Spatial Variability in Disturbed Boreal Ecosystems: Aboveground and Belowground Controls

by

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Abstract

The recent open pit mining for oil sands in the Athabasca Oil Sands Region (AOSR), northern Alberta has created an unprecedented industrial scale disturbance whose ecological consequences is not well understood, and requires intensive investigation. This study focused on the temporal dynamics of spatial variability in aboveground (canopy cover, understory vegetation cover and forest floor) and belowground (soil nutrient availability, microbial biomass, respiration and enzyme activities) processes in wildfire disturbed upland boreal forests to create a benchmark condition for measuring reclamation success.

The wildfire chronosequence used for the spatial study contained three trembling aspen (*Populus tremuloides* Michx.) stands; a one-year old post fire stand (PF), a 9 year old stand at canopy closure (CC) and a 72 year old mature (MA) stand. The PF stand had the highest total inorganic N, P and K availability compared to the CC and MA stands. Most of the above and belowground properties, including macronutrients, in the PF stand either had a large scale spatial pattern or did not show any spatial structure, whereas the CC and MA stands had a spatial range equal to or less than 10 m. The PF stand also showed the weakest spatial coupling between aboveground and belowground properties. The aboveground and belowground properties in the CC stand appear to be more similar to the MA stand. This indicates that natural recovery probably happen much faster rate than what is reported in the literature. The current research also quantified the spatial variability of soil respiration (Rs) in the same fire chronosequence over two growing seasons. No spatial structure was detected in Rs of the PF stand during the peak growing season (June-July), whereas Rs was auto-correlated at a scale of < 6 m in the CC and MA stands, which confirms the disturbance legacies in spatial patterns found in the nutrient study.

Finally, the research investigated whether spatial patterns in biogeochemical properties were developed in a 14-year old aspen stand reclaimed after oil sands extraction. A fine scale (< 10 m) spatial pattern was found in the majority of above and belowground properties. However, soil chemical properties showed large scale spatial auto-correlation indicating persistence of disturbance effect. A strong soil microbial influence on the availability of macronutrients was found when compared to stand characteristics. The weak spatial coupling between nutrient availability and aboveground properties even after a decade of reclamation suggests that the ecosystem recovery rate in the reclaimed area is slower than in wildfire disturbed areas, and might require further time to develop. This research highlights the importance of spatial heterogeneity as a tool for measuring ecosystem recovery after disturbance and data on natural benchmark function to quantify reclamation success in oil sands mine disturbed areas.

Preface

This thesis is an original work by Sanatan Das Gupta. Chapter 4 of this thesis has been published as Das Gupta, S., MacKenzie, M.D. and Quideau, S. A. "Using Spatial Ecology to Examine Above and Belowground Interactions on a Reclaimed Aspen Stand in Northern Alberta" Geoderma, vol. 259-260, 12-22 (2015). I was responsible for conducting the experiment, data collection and analysis as well as manuscript composition. M.D. MacKenzie and S.A. Quideau were the supervisory authors and were involved with concept formation and manuscript editing.

Dedication

I dedicate this work to my beloved parents.

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List of Symbols and Abbreviations

Abbreviation	Definition
AOSR	Athabasca oil sands region
AG	Aboveground
BG	Belowground
BGn	Bare ground
PF	Post fire
CC	Canopy closure
MA	Mature aspen
DBH	Diameter at breast height
Tdist.	Distance to nearest tree
CWD	Coarse woody debris
UV	Understory vegetation
CRB	Coarse root biomass
FRB	Fine root biomass
BA	Basal area
PRS probe	Plant root simulator probe
ICP	Inductively-coupled plasma
MBC/MBN	Microbial biomass C/Microbial Biomass N
BR	Basal Respiration
HSC	Hexose Sugar Complex
PSC	Pentose Sugar Complex
NAG	N-acetyl-β-glucosaminidase
Bglu	β-1,4-glucosidase

Abbreviation	Definition
Phenol	Phenol oxidase
Perox	Peroxidase
Phos	Phosphatase
Sulf	Sulfatase
SAR	Spatial Auto Regression
OLS	Ordinary Least Square
NMDS	Non-Metric Multidimensional Scaling
Rs	Soil Respiration
FC	Flux concentration
ST	Soil temperature
SM	Soil moisture
NEE	Net Ecosystem Exchange
CV	Coefficient of Variation
IRGA	Infrared Gas Analyzer
NEE	Net Ecosystem Exchange
PCA	Principal Component Analysis
TC	Total organic C
TIN	Total inorganic N

Chapter 1. Introduction

1.1 Ecosystem Disturbance and Reclamation

Disturbance is a major natural or anthropogenic event that causes abrupt changes in ecosystem components by altering the distribution of resources. Through partial or complete removal of vegetation it reduces competition, changes microsite conditions, root morphology and foraging behavior, and nutrient biogeochemistry (Fraterrigo and Rusak 2008; Pickett and Cadenasso 1995). Natural ecosystems have evolved to recover after disturbance, which generally occurs within a known time frame. For example, boreal ecosystem is fire adapted and fire return interval generally ranges between 35 years to 250 years (Cumming 2000; Rogeau et al. 2007; Barrett et al. 2010). Depending on intensity, key biogeochemical properties recover back within several years to couple of decades after fire disturbance (Grandpre et al. 1993; Lynham et al. 1998; Certini 2005; Maynard et al. 2014). Human disturbed ecosystems, however, may require intervention to fully recover as the mode and magnitude of disturbances can be different from that of natural disturbances (Everett et al. 2000). For example, open pit mining completely remove biomass from the system, whereas natural disturbances such as fire and windstorm return biomass and nutrients to the system. Restoring ecosystem integrity (coupling between ecosystem components) should be the central focus of reclaiming areas affected by anthropogenic disturbances (Mummey et al. 2002). The spatial relationship among biotic and abiotic components of ecosystem is a key concept in understanding ecosystem integrity (Kardol and Wardle 2010). Establishing a functional relationship among ecosystem components, identifying above and below ground control mechanisms, and finding the relationship ecosystem resilience extending the idea of long term sustainability have been found to be a challenging task for both natural and man-made disturbances (Balser and Firestone 2005; MacKenzie and Quideau 2010).

Out of several anthropogenic disturbances in the boreal northern Alberta such as mining, harvesting, road construction, pipeline, powerline and seismic line, oil sands mining is one of the major one which produced industrial scale disturbances (Lee 2004; Pickell et al. 2015). These ores are distributed under approximately 142 000 km^2 area of the province and of the total reserve, ten percent lies very close (within 100 m) to the ground surface, and is currently being extracted by open pit mining (Government of Alberta, 2014). Open pit mining creates massive ecological and environmental disturbance by removing all the biotic components (vegetation and living forest floor), as well as completely removing soil. The current disturbance footprint from surface mining in the area is about 815 sq. km which has a potential to increase up to 2000 km^2 by 2020 (Government of Alberta 2014; CAPP 2015). As a legislative mandate, oil sand companies are required to reclaim the sites disturbed by mining activities to "equivalent land capability conditions". To date, a significant portion of the disturbed area (> 75 000 ha) has not received any treatment and there is very limited information regarding benchmark conditions that the reconstructed ecosystems should meet.

Among the biogeochemical properties of interest in ecosystems recovering from disturbances, nutrient availability and microbial metabolisms are the two important ones that can be used to understand how aboveground (AG) and belowground (BG) components are interconnected (MacKenzie and Quideau 2010). Proper characterization of nutrient dynamics and the biogeochemical processes associated with them is crucial for understanding the recovery pattern of disturbed ecosystems compared to natural analogues. Such information may also prove useful for following the temporal trajectory of ecosystem development in the reconstructed landscape. Currently oil sands reclamation in Alberta seem more heavily focused on AG productivity rather than on belowground ecology. The Land capability classification system

(LCCS) was used in the past as a tool for evaluating plant performance and soil nutrient status in reclaimed ecosystems (Leskiw 1998). However, the system lacked important processes and properties such as bioavailability of nutrients, active microbial community, and information on structural heterogeneity. Moreover, land capability might not fully represent structural and functional compositions of key ecosystem components at different scales. Therefore, a holistic approach to evaluate reclamation success is required for oil sands reclamation which should include ecologically meaningful indices of ecosystem functionality. From an ecosystem ecology perspective, oil sands mining in Alberta has created a unique opportunity to study ecosystem development after massive industrial scale disturbances. Characterizing both AG and BG ecosystem processes may help tease apart the complex ecological puzzles, which in turn will be helpful to recreate a more natural like system. Research described in this dissertation addresses these AG and BG processes in fire disturbed and surface mine reclaimed sites in northern Alberta.

1.2 Wildfire Disturbed Ecosystems as Reclamation Benchmark

Disturbance is a ubiquitous phenomenon that creates heterogeneity both in the AG and BG ecosystem components. Fire is the primary mode of natural disturbance in boreal ecosystems (DeLuca et al. 2006). Fire as an ecosystem modifier, has a profound effect on both short-term and long-term nutrient cycling by changing vegetation structure (Green 1989; Schimmel and Granström 1996), soil properties (DeBano 1991; González-Pérez et al. 2004; MacLean et al. 1983; Zackrisson et al. 1996), microbial assemblage (Ball et al. 2010; Hart et al. 2005) as well as the micro and mesoclimatic behaviour of the site (DeBano et al. 1998). Most of the boreal tree species are fire adapted and require fire disturbance to regenerate. Clonal species

such as aspen produces suckers vigorously after fire with a stem density as high as 200 000/ha (Peterson and Peterson 1992). The mosaic structure of stands with abrupt but irregular boundaries further indicate the fire is the integral part of the boreal ecosystem (Rowe and Scotter 1973). The spatial heterogeneity in resources created by fire might be one of the reasons why the mosaic pattern of stand structure persists (Boby et al. 2010). Fire causes nutrients to be redistributed or transferred from one pool to another (Boerner 1982; Grier 1975), and therefore favors or limits plant growth in patches with variable nutrient conditions. Factors that strongly influence spatial distribution of nutrients after stand replacing fire include fire severity (affect organic layer depth, organic matter quality, and plant regeneration), abiotic conditions (affect moisture and temperature), and post-fire vegetation (Smithwick et al. 2005).

Stand replacing fire can create homogenous or random patterns in nutrient availability and other biotic activities, which may become heterogeneous over time as stand structure gets more complex. Such properties in fire disturbed ecosystem can be used for tracking and comparing ecosystem development in oil sands reclaimed sites. Since wildfire is the major natural disturbance in boreal ecosystem (Maynard et al. 2014; Bergeron et al. 2001) and the reclamation goal of oil sands mining is to recreate functionally similar upland boreal forests (Alberta Environment 2010), wildfire disturbed sites can be used as natural benchmark for measuring reclamation success. There is no historical analogue in boreal ecosystem to compare the spatial patterns generated by industrial scale disturbance such as oil sands mining (Pickell et al. 2013; Pickell et al. 2015). Although harvesting has been a common anthropogenic disturbance in boreal forests for long time, its effect on soil and vegetation processes can be very different than that exerted by wildfire disturbance (Niemela 1999; McRae et al. 2001; Simard et al. 2001). The other forms of natural disturbance such as flooding, wind throw, insect and disease, and

snow/frost damage are less frequent in boreal Alberta (Lee 2004) and might not be as important as wildfire for generating targeted patterns in ecosystem properties (Angelstam 1996; Niemela 1999).

1.3 Use of Spatial Ecology in Tracking Ecosystem Recovery

Biotic occurrence of living organisms in nature is not a random process; rather it happens in aggregated fashion, in patches, or in a gradient of several spatial structures (Legendre & Fortin, 1989). Such spatial structures occur at different scales of space, time and organizational complexity (Levin 1992). Most ecological phenomena in nature show patchiness which can ranges from few millimetres to several thousand km (Legendre 1993). Endogenous ecological processes interacting between neighboring individuals may sometime create spatial autocorrelation, thus generating spatial patterns (Stoll and Bergius 2005). Quantifying spatial patterns and determining the underlying mechanistic processes that generate that specific pattern have become a major focus of the current ecological studies (McIntire & Fajardo, 2009). The relationship between pattern and process in ecological systems is not straightforward as there are possibilities that the same pattern can be created by several different processes (Perry et al. 2002; Real and McElhany 1996). Moreover, it is practically not possible to know the exact structure of the process model of the system under investigation, especially when the study is not manipulated or conducted in natural conditions. Thus, deriving inferences on the ecosystem processes has been a challenging task for long time and followed an inductive approach for reaching conclusions rather than supported by apriori hypothetically derived deductive process (Borcard et al. 2004; Dale and Fortin 2014; Jeltsch et al. 1999; McIntire and Fajardo 2009). However, using a combination of right analytical tools and multiple apriori ecological

hypotheses the pattern-process puzzle can be solved without blaming much to our perceptions of biological limitations (Burnham and Anderson 2002).

Non-spatial statistics often ignore the ubiquitous distance dependency and autocorrelation in ecological data by assuming that organisms and their controlling factors are uniformly distributed in nature (McIntosh 1991; Fortin and Dale 2009). Variability and discontinuity in ecosystem properties has been regarded as random noise, although this often happens in predictable patterns at various scales with both spatial and temporal components (Ettema and Wardle, 2002). The spatial relationship can, however, be very useful in inferring ecological processes if considered as the consequence of biological processes (Keitt and Urban 2005). Spatial patterns of ecological variables may provide valuable information on the possible mechanistic processes when tie with testable ecological hypotheses. Ecological inferences can also be derived for process-pattern relationships if space is regarded as a surrogate of unmeasured variables as proposed by McIntire and Fajardo (2009). If a spatial dependency exists for the unmeasured variables, that should be evident in the spatial pattern analysis of the spatial residuals. The inferences can further be maximized by constraining the causal predictors which have biological relationships, rather than empirical or probabilistic (statistical) relationships (Borcard et al. 2004).

Use of 'space' and spatial analyses in natural disturbed ecosystems have been shown to be very effective in inferring key processes about ecosystem recovery such as development of vegetation pattern (Arseneault 2001; Bautista and Vallejo 2002), nutrient dynamics (Rodríguez et al. 2009; Smithwick et al. 2005), and microbial ecology (Smithwick et al. 2012). The similar spatial approach has been used in human disturbed ecosystems (e.g. mining) to track the development of functional ecosystem components (e.g. organic layer, microbial community, and

nutrient cycling) and to compare those with natural benchmarks (Jacinthe and Lal 2006; Mummey et al. 2002; Nyamadzawo et al. 2008). However, variability in ecosystem type and analytical methods used for quantifying different properties has made these studies less comparable. Moreover, inductive reasoning has been used in lot of these studies rather than deductive inferences supported by a priori hypothesis, which perhaps violated a number of testable alternative ecological hypotheses and therefore, made these studies less appropriate for generating ecological inferences.

Understanding the spatial ecology in oil sands reclaimed ecosystem will be helpful in characterizing 'equivalent land capability' as a legal mandate for reclamation certification. Since land reclamation should focus on the overall ecosystem structure including functions, interactions and variability, a mechanistic understanding of process-pattern relationship is must to reach reclamation goal (Kardol and Wardol 2010). Spatial structure of the key ecosystem properties, their driving factors, and the successional development pattern in the reconstructed ecosystem would be more ecologically appropriate than focusing only on average value when comparing the system with natural benchmarks. In this connection, knowing the relative contribution of environmental, biotic, and space factors to the variation in ecosystem properties will be of decisive importance in comparing functional similarity and testing ecological hypothesis (Borcard et al. 1992).

1.4 Methods for Measuring Forested Ecosystem Functions

The bulk of our current knowledge about soil science and plant nutrition is predominantly developed from agricultural practices (Brevik and Hartemink 2010). The nutritional requirement

of crop and the soil ability to supply such demand can be controlled in managed systems such as agriculture and production forestry. Applying agronomic knowledge of soil and plant science in forested and reclaimed ecosystems, however, poses a great risk of misinterpreting ecosystem ecology which is completely different from the agricultural systems. The idea of plant nutritional demand and limitation might not fully apply in natural ecosystems as the very characteristics of nutrient status and seasonal fluctuations are the main reasons that shape the natural ecosystems over a longer temporal trajectory. The same reasoning applies to the intricate belowground interactions in forested ecosystems. However, agronomic application of soil science is still a common practice in natural ecosystem studies as the necessary modifications in the methods and philosophies are yet to be developed. In the current research, I used some non-agronomic methods for measuring nutrient availability and soil biological activities, and spatially modelled their relationship with AG properties.

1.4.1 Plant Root Simulator (PRS) Probes

PRS probes were used for measuring nutrient availability in the current study. These are ion exchange resin membranes which are more efficient and biologically meaningful means of capturing nutrient behavior in soil environment than the traditional batch extraction methods used for agricultural soils (Qian and Schoenau 2002). PRS probes have been successfully used in forested ecosystems, where they produced some of the best results when compared to other methods such as intact soil core incubation and ion exchange resin bags (Huang and Schoenau 1997). These membranes take advantage of ion diffusion chemistry to simulate plant root behavior of nutrient acquisition under field conditions. As soon as nutrients are mineralized and

come in close contact with the membranes, they are trapped and secluded from further biological activity.

1.4.2 Soil Respiration

The CO_2 efflux from soil, known as soil respiration (Rs), is an end product of several amalgamative plant and soil processes. Rs is composed of CO_2 fluxes from two different sources, (i) autotrophic respiration (Ra), mainly from plant roots, rhizosphere micorrhizae and living mosses, and (ii) heterotrophic respiration (Rh), mainly from microbial activity (Hanson et al. 2000). Rs can have several developmental phases in disturbed ecosystems. For example, very low Rs is usually found after stand replacing fire which gradually increases, and depending on ecosystems and vegetation, reaches a peak after which it decreases again at stand maturity (Swamoto et al. 2000; Amiro et al. 2003; Czimczik et al. 2006; Hyvonen et al. 2007). Such behavior of Rs can be used as a good indicator of ecosystem recovery after disturbances. As Rs shows considerable seasonal fluctuations due to several environmental and biotic factors, spatial variability could therefore be used to capture signature of seasonal change in Rs patch sizes.

Due to the advent of new portable technologies such as infrared gas analyzer for CO_2 flux measurement, a huge attention has been given to understand the underlying mechanisms that contribute to Rs both in agricultural and forested ecosystems. The two main state factors of variation as agreed in most of the literature are temperature and moisture. However, other soil properties such as organic matter quality, photosynthates in root, microbial biomass and activity are all responsible for the variation in soil respiration (Tang and Baldocchi 2005). Environmental (temperature and moisture) control on Rs is perhaps more prominent in well managed system like agriculture where other factors such as vegetation, spacing and fertilization scheme are kept

spatially homogeneous both qualitatively and quantitatively. This is, however, not the case in forested ecosystems. To address the complex above and belowground contributions to Rs in disturbed forested ecosystems in the current study, I measured both environmental variables and microbial properties (biomass, basal respiration, and C mineralizing enzymes).

1.4.3 Extracellular Enzyme Activities

Extracellular enzymes are proteins responsible for deconstructing plant and microbial cell wall and convert complex organic macromolecule to simple soluble substrates for plant uptake and microbial assimilation (Sinsabaugh et al. 2008). These proteins are important catalyzing agents for organic matter decomposition thus contribute to a great extent to nutrient cycling. Relative activities of extracellular enzymes reflect the biochemical environment in soils as different enzymes are associated with organic matter with varying quality and interaction with soil microbial community over a certain period of time. The proteins are long lived in the soil environment and represent a holistic view of decomposition, humification and nutrient mineralization (Decker et al. 1999). As most of the biochemical processes related to decomposition and nutrient mineralization happen at the microbial scale, extracellular enzymes produced during the mineralization process should also have an identifiable spatial pattern at similar scale. Such fine scale patterns have been found in different layers of forest floor (Šnajdr et al. 2008) and have been related to decomposition and nutrient mineralization processes in forested ecosystems (Antibus et al. 1992; Sinsabaugh 1994). Therefore, if the mechanistic relationship between enzyme activity and nutrient availability in disturbed ecosystems can be resolved through spatial analyses, such information would be very useful in monitoring ecosystem recovery from the perspective of microbial activity and patch dynamics. In the current

study, I measured six major extracellular enzymes responsible for C, N, P and S mineralization, and determined their relationships with nutrient availability measured *in-situ*.

1.5 Ecosystem Heterogeneity: A Key Concept in Spatial Ecology

The current concern about ecosystem heterogeneity is a consequence of relatively recent paradigm shift. Environmental homogeneity was the starting assumption of the old ecological paradigm, which was much simplified at the expense of reality (Wiens 2000). Heterogeneity is now being considered as an integral part of natural ecosystem rather than random noise and complexity (Stewart 1999). Heterogeneity is rather a complex term to be defined in ecological context, as depending on approaches heterogeneity can mean different qualitative and quantitative attributes of a system (Li and Reynolds 1995). Milne (1991) defined heterogeneity as 'complexity that results from interaction between the spatial distribution of environmental constraints and the differential responses of organisms to the constraints'. According to Weins (2000), heterogeneity can be expressed as 'spatial variation', which is a measure of aggregate variation in a given area. In its simplest form, heterogeneity is the uneven distribution of attributes in space and time. Li & Reynolds (1995) identified four different forms of heterogeneity created from patterns, either different quantitatively or qualitatively, or have spatially explicit compositional difference.

Ecological phenomena are spatially and temporally variable, and might operate at multiple spatial scales (Hutchings et al. 1999; Koenig, 1999; Fortin et al. 2006). Understanding ecosystem heterogeneity requires a wide consideration of qualitative or quantitative factors responsible for creating heterogeneity. Fortin and Dale (2005) suggested three basic mechanisms

of spatial patchiness or heterogeneity, viz. i) inherent spatial dependence, which may result from the causal interaction between ecological processes, ii) induce spatial dependence, where pattern develops due to environmental response of organisms, and iii) the spurious pattern, which can either arise from the unmeasured processes or environmental factors.

Heterogeneity in ecosystem level processes and properties is the consequence of the interactions between AG and BG components. There are both positive and negative feedbacks among ecosystem processes, where one process either influences or get influenced by the others, and sometimes these forces work together under the same spatio-temporal scale to generate specific ecosystem pattern (Wardle et al., 2004). The following section will address some of the key processes that generate heterogeneity in both AG and BG processes and properties.

1.5.1 Aboveground and Belowground Components of Ecosystems

Terrestrial ecosystems are composed of AG and BG components that interact together to drive ecosystem level processes and properties (Wardle et al. 2004). The two components have long been studied in isolation in traditional ecosystem studies and only recently have AG-BG feedbacks been considered as key regulating factor in ecosystem processes (Bardgett and Wardle 2003). Aboveground properties such as tree distribution, canopy cover, and forest floor depth can directly or indirectly affect BG components such as soil microbes, including composition and function (Wardle 2002; Weber and Bardgett 2011). Plants can modify the distribution of understory species and BG biota by changing resources such as light, moisture, and organic matter that accumulates under their zone of influence (Saetre and Baath 1999; Wardle 2002). Individual trees play significant role in BG processes by their variable rate of litter input and nutrient uptake from soil (Weber and Bardgett 2011). Plant species and intra-species

relationships also determine the specific decomposer community by their direct effect on leaf litter and root exudate quality, and therefore contribute to BG processes (Wardle et al. 2004).

Belowground organisms also significantly influence AG vegetation dynamics and distribution. Changes in soil microbial community structure can directly affect organic matter quality by changing decomposition pathways, which in turn may alter nutrient dynamics in belowground ecosystem and consequently favor certain group of plant species (Bradford et al. 2002; John et al. 2007). Microbes are also very important biogeochemical agents in marginal or heavily disturbed soil, where they are responsible for increasing resource variability and initiating ecosystem development processes (DeGrood et al. 2005; Smithwick et al. 2012). Soil microbes exert strong control on nutrient availability at the initial stage of stand development in naturally disturbed sites (Wardle 2002). Above and belowground feedback loops in boreal ecosystems are tightly linked among plants, accumulated organic matter, and belowground decomposer groups. For example, C fixation is heavily dependent on nutrient availability, especially N (Magnani et al. 2007), and nutrient availability is further determined by the decomposability of the C compound produced by the growing vegetation (Pastor and Naiman 1992; Eskelinen et al. 2009).

1.5.1.1 Causes of Aboveground Heterogeneity

Heterogeneity in AG components of ecosystems can arise from several factors including competition (Tilman 1994), canopy cover and gap, tree location (Nicotra et al. 1999; Collins and Battaglia 2002; Dusan et al. 2007), microsite variation e.g. microtopography, aspect and slope position (Beatty 1984; Bestelmeyer et al. 2006), understory vegetation (Nilsson and Wardle

2005), coarse woody debris (Laiho and Prescott 2004), and BG factors such as mycorrhizal association, soil organic matter quality, and variability in nutrient availability (Roy et al. 2012).

Soil patchiness is considered to be one of the most important drivers of plant heterogeneity; however, such patchiness can arise from both biotic (e.g. microbial assemblages and nutrient mineralization) (Tilman 1984) and abiotic factors (e.g. moisture). Plant derived influences can sometime override the heterogeneity from the abiotic factors. Seed dispersal pattern is one of such mechanisms that have been reported to outweigh soil heterogeneity. The combined effect of both soil patchiness and seed dispersal might create a forest floor that varies greatly in soil seed banks (Pickett and McDonnell 1987).

i. Tree Location

The spatial pattern of trees in forested ecosystem may reflect the initial variability in soil, competition from neighboring vegetation, and climate and light conditions during the stand establishment phase (Moeur 1993). Individual tree create zone of influence near the stem and under the canopy, where the physical and microclimatic conditions are different than the surrounding open areas. Individual tree or tree clusters can generate AG heterogeneity through modification of several stand level processes such as seedling recruitment and understory vegetation pattern (Beckage et al. 2000), litter chemistry (Facelli and Pickett 1991), and microsite conditions (Vetaas 1992). Location of tree stem can also influence nutrient availability through processes such as throughfall and canopy interception (Gallardo 2003).

ii. Canopy Cover

Among the stand level properties, canopy cover probably exerts the most influence on AG heterogeneity through its direct influence on light availability, microhabitat condition, nutrient interception, and organic matter input (Armesto et al. 1991). Regenerating vegetation in young stand recovering from disturbance (e.g. stand replacing fire) experiences somewhat uniform environmental condition (e.g. light and precipitation) due to having an open canopy structure. In pyrogenic boreal ecosystem such stand level uniformity may operate only during the first several years after fire and patchy structures in vegetation develop as stands grow older due to competition and density dependent mortality (Grandpré et al. 1993; Peterson and Peterson 1992; Rowe and Scotter 1973). Canopy of dominant vegetation in mature stands reduces light availability to understory vegetation, but canopy gap creates space for those species that were inhibited by the shading effect (Armesto and Pickett 1985). In this way growing vegetation maintain their social sphere and contribute to the overall ecosystem heterogeneity. Wilson (2000) described two main types of heterogeneity responsible for AG diversity that can be mediated through canopy effect, i) abiotic heterogeneity; originating from abiotic processes (all the environmental and chemical factors), and biogenic heterogeneity; caused by organisms as a result of resource consumption or non-consumptive effect on abiotic processes.

iii. Understory Vegetation

The understory vegetation in forested ecosystems is the second lowest layer from the top-down canopy stratification, which can directly influence AG heterogeneity through litter input (Maguire and Forman 1983), nutrient uptake (Lavoie and Mack 2012a), and modification of microbial assemblages (Saetre 1999) and decomposition processes (Beatty 1984). Mosses, algae and lichens are probably the lowest layer from which AG heterogeneity can be generated. The causal pathways that generate AG heterogeneity due to the variation in understory vegetation

may have similarity to that of canopy effect from dominant tree species. However, the spatial scale might vary. For example, a number of annual herbs and perennial shrubs vigorously regenerate immediately after fire, and depending on the fire severity, random (no spatial pattern) or patchy structure may develop in the understory vegetation (Grandpré et al. 1993). Such patterns are however transient and very likely to change within several years due to the development of overhead canopy layer of the dominant tree species. The heterogeneity of understory vegetation might follow several patterns throughout the stand development trajectory, which could be directly related to the pattern of canopy cover of dominant tree species.

iv. Coarse Woody Debris

Coarse woody debris (CWD) is one of the most visible components of spatial heterogeneity in old growth forest, as well as in post-fire stands. Stand replacing fire generally consumes most of the living biomass and turn them into standing dead and other partially or fully charred CWD. Depending on the environmental factors (temperature, moisture and wind activity) and decomposition rate, all the standing snags end up being on the ground in several years, where they become an active component of AG heterogeneity. CWD can contribute to AG heterogeneity by modifying several factors including microsite conditions (Forrester et al. 2012), nutrient availability (Laiho and Prescott 2004), microbial and meso-faunal habitat (Marra and Edmonds 1998), and germination and subsequent growth pattern of seedlings and understory vegetation (Harmon et al. 1986; Stokland 2001).

1.5.1.2 Causes of Belowground Heterogeneity

Belowground resources in terrestrial ecosystems are heterogeneously distributed (Ettema and Wardle 2002; Hutchings et al. 2003). Several factors can cause this heterogeneity; however they are different in plot scale vs landscape scale. At the landscape scale, heterogeneity could be imposed by geomorphological features such as glacial redistribution of parent materials (Turner 1989; Stark 1994; Moles and Moles 2002) and by disturbances such as fire and flooding. At the plot scale, heterogeneity can results from patchy distribution of plants, soil properties (Robertson and Gross 1994; Ettema and Wardle 2002; Wardle 2002), microorganisms and large animal (Parkin 1993; Burke et al. 1999; Ettema and Wardle 2002), and also from disturbances such as fire (Smithwick et al. 2012), or agriculture, mining and forestry practices (Cambardella et al. 1994; Mummey et al. 2007). Disturbance driven heterogeneity might arise from the alteration of key biogeochemical factors such as soil microbial community and nutrient dynamics (Smithwick et al. 2012), root biomass and rhizosphere activity (Hassett and Zak 2005; Shepperd 1993), organic matter quality (González-Pérez et al. 2004), and microsite conditions (Guo et al. 2002). Although spatial variation in BG properties has been studied quite extensively in recent decades, the scale to which heterogeneity occurs and the mechanistic relationship between BG processes and patterns in different ecosystems remain poorly understood. In the following sections, I will discuss some of the main drivers of BG heterogeneity in the context of currently available literature.

i. Parent Materials and Soil Types

Patchiness is the inherent nature of soil systems (Fitter et al. 2000). Soil is composed of all states of matter, including solid, liquid and gaseous phases. Solid phase of pedosphere is equally important for generating heterogeneity in soil systems. According to Fitter et al. (2000) material movement in the solid phase is a very slow process which limits the extent of local

variations, but can be important for the landscape scale heterogeneity. The geophysical template

of soils is also heterogeneous. The composition and pattern of bedrock or sedimentary geology

(especially important for the geologic heterogeneity in western Alberta) mainly determine the

heterogeneity in soil type. These geologic materials are called parent materials and may consists

of unweathered rock of geologic origin, loose gravel, sand, silt and clay, or organic materials.

The complex geology of tectonically active regions is often the principal driver of patchy

distribution in parent materials (Naiman et al. 2005). The geologic processes in these active

zones shape the landscape forms i.e. topography, terrain and elevation, which eventually

influence other environmental and biotic factors of soil formation.

A certain degree of variation is usually found in most parent materials as a result of

bedrock formation. The degree to which the heterogeneity in parent materials is reflected in soil

processes will depend on the rate of transformation (Stark 1994). Physical and chemical

processes of soil formation can occur in a broad range of time scale; from geological scale (e.g. 1

x 10^6 years for the full development of soil profile) to annual and seasonal scales similar to that

in plant community (Lavelle and Spain 2001). Spatial heterogeneity in geology or parent

materials is usually found at continental and regional scales (Lavelle and Spain 2001). However,

clay and organic matter distribution often shows clearly-defined patterns at the scales of their

formation.

ii. Organic Matter

Organic matter (OM) input from the growing vegetation is another key factor for BG

heterogeneity. Chemical composition of OM can have localized effect on the heterogeneity in

soil properties through their variable rate of decomposition and nutrient release. This effect is

predominant in a system where plants are spaced enough to exert influence on competitive resources such as moisture, light and nutrients (Wardle 2002). Works by Schlesinger et al. (1996) ("Island of fertility" hypothesis in grassland ecosystem) and Seastedt and Adams (2001) ("Tree island" hypothesis in alpine tundra ecosystem) clearly showed that patches of conspecific individuals can have direct effect on soil properties (biota and nutrient availability). Individual tree effect on the spatial distribution of organic matter quality in forested ecosystems is also well documented. Wardle and Lavelle (1997) showed that co-existence between two tree species can promote patches of forest floor with differing litter quality and decomposablility. In oligotrophic ecosystems, where resource transfer and acquisition rate is slow, co-existence of several species can generate patchy structure of resource availability (Wardle 2002).

Landuse history and input from previous vegetation can also be important for BG heterogeneity through their effect on OM quality and distribution (Flinn and Marks 2007; Lesschen et al. 2008). This is commonly the case in landuse conversion (e.g. agriculture to forestry and vice versa) or reconstruction of degraded ecosystem such as reclamation of mine disturbed lands, where soils can be very different from the target ecosystem.

iii. Root Activity

Spatial pattern of root development in soil and its effect on the heterogeneity in BG processes are poorly understood (Lavelle et al. 2005). Roots of individual plant maintain a minimum distance with other plants to optimize nutrient and moisture extraction. This distance increases with increasing soil depth (Fitter et al. 2000). Plant roots create heterogeneity by modifying soil structures and creating zones of nutrient depletion and accumulation of secondary metabolites (exudates). The zone of depletion and accumulation can range from nanometers to

meters depending on the type of nutrients, physicochemical properties of soil, and plant-organism (microbes, pathogen or large herbivores) interactions. Rhizosphere heterogeneity can also results from other processes such as the release of H+, enzymes, and labile C compounds, root sloughing and exudation (Fitter et al. 2000).

iv. Soil Microbial Community and Functions

The microbial community in soil is probably the most diverse biotic factor and can influence soil ecosystem ecology in many ways. Significant developments have been accomplished over the past few decades in terms of microbiology methods. However, our knowledge about soil microbial ecology is still a frontier. As emphasized by Ettema and Wardle (2002), empirical and modeling studies focused on the spatial ecosystem ecology tried to focus more on the AG components, and mostly covered abiotic factors such as moisture, nutrients, and soil mineralogical aspects. The whole microscopic world of soil is under-represented in spatial studies perhaps due to the limitation in sampling and quantification methods.

Soil organisms show predictable spatial structure in space and time (Bardgett et al. 2005). Belowground microbiota can exerts strong influences on the spatial patterns of processes such as organic matter decomposition (Saetre 1999; Saetre and Bååth 2000), nutrient release and acquisition (Bengtson et al. 2007), root symbiosis (Van der Heijden et al. 1998), as well as the pattern of vegetation (Wardle 2002). In forested ecosystems, soil microbial properties and functions are often structured at one to several meters, which might reflect the patch size individual tree or tree cluster (Saetre 1999; Ettema and Wardle 2002; Wardle et al. 2004).

Spatial patterns of soil microbes are closely associated with the quality of litter produced by the AG vegetation (Ettema and Wardle 2002). Association of different species can therefore

promote diverse group of microorganisms due to the difference in litter quality. Managed landscape like mono-species plantation forestry or single crop agriculture might not have compositional heterogeneity in soil microbial community. Forested ecosystem, however, nurture both compositional and functional heterogeneity through the different combination of ecological trophic system (Kuuluvainen 2002; Wardle 2002).

Spatial aggregation of soil organisms can also happen due to their intrinsic population biology e.g. reproduction, foraging behavior, and competition. The aggregation pattern of soil microbial structure could be different than that of underlying abiotic factors. Current prokaryotic biogeography and diversification theory proposes two main factors responsible for the variation of microbial communities at the landscape scale, i) environmental heterogeneity, and ii) disturbance, and current or historical landuse (Ramette and Tiedje 2007). Niche based mechanisms of microbial diversity and heterogeneity in soil matrix has long been the accepted explanations in microbial ecology as it is based on the fact that microbial communities respond very quickly to environmental heterogeneity (McArthur et al. 1988; Travisano and Rainey 2000). Disturbance and landuse history have been shown as reasons for spatial isolation between microbial population, and as significant contributor to the ecosystem heterogeneity (Borcard and Legendre 1994).

1.6 Soil Nutrient Heterogeneity at Different Scales

Spatial and temporal patterns of nutrient in soil system are complex. Although there are substantial number of studies examined the spatial pattern of soil nutrients in different ecosystems, the functional range of nutrient availability in soil relevant to microbial community

and plant root is yet to be confirmed (Stark and Hart 1997). Understanding the heterogeneity in soil nutrients will require precise identification of nutrient production and consumption rates (Stark 1994).The mobility of nutrient ions in soil is restricted by interactions with charged surfaces. Solubility and diffusion rates are the two important factors responsible for the heterogeneous nutrient patches in soil. Nitrate, for example, is very soluble in water, but the barrier from the competition between plants and microbes, and the limitation from the physical path distance to reach the receptor (plant root or microbes) might create heterogeneous patches of this nutrient. Phosphate, on the other hand, produces insoluble complexes with almost all the cations, and as a consequence, its diffusion rate is very slow. The spatial scale of variability in N and P, therefore can be different unless both nutrients are generated from the common source process (organic matter decomposition) and did not get enough time to be affected by other environmental factors (Tinker and Nye 2000). Such differences in mobility of nutrient ions largely contribute to their heterogeneity.

Heterogeneity in nutrients mediated by soil organisms can be generated from several related factors such as the enzymes and substrates present in the system, availability of reactants, and environmental controls on enzymatic activity (Allison 2005).Soil colloids also have great impact on the variability of nutrient patches as they can simultaneously work as the source and sink of nutrients. Variations in colloids happen mainly due to the differences in parent materials mineralogy, environmental factors, and organic compounds (Stark 1994; Chadwick et al. 1999).

Variations in flow rate from nearby microsites can also result heterogeneity in soil nutrients. Out of the three main mechanisms of nutrient transport process in soils, diffusion always tends to create homogeneity, whereas mass flow and transport by organisms can either increase homogeneity or heterogeneity. Diffusion rate again depends very much on the

volumetric water content of soil. Stark (1994) presented a hypothetical relationship between nutrient heterogeneity and soil moisture content, where he hypothesized that heterogeneity in nutrients will be low at near saturation moisture content of soil due to higher diffusion and less biological activity, and heterogeneity will increase as moisture content declines at or below field capacity as a result of non-uniform distribution of moisture and diffusional limitation.

Spatial variability in nutrient availability to a range beyond the foraging area of plant root will not have direct impact on the AG heterogeneity, although it might affect the microbial community structure. The temporal scale of nutrient release from soil mineral complexes due to weathering process is far longer than the lifetime of plants and has limited contribution to vegetation heterogeneity (Stark 1994).

1.7 Aboveground-Belowground Feedback and Heterogeneity

Although individual component of ecosystem has their unique role in creating heterogeneity and patchy structure, many of these relationships are not independent (Bardgett and Wardle 2010). It is now well recognized that the interaction between plant and soil works in several feedback loops where both components of the framework can affect or be affected by the other half (Wardle 2002). The outcomes of these loops are again dependent on the space and time dimensions of ecosystems. Depending on the strength and mode of interactions, the consequences can be manifested through either AG or BG processes, or it could also affect a third process, where clear a manifestation might not be observed in either AG or BG processes due to the dilution of spatial and temporal scales (Wiens 1989; Kolasa and Rollo 1991).

Ecosystem functions and heterogeneity thus can be thought in a five dimensional view such as aboveground, belowground, horizontal and vertical space, and temporal.

Wardle et al. (2004) mentioned positive and negative feedback through which AG heterogeneity can be affected. Negative response can happen by pathogenic or parasitic effect in plant rhizosphere through removal of C and nutrients, whereas symbiotic association between beneficial microorganisms can generate positive feedback, and all of these can change the spatial distribution of vegetation. Likewise, positive association can also be species specific; maximum flux of nutrients or mutual benefit may occur in plants in case of specific association with certain microbial species.

Ecosystem development after disturbance is rather a dynamic process (Fattorini and Halle 2004). Vegetation development in post-disturbed ecosystem usually follows a specific trend, where AG stand level processes affects BG processes and vice-versa, as described in the above sections. So, it could be assumed that the spatial variability in key plant and soil processes, and their interactions at different stand developmental stages might show predictable patterns, which can be quantified and the mechanistic relationships can be identified using appropriate spatial analyses.

The overall objective of the current research was to characterize spatial variability in nutrient availability and associated biogeochemical properties, and to identify the key mechanistic relationships that drive nutrient availability in disturbed upland boreal ecosystems. Both naturally and anthropogenically disturbed boreal forests were selected to achieve these goals. A chronosequence of fire disturbed aspen forest stands (1, 9 and 72 years old) was selected as natural benchmark and an oil sands mine reclaimed stand (14 years old) was used as

the anthropogenically disturbed ecosystems. A number of AG and BG variables were then measured using a spatially explicit sampling protocol. Spatial behaviour and mechanistic relationships were then analyzed using several variability indices such as semi-variogram, cross-variograms, spatial regression models, and non-parametric spatial measures such as ordination and index of spatial concordance. Aboveground attributes included stand properties such as canopy cover, forest floor depth, tree location, understory vegetation cover, coarse woody debris cover, percent bare ground, and seedling density. Key BG properties included nutrient availability, soil microbial biomass, dissolved organic C and N, extracellular enzyme activity, basal respiration, total C and N, and soil pH and EC. The wide array AG and BG variables was selected due to the complex nature of nutrient biogeochemistry in the disturbed boreal ecosystems, and to ensure the identification of true mechanistic relationships, which can be obscured by unknown missing variables. A priori ecological hypotheses were grounded for each study and findings were tested against those hypotheses. Chapter 2 and 3 of the dissertation dealt with the spatial variability in nutrient availability and soil respiration in the natural fire chronosequence. Chapter 3 described the seasonal variation in the spatial pattern of soil respiration and the key factors governed soil respiration along the fire chronosequence. These two chapters developed the natural benchmark of spatial biogeochemical properties in fire disturbed upland boreal ecosystems and guided the research component of chapter 4, which characterized the spatial pattern of some of the key biogeochemical properties that were also measured in the natural fire chronosequence and related this to the spatial variability of nutrient availability in the reclaimed system.

Finally, the synthesis chapter summarizes outcomes from all the 3 studies and describes how the overall thesis objectives were met. Research limitations and future research possibilities

are also discussed. The overall synthesis is then used to propose a new ecosystem recovery evaluation guideline for the disturbed oil sands mining areas.

The current research will contribute to the growing body of literature on the disturbance effect on the spatial pattern in ecosystems properties and its temporal dynamics. With special focus on pyrogenic boreal ecosystem, this research showed evidences on how spatial pattern of biogeochemical properties change over time after stand replacing fire in a conspecific set-up. A new hypothesis on the successional development of AG-BG control on nutrient availability is also proposed. The hypotheses presented and tested in the current research can be tested in different ecosite conditions in boreal ecosystem to get more insight on the nature of recovery in mixedwood stands or in coniferous stands.

Chapter 2. Spatial Variability of Nutrient Availability in Pyrogenic Boreal Aspen Ecosystems: Aboveground and Belowground Controls

2.1 Introduction

Wildfire is a major natural disturbance in upland boreal forests that causes abrupt changes in the aboveground (AG) and belowground (BG) components of the ecosystem (Kasischke and Turetsky 2006). Although boreal ecosystem is fire adapted, crucial biogeochemical and community level processes such as nutrient cycling, vegetation dynamics, and ecosystem productivity depend on the frequency and intensity of fire (Neary et al. 1999; Ryan 2002). Besides influencing key biogeochemical processes, fire alters the spatial variability and coupling of these processes (MacKenzie et al. 2008), which eventually translates into the multi-scalar patterns that develop over time and create a mosaic on the landscape. The role of wildfire in creating ecosystem heterogeneity depends very much on the severity and extent of the disturbance (McKenzie and Kennedy 2011). Nutrient availability and vegetation structure are perhaps the ecosystem attributes mostly affected by fire disturbance (Harden et al. 2004). There is ample evidence for how fire affects nutrient stocks and biomass in different ecosystems (DeBano and Conrad 1978; Grandpré et al. 1993; Johnstone and Chapin III 2006; Murphy et al. 2006; Neary et al. 1999; Neff et al. 2005), but less is known about their spatial distribution and temporal changes.

In recent years, significant attention has been given to understand post-disturbance ecosystem recovery by integrating different AG and BG components (Kardol and Wardle 2010). Such spatial information is very important for managing and restoring disturbed forest

ecosystems, not only of natural origin such as fire, but also after anthropogenic disturbance such as mining for resource extraction, e.g. oil sands mining in northern Alberta. However, our understanding about the mechanisms that govern key ecosystem processes in post-disturbed environments such as nutrient cycling and soil microbial activities, and the scales at which these processes take place remained at rudimentary level. There are only few evidences that show development of spatio-temporal pattern in post-fire ecosystem processes and studies in boreal ecosystems are even scarce (Lavoie and Mack 2012; Rodríguez et al. 2009a; Smithwick et al. 2012; Turner et al. 2011). In this study, we asked four questions. (1) How variable is nutrient availability in stands recovering from fire? (2) Does the spatial variability of nutrient availability change with time since fire? (3) What degree of spatial coupling does nutrient availability have in different post-fire stands? and (4) What aboveground and belowground factors control the spatial variability in nutrient availability in these stands?

High global variation or large scale spatial structure in nutrient availability was expected in the post fire stand (Question 1 and 2). Thus, the semi-variograms were expected to follow either a linear or nugget model without any detectable spatial range and we hypothesized that spatial heterogeneity in nutrient availability would increase with time since fire (Figure 2-1a). Several studies have indicated that the magnitude of nutrient heterogeneity decreases after stand replacing fire due to the homogenization of resources (Blair 2005; Grier 1975) and the redistribution of ash (Grogan et al. 2000). However, development of fine scale patchy structure in soil nutrients and microbial properties has been observed one to ten years after disturbance in boreal ecosystems recovering from wildfire (Lavoie and Mack 2012; Smithwick et al. 2005).

Spatial heterogeneity in stand structure and resources may increase with stand age due to competition, thinning and gap formation (Cumming et al. 2000). Aspen stands reach canopy

closure quickly after fire, usually within 7 to 11 years, and significant changes take place in both aboveground and belowground attributes related to nutrient availability at canopy closure (Petersen and Petersen 1992; Valverde and Silvertown 1997). Therefore, we expected to see spatially structured behavior in nutrient availability at this stage. Spatial patterns that originate from such stand level processes are evident at tree to tree scale, with very fine spatial structure (1 – 4.5 m) (Fajardo and McIntire 2007; Liski 1995). We speculated that the nutrients mostly mediated through microbial processes such as N, P and S should have fine to intermediate scale spatial range (~4 and 23 m) due to individual tree or tree cluster influence at this stage. A large scale ($\geq$ 23 m) spatial range was expected for cation availability (Ca, Mg and K) at canopy closure due to their potential leachability after severe fire, and relatively longer timeframe required to develop patchiness due to aboveground inputs, mostly through litter deposition (Chorover et al. 1994; Paré and Bergeron 1996). In mature stands, we expected to see a fine scale (< 4 m) spatial pattern and distinct patchiness in nutrient availability due to an established microbes-root-canopy linkage.

For question 3, I hypothesized that spatial coupling between nutrient availability, AG and BG properties would increase with stand age due to an increased contribution from both microbial and tree level processes. Degeneration between humus nutrient build-up and vegetation structure after fire has been reported in several studies (e.g. Engelmark et al. 1998; Hart et al. 2005). In boreal ecosystem, Lavoie and Mack (2012) found increasing trend of correlation between organic layer depth and soil properties with time since last fire; however, their study did not account for spatial relationships in this correlation. Spatial coupling between AG and BG processes must increase over time as stands recover from fire disturbances. One of the Odum's classic hypotheses about nutrient retention was that biogeochemical cycling of major

nutrients would have a tighter coupling in mature system than the developing ones (Odum 1969).

Vitousek and Reiners (1975) and Leuschner and Rode (1999) showed partial evidence in support of this hypothesis in different disturbed forested ecosystems. Although none of these studies tested the hypothesis from spatial point of view, the idea of spatial connectedness is strongly embedded and reflected in their findings. In subalpine coniferous forest, Turner et al. (2011) did not find spatial coupling between AG cover and N availability upto 4 years after wildfire and suggested a difference in scale between AG and BG processes. Development of multiscalar spatial coupling between soil N mineralization and AG-BG properties has been reported in boreal ecosystem one year after stand replacing fire (Smithwick et al. 2005). Other evidence suggests that an increase in spatial coupling between vegetation and soil resources will occur with stand age as nutrient demand will surpass the supply as a result of tree competition (Kaye and Hart 1997).

Finally, I expected to see a strong BG control on nutrient availability in the post fire stand followed by stronger AG controls in the canopy closure stand, and a joint AG-BG control in the mature stand (Question 4) (Figure 2-1b). Immediate post-fire patterns are likely to be associated with fire induced mortality of AG features which may take several years to re-establish (Rowe 1973; Turner et al. 2011). In boreal ecosystems, understory vegetation and suckering species usually take over the AG space, but I believe their control on nutrient dynamics will not be evident for a decade.

2.2 Methods

2.2.1 Study sites

The study was conducted in the Athabasca oil sand region (AOSR) at Fort McMurray, Alberta, Canada (56° 43′ N 111° 21′ W). The mean annual temperature in this region is 0.9°C and mean growing season (May – September) temperature is 13.3°C. Mean annual precipitation is 418.6 mm, of which 283.4 mm fall as rainfall during the growing season (Environment Canada 2014). Soils in the study area are sandy loamy to silty loamy, well to moderately-well drained, and developed from till and glaciofluvial sediments (Crown and Twardy, 1970). Three boreal aspen stands along a fire chronosequence were used in this study; a one year old post fire (PF) stand, a 9 year old stand at canopy closure phase (CC), and a mature 72 year old stand (MA). Trembling aspen (*Populus tremulides* Michx.) was the most dominant tree species represented more than 95% of the basal area in all the three sites and only a few sporadic white spruce (*Picea glauca* (Moench) Voss.) were found in the CC and MA stands. The maximum distance between the sites was 34 km. According to the ecosite classification of northern Alberta, all the three sites fall under the d1 ecosite phase (low-bush cranberry Aw) (Beckingham and Archibald 1996). Geographic location, fire history and dominant shrub, forb, grass and moss species in the study sites are given in the Appendix II.

2.2.2 Sampling protocol

Sampling and field measurements were carried out in a 50 m × 20 m plot in all the three sites. A cyclic spatial sampling protocol (Clayton & Hudelson 1995) was used to capture both the scale and directionality in the measured variables (Figure 2-2). In total 81 sampling points were established in 9 transects within a 1000 m^2 plot which ensured a minimum detectable spatial lag of 0.5 m. Spacing between the sampling points along the transect were 0.5, 3, 6 and 9 m, and inter-transect spacing were 2 m and 4 m. The sampling orientation was reversed in the

middle two transects to capture the anisotropy. All field measurements and sampling were done in May - August 2012.

2.2.3 Aboveground properties

Aboveground properties were measured around each spatial point. Measured aboveground properties included tree location (XY coordinates), tree diameter (at breast height; DBH), number of aspen seedlings, canopy cover (%), understory vegetation cover (%; UV), bare ground (%; BGn), coarse woody debris (volume and % cover; CWD), and forest floor depth (cm; FD). Tree locations were only measured in the MA stand using a Nikon total station (Nikon DTM 352). Forest floor depth was measured at each spatial point by taking average of three measurements. Tree canopy cover (%) was measured using a convex densitometer and percent cover of understory vegetation and coarse woody debris cover were measured using a 0.25 m^2 sampling frame. Number of aspen seedling was counted near each sampling point using a 1 m^2 sampling frame. Basal area (BA) of nearest tree was calculated from the tree DBH. Coarse root biomass (CRB) and fine root biomass (FRB) were calculated from allometric equation using tree diameter (Appendix IV).

2.2.4 Nutrient availability

Nutrient availability was measured using PRS^{TM} probes (plant root simulator probes; Western Ag Innovations Inc., Saskatoon, SK, Canada). These probes (cations and anions) have ion-exchange resin membrane which trap nutrient ions and nutrient supply rates are estimated based on the ion sink adsorbed per surface area of membrane over the burial period (Qian and

Schoenau 2002). Two pairs of cation and anion probes were vertically installed at the organic

and mineral soil interface at each sampling point, and left for 8 weeks to measure available

nutrients under field condition. Upon retrieval, probes were extracted with 0.5 M HCl and elutes

were analyzed for nutrients. Ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4^{2-}) were

analyzed colourimetrically using a segmented flow Autoanalyzer III (Brand and Lubbe, Inc.,

Buffalo, NY.). Potassium (K^+), sulfate (SO_4^{2-}), calcium (Ca^{2+}) and magnesium (Mg^{2+}) were

quantified by inductively-coupled plasma (ICP) spectrophotometry (PerkinElmer Optima 3000-

DV, PerkinElmer Inc., Shelton, CT). Nutrient availability was expressed as μg ion. 10 cm^{-2} 8

weeks^{-1}.

2.2.5 Microbial properties

Soil samples (organic layer + 5 cm mineral soil) were collected from each spatial point

using a bulk density core. The core was surface sterilized and washed using ethanol (70%) in

between samples to minimize any possible contamination and denaturation of enzyme products.

Immediately after collection, soils were kept in a cooler with ice bags and brought back to the

laboratory. Samples were then homogenized properly after carefully removing the coarse

fragments (roots, twigs and stones). A sub-set of the samples were then stored at -20°C for

extracellular enzyme activity and rest of the samples were stored at 4°C until further processing.

Soil microbial biomass C (MBC), N (MBN), and basal respiration (BR) were measured

after an incubation experiment conducted using the soils stored at 4°C. Approximately 75 to 100

g soil was incubated for 10 days at 25°C in sealed Mason jar with alkali trap inside (0.5 M

NaOH). Soil basal respiration was calculated from the alkali trap after titrating with HCl (0.5 M).

Microbial biomass C and N were measured on the incubated samples using the fumigation

extraction method (Vance et al. 1987). Approximately 20 to 25 g soil was extracted in 0.5 M

K_2SO_4 with a ratio of 1:2. Dissolved organic C (DOC) and N (DON) were measured on the

unfumigated fractions of the soil extraction using Shimadzu TOC-V/TN analyzer

(Shimadzu Corp., Kyoto, Japan).

Extra-cellular enzyme activity was measured on soils stored at $-20°C$. Four enzymes

were analyzed to quantify the potential extracellular enzyme activity responsible for C, N, P and

S mineralization: (i) β-glucosidase (Bglu) (EC 3.2.1.21) responsible for breaking labile cellulose

and other carbohydrate polymer chains, (ii) N-acetyle-β-D-glucosaminidase (NAGase) (EC

3.2.1.30), enzyme mainly catalyzes the hydrolysis of chitin, and convert it to amino sugars which

are major sources of N mineralization in soils (Ekenler and Tabatabai 2004), (iii) Phosphatase

(Phos) (E.C. 3.1.3.2), phosphomonoesterases responsible for catalyzing the hydrolysis of esters

and anhydrides of phosphoric acid (Tabatabai 1982), and (iv) Arylsulfatase (Sulf) (EC 3.1.6.1),

enzyme that catalyzes hydrolysis of arylsulfate by breaking O-S bond and regulate

mineralization of ester sulfate in soils (Deng and Tabatabai 1997). Enzyme activities were

measured using 4-methylumbelliferone (MUB; 10 mM) as a fluorimetric substrate. Details on

the enzyme assay can be found in Sinsabaugh et al. (2008) and Das Gupta et al. (2015). Briefly,

200 µl soil suspension (1 g soil homogenized in 100 ml 0.1M, pH 5 sodium acetate) and 50 µl

(200 µM) substrates were pipetted into 96 well microplates at 6 samples per plate. Microplates

were then incubated at 20° C in dark for 3 hours for β-glucosidase, N-acetyle-β-D-

glucosaminidase and Arylsulfatase, and for 2 hours for phosphatase enzyme. Fluorescence was

measured at 365 nm excitation and 460 nm emission using a microplate spectrophotometer

(Synergy HT, BioTek, Winooski, VT). Assay and control wells were replicated 8 times. Activity

rates (µmol of converted substrate g^{-1} soil $hour^{-1}$) were calculated on an oven dry mass (105°C)

basis. Total C and N in soils were measured on ground samples using a Costech 4010 Elemental Analyzer System (Costech Analytical Technologies Inc., Valencia, CA, USA). Soil pH and EC were measured in 1:2 solution of deionized water.

2.2.6 Statistical analyses

Coefficient of variation (CV) was used as an index of global variation in the measured variables. The CV is a simple metric of variability which can be interpreted easily and is comparable between different ecological properties (Fraterrigo and Rusak 2008). Semi-variogram analysis was used to measure local variation i.e. spatial dependence of nutrient availability and other properties. Data were log transformed prior to analyzing semi-variogram and variogram modeling. Five variogram models viz. Linear, Gaussian, Exponential, Spherical and Nugget were tested. A combination of highest coefficient of determination (R^2) and the lowest residual sum of square error was used to select the final model. Spatial dependence was calculated using the nugget coefficient, n_c which is a ratio of total variance ($c_0 + c_1$) and nugget variance (c_0) (Legendre and Legendre 2012).

Cross-variogram analysis was conducted between nutrients, soil and stand properties to check for any scale dependent relationship. A positive cross-variance indicates spatial association, whereas a negative variance means dissociation (Yates and Warrick 2002). The spatial connection between AG and BG properties, and the degree at which all these three components (space, AG, and BG properties) are coupled together is termed here as spatial congruence. Spatial congruence among variables was measured by Kendall's coefficient of concordance (W) (Carlton and Bazzaz 1998; Legendre 2005). Variables were standardized and converted to a common scale between 0 and 100 before performing the test. Spatial congruence

(W) is measured between 0 and 1, where 0 means completely incongruent and 1 means perfect congruence. Spearman rank correlations between variables were also examined to know the strength and mode of bivariate relationships. Kendall's W and Spearman rank correlations were done in in R (R Core Team, 2013, version 3.0.1). The 'vegan' package was used for calculating the Kendall's W. Variograms were created using GS+ geostatistic software (V9.0, Gammadesign software). Spatial autoregressive (SAR) models were developed between nutrients and environmental variables, and contribution of space was estimated using two SAR models viz. spatial error model and spatial lag model (Besag 1974; Anselin 1988). SAR analysis was done in R (R Core Team, 2013, version 3.0.1) and Geoda, an R based open source geospatial software (Anselin 2004). Details on the semi-variogram modeling, SAR calculation, and interpretations are given in the Appendix I.

Nutrient profiles of different sites were compared in ordination space using the Non-metric multidimensional scaling (NMDS) in the "ecodist" package (R Core Team, 2013, version 3.0.1). Most influential variables contributing to nutrient availability were determined using Random Forest technique (Breiman 2001). Random Forest is a non-parametric classification and regression technique which generates many trees using boot strap method. About a third of the samples in the dataset are used for model validation. Principal Component (PC) axis explained the highest variation in macronutrients was used as dependent variable in the Random Forest analysis. All the AG and BG properties were included as independent variable. Random Forest technique has been previously applied successfully for correlated data (Genuer et al. 2010). Random forest and PCA analysis were done using the randomForest and stats packages in R, (R Core Team, 2013, version 3.0.1).

2.3 Results

2.3.1 Nutrient availability

Significant differences were found in nutrient profile among the three fire affected stands. Total inorganic nitrogen (NH_4^+ and NO_3^-), P and K availability were the highest and Mg availability was the lowest in the PF stand. The CC stand had the lowest S availability followed by the PF and MA stand. Nitrate was the main form of N in all the three stands and the availability was highest in the PF stand (4.09 ± 2.45 μg 10 cm^{-2} 8 weeks^{-1}) followed by the CC (2.18 ± 1.26 μg 10 cm^{-2} 8 weeks^{-1}) and the MA (2.37 ± 1.30 μg 10 cm^{-2} 8 weeks^{-1}) stand. Likewise, P availability in the PF stand was 31.7 (± 26) followed by 5.67 (± 3.67) in the CC and 6.84 (± 4.84) μg 10 cm^{-2} in the MA stand (Table 2-1).

The nutrient profile, soil microbial properties, and stand characteristics in different stands are shown in the NMDS ordination graphs (Figure 2-3). The CC and MA stands had similar distribution in the ordination space for all the three ecosystem matrices. The PF stand, on the other hand, had quite distinct patterns and occupied a space further from the CC and MA stands.

2.3.2 Spatial variability

Higher global variation (CV) in N, P, Ca and Mg availability was found in the PF stand than the other stands, which gradually decreased over time with the lowest in the MA stand. For example, CV of available TIN was 133.17, 63.64 and 37.37% in the PF, CC and MA stand, respectively. On the other hand, lower global variation was also observed in the PF stand than the older stands for certain other nutrients such as S (62.18%) and K (46.68%) (Table 2-1).

Most of the nutrients in the PF stand either had large scale or no spatial pattern, except S and Ca. Nutrients in the CC and MA stands, however showed spatially structured patterns. Sulfur and Ca availability had strong spatial dependency in the PF stand (≤ 6.5 m), which showed large scale dependency (≥ 21 m) in the CC and MA stands. Nitrogen and P availability were both spatially structured at < 10 m in the CC and MA stands but had either a pure nugget model or large scale structure in the PF stand (Table 2-1 and Figure 2-4).

2.3.3 Spatial association

Spatial congruence (as measured by Kendall's W) between nutrient availability, AG and BG properties was the lowest in the PF stand which gradually increased with stand age (Figure 2-6). Spatial congruence was 0.28, 0.33, and 0.40 in the PF, CC and MA stand, respectively. Spatial congruence among the available nutrients, however, was the highest in the PF stand followed by the CC and MA stands.

Number of significant correlations between nutrients, AG and BG properties is presented in Appendix III (Table A3-2). Out of 126 possible correlations (6 nutrients x 21 variables), the PF stand had only 18 significant cases (14%), the CC stand had 20 significant cases (16%), and the MA stand had 28 significant cases (22%). Similar trend was also found when only belowground resources such as DOC, DON, MBC, MBN, C, N, and FD (proxy of organic matter) were considered. Out of such 42 possible correlations (6 nutrients x 7 resources), PF stand had only 6 significant cases (14%), which was 8 (19%) and 11 (27%) in the CC and MA stands, respectively. Number of significant correlations between nutrients was, however, the highest in the PF stand (66%; 10 out of 15 correlations) than the CC (27%; 4 out of 15) and MA (40%; 6 out of 15) stands (Table 2-2). Correlations between nutrients in the PF stand were all

positive, whereas the relationships changed in most cases in the CC and MA stands. For example, P showed a positive relationship with S and Mg in the PF stand, but the relationship was negative in the CC and MA stands.

Spatial associations between nutrients, AG, and BG properties were measured using cross-variance analysis (Figure 2-5). Nitrogen, P, and S in the PF stand had spatial association with enzyme activities at ≤ 10 m scale, but no aboveground association was detected for these nutrients (Figure 2-5; a, f and i). The CC and MA stands, on the other hand, showed spatial association of these nutrients with both enzymes, substrates (DOC), and AG variables such as understory vegetation cover and tree distance, although nutrient-enzyme association was only detected in the CC stand (Figure 2-5; b and j). The spatial control from UV and FD on the availability Mg and K was also found only in these stands, except Mg had a fine scale (2.4 m) negative association with UV in the PF stand (Figure 2-5; l, m and n).

2.3.4 Aboveground-belowground control on nutrient availability

Spatial regression models (Error and Lag) were used to account for the AG and BG contribution to nutrient availability in different stands. A clear influence of microbial processes (especially enzyme activity) was found in the PF stand. The only nutrient showed control from AG variable in this stand was TIN through FD and bare ground (BGn). Phosphorus and Ca appeared to be influencing the availability of most of the macronutrients in the PF stand. On the other hand, both AG and BG properties exerted significant influence on the nutrient availability in the CC and MA stands. Different sets of AG variables appeared to have significant control on nutrients in these two stands. For example, FD and UV were significant drivers for most nutrients in the CC stand, whereas Tdist. and BA were also significant in the MA stand.

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Microbial variables that had significant control in these stands were DOC, MBCN, BR and enzyme activities. Significant space effect in the nutrient availability was detected only for Ca in the PF stand, K and Ca in the CC stand, and for all other nutrients except Ca and K in the MA stand (Table 2-3).

Finally, the most influential AG and BG variables controlling the overall nutrient availability in the three aspen stands were analyzed using RandomForest, a non-parametric recursive partitioning technique (Figure 2-7a). Belowground biotic variables such as NAG, Sulf, MBN, TC, and DOC appeared as the most influential variables in the PF stand, whereas space, FD, and canopy cover were the topmost influential variables in the CC stand. On the other hand, a combination of BG properties (BR and TC) and AG variables (FD and BA) were found as the most influential controlling factors in the MA stand.

To get more insight on the controlling factors of the microbially mediated nutrients (N, P, and S), randomForest permutations were performed using the principal components of these nutrients as dependent variables in the models (Figure 2-7b). Unlike the overall nutrient model, only BG properties (MBN, Sulf, and TC) were the most influential in the PF stand. Substrate availability seems mostly influencing the microbially mediated nutrients in the CC stand as DOC, TC, DON, and FD were the few topmost influential variables in the model. Substrate quality (C:N) and chemical environment (pH) appeared as the most influential drivers in the MA stand after CWD, BGn and NAG.

2.4 Discussion

2.4.1 Nutrient availability and spatial variability

The current study presents evidence of changes in nutrient availability and their spatial variability in pyrogenic boreal aspen ecosystems. Although post-fire ecosystem properties are generally assumed to be heterogeneous (Blair 2005; Boerner et al. 2000; Rodríguez et al. 2009b), there are only a few studies that have actually looked at the spatial relationships and their dynamics from an AG and BG perspective, and a lot of these studies were done in coniferous stands with a few in boreal ecosystems. I hypothesized that post-fire nutrient availability would be high, with a high global variation (CV) and less spatial predictability. This was true in the PF stand and heterogeneity increased with development through CC and into MA stands. The findings are also in line with our expectation to observe a nugget or linear semi-variogram models in the PF stand and more spherical models in the MA stand due to patchiness in nutrient availability.

Fire effects on soil nutrients have been studied extensively in different ecosystems. A significant number of studies have reported an increase in mineral nutrients in post-fire environment (Chandler et al. 1983; Christensen 1987; DeBano 1991). Although fire causes an overall immediate loss in nutrient stocks in soil, the thermal and chemical changes in OM creates more labile and shorter chain structures that can be easily mineralized by microbes, and this might result in high nutrient availability in post-fire environment (Certini 2005; Harden et al. 2002). In a comprehensive review, Certini (2005) reported that fire usually increases the long term availability in nutrients, especially N and P, whereas the increase in Ca, Mg and K availability is relatively ephemeral. Effect of recent burn on major elements and plant available nutrients in boreal aspen stand is scarce (Harden et al. 2002). In boreal forest ecosystems, Neff et al. (2005) did not find any significant fire effect on P, Ca, Mg and K stocks which they attributed to the post-fire erosional loss and chemical immobilization due to the increased availability of Al

and Fe. In an experimental burn in boreal Alaska, Harden et al. (2004) found higher N, P, Ca, Mg and K in the burned soil which corroborates with our findings except for Mg.

The rate at which these nutrients recover to a pre-fire level depends on the ecosystem type, fire severity, and vegetation at the time of fire (Harden et al. 2002). Similar nutrient profile in the CC and MA stands in the current study might suggest that ecosystem recovery from wildfire disturbance can happen at a faster pace, i.e. within 10 years of disturbance. The stand and soil microbial properties from these two sites also showed closer distribution in the ordination biplot, which further support this assumption. A variable recovery timeframe in pre-fire nutrient availability is reported in the literature with a maximum of 35 years after fire (Knicker 2007; Neary et al. 1999). Belowground biomass, on the other hand, has been shown to recover within 12 years after fire (Fritze et al. 1993b). Adams and Boyle (1980) reported an ephemeral increase in P, Ca, K and Mg in a mixed aspen stand one month after fire which decreased to pre-fire level within 5 months. The initial soil heterogeneity in the post-fire environment is assumed to be created by spatial variability in fire intensity and the understory vegetation that survived from fire (Boerner et al. 2000; Grandpré et al. 1993). Ephemeral post-fire heterogeneity in major plant available nutrients may become homogenized quickly due to uniform abiotic condition and vigorous regeneration that stands experience, which is especially true for aspen since root suckering is the main form of regeneration (Petersen and Petersen 1992).

The findings from this study are contradictory with Smithwick et al. (2005), who found that predictable spatial structure in post-fire N mineralization (8.3 m) and C pool (extractable organic C and %C) (2.5 m and 16 m, respectively) in a boreal black spruce stand. The multiple scale dependency of C and N availability in their study was attributed to topographical and

microclimatic variation. In a boreal black spruce-trembling aspen fire chronosequence, Lavoie and Mack (2012) did not find any spatial structure in N mineralization and C pools (TC, C:N and BR) in the post-fire stand, which gradually appeared in the older stands. Although their study tried to link the BG spatial pattern to the stand characteristics (organic layer thickness and vegetation cover), the evidence for this spatial mechanism was not clear.

In a dry tropical forest, Hirobe et al. (2003) found the similar fire effect on N mineralization as in our study. The spatial range decreased within the fire chronosequence from ≥ 9 m to 3.2 m with time since last fire. They also found strong spatial dependence for soil properties in the stand which had the longest (35 years) fire exclusion history. Adams and Boyle (1980) in an oak-aspen forest, found that irrespective of fire intensity and variation due to coarse woody debris on site, the fire induced nutrient availability was fairly uniform and did not show any significant differences among treatments. However, they found significant differences in cation concentrations (Mg and K) in sub-soil layers shortly after the fire burn, and attributed this variation to the accelerated mineralization of combusted organic matter and reduced plant uptake.

Spatial information on the availability of macronutrients other than N is limited in pyrogenic boreal ecosystems. Variability in the methods used for measuring nutrient availability in different studies is another constraint that made such comparisons difficult. We did not find any detectable spatial pattern in K and Mg, but a very fine scale pattern in Ca availability in the post-fire stand. Large scale patterns were detected for these nutrients in the CC and MA stands. The missing spatial pattern in base cations in the post-fire environment might be related to leaching loss and absence of canopy input to the forest floor layer. Tree canopy and forest floor play significant role in base cation cycling through microclimatic modification, litter fall input,

and throughfall (Prescott 2002). The observed spatial pattern in base cations in the CC and MA stands can similarly be attributed to the development of canopy structure and forest floor. However, spatial variation in cations can also be originated from the geological variability (i.e. variability in parent materials) and the weathering rate (Gallardo 2003). Bengtson et al. (2007) reported a large scale patterns in cation availability in a mature coniferous forest in coastal British Columbia, which they think were generated due to abiotic factors such as topography and might not be related to the spatial variability in the organic and mineral soil horizons. However, the studied aspen ecosystems reported here, are largely fire dependent and might have a long term fire signature on the spatial pattern of base cations.

2.4.2 Spatial congruence

Disturbance (e.g. fire) dramatically alters the biogeochemical and other abiotic fluxes, and can also significantly change the spatial connections between the AG and BG factors (Carlton and Bazzaz 1998). I hypothesized a weak spatial congruence between AG and BG properties in the PF stand, which was expected to increase with stand recovery from fire. Spatial congruence, as measured by Kendall's W, in different stands supported the hypothesis. However, post-fire nutrient availability showed significant correlation which was not observed in the other two stands (Table 2-2). The strong positive correlations between macronutrients in the PF stand indicate a clear effect of fire on the availability of these nutrients, which could be through ash convection or downward movement of nutrients (DeBano 1991). The missing relationship between N and other nutrients further indicates the high demand for this nutrient in post-fire environment (Table 2-2). The consistent mode of nutrient interaction in the CC and MA stands points out that the observed nutrient relationship in the PF stand is ephemeral and might not have

originated from spatial regulatory processes. Several other studies reported a positive correlation among nutrients after fire. For example, Chorover et al. (1994) found a strong correlation between anions and cations in a mixed conifer forest in California four months after fire. They attributed this to the leaching of nutrient ions through forest floor as a result of increased water movement. Murphy et al. (2006) also reported similar findings one year after an experimental wildfire in a mixed coniferous forest and identified leaching as the principal mechanism. Post-fire plant functional groups can sometime be more determinative for spatial structuring of belowground biotic community and the related processes such as nutrient availability (Hart et al. 2005). Wildfires have strong effect on the plant functional traits which can change the spatial connections between BG processes by killing most of the dominant tree species and creating areas with homogenous microclimatic conditions (Wardle 2002). As the current study shows, the broken spatial link between AG and BG properties in fire disturbed boreal forests can recover quickly through vigorous regeneration and development of forest floor.

Since the aboveground structure in the PF stand is yet to develop, a strong correlation in nutrient availability can be interpreted as indirect fire-induced effect and not of spatial origin. The lack of spatial autocorrelations in some of these nutrients in the PF stand and gradual increase of spatial congruence (Kendall's W) between AG and BG properties in the CC and MA stands also support this (Figure 2-6). Lavoie and Mack (2012) corroborates with the higher number of significant correlations among resources in the mature stands in our study. In their study, the number of significant correlations between AG and BG properties increased from 3, in the youngest post-fire site, to 17 in the oldest site of the fire chronosequence. In a dry tropical forest, Hirobe et al. (2003) reported a gradual increase in the strength of correlation between N mineralization, nitrification, and soil moisture with increasing stand age after fire. All these

evidences suggest that the spatial coupling between AG and BG properties in pyrogenic ecosystems might follow the hypothesized pattern of spatial autocorrelation (large scale to fine scale and weak to strong). The findings from this study can be a unique example of the development of such spatial relationship in boreal ecosystem; however, caution should be made before making any generalization of the processes in other ecosystems.

2.4.3 Aboveground-Belowground control on nutrient availability

A number of detail studies were done in the boreal ecosystems to understand the change in nutrient availability along the course of stand development after fire, but only a few (e.g. Lavoie and Mack 2012; Smithwick et al. 2005) have focused on their spatial mechanisms. To our knowledge this is the first study which addressed some of the key spatial AG and BG controls of nutrient availability in pyrogenic boreal ecosystems. A strong BG control was expected in the PF stand with a gradual increase in AG control in the CC and MA stands. The findings indicate a combined microbial and chemical control on nutrient availability in the PF stand with almost no spatial structure, and a joint AG-BG control in the CC and MA stands with significant spatial structures.

Spatial regression models of individual nutrient indicated that substrate availability (DOC and MBC:TC) and C mineralization were probably driving the availability of most of the macronutrients in the CC stands, whereas substrate quality (C:N) appeared as the most consistent BG driver of nutrients in the MA stand. On the other hand, enzyme activity seems to be controlling the availability of almost all the macronutrients in the PF stand (Table 2-3). As indicated by the randomForest models, the hypothesized cyclic BG-AG-AGBG control on nutrient availability was more evident for the overall macronutrient availability, except

understory vegetation (UV) appeared to be the most influential variable in the PF stand. The strong control from UV disappeared when principal component scores of microbially mediated nutrients (N, P and S) were used as dependent variable. Total organic C, microbial N and enzyme activity appeared as the most influential variables for N-P-S availability in the modified model, which corroborates with the respective SAR model (Table 2-3). However, microbially mediated nutrients still showed a BG control in the CC stand (Figure 2-7). This may indicate that establishment of aboveground synergy for these nutrients probably extend beyond the canopy closure phase. The gradual increase in the AG-BG contribution to overall nutrient availability and the increasing trend of spatial congruence with stand age suggest that the cyclic pattern might continue as a joint control at stand maturity. Significant space term in the regression models of nutrient availability in the MA (mostly) and other stands might indicate nested patterns which were not captured by the current sampling protocol.

Strong enzymatic control on nutrient availability in the PF stand might be due to the thermal conversion of OM to more labile forms. Fire can create a flush of lower molecular weight compounds in soil, which in turn can trigger higher microbial activity. The energetics of OM decomposition dictates microbes to work first on the labile, low molecular weight substrate and then shift towards more recalcitrant compound (Glanville et al. 2012; Moorhead et al. 2013). No significant enzymatic control was found on N availability in the PF stand, but a strong DON control indicates that labile N was probably abundant and microbes were not utilizing N from other recalcitrant sources. Fire can preferentially favor chitonolytic organisms (mainly bacteria) to produce more chitin in the post-fire environment (Jorgensen and Hodges Jr 1970). In high N environment, as in the PF stand, chitin can depress chitinase (NAG) activity (Hanzlikova and Jandera 1993). A positive correlation between N and NAG in the PF stand however, indicates

that this enzyme might be important for N acquisition in post-fire environment. A negative relationship between P and phosphatase, and S and sulfatase may indicate an end product inhibition (Maynard et al. 1985; Goldstein et al. 1988).

The CC and MA stands showed significant AG control on nutrient availability which was expected as a result of biomass accumulation, forest floor and canopy development, and changes in forest composition (Brais et al. 1995). In a coniferous fire chronosequence in Montana, MacKenzie et al. (2004) showed that forest floor thickness and aboveground biomass gradually increased with time since fire following a log-linear pattern, and significantly influenced the speciation of available N along the trajectory of secondary succession. Their results also indicated a higher N mineralization rate during the early stages of the succession and a lower mineralization rate during the later stages, which were attributed to the difference in organic matter quality. In boreal forest ecosystems, DeLuca et al. (2002) also reported similar findings. Interestingly, the aboveground drivers of nutrient availability were not the same in the CC and MA stands. Stand level attributes such as FD, UV and CWD were mostly significant in the CC stand, whereas more individual tree based attributes such as distance to nearest tree, tree basal area and canopy cover were mostly significant in the MA stand.

2.5 Conclusions

Nutrient availability in pyrogenic environment often evolves through complex multi-scalar interactions, which might determine the mosaic pattern of vegetation and biogeochemistry in mature landscape; however, such relationships and their temporal patterns depend very much on the mode of disturbance and ecosystem types. Understanding the complex spatio-temporal

interactions between nutrient availability and biogeochemical agents in post-fire environment may explain the mechanisms of heterogeneity in ecosystem functions and their relationships with disturbance. Pyrogenic boreal aspen forests are some of the least studied ecosystems in terms of the development in spatio-temporal pattern in biogeochemical properties and responsible mechanisms. In the current study, I quantified temporal pattern of spatial structures in major plant nutrients and characterized the key mechanistic relationships that govern nutrient availability in pyrogenic boreal aspen ecosystems. Through a deductive reasoning approach using a priori hypotheses, I found that in general, post-fire nutrient availability is not spatially structured and spatial heterogeneity developed as the stand recovered from fire disturbance. Spatial congruence between nutrients, AG and BG properties also indicated a least connectivity in the post-fire stand and a strong linkage in the mature stand. Finally, spatial predictive models of nutrient availability confirmed that biotic drivers (mostly enzymes) are more actively controlling nutrient availability in the post-fire environment, which gradually shifted towards a control of substrate availability during the canopy closure phase, and a control of substrate quality and chemical environment in the mature stand.

I proposed a new ecological hypothesis of cyclic control in nutrient availability in pyrogenic boreal ecosystem and presented some evidences in support of the hypothesis. The current findings suggest that nutrient availability in pyrogenic boreal aspen ecosystems might cycle through a BG (heterotrophic) dominance in the young post-fire stand to a synergistic AG (canopy cover and forest floor depth) and BG control (substrate availability and quality) at stand maturity. Such spatial predictive models and the cyclic control mechanisms of nutrient availability at different stages of stand development might be useful for studies that are designed to compare changes in ecosystem properties before and after any large scale natural disturbance

such as fire, draught, insect attack, or anthropogenic disturbance such as harvesting and mining. Of special interest to ecosystem reconstruction after resource mining, this study will work as natural benchmark and will help creating a target ecosystem with specific spatial pattern in AG and BG properties.

Table 2- 1. Mean, coefficient of variation (CV), and variogram model parameters for available macronutrients ($\mu g\ 10\ cm^{-2}\ 8\ weeks^{-1}$) in three aspen stands along a fire chronosequence in boreal northern Alberta.

Stands	Nutrients	Mean (SE)	CV (%)	Range (m)	Spatial dependence	Model	R^2
Post fire	TIN	7.25 ± 1.07	133	-	-	NUG	-
	P	31.7 ± 2.89	82.0	> 23	0.24	LIN	0.14
	S	36.07 ± 2.49	62.2	6.5	0.81	GAU	0.40
	K	344.4 ± 17.8	46.7	-	-	NUG	-
	Ca	1216 ± 61.4	45.4	1.1	0.88	GAU	0.12
	Mg	90.43 ± 4.38	43.6	-	-	NUG	-
Canopy closure	TIN	3.34 ± 0.24	63.7	8.0	0.50	GAU	0.17
	P	5.74 ± 0.40	62.8	3.1	0.83	SPH	0.18
	S	25.9 ± 2.88	98.7	> 23	0.36	LIN	0.25
	K	177.5 ± 13.6	68.8	> 23	0.52	GAU	0.48
	Ca	1326.1 ± 64.6	43.8	> 23	0.38	LIN	0.28
	Mg	144.3 ± 5.2	32.2	-	-	NUG	-
Mature stand	TIN	3.96 ± 0.16	36.4	9.8	0.60	SPH	0.39
	P	6.64 ± 0.50	68.1	5.8	0.51	SPH	0.15
	S	54.3 ± 5.1	83.7	10	0.61	SPH	0.40
	K	250.5 ± 17.1	61.6	> 23	0.50	LIN	0.21
	Ca	1079.4 ± 34.7	28.9	> 23	0.53	EXP	0.26
	Mg	308.5 ± 9.24	27.9	17.6	0.51	GAU	0.46

Table 2- 2. Spearman rank correlations between macronutrients in three aspen stands along a fire chronosequence in boreal northern Alberta. Significance level: * <0.05; ** <0.01.

		Mg	Ca	K	S	P
PF	TIN	0.05	0.13	0.08	-0.04	0.20
	P	0.39**	0.48**	0.41**	0.51**	
	S	0.50**	0.46**	0.16		
	K	0.47**	0.25*			
	Ca	0.80**				
CC	TIN	0.07	-0.05	0.17	0.14	-0.24*
	P	-0.16	-0.08	0.18	-0.15	
	S	0.12	0.22*	-0.05		
	K	-0.19	-0.54**			
	Ca	0.76**				
MA	TIN	0.20	0.06	-0.04	0.08	-0.24*
	P	-0.01	0.01	0.16	-0.09	
	S	0.54**	0.36**	-0.19		
	K	-0.25*	-0.28*			
	Ca	0.80**				

Table 2- 3. Spatial regression models and parameters for available macronutrients (µg 10 cm-2 8 weeks-1) in three aspen stands along a fire chronosequence in boreal northern Alberta; § p ≤ 0.10; † p ≤ 0.05; †† p ≤ 0.005; †§ p ≤ 0.0005; §§ p ≤ 0.00005

	Spatial regression models	Lag coeff. (ρ)	Error coeff. (λ)	LogL	LR	F value, p	AIC	R^2_{adj}
Post fire	†TIN ~ f(††DON, §pH, †FD, ††FRB, ††BGn, †P)	-	0.14 (0.26)	56.3	0.98 (0.32)	$5.05_{6,73}$; < .0005	-98.6	0.21
	P ~ f(†Bglu, ††NAG, ††Phos, †TN, †Ca, †K, §§S)	-	-0.22 (0.12)	24.5	1.64 (0.19)	$10.83_{7,72}$; < .0000	-33.1	0.42
	S ~ f(†Phos, ††Sulf, †MBC:TC, †TN, §§P, §§Mg)	0.18 (0.06)	-	37.2	3.82 (0.05)	$14.81_{7,72}$; < .0000	-59.4	0.48
	K ~ f(§BR, †NAG, †pH, †P, §§Ca, §§Mg)	-	-0.14 (0.33)	38.9	0.71 (0.40)	$11.14_{6,74}$; < .0000	-63.8	0.38
	Ca ~ f(§DOC:DON, §§P, †§K, §§Mg)	**0.23 (0.00)**	-	82.3	7.74 (0.00)	$54.76_{4,77}$; < .0000	-152.6	0.70
	Mg ~ f(†Bglu, †P, †S, §§K, §§Ca)	-	-	84.9	-	$52.92_{5,76}$; < .0000	-157.9	0.76
Canopy closure	TIN ~ f(†Bglu, ††MBC:TC, §§qCO2, †FD, BGn, †pH)	0.17 (0.12)	-	52.4	2.09 (0.15)	$5.75_{6,75}$; < .0000	-88.9	0.25
	P ~ f(††DOC, †BR, †FD, K)	-	0.11 (0.43)	29.7	0.51 (0.47)	$5.09_{4,77}$; < .005	-49.3	0.16
	S ~ f(††MBCN, †§DOC, pH, †CWD, ††NH4, †Ca)	-	0.22 (0.08)	5.13	2.29 (0.13)	$7.19_{6,75}$; < .0000	3.74	0.31
	K ~ f (†qCO2, †§UV, §§CWD, §§P, §§Ca, §§Mg)	-	**-0.33 (0.01)**	14.8	4.34 (0.03)	$24.13_{6,75}$; < .0000	-15.7	0.59
	Ca ~ f (†§MBC:TC, §§BA, ††UV, †§NO3, §§K, §§Mg)	-	**0.31 (0.00)**	105.8	3.67 (0.05)	$103.5_{6,75}$; <.0000	-197.7	0.80
	Mg ~ f (†UV, †BGn, †§CRB, †§P, §§Ca, §§K)	-	0.03 (0.80)	116.7	0.04 (0.84)	$74.77_{6,75}$; < .0000	-219.5	0.75
Mature stand	TIN ~ f(§NAG, DON††, †DOC:DON, §Tdist., BA, P††)	**0.31 (0.00)**	-	80.0	7.06 (0.00)	$4.51_{6,75}$; <.005	-144.1	0.25
	P ~ f(††Bglu, †NAG, †DOC:DON, †BR, FRB, †TIN, S)	-	**0.29 (0.01)**	25.5	5.56 (0.01)	$3.11_{7,74}$; < .05	-37.1	0.18
	S ~ f(†qCO2, †Tdist., †BA, †§UV, P, §§Mg)	**0.30 (0.00)**	-	20.9	7.75 (0.00)	$12.24_{6,75}$; < .0000	-25.9	0.47
	K ~ f(†MBCN, ††EC, †§FD, †Canopy, ††CRB, ††Ca)	-	0.21 (0.09)	17.7	2.45 (0.12)	$7.86_{6,75}$; < .0000	-21.4	0.32
	Ca ~ f(†DOC:DON, ††Sulf, §EC, §Tdist., †CWD, ††TIN, §§Mg)	-	0.22 (0.08)	109.6	2.90 (0.08)	$33.6_{7,74}$; < .0000	-203.3	0.67
	Mg ~ f(§§pH, §§EC, †UV, §§Ca, ††S)	-	**0.25 (0.03)**	125.4	3.25 (0.07)	$59.21_{5,76}$; < .0000	-238.8	0.73

[†]MBC = Microbial biomass C (µg g^{-1} soil); MBN = Microbial biomass N (µg g^{-1} soil); MBCN = Microbial C to N ratio; BR = Basal respiration (µg CO_2-C g^{-1} soil day^{-1}); DOC = Dissolved organic C (µg g^{-1} soil); DON = Dissolved organic N (µg g^{-1} soil); Bglu = β-1,4 glucosidease (nmol g^{-1} soil hour^{-1}); NAG = N-acetylegluccosaminidase (nmol g^{-1} soil hour^{-1}); Phos = Phosphatase (nmol g^{-1} soil hour^{-1}); Sulf = Sulfatase (nmol g^{-1} soil hour^{-1}); TC = Total C (%); TN = Total N (%); FD = Forest floor depth (cm); FRB = Fine root biomass (kg stem^{-1}; g stem^{-1} in CC); BGn = Bare ground (%); Tdist = Distance to nearest tree (cm); UV = Understory vegetation cover (%); BA = Basal area of nearest tree (cm^2; cm^2 m^{-2} in CC); CWD = Coarse woody debris cover (%).

Figure 2- 1. Illustrations showing the hypothesized spatial pattern of nutrient availability (a) and its aboveground-belowground control (b) in three aspen stands along a fire chronosequence in boreal northern Alberta.
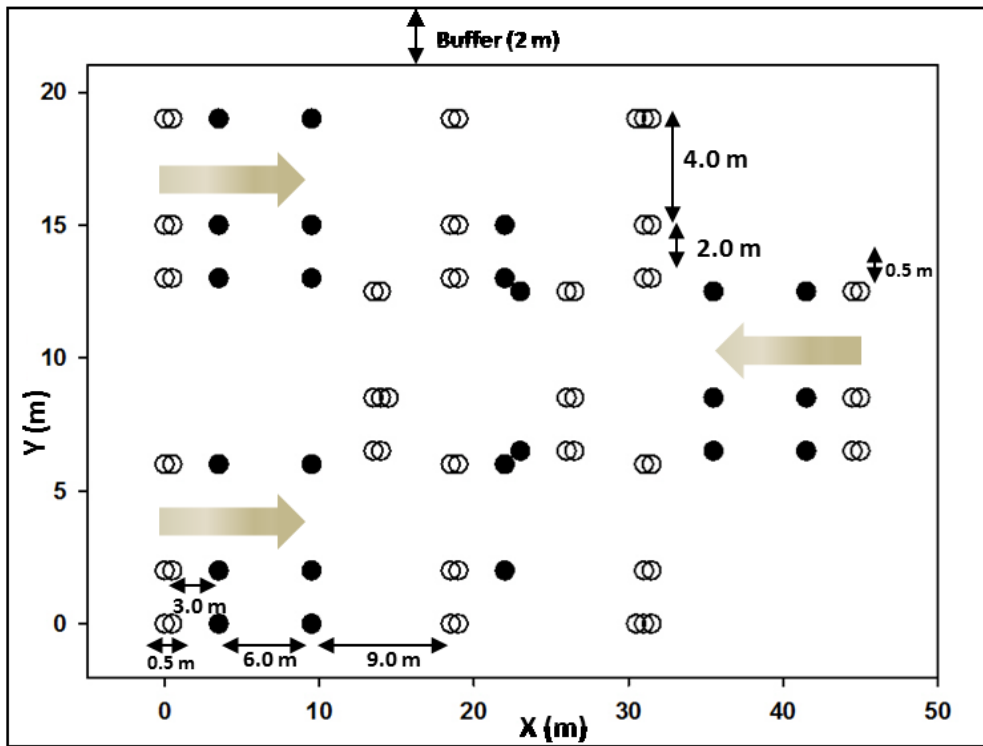
Figure 2- 2. Layout of the sampling protocol used to measure spatial patterns in the aboveground and belowground properties along a fire chronosequence of aspen stands in boreal northern Alberta. Three middle rows were laid out in reverse direction (as indicated by the arrow) to account for any potential anisotropy. Open circle points have 50 cm intervals in between. A 2 m buffer was maintained around the plot to minimize disturbance from trampling.
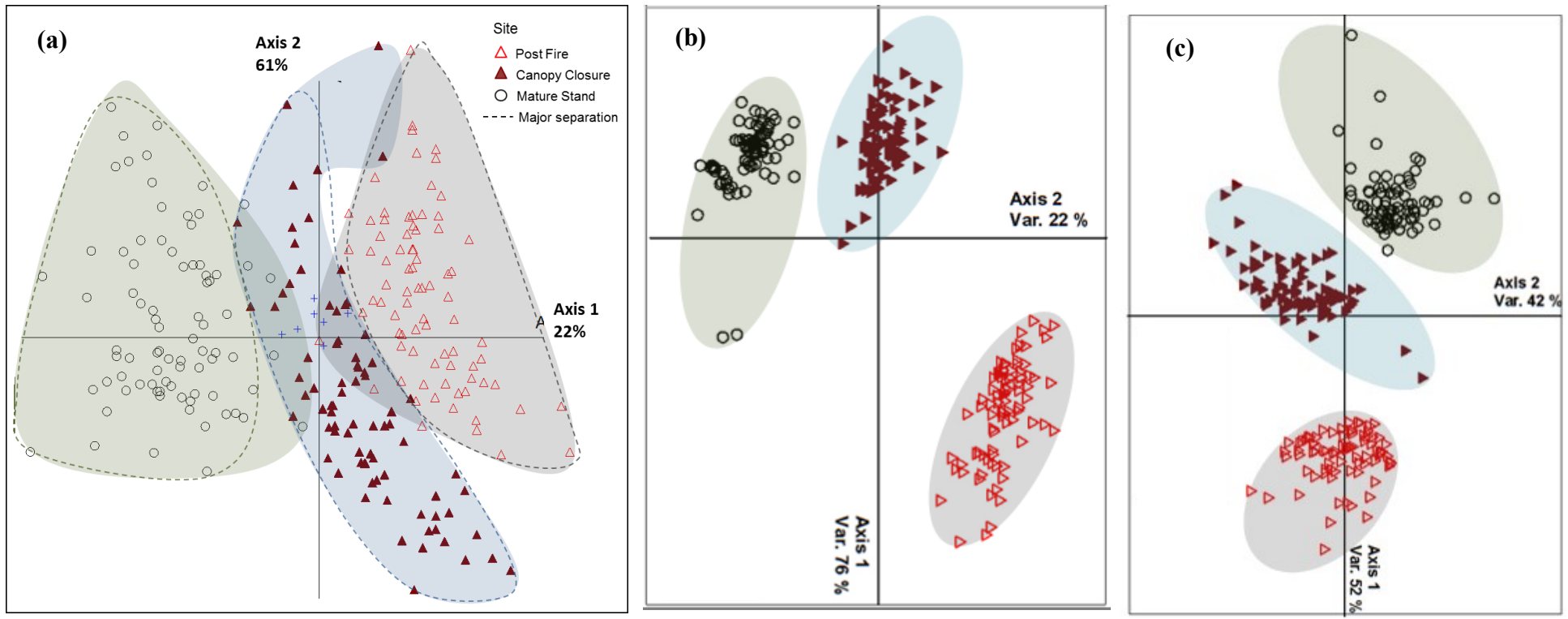
Figure 2- 3. Nonmetric Multidimentional Scaling (NMDS) ordination of available macronutrients (a), aboveground (b) and soil microbial properties (c) in three aspen stands along a fire chronosequence in boreal northern Alberta.
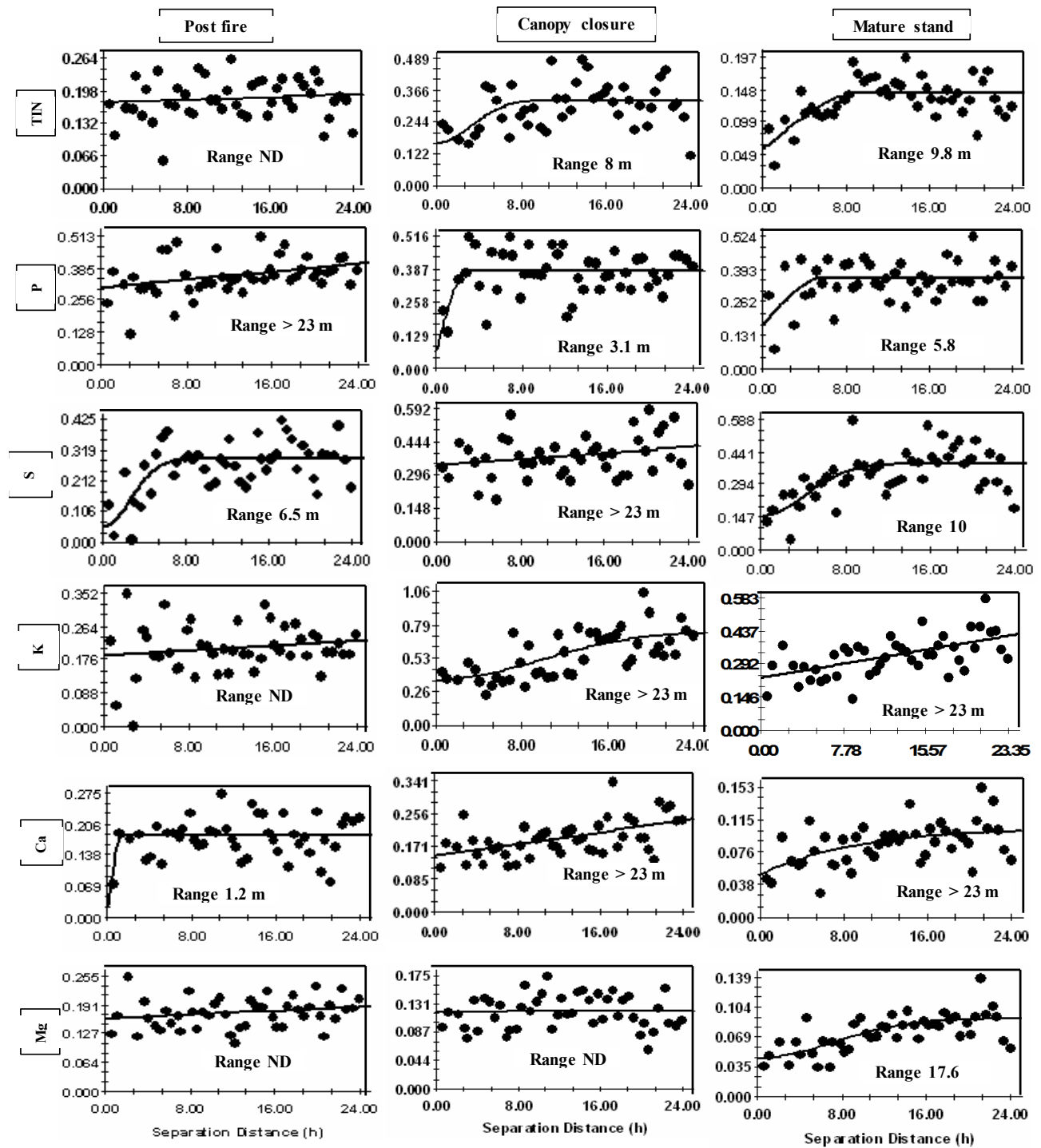
Figure 2- 4. Semi-variograms of available macronutrients (µg 10 cm^{-2} 8 weeks^{-1}) in three aspen stands along a fire chronosequence in boreal northern Alberta.
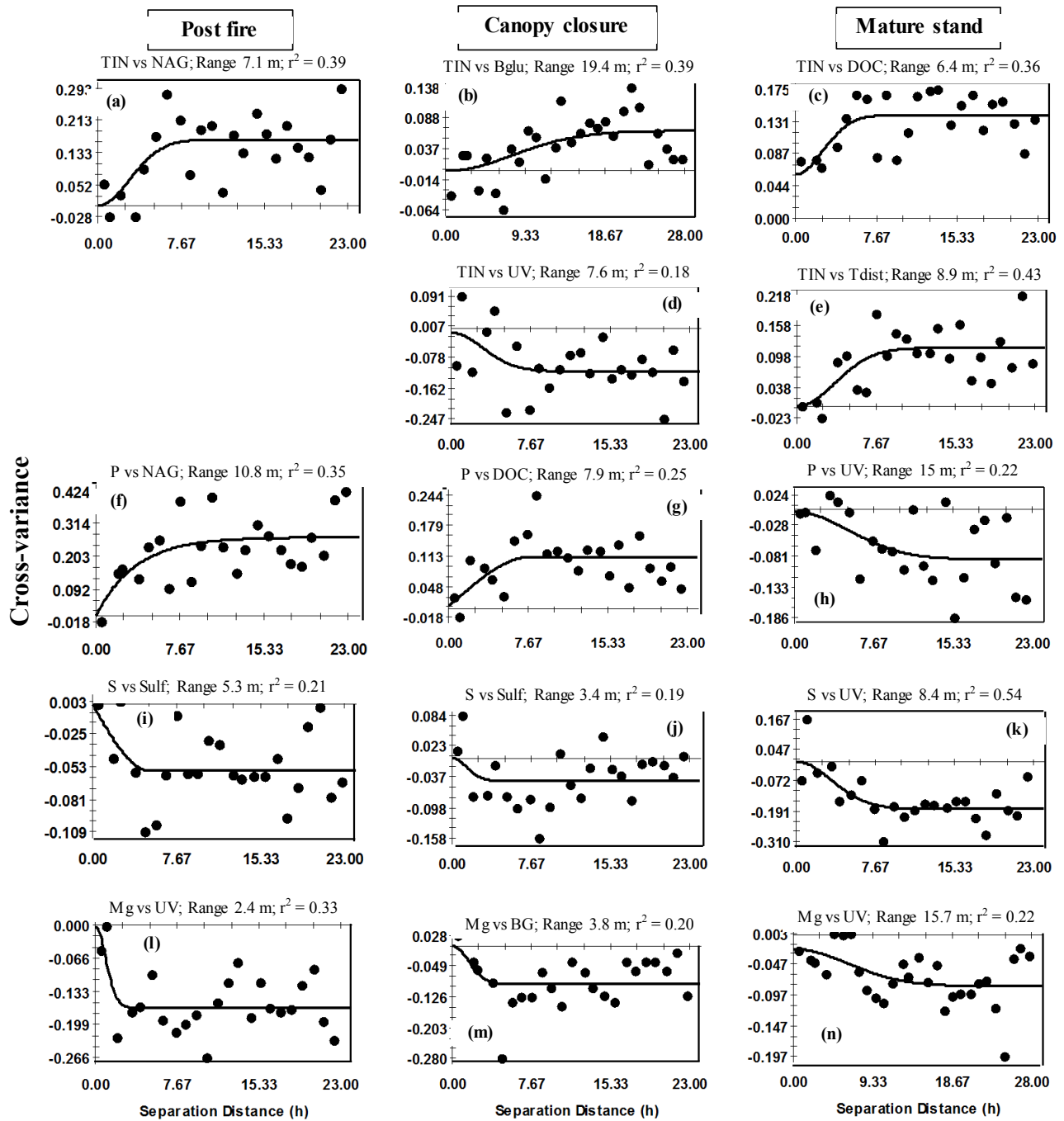
Figure 2- 5. Cross-variograms between available N, P, S and Mg (μg 10 cm^{-2} 8 weeks^{-1}), and soil and stand variables in three aspen stands along a fire chronosequence in boreal northern Alberta.
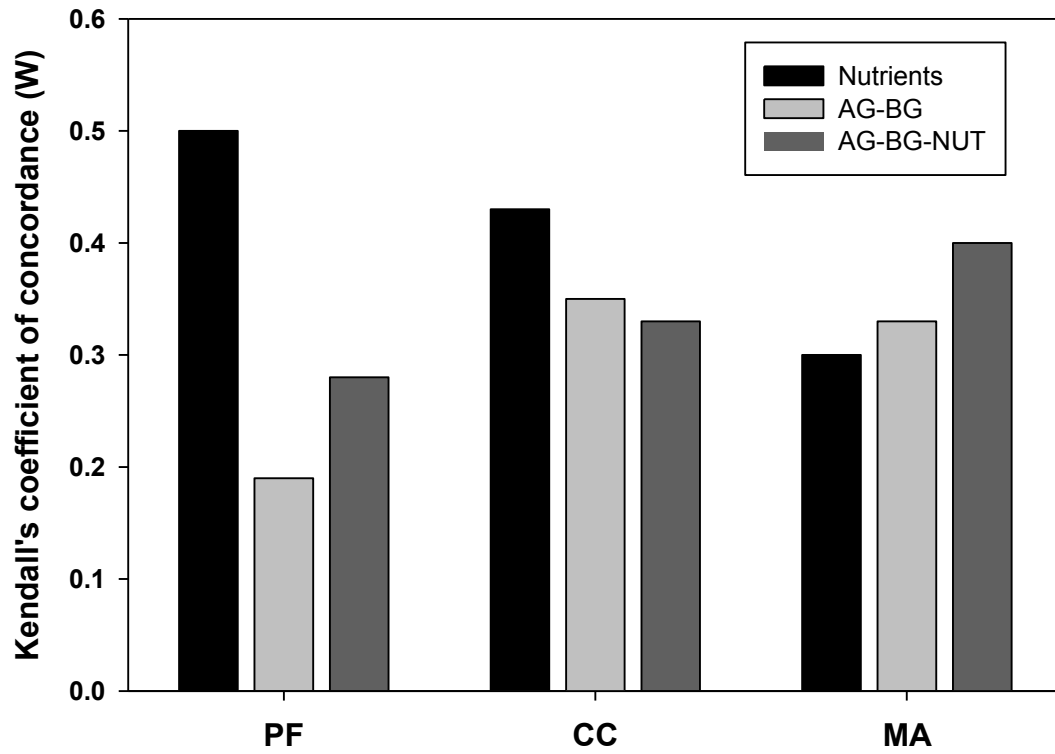
Figure 2- 6. Spatial congruence among available nutrients (NUT), aboveground (AG), belowground (BG) properties in three aspen stands along a fire chronosequence in boreal northern Alberta.
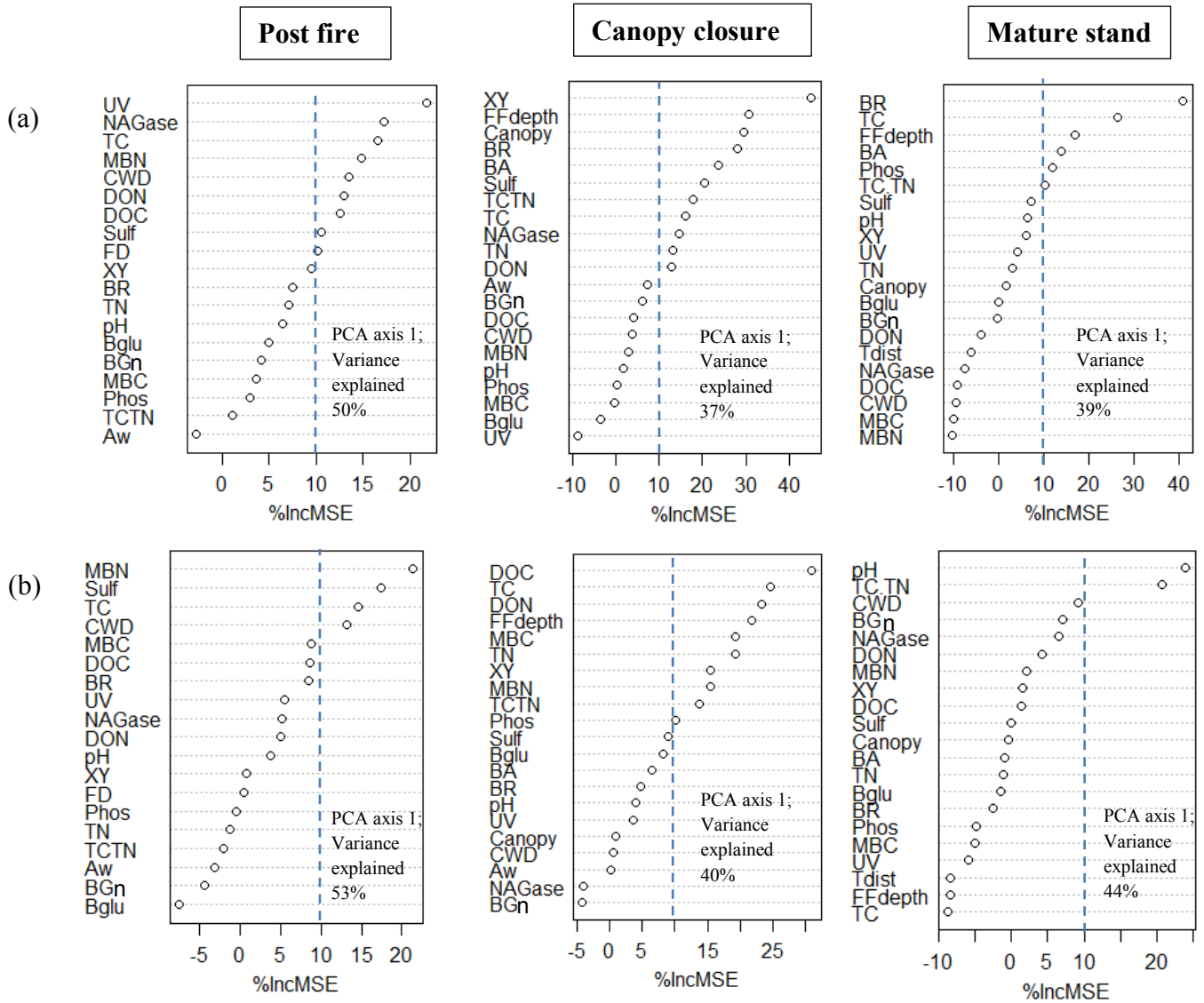
Figure 2- 7. Variable importance derived from the random forest (RF) models for overall available macronutrients (a) and microbially (N, P and S) (b) mediated nutrients in three aspen stands along a fire chronosequence in boreal northern Alberta. Principal component scores of nutrients were used as dependent variable in each RF model.

Chapter 3. Spatial heterogeneity in Soil Respiration in a Boreal Aspen Forest Fire Chronosequence

3.1 Introduction

The boreal forest is the largest terrestrial biome on earth, represents about 25% of the global forested areas, and accounts for 289 Pg of C most of which is in soils (Bond-Lamberty et al. 2004; Kasischke et al. 1995; Khomik et al. 2006). Wildfire is one of the main drivers of C exchange in these forested ecosystems. Boreal forest ecosystems are fire adapted, however periodic wildfire is required to maintain vegetation dynamics, stand renewal, landscape patchiness, and overall biogeochemical cycling (Flannigan et al. 1991; Chen et al. 2000; Stocks et al. 2002, Czimczik et al. 2006). One of the key ecosystem processes affected by wildfire is soil respiration (Rs) which is composed of CO_2 fluxes from two different sources, (i) autotrophic respiration (Ra), mainly from plant roots, rhizosphere micorrhizae and living mosses, and (ii) heterotrophic respiration (Rh), mainly from microbial activity (Hanson et al. 2000). *In-situ* soil respiration has been shown to be effective in tracking ecosystem recovery after stand replacing disturbance such as wildfire (Weber 1990).

Significant efforts have been devoted to understand the potential sources of variation in Rs in different ecosystems including the pyrogenic boreal ecosystem (Czimczik et al. 2006; Rayment and Jarvis 2000; Singh et al. 2008; Yang et al. 1999). The two main state factors of variation as agreed in most of the literature are temperature and moisture. However, other soil properties such as organic matter quality, concentration of photosynthates in root, and enzyme activity are all responsible for the variation in Rs (Allison et al. 2008; Tang and Baldocchi 2005).

Despite the technological progress in measuring Rs, there are few studies that have actually looked at the spatial variation of Rs and quantified the potential sources of variation other than the temperature and moisture. Environmental factors are not always very useful in explaining spatial patterns in Rs as the variation comes from a gradient of soil properties which might not be directly affected by these factors (Tang and Baldocchi 2005). The current prediction models are mainly based on the empirical relationship between Rs and soil temperature which might not reflect the nature of relationship between Rs and other biotic and abiotic drivers, and therefore limits the modeling efforts of future net ecosystem C exchange (NEE) (Czimczik et al. 2006). Among the studies done in the boreal ecosystems, variation in Rs was attributed to the forest floor depth (Khomik et al. 2006; Lavoie and Mack 2012b; Rayment and Jarvis 2000), substrate quality (Khomik et al. 2006), root biomass (Ruess et al. 1996; Singh et al. 2008), vegetation type (Khomik et al. 2006; Raich and Tufekciogul 2000), and soil temperature and moisture (Drewitt et al. 2002; Gulledge and Schimel 2000; Russell and Voroney 1998; Shibistova et al. 2002; Van Cleve and Sprague 1971). However, most of these studies either used coefficient of variation as a measure of spatial variation, or used non-spatial least square regression approach for modeling Rs, which is prone to give biased and erroneous parameter fit if data are spatially autocorrelated (Beale et al. 2010; Kissling and Carl 2008). Moreover, the boreal literature on Rs are heavily focused on the CO_2 efflux in coniferous stands, especially the black spruce mix stand, and therefore might not fully reflect the mechanisms of Rs in pure and mixedwood stands with broadleaf species. Wildfire disturbance, a very likely scenario in boreal ecosystems, was not also represented adequately in the spatial Rs studies, which is limiting our total understanding of the regulatory mechanisms of CO_2 efflux in these ecosystems.

Wildfire may create or reshuffle spatial structure in soil processes by fully or partially consuming the overstory and organic layers (Boby et al. 2010; Wang et al. 2002). Stand-replacing fire, where aboveground canopies and most of the organic layer are consumed, can decrease the spatial variation in biotic processes to a large extent due to the homogenization of abiotic environmental conditions such as temperature and moisture. However, other factors such as organic matter quality, charcoal, forest floor depth and understory vegetation cover can also exert significant control where temperature and moistures are not limiting (Czimczik et al. 2006; Smithwick et al. 2005). We hypothesized that post fire soil respiration would have less heterogeneity and large scale spatial dependency. The spatial dependency in Rs should, however, develop over time as stands grow older and recreate the structural complexity lost during fire disturbance (Hypothesis 1). We expected to see a seasonal effect, with higher summer spatial variability (i.e. fine scale patchiness) than in the spring, as summer is the main growing season and should stimulate all the major autotrophic and heterotrophic drivers of Rs (Griffis et al. 2004; Weber 1990). We assume that these effects would be more localized during the peak growing months (June to August) (Hypothesis 2). Availability of moisture and labile C are two major drivers that we expected to have significant influence on post fire Rs (Hypothesis 3). PF should experience a moisture limitation due to high temperature caused by the black charred forest floor and an open canopy structure (O'Neill et al. 2002). High number of aspen suckers in post-fire environment might also exacerbate the moisture condition through a high evapo-transpirative demand. Availability of soluble C generally decreases after fire and can affect Rs in post fire stands since C is the main fuel for microbial activity (Certini 2005). We also assumed that the belowground (BG) biotic control on Rs would be stronger than the aboveground (AG) factors in the post fire stands and this would emerge to a joint AG-BG control with stand

maturity (Hypothesis 4) (Czimczik et al. 2006; Grant et al. 2007; O'Neill et al. 2002; Richter et al. 2000).

Understanding the regulatory mechanisms of spatial heterogeneity of Rs in post-fire aspen stands is important as the regeneration and subsequent stand dynamics of aspen in boreal ecosystem heavily rely on wildfire disturbance (Weber 1990). I took this unique vegetation dynamics of pyrogenic boreal aspen ecosystems to understand the evolution of Rs in a conspecific set-up. Besides deepening our ecological understanding, this study can also be used as a benchmark for measuring reclamation success of similar areas disturbed by oil sand mining, a major anthropogenic disturbance in northern Alberta. The specific objectives of this study were: i) to quantify the spatial variation in Rs, iii) to characterize the seasonal pattern of spatial variation in Rs, and iii) to determine the principal factors controlling the spatial variation in Rs along a boreal aspen fire chronosequence.

3.2 Methods

3.2.1 Study sites

The study was conducted in the Athabasca oil sand region (AOSR) around Fort McMurray, Alberta, Canada (56° 43′ N 111° 21′ W). The mean annual temperature in this region is 0.9°C and mean growing season (May – September) temperature is 13.3°C. Mean annual precipitation is 418.6 mm, of which 283.4 mm fall as rainfall during the growing seasons (Environment Canada 2014). Soils in the study areas are sandy loamy to silty loamy, moderately well drained, and developed from till and glaciolacustrine sediments (Crown and Twardy, 1970). Three boreal aspen stands were used to create a fire chronosequence, a one year post fire (PF)

stand, a 9 years stand at canopy closure phase (CC), and a 72 years mature stand (MA). Trembling aspen (*Populus tremulides* Michx.) was the most dominant tree species and represented more than 95% of the basal area in all the three sites. The maximum distance between the sites was 34 km. The number of aspen suckers in the PF stand was counted as 230, 000 – 270, 000 per hectare. The CC stand had a tree density of 1900 stems per/ha and was different from the other two sites in that it had a large amount of coarse woody debris on the ground. The density in the MA stand was approximately 2150 stem per hectare. According to the ecosite classification of northern Alberta, all the three sites fall under the d1 ecosite phase (low-bush cranberry Aw) (Beckingham and Archibald 1996). Geographic location, fire history and dominant shrub, forb, grass and moss species in the study sites are given in the Appendix II.

3.2.2 Respiration measurements

Sampling and *in-situ* measurements were carried out in a 50 m × 20 m plot at all the three sites. A cyclic spatial sampling protocol with variable intervals (Clayton & Hudelson 1995) was used to capture both the scale and directionality in measured properties (Figure 3-1). In total 42 sampling points were established in 7 transects within a 1000 m^2 plot which ensured a minimum detectable spatial lag of 2.0 m. Intervals between the sampling point along the transect were 3, 6 and 9 m, and inter-transect intervals were 2 m and 4 m. The sampling orientation was reversed in the middle two transects to capture anisotropy. Respiration collars made of high grade PVC pipe (10 cm internal diameter) were installed at each sampling point. Collars were inserted 8 cm deep into the soil and a 2 cm edge was kept above the soil surface to be used as housing for the respiration chamber rim. Side walls of the collars were drilled (3 to 5 holes) to allow lateral water movement. Collars were installed 48 hours prior to respiration measurements to avoid the

initial flush of CO_2 due to ground disturbance. Soil respiration and flux concentration (FC) were measured using a portable dynamic closed chamber infrared gas analyzer (CIRAS 1) with a SRC-1 soil respiration chamber (PP systems, Hitchin Herts, UK). Respiration was measured monthly from June to August, 2012, May 2013. Soil temperature (ST) (at 8 cm depth) and volumetric moisture content (SM) (Theta probe and HH2 moisture meter, Delta-T, UK) were also measured at each sampling point during the respiration measurements. Air temperature was also recorded at every 30 minutes during the whole measurement period. All the measurements were done between 8:30 am to 1:30 pm to reduce the diurnal variation in soil respiration.

3.2.3 Lab analyses

Soil samples were collected at each spatial sampling point in August 2012 and included the entire forest floor depth and 5 cm of mineral soil. Samples were kept chilled with ice packs in the field and then stored at 4°C in the lab until further processing. After carefully removing the coarse roots and coarse fragments, samples were homogenized. A sub-set of the samples were frozen at -20°C for extracellular enzyme activity. Approximately 75 to 100 g soil was incubated for 10 days at 25°C in sealed Mason jar with alkali trap (0.5 M NaOH) and basal respiration was calculated after titrating with 0.5 M HCl (Pell et al. 2006). Microbial biomass C and N were measured on the incubated samples using the fumigation extraction method (Vance et al. 1987). Approximately 20 to 25 g soils were extracted in 0.5 M K_2SO_4 (1:2 ratio) after exposing to chloroform ($CHCl_3$) fume for 96 hours. Dissolved organic C and N were measured on both the unfumigated and fumigated fractions of the soil extractions using Shimadzu TOC-V/TN analyzer (Shimadzu Corp., Kyoto, Japan), and microbial biomass was determined taking the difference between the two fractions.

Three enzymes were examined in this study including: (i) β-glucosidase (EC 3.2.1.21) which is responsible for breaking labile cellulose and other carbohydrate polymer chains, (ii) phenol oxidase (EC 1.10.3.2), which mainly degrades lignin and laccases, , and (iii) peroxidase (EC 1.11.1.7) which also degrades lignin and polysachharide but uses H_2O_2 or secondary oxidants as electron acceptor (Bach et al. 2013). β-glucosidase (Bglu) activity was measured using 200 mM of 4-methylumbelliferyl (MUB)-β -D-glucopyranosidase as a fluorimetric substrate, while the phenol oxidase (Phenol) and peroxidase (Perox) activity were measured using 3,4-dihydroxy-L-phenylalanine as a colorimetric substrate (Sinsabaugh et al. 2008; Quideau et al. 2013). Assay and control wells were replicated 8 times. Activity rates (μmol of converted substrate g^{-1} soil $hour^{-1}$) were calculated on an oven dry mass basis.

3.2.4 Measurement of stand attributes

Stand characteristics were measured around each spatial sampling point. Coarse woody debris cover (CWD; %) and number of aspen seedlings were counted using a 0.25 m^2 and 1 m^2 sampling frame, respectively. Tree location (XY coordinates) was measured in the PF and MA stand using a Nikon total station (Nikon DTM 352). Canopy cover (%) estimation was done using a convex densitometer and forest floor depth (FD) was measured using a ruler (average of three measurements).

Aspen fine root biomass (< 5 mm; FRB) in MA stand was estimated using the allometric equation developed by Chen et al. (2004) (Appendix IV). Fine root biomass value for each spatial point was taken from the estimated root biomass of the nearest tree (as close as 0.10 m), as we think, tree closer to the point would have much stronger spatial control than the tree farther apart.

3.2.5 Geo-statistics and other statistical analyses

Isotropic semi-variograms of the measured variables were calculated to examine the spatial autocorrelation in Rs and other attributes (Yates and Warrick 2002). Data were log transformed prior to analyzing semi-variograms and variogram models. Five variogram models (Linear, Gaussian, Exponential, Spherical and Nugget) were tested to fit the empirical data. A combination of highest coefficient of determination (R^2) and the lowest residual sum of square error was used to select the final model. Spatial dependence was calculated using the nugget coefficient, n_c which is a ratio of total variance ($c_0 + c_1$) and nugget variance (c_0). A nugget coefficient > 75 indicates strong spatial dependence, between 25 and 75 indicates moderate dependence, and < 25 indicates poor or no spatial dependence (Camberdalla et al. 1994). Coefficient of variation (CV) was used as a measure of global variation which was calculated by dividing the standard deviation by the mean and taking a percentage. Cross-variograms were calculated between Rs and the aboveground and belowground variables to check for any scale dependent spatial relationships. A positive cross-variance indicates spatial association, whereas a negative variance means spatial dissociation. Fitted semi-variogram models were used for creating ordinary kriged maps of Rs. Variogram modeling and krieging interpolation were done using GS+ geostatistic software (V9.0, Gammadesign software). Details on the semi-variogram modeling are given in the Appendix I.

Driving factors of Rs and their seasonal influence in different stands were tested using spatial autoregressive (SAR) models. Both the spatial error (SAR_{err}) and spatial lag (SAR_{lag}) models were tested, and the one with lowest AIC and highest R^2_{adj} (adjusted for number of predictors in the model) was finally selected (Besag 1974; Anselin 1988). SAR analysis was

done in R (R development Core Team, 2013) and Geoda an R based open source geospatial software (Anselin 2004). Details on SAR calculation and interpretations are given in the Appendix I.

In order to quantify how variability influenced the predictability of Rs in different stands, we calculated the sample size required to estimate Rs within a specified confidence interval according to Petersen & Calvin (1986) using the Student's t statistic at α level of 0.05. The following equation was used:

$n = t_\alpha^2 s^2 / D^2$, where n is the required sample size, t_α is the Student's t statistic at α level of confidence, s is the standard deviation, and D is the specified error limit. We used 95% confidence level and errors equal to 10 and 20% of the sample mean.

3.3 Results

3.3.1 Soil respiration (Rs) and aboveground and belowground factors

Soil respiration showed significant differences between stands ($p < 0.01$) and seasons ($p < 0.000$). Post fire stand had the lowest growing season Rs (0.73 ± 0.02 g CO_2 m^{-2} hour^{-1}) followed by the CC (0.86 ± 0.04 g CO_2 m^{-2} hour^{-1}) and MA stand (1.16 ± 0.05 g CO_2 m^{-2} hour^{-1}). Lowest early growing season (May) Rs was found in the CC stand whereas lowest summer season (June – August) Rs was in the PF stand (Table 3-1). Concentration of CO_2 constantly increased from 440 ppm in May to 531 ppm in August in the CC stand, however dropped in August in the PF and MA stands. Flux concentration ranged from 445 to 486 ppm in the PF stand, and 472 to 540 ppm in the MA stand. Significant ($p < 0.000$) differences were also found

in ST and SM of different stands (Table 3-2). A constant trend of increasing ST was observed in all stands from May to July which then dropped in August. Soil temperature ranged from 11.4 to 16.1°C in the PF stand, 6.9 to 16.1° in the CC stand, and 7.5 to 13.8°C in the MA stand. Soil moisture also decreased constantly in all stands over the growing season except July in the PF stand.

Significant (p < 0.10) differences were also found in the aboveground and belowground properties in the three aspen stands (Table 3-3). The MA stand had significantly higher MBC, Bglu, Phenol, TC, TN, canopy cover, and FD. Dissolved organic C did not differ significantly between the stands, however, followed an increasing trend with stand age. Dissolved organic N, on the other hand, was significantly higher in the PF stand than the CC and MA stand. Basal respiration (BR) was significantly higher in the PF stand than the CC stand but not than the MA stand. Fine root biomass calculated from the allometric equation had higher values in the MA stand than the PF stand. However, most of these fine aspen roots in the PF stand are likely to be dead due to the fire effect.

3.3.2 Spatial variation in Rs, ST and SM

Strong to moderate spatial dependency was observed in Rs, ST and SM, and other AG and BG properties in all the three aspen stands (Table 3-1). Global variation (coefficient in variation) in Rs did not follow any specific trend, but generally showed higher value during the peak growing season (June and July). Overall, the CC stand showed the highest global variation in Rs (35.8 - 48.6 %) (Table 3-1). A gradual decrease in the CV of ST was observed from May to August in all the stands. The CV of SM also showed similar trend from May to July in the PF

and MA stand. The CC stand had the highest CV in ST (5 – 29%), and the MA stand had the highest CV in SM (22 – 28%).

Soil respiration in the PF stand had spatial autocorrelation at maximum 6 m in May and August. Either a very coarse scale (> 23 m) or no detectable spatial autocorrelation was found in June and July. Autocorrelation in Rs varied between 4.4 m (May) to 5.6 m (June) in the CC stand, and no spatial autocorrelation was detected in August at the measured scale (Table 1). However, CO_2 concentration (FC) in August showed a large scale (> 23 m) autocorrelation. Soil respirations in the MA stand showed spatial autocorrelation mostly at ≤ 5 m scale throughout the growing season except in May when the range was 8 m. CO_2 concentration also followed similar spatial trend as Rs except the June and August measurements. Seasonal changes in Rs in different stands are also shown in interpolated krieged maps (Appendix IV; Figure A4-1).

Large scale spatial autocorrelation (≥ 19 m) was detected in ST in the PF and CC stand during most of the growing season, and SM did not show any detectable spatial autocorrelation except in July in the PF stand (4.8 m), and in August in the CC stand (3.6 m) (Table 3-2). The MA stand also showed a large scale (> 23 m) spatial autocorrelation in ST and SM in the early growing season which gradually became finer with a minimum of 4.2 m in August.

Cross-variogram analysis between Rs and, AG and BG variables showed a spatial association at > 13 m range in the PF stand, and < 9 m range in the CC and MA stand (Figure 3-2). For example, Rs in the PF stand had spatial association with TC at 20 m and with FD at 14 m, whereas the CC stand had association with Cenz at 7 m and with canopy at 8 m. Likewise, Rs in the MA stand showed association with MBC at 9 m and with canopy at 7 m.

Variability in Rs seems affected the required sample size to correctly estimate Rs within 10% error of mean, especially in the CC stand. According to the estimated required sample size, the current sampling protocol (n = 42) falls within the seasonal boundary for the PF (average n = 51) and MA (average n = 48) stands. The estimated sample size in the CC stand is, however, nearly two-fold higher than the current sample size during the May to July measurements (Table 3-3).

3.3.3 Spatial regressions

Spatial regression models indicated significant spatial and non-spatial control on Rs in all three stands along the fire chronosequence (Table 3-4). These models explained 18 to 52% of the variation in Rs in all stands. In the PF stand, a significant space effect on Rs was only detected in May. Forest floor depth and SM were the two most significant predictors of Rs in the PF stand, except in July when DOC and DON appeared to be the principal controlling factors. Soil respiration showed variable dependency in the CC stand with a significant space effect in June. Aboveground properties such as FD and aspen sapling density showed a consistent positive control on Rs in the CC stand during the growing season; however, the strongest control came from the BG properties such as Bglu, Perox and DOC, especially during June to August. Spatial relationships between Rs and the driving factors seem more complex in the MA stand. Like the CC stand, a consistent control of AG and BG variables on Rs was also observed in this stand, except in May when MBN had the strongest control. The most significant AG control was found during July and August through the effect of FD, canopy and tree distance. The control from tree distance and canopy were much stronger than FD in August. Among the BG factors, FRB appeared to be the most significant driver of Rs throughout the growing season. Soil microbial

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biomass C (MBC) and enzyme activities were the other belowground factors that showed consistent significant positive control on Rs, whereas enzymes had mostly negative control on Rs in the PF and CC stands. Significant spatial control on Rs in the MA stand was only found in August.

3.4 Discussion

The ranges and seasonal patterns in Rs found in this study corroborate previous studies done in the boreal aspen forests (Gaumont-Guay et al. 2006; Griffis et al. 2004; Russell and Voroney 1998). Russell and Voroney (1998) reported a flux of 0.10 mg CO_2 m^2 s^{-1} in May and maximum 0.40 mg CO_2 m^2 s^{-1} in July in a 70 years old boreal aspen forest. The corresponding values in our study were 0.14 and 0.41 in May and July, respectively. Weber (1990) also reported a similar seasonal fluctuation in Rs with a lowest in May and highest in July in a mixed aspen-Jack pine stand, and the trend was distinct 1 year after fire. With the measured rate, the growing season (May – August) annual daytime C flux from the forest floor of mature aspen stand is 11.2 Mg C ha^{-1}. In the PF and CC stands these values are 7.1 and 8.3 Mg C ha^{-1}, respectively. The peak Rs in the PF and CC stands was found in June and August, respectively. The lower Rs in July in the PF stand can be attributed to the decrease in autotrophic respiration due to the premature defoliation of aspen seedlings in July caused by the ink spot disease, a common problem in young aspen stands regenerating from suckers (Gross and Basham 1981). On the other hand, the gradual rise in Rs in the CC stand until August could have resulted from the continuous root proliferation as happens in stands recovering from fire disturbance.

Mean growing season Rs in the PF stand was lower by 15% and 37% than the CC and MA stands, respectively. Fire can have direct negative effect on Rs through a number of ways such as removal of organic layer, reduction in microbial biomass, and thermal conversion of C to more recalcitrant forms (González-Pérez et al. 2004). Studies performed in the pyrogenic boreal ecosystems often reported similar effects of fire on soil respiration (see review by Amiro et al. 2003). The decrease in Rs in the PF stand can most likely be attributed to a decrease in the autotrophic respiration, however other factors such as soil moisture and microbial activity have also been found to be important in some studies (Fritze et al. 1993a; Pietikäinen and Fritze 1996). Results from this study confirm the hypothesized trend of C flux in pyrogenic aspen ecosystem that fire reduces respiration (Amiro et al. 2003) and that post fire upland boreal ecosystems are probably a C sink rather than a source as indicated by some models (Kurz and Apps 1999; O'Neill et al. 2006).

3.4.1 Spatial variation in Rs, ST and SM

The current study showed that spatial heterogeneity in Rs in pyrogenic boreal aspen ecosystems may increase with increasing stand age and structural complexity (Table 3-1). Soil respiration in the CC and MA stands had stronger spatially predictable heterogeneity than that in the PF stand, which appeared to be less heterogeneous and random. These findings support our first hypothesis that Rs in the PF stand would have less heterogeneity and weak spatial dependency, and a fine scale heterogeneity would develop overtime. The large scale (> 11 m) spatial association between Rs, TOC, and FD in the PF stand, and fine spatial association (≤ 8 m) with microbial properties and canopy in the CC and MA stands further confirm this (Figure 3-2).

Lack of spatial structure in Rs in the PF stand can be attributed to the less variability in FD, open canopy structure, and low fine root biomass (Khomik et al. 2006; Rayment and Jarvis 2000; Singh et al. 2008). Although mid growing season (June and July) Rs in the PF stand had large scale spatial structure, fine scale structure was found in the early and late growing season when aspen growth was probably delimited by environmental and physiological conditions such as low soil temperature in May and defoliation in August. This indicates that fire disturbance might have created patchiness in heterotrophic respiration, but homogenized major component of autotrophic respiration i.e. fine root biomass. Stand replacing fire generally consumes total above ground living biomass, which causes mortality in fine roots and decomposition thereafter. Yuan and Chen (2012) in a boreal mixedwood forest found that turnover rate of aspen fine root was highest during the first few years (3 – 11 years) after fire. In aspen dominated southern boreal forests, Finér et al. (1997) also reported a gradual increase in fine root (5 – 10 mm) biomass in organic layer with increasing stand age after fire. Thus a homogenous spatial structure in the autotrophic source of respiration can be expected in the post fire ecosystems as might have happened in the PF stand.

The fine scale spatial autocorrelation of Rs in the CC and MA stands might have originated from fine scale spatial association with stand (canopy cover and FRB) and soil microbial attributes (Table 3-1 and Figure 3-2). In a boreal mixedwood (aspen-black spruce) fire chronosequence, Lavoie and Mack (2012) showed a gradual increase in soil microbial biomass, basal respiration, soil C, and organic layer depth with time since fire. They also found a fine scale spatial autocorrelation in basal respiration in the mature sites, which they attributed to the development of organic layer and understory vegetation. In a boreal black spruce fire chronosequence, Singh et al. (2008) however, did not find any increase in spatial heterogeneity

in Rs among the three stands at an age of 6, 15 and 27 years after fire, and the spatial ranges were mostly > 20 m. They attributed this partly to the spatial variability in Rs that was not captured by their sampling protocol and partly due to the decrease in fine root biomass by the fire event. Soil physical conditions in post-fire environment also control Rs, mainly through the fluctuations in soil temperature and moisture conditions. However, such physical control remains significant only for a short period of time before the vegetation control takes over (Lavigne et al. 2003; Melillo et al. 2002).

The large scale or non-detectable spatial pattern in ST and SM in the PF stand was expected, and might represent the typical spatial structure of abiotic environmental variables in fire disturbed ecosystems with open canopy (Gimeno-García et al. 2004). The detectable spatial pattern in these variables in the CC stand, and the relatively short spatial scale (≤ 13 m) in the MA stand indicate the recovery of spatial variability due to the development in AG and BG features.

3.4.2 Seasonal variation in Rs

The spatial variation in Rs was expected to have localized, fine scale structure during the peak growing months (June and August) (hypothesis 2). Only the MA stand followed the hypothesized trend (Table 3-1). The PF stand did not show any detectable spatial structure in Rs during these months except August, although the CC stand showed fine scale spatial autocorrelation. Similarly, no spatial trend was also detected in ST and SM in these stands. A gradual increase in spatial heterogeneity (as indicated by the decrease in spatial range) in ST and SM was observed in MA stand (Table 3-2). This could be used as evidence that not only the spatial structure in Rs was disturbed by wildfire, but the seasonal pattern of the spatial

relationships was also disrupted, and the recovery was not fully established even at the canopy closure phase. The stand structure (e.g. canopy overlap, understory vegetation, and sapling density) in the CC stand was probably not complex enough to create the hypothesized seasonal trend. Moreover, the huge pile of coarse woody debris in the CC stand might have masked the effect exerted by the AG factors. This suggests that there might be a successional phase up to which the effect from CWD on the spatial distribution of key biogeochemical processes would be distinct and this would disappear gradually after that due to decomposition. Lee (1998), in a boreal aspen stand, found that all the standing snags had fallen down within 15 years of the fire event. Such pulse of CWD after fire disturbance may take 100 years or more to disappear and any new accumulation of CWD afterwards develops from new growth (Hély et al. 2000; Pedlar et al. 2002).

In general, the current study corroborated the seasonal pattern observed by other studies in boreal ecosystems. Khomik et al. (2006) studied seasonal variation in Rs in a boreal mixwood forests and showed that it peaks in June and July due to stand physiological processes such as canopy and root development. Highest summer season Rs in boreal aspen stands was also reported by Russel and Voroney (1998). Lower early growing season (May) Rs in this study is probably due to the lower biotic activity (e.g. root development, microbial activity) resulted from the low soil temperature.

3.4.3 Spatial control on Rs

The spatial pattern in residual error of the Rs regression models in this study was quantified through SAR approach. Therefore the resulting relationships between Rs and predictor

variables can be treated as mechanistic (Keit et al. 2002). A significant negative control of SM and a positive control of FD on Rs were found in the PF stand throughout the growing season. Interestingly, enzyme activities and DOC also showed negative relationships with Rs (Table 4). The findings support our hypothesis of having a moisture and DOC control on Rs in the PF stand (hypothesis 3), although a positive effect of these variables on Rs was expected. The significant positive effect of FD on Rs reconfirms similar finding from several other studies in boreal ecosystems (Khomik et al. 2006; Rayment and Jarvis 2000; Singh et al. 2008). Forest floor layer along with the top 3 - 5 cm mineral soil is the most biotic active zone in the boreal ecosystems (Mariani et al. 2006). Most the of fine root biomass in boreal ecosystems is found in the organic layer and mineral soil interface, which makes the forest floor a very important regulator of soil respiration (Strong and La Roi 1985). As fire probably consumed a significant portion of the organic layer in the PF stand, the residual intact organic layer was very likely to become an important microbial hub and root proliferation zone. Organic matter in the intact zone might have captured thermally altered labile C substrates percolated from the upper layers and this could have initiated the positive feedback to Rs.

The significant positive control of FD on Rs in the CC stand appeared to have resulted from the fresh organic matter and fine root biomass in that layer as aspen sapling density (proxy of organic matter input and root biomass) was also one of the significant drivers of Rs (Table 3-4). However, a stronger positive microbial control (e.g. peroxidase, DOC) was also observed, which might be due to microsite modification (through temperature and moisture) and a continuous supply of C substrate from the lying CWD (Pedlar et al. 2002). Unlike the CC stand, FD did not appear to be a significant predictor of Rs in the MA stand until July, although a positive microbial and DOC control existed. This might be due to the negative relationship

between FD and SM. A negative effect of SM on Rs was found during the early growing season (May - June) in MA and other stands. Such negative control of moisture could be a residual signature of snow melting event. High moisture (> 20%) content had an overall negative relationship with Rs in all the stands, but lower moisture relationship did not follow any specific trend (data not shown).

A joint aboveground and belowground control on Rs was more evident in the CC and MA stands than the PF stand (Hypothesis 4). Forest floor depth, sapling density, and enzyme activity showed a consistent positive control on Rs in the CC stand throughout the growing season (except May), which indicates a recovery of spatial coupling in this stand. The MA stand, however showed the strongest relationship between AG-BG variables and Rs (maximum R^2 0.52). Higher microbial control on Rs than the AG factors in May in the MA stand is probably due to having less pronounced tree influence such as canopy shading, litter input, and fine root growth. These variables became significant driver of Rs in the mid to late growing season (Table 3-4). The strongest aboveground (FD, Canopy, FRB) and belowground (MBC, Bglu, Perox) control in July and August suggests that Rs was mostly regulated through a recovering spatially coupled process in the CC stand and a functioning dynamic process in the MA stand. Evidence of such AG-BG spatial coupling have been reported previously in pyrogenic ecosystems for other biogeochemical properties such as nutrient cycling (e.g. Smithwick et al. 2005), but findings from the current study suggest that the regulating mechanisms of Rs might have similar signature in both canopy closure and mature stands through the cumulative effect of forest floor, microbes, and roots (Weber 1990).

The negative enzymatic control on Rs might be due to the end product inhibition of C mineralizing enzymes. Presence of readily available C inhibits C mineralizing activity (Carreiro

et al. 2000; Shackle et al. 2000). Fire effect on broadleaf forest with low auto-combustibility, as in the case of aspen, has been shown to be responsible for higher input of biodegradable C in soil (González-Pérez et al. 2004). Although the PF stand has overall lower DOC than the MA stand, the soluble C in this stand is probably more bioavailable, as the thermally altered humus layer is likely to have less exchange sites to attract these ions, and this might have generated the negative enzyme-respiration feedback. Humus-aggregate seclusion of enzyme proteins released during wildfire due to microbial death and cell lysis might also have a role to play in generating this negative relationship. These trapped proteins might get freed during the decomposition of organo-mineral aggregates, which can further induce synthesis of extracellular enzymes without necessarily increasing the microbial activity (Dilly and Nannipieri 2001).

Soil respiration in the CC and MA stands also had significant negative control from enzyme activity but only during the early growing season (May). This may suggest that Rs in the pyrogenic boreal ecosystem is not substrate limited in the early growing season, and the concentration of labile C is probably higher than the microbial demand. Significant positive relationship in the later months (June – August), particularly in the CC and MA stands, indicates that there is a biotic demand for C during the peak growing season. The source of respiration in boreal ecosystems has been shown to be changing from stored C pool during the early growing season to photosynthetic products during the peak growing season (Czimczik et al. 2006; Desrochers et al. 2002). Hogberg et al. (2001) emphasized that photosynthates drive the peak to late growing season Rs in boreal ecosystem, and belowground C allocation needs to be considered more than the seasonality in determining the respiratory loss of C. Our findings corroborate these studies from a microbial perspective.

Significant space effect in the Rs of PF stand in May is somewhat confounding, but not surprising given that the some of the variables important for biogeochemical cycling in the post fire ecosystems such as charcoal and organic matter quality were not measured directly in our study (Table 3-5). Distribution of charcoal can have significant control on the spatial variability of biotic properties through its high sorption capacity and porous structure, and the effect is manifested well in recent fire disturbed sites (MacKenzie and DeLuca 2006; MacKenzie et al. 2008). In pyrogenic boreal ecosystems, this can particularly be important during the early growing season when there is a moisture flush from snow melt. The space effect in the May Rs of the PF stand might have resulted from the missing charcoal distribution which indirectly affected C mineralization through the variable water retention in the forest floor. Despite having a very complex spatial model, a significant space effect was also detected in the August Rs of the MA stand. This indicates that a finer spatial lag would probably be more appropriate for quantifying Rs dependency in this stand.

3.5 Conclusions

Studies on the post fire spatial heterogeneity in Rs in boreal ecosystems are few despite its importance in modeling and predicting future net C exchange. To my knowledge, this is the first study which simultaneously looked at the development of spatial heterogeneity in Rs, both seasonally and along a chronosequence of fire disturbance, and modelled the mechanistic relationships between Rs and the driving factors (abiotic, plants and microbes) after considering their spatial autocorrelations. Based on the findings, I conclude that stand-replacing fire has created large scale spatial pattern (less spatial variability) in the Rs of boreal aspen ecosystem, and a development of fine scale heterogeneity (more spatial variability) was found along the

chronosequence. The spatial structure in Rs and the driving mechanisms at the canopy closure phase showed similarity to the mature stand implies a quick recovery in the spatial heterogeneity within 9 years after fire disturbance.

A belowground microbial control on Rs in the PF spatial model suggests a dominance of heterotrophic contribution. However, the emergence of both autotrophic and heterotrophic factors in the spatial models of the CC and MA stands indicates an established AG-BG feedback loop. Forest floor depth could be used as a prime predictor of Rs in all seasons; however, variable combinations of FRB, enzyme activity, and environmental factors would be required for seasonal prediction. Significant space term in the MA stand during the late growing season indicates spatial mechanisms of Rs operate at much finer scale than the used 2 m scale in this study.

Finally, the CV of Rs in this study indicates that our spatial sampling protocol has satisfied the required number of observation to calculate Rs within 10% error limit except in the CC stand which requires almost double number of observation during the peak growing season. This should be considered in all the future spatial studies in similar stands.

Table 3- 1. Seasonal mean, coefficient of variation (CV) and variogram parameters of soil respiration (Rs) measured in three boreal aspen stands in northern Alberta along a fire chronosequence.

Site	Month	Factors	Mean (± SE)	CV (%)	Range (m)	Spatial dependence	Dependence class	Model	R^2
Post Fire	May	†Rs	0.50 (0.02)	30.4	5.8	0.86	Strong	Spherical	0.34
	May	FC	445.21 (2.85)	4.14	ND	-	-	-	-
	Jun	Rs	0.99 (0.06)	39.4	>23	0.53	Moderate	Exponential	0.45
	Jun	FC	439 (1.92)	2.8	ND	-	-	-	-
	Jul	Rs	0.85 (0.05)	36.5	ND	-	-	-	-
	Jul	FC	493 (2.51)	3.3	5.8	0.99	Strong	Gaussian	0.79
	Aug	Rs	0.56 (0.03)	35.4	5.2	0.98	Strong	Spherical	0.21
	Aug	FC	486 (3.41)	4.5	5.7	0.99	Strong	Spherical	0.42
Canopy Closure	May	Rs	0.29 (0.02)	48.3	4.4	0.97	Strong	Spherical	0.28
	May	FC	439.7 (2.94)	4.3	ND	-	-	-	-
	Jun	Rs	0.68 (0.05)	47	5.6	0.96	Strong	Spherical	0.41
	Jun	FC	467.5 (4.49)	6.2	ND	-	-	-	-
	Jul	Rs	1.15 (0.08)	48.6	4.8	0.84	Strong	Spherical	0.26
	Jul	FC	508.5 (4.66)	5.9	ND	-	-	-	-
	Aug	Rs	1.31 (0.07)	35.8	ND	-	-	-	-
	Aug	FC	531.3 (4.90)	5.9	> 23	0.78	Strong	Gaussian	0.93
Mature Stand	May	Rs	0.514 (0.03)	34.2	8.0	0.95	Strong	Exponential	0.21
	May	FC	471.8 (4.90)	6.73	3.6	0.92	Strong	Spherical	0.19
	Jun	Rs	^{c}1.46 (0.08)	35.6	4.0	0.94	Strong	Gaussian	0.58
	Jun	FC	510.3 (3.86)	4.9	21	0.63	Moderate	Exponential	0.50
	Jul	Rs	1.49 (0.07)	32.8	3.6	0.98	Strong	Spherical	0.28
	Jul	FC	556.5 (6.39)	7.4	4.0	0.99	Strong	Exponential	0.46
	Aug	Rs	1.17 (0.07)	40.1	5.0	0.99	Strong	Gaussian	0.78
	Aug	FC	540.3 (4.99)	5.9	18.9	0.62	Moderate	Gaussian	0.84

†Rs = Soil CO_2 efflux (g CO_2 m^{-2} hour^{-1}); FC = Flux CO_2 concentration (ppm); ND = not detected

Table 3- 2. Seasonal mean, coefficient of variation (CV), and variogram parameters of soil temperature (ST) and soil moisture content (SM) measured in three boreal aspen stands in northern Alberta along a fire chronosequence.

	Month	Factors	Mean (± SE)	CV (%)	Range (m)	Spatial dependence	Dependence class	Model	R^2
Post fire	May	†ST	11.38 (0.11)	6.4	ND	-	-	-	-
		SM	0.22 (0.01)	26.5	ND	-	-	-	-
	Jun	ST	12.2 (0.14)	7.5	19	0.52	Moderate	Gaussian	0.33
		SM	0.20 (0.01)	23	ND	-	-	-	-
	Jul	ST	16.1 (0.11)	4.4	> 23	0.50	Moderate	Linear	0.24
		SM	0.22 (0.01)	19	4.8	0.96	Strong	Spherical	0.22
	Aug	ST	15.2 (0.07)	2.9	7.6	0.86	Strong	Gaussian	0.86
		SM	0.14 (0.003)	18.5	ND	-	-	-	-
Canopy Closure	May	ST	6.9 (0.31)	28.9	6.4	0.99	Strong	Gaussian	0.82
		SM	0.23 (0.01)	24.7	> 23	0.71	Moderate	Gaussian	0.73
	Jun	ST	11.4 (0.17)	9.5	> 23	0.85	Strong	Spherical	0.94
		SM	0.21 (0.01)	16.2	20	0.50	Moderate	Gaussian	0.47
	Jul	ST	16.1 (0.12)	4.8	> 23	0.80	Strong	Gaussian	0.96
		SM	0.15 (0.01)	26.6	> 23	0.63	Moderate	Gaussian	0.56
	Aug	ST	15.1 (0.10)	4.4	> 23	0.99	Strong	Spherical	0.89
		SM	0.15 (0.004)	20.5	3.6	0.99	Strong	Gaussian	0.42
Mature Stand	May	ST	7.49 (0.18)	15.2	ND	-	-	-	-
		SM	0.25 (0.01)	27.5	> 23	0.53	Moderate	Linear	0.52
	Jun	ST	9.8 (0.08)	5.4	> 23	0.67	Moderate	Spherical	0.76
		SM	0.22 (0.01)	27.2	13.1	0.59	Moderate	Spherical	0.50
	Jul	ST	13.8 (0.06)	3.1	6.4	0.91	Strong	Gaussian	0.52
		SM	0.15 (0.004)	21.7	ND	-	-	-	-
	Aug	ST	13.7 (0.06)	2.8	6.5	0.89	Strong	Exponential	0.19
		SM	0.09 (0.003)	25.3	4.2	0.99	Strong	Gaussian	0.56

†ST = Soil temperature (°C); SM = Soil moisture ($m^3\ m^{-3}$);

Table 3- 3. Seasonal variation in the required sample size for estimating soil respiration (Rs) in fire disturbed boreal aspen stands within ±10 and ±20% of the sample mean at the 95% probability level.

	May			June			July			August		
	PF	CC	MA	PF	CC	MA	PF	CC	MA	PF	CC	MA
Sample size (n)							42					
Std. deviation	0.15	0.14	0.18	0.39	0.32	0.53	0.31	0.57	0.49	0.21	0.47	0.47
Req. sample size (± 10%)	37	89	31	63	90	52	54	99	45	51	52	67
Req. sample size (± 20%)	9	22	7	16	23	13	14	25	11	13	13	17

Table 3- 4. Spatial regression models and parameters of the seasonal relationships between soil respiration (Rs) and aboveground and belowground properties in three boreal aspen stands in northern Alberta along a fire chronosequence.

		Spatial regression models	Lag coeff. (ρ)	Error coeff. (λ)	Log Likelihood	F	p	AIC	R^2_{adj}
Post fire	**May**	Rs = §§**0.44** + §§**0.07*** FD – †**0.003***CWD – 0.002*BR – ††**0.92***SM	-	†**-0.58**	39.71	$5.42_{5,33}$	0.001	-69.43	0.34
	June	Rs = §§**1.33** + §§**0.16***FD – †**0.01***CWD – †**0.07***FRB – †**0.003***DOC – §**0.06***Perox – **2.53***SM	-	-0.04	1.05	$3.78_{7,32}$	0.005	11.88	0.30
	July	Rs = †§**1.46** + ††**0.001***DOC + 0.004*BR – ††**0.007***DON – †**0.05***ST	-	0.16	34.11	$5.80_{5,31}$	0.001	-58.23	0.34
	Aug	logRs = 0.02 + ††**0.28***logFD – §**0.02***logCWD – §**0.28***logPhenol	-	-0.08	71.24	$4.26_{4,37}$	0.01	-134.49	0.18
Canopy closure	**May**	Rs = †**0.24** + ††**0.02***FD + †**0.01***Sapling – §**0.23***Bglu – †**0.23***Phenol – †**0.02*** MBCN + †**0.01***ST	-	0.07	-54.44	$3.99_{7,30}$	< 0.001	-94.88	0.31
	June	Rs = 0.26 + §**0.03***FD + ††**0.04***Sapling – ††**1.29***Bglu + 0.05*Perox + †§**0.002***DOC – †**1.68***SM	-	†**0.30**	-10.47	$3.46_{7,32}$	< 0.001	-6.95	0.33
	July	Rs = ††**-0.38** + †**0.07***FD + †**0.04***Sapling + ††**0.14***Perox + 1.62*TN + †**0.21***ST	-	0.18	-8.85	$5.73_{6,31}$	< 0.001	29.7	0.40
	Aug	Rs = §§**1.60** + †**0.09***FD + ††**0.003***DOC – †§**7.16***SM	-	0.15	-16.52	$8.13_{4,37}$	< 0.001	41.04	0.36
Mature stand	**May**	Rs = †**0.39** + §§**0.006***MBN + §**0.03***Perox + §**0.002***DOC – †**0.02***DON – †**0.05***TC – †**0.58***SM	-	0.15	24.94	$3.91_{7,34}$	< 0.005	24.94	0.29
	June	Rs = 0.25 + 0.04*FD + §§**0.09***FRB + †**0.003***DOC + †**2.7***Bglu + †**0.14***Phenol – §**1.60***SM	-	-0.01	-12.08	$6.24_{7,32}$	0.0001	38.18	0.43
	July	Rs = 0.12 + ††**0.08***FD – †**0.18***Tdist + §§**0.10***FRB + ††**0.001***MBC + §**2.28***Bglu + 0.10*Phenol – 0.01*BR	-	- 0.18	-14.29	$4.75_{8,33}$	0.0008	44.58	0.40
	Aug	Rs = -2.68 + ††**0.025***Canopy + §**0.03***FD – †§**0.16***Tdist + §§**0.08***FRB + †§**0.001***MBC + ††**0.09***Perox – §**0.07***TC	††**0.29**	-	3.34	$5.96_{8,32}$	0.0001	11.31	0.52

§ $p \leq 0.10$; † $p < 0.05$; †† $p < 0.005$; †§ $p < 0.0005$; §§ $p < 0.00005$

[†]MBC = Microbial biomass C (μg g^{-1} soil); MBN = Microbial biomass N (μg g^{-1} soil); MBCN = Microbial C to N ratio; BR = Basal respiration (μg CO$_2$-C g^{-1} soil day^{-1}); DOC = Dissolved organic C (μg g^{-1} soil); DON = Dissolved organic N (μg g^{-1} soil); Bglu = β-1,4 glucosidease (nmol g^{-1} soil hour^{-1}); Phenol = Phenol Oxidase (nmol g^{-1} soil hour^{-1}); Perox = Peroxidase (nmol g^{-1} soil hour^{-1}); TC = Total C (%); TN = Total N (%); FD = Forest floor depth (cm); FRB = Fine root biomass (kg stem^{-1}; g stem^{-1} in CC); Tdist = Distance to nearest tree (cm); CWD = Coarse woody debris cover (%).
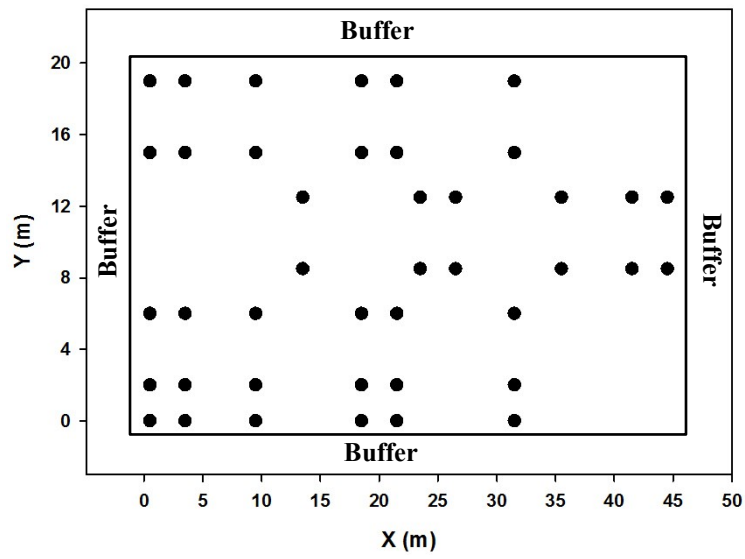
Figure 3- 1. Lay-out of the spatial sampling protocol used in the current study.
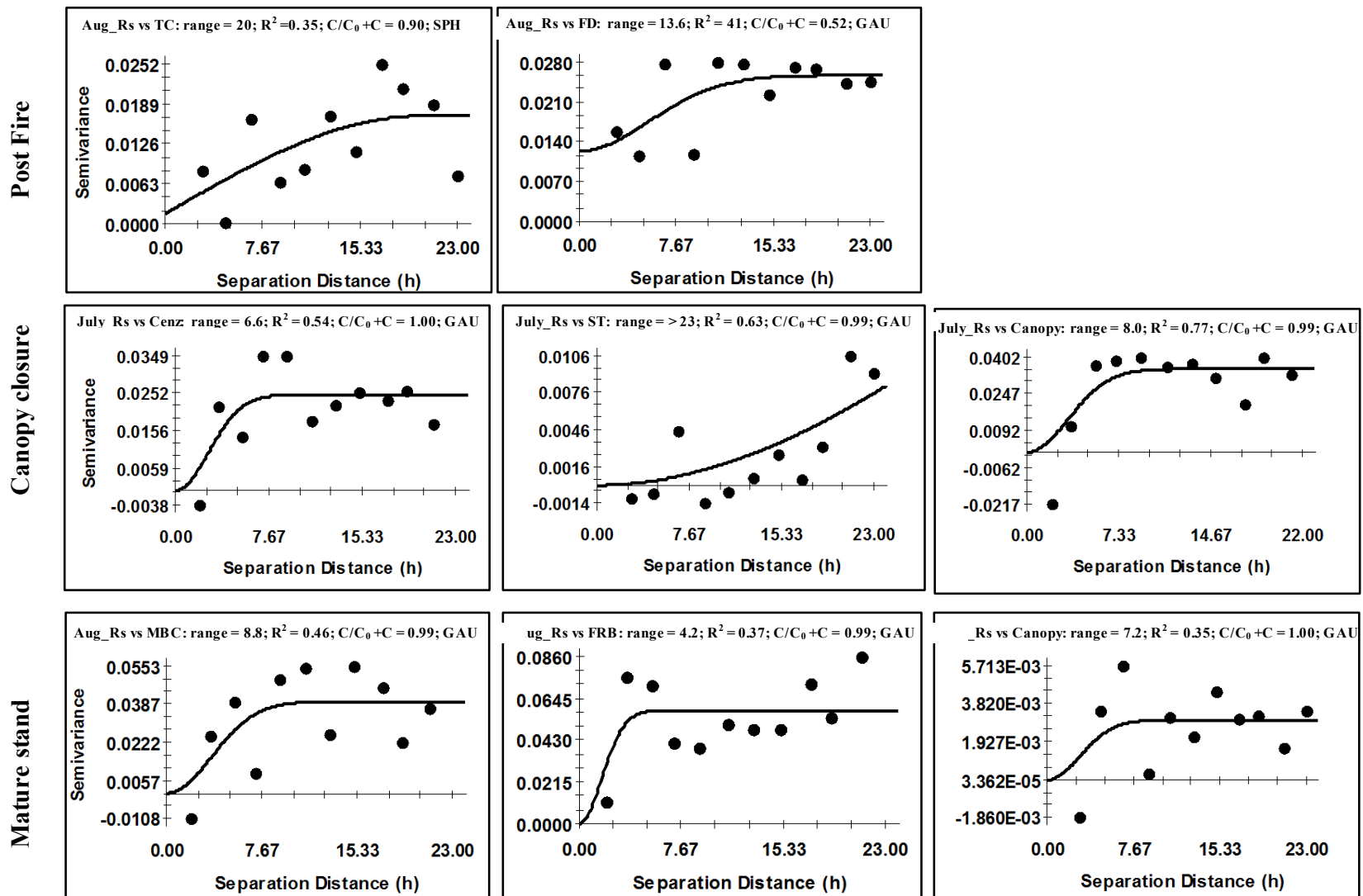
Figure 3- 2. Cross-variograms between soil respiration (Rs) and the aboveground and belowground properties in the boreal aspen stands in northern Alberta along a fire chronosequence (TC = Total organic C; MBC = Microbial Biomass C; Cenz = C mineralizing enzymes; FD = Forest floor depth; Tdist. = Distance to nearest tree; ST = Soil temperature; Canopy = Canopy cover; FRB = Fine Root Biomass; SPH = Spherical; GAU = Gaussian). Only significant cross-variograms are presented here.

Chapter 4. Using Spatial Ecology to Examine Above and Belowground Interactions on a Reclaimed Aspen Stand in Northern Alberta

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4.1 Introduction

Heterogeneity in ecosystem processes may arise from interactions between above and belowground components (Kardol and Wardle 2010). There are both positive and negative feedback loops through which one component influences the other, and sometimes these forces work together under the same spatio-temporal scale to generate specific ecosystem patterns (Wardle et al. 2004). Above and belowground linkages at one level of ecosystem organization can transcend to a higher level of organization; for example the interaction between soil microbes and plant functional traits can directly shape community level biodiversity, which has the potential to affect ecosystem level C and nutrient fluxes (Kardol and Wardle 2010; Van Der Heijden et al. 2008). Aboveground properties such as tree distribution, tree cluster, and forest floor depth can directly or indirectly affect variability in soil microbes, including composition and function (Wardle 2002; Weber and Bardgett 2011). Trees can influence the spatial distribution of under-storey species and belowground biota by modifying resources such as light, moisture, and by their variable rate of litter input and nutrient uptake from soil (Saetre 1999; Wardle 2002; Weber and Bardgett 2011). Belowground organisms can also significantly

influence aboveground vegetation dynamics and distribution. Changes in the soil microbial community can favor plant associations of a certain type by directly modifying organic matter decomposition pathways, and altering belowground nutrient dynamics (Bradford et al. 2002; John et al. 2007).

Microbes are very important biogeochemical agents in marginal or heavily disturbed soil, where they are responsible for initiating ecosystem development and creating resource heterogeneity (DeGrood et al. 2005; Smithwick et al. 2012; Van Der Heijden et al. 2008). Stolp (1988) proposed that microbially driven biogeochemical heterogeneity in soils is determined by the availability of microbial resources and abiotic reaction conditions. Soil microbial control on nutrient availability, therefore, could be stronger at the initial stage of stand development in disturbed ecosystems (Wardle 2002), when the disturbance creates large amounts of labile soil organic matter, as is the case after wildfire (Certini 2005; Choromanska and DeLuca 2002; Fernández et al. 1997) and after tillage in agriculture (Marriott and Wander 2006). Strong microbial influence on vegetation dynamics and nutrient biogeochemistry at the stand initiation phase has also been reported in human disturbed ecosystems such as in ecosystems recovering from surface mining and harvesting (Holmes and Zak 1999; Ingram et al. 2005; Mummey et al. 2002). In nutrient limited northern ecosystems such as the boreal, soil microbial influence on the spatial distribution of nutrients is likely to have similar magnitude as plant contributions since the aboveground and belowground feedback loops in these ecosystems are tightly linked through the accumulation of organic matter (Eskelinen et al. 2009; Van Der Heijden et al. 2008). Disturbance, especially surface mining and reclamation with novel soil substrates, can reshuffle the established spatial structure in the aboveground and belowground processes, and these

patterns might take decades to recover as seen in abandoned agricultural fields Flinn and Marks (2007).

In this study, I seek to tie patterns of nutrient availability to above and belowground properties with spatially explicit sampling and geostatistics. Figure 4-1 and the following outline my specific hypotheses with the objective of: 1) examining spatial predictability of above and belowground properties, 2) isolating the microbial influence on nutrient availability, and 3) examining tree influence on microbial activity.

Hypothesis 1: Young oil sands reclaimed sites usually have less heterogeneity in terms of geomorphological features, including: micro-topography, slope, and sub-surface materials (Figure 4-1). Low heterogeneity in juvenile reclaimed ecosystems has been reported in previous studies (e.g. Nyamadzawo et al. 2008; Shukla et al. 2005). Heterogeneity might develop in such reclaimed ecosystems over time through continuous organic matter input (Boerner et al., 1996; Boerner et al., 1998), modification of soil physico-chemical conditions (Shukla et al., 2007), and proliferation of a diverse soil microbial community (Anderson et al. 2008; Boerner et al. 1996; Boerner et al. 1998; Gibson et al. 1985; Shukla et al. 2007). However, the amount of time it might take for heterogeneity to develop has not been well documented. The most significant aboveground changes in forest ecosystems happen during the canopy closure phase of stand development. Natural fire disturbed aspen ecosystems usually reach canopy closure by 7 to 11 years after initiation (Petersen and Petersen 1992; Valverde and Silvertown 1997). During this time forest floor litter and stand structure will develop predictable patterns that may increase with tree gap or cluster formation (Cumming et al. 2000). Development of heterogeneity in soil nutrients and microbial properties has also been observed within ten years of natural disturbance, such as wildfire in boreal ecosystems (Lavoie and Mack 2012b; Smithwick et al. 2005;

Smithwick et al. 2012; Turner et al. 2011). Therefore, I assume that spatial heterogeneity in above and belowground properties might develop in oil sands reclaimed ecosystem, and examined this in a 14 years old reclaimed site using semi-variogram approach.

Hypothesis 2: Spatial associations with available nutrients occur mostly at the scales of enzymatic reactions necessary to break litter polymers into smaller molecules (Allison 2005), microbial metabolism (Stoyan et al. 2000), nutrient uptake (Selles et al. 1999), and their combined effect (Schimel and Chapin III 2006) (Figure 4-1). The quantity and nature of extracellular enzymes produced by microbes depend mostly on the biochemical characteristics of the native organic matter. Thus, the relative activity of enzymes associated with decomposition should better represent mineralization and nutrient release than other less specific indices, such as total microbial count (Decker et al. 1999). Soil enzymes and microbial metabolism have been shown to be related to nutrient mineralization at variable hierarchical scales in ecosystems recovering from natural disturbances. The scale of such spatial association ranges from < 1 m to 10 m (Ettema and Wardle 2002; Groffman et al. 2009; Smithwick et al. 2005). I believe that nutrient availability in oil sands reclaimed ecosystem would have a fine scale spatial association with microbial properties. I hope to tease apart these belowground interactions using cross-variogram analysis and spatial regression.

Hypothesis 3: Trees can directly or indirectly influence above- and belowground processes through modifications of site condition (Figure 4-1). The major influence of trees on soil properties results from modifications in litter quality, soil temperature, and hydrological regimes, and all these in turn shape the belowground microbial assemblage (Schimel and Chapin III 2006). Consequently, the modifications in decomposer community could be directly linked to nutrient availability (Hypothesis 2). Several studies (e.g. Boettcher and Kalisz 1990;

Kuuluvainen et al. 1993) have been conducted which provide evidence for a "zone of influence" under single tree or tree cluster (Zinke 1962). The spatial range at which individual trees or tree clusters influences belowground processes usually occurs at the scale of either the canopy or root distribution (Saetre 1999). Competition is also responsible for creating patterns and in planted stands, such spatial range has been shown to be 1 – 4.5 m (Fajardo and McIntire 2007; Liski 1995). Therefore, I expected to see a strong spatial association between tree cluster and soil microbial properties at $\geq$ 3 m (the maximum spacing between plants), and used cross-variogram analysis and spatial regression approach to tease these apart.

Re-establishing aboveground and belowground linkages should be the primary goal of reclaiming ecosystems that are disturbed by human resource extraction (Kardol and Wardle 2010). Surface mining in the Athabasca Oil Sands Region (AOSR) of northern Alberta has created a unique opportunity to study the development of heterogeneity in these components. The legal mandate requires extraction companies to reclaim the disturbed landscape to the equivalent land capability that existed prior to disturbance and to selectively salvage soils for use in reclamation (Alberta Government 2014). Recently, a land capability classification system (LCCS) (Leskiw 1998a) was used for measuring the potential of reclaimed sites to grow upland boreal forests. However, capability might not fully represent structural and functional compositions at different scales, and therefore mislead the ecological fidelity of reclamation (see Higgs 1997; Kelly and Harwell 1990). What I am proposing is that ecosystem heterogeneity (or spatial pattern analysis) can be used as a tool for measuring reclamation success/function, either in combination with the LCCS or separately. To my knowledge, only one other spatial study has been done in the AOSR region, which did not account for the belowground spatial control on nutrient availability (see Sorenson et al. 2011). Identifying fine scale heterogeneity in nutrient

availability and their aboveground-belowground control mechanisms in novel, reconstructed ecosystem would enhance our understanding of ecosystem progression after severe disturbance, and at the same time, can assist in measuring reclamation success when compared with natural analogues.

4.2 Methods

4.2.1 Study area

The study site, a 14 year old aspen (*Populus tremuloides* Michx.) stand reclaimed in 1994, is located 40 km north of Fort McMurray, Alberta (57°05'00.9420''N 111°36'44.5654''W). The climate in this region is characterized by short summers and long cold winters. The mean monthly air temperature in the region ranges from -17.4°C in January to 17.1°C in July, with a mean annual temperature of 0.9°C. The mean annual precipitation is 418 mm, with 283 mm occurring as rainfall during the growing season (Environment Canada 2014). Details about reconstruction of soil profiles following oil sand mining can be found in Rowland et al. (2009) and Sorenson et al. (2011). Briefly, soil profiles were reconstructed with surface salvaged organic and geologic materials removed during oil sands mining, and placed as a 10 cm cap of peat and 40 cm of mineral soil as a clean top layer (peat mineral mix; PMM). After placement of capping substrates, the site was offset disked and aspen seedlings were planted at a density of 1700 stem ha^{-1} with an average spacing of 2 – 3 m between trees. Complete fertilizer (N-P-K-S) was applied at a rate of 500 kg ha^{-1} with a blending ratio of 10:30:15:4 to favor the initial establishment of aspen seedlings.

4.2.2 Sampling design

Sample locations were established using a spatially explicit sampling protocol (Appendix V; Figure A5-1). A random walk design (Underwood 1997) was followed, where sampling locations and directions were fixed from a list of randomly generated numbers. A minimum of 30 paired points at each lag distance were selected in order to increase detectable spatial relationships (Journel and Huijbregts 1978). With the random walk method, 15 initial points were located with an interval of 2 -10 m between points, and at each of these, four points were established in cardinal directions at random distances ranging from 0.5 m to 2 m, giving a total of 75 sample points. The minimum spatial resolution of the current sampling protocol was 0.5 m.

All field measurements and sampling were done in August 2008. Key aboveground and belowground variables linked to nutrient availability were measured. Soil variables were selected from the areas that directly influence nutrient bio-geochemistry such as substrate quality, microbial activity and chemical environment (Ingram et al. 2005; Mummey et al. 2002). Plant root simulator (PRS™) probes (Western Ag Innovations Inc., Saskatoon, SK, Canada) were used to measure nutrient availability under field conditions. Cation and anion probes were installed vertically at each sampling point with the top of the probe membrane at the interface of the forest floor and PMM, and left for 12 weeks. Upon retrieval, probes were extracted with 0.5 M HCl and elutes were analyzed for nutrients. Inorganic nitrogen (NH_4^+ and NO_3^-; TIN), and phosphate were analyzed colourimetrically using a segmented flow Autoanalyzer III (Brand and Lubbe, Inc., Buffalo, NY.). Potassium, sulfate, calcium, magnesium and other micronutrients were quantified by inductively-coupled plasma (ICP) spectrophotometry (PerkinElmer Optima 3000-DV, PerkinElmer Inc., Shelton, CT).

Forest floor and PMM samples were collected using bulk density cores (15.2 cm and 5 cm diameter, respectively). PMM samples were collected to a depth of 5 cm. Forest floor depth (FFdepth) was recorded at each point and forest floor mass (FFmass) was calculated on an areal basis from bulk density (Mg ha^{-1}) determined by drying the samples at room temperature (23°C). Finally, location of each tree within 10 m of a sampling point was surveyed using a Vertex III and Transponder T3 with an automatic level. Distance to nearest tree and number of overlapping canopies (stated here as tree cluster) on each sampling point was computed.

4.2.3 Incubation experiment

PMM samples were brought back to the laboratory, sieved (2 mm) and air dried. Total organic C (C) and total N (N) were measured by the Dumas Combustion Method using a Costech 4010 Elemental Analyzer System (Costech Analytical Technologies Inc., Valencia, CA, USA). Soil pH was measured with a 2:1 ratio of 0.01M CaCl$_2$ (Kalra and Maynard 1991).

A 45 day lab incubation experiment was conducted to characterize the key microbial and biochemical properties of these PPM samples. Before incubation, samples were mixed with 20% quartz sand (pH 7.0) to ensure aeration and uniform moisture distribution. Sample moisture was adjusted to 60% of field capacity determined by a pressure plate experiment (at -33kPa pressure). Approximately 100 g of soil-sand mix was pre-incubated for 3 weeks at constant temperature of 25°C to avoid the sudden flush of soil respiration and to re-establish microbial function. During this period, CO$_2$ generation was monitored using gas chromatography (HP 5890, Supelco 8 ft. x 1/8" O.D. stainless steel column, matrix 80/100 HayeSep Q) at 2-3 day intervals until a stable respiration point was reached. After the pre-incubation, soils were mixed with ion exchange resin (J. T. Baker, mixed-bed exchange resins) to adsorb mineralized nutrients. The experimental

incubation was then conducted for 4 weeks. Sub-samples (15 to 20 g) were collected at the beginning and end of incubation, and extracted with 2 M KCl (1:3) for inorganic N (TIN$_{inc.}$; NH$_4^+$$_{inc.}$ and NO$_3^-$$_{inc.}$). Gravimetric moisture content was adjusted by taking jar weight at every 3 to 4 days during the incubation experiment. Basal respiration was measured for three successive days before the end of the incubation using gas chromatography. Finally, samples were analyzed for different microbial properties at the end of the incubation. Measured properties included microbial biomass C and N (MBC and MBN), dissolved organic C and N (DOC and DON), hexose sugar complex (HSC), and extracellular enzyme activities related to C, N, P and S mineralization.

Microbial biomass C and N were measured according to the chloroform fumigation extraction method (Vance et al. 1987) using 20 g soil, extracted in 0.5 M K$_2$SO$_4$ with a ratio of 1:2. Dissolved organic C and N were measured on the unfumigated samples using a Shimadzu TOC-V/TN analyzer (Shimadzu Corp., Kyoto, Japan). Soluble hexose sugar complex (HSC) was measured in unfumigated soil extraction by Anthrone reactive C method as described in DeLuca & Keeney (1993). The amount of pentose and other sugar complexes (PSC) was calculated by taking the difference between DOC and HSC. Microbial quotient (respiration per unit biomass; qCO$_2$) was calculated by dividing the BR with MBC. Ammonium and nitrate (NH$_4^+$$_{inc}$ and NO$_3^-$$_{inc}$, respectively) from the incubation experiment were measured colorimetrically on a SmartChem Discrete Wet Chemistry Analyzer (Westco Scientific Instruments, USA).

Extracellular enzyme activities were measured using microplate assays as described by Sinsabaugh et al. (2003). The activities of β-1, 4-glucosidase (β-glucosidase, E.C. 3.2.1.21), N-acetyl- β-glucosaminidase (NAGase, EC 3.2.1.30), acid phosphatase (E.C. 3.1.3.2) and sulfatase

(E.C. 3.1.6.1) were measured using 4-methylumbelliferyl (MUB) derived substrates. A 200 µl

volume from a soil suspension (1 g soil homogenized in 100 ml 0.1M, pH 5 sodium acetate), and

50 µl of 200 µM substrate were pipetted into each sample well of a 96 well plate. Fifty

microliters of 4-methylumbelliferone (10 µM) plus 200 µl of acetate buffer were used in the

reference standard wells. Quench control wells received 200 µl of soil suspension plus 50 µl of

MUB standard. Each sample was replicated eight times per enzyme assay. Microplates were

incubated at 20° C in the dark for up to 3 hours depending on the assay (a 2 hour incubation was

used for acid phosphatase). Fluorescence was measured at 365 nm excitation and 460 nm

emission, using a microplate spectrophotometer (Synergy HT, BioTek, Winooski, VT). Activity

rates (µmol of converted substrate g^{-1} soil h^{-1}) were calculated on an oven dry basis.

4.2.4 Spatial statistics

Significant spatial patterns were found in the data, therefore I could not consider the samples to

be spatially independent, making parametric statistics of limited use because of inflated degrees

of freedom (Fortin and Dale, 2005; MacKenzie et al., 2008). Failing to account for any

significant spatial structure in data has been demonstrated to have resulted in dramatically

different conclusions on ecosystem processes (Fortin and Dale 2005; Keitt et al. 2002).

Therefore, spatial statistics were used to account for the residual spatial pattern in the data.

4.2.4.1 Spatial autocorrelation

The coefficient of variation (CV) was used as a measure of global variation in the soil

and stand properties, and a semi-variogram approach was used to detect spatial autocorrelation

(local variation). Individual variables were first tested to check for any large scale directional trend, and, if found, trends were removed by polynomial functions using X, Y coordinates (Lloyd 2010). Semi-variograms were calculated with a minimum lag spacing of 0.5 m and a maximum lag distance of 30 m. The nugget to total variance ratio was used to determine spatial dependency. A ratio of less than 25 was treated as weak, between 25 and 75 as moderate, and greater than75 was considered strong spatial dependency (Cambardella and Elliott 1994). Here, spatial dependency was expressed on a scale of 0 to 1, where 1 means perfect spatial dependence. Spatial autocorrelation at > 10 m range (from semi-variogram) was termed as 'Large scale', and all the spatial structure < 10 m was termed as 'Fine scale'. Trend surface analysis was done in openGeoDa package (Anselin 2004). Semivariograms and ordinary kriging maps were produced using ArcGIS Geostatistical analyst module (ArcGIS v 9.3) and GS+ version 9.0 (Robertson 2008). The nearest-neighbor distribution ($G(r)$) was calculated for aspen trees using spatstat library (Baddeley and Turner 2005) in R (R Development Core Team 2011). The upper and lower envelopes of $G(r)$ were computed from 99 Monte carlo simulations. Nearest-neighbor values above the upper envelop indicate tree aggregation, within the envelopes indicate random distribution, and below the lower envelope indicate regular distribution (Baddeley and Turner 2005).

Cross-variograms were calculated to examine the spatial dependence between two variables, and to detect at which distance this association occurs. Assumptions of stationarity and isotropy also hold true for cross-variogram (Journel and Huijbregts 1978; Yates and Warrick 2002b). Log and square root transformed variables were used in calculating cross-variogram to avoid any outlier effect. Positive cross-variance means a positive spatial association, whereas,

negative cross-variance indicates spatial dissociation (McBratney and Webster 1983). Equations for both semi-variogram and cross-variogram are given in the Appendix I.

4.2.4.2 Spatial regression modeling

Spatial regression models (Anselin 1988; Besag 1974) were used to determine what factors were responsible for the variation in available nutrients, as well as to quantify their proportional contribution to this variation after accounting for spatial residuals. A two-step process combining both standard regression and geostatistical techniques were used. As spatial pattern of nutrient availability very much depends on the pattern of multitude of factors such as substrate quality (C:N and labile C), microbial activity (enzyme production and mineralization), and chemical environment (pH, moisture and temperature), I built the initial spatial model with the variables that mostly represents the three categories. Soil properties and stand characteristics were used as covariates, and resin available nutrients were the dependent variables in the regression models. Spatial structures in the selected models were tested by ordinary least square regression (OLSR) with spatial error term and the spatial autoregressive model (SAR). Space term in the model can be regarded as a proxy of unmeasured variables (McIntire and Fajardo 2009b). SAR model was used for its ability to propagate local neighborhood effect in the final model, and to detect spatial autocorrelation due to any unmeasured variables (Keitt et al. 2002). These specific traits of the spatial model are important as the right combination of variables controlling nutrient availability in the novel ecosystem was unknown. SAR was only used when there was significant spatial autocorrelation detected in the model residuals, tested by calculating the global Moran's I (Anselin 2004). Spatial regression analysis was done using Geoda (Anselin

2004) and spdep packages (Bivand et al. 2011) in R program (R Development Core Team 2011). Details of model selection and SAR are given in the Appendix I.

4.3 Results

4.3.1 Spatial autocorrelation

Spatial autocorrelation was found for all the measured soil properties and stand characteristics (Table 4-1). Most of the available macronutrients had fine scale (<10 m) spatial range (Table 4-2). No spatial autocorrelation was found for micronutrients except for Al and Zn. Aluminium had a strong spatial dependency whereas Zn displayed a much weaker relationship. Fine scale spatial range and high global variability (CV from 34 - 63%) were found in soil microbial properties. On the other hand, soil chemical properties such as C, N, and pH showed a spatial range exceeding 10 m with low global variability (CV from 2 - 21%). The spatial range of stand characteristics varied between 2.6 m (forest floor mass) and 4.2 m (tree cluster). Tree distribution showed an aggregated pattern from 0.75 m to 2 m (Figure 4-2). The degree of spatial dependence ranged from 3 – 68% for nutrient availability, 55 – 90 % for soil microbial properties, and 30 – 60 % for stand characteristics. Most of the soil microbial properties had moderate spatial dependency (Table 4-1).

4.3.2 Spatial association

Spatial associations were detected between nutrient availability, microbial properties and stand characteristics as indicated by cross-variance analysis (Figure 4-3). Fine scale (< 10 m) spatial association was found between N-P-S availability and microbial properties (Figure 3a, b and c). $NO_3^-{}_{inc.}$ showed a positive association with MBC (7 m) as evident from the fitted

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variogram model (Figure 4-3a line), but cross-variance also followed a cyclic pattern with maximum amplitude at 8 m, gradually decreasing to 12 m (Figure 4-3a points). Such cyclic pattern was observed in most of the cross-variograms between N-P-S availability and microbial properties. For example, cross-variance between P availability, acid phosphatase and β-glucosidase had a cyclic pattern at every 10 m and the fitted variogram models indicated a spatial range < 4 m (Figure 4-3b). The similar cyclic pattern was also found in the cross-variance between S availability and metabolic quotient, although no spatial range was detected for the current scale of measurement (Figure 4-3c). Potassium, Ca and Mg did not show any clear spatial association with microbial properties.

Spatial associations between microbial properties and stand characteristics showed either large scale (>15 m) or very weak pattern. For example, MBC and DOC showed negative association with tree clustering at 16 m and 21.1 m, respectively (Figure 4-3d). Enzyme activities such as β-glucosidase and acid phosphatase, on the other hand, had very weak to random association with tree cluster. Cross-variance analysis between nutrients and stand characteristics also revealed spatial associations at larger scales ($\geq$ 23 m) and did not show any cyclic pattern (data not shown). Bivariate correlation analysis (global correlation) between microbial properties and stand characteristics further confirmed the poor dependency between these variables (Appendix V; Table A5-1).

Spatial distribution of available nutrients was more similar to the spatial distribution of soil microbial properties as indicated by Krigging (Figure 4-4). Hot and cold spots in P availability matched well with that of BR, phosphatase, and β-glucosidase activity. The TIN (both resin available and incubation) map had patch similarity with DON maps. The $TIN_{inc.}$ map also exhibited patch similarity with MBC, BR, and β-glucosidase activity. Sulfur availability did

not show any distinct patch similarity with a single property, however, it had a mixed pattern similar to β-glucosidase activity and BR.

4.3.3 Spatial regression models

Both the separate and combined effects of above and belowground attributes were tested on nutrient availability. Models with predictor variables including stand characteristics and soil chemical properties (pH, C and N) indicated a significant space effect for TIN, S, P, Al and Cu availability. However, after incorporating soil microbial properties in the model, the significant space effect disappeared, indicating a sufficiency of predictor variables in the model at the scale of measurement (Table 4-3 & 4-4). Nitrogen availability was mostly controlled by MBC (positively) and pH (negatively), whereas β-glucosidase activity and soil C were the most significant controlling factors for P availability. HSC and DON were found to be the most significant factors for S availability. No significant spatial structure was detected for Ca, K, Mn and B when only stand characteristics were in the regression model; however, including soil microbial properties in the model lowered the AIC and almost doubled the R^2. Stand properties, specifically forest floor depth and soil pH, were significant predictors of Mg, Ca, K, Fe, Zn and Al. Significant microbial control through BR, β-glucosidase, and phosphatase activity was found for micronutrients such as Mn, B and Cu. Aluminium and $TIN_{inc.}$ both had significant spatial structure in the regression model even after incorporating stand characteristics and microbial properties (Appendix V; Table A5-2).

4.4 Discussion

4.4.1 Spatial pattern of soil and stand properties

Fine scale spatial patterns in nutrient availability, soil microbial properties, and stand characteristics indicate that aboveground and belowground processes in this reclaimed aspen ecosystem have developed some heterogeneity. This finding supports the first hypothesis that aspen stands should develop spatially predictable variability in soil and stand attributes; however, the relationships are not as strong as we would expect after 14 years of recovery from oil sands reclamation. Heavily disturbed and managed systems (e.g. agricultural sites) tend to have either large scale or no spatial pattern in soil properties (Fraterrigo et al. 2005; Robertson et al. 1993). I believe that at initiation oil sand reclamation sites are comparable to agricultural sites, because homogenization had happened at different stages during soil salvage and placement when the site was built. There might be a possibility that larger blocks of soil and organic materials might have retained some of the spatial variability from the donor sites, however, offset disking done after soil placement was very likely to have destroyed the ecological legacies that had created the variability. Over time, heterogeneity must develop in the reclaimed system through contributions of mass and energy from plants and soil microbes (Anderson et al. 2008; Shukla et al. 2007). Cambardella et al. (1994) reported > 100 m spatial range of soil microbial biomass and N availability in a no-till agricultural field which had been previously managed through tillage. Flinn and Marks (2007) found that spatial homogenization of soil properties and altered vegetation composition remained as a legacy of former agricultural practices even after 100 years of reforestation. Lesschen et al. (2008), in semi-arid ecosystem, showed that recovery of spatial heterogeneity in vegetation and soil properties takes at least 40 years after abandonment of agriculture field. On the other hand, Banning et al. (2008) and Graham and Haynes (2004) reported the development of natural levels of variation in soil microbial properties 18 to 22 years after reclamation and attributed this to aboveground factors

such as litter quality. Mummey et al. (2002) found a fine scale structure (< 14 cm) in soil microbial community composition and N availability in a 22 year old reclaimed grassland and proposed that belowground controls, including plant root activity and nutrient foraging, had contributed to this heterogeneity.

4.4.2 Spatial coupling between aboveground and belowground properties

Common spatial association between nutrient availability and soil microbial properties supports the second hypothesis. However, the spatial associations between soil microbial properties and tree cluster were either weak or occurred at a scale greater than 15 m, which is contrary to hypothesis 3, that these properties would be associated at the scale of tree clustering (~ 2 - 3 m; Figure 4-2). Fine scale spatial association between nutrient availability and microbial properties indicates that belowground connections have been re-established in the reclaimed system. Spatial range of nutrients such as TIN, P and S had similar scale with most of the microbial properties (5 to 8 m), which suggests joint spatial processes at the given scale. The fine scale cyclic spatial association between nutrients and microbial properties (< 10 m) also supports the idea of re-established belowground connection. This type of periodicity might arise from evenly distributed interactions between two or more spatial processes (Bruckner et al. 1999), for example the coupling between MBC and labile C (HSC), as both of these properties showed a spatial range close to 10 m. Such regular distribution in belowground properties can result from the symmetric root and microbial competition for resources due to microsite variations, which ultimately determine the availability and spatial pattern of nutrients (Fajardo and McIntire 2007; Raynaud and Leadley 2005).

However, the expected cyclic pattern in aboveground attributes necessary to create regular microsite variations was not observed. The weak and/or mostly large scale spatial associations between stand characteristics and nutrient availability suggests that aboveground factors in the reclaimed aspen stand were not strong enough to directly contribute to heterogeneity in belowground biological properties, at least in a spatial context. This is surprising given that a companion paper indicated that forest floor depth had a significant influence on microbial community structure as indicated by phospholipid analysis (Sorenson et al. 2011). It is possible that the organic matter quality of the evenly distributed peat substrate is overriding the aboveground controls. A comparative study done in the AOSR found that sites reclaimed with peat have significantly different microbial biota and nutrient profiles than that of undisturbed natural analogues (Quideau et al. 2013). The organic matter structure of peat has also been shown to be different from that found in the forest floor of upland boreal ecosystems (Turcotte et al. 2009). Finally, a greenhouse study conducted by Pinno et al. (2012) showed that the performance of aspen seedlings was better on a salvaged forest floor substrate than a peat substrate similar to the one used here.

4.4.3 Mechanistic relationship between nutrient availability, soil and stand properties

Spatial regression models were used to account for the above and belowground control of nutrient availability in the reclaimed system. Strong soil microbial control on N-P-S availability in the regression models confirms that these nutrients are microbially mediated in the reclaimed environment (Table 4-3). This finding also supports the second hypothesis that microbial control on nutrient availability will be strong. Extracellular enzyme activity and labile C were the two important microbial predictors of nutrient availability besides soil pH. A few studies have

reported similar observations of microbial control on nutrient availability in reclaimed ecosystems (Banning et al. 2008; Mummey et al. 2002); however, they did not quantify the spatial relationships among these processes. I treated the spatial pattern of residuals separately in the regression models, and the resulting relationships between nutrient availability and predictor variables can be treated as mechanistic (Keitt et al. 2002).

A negative relationship has been found between P availability and phosphatase activity in the spatial regression model. Negative feedback between P and phosphatase activity in previous studies was mostly attributed to the biotic demand for P (Juma and Tabatabai 1978; Olander and Vitousek 2000; Sinsabaugh et al. 1993; Tadano et al. 1993); however the actual mechanism of this relationship is not well understood. Goldstein et al. (1988) theorized that phosphatases are inducible enzymes dependent on end product inhibition. Plant roots and microbes do not usually exude phosphatase unless P availability does not meet their growth requirements. The negative relationship found in this study and the fact that the peat substrate used for oil sand reclamation is low in available P (Pinno et al. 2012), represents evidence that biologically mediated belowground processes are trying to alleviate low P availability to satisfy growth requirements. Beta-glucosidase activity and TOC were the other two significant predictors of P availability as indicated by the regression model. Release of P from organic forms can either be a byproduct of C mineralization, where processes are mainly mediated by microbial energy (C) requirements, or can be a result of biochemical mineralization, where organisms are actively seeking P for biochemical reactions (McGill and Cole 1981; Turner and Haygarth 2005). Depolymerisation of complex organic P polymers might require additional enzymes before the organic intermediates are available to phosphatases (McGill and Cole 1981; Spears et al. 2001). Therefore, we can interpret the observed positive relationship between β-glucosidase activity and P availability to

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be the consequence of biochemical mineralization to cleave off the ester bound P (C-O-P) since

the reclaimed system is P limited. A negative relationship was also detected between S and

sulfatase activity in the spatial regression models. Similar to phosphatase, sulfatase is also

subject to end product (SO_4^{2-}) inhibition. Several other studies reported a similar negative

relationship between inorganic S and sulfatase activity (Maynard et al. 1985; Prietzel 2001;

Saviozzi et al. 2006). Maynard et al. (1985) found that sulfatase activity decreases when

inorganic S concentration is high in soil solution. Wet deposition of S in the AOSR has been

reported to be between $11 - 39$ kg ha^{-1}year^{-1} (Proemse et al. 2012), which is much higher than

the natural background of surrounding forested areas. Sulfate concentration in wet deposition

often occurs in excess of vegetation requirements (Lindberg et al. 1986), likely moves through

mineral soil, and this might have generated the inhibition of sulfatase activity in the study area. A

positive relationship was observed between NAGase and S availability. This could happen when

microbes use N rich compound as energy substrate to mineralize organically bound S (C-S or C-

N-S) to meet C demand (McGill and Cole 1981). This might be a possible mechanism of C

mineralization in the reclaimed site, since S is already abundant in the system.

Although aboveground attributes in this study seem to have weak contribution to the

availability of most of the essential macronutrients, forest floor depth showed a significant

positive relationship with the availability of most base cations and micronutrients. The role of

aspen as a cation pump has been recognized previously by different studies (Hobbie et al. 2006;

Paré and Bergeron 1996). Returning cations to mineral soils through leaf litter is an important

mechanism by which aspen might re-establish aboveground control on nutrient cycling and a

return to natural function in the reclaimed environment. Aspen was previously found to initiate

rapid forest floor development and establish links between aboveground and belowground

processes in the AOSR (Sorenson et al. 2011). However, development of spatial structure in micronutrients and base cations might take longer than the microbially mediated nutrients, as indicated by this study.

4.5 Conclusions

I used spatial analysis to tease apart scale dependent mechanistic relationships between nutrient availability, microbial properties and stand attributes 14 years after reclamation. This study revealed some interesting spatial control mechanisms of nutrient availability in the novel reclaimed ecosystem which might be useful for the management of such areas. Spatially structured variability in nutrient availability, microbial properties, and stand attributes indicated that the reclaimed ecosystem developed heterogeneous structure, although the spatial coupling between some of these properties was not well established. Stand attributes showed large scale spatial association and weak control on essential macronutrients (N, P and S) which suggests that availability of these nutrients in the reclaimed environment is more strongly regulated by belowground processes. In this young reclaimed system, N, P, and S availability was spatially predicted at less than 10 m scale from microbial properties such as extracellular enzyme activity and labile C. Availability of micronutrients, although not spatially structured, seemed to be controled by forest floor thickness, soil microbial activity, and pH. Examining spatial patterns in ecosystem function will provide some of the data necessary to assess boreal forest reclamation, where interactions between many different woody perennial species and a living forest floor dominates. Future studies in the reclaimed ecosystems can also take advantage of the current spatial information to design ecologically meaningful sampling designs.

Acknowledgements

Table 4- 1. The mean, coefficient of variation (%), spatial range, spatial dependence class and semi-variogram models fitted to soil properties and stand characteristics of a 14 year old aspen reclaimed site.

	Factors	Mean (± SE)	CV (%)	Range (m)	Spatial dependence	Dependence class	Model	RMSE[†]
Stand characteristics	FFdepth (cm)	2.1 ± 0.05	21.1	2.2	0.44	Moderate	Gaussian	1.10
	FFmass (Mg ha^{-1})	40 ± 10	31.4	2.6	0.32	Moderate	Spherical	1.13
	Tree cluster (canopy overlap)	1.3 ± 0.13	84.5	4.2	0.68	Moderate	Exponential	1.06
	Treedist. (m)	0.85 ± 0.06	57.5	3.2	0.62	Moderate	Gaussian	1.04
Soil properties — Microbial	MBC (µg g^{-1} soil)	178.3 ± 9.41	45.7	7.7	0.64	Moderate	Gaussian	1.07
	MBN (µg g^{-1} soil)	17.1 ± 1.57	62.5	8.5	0.71	Moderate	Gaussian	1.08
	HSC (µg g^{-1} soil)	41.4 ± 2.44	51.2	8	0.90	Strong	Exponential	1.09
	PSC (µg g^{-1} soil)	154.8 ± 7.69	43.0	18.6	0.76	Strong	Circular	0.99
	DON (µg g^{-1} soil)	48.3 ± 1.97	35.5	4.7	0.67	Moderate	Gaussian	1.13
	BR (mg CO_2-C kg^{-1} soil day^{-1})	4.1 ± 0.26	54.6	6.7	0.73	Moderate	Circular	1.10
	qCO2	0.02 ± 0.001	40.1	12.3	0.60	Moderate	Circular	1.05
	βglucosidase (µmol g^{-1} soil hour^{-1})	0.12 ± 0.005	35.5	5.8	0.55	Moderate	Circular	1.12
	NAGase (µmol g^{-1} soil hour^{-1})	0.07 ± 0.003	34.5	4.0	0.79	Strong	Exponential	1.25
	Phosphatase (µmol g^{-1} soil hour^{-1})	0.08 ± 0.004	43.5	5.3	0.52	Moderate	Gaussian	1.09
	Sulfatase (nmol g^{-1} soil hour^{-1})	1.47 ± 0.06	35.2	7.2	0.61	Moderate	Circular	1.13
Chemical	C (g kg^{-1} soil)	92.4 ± 2.26	21.2	23	0.50	Moderate	Gaussian	1.06
	N (g kg^{-1} soil)	4.1 ± 0.12	24.8	19	0.47	Moderate	Gaussian	1.04
	C:N	22.5 ± 0.22	8.4	13.5	0.40	Moderate	Gaussian	0.98
	pH	6.7 ± 0.02	2.2	13	0.16	Weak	Gaussian	0.97

[†]RMSE = Root mean square error

Table 4- 2. The mean, coefficient of variation (%), spatial range, spatial dependence class and semi-variogram models fitted to the available nutrients in a 14 year old aspen reclaimed site measured using PRS probes (µg 10 cm-2) and lab incubation experiment.

	Factors	Mean (SE)	CV (%)	Range (m)	Spatial dependence	Dependence class	Model	RMSE
Macro Nutrients	[†]$NH_4^+{}_{inc.}$	0.35 ± 0.03	70.9	6.8	0.66	Moderate	Gaussian	1.06
	$NO_3^-{}_{inc.}$	30.1 ± 2.42	69.7	6.5	0.68	Moderate	Gaussian	1.05
	NH_4^+	2.55 ± 0.31	104.3	5.5	0.13	Weak	Circular	0.98
	NO_3^-	7.83 ± 1.47	162.8	2.0	0.28	Moderate	Circular	0.81
	P	4.78 ± 0.35	63.4	3	0.28	Moderate	Gaussian	0.98
	K	103.2 ± 7.12	59.8	4.2	0.07	Weak	Exponential	0.97
	S	631.8 ± 22.4	30.7	5.7	0.21	Weak	Gaussian	0.97
	Ca	2989.8 ± 36.5	10.5	25	0.03	Weak	Circular	0.95
	Mg	390.7 ± 6.23	13.8	ND	ND	ND	ND	ND
Micro Nutrients	Fe	18.67 ± 1.36	63.1	ND	ND	ND	ND	ND
	Zn	2.94 ± 0.19	57.9	14	0.15	Weak	Exponential	1.05
	B	3.08 ± 0.20	56.8	ND	ND	ND	ND	ND
	Mn	0.63 ± 0.05	72.7	ND	ND	ND	ND	ND
	Al	79.4 ± 2.85	31.1	10.3	0.79	Strong	Gaussian	0.99
	Cu	0.41 ± 0.01	20.0	ND	ND	ND	ND	ND

[†]inc. = From incubation experiment; ND = Not detected;

Table 4- 3. Standardized spatial regression coefficients for predictive variables of available macronutrients in a 14 year old aspen reclaimed stand (models shown in bold text has significant spatial structure).

Properties	TIN			P			S			Ca			Mg		K	
	Full	WOSC‡	**WOMP†**	Full	WOSC	**WOMP**	Full	WOSC	**WOMP**	Full	WOSC	WOMP	Full	**WOSC**	Full	WOMP
	Adj. R² 0.18	Adj. R² 0.17	Adj. R² 0.12	Adj. R² 0.20	Adj. R² 0.18	Adj. R² 0.09	Adj. R² 0.21	Adj. R² 0.18	Adj. R² 0.12	Adj. R² 0.12	Adj. R² 0.06	Adj. R² 0.06	Adj. R² 0.11	Adj. R² 0.05	Adj. R² 0.06	Adj. R² 0.05
	AIC 603	AIC 602	AIC 606	AIC 367	AIC 368	AIC 375	AIC 992	AIC 993	AIC 996	AIC 1070	AIC 1074	AIC 1073	AIC 807	AIC 810	AIC 830	AIC 829
Tree cluster	-	-	0.48*	-	-	-	-	-	0.11**	-	-	-	-	-	0.09	-
Treedist.	-	-	0.49	-	-	-	-	-	-	-	-	-	0.05	-	-	-
FFdepth	-	-	-	0.53	-	0.65	-	-	-	0.14*	-	0.14*	0.15*	-	-	-
FFmass	0.58	-	-	-	-	-	-	-	-	-	-	-	-	-	0.46*	0.48*
MBC	1.04*	0.87*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BR	-	-	-	-	-	-	-	-	-	0.05*	0.06*	-	-	-	-	-
HSC	-	-	-	-	-	-	0.33**	0.32**	-	-	-	-	-	-	0.16	-
PSC	-	-	-	-	-	-	-0.28*	-0.32**	-	-	-	-	-	-	-	-
DON	-	-	-	-	-	-	-0.49**	-0.44**	-	-	-	-	-	-	-	-
βglucosidase	-	-	-	0.96**	1.03**	-	-	-	-	-	-	-	-	-	-	-
NAGase	-	-	-	-	-	-	0.27*	0.19	-	-	-	-	-	-	-	-
Phosphatase	-	-	-	-0.36	-0.40	-	-	-	-	-	-0.04	-	-	-	-	-
Sulfatase	-1.86**	-1.87**	-	-	-	-	-0.09	-	-	-	-	-	-	-	-	-
C	-	-	-	0.58*	0.58*	-	-	-	-	-	-	-	-	-	-	-
N	-	-	-	-	-	0.65*	-	-	-	-	-	-	-	-	-	-
C:N	-	-	-	-	-	-	-	-	-	-	-	-	0.43*	0.34	-	-
pH	-18.6**	-18.2**	-15.9*	-	-	-	-	-	-	-	-	-	-1.73*	-1.62*	-	-
P	-	-	-	-	-	-	-0.11*	-	-0.09	-	-	-	-	-	-	-

Table 4- 4. Standardized spatial regression coefficients for predictive variables of available micronutrients in a 14 year old aspen reclaimed stand (models shown in bold text has significant spatial structure).

Properties	Al			Mn			B			Cu		
	Full Adj. R² 0.32 AIC 671	**WOSC‡** Adj. R² 0.27 AIC 674	**WOMP†** Adj. R² 0.21 AIC 680	Full Adj. R² 0.23 AIC 81	WOSC Adj. R² 0.23 AIC 81	WOMP Adj. R² 0.14 AIC 88	Full Adj. R² 0.16 AIC 288	WOSC Adj. R² 0.10 AIC 292	WOMP Adj. R² 0.08 AIC 293	Full Adj. R² 0.22 AIC -175	WOSC Adj. R² 0.14 AIC -168	**WOMP** Adj. R² 0.09 AIC -165
Treedist.	-	-	-0.13*	-	-	-	-	-	0.18	-	-	-
FFdepth	0.33*	-	0.26	-0.86*	-	-0.92*	0.73*	-	0.81**	0.30**	-	0.30**
BR	-	-	-	0.72**	0.85**	-	0.38**	0.38**	-	0.08	0.08	-
HSC	0.44**	0.43**	-	-	0.53*	-	-	-	-	-	-	-
DON	-0.56**	-0.55**	-	-0.77**	-1.54**	-	-	-	-	-	-	-
βglucosidase	-	-	-	-0.45	-0.50	-	-	-	-	0.17*	0.18*	-
Phosphatase	-	-	-	-	-	-	-0.36*	-0.37*	-	-	-	-
C	-	-	-	-	-0.89*	-	-	-	-	-	-	-
N	-0.29*	-0.29	-	-	-	-	-	-	-	-	-	-
C:N	-	-	-	-	-	2.16*	-	-	-	0.55*	0.55*	-
pH	-5.1**	-5.2**	-4.8**	-10.9**	-9.4*	-9.4*	-	-	-	-	-	-1.29

‡ WOSC = Regression model without stand characteristics
† WOMP = Regression model without microbial and chemical properties
* p value < 0.05 ; ** p value < 0.005; "-" indicates variables were not selected in the spatial regression model

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Tree scale (m)

Scale of tree cluster (m)

Zone of influence

OM input

H1: Spatial predictability

Zone of influence

H3: Tree influence on microbes

Root exudate

Soil aggr.

SOM

Microbe Scale (μm)

H1: Spatial predictability

H2: Microbial influence on nutrient availability
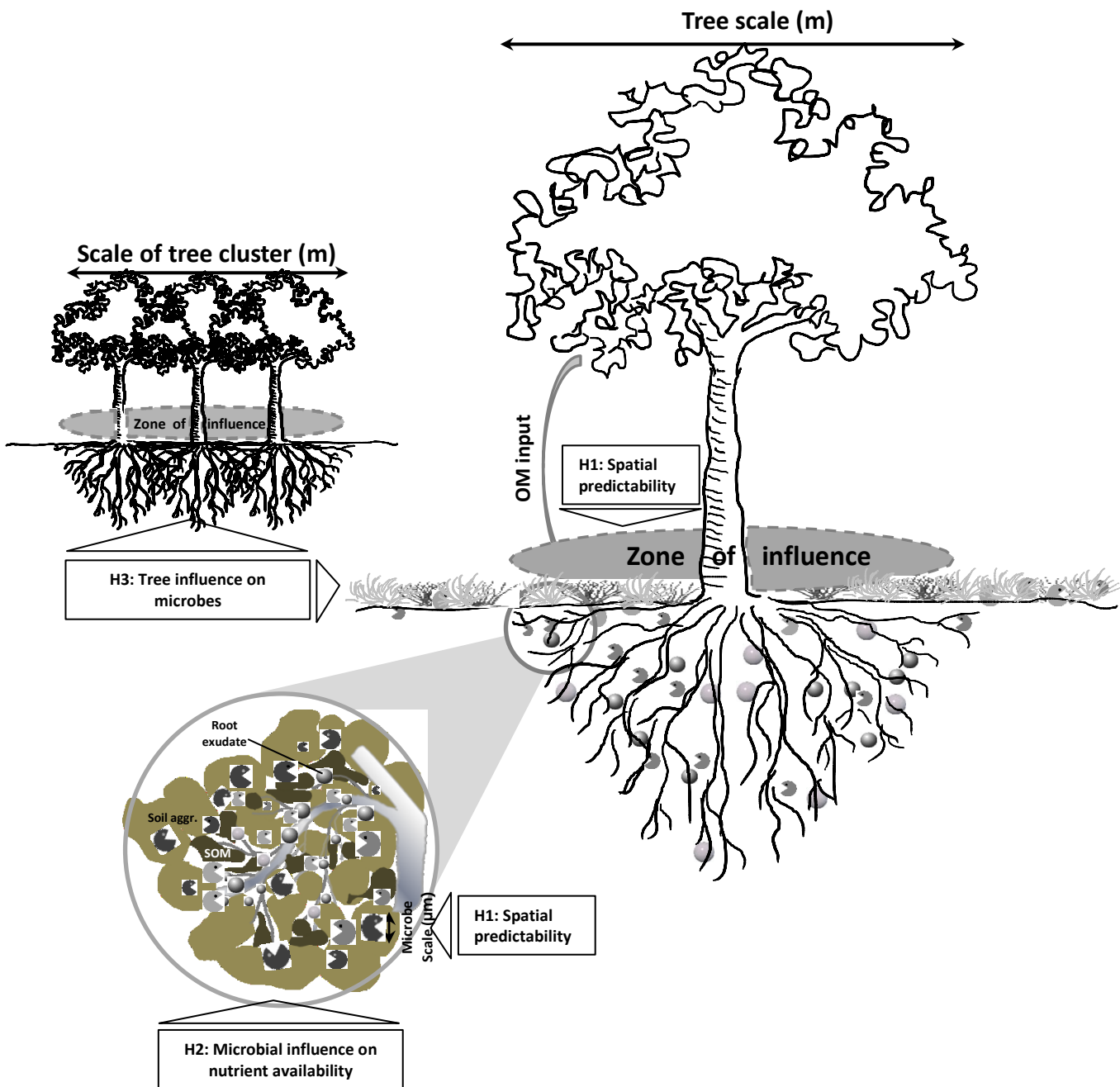
Figure 4- 1. Schematic diagram showing different parts of the working hypotheses.

Aspen Tree Distribution
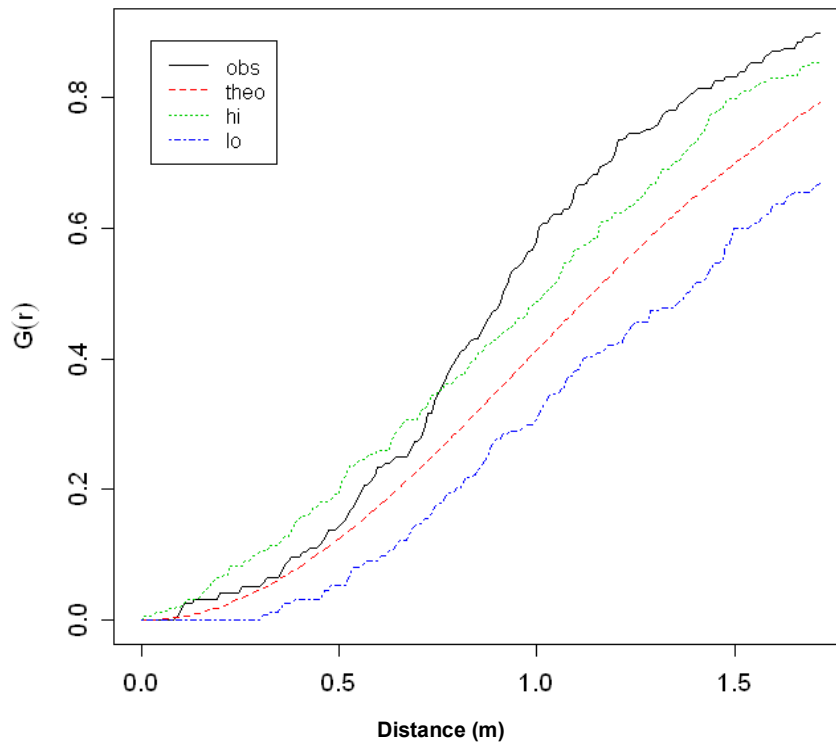
Figure 4- 2. Spatial distribution of aspen trees in a 14 year old oil sands reclaimed stand as estimated from the nearest-neighbor function G(r). Observed G(r) value above the simulation envelope indicates an aggregated pattern and within the envelope indicates a regular pattern. (Obs = Observed value of G(r); Theo = Theoretical value of G(r); hi = Upper envelop of G(r); lo = Lower envelop of G(r)).
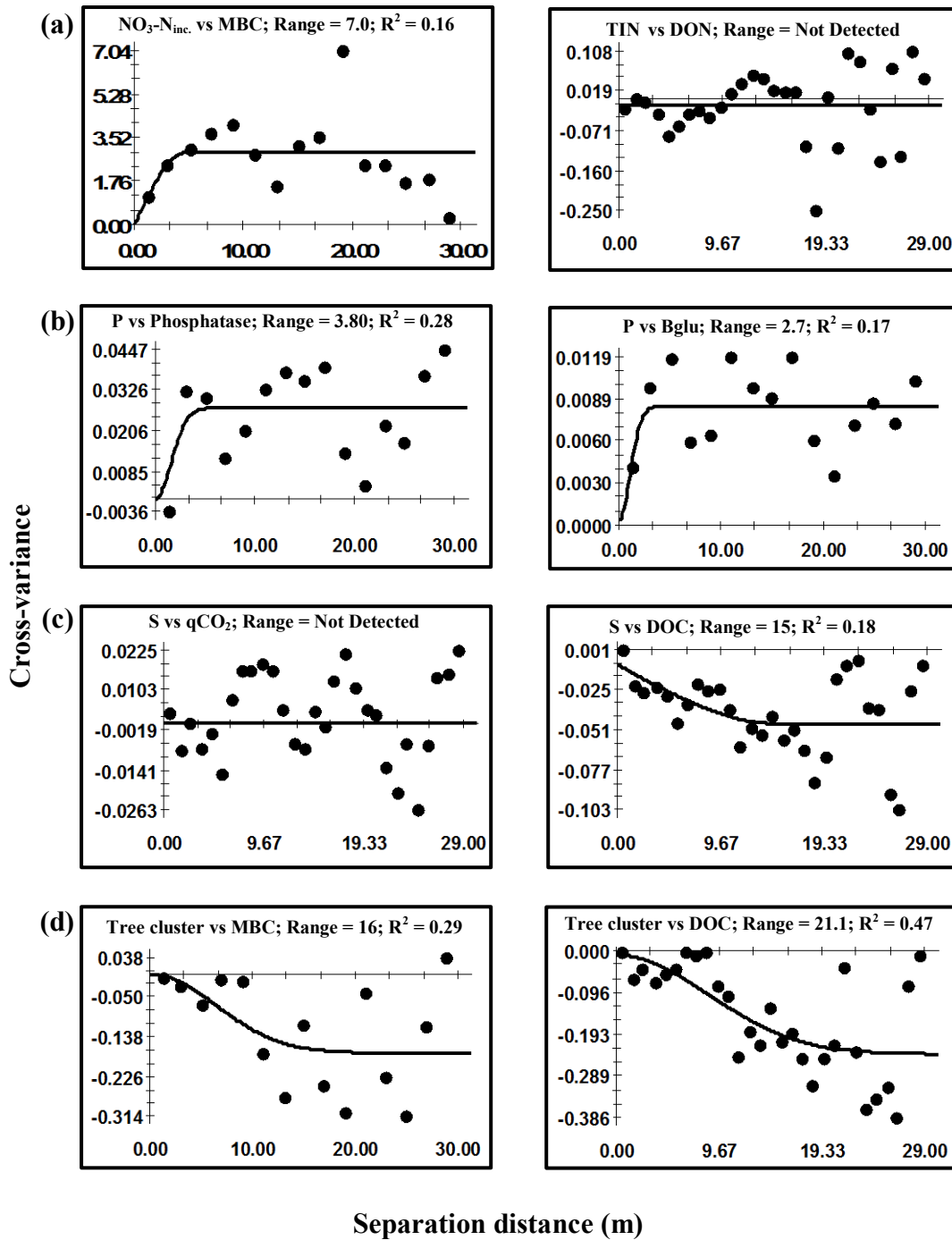
Figure 4- 3. Cross-variograms between available nutrients, soil properties, and stand characteristics of a 14 year old reclaimed aspen stand. Only significant cross-variograms are presented here.
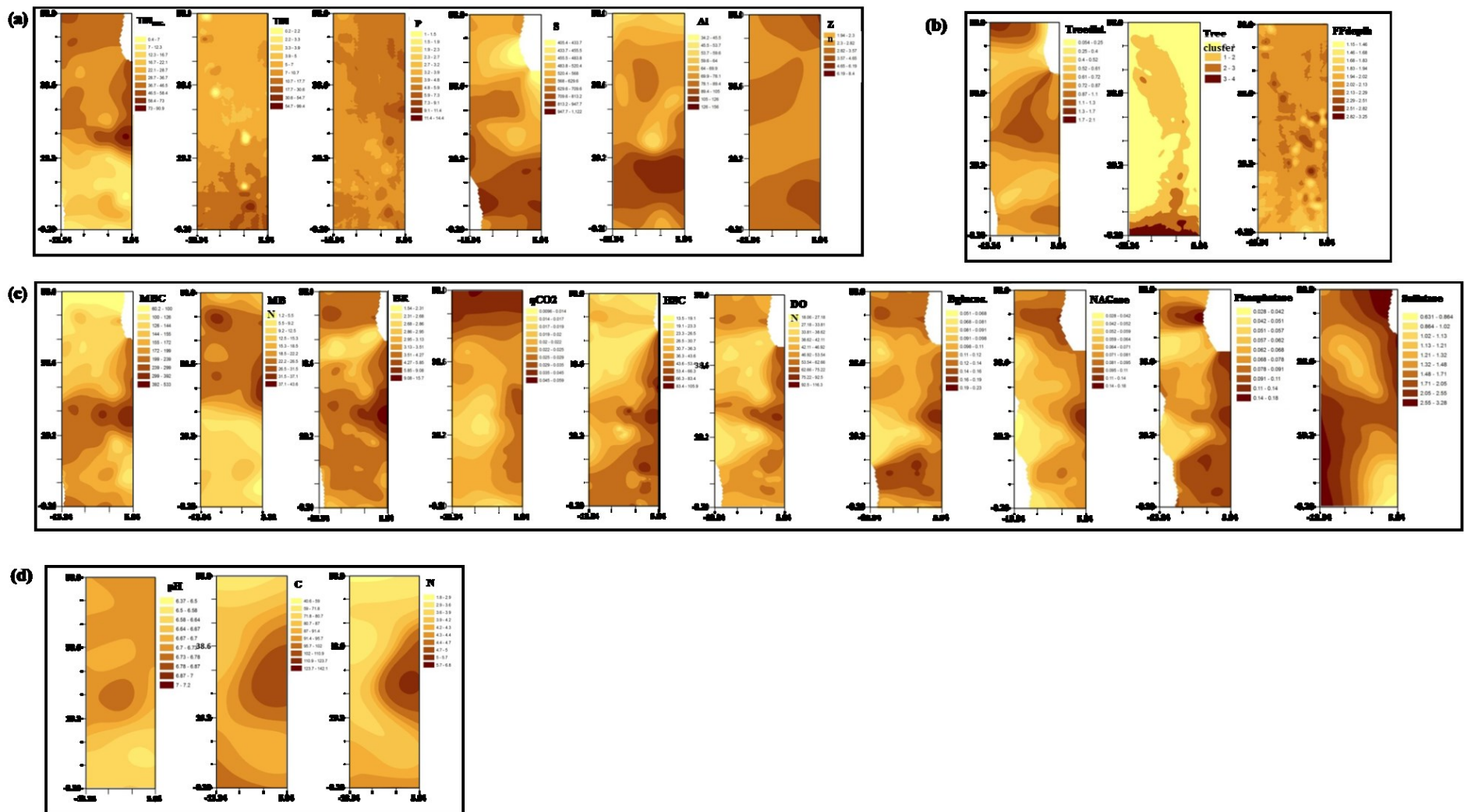
Figure 4- 4. Krieged contour map of TIN$_{inc.}$ and available nutrients measured by PRS probe (a), stand characteristics (b), soil microbial (c), and chemical (d) properties. X and Y axes indicates the coordinates of sample plot. Interpolation did not create complete map where contour lines were either too noisy or had island effect, and were removed from the maps as in the case of most of the microbial properties, S availability, and Treedist.

Chapter 5. Chapter Summaries and Conclusions

5.1 Research Objectives

The main objective of the work presented in this dissertation was to create a benchmark database of biogeochemical properties for reclaiming oil sands mine disturbed ecosystems. An aboveground-belowground approach was used for this purpose with an in-depth characterization of spatial heterogeneity in key biogeochemical properties in natural fire disturbed and oil sands mine reclaimed boreal forests. Chapter two mainly focused on the spatial variability in nutrient biogeochemistry in a chronosequence of fire disturbed aspen stands. A post-fire homogenization of nutrient availability with a gradual increase in spatial variability was detected in this study. Chapter three then tested whether the observed spatial patterns in the nutrient study hold true for C mineralization, measured as soil respiration, and indirectly partitioned the heterotrophic and autotrophic contribution to the total soil respiration from the root biomass. Finally, chapter four characterized spatial variability in nutrient availability in a young oil sands reclaimed site and identified the key regulatory aboveground and belowground mechanisms.

5.2 Chapter Summaries

The three data chapters presented in this dissertation were designed with specific objectives; although the main focus remained on the spatio-temporal pattern of the biogeochemical properties in post-disturbed boreal ecosystems. A number of key findings emerged from these chapters which are described below:

Chapter 2: Spatial variability of nutrient availability in pyrogenic boreal aspen ecosystems: Aboveground and belowground controls

i) Stand replacing fire in boreal ecosystems caused a nutrient flush and uniformity in nutrient availability.

ii) Spatial heterogeneity in nutrient availability seems to be increasing and becoming more spatially predictable over time since fire.

iii) Strong belowground control on nutrient availability was found in the post-fire and canopy closure stands, and a joint aboveground and belowground control was found in the mature stand.

iv) Spatial coupling among nutrient availability and aboveground and belowground factors was the lowest in the post-fire stand and showed stronger coupling in the canopy closure and mature stands.

Chapter 3: Spatial heterogeneity in soil respiration in a boreal aspen forest fire chronosequence

i) The lowest CO_2 flux was found in the post-fire stand during the peak growing months (July and August) and the highest flux was found in the mature stand.

ii) Large scale or no spatial pattern in soil respiration was detected in the post-fire stand, whereas the canopy closure and mature stands showed fine scale (< 10 m) patterns.

iii) Soil respiration showed positive correlation with soil temperature in the canopy closure and mature stands, whereas a negative correlation was observed in the post fire stand when soil moisture is low; however, a positive feedback was also found in case of high soil moisture (Appendix 4: Figure A4-2).

iv)   Variable seasonal control from coarse woody debris, forest floor depth, and soil moisture on soil respiration was found in the post-fire stand with no direct influence from the autotrophic variables, whereas a joint autotrophic-heterotrophic control (tree and soil microbial input) was detected in the canopy closure and mature stands. Significant space effect in the mature stand indicates that control on soil respiration is happening at much finer scale than the 2 m resolution used in this study.

v)   Higher autotrophic respiration in the post-fire stand, higher heterotrophic respiration in the canopy closure stand, and again a higher autotrophic control in the mature stand suggesting shifting control from vegetation to microbial processes on soil respiration along the stand development trajectory (Appendix 4: Figure A4-3).

Chapter 4: Using spatial ecology to examine above and belowground interactions on a reclaimed aspen stand in northern Alberta

i)   Fine scale spatial variability was detected in most of the aboveground and belowground properties, although the spatial dependency of nutrients and aboveground variables was very weak.

ii)   N-P-S availability showed fine scale associations with microbial properties, especially with extracellular enzymes.

iii)   Cyclic spatial associations between nutrients and microbial properties at 10 m scale indicate there might be nested processes happening at much finer scale than that used (0.5 m spatial resolution).

iv)   Large scale spatial associations were detected between tree cluster and soil microbial properties.

v)   Strong belowground control on N-P-S availability through enzymes and substrate

quality with no aboveground influence. Availability of cations was strongly

controlled by the aboveground factors such as forest floor depth and tree distance.

5.3 Project Limitations and Future Research

The overall experimental design of the current study was based on the chronosequence

approach, a very common technique used in ecological studies for the sake of practicality or

necessity. The main assumption of this approach is the homology of spatial variation and

temporal sequences i.e. processes are independent of space and time (Pickett 1989). This was,

however, not assumed in the current study as detecting the temporal pattern of spatial variability

in ecosystem properties along the chronosequence was the main objective of this research. The

underlying assumption of chronosequence approach of this research was rather the similar

microclimatic, pedogenic and disturbance conditions in all the sites. A rigorous site searching

was deployed using GIS, forest inventory and fire data to match the chronosequence sites

according to the vegetation, soil and disturbance conditions. The selected chronosequence sites

were the best possible matches found that satisfied the criteria of experimental design. All the

three sites were within 30 km radius, so most likely experienced a similar weather condition. The

sites were also matched with the ecosite classification (lowbush cranberry ecosite; type d) of

northern Alberta (Beckingham and Archibald 1996), thus confirm a comparable moisture and

nutrient regime among the sites. Terrain conditions (flat) and soil textures (sandy loam to silty

loam) were also similar in all the sites. Although I tried to minimize the potential confounding

factors to make the experimental design sound and ecologically comparable, there are certain

factors that could not be overruled such as the assumption of similar fire disturbance conditions, pre-disturbance species assembly, and post-disturbance vegetation dynamics. In an ideal situation, a permanent sampling plot would remove all these confounding factors if monitored over time. Using process based spatial ecosystem models, one can easily validate the cause and effect relationships between fire disturbance and nutrient biogeochemistry of such field based chronosequence approach; however, there are only few models that simulate spatial ecosystem dynamics, and most of them focus heavily either on the aboveground or the belowground components (e.g. Grant 2001; Pacala et al. 1993; Pacala et al. 1994).

Another major limitation of the current research was the limited number of replicated sites. Each chronosequence site had a sample size of one. However, I used spatially explicit sampling design which was able to capture spatial variation with a minimum resolution of 0.5 m. Such single stand intensive spatial sampling is very common in ecological studies as capturing variability in two dimensional space require fairly large number of spatially explicit samples which often limits the luxury of having several replicated sites (e.g. see Bengtson et al. 2007; Lavoie and Mack 2012a; Saetre and Bååth 2000; Smithwick et al. 2005a; Smithwick et al. 2012b)

The chronosequence sites established for the current research have valuable future research implications to monitor temporal changes in a number of biogeochemical properties that were not possible to test during this research. In study one, nutrient availability was only measured for one growing season, and was only measured until August. However, there are evidences that boreal broadleaf plants are able to recycle nutrients in a temperature condition as low as 0°C (Tanja et al. 2003) and in Fort McMurray weather condition this might not happen

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until the late October (Environment Canada 2015). Thus, future research can focus on repeated longer term nutrient measurements to capture the seasonal variations. Microhabitat factors such as temperature and moisture exert significant influence on ion diffusion through which resin membrane works (Qian and Schoenau 2002). Due to logistic limitation, soil moisture and temperature could not be captured according to the spatial design during the PRS probe burial period. It is, however, strongly recommended to have the spatial pattern of these variables for a total understanding of nutrient dynamics in the wild ecosystems. Soil samples for this study were collected once at the end of the growing season which might not have the same spatial pattern in the other months, although previous studies suggest that spatial structures in microbial processes do not change rapidly unless there is perturbation in soil physical structure and organic layers (Robertson et al. 1993). If resources are available, it would probably be more ideal to sample nutrients and soils during the seasonal transitions such as before and after snow melting in spring, during summer and fall months, and for an extended period during winter months.

In study two, I measured spatial variation of growing season soil respiration with a view to find an easily measurable index to track ecosystem recovery after disturbance. Soil respiration and environmental factors (moisture and temperature) were measured monthly from May – August. The main controlling factors of respiration in different months were then identified using mechanistic spatial models. Stand and soil biochemical attributes were used as independent variables in the model. Although spatial patches of respiration in different months showed consistent patches in different stands, weekly measurement of respiration could detect more spatial signature which might have been missed due to longer time lag. The measured soil respiration is the total of autotrophic and heterotrophic respiration. An indirect multivariate regression approach (Rodeghiero and Cescatti 2006) was used for separating autotrophic and

heterotrophic respiration with an assumption that autotrophic respiration is linearly related with root biomass (Xu and Qi 2001). A direct quantification soil respiration with and without root would generate more concrete evidence of respiration partitioning to its autotrophic and heterotrophic components, and would allow characterizing their spatial patterns as well.

Although nutrient availability was measured in-situ in the reclaimed site (Chapter 4), collected soil samples were air dried and later rewetted to field capacity for incubation experiment. This might have an effect on the microbial properties and processes different than what would be the case in freshly collected soils (e.g. Thomson et al. 2010). However, there are studies also showing that after the initial flush of rewetting cycle, respiration, biomass and enzyme activities quickly recover to the actual level (Wu and Brookes 2005; Zornoza et al. 2006). A three week pre-incubation was conducted before starting the main incubation experiment which might have avoided the initial flush of microbial activity and stabilized the microbial community and functions. Nevertheless, analysis with freshly collected soil samples would be the most ideal condition for microbial analyses to avoid all the confounding factors. The effect of drying and rewetting on the microbial properties and processes have not been adequately tested for soils already disturbed by other events such as fire and mining. Future research can focus on this aspect of soil quality alteration due to soil handling and processing, which often cannot be avoided due to remote sampling locations such as boreal forests.

5.4 Implications for Forest Management and Land Reclamation: Technology Transfer

The research described in this dissertation was conducted for an overall understanding of ecosystem recovery in naturally disturbed upland boreal forest with a view to use the information

in reclaiming oil sands mine disturbed ecosystems in northern Alberta. However, boreal landscapes, in general, are now under pressure for resource extraction, so the findings of the current research have some general applicability, where ecosystem conditions and mode of disturbances are somewhat comparable. Identifying temporal patterns of spatial variability and key mechanisms governing biogeochemical properties were in the core of the current research. There are only limited evidences in upland boreal ecosystems on how spatial patterns of biogeochemical properties recover over time after stand replacing disturbances such as wildfire. From a ecosystem management perspective, current research has utmost importance to spatially model disturbance effect on poorly understood biogeochemical processes such as nutrient cycling, microbial biochemistry and stand dynamics.

5.4.1 Implication for Forest Management

Study one (Chapter 2) of my research identified spatial patterns of nutrient availability along a fire chronosequence. Very low to no post-fire spatial variability in the major plant macronutrients (N and P) indicated a random homogenization effect of fire. This information might be useful for forest and ecosystem managers who are trying to emulate natural condition in restoring ecosystem. The high availability of nutrients after fire also suggests a fertilization effect; thus, fire can be used as an *in-situ* stand management technique without applying inorganic fertilizer for plant establishment. In this study, I proposed a rather new ecological hypothesis on the nutrient control in fire disturbed ecosystems and generated some evidence in support of that. Spatially mechanistic models indicated a strong microbial (mainly extracellular enzyme activities) control on the nutrient availability in the post fire stand. This finding is

challenging some of the earlier literature which suggested that understory vegetation in post-fire stands mostly drive nutrient availability and ecosystem processes (see the review by Nilsson and Wardle 2005). From the management perspective, this could indicate that there is a time lag when growing vegetation in post-fire stand relies on readily bio-available nutrients, after which nutrient cycling from aboveground input becomes more important. Although such time lag is very much dependent of vegetation type and mode of disturbance, careful experimental design with enough stand replicates might be able to identify this, which will give ecosystem managers more flexibility on when to focus on aboveground tending operation, if necessary at all. The spatial scales at which different nutrients were patterned might also be useful in determining boundaries of management prescriptions such as selective harvesting or prescribed burning were to be conducted.

Soil respiration study in Chapter three revealed several interesting facts which might be useful for managing upland boreal forest ecosystems. Contrary to several other studies (Bibliography in Amiro et al. 2003b; Bergner et al. 2004; Bissett and Parkinson 1980), the post fire stand showed the lowest soil respiration than the other older stands. This indicates that burning can be used as an ecological tool to manage forest biogeochemistry without affecting much of the belowground functionalities. Study done by Swallow (2012) in the upland boreal forests of Alberta also postulated similar effect that prescribed burning did not alter microbial community structure. Mechanisms controlling soil respirations in different stands as estimated using the spatial regression models clearly indicated that biotic factors and substrate quality can have much stronger effect than the environmental factors such as soil temperature and moisture, which has been traditionally used to model soil respiration (Buchmann 2000; Fang and Moncrieff 2001; Tang and Baldocchi 2005). Driving factors of soil respiration were also

changing at different time points in different stands during the growing season, which limits the development of a general mechanistic model of soil respiration for stands having different recovery stages. Future research can invest more resources in the total understanding of mechanisms driving soil respiration in disturbance prone boreal ecosystems. Seasonal pattern of spatial variability of soil respiration in different post-fire stands can be used as benchmark condition for oil sands reclamation; however, caution must be exercised while considering the scale and spatial dependency information as the temporal resolution of the measurement in the current study was coarse.

Chapter four raised some concerns about the use of peat substrate in reclaiming upland boreal forest. A clear gap was identified between the aboveground and belowground factors controlling nutrient availability. The findings from this study are suggesting that future construction of reclaimed ecosystem must consider using substrate that favors biogeochemical conditions congenial for growing upland vegetation. Limitation of P and high availability of S in the studied reclaimed site are further indicating that fertilization schemes in the juvenile reclaimed sites must be matched with the potential nutrient supply ability of the substrates. Creating a targeted spatial pattern in above and belowground properties in reclaimed systems will be a challenging task as we do not have enough knowledge about all the governing biogeochemical factors in such novel ecosystems. Some management considerations can, however, be derived from this and the natural fire chronosequence studies, which might help generating spatial heterogeneity in reclaimed ecosystems at a faster pace. Management practice such as the application of coarse woody debris on newly reclaimed sites has already been started (Brown and Naeth 2014). Other possible means for creating ecosystem heterogeneity in the reclaimed systems might be the application of variable substrate mixture (selectively salvaged

forest floor and organic substrates), planting seedlings with variable ages (possibly, some at

sapling stage), applying charcoal as a legacy substrate of fire disturbance, and variable

fertilization schemes matching with the potential nutrient supply rate of topsoil substrates.

However, without a continuous research and monitoring program, it would not be possible to

fully understand the mechanisms of heterogeneity in the reclaimed ecosystems. Given that all the

necessary above and belowground components of forested ecosystem can be put together to

jump start the ecosystem recovery after oil sands mining, these disturbed sites are scientific gold

mines for testing unresolved hypothesis of ecosystem heterogeneity after disturbances, such as

intermediate disturbance hypothesis of heterogeneity (Kolasa and Rollo 1991).

5.4.2 Implication for Land Reclamation

The regulatory mandate for oil sands companies mining in Alberta require all the

disturbed areas to be returned to a functioning landscape of equivalent land capability (Alberta

Environmental Protection and Enhancement Act - EPEA) (Alberta Environment 2010).

Therefore the forested component of the reclaimed sites needs to be within the natural range of

ecosite types found in the Central Mixed Wood Sub-Region of the Boreal forest (Eaton et al.

2014; Alberta Environment 2010;) and the soil quality must be improved to the conditions

similar to or better than that of pre-disturbance conditions (Hemstock et al. 2010). However,

reclamation practice in Alberta is missing appropriate techniques to derive ecologically

meaningful information from natural benchmark conditions which can be used for evaluating

reclamation success. One of the main reasons for this is that the ecology of upland boreal forest

is yet to be well understood, and many biogeochemical processes and their interactions with disturbances are also not well studied (Chapin III et al. 2000).

Until 2014, a land capability classification system (LCCS) used to be the main tool for evaluating land capability of reclaimed ecosystems (CEMA 2006; AER 2014). LCCS is mainly based on the soils and landscape features. The main evaluating criteria in LCCS are available water holding capacity and water table depth, salinity, and soil nutrient status measured based on the total organic C and total N. However, the LCCS system has recently been criticized and removed from the predisturbance assessment and conservation and reclamation (PDA/C&R) guideline due to a number of limitations identified for its inadequacy to characterize the 'equivalent land capability' conditions similar to targeted natural ecosites (AER 2014). Although LCCS has been removed from the PDA/C&R guideline, no other matrix has been suggested or put in place to evaluate reclamation success. The ecosite classification system might be a potential solution that is currently being reviewed by the restoration ecology researchers at the university of Alberta; however, a significant portion of belowground ecosystem components would be excluded if only ecosite classification is considered as the system is heavily dependent on indicator vegetation and forest productivity (Beckingham and Archibald 1996). A hybrid classification system using the edatopic grid and a number of significant ecosystem functionality indicators (e.g. nutrient bioavailability, soil microbial attributes, and organic matter accumulation) might work better. Therefore, there is a huge knowledge gap and demand for an ecologically meaningful index which can be used both for pre and post disturbance evaluation of land capability. The Criteria and Indicators Framework for Oil Sands Mine Reclamation Certification (CIFOSMR) (Government of Alberta 2014) has listed 44 soil, vegetation, wildlife

and ecosystem service indicators to be considered in the reclamation certification process which are more ecologically meaningful; yet not complete.

The current research has generated some ecologically informative indices which can be included in the proposed criteria and indicator for reclamation certification, and can directly be used in evaluating reclamation success. One of my main arguments through this research was that spatial variability in ecosystem properties can be used as an index of reclamation success. A number of restoration ecology and reclamation studies have suggested such index to be more ecologically meaningful to compare recovery pattern after disturbances (Higgs 1997; Ruiz-Jaen and Mitchell Aide 2005).

Along with soil nutrient (N and P), moisture, pH, salinity, and plant composition as proposed in the CIFOSMR to be used as key soil and plant criteria of reclamation certification, I am proposing to include three more detail indices in the evaluation process viz. spatial variability index, soil microbial index and soil nutrient profile index. Each of these indices and their calculations are described below with examples:

i) Spatial Variability Index (SVI): This will include scale of spatial dependency of key aboveground and belowground variables. Aboveground variables might include properties like forest floor depth and canopy cover, and belowground properties could be major macronutrients (N, P, K, and S), microbial attributes (biomass and enzyme activities), and substrate quality (DOC and C:N ratio). However, selection of variables can take advantage of smaller sub-set of aboveground and belowground properties if a clear connection can be established, for example, forest floor depth and nutrient availability. For simplification purpose, three different ratings can be defined

for spatial scale. A fine scale variability (< 5 m) would be rated as 3, medium scale variability (≥ 5 m but < 10 m) would get a rating of 2, and finally a coarse scale variability (> 10 m) would get a rating of 1. Sum of all the rating from the aboveground and belowground properties will finally define the spatial variability index.

ii)   Soil Microbial Index (SMI): This index will predominantly include variables related to microbial properties and functions such as biomass C and N, extracellular enzyme activities, community structure, and physiological functions. Enzyme activities showed some of the strongest control on nutrient availability in both natural fire disturbed and reclaimed sites in the current research. A number of earlier studies in disturbed ecosystem have demonstrated the importance of enzymes in microbial nutrient acquisition (Boerner and Brinkman 2003; Das Gupta et al. 2014). Study conducted in the oil sands reclaimed sites by Quideau et al. (2013a) showed the importance of microbial community structure while comparing ecosystem recovery with natural benchmarks. Thus, all these variables have very firm ecological rationale to be included in the reclamation evaluation process, although might not always be practical for industrial scale disturbance as in the case of oil sands mining. However, reclaimed sites are often built with greater homogeneity both structurally (substrates) and topographically (terrain conditions). Having a soil microbial index from a few subplots of the total reclamation unit would, at least, indicate the biological health status of reclaimed soils. The most practical way of formulating this index would be performing a principal component analysis (PCA) among the variables. The higher variability explained with high number of variables, and a threshold correlation of

minimum 0.20 should be considered as the basis of overall rating. For example, if principal component axis 1 explain 60% variability and include 5 variables with over threshold correlations, this would get higher rating than that explaining 80% with only 2 variables. The ecological rationale behind such assumption of higher rating with high number of correlated variable is that the higher number might suggest strong coupling between microbial biochemistry, substrate quality, and other chemical properties (Bååth et al. 1995; Ritz et al. 2004).

iii) Soil Nutrient Index (SNI): Such an index already existed in the land capability classification system (termed as soil nutrient regime; SNR) and has been suggested to be included in more rigorous form in the Criteria and Indicators Framework for Oil Sands Mine Reclamation (CIFOSMR) certification, where plant available N and P are also included besides total organic C and N (Government of Alberta 2014). Aerobic and anaerobic laboratory incubations are the suggested methods for measuring plant available nutrients in the CIFOSMR. Here, I would argue that laboratory incubation with collected soil samples might not provide the appropriate measure of plant available nutrients due to several limitations such as altered soil physical structure and abiotic conditions (moisture and temperature), changed microbial functionality, and absence of rhizosphere effect and plant competitions. *In-situ* measurement of nutrient conditions would rather give more realistic nutrient regimes. Ionic resin membranes can be used for this purpose which can readily be installed in field condition and have been demonstrated to produce better results (well correlated with plant growth and nutrition) (Huang and Schoenau 1997; Qian and Schoenau 2002). At least, major plant macronutrients (N, P, S, K, Ca and Mg) should be measured and

used while calculating the SNI. As resin measured nutrient availability is expressed in

ug/10 cm^2 surface, the SNI can be additive in this case. The site with higher nutrient

availability should get higher rating. Two different rating schemes can be developed,

one for the microbially mediated nutrients such as N, P, and S; the other one is for the

cations (K, Ca, and Mg).

Finally, all the measured biogeochemical properties can be fitted in spatial regression

models to tease apart the potential mechanisms that drive certain ecosystem properties in the

reclaimed systems. This will generate more concrete evidence that the strongest or weakest

driving factors for specific properties of interest in the reclaimed systems are either similar or

different than the benchmark conditions.

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Appendix I

A1.1 Semi-variogram

Semi-variograms were calculated on the residual of trend surface models. Four theoretical semi-variogram models (Gaussian, Spherical, Circular and Exponential) were tested to fit the empirical semi-variogram calculated from the actual observations. Maximum 30 m lag distance was covered for semi-variogram calculation as this was the reliable limit for detecting any spatial structure given that the maximum distance in the sampling protocol was 60 m. The lowest root mean square error (RMSE) was used for selecting the best appropriate model. The following equation was used for calculating semi-variogram (Yates and Warrick 2002b) –

$\gamma_x(h) = \frac{1}{2N(h)}\sum_{i=1}^{N(h)}(X_i - X_{i+h})^2$ where, γ(h) is semi-variance, h is separation distance, X is variable of interest, and N(h) is the total pair of sample points separated by distance h.

A1.2 Cross-variogram

Cross-variograms were used to detect the scale dependant spatial association between above and belowground properties. The following equation was used for calculating cross-variance (Yates and Warrick 2002b) –

$\gamma_{xy}(h) = \frac{1}{2N(h)}\sum_{i=1}^{N(h)}(X_i - X_{i+1})(Y_i - Y_{i+h})$ where, γ_{xy}(h) is the experimental cross-variance of n spatial observations of variable X and Y, N(h) is the number of observations separated by a distance h and X_i is the location, i = 1, ... n.

A1.3 Moran's I

Moran's index was used to determine the spatial dependency of regression model residual. The equation was used for calculating Moran's I :

$$I = \frac{n}{\sum_{i=1}^{n}(X_i - \bar{X})^2} \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} W_{ij}(X_i - \bar{X})(X_j - \bar{X})}{\sum_{i=1}^{n}\sum_{j=1}^{n} W_{ij}}$$

where, n is the number of observations, X is the model residual value for each sampling point, $\bar{X}$ is the mean of the residuals, and W_{ij} is the weight matrix. Distance based contiguity spatial weights matrix was used in this analysis. The threshold distance to avoid island formation was calculated by Euclidean distance between sampling points. Threshold distance for the current sampling protocol was 1.96 m.

A1.4 Spatial regression model

Spatial regression modeling was performed to detect what factors spatially controls nutrient availability in the reclaimed system. Theoretically, the spatial autoregression (SAR) model adds a spatial autocorrelation term in the standard OLSR model, where contiguity of sampling location is defined by a spatial weight matrix (Anselin 2001). SAR models commonly take two forms, spatial lag model (SARlag) where spatial autocorrelation term is associated with the response variables and the spatial error model (SARerr) which accounts for spatial trend by incorporating the autoregressive process in the error term. SARlag has the following form:

$Y = X\beta + \rho WY + \varepsilon, \ \varepsilon \sim N(0, \sigma^2)$

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where, X is independent variable, β is regression coefficient, and ρ is the autoregression coefficient. *WY* expresses the spatial autocorrelation in the response variable Y (spatially lagged dependent variable) and ε is the random error term.

SARerr model has the following form:

$$Y = X\beta + \varepsilon; \; \varepsilon = \lambda W\varepsilon + \xi, \; \varepsilon \sim N(0, \sigma^2),$$

where, ε is the random error term and λ is the spatial autoregression coefficient. *Wε* represents the spatial structure (W) in error term (ε) and ξ is the independent error term after accounting for spatial relationship.

Best candidate models for available nutrients were selected by stepwise regression using the "step" function in R (Venables and Ripley 2002). The models with lowest AIC were then tested for further improvement in AIC value (lower) by using "drop1" function as suggested by Burnham and Anderson (1998). Finally, the multicollinearity in the models with lowest AIC were tested by variance inflation factor (VIF) using the "vif" function in the car package of R (Kutner et al. 2005). Variables with VIF more than 5 were removed from the model. Normality in the model residuals was tested by Jarqua-Bera test (Kutner et al. 2005) and heteroscedasticity was tested by Breusch-Pagan and Koenker-Bassat test (Anselin 2004).

In order to eliminate unit dimension of variables in the regression model and make all the regression coefficients comparable (both in OLSR and SAR), the regression coefficient β was standardized to partial regression coefficient β' using the following equation (Bring 1994):

$$\beta' = \beta \sqrt{\frac{\sum x_i^2 - (\sum x_i)^2 / n(n-1)}{\sum y_i^2 - (\sum y_i)^2 / n(n-1)}}$$

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The spatial analyses, including OLSR and SAR were done using openGeoDa package (Anselin 2004) and spdep packages in R v.2.15.2 (Bivand et al. 2011).

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Appendix II

Table A2- 1. Geographic location, fire history and top soil texture of the study sites.

Site	GPS coordinates	Fire year	Soil Texture
Post Fire (PF)	57° N 18′ 0.73″ N 111° 40′ 49.28″ W	2011	Sandy Loam
Canopy Closure (CC)	57° 07′ 9.78″N 111° 36′ 22.74″ W	2003	Sandy Loam
Mature Stand (MA)	57° 1′ 26.41″N 111° 55′ 39.81″ W	1942	Silty Loam to Sandy Loam

A2.1 Ecosite Classification

Post-fire Stand (PF)

Age: 1 year old

Pre-fire dominant species: Aspen (*Populus tremuloides*) and White Spruce (*Picea glauca*)

Pre-fire site index: 18

Topographic position: Level

Organic layer thickness: 6 cm

Post fire understory vegetation:

Green Alder (*Alnus crispa*); Lowbush cranberry (*Viburnum edule*); Sarsaparilla (*Aralia nudicaulis*); Wild geranium (*Geranium maculatum*); Bunchberry (*Cornus canadensis*); Raspberry (*Rubus spp.*); Wild strawberry (*Fragaria virginiana*); Northern bedstraw (*Galium boreale*); Star flowered solomon seal (*Maianthemum stellatum*); Prickly rose (*Rosa acicularis*); Twinflower (*Linnea borealis*); Palmate-leaved coltsfoot (*Petasites palmatus*); Pink wintergreen

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(*Pyrola asarifolia*); Bishop's cap (*Mitella ruda*); Creeping raspberry (*Rubus spp.*); Fireweed (*Chamerion angustifolium*); Stair step moss (*Hylocomium splendens*);

Drainage: Moderate to well drain

Matching Ecosite: low-bush cranberry Aw-Sw (d2)

Canopy Closure Stand (CC)

Age: 9 years old

Pre-fire dominant species: Aspen (*Populus tremuloides*) and White Spruce (*Picea glauca*)

Pre-fire site index: 18

Topographic position: Level

Organic layer thickness: 7.5 cm

Post fire understory vegetation:

Fireweed (*Chamerion angustifolium*); Lowbush cranberry (*Viburnum edule*); Bunchberry (*Cornus canadensis*); Dandelion (*Taraxacum spp.*); Raspberry (*Rubus spp.*); Palmate-leaved coltsfoot (*Petasites palmatus*); Blue bell (*Hyacinthoides spp.*); Cream peavine (*Lathyrus ochroleucus*); Peavine (*Lathyrus venosus*); Horsetail (*Equisetum spp.*); Silverberry (*Elaeagus commutata*); Green Alder (*Alnus crispa*); Stair step moss (*Hylocomium splendens*);

Drainage: Moderate to well drain

Matching Ecosite: low-bush cranberry Aw-Sw (d2)

Mature Stand (MA)

Age: 72 years old

Pre-fire dominant species: Aspen (*Populus tremuloides*) and White Spruce (*Picea glauca*)

Site index: 20

Topographic position: Level

Organic layer thickness: 9.5 cm

Post fire understory vegetation:

Green Alder (*Alnus crispa*); Lowbush cranberry (*Viburnum edule*); Labrador tea (*Ledum latifolium*); Bracted Honeysuckle (*Lonicera involucrata*); Saskatoon (*Amelanchier alnifolia*); Sarsaparilla (*Aralia nudicaulis*); Bunchberry (*Cornus canadensis*); Raspberry (*Rubus spp.*); Wild strawberry (*Fragaria virginiana*); Gooseberry (*Ribes spp.*); American vetch (*Vicia americana*); Prickly rose (*Rosa acicularis*); Twinflower (*Linnea borealis*); Palmate-leaved coltsfoot (*Petasites palmatus*); Pink wintergreen (*Pyrola asarifolia*); Cream peavine (*Lathyrus ochroleucus*); Peavine (*Lathyrus venosus*); Star flowered solomon seal (*Maianthemum stellatum*); Bishop's cap (*Mitella ruda*); Creeping raspberry (*Rubus spp.*); Fireweed (*Chamerion angustifolium*); Stair step moss (*Hylocomium splendens*); Schreber's moss (*Pleurozium schreberi*).

Drainage: Moderate to well drain

Matching Ecosite: low-bush cranberry Aw-Sw (d2)

Appendix III

Table A3- 1. Parameters of the spatial regression models for available macronutrients (µg 10 cm-2 8 weeks-1) in three aspen stands along a fire chronosequence in boreal northern Alberta.

	Spatial regression models	*F value, p*	*AIC*	R^2_{adj}
Post fire	TIN = 0.72 + 0.22*DON − 0.70*pH − 0.41*FD + 0.25*FRB + 0.29*BG + 0.15*P + 0.14*W*ε + ξ	$4.343_{80,\,8}$; < 0.0005	-93.4	0.21
	P = -2.41 − 0.32*Bglu + 0.64*NAG − 0.39*Phos + 6.12*TN + 0.28*Ca + 0.24*K + 0.46*S - 0.22*W*ε + ξ	$10.83_{80,\,8}$; < 0.0000	-33.1	0.42
	S = **2.40** + 0.26*Phos − 0.57*Sulf − 1.08*MBC:TC − 6.73*TN + 0.32*P + 0.48*Mg + 0.19*W*S + ε	$14.81_{80,\,7}$; < 0.0000	-59.4	0.48
	K = **1.53** + 0.38*BR − 0.30*NAG +0.97*pH + 0.25*P − 0.73*Ca + 0.99*Mg - 0.14*W*ε + ξ	$11.14_{80,\,7}$; < 0.0000	-63.8	0.38
	Ca = **1.71** − 0.13*DOC:DON + 0.19*P − 0.22*K + 0.81*Mg + **0.23*W*Ca** + ε	$54.76_{80,\,5}$; < 0.0000	-152.6	0.70
	Mg = **-1.17** + 0.11*Bglu − 0.10*FRB − 0.12*P + 0.13*S + 0.32*K + 0.69*Ca + 0.02*W*ε + ξ	$45.51_{80,\,7}$; < 0.0000	-158.8	0.69
Canopy closure	TIN = **-1.99** + 0.14*Bglu + 1.75*MBC:TC + 7.03*qCO2 - 0.27*FD + 0.18*BG − 0.86*pH + 0.17*W*TIN + ε	$5.75_{80,\,7}$; < 0.0000	-88.9	0.25
	P = 0.03 + 0.32*DOC − 0.25*BR +0.46*FD + 0.08*K + 0.11*W*ε + ξ	$5.09_{80,\,5}$; < 0.005	-49.3	0.16
	S = 0.32 + 1.52*MBCN − 0.49*DOC − 0.93*pH + 0.21*CWD + 0.38*NH₄ + 0.30*Ca + 0.22*W*ε + ξ	$7.19_{80,\,7}$; < 0.0000	3.74	0.31
	K = **3.18** + 4.87*qCO2 − 0.38*UV − 0.26*CWD + 0.53*P − 2.27*Ca + 2.26*Mg - **0.33*W*ε** + ξ	$24.13_{80,\,7}$; < 0.0000	-15.7	0.59
	Ca = **1.40** + 0.84*MBC:TC − 0.08*BA − 0.09*UV − 0.19*NO₃ - 0.18*K + 1.01*Mg + **0.31*W*ε** + ξ	$103.5_{80,\,7}$; < 0.0000	-197.7	0.80
	Mg = **-0.83** + 0.09*UV − 0.08*BG + 0.09*CRB − 0.14*P + 0.81*Ca + 0.18*K + 0.03*W*ε + ξ	$74.77_{80,\,7}$; < 0.0000	-219.5	0.75
Mature stand	TIN = **0.48** - 0.12*NAG + 0.25*DON + 0.23*DOC:DON + 0.19*Tdist. - 0.07*BA - 0.17*P + **0.31*W*TIN** + ε	$4.51_{80,\,7}$; < 0.005	-144.1	0.25
	P = 0.56 + 0.36*Bglu − 0.21*NAG + 0.51*DOC:DON + 0.49*BR − 0.27*FRB − 0.17*UV − 0.06*CWD − 0.56*TIN - 0.13*S + **0.23*W*ε** + ξ)	$2.85_{80,\,10}$; < 0.05	-35.3	0.16
	S = -1.67 + 5.67*qCO2 − 0.45*Tdist. − 0.20*BA − 0.39*UV − 0.10*P + 0.99*Mg + **0.30* W*S** + ε)	$12.24_{80,\,7}$; < 0.0000	-25.9	0.47
	K = 1.39 + 1.22*MBCN + 0.24*EC + 1.06*FD − 0.41*Canopy + 0.33*CRB − 0.51*Ca + ε	$7.86_{80,\,7}$; < 0.0000	-21.4	0.32
	Ca = **0.97** − 0.17*DOC:DON - 0.15*Sulf - 0.03*EC + 0.13* Tdist. + 0.04*CWD − 0.21*TIN + 0.99*Mg + **0.22*W*ε** + ξ	$33.6_{80,\,8}$; < 0.0000	-203.3	0.67
	Mg = **0.51** − 0.41*pH + 0.15*EC − 0.13*UV + 0.70*Ca + 0.09*S + **0.25*W*ε** + ξ)	$59.21_{80,\,6}$; < 0.0000	-238.8	0.73

Table A3- 2. Spearman correlation between macronutrients and aboveground and belowground properties in three aspen stands along a fire chronosequence in boreal northern Alberta. Significance level: * <0.10; ** <0.05.

		TIN			P			S			K			Ca			Mg		
		PF	CC	MA	PF	CC	MA	PF	CC	MA	PF	CC	MA	PF	CC	MA	PF	CC	MA
Belowground properties	DOC	-	-	0.30**	0.22*	0.30*	-	-	-0.26*	-	-	-	-	-	-	-	-	-	-
	DON	-	-	0.27*	-	0.26*	-	-	-0.31**	-	-	-	-	-	-	-	-	-	-
	MBC	0.22*	-	-	-	-	-	-	-0.24*	0.23*	-	-	-	-	0.26**	-	-	-	0.32**
	MBN	0.25*	-	-	-	-	-	-0.27*	-0.26*	-	-	-	-	-	0.31	-	-	-	0.32**
	MBCN	-	-0.34**	0.24*	0.22*	-	-	0.35**	-	-	-0.36**	-	-	-	-	-	-	-	-
	BR	-	-	-	-	-	-	-	-0.24*	0.45**	0.23*	-	-	-	0.36**	-	-	-	0.47**
	βglu	-	-	-	-	-	-	-	-	-	-	-	-	0.25*	-	-	-	-	-
	NAG	0.22*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Phos	-	-	-	-	-	-	-	-	0.36*	-	-	-	-	-	-	-	-	0.26*
	Sulf	-	-	-	-	-	-	-0.33**	-	0.38*	-	-	-	-	-	-	-	-	0.31**
	C	-	-	-	0.21*	-	-	-	-	0.40*	-	-	-	-	-	0.27*	-	-	0.44**
	N	0.25*	-0.26*	-	-	-	-	-	-	0.28*	-	-	-	-	-	-	-	-	0.30**
	pH	-	-	-0.35**	-	-	-	-	-	-	0.23*	-0.26*	-	-	-	0.31**	-	-	-
	EC	-	-	-	-	0.23*	-	-	-	035**	-	-	-	-	-	0.23*	-	-	0.37**
Aboveground properties	FD	-	-	-	-	-	-	-	-	-	-	-	-	0.30**	-	-0.27*	-	-	-
	Canopy	-	-	-	-	-	-	-	-0.22*	-	-	0.22*	-	-	-0.38**	-	-	-	-
	Tdist.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	BA	-	-	-	-	-	-	-	-0.22*	-	-	0.27*	0.27*	-	-0.27*	-	-	-	-
	UV	-0.27*	-	-	-	-	-	-	-0.28	-	-	-	-	-0.35**	-	-	-0.31**	-	-
	BG	0.24*	-	-	-	-	-	-	-	-	-	-	-	0.25*	-	-	0.27*	-	-

[†]MBC = Microbial biomass C (µg g^{-1} soil); MBN = Microbial biomass N (µg g^{-1} soil); MBCN = Microbial C to N ratio; BR = Basal respiration (µg CO_2-C g^{-1} soil day[-1]); DOC = Dissolved organic C (µg g^{-1} soil); DON = Dissolved organic N (µg g^{-1} soil); Bglu = β-1,4 glucosidease (nmol g^{-1} soil hour[-1]); NAG = N-acetyleglucosaminidase (nmol g^{-1} soil hour[-1]); Phos = Phosphatase (nmol g^{-1} soil hour[-1]); Sulf = Sulfatase (nmol g^{-1} soil hour[-1]); TC = Total C (%); TN = Total N (%); FD = Forest floor depth (cm); FRB = Fine root biomass (kg stem[-1]; g stem[-1] in CC); BGn = Bare ground (%); Tdist = Distance to nearest tree (cm); UV = Understory vegetation cover (%); BA = Basal area of nearest tree (cm[2]; cm[2] m^{-2} in CC); CWD = Coarse woody debris cover (%);

Appendix IV

A4.1 Allometric equation

Aspen fine root biomass (< 5 mm; FRB) in the PF and MA stands was estimated using the allometric equation developed by Chen et al. (2004). Fine root biomass for each spatial point was taken from the estimated root biomass of the nearest tree (as close as 0.10 m).

The following equation was used to calculate the FRB:

Fine root biomass (kg) = (0.0113 × 2.0711*DBH) * 1.125   (1)

where, DBH = Diameter at breast height (1.37 m)

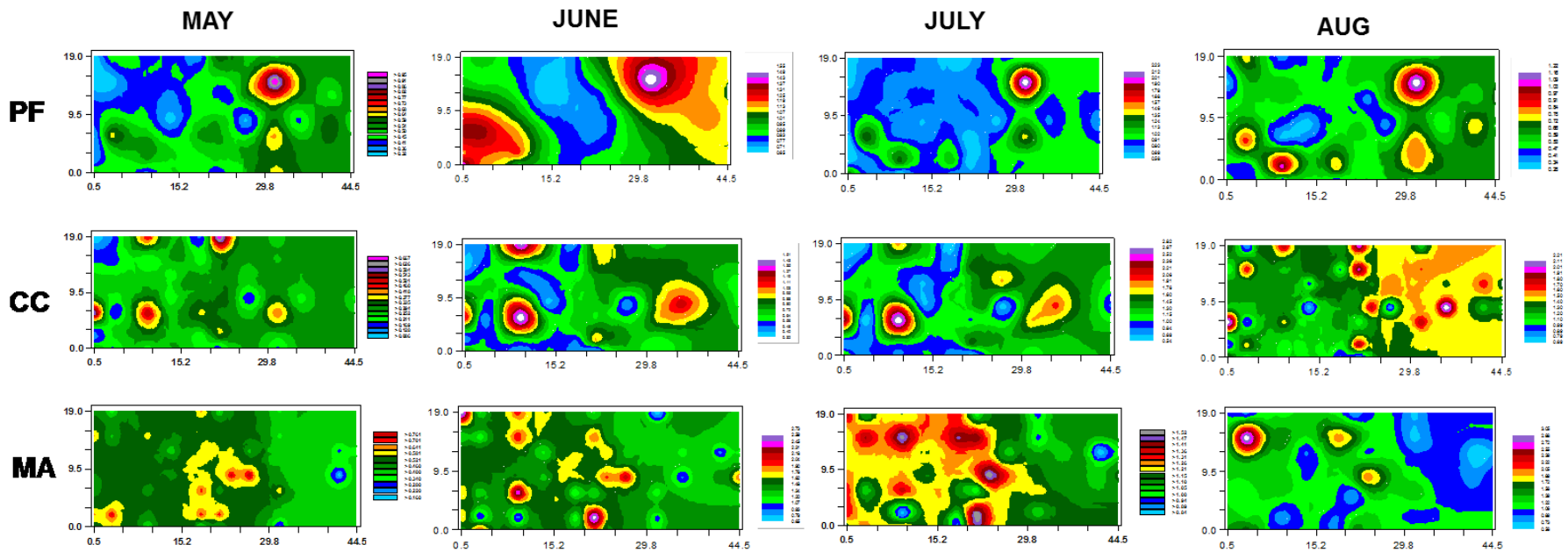Figure A4- 1. Krieged map of soil respiration (g CO_2 m^{-2} hour^{-1}) showing changes in different growing season months along a fire chronosequence of boreal aspen stands in northern Alberta (PF = Post Fire; CC = Canopy Closure; MA = Mature Stand).
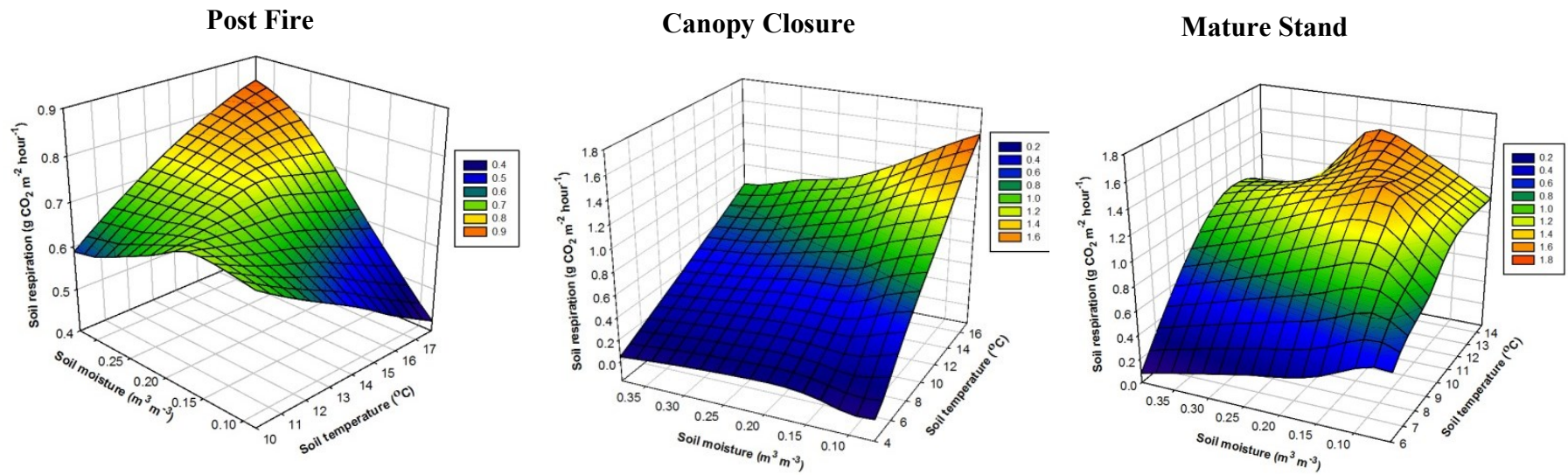
Figure A4- 2. Pooled relationship between soil respiration (Rs), soil temperature (ST), and soil moisture (SM) in the boreal aspen stands in northern Alberta along a fire chronosequence.
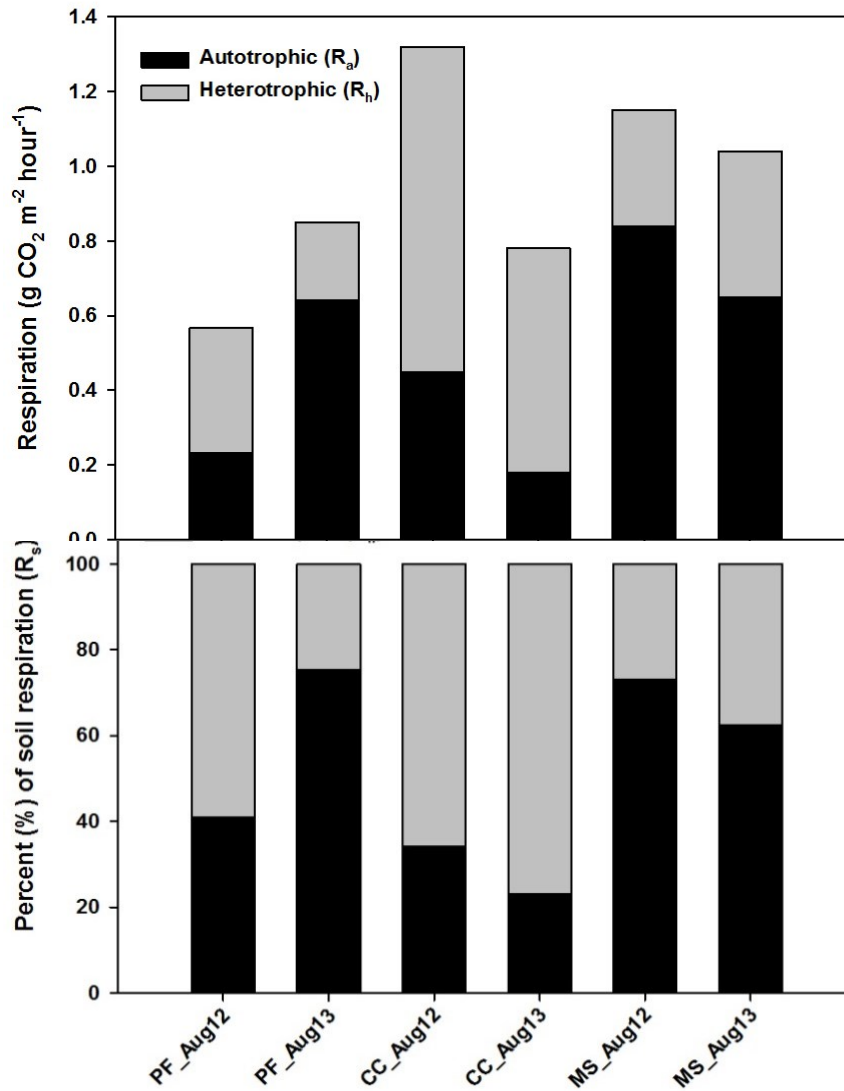
Figure A4- 3. Forest floor and mineral soil root (< 1 cm) density (mg g-1) (a), and the autotrophic (Ra) and heterotrophic (Rh) components of total soil respiration (Rs) (b) in three boreal aspen stands in northern Alberta along a fire chronosequence.

Appendix V

A5.1 Variance explained by spatial regression models

Semi-variograms of spatial regression model residual were calculated and partial sills were divided by the partial sills of dependent variables (nutrients). This accounted for the proportion of spatial variance in nutrient availability actually explained by the selected soil and stand properties in regression models. The proportion of spatially structured variance in the available nutrients that is explained by the soil and stands properties was estimated by dividing the partial sill of spatial regression model of a nutrient with the partial sill of that nutrient. This estimate indicates how well spatial distribution of available nutrients is explained by the related covariates in the regression model. Below and aboveground properties in the spatial regression model together explained 63% (Mg) to 92% (N) of the spatially structured variance in the available nutrients (Table A5-2). Only 21% of the spatially structured variance in Al was explained by the covariates in the spatial regression model.

Table A5- 1. Bivariate spearman correlation between macronutrients, microbial and stand characteristics in a 14-years-old reclaimed aspen stand.

	DOC	HSC	BR	Bglu	NAGase	Phos	Sulf	FD	FFmass	Tdist.	Tree cluster	pH
N	ns†	0.29*	ns	ns	ns	ns	-0.35**	ns	ns	ns	0.30**	ns
P	0.28**	ns	0.32**	0.32**	0.37**	ns	0.26*	0.24*	ns	ns	ns	ns
S	-0.25*	ns	-0.24*	ns	ns	ns	-0.30**	ns	ns	ns	0.34**	ns
K	ns	ns	ns	ns	ns	ns	ns	ns	0.35**	ns	ns	ns
Ca	ns	ns	ns	ns	ns	ns	ns	0.28*	ns	ns	ns	ns
Fe	-0.28*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Zn	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.39**	ns
Al	ns	0.25*	ns	ns	ns	ns	ns	ns	ns	-0.23*	0.24*	-0.40**
Cu	ns	ns	0.25*	0.26*	ns	ns	ns	0.31*	ns	ns	ns	ns
							MBC	ns	ns	ns	ns	ns
							DOC	ns	ns	ns	-0.25*	ns
							HSC	ns	ns	ns	ns	-0.36**
							BR	ns	ns	ns	ns	-0.34**
							Bglu	ns	ns	ns	ns	-0.51**
							NAGase	ns	-0.26*	ns	ns	-0.28*
							Sulf	ns	ns	ns	-0.48**	ns
							Phos	ns	ns	ns	ns	-0.49**

†ns = Not significant at 0.05 level; * means significant at 0.05 level; ** means significant at 0.01 level

Table A5- 2. Spatial regression model and model parameters of nutrient availability in a 14-years-old reclaimed aspen stand.

Spatial regression models	Moran`s I (p value)	ρ (p value)	λ (p value)	LR[†] (p value)	Prop. Spatial var. (%)
TIN ~ f(Sulfatase, pH, MBC, FFmass)	1.23 (0.22)	-	-	-	92.0
TIN$_{inc.}$ ~ f(DON, pH, Canopy, BR, Nagase, DOC, TOC:TN)	4.79 (<0.005)	-	0.61 (<0.005)	22.7 (<0.005)	40.0
S ~ f(HSC, DON, Nagase, P, PSC, Sulfatase)	1.62 (0.10)	-	-	-	75.0
P ~ f(βglucosidase, TOC, FFdepth, Phosphatase)	0.76 (0.44)	-	-	-	91.0
Ca ~ f(FFdepth, BR)	-0.58 (0.56)	-	-	-	76.0
Mg ~ f(pH, TOC:TN, FFdepth, Treedist)	1.16 (0.24)	-	-	-	-
K ~ f(FFmass, HSC, Canopy)	0.50 (0.61)	-	-	-	-
Fe ~ f(PSC, Treedist.)	-0.30 (0.76)	-	-	-	-
Zn ~ f(Canopy, FFmass)	0.70 (0.48)	-	-	-	77.0
Al ~ f(DON, pH, HSC, FFdepth, TN)	2.86 (<0.05)	0.46 (<0.005)	-	17.9 (<0.005)	21.0
Mn ~ f(BR, DON, pH, FFdepth, Bglucosidase)	0.09 (0.93)	-	-	-	-
B ~ f(BR, Phosphatase, FFdepth)	-0.13 (0.89)	-	-	-	-
Cu ~ f(FFdepth, TOC:TN, Bglucosidase, BR)	-1.23 (0.22)	-	-	-	-

[†] LR = Likelihood Ratio

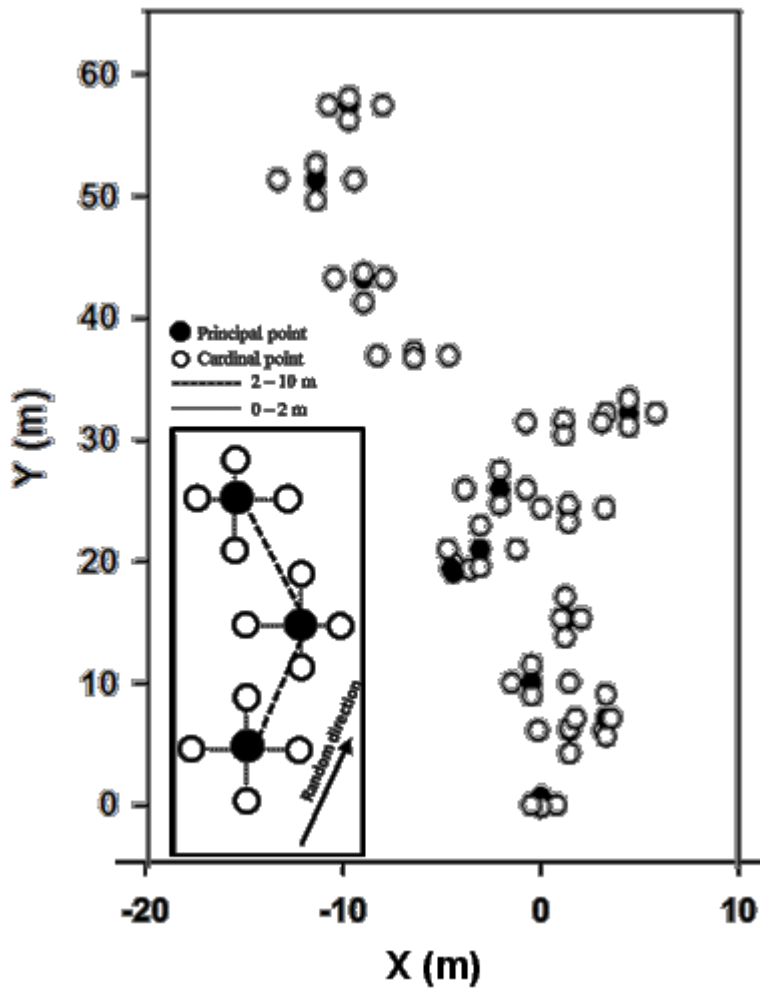"-" indicates non-significant spatial structure

Figure A5- 1. Schematic layout of the sampling protocol. Inset figure shows the principal and four cardinal points.