.068 ±0.002
Midslope	2014	0.062 ±0.003
Riparian	2013	0.057 ±0.002
Riparian	2014	0.055 ±0.003
Peatland	2013	0.056 ±0.001
Peatland	2014	0.049 ±0.003

Table 3.3: Aspen leaf stomatal conductance (median ±standard error) across land units in 2013 and 2014

3.5.4 Plot Transpiration

In 2013 and 2014, aspen transpiration across topographic positions was greatest in the recovering forested areas, especially at the midslope position, and decreased into the peatlands (Figure 3.3). In order of increasing transpiration rates (mm $\mathrm{hr^{-1}}$) in 2013: peatland (0.08), riparian (0.18), hilltop (0.35), and midslope (0.37). Similar observations are reported in 2014 where E_{plot} rates were: peatland (0.11), hilltop (0.23), riparian (0.27), and midslope (0.47), respectively. The greatest variability was observed in the peatlands where transpiration rates ranged from 0.01-1.25 mm $\mathrm{hr^{-1}}$ in 2013, and in the riparian zones in 2014 where rates were between 0.01 and 1.38 mm $\mathrm{hr^{-1}}$. Statistically, the Kruskal-Wallis test showed that the sampling area affected transpiration, where E_{plot} rates differed amongst each land unit ($p<0.05$) in both years (Figure 3.3). Further, E_{plot} within individual land units varied between years ($p<0.05$) with overall increases in 2014, with the exception of the hilltop position where rates lowered. Positive correlations between leaf area ($r_s=0.58$) and stem heights ($r_s=0.69$) also existed with transpiration.

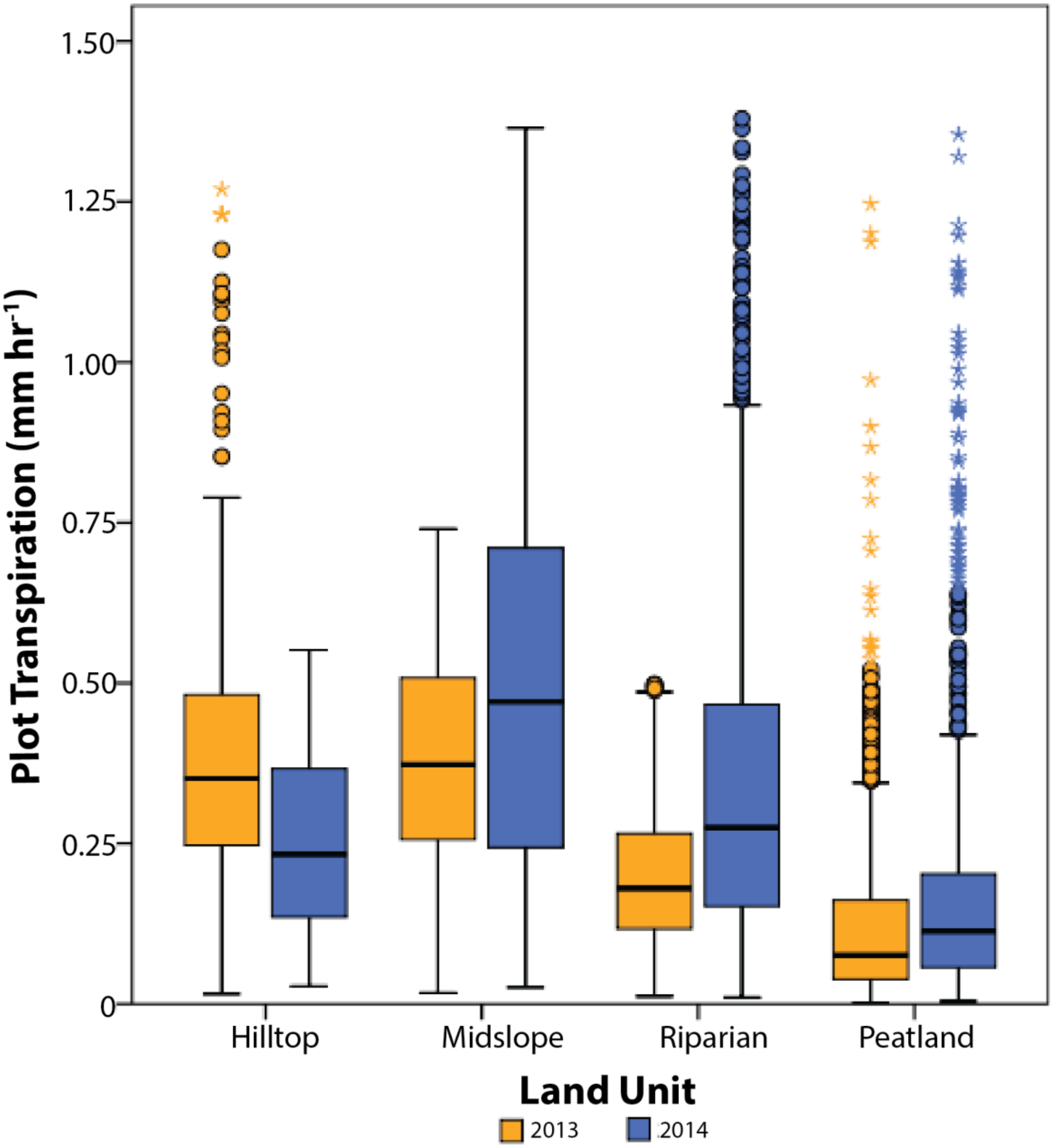


Figure 3.3: Plot transpiration (mm hr^{-1}) during June-August 2013 and 2014, across topographic positions.

3.5.5 D, PAR, and VWC Across Recovering Land Units

In 2013, D did not greatly vary across land units (p<0.05), though the lowest deficits occurred in the recovering hilltops (1.53 kPa) and increased into the peatland (1.89 kPa) (Figure 3.4). Trends were similar in 2014 where D in peatlands (1.80 kPa) exceeded hilltops (1.61 kPa) though medians did not range vastly across the hillslope. There were no relationships between E_{plot} and D in 2013 (r_s=0.004, p=0.74) (Figure

3.4; Table 3.4). Conversely, there was a weak relationship (r_s=0.088) in 2014 where *p*=0.003. The highest transpiration rates occurred at vapour pressure deficits below 1.50 kPa in both years.

PAR did not vary across land units. In 2013, PAR was lowest in the uplands (120 µmol m^{-2} s^{-1}) and increased into riparian areas (214 µmol m^{-2} s^{-1}) and peatlands (210 µmol m^{-2} s^{-1}) (Figure 3.5). Similar trends were observed the following year with highest PAR levels in peatlands (500 µmol m^{-2} s^{-1}) and lowest in aspen hilltops (250 µmol m^{-2} s^{-1}) and differed across land units ($p<0.05$). When PAR was linked to transpiration, r_s=-0.045 and $p<0.05$ (Figure 3.5; Table 3.4). The following growing season showed similar trends where correlations were not observed (*p*=0.51, r_s=0.011).

In 2013, average depths from 0.01 to 0.04 m showed that VWC varied across topographic positions where moisture was lowest in recovering aspen hilltops and increased into peatlands (Figure 3.6). Soil moisture differed across and between topographic positions ($p<0.05$), though medians did not vary statistically between forested areas (*p*=0.54). The greatest variability in VWC occurred in riparian zones, with ranges from 0.08 to 0.87 m^3m^{-3} and in peatlands from 0.01 to 1.01 m^3m^{-3}. In 2014, VWC across all land units lowered (Figure 3.6). Overall trends however, remained where moisture increased into saturated areas, though riparian zones had slightly lower VWC than peatlands (0.42 vs. 0.49 m^3m^{-3}) (Figure 3.6). Aspen transpiration was greatest at the midslope position and aligned with VWC values around in recovering midslopes (Figure 3.3).

Soil moisture over depths showed similar trends with averaged data, where VWC was lowest in forests and increased into lowlands in both years (Figure 3.7). At the beginning of the 2013 growing season, VWC in all land units usually increased with depth, but decreased at 0.4 m from the surface at later sampling periods at all topographic positions. In 2014, soil moisture increased with depth at recovering hilltops, except on DOY 188 and 202 (the middle of the growing season) 0.6 m from the surface. A similar trend was observed in midslopes where the soil was most moist at depth, but often decreased at 0.3 and 0.4 m from the beginning to the middle of study period. Similar decreases at this depth were also seen in riparian areas midseason, though VWC increased typically to 0.6 m in depth, before decreasing. Soil moisture patterns in peatlands were less predictable. At the start and end of the sampling period, VWC increased with depth. While this trend was observed at the middle of the growing season, VWC significantly decreased 1.0 m from the surface.

When VWC values were averaged from 0.1 to 0.4 m from the surface, r_s values with plot transpiration in 2013 and 2014 were -0.21 and -0.34, respectively ($p<0.05$) (Table 3.4). The depth most strongly correlated with E_{plot} occurred at 0.3 m (r_s=-0.24) during the first growing season followed by 0.4

m in the latter (r_s=-0.37). Linking surface VWC to stem heights in 2013 and 2014, r_s=-0.65, r_s=-0.62, respectively. Similarly, r_s=-0.68 and r_s=-0.64 between moisture and leaf area for 2013 and 2014.

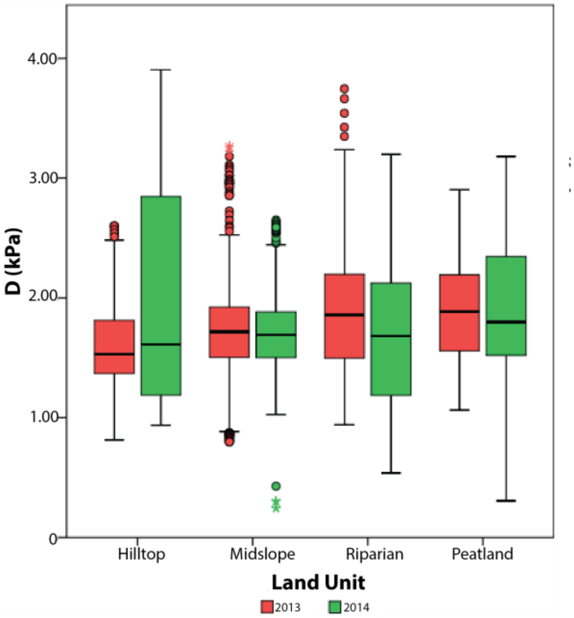


Figure 3.4: Vapour pressure deficit, D, across topographic positions during 2013 and 2014

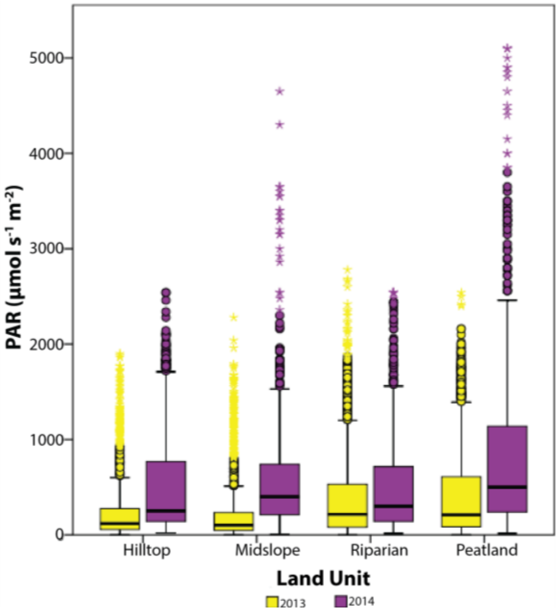


Figure 3.5: Photosynthetic active radiation, PAR, during 2013 and 2014 across land units

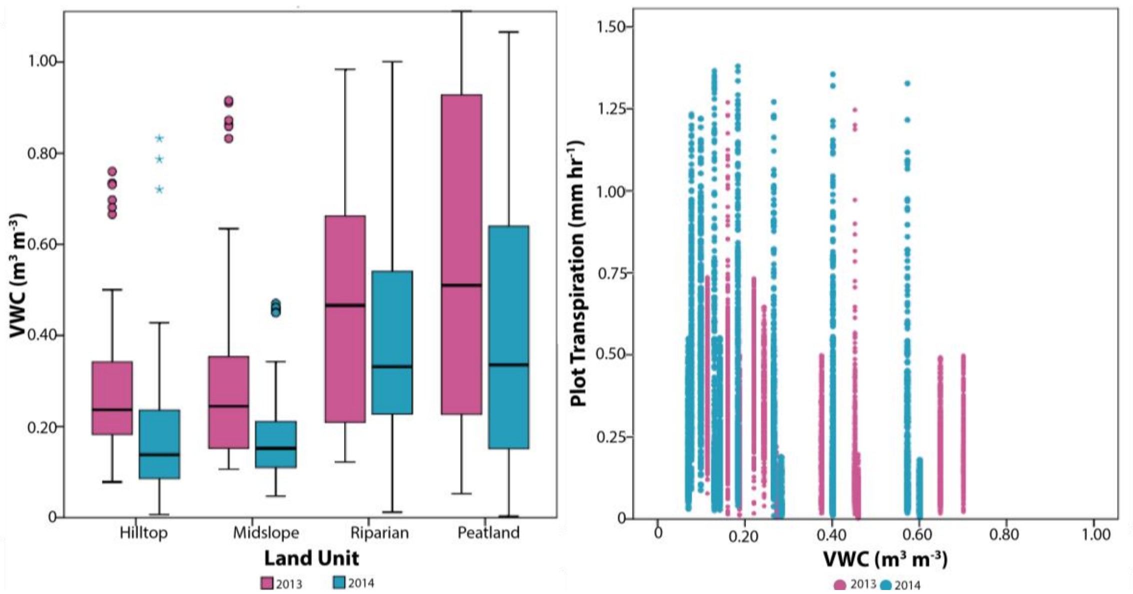


Figure 3.6: Median volumetric water content (m^3 m^{-3}) from 0.01 to 0.04 m from the surface across land units, and VWC across land unit during 2013 and 2014.

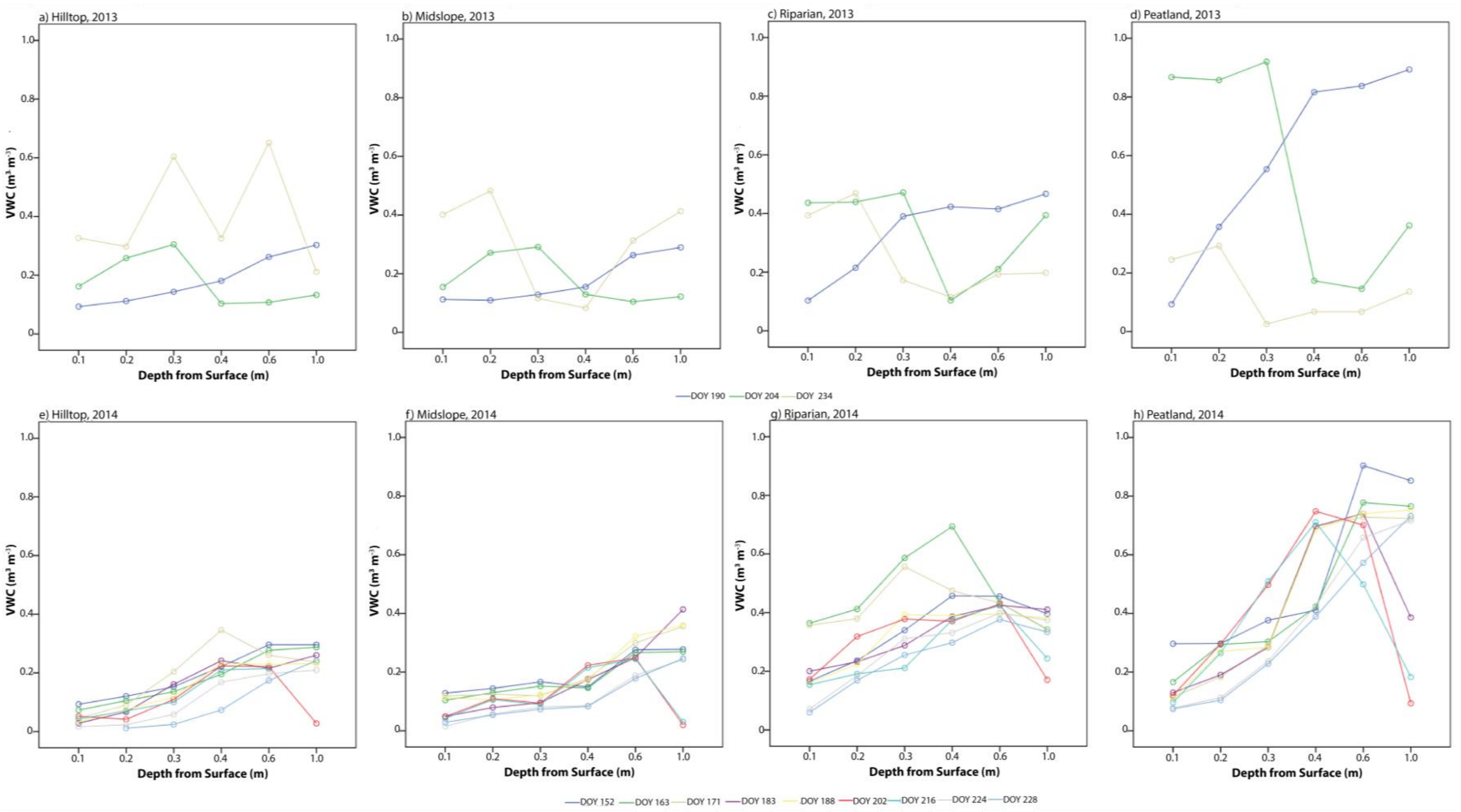


Figure 3.7: Median VWC (m^3 m^{-3}) across land units at varying depths during 2013 and 2014.

Year	**Factor**	$\mathbf{r_s}$	$\mathbf{r^2}$
2013	Plot Transpiration x PAR	**-0.05**	**0.01**
2013	Plot Transpiration x D	0.04	<0.01
2013	Plot Transpiration x VWC	**-0.21**	**0.12**
2014	Plot Transpiration x PAR	0.01	<0.01
2014	Plot Transpiration x D	**0.09**	**<0.01**
2014	Plot Transpiration x VWC	**-0.34**	**0.09**

Table 3.4: Spearman's rank correlation (r_s) and r^2 between transpiration and PAR, D, and VWC in 2013 and 2014. Bolded values include values where $p<0.05$.

3.5.6 Isotopic Composition of Aspen and Soil

Isotopic analysis of $\delta^{18}O$ and $\delta^{2}H$ and showed soil samples at 0.1 m were more isotopically enriched than those collected at depth (Figure 3.8), though each land unit did not statistically vary between depths ($p>0.05$). Across the topographic gradient, oxygen and hydrogen ($\delta^{18}O$, $\delta^{2}H$ expressed in ‰) were greatest at the 0.1 m depth across all units, and indicate that forested areas were more enriched (Figure 3.8, Table 3.5). With the exception of hilltops and peatlands where $p=0.018$, the ratios for both isotopes did not significantly vary between land units ($p>0.05$). Soils at 0.5 m showed a similar trend, though the tops of hills were more enriched than the middle of the slope (Figure 3.8, Table 3.5). At depth, isotopic signatures of $\delta^{18}O$ and $\delta^{2}H$ varied statistically between topographic positions where $p=0.006$ and $p=0.004$, respectively.

Aspen plant matter ($\delta^{18}O$, $\delta^{2}H$ expressed in ‰) was most enriched in the midslopes (-9.9 ‰, -119.9 ‰) followed by hilltops (-10.0 ‰, -117.8 ‰), riparian areas (-6.7 ‰, -102.0 ‰), and peatlands (-7.5 ‰, -102.8 ‰) (Figure 3.8, Table 3.5), though they were not statistically statistically different ($p>0.05$). Similarly, the only differences in isotopic signature occurred between midslopes and riparian areas where $p=0.025$ and $p=0.016$ for $\delta^{18}O$ and $\delta^{2}H$, respectively.

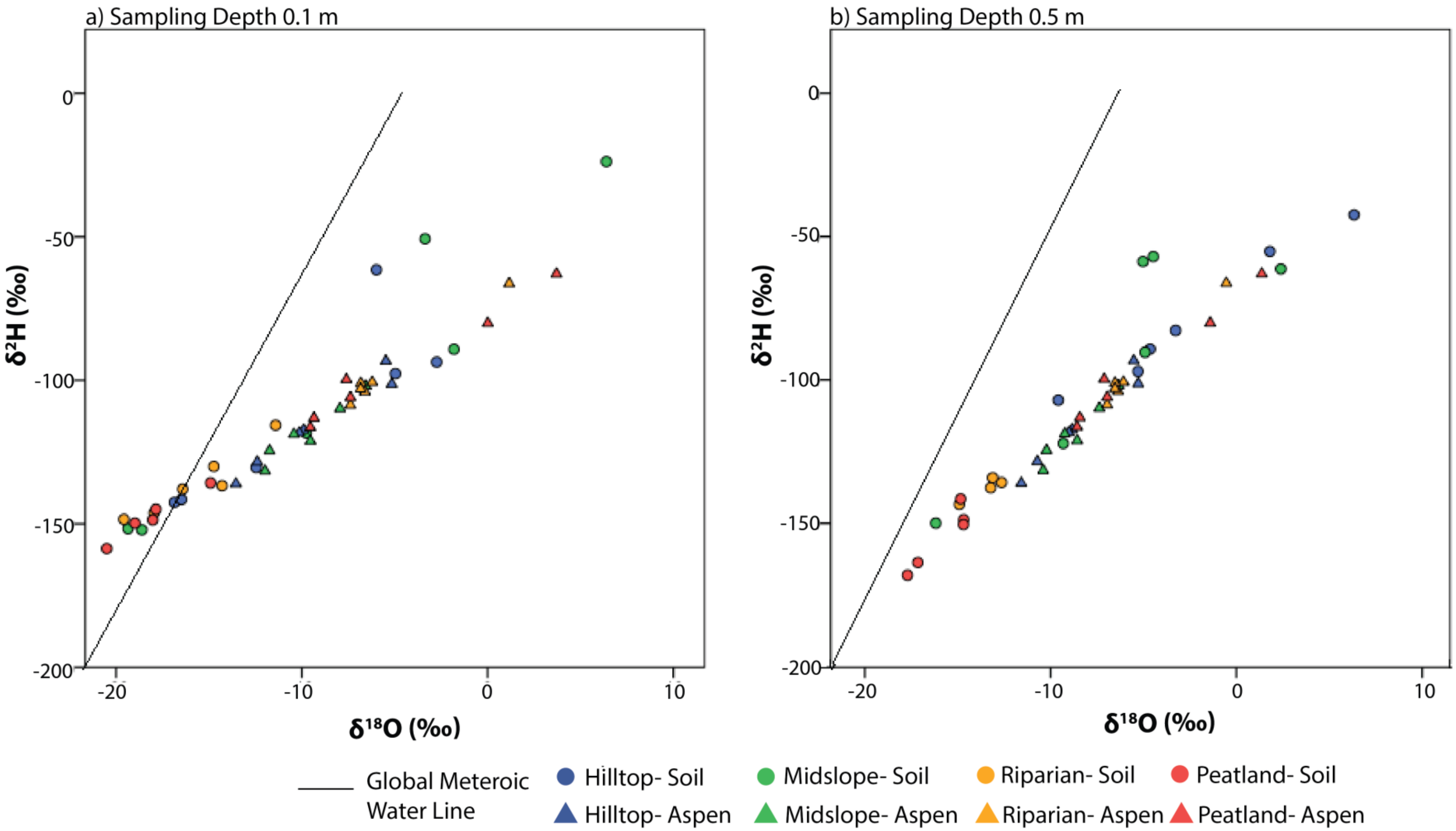


Figure 3.8: Isotopic composition of $\delta^{18}O$ and $\delta^{2}H$ of soil 0.1 m (a) and 0.5 m (b) from the surface and isotope signatures of aspen xylem.

Land Unit	**Depth**	δ^{18}O **Soil**	δ^{2}H **Soil**	δ^{18}O **Plant**	δ^{2}H **Plant**
Hilltop	.10 m	-9.2	-114	-10	-117.8
Midslope	.10 m	-6.6	-103.8	-9.9	-119.9
Riparian	.10 m	-15.6	-137.3	-6.7	-102
Peatland	.10 m	-18	-148.6	-7.5	-102.8
Hilltop	.50 m	-3.4	-85.9	-10	-117.8
Midslope	.50 m	-4.5	-75.8	-9.9	-119.9
Riparian	.50 m	-15.7	-136.7	-6.7	-102
Peatland	.50 m	-17.9	-150.4	-7.5	-102.8

Table 3.5: Median isotopic signatures of δ^{18}O and δ^{2}H in per-mille (‰) of soil water 0.1 m and 0.5 m from the surface, and aspen xylem water.

3.6 Discussion

3.6.1 Aspen Distribution in Peatlands

Most aspen in peatlands were classified as seedlings and were likely distributed through wind, where seed survival often depends on soil texture and moisture (e.g., Peterson and Peterson, 1992). Romme *et al.* (1997) and Turner *et al.* (2003) also saw high aspen seedling densities at low elevations near parent trees as seen in subalpine environments post-fire.

Re-establishment did not occur in hummocks and instead appeared in hollows, likely due to differences in burn patterns. Linked to the dominant moss species and tree cover, burn severities often dictate the depth of burn (*Lukenbach ei al.*, 2015b). For example, during a high severity fire, the median depth of burn (DOB) in feathermoss hollows was ~0.1, whereas the DOB in *Sphagnum fuscum* hummocks was <0.05 m (Lukenbach *et al.*, 2015b) leaving a surface mineral layer. In addition to mineral soils, the distance to the water table in peatlands, especially in severely burned hollows were closer to the surface compared to hummocks (Lukenbach *et al.*, 2015b) thus overall acting as a more suitable soil substrate for seedling re-establishment. The lack of ramets in peatlands supports the lack of oxygen to maintain roots respiration under wet soils (Ländhausser *et al.*, 2003). Aspen in peatlands and peatland margins were of a mix of seedlings and suckers,. This is not unusual as Turner *et al.* (2003) reported the closet parents trees ranging from 0.1-14.1 km from seedlings, which is well-within the distances between uplands and peatlands in the burned catchment.

Margins experienced higher severe burns (DOB ~0.5 m) than peatland centres resulting in exposed mineral soils (Lukenbach *et al.*, 2015a; Hokanson *et al.*, 2015). Parent aspen roots have been recorded to be 15 m in length (Gifford, 1966), which is the approximate distance between aspen at the base of the hill into peatland margins, thus explaining the presence of clones at the edges. Suckers in riparian zones and peat margins had larger leaf areas and stem heights compared to seedlings may be due their connectivity to uplands (Kemperman and Barnes, 1976).

3.6.2 Controls on Aspen Transpiration and Recovery

PAR across topographic positions did not greatly vary across land units and may be due to similar amounts of shading. Similarly, D may have not affected transpiration because of the little difference in elevation across topographic positions may have prevented significant gradients in vapour pressure. This suggests that differences were not significant enough to influence transpiration (Hogg and Hurdle, 1997). Further, other forest studies in the Boreal Plains suggest that vapour pressure deficit only becomes the limiting factor with low soil-water and leaf-water potential (Oren *et al.*, 1999; Hogg *et al.*, 2000; Brown *et al.*, 2013). This indicates that water must be accessible to roots for uptake and implies that soil moisture may dictate E (Brown *et al.*, 2013; Petrone *et al.*, 2015).

In this study, soil moisture relative to light and vapour pressure deficit, was best correlated with plot transpiration where r_s=-0.21 and r_s=-0.34 in 2013 and 2014, respectively. Brown *et al.* (2013) and Petrone *et al.* (2015) also found that other growth parameters, such as net ecosystem production (NEP) and to an extent, ET, in recovering aspen stands immediately after harvesting were affected by soil moisture in wet and dry climate cycles in the WBP. The linkages between soil moisture and transpiration have been well-cited in the literature (e.g. Hogg and Hurdle, 1997), and is attributed to stomatal opening and closing to prevent desiccation (Ewers *et al.*, 2007; MacKay *et al.*, 2007; Brown *et al.*, 2013; Petrone *et al.*, 2015). While mean average P was 481 mm and PET was 518 mm (Marshall *et al.*, 1999), during the 2013 study period, the WBP was in the wet phase of the climate cycle that occurs every 10-15 years (Devito *et al.*, 2005a; Devito *et al.*, 2005b) where P approaches PET. Cumulative precipitation from November 2012 to October 2013, and November 2013 to October 2014 was 447 mm and 350 mm, respectively. Much of precipitation was in the form of snow may have contributed to soil storage and potential increases in soil moisture during the beginning of the growing seasons of 2013 and 2014. Notably, the summer of 2014 received less precipitation than historical averages likely indicating the beginning of a drying period (Lukenbach *et al.*, 2015b). While not measured in this study, it is likely that leaf-water potential was high reflecting soil moisture ultimately enabling aspen transpiration (Brown *et al.*, 2013). Thus, stomatal closures in this study is similar to the findings of Krishnan *et al.* (2006), Bernier *et al.* (2006), and Wang (2012) in Boreal regions who linked stomatal aperture to either high sensible heat and soil water content during periods of drought. This study found that g_s, and E_{plot} was highest in midslopes (with optimal VWC), and lowest in peatlands with high VWC in both years, which corresponded with lowered leaf area and stem height. Thus, understanding that *P. tremuloides* are intolerable of extreme water-stressed conditions can suggest that aspen respond similarly in terms of transpiration under waterlogged areas thus reducing growth.

Figure 3.3 demonstrated that soil moisture is the largest control on transpiration in this setting. However, it is unusual that uplands, specifically midslopes, exhibited the highest rate as VWC was below field capacity where wilting point usually approximates 30% (Hart *et al.*, 2000; Ewers *et al.*, 2007;Liu *et al.*, 2014). This suggests the contribution of additional sources of water to these forests. Since soil moisture in the recovering uplands was approximately 25%, and the water table position in hilltops often exceeded 2.0 m from the surface, aspen roots may not have been able to tap into the water table for hydraulic uplift (Strong and La Roi, 1983; Dawson *et al.*, 1993; Hultine *et al.*, 2006). Although not reflected in VWC, it is probable that the additional source of water for aspen in uplands was peat water (Figure 3.8) that may have been immediately transpired.

In contrast to forested areas, VWC in peatlands was highest and coincided with low transpiration rates in both years. This suggests that saturated soils inhibit aspen growth and further regeneration in this land unit where long-term inundated soils limits the diffusion of oxygen into aspen roots (Bradford and Hsiao, 1982; Ländhausser *et al.*, 2003; Rodriguez-Gamir *et al.*, 2011). In lowering root conductance in inundated soils, stomatal conductance and transpiration also decrease (Bradford and Hsiao, 1982; Rodriguez-Gamir *et al.*, 2011) inferring that aspen respond similarly to dry and waterlogged soils to prevent wilting in stressful environments. Therefore, such conditions do not favour further regeneration in peatlands (Kay, 1993; Romme *et al.*, 1997; Krasnow and Stephen, 2015). Further, although the surface of peatland was likely covered by mineral soils through burning, high OM content of peat at depth may also inhibit seedling re-establishment (Johnstone and Chapin, 2006b; Wolken *et al.*, 2010; Lafleur *et al.*, 2015). This suggests that aspen do not require inundated soils require for further growth.

Like peatlands, soil moisture in riparian areas exceeded field capacity in 2013 (Figure 3.6; Figure 3.7). As a result of low bulk density and low moisture at the margins pre-fire, riparian zones experienced high burn severity (Lukenbach *et al.*, 2015b; Hokanson *et al.*, 2015) exposing the mineral layer of soil and may have acted as suitable substrate for aspen seedlings (Kay, 1993). Further, VWC lowered to only slightly above field capacity in 2014 particularly at the beginning of the growing season, which suggests that drying and subsequent decreases in soil moisture conditions in burned riparian areas may be more suited—relative to peatlands—for aspen regeneration. This is under the assumption that VWC remains around field capacity as Wolken *et al.* (2010) reported limited soil moisture windows where *P. tremuloides* seedling radicles and leaf area grew.

3.6.3 Water Sources Along a Topographic Gradient

The isotopic analysis of this study showed highest isotopic enrichment in forested soils whereas $\delta^{18}O$ and $\delta^{2}H$ was highest in peatlands (Figure 3.8, Table 3.5). This may be due to differences in evaporation and transpiration across land units (Barnes and Allison, 1983; Allison and Barnes, 1983; Hsieh *et al.*, 1998). While evaporation was not measured in this study, it can act as the main mechanism that drives enrichment in drier soils whereas transpiration usually dominates water losses in wetter areas (Allison and Barnes, 1983; Hsieh *et al.*, 1998). In *Sphagnum*, $\delta^{18}O$ and $\delta^{2}H$ has shown to be less enriched in the upper 0.1 m of soil cores due to capillary rise of depleted water (Price *et al.*, 2009). This further suggests the water table may be the source of less enriched water at the margins and peatlands. Despite the different processes that dictate isotope partitioning, the isotopic composition of $\delta^{2}H$ and $\delta^{18}O$ of soils did not vary statistically across land units. This observation has been recorded elsewhere in the WBP (Lazerjan, 2014) and supports the occurrence of peatland and margin water that is re-released into forested areas. An exception occurred in hilltops where the isotopic composition of soils was different than those of peatlands (Figure 3.8). While groundwater and water table isotopes were not collected, parent aspen tree roots could have been able to tap into deep water sources further explaining differences in hilltop soils (Dawson, 1993; Caldwell, 1998; Burgess *et al.*, 1998; Hultine *et al.*, 2006).

Aspen xylem samples showed heavier isotopes in hilltops and midslopes, further supporting hydraulic redistribution through the similarities between aspen xylem in the forested hilltops to peat and riparian zone soil water (Table 3.5). Although burn severity was highest at peatland margins and riparian zones, hydraulic redistribution could have occurred through midslope aspen roots present in the peatland margins. These roots could have been present in the mineral layer of riparian zones pre-fire and may not have been damaged (Brown and Debyle, 1987; Wang, 2003). Therefore, root connectivity may explain the subtle differences in aspen xylem and soil isotopic signatures across the hillslope. Between land units, xylem water composition only varied statistically between aspen in the midslopes and peatlands. The water table in 2013 and 2014 at the toe of the slope may have also acted as a source of water to the midslopes, especially in the areas where mounding occurred in the burned area. The mounding and flow reversal at the riparian area may have also allowed the uptake of water at the base of slope (Smerdon *et al.*, 2005) and was incorporated into aspen tissue. Hydraulic redistribution may explain aspen regeneration in forested areas where water transport from peatlands and margins may be occurring at an amount that is sufficient for aspen regeneration and transpiration (Burgess *et al.*, 1998; Brown *et al.*, 2013). This may explain aspen survival in dry soils with limited soil moisture, and may have implications for areas that act as sources of water.

3.6.4 Implications for Succession

Much of the literature reports aspen intolerance of saturated soils (e.g., Peterson and Peterson, 1992), a study by Roy *et al.* (2000) in Quebec—classified with a humid climate where P > ET—predicted that the presence of aspen in riparian areas post-harvesting was temporary. Since ET > P in the WBP however, there is an increased potential for VWC in riparian areas to change (Macrae *et al.*, 2005, Macrae *et al.*, 2006). While decreases in aspen transpiration have been reported during periods of drought (Hogg *et al.*, 1997), if aspen roots in uplands receive water from peatlands and riparian areas, continued decreases in soil moisture may occur and be accelerated when the climate period of the Boreal Plains enters its dry cycle. This suggests that at a certain soil moisture threshold, riparian areas may exhibit increased vulnerability to upland species. While this study captured both a wet climate cycle in 2013 with storage contributing to soil moisture, in 2014, precipitation during the summer was less than historical summer averages resulting in lowered riparian VWC and the likely start of a drying period. This may explain increased aspen LA and stem height in riparian areas in 2014 reflecting more suitable conditions, though longer-term studies are needed to monitor the trajectory of margins and moisture required for upland transformation in later successional stages. A recent study by Kettridge *et al.* (2015) suggests potential shifts in *Sphagnum* dominated peatland vegetation to grasses and shrubs due to lowered water tables as a result of draining and drying peat at the margins. While not drained, the depth of burn in this peatland exceeded those of Kettridge *et al.* (2015) indicating that peatlands that are ephemerally perched (see Lukenbach *et al.*, 2015c; Hokanason *et al.*, 2015) may be vulnerable to upland transformation.

3.7 Conclusion

Aspen transpiration varied across burned a hillsope where the highest rates occurred in forests and decreased in riparian areas and peatlands. Although PAR and D typically have larger roles on E than reported in this study, the burn severity and little differences in topographic gradients prevented significant variability in such controls, and subsequently on transpiration. Further, PAR and D usually limit transpiration only when moisture is sufficient, though waterlogged peat in this study further inhibited aspen water release indicating the importance of soil moisture. With an abundance of water and the detection of aspen two and three years after fire in peatlands, reductions in stomatal conductance may have prevented transpiration losses likely due to oxygen deficiencies in roots. Conversely, in forested areas where soil moisture was below wilting point, regeneration continued suggesting that moisture was sufficient in uplands and that aspen do not wet soils for regeneration. This was likely due to hydraulic redistribution from aspen clones with parent trees originating in uplands. Belowground roots likely extended into peatlands and margins pre-disturbance further explaining clonal distribution at peatland edges, though these areas may be vulnerable to upland transformations through continued drying.

4.0 Conclusions and Implications

4.1 Controls of Aspen Regeneration in Peatlands

While aspen have been detected in wet areas, this is the first study that reports their presence in Western Boreal Plain peatlands after fire disturbance. To determine if aspen were in peatlands as a result of nutrient deficiencies in recovering uplands, plant available N and P in soil was investigated, and showed that NO_3^-, NH_4^+, and Ext-P varied across land units. While inorganic N levels appeared to be restored to pre-fire levels, extractable P remained elevated in the burned peatland. Furthermore, no relationships were observed between aspen stem height, leaf area, and nutrient availability. This suggests that soil nutrition did not play the largest role in determining regeneration, and that soil nutrients are sufficient in uplands through the cycling of aspen litter.

Instead, there were strong negative correlations between soil organic matter content, texture, and moisture with growth indicating that soil physical properties, particularly VWC, may dictate establishment. This implies that peatlands are unsuitable areas for seedling regeneration. While previous work has measured aspen growth in different moisture conditions that were strictly wet or dry, this is first study that quantifies aspen stress in contrasting field conditions. At a certain soil moisture threshold, aspen likely initiates stomatal closures resulting in decreased transpiration as a response to unfavourable growing conditions such as waterlogging. Although this was observed in peatlands, opposite findings were observed in uplands where transpiration was greatest regardless of moisture levels below field capacity.

As a result of sufficient nutrients and water in regenerating forests, aspen detection in riparian areas and peat margins could be explained through their large role in transporting water to uplands. This process, or hydraulic redistribution, was likely mediated through aspen roots originating in uplands with extensions to areas, such as peatlands, with high water availability pre-fire. The successful use of $\delta^{18}O$/ $\delta^{2}H$ isotopes in this research has been applied in previous transpiration studies and may be beneficial in determining the extent that upland aspen are using peat water. This may be useful in understanding peatland sustenance with continued hydraulic redistribution.

When considering the recovery of burned peatlands in the presence of upland species, such as aspen, the lack of oxygen in the rooting zone will likely result in aspen death in peatlands. This could suggest that aspen trees are restricted to mineral soils with moisture content well-below saturation, with parent tree roots undergoing hydraulic redistribution. A limitation to this prediction however was the timing, or climate cycle at which this study was conducted. This research was preformed when P approached PET, which occurs every 10-15 years, and the likely beginning of a dry climate cycle, thus not reflecting long term WBP climate patterns. Thus, similar measurements during dry climates cycles may better indicate how stress or successful aspen regenerate in forests and peatlands. This may be important in determining if the amount of hydraulic redistribution is sufficient to uplands if water table fluctuations occur at margins and if it is accessible to roots. Answering this could be aided through longer term monitoring which will help in determining how riparian areas undergo succession. Overall, study this shows that aspen may be limited to margins and highlights that nutrients and moisture in peatlands post-fire are not conducive to aspen further. This further supports that peatlands may remain resilient to becoming forests during later succession.

4.2 Future Considerations for Land Management and Reclamations

During the reclamation of disturbed sites, such as those affected by oil exploration and mining in Alberta, the conditions for re-establishment and the location of which upland species, such as aspen, are placed must be considered. In this study, the severe burning and mineralization of the forest floor litter released sufficient N and P, which along with the simultaneously exposed mineral soils allowed aspen reestablishment in uplands. With this data, future reclamation projects may need to consider planting aspen seeds in well-drained mineral soils and the maximum depth of organic matter required for establishment without the expense of adequate nutrients. Upon successful aspen seedling establishment, monitoring of growth and the re-establishment of rooting systems must be monitored especially if one of the functions of aspen is to aid in hydraulic redistribution as seen in natural sites.

When planning the amount of desired wetland or peatland cover in reclamation projects, it is important to consider the possible effects of surrounding forests. If aspen are used for hydraulic redistribution with roots originating in uplands spread into peatlands for water, potential losses of riparian areas to adjacent uplands must be considered. This can be extended to further losses of peatlands to riparian areas. Continued uptake in peatlands and margins can be brought upon by of a lack of insufficient soil moisture in forests, prolonged periods of drought, and/or continued water uptake by aspen in uplands. To prevent this, soil moisture must be sufficient at the margins and saturation in peatlands must be high enough to avoid root survival and sucker regeneration. To further mitigate loss, immediate water sources such as the water table immediately below aspen tap and sinker roots may be more favourable for uptake rathan than allocating reserves to lateral roots. Therefore, when designing reclaimed sites, long-term succession and the possible trajectories peatlands may take must be considered.

References

Aerts, R. (1990). Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oecologia*, 84(3), 391-397. doi:10.1007/bf00329765

Aerts, R., Wallen, B., & Malmer, N. (1992). Growth-Limiting Nutrients in *Sphagnum*-Dominated Bogs Subject to Low and High Atmospheric Nitrogen Supply. *Journal of Ecology*, 80(1), 131-140. doi:10.2307/2261070

Aerts, R., Verhoeven, J. T. A., & Whigham, D. F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology*, 80(7), 2170-2181. doi:10.1890/0012-9658(1999)080[2170:PMCONC]2.0.CO;2

Allison, G. B., Barnes, C. J., & Hughes, M. W. (1983). The distribution of deuterium and 18O in dry soils 2. Experimental. *Journal of Hydrology*, 64(1–4), 377-397. doi:http://dx.doi.org/10.1016/0022-1694(83)90078-1

Anderegg, W. R. L. (2012). Complex aspen forest carbon and root dynamics during drought. *Climatic Change*, 111(3), 983-991. doi:10.1007/s10584-012-0421-9

Ball, P. N., MacKenzie, M. D., DeLuca, T. H., & Montana, W. E. H. (2010). Wildfire and Charcoal Enhance Nitrification and Ammonium-Oxidizing Bacterial Abundance in Dry Montane Forest Soils All rights reserved. *Journal of Environmental Quality*, 39(4). doi:10.2134/jeq2009.0082

Barnes, C. J., & Allison, G. B. (1983). The distribution of deuterium and 18O in dry soils: 1. Theory. *Journal of Hydrology*, 60(1–4), 141-156. doi:http://dx.doi.org/10.1016/0022-1694(83)90018-5

Bartos, D.L., & Meuggler, W.F., (1981). Early succession in aspen communities following fire in western Wyoming. *Journal of Range Management*, 34(4), 315-318

Bayley, S. E., Thormann, M. N., & Szumigalski, A. R. (2005). Nitrogen mineralization and decomposition in western boreal bog and fen peat. *Ecoscience*, 12(4), 455-465. doi:10.2980/i1195-6860-12-4-455.1

Bella, I.E.; DeFranceschi, J.P., (1980) Biomass productivity of young aspen stands in western Canada. Environment Canada, Canadian Forestry Service, Northern Forest Research Centre, Edmonton, Alberta. Information Report NOR-X-219.

Benscoter, B. W., & Wieder, R. K. (2003). Variability in organic matter lost by combustion in a boreal bog during the 2001 Chisholm fire. *Canadian Journal of Forest Research*, 33(12), 2509-2513. doi:10.1139/x03-162

Bernier, P. Y., Bartlett, P., Black, T. A., Barr, A., Kljun, N., & McCaughey, J. H. (2006). Drought constraints on transpiration and canopy conductance in mature aspen and jack pine stands. *Agricultural and Forest Meteorology*, 140(1–4), 64-78. doi:http://dx.doi.org/10.1016/j.agrformet.2006.03.019

Binkley, D., & Hart, S. C. (1989). The Components of Nitrogen Availability Assessments in Forest Soils. In B. A. Stewart (Ed.), *Advances in Soil Science* (Vol. 10, pp. 57-112): Springer New York.

Bodí, M. B., Martin, D. A., Balfour, V. N., Santín, C., Doerr, S. H., Pereira, P., Mataix-Solera, J. (2014). Wildland fire ash: Production, composition and eco-hydro-geomorphic effects. *Earth-Science Reviews*, 130, 103-127. doi:http://dx.doi.org/10.1016/j.earscirev.2013.12.007

Bradford, K.J., & Hsiao, T.C., (1982). Stomatal Behavior and Water Relations of Waterlogged Tomato Plants. *Plant Physiology, 70(5), 1508-1513. doi:* doi: http://dx.doi.org/10.1104/pp.70.5.1508

Bréda, N. J. J. (2003). Ground- based measurements of leaf area index: a review of methods, instruments and current controversies. *Journal of Experimental Botany*, 54(392), 2403-2417. doi:10.1093/jxb/erg263

Brown, J. K., & DeByle, N. V. (1987). Fire damage, mortality, and suckering in aspen. *Canadian Journal of Forest Research*, 17(9), 1100-1109. doi:10.1139/x87-168

Brown, S.M., Petrone, R.M., Mendoza, C., and Devito, K.J. (2010). Surface vegetation controls on evapotranspiration from a sub-humid Western Boreal Plain wetland. *Hydrological Processes,* 24(8), 1072-1085. doi: 10.1002/hyp.7569.

Brown, S. M., Petrone, R. M., Chasmer, L., Mendoza, C., Lazerjan, M. S., Landhäusser, S. M., Devito, K. J. (2014). Atmospheric and soil moisture controls on evapotranspiration from above and within a Western Boreal Plain aspen forest. *Hydrological Processes*, 28(15), 4449-4462. doi:10.1002/hyp.9879

Burgess, O. S. S., Adams, A. M., Turner, C. N., & Ong, K. C. (1998). The redistribution of soil water by tree root systems. *Oecologia*, 115(3), 306-311. doi:10.1007/s004420050521

Burgess, S., & Bleby, T. (2006). Redistribution of soil water by lateral roots mediated by stem tissues. *Journal of Experimental Botany*, 57(12), 3283-3291. doi:10.1093/jxb/erl085

Burke, J. M., Prepas, E. E., & Pinder, S. (2005). Runoff and phosphorus export patterns in large forested watersheds on the western Canadian Boreal Plain before and for 4 years after wildfire. *Journal of Environmental Engineering and Science*, 4(5), 319-325. doi:10.1139/s04-072

Calder, W. J., Horn, K. J., & St. Clair, S. B. (2011). Conifer expansion reduces the competitive ability and herbivore defense of aspen by modifying light environment and soil chemistry. *Tree Physiology*, 31(6), 582-591. doi:10.1093/treephys/tpr041

Certini, G. (2005). Effects of fire on properties of forest soils: a review. *Oecologia*, 143(1), 1-10. doi:10.1007/s00442-004-1788-8

Chambers, R. M., & Pederson, K. A. (2006). Variation in soil phosphorus, sulfur, and iron pools among south Florida wetlands. *Hydrobiologia*, 569(1), 63-70. doi:10.1007/s10750-006-0122-3

Chen, J. M., Rich, P. M., Gower, S. T., Norman, J. M., & Plummer, S. (1997). Leaf area index of boreal forests: Theory, techniques, and measurements. *Journal of Geophysical Research: Atmospheres*, 102(D24), 29429-29443. doi:10.1029/97JD01107

Cleve, K. V., & Noonan, L. L. (1975). Litter Fall and Nutrient Cycling in the Forest Floor of Birch and Aspen Stands in Interior Alaska. *Canadian Journal of Forest Research*, 5(4), 626-639. doi:10.1139/x75-089

Coop, J. D., Barker, K. J., Knight, A. D., & Pecharich, J. S. (2014). Aspen (Populus tremuloides) stand dynamics and understory plant community changes over 46 years near Crested Butte, Colorado, USA. *Forest Ecology and Management*, 318, 1-12. doi:http://dx.doi.org/10.1016/j.foreco.2014.01.019

Côté, L., Brown, S., Paré, D., Fyles, J., & Bauhus, J. (2000). Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. *Soil Biology and Biochemistry,* 32(8–9), 1079-1090. doi:http://dx.doi.org/10.1016/S0038-0717(00)00017-1

Dancer, W. S., Peterson, L. A., & Chesters, G. (1973). Ammonification and Nitrification of N as Influenced by Soil pH and Previous N Treatments1. *Soil Science Society of America Journal*, 37(1). doi:10.2136/sssaj1973.03615995003700010024x

Dawson, T. E. (1993). Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia*, 95(4), 565-574. doi:10.1007/bf00317442

Debano, L.F., Mann, L.D., & Hamilton, D.A. (1973). Translocation of Hydrophohic Substances into Soil by Burning Organic Litter. *Soil Science of Society of America Journal,* 39(1), 130-133. doi: 10.2136/sssaj1970.03615995003400010035x

Debano, L. F., & Conrad, C. E. (1978). The Effect of Fire on Nutrients in a Chaparral Ecosystem. *Ecology*, 59(3), 489-497. doi:10.2307/1936579

DesRochers, A., & Lieffers, V. J. (2001). Root biomass of regenerating aspen (Populus tremuloides) stands of different densities in Alberta. *Canadian Journal of Forest Research*, 31(6), 1012-1018. doi:10.1139/x01-037

Desrochers, A., Landhäusser, S. M., & Lieffers, V. J. (2002). Coarse and fine root respiration in aspen (Populus tremuloides). *Tree Physiology*, 22(10), 725-732. doi:10.1093/treephys/22.10.725

Desrochers, A., van den Driessche, R., & Thomas, B.R., (2003). Nitrogen fertilization of trembling aspen seedlings grown on soils of different pH. *Canadian Journal of Forest Research*, 33(4), 552-560. doi: 10.1139/x02-191

Devito, K. J., Westbrook, C. J., & Schiff, S. L. (1999). Nitrogen mineralization and nitrification in upland and peatland forest soils in two Canadian Shield catchments. *Canadian Journal of Forest Research,* 29(11), 1793-1804. doi:10.1139/x99-148

Devito, K. J., Creed, I. F., Rothwell, R. L., & Prepas, E. E. (2000). Landscape controls on phosphorus loading to boreal lakes: implications for the potential impacts of forest harvesting. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(10), 1977-1984. doi:10.1139/f00-148

Devito, K., Creed, I., Gan, T., Mendoza, C., Petrone, R., Silins, U., & Smerdon, B. (2005). A framework for broad-scale classification of hydrologic response units on the Boreal Plain: is topography the last thing to consider? *Hydrological Processes*, 19(8), 1705-1714. doi:10.1002/hyp.5881

Devito, K. J., Creed, I. F., & Fraser, C. J. D. (2005). Controls on runoff from a partially harvested aspen-forested headwater catchment, Boreal Plain, Canada. *Hydrological Processes*, 19(1), 3-25. doi:10.1002/hyp.5776

Devito, K., Mendoza, C., Qualizza, C. (2012). *Conceptualizing water movement in the Boreal Plains. Implications for watershed reconstruction.* Synthesis report prepared for the Canadian Oil Sands Network for Research and Development, Environmental and Reclamation Research Group. 164 pp.

Dimitrov, D.D., Bhatti, J.S., & Grant, R.F., (2014). The transition zones (ecotone) between boreal forests and peatlands: Modelling water table along a transition zone between upland black spruce forest and poor forested fen in central Saskatchewan. *Ecological Modeling*, 274, 57-70. doi:10.1016/j.ecolmodel.2013.11.030.

Drimmie, R.J., Shouakar-Stash, O., Walters, R., Heemskerk, A.R., (2001). Hydrogen isotope ratio of H_2O by Automatic Elemental Analysis-Continuous Flow-Isotope Ratio Mass Spectrometry. Technical Procedure 4.1 Revision 00, 8 pages. Environmental Isotope Laboratory, Department of Earth Sciences, University of Waterloo.

Dunn, P. H., DeBano, L. F., & Eberlein, G. E. (1979). Effects of Burning on Chaparral Soils: II. Soil Microbes and Nitrogen Mineralization1. *Soil Science Society of America Journal*, 43(3). doi:10.2136/sssaj1979.03615995004300030016x

Dytham, C., (2011). *Choosing and Using Statistics: A Biologist's Guide* (3rd ed.). West Sussex, UK: John Wiley & Sons, Ltd.

Dyrness, C. T., Cleve, K. V., & Levison, J. D. (1989). The effect of wildfire on soil chemistry in four forest types in interior Alaska. *Canadian Journal of Forest Research*, 19(11), 1389-1396. doi:10.1139/x89-213

Elena S. F. Berman, E.F.S., Levin, N.E., Landais, A., Li, S., & Owano, T., (2013) Measurement of $\delta^{18}O$, $\delta^{17}O$, and ^{17}O-excess in Water by Off-Axis Integrated Cavity Output Spectroscopy and Isotope Ratio Mass Spectrometry. *Analytical Chemistry*, 85, 10392−10398.

Elliott, K. J., & Vose, J. M. (2005). Initial Effects of Prescribed Fire on Quality of Soil Solution and Streamwater in the Southern Appalachian Mountains. *Southern Journal of Applied Forestry*, 29(1), 5-15.

Eno, C.F., (1960). Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Science Society of American Journal*, 24, 277-279.

Ewers, B. E., Mackay, D. S., & Samanta, S. (2007). Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species. *Tree Physiology*, 27(1), 11-24. doi:10.1093/treephys/27.1.11

Farquhar, G., & Wong, S. (1984). An Empirical Model of Stomatal Conductance. *Functional Plant Biology*, 11(3), 191-210. doi:http://dx.doi.org/10.1071/PP9840191

Finklestein, M. (1990). National Parks System Plan. Supplies and Services Canada, Ottawa, Ont.

Ferone, J. M., & Devito, K. J. (2004). Shallow groundwater–surface water interactions in pond–peatland complexes along a Boreal Plains topographic gradient. *Journal of Hydrology*, 292(1–4), 75-95. doi:http://dx.doi.org/10.1016/j.jhydrol.2003.12.032

Fraser, E. C., Lieffers, V. J., & Landhäusser, S. M. (2004). Wounding of aspen roots promotes suckering. *Canadian Journal of Botany*, 82(3), 310-315. doi:10.1139/b04-009

Fritz, C., Lamers, L. P. M., Riaz, M., van den Berg, L. J. L., & Elzenga, T. J. T. M. (2014). *Sphagnum* Mosses - Masters of Efficient N-Uptake while Avoiding Intoxication. *PLoS ONE*, 9(1), e79991. doi:10.1371/journal.pone.0079991

Farquhar, G.D, & Sharkey, T. D. (1982). Stomatal Conductance and Photosynthesis. Annual Review of *Plant Physiology*, 33(1), 317-345. doi:doi:10.1146/annurev.pp.33.060182.001533

Galang, M. A., Markewitz, D., & Morris, L. A. (2010). Soil phosphorus transformations under forest burning and laboratory heat treatments. *Geoderma*, 155(3–4), 401-408. doi:http://dx.doi.org/10.1016/j.geoderma.2009.12.026

Galvez, D. A., Landhäusser, S. M., & Tyree, M. T. (2011). Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? *Tree Physiology*, 31(3), 250-257. doi:10.1093/treephys/tpr012

Gifford, G. F. (1966). Aspen Root Studies on Three Sites in Northern Utah. *The American Midland Naturalist*, *75*(1), 132–141. http://doi.org/10.2307/2423485

Gimeno-García, E., Andreu, V., & Rubio, J. L. (2000). Changes in organic matter, nitrogen, phosphorus and cations in soil as a result of fire and water erosion in a Mediterranean landscape. *European Journal of Soil Science, 51(2), 201-210. doi:10.1046/j.1365-2389.2000.00310.x*

Gray, D. M., & Dighton, J. (2006). Mineralization of forest litter nutrients by heat and combustion. Soil Biology and Biochemistry, 38(6), 1469-1477. doi:http://dx.doi.org/10.1016/j.soilbio.2005.11.003

Hájek, T., Ballance, S., Limpens, J., Zijlstra, M., & Verhoeven, J. T. A. (2010). Cell-wall polysaccharides play an important role in decay resistance of *Sphagnum* and actively depressed decomposition in vitro. *Biogeochemistry*, 103(1), 45-57. doi:10.1007/s10533-010-9444-3

Hart, S. C., Nason, G. E., Myrold, D. D., & Perry, D. A. (1994). Dynamics of Gross Nitrogen Transformations in an Old-Growth Forest: The Carbon Connection. *Ecology*, 75(4), 880-891. doi:10.2307/1939413

Hauer, F., & Spencer, C. (1998). Phosphorus and Nitrogen Dynamics in Streams Associated With Wildfire: a Study of Immediate and Longterm Effects. International Journal of Wildland Fire, 8(4), 183-198. doi:http://dx.doi.org/10.1071/WF9980183

Hemming, J. D. C., & Lindroth, R. L. (1999). Effects of Light and Nutrient Availability on Aspen: Growth, Phytochemistry, and Insect Performance. *Journal of Chemical Ecology*, 25(7), 1687-1714. doi:10.1023/a:1020805420160

Hill, A. R. (1996). Nitrate Removal in Stream Riparian Zones. *Journal of Environmental Quality*, 25(4). doi:10.2134/jeq1996.00472425002500040014x

Hobbs, N. T., & Schimel, D. S. (1984). Fire Effects on Nitrogen Mineralization and Fixation in Mountain Shrub and Grassland Communities. *Journal of Range Management*, 37(5), 402-405. doi:10.2307/3899624

Hogg, E.H., & Hurdle, P.A., (1997). Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. *Tree Physiology*, 17, 501-509.

Hogg, E. H., Saugier, B., Pontailler, J.-Y., Black, T. A., Chen, W., Hurdle, P. A., & Wu, A. (2000). Responses of trembling aspen and hazelnut to vapor pressure deficit in a boreal deciduous forest. *Tree Physiology*, 20(11), 725-734. doi:10.1093/treephys/20.11.725

Hokanson, K. J., Lukenbach, M. C., Devito, K. J., Kettridge, N., Petrone, R. M., & Waddington, J. M. (2015). Groundwater connectivity controls peat burn severity in the boreal plains. *Ecohydrology*, n/a-n/a. doi:10.1002/eco.1657

Hsieh, J. C. C., Chadwick, O. A., Kelly, E. F., & Savin, S. M. (1998). Oxygen isotopic composition of soil water: Quantifying evaporation and transpiration. Geoderma, 82(1–3), 269-293. doi:http://dx.doi.org/10.1016/S0016-7061(97)00105-5

Huang, W. Z., & Schoenau, J. J. (1998). Fluxes of water-soluble nitrogen and phosphorus in the forest floor and surface mineral soil of a boreal aspen stand. *Geoderma*, 81(3–4), 251-264. doi:http://dx.doi.org/10.1016/S0016-7061(97)00092-X

Huffman, E. L., MacDonald, L. H., & Stednick, J. D. (2001). Strength and persistence of fire-induced soil hydrophobicity under ponderosa and lodgepole pine, Colorado Front Range. *Hydrological Processes*, 15(15), 2877-2892. doi:10.1002/hyp.379

Hultine, K. R., Koepke, D. F., Pockman, W. T., Fravolini, A., Sperry, J. S., & Williams, D. G. (2006). Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte. *Tree Physiology*, 26(3), 313-323. doi:10.1093/treephys/26.3.313

Irwin H., Curtis C., & Coleman M., (1977). Isotopic evidence for source of diagenetic carbonates formed during burial of organic-rich sediments. *Nature*, 269,209-213

Jarvis A.J. & Davies W.J. (1998) The coupled response of stomatal conductance to photosynthesis and transpiration. *Journal of Experimental Botany* Special Issue, 49, 399–406.

Jerabkova, L., & Prescott, C. E. (2007). Post-harvest soil nitrate dynamics in aspen- and spruce-dominated boreal forests. *Forest Ecology and Management*, 242(2–3), 209-216. doi:http://dx.doi.org/10.1016/j.foreco.2007.01.003

Johnson, J. D., & Ferrell, W. K. (1983). Stomatal response to vapour pressure deficit and the effect of plant water stress. *Plant, Cell & Environment*, 6(6), 451-456. doi:10.1111/1365-3040.ep11588103

Johnstone, J. F. (2005). Effects of aspen (Populus tremuloides) sucker removal on postfire conifer regeneration in central Alaska. *Canadian Journal of Forest Research*, 35(2), 483-486. doi:10.1139/x04-171

Johnstone, J. F., & Chapin, F. S. (2006). Effects of Soil Burn Severity on Post-Fire Tree Recruitment in Boreal Forest. *Ecosystems*, 9(1), 14-31. doi:10.1007/s10021-004-0042-x

Johnstone, J. F., & Chapin, F. S. (2006). Fire Interval Effects on Successional Trajectory in Boreal Forests of Northwest Canada. *Ecosystems*, 9(2), 268-277. doi:10.1007/s10021-005-0061-2

Johnstone, J. F., & Kasischke, E. S. (2005). Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. *Canadian Journal of Forest Research*, 35(9), 2151-2163. doi:10.1139/x05-087

Kaelke, C. M., Kruger, E. L., & Reich, P. B. (2001). Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light-availability gradient. *Canadian Journal of Forest Research*, 31(9), 1602-1616. doi:10.1139/x01-090

Keech, O., Carcaillet, C., & Nilsson, M.C. (2005). Adsorption of allelopathic compounds by wood-derived charcoal: the role of wood porosity. *Plant and Soil*, 272(1), 291-300. doi:10.1007/s11104-004-5485-5

Keeley, J. E., Brennan, T., & Pfaff, A. H. (2008). fire severity and ecosytem responses following crown fires in california shrublands. *Ecological Applications*, 18(6), 1530-1546. doi:10.1890/07-0836.1

Kemperman, J. A., & Barnes, B. V. (1976). Clone size in American aspens. *Canadian Journal of Botany*, 54(22), 2603-2607. doi:10.1139/b76-280

Kettridge, N., Turetsky, M. R., Sherwood, J. H., Thompson, D. K., Miller, C. A., Benscoter, B. W.,Waddington, J. M. (2015). Moderate drop in water table increases peatland vulnerability to post-fire regime shift. *Scientific Reports*, 5, 8063. doi:10.1038/srep08063

Kettridge, N., & Waddington, J. M. (2014). Towards quantifying the negative feedback regulation of peatland evaporation to drought. *Hydrological Processes*, 28(11), 3728-3740. doi:10.1002/hyp.9898

Kielland, K. (2001). Short-Circuiting the Nitrogen Cycle: Ecophysiological Strategies of Nitrogen Uptake in Plants from Marginal Environments. In N. Ae, J. Arihara, K. Okada, & A. Srinivasan (Eds.), Plant Nutrient Acquisition (pp. 376-398): Springer Japan.

Kim, D., Oren, R., Oishi, A. C., Hsieh, C.-I., Phillips, N., Novick, K. A., & Stoy, P. C. (2014). Sensitivity of stand transpiration to wind velocity in a mixed broadleaved deciduous forest. *Agricultural and Forest Meteorology*, 187, 62-71. doi:http://dx.doi.org/10.1016/j.agrformet.2013.11.013

Kishchuk, B. E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T., & Sidders, D. (2014). Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada. *Canadian Journal of Forest Research*, 45(2), 141-152. doi:10.1139/cjfr-2014-0148

Klein, E., Berg, E. E., & Dial, R. (2005). Wetland drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. *Canadian Journal of Forest Research*, 35(8), 1931-1941. doi:10.1139/x05-129

Kneeshaw, D. D., & Bergeron, Y. (1998). Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*, 79(3), 783-794. doi:10.1890/0012-9658(1998)079[0783:CGCATR]2.0.CO;2

Knicker, H., González-Vila, F. J., Polvillo, O., González, J. A., & Almendros, G. (2005). Fire-induced transformation of C- and N- forms in different organic soil fractions from a Dystric Cambisol under a Mediterranean pine forest (Pinus pinaster). *Soil Biology and Biochemistry*, 37(4), 701-718. doi:http://dx.doi.org/10.1016/j.soilbio.2004.09.008

Krasnow, K. D., & Stephens, S. L. (2015). Evolving paradigms of aspen ecology and management: impacts of stand condition and fire severity on vegetation dynamics. *Ecosphere*, 6(1), 1-16. doi:10.1890/ES14-00354.1

Krishnan, P., Black, T. A., Grant, N. J., Barr, A. G., Hogg, E. H., Jassal, R. S., & Morgenstern, K. (2006). Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought. *Agricultural and Forest Meteorology*, 139(3–4), 208-223. doi:http://dx.doi.org/10.1016/j.agrformet.2006.07.002

Ku, SB., Edwards, G.E., & Tanner, C.B., (1977). Effects of Light, Carbon Dioxide, and Temperature on Photosynthesis, Oxygen Inhibition of Photosynthesis, and Transpiration in *Solanum tuberosum*[1] *Plant Physiology*, 59(5), 868-872.doi: http://dx.doi.org/10.1104/pp.59.5.868

Kuiters, A. T., & Denneman, C. A. J. (1987). Water-soluble phenolic substances in soils under several coniferous and deciduous tree species. *Soil Biology and Biochemistry*, 19(6), 765-769. doi:http://dx.doi.org/10.1016/0038-0717(87)90061-7

Kulakowski, D., Veblen, T. T., & Kurzel, B. P. (2006). Influences of infrequent fire, elevation and pre-fire vegetation on the persistence of quaking aspen (Populus tremuloides Michx.) in the Flat Tops area, Colorado, USA. Journal of Biogeography, 33(8), 1397-1413. doi:10.1111/j.1365-2699.2006.01529.x

Lafleur, B., Cazal, A., Leduc, A., & Bergeron, Y. (2015). Soil organic layer thickness influences the establishment and growth of trembling aspen (Populus tremuloides) in boreal forests. *Forest Ecology and Management,* 347, 209-216. doi:http://dx.doi.org/10.1016/j.foreco.2015.03.031

Lamontagne, S., Carignan, R., D'Arcy, P., Prairie, Y. T., & Paré, D. (2000). Element export in runoff from eastern Canadian Boreal Shield drainage basins following forest harvesting and wildfires. *Canadian Journal of Fisheries and Aquatic Sciences,* 57(S2), 118-128. doi:10.1139/f00-108

Landhäusser, S. M., & Lieffers, V. J. (2001). Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. *Tree Physiology*, 21(4), 243-250. doi:10.1093/treephys/21.4.243

Landhäusser, S. M., & Lieffers, V. J. (2002). Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. *Journal of Ecology*, 90(4), 658-665. doi:10.1046/j.1365-2745.2002.00699.x

Landhäusser, S. M., Silins, U., Lieffers, V. J., & Liu, W. (2003). Response of Populus tremuloides, Populus balsamifera, Betula papyrifera and Picea glauca Seedlings to Low Soil Temperature and Water-logged Soil Conditions. *Scandinavian Journal of Forest Research*, 18(5), 391-400. doi:10.1080/02827580310015044

Landhäusser, S. M., Wan, X., Lieffers, V. J., & Chow, P. S. (2010). Nitrate stimulates root suckering in trembling aspen (Populus tremuloides). *Canadian Journal of Forest Research*, 40(10), 1962-1969. doi:10.1139/X10-141

Lazerjan, M.S., (2014). Moisture Controls on Regenerating and Reclaimed Aspen Forest Evapotranspiration in the Western Boreal Plain. MSc Thesis. Department of Geography and Environmental Studies, Wilfrid Laurier University, Waterloo, ON.

Liang, H., & Chang, S. X. (2004). Response of trembling and hybrid aspens to phosphorus and sulfur fertilization in a Gray Luvisol: growth and nutrient uptake. *Canadian Journal of Forest Research*, 34(7), 1391-1399. doi:10.1139/x04-022

Liu, J., Equiza, M. A., Navarro-Rodenas, A., Lee, S. H., & Zwiazek, J. J. (2014). Hydraulic adjustments in aspen (*Populus tremuloides*) seedlings following defoliation involve root and leaf aquaporins. *Planta*, 240(3), 553-564. doi:10.1007/s00425-014-2106-2

Lis, G., Wassenaar, L. I. & Hendry, M. J., (2008). High-Precision Laser Spectroscopy D/H and ^{18}O/^{16}O Measurements of Microliter Natural Water Samples. *Analytical Chemistry*, 80, 287-293.

Longpré, M.-H., Bergeron, Y., Paré, D., & Béland, M. (1994). Effect of companion species on the growth of jack pine (Pinusbanksiana). *Canadian Journal of Forest Research*, 24(9), 1846-1853. doi:10.1139/x94-238

Loranty, M.M., Mackay, D. S., Ewers, B. E., Adelman, J. D., & Kruger, E. L. (2008). Environmental drivers of spatial variation in whole-tree transpiration in an aspen-dominated upland-to-wetland forest gradient. *Water Resources Research*, 44(2), n/a-n/a. doi:10.1029/2007WR006272

Lukenbach, M.C., Devito, K. J., Kettridge, N., Petrone, R. M., & Waddington, J. M. (2015). Burn severity alters peatland moss water availability: implications for post-fire recovery. *Ecohydrology*, n/a-n/a. doi:10.1002/eco.1639

Lukenbach, M. C., Hokanson, K.J., Moore, P.A., Devito, K. J., Kettridge, N., Thompson, D. K., & Waddington, J. M. (2015). Hydrological controls on deep burning in a northern forested peatland. *Hydrological Processes*, 29(18), 4114-4124. doi:10.1002/hyp.10440

Lukenbach M.C., Kettridge N., Devito K.J., Petrone R.M., & Waddington J.M. (2015). Hydrogeological controls on post-fire moss recovery in peatlands. *Journal of Hydrology* in press, doi: 10.1016/j.jhydrol.2015.09.075.

Macias Fauria, M., & Johnson, E. A. (2008). Climate and wildfires in the North American boreal forest. Philosophical Transactions of the Royal Society of London B: *Biological Sciences*, 363(1501), 2315-2327. doi:10.1098/rstb.2007.2202

Mackay, D. S., Ewers, B. E., Cook, B. D., & Davis, K. J. (2007). Environmental drivers of evapotranspiration in a shrub wetland and an upland forest in northern Wisconsin. *Water Resources Research*, 43(3), n/a-n/a. doi:10.1029/2006WR005149

Macrae, M. L., Redding, T. E., Creed, I. F., Bell, W. R., & Devito, K. J. (2005). Soil, surface water and ground water phosphorus relationships in a partially harvested Boreal Plain aspen catchment. *Forest Ecology and Management*, 206(1–3), 315-329. doi:http://dx.doi.org/10.1016/j.foreco.2004.11.010

Macrae, M. L., Devito, K. J., Creed, I. F., & Macdonald, S. E. (2006). Relation of soil-, surface-, and ground-water distributions of inorganic nitrogen with topographic position in harvested and unharvested portions of an aspen-dominated catchment in the Boreal Plain. *Canadian Journal of Forest Research*, 36(9), 2090-2103. doi:10.1139/x06-101

Marshall IB, Schut P, Ballard M. (compilers). 1999. Canadian Ecodistrict Climate Normals for Canada 1961–1990. A national ecological framework for Canada: Attribute Data. Environmental Quality Branch, Ecosystems Science Directorate, Environment Canada and Research Branch, Agriculture and Agri-Food Canada, Ottawa/Hull.

Mast, M. A., & Clow, D. W. (2008). Effects of 2003 wildfires on stream chemistry in Glacier National Park, Montana. *Hydrological Processes*, 22(26), 5013-5023. doi:10.1002/hyp.7121

Mataix-Solera, J., & Doerr, S. H. (2004). Hydrophobicity and aggregate stability in calcareous topsoils from fire-affected pine forests in southeastern Spain. *Geoderma*, 118(1–2), 77-88. doi:http://dx.doi.org/10.1016/S0016-7061(03)00185-X

Maynard, J. J., O'Geen, A. T., & Dahlgren, R. A. (2011). Sulfide Induced Mobilization of Wetland Phosphorus Depends Strongly on Redox and Iron Geochemistry. *Soil Science Society of America Journal,* 75(5). doi:10.2136/sssaj2011.0031

McEachern, P., Prepas, E. E., Gibson, J. J., & Dinsmore, W. P. (2000). Forest fire induced impacts on phosphorus, nitrogen, and chlorophyll a concentrations in boreal subarctic lakes of northern Alberta. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(S2), 73-81. doi:10.1139/f00-124

Michaelian, M., Hogg, E. H., Hall, R. J., & Arsenault, E. (2011). Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, 17(6), 2084-2094. doi:10.1111/j.1365-2486.2010.02357.x

Milberg, P., & Lamont, B. B. (1995). Fire enhances weed invasion of roadside vegetation in southwestern Australia. *Biological Conservation,* 73(1), 45-49. doi:http://dx.doi.org/10.1016/0006-3207(95)90061-6

Min, X., Siddiqi, M. Y., Guy, R. D., Glass, A. D. M., & Kronzucker, H. J. (1998). Induction of nitrate uptake and nitrate reductase activity in trembling aspen and lodgepole pine. *Plant, Cell & Environment,* 21(10), 1039-1046. doi:10.1046/j.1365-3040.1998.00340.x

Mitton, J. B., & Grant, M. C. (1996). Genetic Variation and the Natural History of Quaking Aspen. *BioScience*, 46(1), 25-31. doi:10.2307/1312652

Moore, T., & Basiliko, N. (2006). Decomposition in boreal peatlands. In Wieder, R.K., & Vitt, D.H. (Eds.), *Boreal Peatland Ecosystems* (125-143). Berlin, Heidelberg: Springer Publishing Company

Monteith, J. L. (1995). A reinterpretation of stomatal responses to humidity. *Plant, Cell & Environment,* 18(4), 357-364. doi:10.1111/j.1365-3040.1995.tb00371.x

Morrison, J., Brockwell, T., Merren, T., Fourel, F., & Phillips, A.M. (2001), On-Line High-Precision Stable Hydrogen Isotopic Analyses on Nanoliter Water Samples. Micromass UK Ltd., Floats Road, Wythenshawe, Manchester, M23 9LZ U.K., *Analytical Chemistry*, 73, 3570-3575

Mutch, R. W. (1970). Wildland Fires and Ecosystems--A Hypothesis. *Ecology*, 51(6), 1046-1051. doi:10.2307/1933631

Neff, J. C., Harden, J. W., & Gleixner, G. (2005). Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. *Canadian Journal of Forest Research*, 35(9), 2178-2187. doi:10.1139/x05-154

Oren, R., Phillips, N., Ewers, B. E., Pataki, D. E., & Megonigal, J. P. (1999). Sap-flux-scaled transpiration responses to light, vapor pressure deficit, and leaf area reduction in a flooded Taxodium distichum forest. *Tree Physiology*, 19(6), 337-347. doi:10.1093/treephys/19.6.337

Paré, D., & Bergeron, Y. (1996). Effect of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. *Canadian Journal of Forest Research*, 26(6), 1022-1031. doi:10.1139/x26-113

Penna, D., Stenni, B., Šanda, M., Wrede, S., Bogaard, T. A., Michelini, M., Fischer, B. M. C., Gobbi, A., Mantese, N., Zuecco, G., Borga, M., Bonazza, M., Sobotková, M., Čejková, B., & Wassenaar, L. I., (2012): Technical Note: Evaluation of between-sample memory effects in the analysis of δ^2H and δ^{18}O of water samples measured by laser spectroscopes, *Hydrology and Earth System Sciences*, 16, 3925-3933

Peterson, E.B., & Peterson, N.M. (1992). *Ecology, management and use of aspen and balsam poplar in the prairie provinces, Canada.* Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, Alberta, Special Report 1. Vol. 1. 252 p.

Petrone, R. M., Chasmer, L., Hopkinson, C., Silins, U., LandhÃ¤usser, S. M., Kljun, N., & Devito, K. J. (2015). Effects of harvesting on CO_2 and H_2O fluxes in an aspen dominated Western Boreal Plain forest". *Canadian Journal of Forest Research, ,* 45: 87-100., DOI: 10.1139/cjfr-2014-0253

Phuyal, M., Artz, R. R. E., Sheppard, L., Leith, I. D., & Johnson, D. (2007). Long-term nitrogen deposition increases phosphorus limitation of bryophytes in an ombrotrophic bog. *Plant Ecology*, 196(1), 111-121. doi:10.1007/s11258-007-9338-1

Pieruschka, R., Huber, G., & Berry, J. A. (2010). Control of transpiration by radiation. Proceedings of the National Academy of Sciences, 107(30), 13372-13377. doi:10.1073/pnas.0913177107

Prévost, M., & Pothier, D. (2003). Partial cuts in a trembling aspen □ conifer stand: effects on microenvironmental conditions and regeneration dynamics. *Canadian Journal of Forest Research*, 33(1), 1-15. doi:10.1139/x02-147

Prieto-Fernández, A., Acea, J. M., & Carballas, T. (2012). Soil microbial and extractable C and N after wildfire. *Biology and Fertility of Soils*, 27(2), 132-142. doi:10.1007/s003740050411

Redding, T. E., & Devito, K. J. (2008). Lateral flow thresholds for aspen forested hillslopes on the Western Boreal Plain, Alberta, Canada. *Hydrological Processes*, 22(21), 4287-4300. doi:10.1002/hyp.7038

Redding, T., & Devito, K. (2010). Mechanisms and pathways of lateral flow on aspen-forested, Luvisolic soils, Western Boreal Plains, Alberta, Canada. *Hydrological Processes*, 24(21), 2995-3010. doi:10.1002/hyp.7710

Riddell, J. (2008). Assessment of surface water-groundwater interaction at perched boreal wetlands, north-central Alberta. M.Sc. thesis, Department of Earth and Atmospheric Sciences, University of Alberta.

Roden, J. S., & Pearcy, R. W. (1993). Photosynthetic gas exchange response of poplars to steady-state and dynamic light environments. *Oecologia*, 93(2), 208-214. doi:10.1007/bf00317673

Rodríguez-Gamir, J., Ancillo, G., González-Mas, M. C., Primo-Millo, E., Iglesias, D. J., & Forner-Giner, M. A. (2011). Root signalling and modulation of stomatal closure in flooded citrus seedlings. *Plant Physiology and Biochemistry*, 49(6), 636-645. doi:http://dx.doi.org/10.1016/j.plaphy.2011.03.003

Rooney, R. C., Bayley, S. E., & Schindler, D. W. (2012). Oil sands mining and reclamation cause massive loss of peatland and stored carbon. *Proceedings of the National Academy of Sciences*, 109(13), 4933-4937. doi:10.1073/pnas.1117693108

Roy, V., Ruel, J.C., & A.P. Plamondon, A.P (2000). Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. *Forest Ecology and Management*, 129, 253–267

Ryan, K.C., & Noste, N.V., (1983). Evaluating prescribe fires. In: Lotan, J.E., Kilgore, B.M., Fischer, W.C., Mutch, R.W. (Tech. Coord.), Symposium and Workshop of Wilderness Fire: Proceedings Gen. Tech. Rpt. INT-182. USDA Forestry Service., Intermountain Res. Sta., Ogden, UT, pp. 230–238.

Schier, G.A., & Campbell, R., (1978). Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. *Forest Science*. 24, 303-312

Schier, G.A., Jones, J.R., & Winokur, R.P., (1985). Vegetative regeneration. In: DeBye, N.V, Winokur, R.P., editors. Aspen: Ecology and management in the western United States. USDA Forest Service General Technical Report RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. pp. 29-33

Schlesinger, W. H., Ward, T. J., & Anderson, J. (1997). Nutrient losses in runoff from grasslandand shrubland habitats in southern New Mexico: II. Field plots. Biogeochemistry, 49(1), 69-86. doi:10.1023/a:1006246126915

Schlesinger, W.H. (1997). Biogeochemistry: an analysis of global change (2nd ed.). San Diego: Academic.

Shenker, M., Seitelbach, S., Brand, S., Haim, A., & Litaor, M. I. (2005). Redox reactions and phosphorus release in re-flooded soils of an altered wetland. *European Journal of Soil Science*, 56(4), 515-525. doi:10.1111/j.1365-2389.2004.00692.x

Shetler, G., Turetsky, M. R., Kane, E., & Kasischke, E. (2008). *Sphagnum* mosses limit total carbon consumption during fire in Alaskan black spruce forests. *Canadian Journal of Forest Research*, 38(8), 2328-2336. doi:10.1139/X08-057

Sherman, E. R., Fahey, J. T., & Howarth, W. R. (1998). Soil-plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. *Oecologia*, 115(4), 553-563. doi:10.1007/s004420050553

Simard, D. G., Fyles, J. W., Paré, D., & Nguyen, T. (2001). Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. *Canadian Journal of Soil Science*, 81(2), 229-237. doi:10.4141/S00-028

Sinclair, T. R., Tanner, C. B., & Bennett, J. M. (1984). Water-Use Efficiency in Crop Production. *BioScience*, 34(1), 36-40. doi:10.2307/1309424

Smart, D. R., Carlisle, E., Goebel, M., & NÚÑEz, B. A. (2005). Transverse hydraulic redistribution by a grapevine. *Plant, Cell & Environment*, 28(2), 157-166. doi:10.1111/j.1365-3040.2004.01254.x

Smerdon, B. D., Devito, K. J., & Mendoza, C. A. (2005). Interaction of groundwater and shallow lakes on outwash sediments in the sub-humid Boreal Plains of Canada. *Journal of Hydrology*, 314(1–4), 246-262. doi:http://dx.doi.org/10.1016/j.jhydrol.2005.04.001

Smith, D. W., Prepas, E. E., Putz, G., Burke, J. M., Meyer, W. L., & Whitson, I. (2003). The Forest Watershed and Riparian Disturbance study: a multi-discipline initiative to evaluate and manage watershed disturbance on the Boreal Plain of Canada. *Journal of Environmental Engineering and Science*, 2(S1), S1-S13. doi:10.1139/s03-030

St. Clair, S. B., Cavard, X., & Bergeron, Y. (2013). The role of facilitation and competition in the development and resilience of aspen forests. *Forest Ecology and Management*, 299, 91-99. doi:http://dx.doi.org/10.1016/j.foreco.2013.02.026

Ste-Marie, C., & Paré, D., (1999). Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. *Soil Biology and Biochemistry*, 31, 1579-1589.

Startsev, N. A., Lieffers, V. J., Landhäusser, S. M., & Velazquez-Martinez, A. (2008). N-transfer through aspen litter and feather moss layers after fertilization with ammonium nitrate and urea. *Plant and Soil*, 311(1), 51-59. doi:10.1007/s11104-008-9657-6

Strong, W. L., & Roi, G. H. L. (1983). Root-system morphology of common boreal forest trees in Alberta, Canada. *Canadian Journal of Forest Research*, 13(6), 1164-1173. doi:10.1139/x83-155

Turetsky, M. R. (2003). The Role of Bryophytes in Carbon and Nitrogen Cycling. *The Bryologist*, 106(3), 395-409. doi:10.1639/05

Turetsky, M. R., Kane, E. S., Harden, J. W., Ottmar, R. D., Manies, K. L., Hoy, E., & Kasischke, E. S. (2011). Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nature Geoscience*, 4(1), 27-31. doi:http://www.nature.com/ngeo/journal/v4/n1/abs/ngeo1027.html#supplementary-information

Turner, M. G., Hargrove, W. W., Gardner, R. H., & Romme, W. H. (1994). Effects of Fire on Landscape Heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, 5(5), 731-742. Retrieved from http://www.jstor.org/stable/3235886

Turner, M. G., Romme, W. H., Reed, R. A., & Tuskan, G. A. (2003). Post-fire aspen seedling recruitment across the Yellowstone (USA) Landscape. *Landscape Ecology*, 18(2), 127-140. doi:10.1023/a:1024462501689

Van Cleve, K., & Noonan, L. (1975). Litterfall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. *Canadian Journal of Forest Research*. 4(5), 626-639.

Vance, E. D., & Chapin Iii, F. S. (2001). Substrate limitations to microbial activity in taiga forest floors. *Soil Biology and Biochemistry*, 33(2), 173-188. doi:http://dx.doi.org/10.1016/S0038-0717(00)00127-9

Venterink, H. O., Davidsson, T. E., Kiehl, K., & Leonardson, L. (2002). Impact of drying and re-wetting on N, P and K dynamics in a wetland soil. *Plant and Soil*, 243(1), 119-130. doi:10.1023/a:1019993510737

Vidon, P., Allan, C., Burns, D., Duval, T. P., Gurwick, N., Inamdar, S., Sebestyen, S. (2010). Hot Spots and Hot Moments in Riparian Zones: Potential for Improved Water Quality Management. *Journal of the American Water Resources Association*, 46(2), 278-298. doi:10.1111/j.1752-1688.2010.00420.x

Vitt, D.H., Halsey, L., Thormann, M.N. and Martin, T. 1996. *Peatland Inventory of Alberta*. Alberta Peat Task Force, University of Alberta. Edmonton, AB.

Vogwill R. 1978. *Hydrogeology of the Lesser Slave Lake Area, Alberta*. Edmonton AB. Alberta

Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K., & Moore, P. A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8(1), 113-127. doi:10.1002/eco.1493

Walbridge, M., & Navaratnam, J. (2006). *Phosphorous in Boreal Peatlands*. In R. K. Wieder & D. Vitt (Eds.), Boreal Peatland Ecosystems (Vol. 188, pp. 231-258): Springer Berlin Heidelberg.

Wang, G. G. (2003). Early regeneration and growth dynamics of Populus tremuloides suckers in relation to fire severity. *Canadian Journal of Forest Research*, 33(10), 1998-2006. doi:10.1139/x03-123

Wang, S. (2012). Evaluation of Water Stress Impact on the Parameter Values in Stomatal Conductance Models Using Tower Flux Measurement of a Boreal Aspen Forest. *Journal of Hydrometeorology*, 13(1), 239-254. doi:10.1175/JHM-D-11-043.1

Wang, G., Yu, X., Bao, K., Xing, W., Gao, C., Lin, Q., & Lu, X. (2015). Effect of fire on phosphorus forms in *Sphagnum* moss and peat soils of ombrotrophic bogs. *Chemosphere*, 119, 1329-1334. doi:http://dx.doi.org/10.1016/j.chemosphere.2014.01.084

Weber, M.G., & Stocks, B.J., (1998). Forest fires and sustainability in the boreal forests of Canada. *Ambio* 27(7), 545-550.

Whitson, I. R., Chanasyk, D. S., & Prepas, E. E. (2005). Effect of forest harvest on soil temperature and water storage and movement patterns on Boreal Plain hillslopes. *Journal of Environmental Engineering and Science*, 4(6), 429-439. doi:10.1139/s04-081

Wilbur, R. B., & Christensen, N. L. (1983). Effects of Fire on Nutrient Availability in a North Carolina Coastal Plain Pocosin. *American Midland Naturalist*, 110(1), 54-61. doi:10.2307/2425213

Wolken, J. M., Landhäusser, S. M., Lieffers, V. J., & Dyck, M. F. (2010). Differences in initial root development and soil conditions affect establishment of trembling aspen and balsam poplar seedlings. *Botany*, 88(3), 275-285. doi:10.1139/B10-016

Wu, Y., Rutchey, K., Newman, S., Miao, S., Wang, N., Sklar, F. H., & Orem, W. H. (2012). Impacts of fire and phosphorus on sawgrass and cattails in an altered landscape of the Florida Everglades. *Ecological Processes*, 1(1), 1-11. doi:10.1186/2192-1709-1-8