Understanding aspen in the James Bay
area of Quebec at multiple scales

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DEDICATION

This thesis is dedicated to my late grandfather Alvin T. Whitbeck and my first academic mentor and friend Dr. Edward Jensen. Thank you for always believing in me and providing unconditional love and support, it helped me climb many mountains.

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ABSTRACT

Understanding tree species distributions and dynamics in northern boreal forests is necessary for appropriate societal action and response to critical issues such as climate change, increased economic development of northern natural resources, and the collateral damage to cultures of indigenous communities. Northern tree species are expected to be sensitive to ongoing and anticipated climate change. Due to their remoteness and lack of a history of management-oriented research, information that is available for temperate areas, such as species distribution maps, soils, and climatology is often poorly quantified in the North. Consequently, our understanding of the factors controlling tree species northern distributional limits (NDL) and our ability to predict how future environmental change will affect their range distributions is limited. Moreover, very little attention has been devoted to understanding the dynamics of the few broadleaf tree species, such as trembling aspen, which are important components of northern boreal forest systems, from both an ecological and an economical perspective.

This thesis was inspired by observations of aspen growing in uncharacteristic abundance near the extremes of its NDL in Quebec in conjunction with the pressing need to answer questions regarding how individual boreal tree species may respond to current and future environmental change. Here, I investigate the factors driving the variation in observable patterns of aspen distribution and abundance at regional and landscape scales in the James Bay area of northwestern Quebec, as well as the influence of a range of ecological conditions on aspen growth. The four specific objectives of this research were: (i) to map aspen's regional distribution and abundance using a combination of field, GIS, and remote sensing techniques, (ii) to determine how aspen height growth responds to change in environmental conditions across a broad latitudinal gradient from 46° to 54°N latitude, (iii) to determine the factors organizing vegetation community composition in and around aspen-dominated communities at the landscape scale, and (iv) to explore the influence of specific environmental factors on aspen abundance at the landscape scale near aspen's NDL.

The key scientific merits of this thesis are: (i) creation of baseline data characterizing aspen's geographic range and associated land cover in northwestern

Quebec to allow for more accurate comparative and quantitative studies now and in the future, (ii) development and application of a new method for rapid extraction of land cover classification data in remote areas, (iii) demonstration that the regional scale pattern of aspen occupancy in the James Bay area of QC appears influenced by anthropogenic driven disturbance, (iv) demonstration that aspen's NDL in QC is not predominately governed by harsh climate, thus highlighting the need for more in depth species specific research on determinants of range limits, and the subsequent factors most appropriate for use in predictive modelling of future tree species' distributions, and (v) demonstration that gradients related to soil moisture and soil fertility best characterize forest composition and structure at the landscape scale in the study area, while aspen abundance, in particular, is associated with soils high in K, and inland areas where fire events are more frequent than those on the coast. Together these tools and findings suggest that identifying and understanding species' distribution and abundance patterns is complex and a further grasp of change in species specific patterns across their entire ranges is necessary to make informed forest management decisions and predict future outcomes.

RÉSUMÉ

Une meilleure compréhension de la dynamique et de la répartition des espèces d'arbres en forêt boréale permettra d'intervenir socialement de façon plus appropriée face aux pressions exercées par les changements climatiques et par le développement accru du Nord, en plus de limiter les effets néfastes de ces pressions sur les communautés autochtones. Les espèces d'arbres nordiques peuvent s'avérer sensibles aux changements climatiques. Or, les données sur la répartition des espèces, la climatologie et les sols sont souvent manquantes en milieux nordiques étant donné l'isolement et le manque de recherche sur la gestion de ces milieux. En conséquence, notre compréhension des facteurs contrôlant les limites nordiques de répartition des espèces ligneuses et notre capacité à prédire les effets des changements environnementaux sur leurs aires de répartition sont limités. De plus, les dynamiques des essences d'arbres feuillus tels que le peuplier faux-tremble ont été très peu étudiées malgré la très grande importance écologique et économique de ces espèces pour l'écosystème forestier boréal.

Ce projet, initié suite à l'observation de quantités surprenantes de peupliers à la limite nordique de répartition de l'espèce au Québec, vise à améliorer les connaissances sur la réponse possible des espèces d'arbres boréales face aux changements environnementaux présents et futurs. Dans cette thèse, j'étudie les facteurs contrôlant la répartition du peuplier dans la région de la Baie James du nord-ouest québécois et j'évalue l'influence d'un nombre de conditions écologiques sur la croissance du peuplier. Les quatre objectifs principaux de cette étude étaient de (i) cartographier, avec l'aide d'un SIG, la répartition et l'abondance régionale du peuplier en utilisant des données de terrain et de télédétection, (ii) déterminer de quelle façon la croissance du peuplier varie en fonction d'un large gradient de latitude (de 46° à 54°N), (iii) au niveau du paysage, déterminer les facteurs responsables de l'organisation et de la composition des communautés végétales dominées par le peuplier, et des communautés environnantes, (iv) explorer l'influence de facteurs environnementaux spécifiques au niveau du paysage sur l'abondance du peuplier près de la limite nordique de sa répartition.

Les contributions scientifiques principales de cette thèse sont : (i) l'obtention de données sur la répartition géographique et la couverture terrestre du peuplier dans le nord-ouest du Québec qui pourront servir de base à des études comparatives et quantitatives plus précises, (ii) le développement et l'application d'une nouvelle méthode pour l'extraction rapide de classification de la couverture terrestre dans des régions éloignées, (iii) la démonstration que les patrons de répartition du peuplier à l'échelle régionale dans la région de la Baie James sont influencés par des perturbations anthropiques, (iv) la démonstration que la limite nord de répartition du peuplier au Québec n'est pas contrôlée principalement par le climat. Cette observation met en évidence le besoin d'effectuer des recherches plus approfondies sur les facteurs déterminant les limites de répartition, et d'évaluer lesquels permettront de prédire de façon précise la répartition future des espèces d'arbres, (v) la démonstration que les gradients liés à l'humidité et à la fertilité du sol caractérisent la composition et la structure de la forêt à l'échelle du paysage. De façon particulière, le peuplier est associé à des sols avec des teneurs élevées en potassium et à des sites éloignés des côtes où les feux sont moins fréquents. La mise en commun de ces outils et de ces résultats suggère que l'identification et la compréhension des patrons d'abondance et de répartition des espèces sont complexes. Plus de connaissances sur les patrons complets des aires de répartition spécifiques à chaque espèce sont nécessaires afin de prendre de meilleures décisions relatives à l'aménagement forestier et pour prédire les impacts futurs de ces décisions.

CONTRIBUTIONS OF AUTHORS

The format of this thesis is manuscript-based and consists primarily of three manuscripts that will be submitted for publication review in ecology and forestry scientific journals. I am the primary author of all the chapters of this thesis. Chapter 2 is co-authored with D.R. Oetter and J.W. Fyles and will be submitted to *Forest Ecology and Mangement*[1]. Chapter 3 is co-authored with J.W. Fyles and will be submitted to *ÉCOSCIENCE*[2]. Chapter 4 is co-authored with P.M.A. James and J.W. Fyles and will be submitted to *Canadian Journal of Forest Research*[3].

J.W. Fyles has provided academic supervision, ideas, and editorial assistance for the entire thesis, and statistical assistance for chapter 3 and chapter 4. D.R. Oetter provided ideas, training, statistical, and editorial assistance for chapter 2. P.M.A. James provided training, statistical advice, and editorial assistance for chapter 4. Additional advice was given by the project committee members Dr. Benoit Cote and Dr. Murray Humphries.

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[1]   Whitbeck KL, Oetter DR, Fyles JW (to be submitted) Aspen near its northern range edge in Quebec: Is human activity more important than climate? *Forest Ecology and Management.*

[2]   Whitbeck KL and Fyles JW (to be submitted) Aspen growth response to change in environment along a latitudinal gradient in the eastern Canadian boreal forest. *ÉCOSCIENCE.*

[3]   Whitbeck KL, James PMA, Fyles JW (to be submitted) Ecological analyses of trembling aspen near its northern range limit. *Canadian Journal of Forest Research*

CONTRIBUTIONS TO KNOWLEDGE

My thesis provides a multi-scale treatment of trembling aspen (*Populus tremuloides*) ecology in the northern boreal forest of Quebec where aspen nears its northern distributional limits (NDL). Because a substantial portion of Quebec's northern boreal forest is located above the northern limit for timber allocations (~ 51°N latitude) there has historically been little attempt to quantify or characterize this area compared to Quebec's southern boreal forest. Special interest in tree species range edge dynamics is increasingly a practical concern for forest management due to the imminent relevance of the uncertainties around species-specific responses to climate change and shifting land use. Aspen's wide distribution and ecological tolerance, life history, adaptive traits, and uncharacteristic abundance near its NDL in the James Bay Region made it a model tree species for a multi-scale/multi-variate investigation into the dynamic nature of a common tree species growing near a range edge, the ecological patterns that emerge at different spatial scales of examination, and growth patterns associated with the change in environmental conditions that occur along a broad latitudinal gradient.

Chapter 2: A Regional Perspective on the Distribution and Abundance of Aspen and Associated Land Cover in the James Bay Region of Quebec

While the majority of work on the implications of climate change for tree species' geographic distributions are derived from two base criteria: present species' distributions and current environmental conditions, in reality our understanding of most species' geographical range distributions is quite limited. In fact, comprehensive distribution descriptions are still incomplete for even some of our most common species, including aspen, because it is only within the last few decades that sufficient technology has become readily available to map and characterize large geographic areas in detail without the requirement of physically visiting/assessing each square meter. Therefore little is known about the regional scale factors constraining aspen's distribution in the James Bay area. In this chapter, I develop and use a large and spatially precise database to build a land cover map to characterize the distribution and abundance of aspen in the James Bay Region and conduct spatial analyses to explore

the factors driving the observed patterns of distribution. I also present a novel method for rapid extraction of land cover classification data in remote areas. This is the most comprehensive regional scale assessment of aspen's distribution where it nears its NDL to date.

Chapter 3: Aspen growth response to change in environment along a latitudinal gradient in the eastern Canadian boreal forest

Change in climate (specifically temperature and precipitation) is expected to affect tree species' establishment, growth, regeneration, and consequently general forest community structure and composition. Yet, few studies employ robust sampling strategies to document the growth response of individual tree species across broad climatic gradients associated with change in latitude. In this chapter, I present results of a study documenting the growth rates of aspen saplings across a climatic gradient spanning ~8° of latitude in western Quebec. Our results reveal surprisingly weak relationships between aspen growth rates and change in climate as inferred by change in latitude. It can be concluded from this work that the general prediction that climate is the greatest factor limiting tree growth near northern NDL does not equally apply to all tree species. Furthermore, given that all aspen sampled in this study were growing in equivalent edaphic conditions and performed similarly growth-wise across the entire gradient, this study suggests that substrate may be an important indicator of aspen growth potential in the study region.

Ecological Analyses of Trembling Aspen and associated vegetation near Aspen's Northern Distributional Limit (NDL) in Quebec

Trembling aspen sustainability has emerged as a key issue in forest ecology due to changing patterns of aspen distribution and abundance in many different geographic locations and the lack of agreement on the factors most responsible for observed changes. The points of agreement between leading aspen ecologists are that aspen forests differ across the full spectrum of their distribution, and that we need to achieve a clearer understanding of the varying influences different factors have on aspen distribution patterns across its broad geographic range by employing aspen

landscape-or aspen type-specific approaches. Moreover, strong concerns have been expressed regarding the potential impacts of climate warming on aspen forests, particularly near range edges, and have established a critical need for aspen edge related studies. In this chapter, I demonstrate how scaling up detailed tree-, species-, and stand-level data collected on field plots can be used to characterize forest composition and structure across an area where aspen occurs in uncharacteristic abundance near its NDL in QC. The results of chapter 4 establish linkages between aspen abundance and soil K for northern aspen populations in QC at the landscape scale, and build on previous research findings that vegetation abundances of three dominate coniferous trees of the James Bay area varied with spatial variations in the fire cycle; here, I demonstrate that spatial variation associated with the fire cycle also explains differing aspen abundances across our study area.

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Many important and wonderful people spent countless hours helping me learn and develop the critical skills required to complete this thesis, become a better researcher, and hopefully a better person. I would like to thank my supervisor, Dr. James W. Fyles, for his dedicated support, for guiding me when required, yet encouraging me to resolve surmountable research challenges on my own. He taught me many valuable lessons about science and life that I hope to carry forward. Jim is one of those rare breeds who plants seeds of inspiration in all who cross his path and I am sincerely grateful for the privilege of working with him.

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My co-author, colleague, and steadfast friend Dr. Doug R. Oetter has been instrumental in the growth and development of my thesis research. He inspired me to go beyond my limits and is truly an amazing teacher, scholar, and visionary. His boundless energy has the capacity to engage and transform all willing participants.

I am also very fortunate for the advice, perspective, encouragement, and participation from my co-author Dr. Patrick M.A. James. Without a personal stake, he provided his time, expertise, encouragement, and gave me critical guidance. He gently motivated and directed me towards self-study to procure statistical knowledge that had a profound impact on my research, my analytical development, and general competence as a working ecologist.

I am forever grateful for the patience and advice of the Wemindji community at large. The people of Wemindji not only accepted me into their community with exceptional warmth and hospitality, but they allowed me to participate in a way of life, their life, that moves me beyond words.

1 General Introduction

There is a great need to understand tree species distributions and dynamics in northern forests as climate change is predicted to affect different tree species and their distributions in different ways. High latitude environments are predicted to experience the greatest warming and associated impacts (Parmesan & Yohe, 2003; Parmesan *et al.*, 2005). Much research has focused on understanding both current and historic range dynamics of common conifer tree line species in northern forests (black spruce, white spruce, tamarack); however, little attention has been devoted to studies that similarly address the common broadleaf tree species of these forests (Payette, 1983; Ritchie, 2004), such as aspen, which is the most widely distributed broadleaf tree in North America.

Understanding the appropriate responses to critical issues such as climate change rests on the ability to predict how different species will respond over their geographic ranges. Such predictive power hinges on the accuracy with which we can describe the spatial extent of any given species range. Moreover, it is critical that studies address species populations existing on the edges of their range distribution, such as aspen in northwestern Quebec, because they are often more vulnerable to environmental stressors than populations in the center of their range (Gaston, 2009). Research conducted in Yellowstone Park suggests the latitudinal and altitudinal limits of aspen are constrained by low temperature and length of growing season (Turner *et al.*, 2003), while studies of aspen forests in the Western Canadian Rockies conducted by Hogg et al. (2008) show moisture to be the limiting factor at aspen's southern edge.

To date, most edge-related research has focused on changes along the tree line ecotones, the transition between forest and tundra ecosystems (Payette, 1983; Payette, 1993; Sveinbjörnsson, 2000; Kullman, 2001). Current research and satellite imagery yields little evidence of forests moving into the arctic and alpine tundra areas in northern latitudes (Masek, 2001) which implies that current species assemblages in northern forests may not reflect recent warming. We currently lack empirical data to draw conclusions about tree species distributions further south in the boreal forest (Landhäusser *et al.*, 2010).

Understanding the generation of spatial patterns by ecological processes is a major problem in ecological theory (Levin, 1992). Not only do different patterns emerge depending on the scale of observation, but the underlying causes of these patterns also differ (Wiens, 1989). The last two decades of ecological research on species distributions across environmental gradients have strongly reinforced the importance of, and the need for, multi-scale studies that illuminate the various mechanisms driving patterns of species distributions at different scales (Allen & Hoekstra, 1990). Many community and landscape scales have linked species response to environmental gradients at fine spatial or temporal scales (Tilman & Kareiva, 1997) or at broad spatial and temporal scales (Currie & Paquin, 1987). Few studies, however, have investigated species dynamics at multiple scales (Reed *et al.*, 1993; Hollingsworth *et al.*, 2006).

In this thesis I consider regional (200-4000 km) and landscape (20-200 km) scale (Waide *et al.*, 1999) patterns of aspen distribution and abundance as well as aspen's growth response to a wide range of natural climatic conditions across a broad latitudinal gradient in the northern boreal forest of western Quebec, Canada. The first manuscript (Chapter 2) focuses on establishing the biogeographic extent of aspen in the James Bay Region of Quebec and examines patterns of aspen distribution and abundance at the regional scale. The second manuscript (Chapter 3) examines aspen growth rates across a latitudinal gradient of ~ 8° (~750 km). The third manuscript (Chapter 4) employs a multivariate approach to identify and separate the effects of co-varying causal factors influencing aspen abundance at the landscape scale and the factors responsible for the abundances of co-occurring vegetation.

1.1 Literature Review

1.1.1 Theoretical perspectives on the distribution and abundance of species

Comprehending the intricacies of terrestrial ecosystems and establishing an indisputable scientific explanation for observed patterns of species distribution and abundance is a central goal of plant community ecologists, and has been the driver of their studies (Perry *et al.*, 2008). Various methodologies, approaches, and theories

have been developed and used to demystify the underlying processes contributing to shaping such patterns.

Ecological studies at the population level revealed deep insights into the way single populations change and their causal factors; however, they did not and do not allow us to scale up and make broader interpretations of ecosystem function. This predicament moved ecologists toward adopting a community-level approach involving not only the study of intra- and inter-level species diversity, but also the actual structure and assembly of the community as a whole (Tokeshi, 1999). The roots of contemporary theories on community assembly can be traced back to Henry Gleason in the early 1900's who put forth the "individualistic" concept of plant community ecology. Gleason hypothesized that species do not belong to clearly defined communities, rather they are variously distributed (Whittaker, 1975).

Two dominant theories in plant community ecology today that try to explain species distribution and abundance are niche and neutral theory. The ecological concept of the niche dates back to the early 1900's (Grinnell, 1917; Tokeshi, 1999) and despite many different interpretations and modifications of the niche concept (Gause, 1934; Hutchinson, 1957; Whittaker *et al.*, 1973; Silvertown, 2004) its essence still holds a firm stance in current ecological theory. An easy conceptual definition of the niche coined by Hutchinson (1957) is "a description of the ecological space occupied by a species". Hutchinson (1957) suggested that the niche could be modeled as an imaginary space with multiple dimensions, in which each axis represents the range of some environmental condition or resource required by the species. Niche theory explains the co-existence of species by their distribution along environmental (i.e., soil moisture, light, soil pH), resource (i.e., water, soil nutrients, light), or disturbance (i.e., fire, ice storm, flooding) gradients, thus species occupying the same physical space must partition resources in different ways (Whittaker, 1975).

The niche concept expanded with Whittaker's (1975) proposal of alpha diversity (within habitat diversity), beta diversity (between habitat diversity), and gamma diversity (species diversity at the regional scale). Pickett and Bazzaz (1978) modified terminology established by Whittaker (1975) through the substitution of the word "niche" for "diversity"; however, the fundamental concept remained the same.

Niche theory has recently been challenged by neutral theory (Hubbell, 2001). Neutral theory assumes that species are ecologically equivalent in their responses to all constraints and that communities are in fact random assemblages of species resulting from chance, history, and random dispersal. The model asserts that stochastic drift is the explanation for species distribution and abundance and that there should be no relation among species traits and their abundances, or among community composition and environmental conditions (Chesson & Case, 1986; Hubbell & Foster, 1986).

Niche vs. Neutral theory has been a hotly debated topic in the last decade and shaped the way ecologists build predictive models to forecast change in species distributions and abundance patterns. Understanding the processes contributing to the distribution and abundance of species has important implications for predicting the likelihood of species extinctions, the effects of habitat loss or gain on community structure, effective reserve design and factors allowing for species coexistence (Harte *et al.*, 1999).

1.1.2 *Populus tremuloides* – the focal species

Populus tremuloides (Michx.) is a tree that thrives on change. While twenty-first century climate change has been raising temperatures across Canada, aspen has moved into areas previously occupied by other vegetation in several locations and experienced shifting abundance levels (Romme *et al.*, 1997; Elliott & Baker, 2004; Dabros, 2009; Landhäusser *et al.*, 2010).Both the Rocky Mountains of west-central Alberta and the mixedwood-boreal transitional forest of northwestern Quebec have experienced such shifts. Although the warm climate has been given partial credit for localized expansions, other factors, including forest management activities, were also identified as causal agents of aspen's changing distribution and abundance patterns (Dabros, 2009; Landhäusser *et al.*, 2010). How do these results align with current ideas about how North American forests and individual tree species are predicted to be influenced by climate change?

1.1.3 Forest response to climate change

There has been much conjecture that twenty-first century climate change is shifting North American forest communities northward and thus changing the geographic distribution of species (Landhausser & Wein, 1993; Iverson & Prasad, 1998). The general expectation that tree species will track warming climate by shifting their ranges to higher latitudes or elevations (Walther *et al.*, 2002; Parmesan & Yohe, 2003) where changes are predicted to be most severe (Turner *et al.*, 2003), rests on the assumption that all tree species will respond uniformly to the multiple, complex, and often non-linear ecosystem adjustments that take place as climate changes.

Similarly, the main modelling efforts directed at forecasting the impact of climate change on forest community composition operate with the assumption that a specie's current distribution is a function of current climatic conditions - mainly some facet of temperature and/or precipitation (Gaston, 2003; Beaumont *et al.*, 2007), and that models forecasting future tree species distributions need only include information about a species current location and the climatic variables that correlate with that site. This approach is often referred to as "ecological niche modelling" and/or "bioclimatic envelope modelling" in the primary ecological literature (Heikkinen *et al.*, 2006).

The problems associated with expecting a uniform response from trees to climate and the related modelling approaches that follow are:

- we not only have a large ecological literature documenting the varied responses of individual species to different environmental factors at different temporal and spatial scales, but we also have evidence that individual species often have different responses to climate change at contrasting parts of their geographic ranges (Gaston, 2009);

- the capacity for species' range shifts is also typically affected by non-climatic variables known to affect tree species distributions, such as biotic interactions, physical barriers to dispersal, evolutionary change, and soil properties (Pearson & Dawson, 2003); and

- comprehensive range descriptions are still incomplete for some of our most common tree species, such as *Populus tremuloides*, because it is only

within the last few decades that sufficient technology is readily available to map and characterize large geographic areas in detail (Gaston, 2003).

This research arose in response to the growing need to understand the factors affecting different tree species across their geographic ranges in the context of changing climate, and coincidental observations of an important broadleaf boreal tree species displaying uncharacteristic distribution and abundance patterns.

1.1.4 The distribution and abundance of trembling aspen in Quebec

As described by Payette (1983) and others (Foster & King, 1986; Ritchie, 2004), the density of aspen in Quebec is greatest in the southern boreal forest (~48°N latitude) with stands noted to occur as far north as 52°N latitude – particularly around southern James Bay. This provides a coarse view of aspen's geographic extent in Quebec; however, there is no thorough documentation of aspen's distribution and abundance in the northern part of its range (Ritchie, 2004).

In the Abitibi area south of James Bay, much of the forest is dominated by aspen but abundance decreases to small patches and scattered individuals along the gravel shoulders of the James Bay Highway (JBH) within 20 km of Matagami (49°45'N latitude; JBH km 0). Moving further north along the JBH, black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) uplands and bogs dominate the land cover for over 250 km. Upon reaching the Old Factory Lake Watershed (OFLW) (~JBH km 464) the terrain changes from flat lands to undulating hills and aspen is abundant along the hillsides. Further, north of the OFLW, aspen again fades from the surrounding viewshed visible from the JBH. However, despite the fluctuating abundances of aspen across the territory dissected by the JBH, the consistent presence of individual aspen along the roadside demonstrate that it is an effective pioneer of human disturbance; it tracks the road corridor all the way to the end of the JBH in Radisson, while largely remaining absent in surrounding landscapes away from the road The pattern of aspen distribution observed in the James Bay Region seems inconsistent with general literature on current species range distributions and the role of climate, and played a significant role in the development of this thesis.

1.1.5   An ecological perspective of the study area – from biome to landscape

1.1.5.1   Boreal Forest

The boreal forest is one of the largest biomes in the world, blanketing 17% of the terrestrial habitat on earth (Melillo, 1996). Mean global temperatures are increasing and the effects of climate-induced change will be most pronounced in the high latitudes, making boreal forests a high priority zone requiring careful investigation (Soja *et al.*, 2007). Boreal forests are of critical biological importance because they affect climatic, ecological, and biogeochemical processes, both at regional and global scales (Bonan *et al.*, 1992) and through their role in global carbon storage and cycling (Melillo, 1996). Boreal forests are located in some of the coldest environments on Earth where trees can survive and dominate vegetative cover (Waide *et al.*, 1999). The species composition and structure of the boreal forest results from a complex interaction between climate, forest fires, solar radiation, topography, geology, nutrient availability, soil features, ecology of species, and infestations of pests and disease (Soja *et al.*, 2007).

The fire regime is believed to be the "keystone ecosystem process " that organizes the forest's physical and biological attributes through its role in structuring communities via the continual "resetting" of successional dynamics (Weber & Flannigan, 1997). Fire creates and maintains a forest mosaic of successional and subclimax plant communities, paving the way for plant establishment, influencing organic matter accumulation, and largely preventing the forest from converging to uniform dominant vegetation (Whelan, 1995; Hansen *et al.*, 2001). The post-fire matrix pattern, typical of boreal forests around the world, often show clear boundaries between different patches of dominate vegetation, which vary in size across spatial and temporal gradients. Within this matrix, in eastern Canada, lies the James Bay study area, which defines the regional spatial extent of research conducted for this thesis.

1.1.5.2   James Bay Study Area

The James Bay study area, as defined by our study boundaries, occupies a ~51,000 km^2 area in the northern boreal zone of western Quebec. The western edge of the study area is at 79°00' W longitude and extends east to 76°30' W longitude, while

the southern boundary is at 51°10'N latitude and extends north to 53°50'N latitude. The topography of the study area is generally of low relief but rolling hills and rock outcrops (250-350 m above sea level) do occur in the central-eastern part of the study area in the vicinity of Old Factory Lake (52°48'N, 77°30'W) and near the northern extent of the study boundary. Situated in the Canadian Precambrian Shield, the underlying bedrock is dominated by ancient acidic metamorphic rocks with more recent igneous intrusions. This bedrock consists mostly of granite and gneiss; both are felsic and composed mainly of feldspar (specifically orthoclase and microcline) and quartz (Stockwell *et al.*, 1968). At the regional scale, the soils are classified mainly as podzolic on mesic sites with organic fibrisols in the poorly drained areas (Ritchie, 2004); however, the soils prove more variable when examined at increasingly finer spatial scales. Bedrock geology has a strong influence over much of the landscape characteristics such as relief, surface roughness, drainage pattern, vegetation pattern, and soil development because large areas of shield are exposed with little or no mantle of unconsolidated materials (Ritchie, 2004). In the James Bay area, a bedrock 'exposure' gradient of high to low follows a north-south trajectory, with highest exposure occurring north of the 52th parallel, and lowest exposure occurring south of the 49th parallel (Ciesielski, 1998). This exposed bedrock in the north is generally acidic and low in Ca and Mg but high in K (Hocq, 1994). It can be expected to be subject to severe physical weathering processes associated with seasonal freeze-thaw events in conjunction with normal chemical weathering (Chapin III & Matson, 2011). The exposed granitic ridges that top the hills around Old Factory Lake (OFL) illustrate the high exposure end of this gradient and will be discussed in further detail in descriptions of the OFL landscape in particular.

The boreal forest of northern Quebec is dominated by conifers; however, there is a distinct broadleaf component. Black spruce is the most common species and can be found in three distinct forest cover types including mature black spruce forests, open paludified black spruce forests, and forested peatlands (Bergeron & Fenton, 2012). Conversely, jack pine is often limited to well drained, inland sites; white spruce (*Picea glauca* (Moench) Voss) is typically confined to coastal areas and occasionally inland on stream banks and disturbed sites; balsam fir (*Abies balsamea* (L.) Mill.) is

predominately found on sites with long fire intervals; and balsam poplar (*Populus balsamifera* L.) is sparse and mainly on alluvial sites (Parisien & Sirois, 2003). Aspen, tamarack (*Larix laricina* (Du Roi) K. Koch), and paper birch (*Betula papyrifera* Marshall) are also found in the study area – but typically in lower abundances.

The area is affected by cold, dry arctic air from the north during the winter and by warm, moist air originating from the south during the summer which yields long and cold winters, and short and warm summers. The mean annual temperature ranges from -1 to -3°C from south to north. In the south, the average growing season lasts 140 days with 1100 degree-days ≥ 5°C as compared to 120 days and 600 degree-days ≥ 5°C in the north (Environment-Canada, 2002). Total precipitation varies from 868 to 684 mm from south to north, with about one-third falling as snow (Hutchinson *et al.*, 2009). There are also east-west temperature and precipitation gradients caused by the moderating influence of James Bay on the coastal climate. During the ice-free periods along the James Bay coast there are frequent rainfall events and fog that contribute to a localized maritime-type climate in a strip of a few kilometers inland from the coast (Plamondon-Bouchard, 1975). In addition, as moisture decreases with distance from the coast, fire frequency increases (Parisien & Sirois, 2003).

1.1.5.3 Old Factory Lake watershed

The Old Factory Lake Watershed (OFLW), located within the James Bay Region (JBR), defines the extent of the landscape scale investigations described in this thesis. Old Factory Lake (OFL; ~ 100 m a.s.l.) is at the head of the watershed and drains westward ~ 90 km to James Bay via the Old Factory River. The terrain surrounding the OFLW includes rolling hills with large rock outcrops (up to 250 m a.s.l.) that have extensive ridges, and exemplify some of the highest relief in the greater James Bay area (Parisien and Sirois 2003). The composition of these landforms includes high amounts of K-rich pink feldspar (Personal observation and personal communication, Youcef Larbi, Chief Geologist, Cree Mineral Exploration Board). The soils dominating the study area include: dystric brunisols; organic mesisols and humisols; and gleysols (ESWG, 1996). These areas correspond to some of the best developed broadleaf forest identified in the broader James Bay area, which is consistent with high nutrient demands of aspen (Perala & Alban, 1982).

The majority of the aspen stands of the OFLW are regenerating from a fire in 1989 with intermixed small clusters of 75-85 year old (30-40 cm diameter at breast height) individuals that survived the fire (Lavoie & Sirois, 1998). The stands appear to be well-established, productive historical forests. They are not sparse peripheral populations, nor are they new populations that have established following disturbance associated with the construction of the James Bay Highway (JBH) (1971-1974). There has been little study of the relationships between the geological and ecological patterns expressed across the OFLW; however, as expressed later in chapter 4 it appears that the bedrock geology may have played an important role in defining the current patterns of aspen distribution and abundance in this area.

In general, the land cover of the OFLW exhibits species abundance variability not captured in the common literature describing the regional vegetation as dominated by black spruce and jack pine. From a landscape perspective the OFLW consists of mixed conifer species assemblages broken by lowland bogs and wetlands, upland open and semi-open clearings, hill sides with broadleaf cover, and recently burned areas. Within the recent burns, open, semi-open, and shrub areas dominate (Whitbeck *et al.*, 2012). The patterns of the OFLW ecosystem reflect the combined influence of a diversity of factors acting over many scales of time and space, which are of both 'natural' and human origin to varying extents.

1.1.5.4 Human influence in the OFLW and field work in 'the bush'

The Wemindji Cree people and their ancestors have been an integral part of the OFLW for several centuries. Archaeological evidence suggests that significant human habitation around OFL dates back to 3500 BP; however, there is no evidence of landscape level modifications by human activity associated with local occupations around OFL (Scott, 2008). This differs from the coastal environment along James Bay, where the construction of dykes and the cutting of corridors through coastal forest are historic land management tools used by Wemindji Cree hunters to modify the local environment to favor one of their primary food resources, waterfowl (Sayles & Mulrennan, 2010). Construction of the James Bay Highway and access roads to Cree communities in the 1970's made the James Bay area more accessible to people from the south; however, to access the shores of OFL one still needs to hike a 2.5 km canoe

portage trail, or come from upriver via canoe. Due to the remote nature of the OFLW study area there was, and is, no easy way to move through the territory, this makes field research very challenging logistically. Collecting field data in such an isolated area required extensive hiking, abundant bush-whacking and extended canoe travel to navigate the rapids along the ~ 90 km length of the Old Factory River. As such, this thesis required careful field planning and critical assistance from members of the Wemindji community regarding safe land and river-travel. Next, I review the current literature surrounding species range limits and distributions

1.1.6 A general review of the controls over species distribution and abundance

1.1.6.1 The importance of scale

It is well accepted within the scientific community that patterns of ecological organization observed in any given study are inherently linked to both the spatial and temporal scale of the study (Levin, 1992). In his treatise on scale Wiens (1989) provides a good example of how experimental research aimed at determining the causal agents of varying decomposition rates produces different results at different spatial scales of investigation. Experiments conducted at the local scale effectively explained variation in litter decomposition rates between species as a function of litter type, and the assemblage of on-site decomposers. Whereas broader regional scale research linked climatic variables to gross differences in decomposition rates (Meentemeyer, 1984). The relationship between climate and vegetation, that is clearly apparent at broad spatial scales, becomes less visible at finer spatial scales because the effects of local scale processes such as competition and facilitation appear stronger and mask the effects of climate (Woodward, 1987). Similarly, a species distribution may appear stable when viewed from the temporal scale of several decades, yet over geologic time scales species' distributions fluctuate and/or extinctions occur (Gaston & He, 2002). Furthermore, much research has shown that several intercorrelated factors act simultaneously on species' demographics. This makes teasing apart the varying influence different factors have across space and time extremely difficult, and also makes defining and conceptualizing discrete boundaries around scales of influence (i.e., continental, regional, local) a nebulous task (Waide *et al.*, 1999). Thus

the following is a summary of 'generalized' drivers of species distribution and abundance patterns.

1.1.6.2 *Global and continental scale*

At the global and continental scale most species are thought to be limited by current climatic factors (specifically temperature and moisture), historical factors (temporal changes in geology, climate, and other environmental variables), evolutionary history and dispersal (Gaston, 1990; Currie, 2001; Hansen *et al.*, 2001; Parmesan *et al.*, 2005; Morin *et al.*, 2007). Although, the influence of climate on species assemblages extends across all scales of biological organization, temperature and moisture are considered the two main factors delimiting the distribution of life on earth; all organisms are subject to upper and lower temperature thresholds that constrain their physiological limits (Currie, 2001). However it is unlikely that only one or two factors are constraining a species distribution at any particular point in space and time. More likely there are different complexes of interacting factors with varying levels of influence affecting a species distribution in different parts of its range (Renner *et al.*, 2006). Moreover, different mechanisms appear to control the boundaries or edges of a species distribution depending on the scale of observation.

MacArthur (1972) proposed that latitude is responsible for the balance between abiotic and biotic factors explaining species distribution in trees. He suggested that the northern distributional limits were due to physical environmental constraints while the southern distributional limits were a result of competition. For example, it is common to see the pattern among plants of the Northern Hemisphere in which they are increasingly restricted to low elevations and south facing exposures as they reach the northern limit of their ranges, which suggests that their distributions are determined by ambient temperature (Renner *et al.*, 2006). Whether it is the maximum, minimum, average, variability etc…, in temperature, having the largest impact on a particular species at any given time is difficult to determine. While adults of some plant species may be killed by critically low short-term temperatures experienced during a one night episode, others may respond more strongly to bouts of prolonged freezing. Still other species may be restricted by cold climates where the summer growing season is too short to allow for growth and reproduction as opposed to low winter temperatures

(Renner *et al.*, 2006). There is much support in the literature for abiotic factors limiting the northern or altitudinal range of species (Sakai & Weiser, 1973; Körner & Paulsen, 2004). However, conflicting evidence exists for studies on southern distributional limits at the global scale which renders a high level of uncertainty of competition's role (Sax, 2001; Schwarz *et al.*, 2003). Thus the changing patterns of species assemblages observed across changing latitude is complex, and latitude is really a surrogate for one or more factors that are linked to specific geographic locations, hence environments and species assemblages (Rahbek, 2005).

Paleontological records of range changes associated with major climatic shifts such as the glacial to interglacial transitions have been widely used both to highlight strong correlations between climatic variables and species' ranges, and to make predictions about responses of species' across their ranges to present day climatic warming (Parmesan *et al.*, 2005). Classic studies have emerged from records of pollen and plant macro-remains for forest communities (Huntley & Birks, 1983; Davis & Zabinski, 1992; Payette, 1993) and fossils of beetles and other insects (Chironomids) (Coope & Lemdahl, 1995; Lavoie & Arseneault, 2001). Over time spans from the Holocene to 140,000 BP, range shifts of hundreds of kilometers, and as much as 2,000 km, have been documented for individual species associated with mean temperature changes of 4 ° to 8° Celsius over as little as 500 years.

The tree species of northern Quebec-Labrador are all widely distributed in North America, and all of boreal origin. They are believed to have moved into northern areas from a meridional source situated south of Pleistocene ice, and further spread towards their respective northern distributional limits (NDL) post deglaciation. Individual tree species spread at rates relative to their individualistic ability to colonize habitats driven by different disturbance regimes (Davis, 1983). A strong advantage shared among boreal species is the capacity for significant adaptation to changing environmental conditions through local and regional abundances and different growth forms (Payette, 1983). For example, it is thought that boreal tree species responded to postglacial environmental change by expressing change in their regional abundances (Payette, 1993). Payette (1983) suggests that the NDL of black spruce in the Quebec-Labrador region is out of phase with present climate, and that many tree species have

not yet colonized all potential sites in this area. White spruce is in equilibrium with present climate in the eastern part of the region, whereas it continues to expand along the Hudson Bay Coast. Balsam fir is slowly expanding in the James Bay area, whereas Jack pine is also thought to be in equilibrium with current climate at its NDL throughout the Quebec-Labrador region (Payette, 1993). Although it is assumed that *Populus* spp. arrived early after deglaciation, it is not known to what extent the distribution of either species (*P. tremuloides* or *P. balsamifera*) reflects present climatic conditions at their NDL (Payette, 1993).

1.1.6.3 Dispersal

A species is likely to be absent from many places where it could live due to dispersal limitations. Accidental and intentional introduction of non-native species to new environments demonstrates that there are areas which at any given time are unoccupied because individuals have not managed to get there (e.g., purple loostrife, reed canary grass) (Gaston, 2009). Favorable sites are often isolated from inhabited areas by some combination of distance and intervening areas with inhospitable conditions so that individuals are unable to disperse to these areas. At the global and continental scale, large bodies of water and mountain ranges illustrate this point as they are literally physical barriers that block dispersal (Gaston, 2009). In addition, these 'barriers' reinforce the role of history in determining where species occur, with ranges shaped by the interaction between dispersal ability and the timing of events that lead to barriers to movement being formed and destroyed (Renner *et al.*, 2006). However, the extent to which the immediate limits of geographical ranges are dispersal limited is a highly contentious issue. In the context of my research, the high dispersal ability of aspen via light, wind-blown seeds is notable.

1.1.6.4 Regional scale

At the regional scale, patterns of species distribution and abundance are thought to be influenced strongly by factors related to climate, disturbances, geology, and geomorphological processes (Foster, 1983; Brown, 1984; Foster *et al.*, 1998). Wildfires caused by lightning are the main disturbance in the North American boreal forest (Fauria & Johnson, 2008). The nature of fire in the North American boreal forest varies spatially and temporally, in large part due to differences in climate (i.e.,

along an east-west precipitation gradient) and fire's interactions with different landforms (Johnson, 1992; Bergeron *et al.*, 2001).

Climate-induced changes in fire regimes, or "the kind of fire history that characterizes an ecosystem" (Heinselman, 1981), are known to have occurred in the past (Bergeron & Archambault, 1993), and are predicted to have significant effects on boreal forest structure and composition in the future. If Atmosphere-Ocean General Circulation Models are accurate, the expected winter warming across the circumboreal zone will be in excess of 40% above the global mean in 2100, bringing a dramatic increase in fire activity and thus strongly affecting the successional dynamics of the forest at large (Chapin *et al.*, 1994; IPCC, 2007). The fire regime characterizing a region is comprised of: fire type and intensity (e.g., crown fires, surface fires); fire size; seasonality; and fire frequency (e.g., how often a fire occurs on a given piece of land) (Heinselman, 1981; Stocks *et al.*, 2002). These factors are largely affected by climatic control over fuel moisture levels and lightning activity (Fauria & Johnson, 2008). Fire disturbance is high during periods of low fuel moisture and seasonality which in turn, influence the spatial extent and intensity of any given fire, and further impact what vegetation becomes established after fire (Heinselman, 1981). In general, an east-west precipitation gradient underpins regional fire cycles in the North American boreal forest, which are on average ≥200 years in eastern forests where precipitation is high (Foster, 1983; Bergeron *et al.*, 2006), and between 50 and 100 years in the more westerly arid locations, such as Alberta and Alaska (Heinselman, 1981; Johnson, 1992; Larsen, 1997). Large stand-destructive crown fires burning 1000's of hectares are responsible for more than 95% of the area burned, as opposed to small fires that burn under 200 ha (Van Wagner, 1978). These fires generate uneven-aged forest mosaics of burned and unburned vegetation (Foster *et al.*, 1998; Bergeron, 2000), whereas low intensity surface fires are associated with short forest fire cycles, and often result in even-aged stands (Johnson, 1992). The difference in forest development over time, between fires, is reflected in canopy dominance and understory vegetation. The increase in forest fire that is expected to accompany changing climate is thus likely to produce noticeable vegetation change in some areas (Overpeck *et al.*, 1990). Hypothetically, early successional species that respond well to

disturbance, such as aspen, may have more opportunities to establish due to increased fire frequency, while potential later successional species such as black spruce would have fewer (Overpeck *et al.*, 1990). The net result of shifting abundances and dominant species over time and space has the capacity to alter soil environments, biomass accumulation rates, and systems function in general.

The present configuration of eastern James Bay is a result of a series of events that exhibit how influences of geology and geomorphological processes modify environments at regional scales. Change began about 10,000 years ago when the Laurentide ice sheet that had been covering most of North America for several tens of thousands of years began melting. Processes that followed resulted in the formation of the large freshwater Lake Ojibway, which was contained by a large ice dam to the north that if kept separate from the salt waters of the ancient Tyrell Sea (now Hudson Bay). Roughly 8,500 years ago this dam broke and the lake water was released and subsequently drained into, and mixed with, the salt water of the sea. After drainage, the waters of the sea flooded all ice-free lowland areas of eastern James Bay up to the Sakami moraine (essentially easterly as far as the James Bay Highway) and then began to retreat (Vincent & Hardy, 1979; Lajeunesse & Allard, 2003). When the ice melted the land was simultaneously released from the extremely thick and heavy mass, and responded by releasing and rising (Hillaire-Marcel *et al.*, 1981). This isostatic rebound continues today raising the land and moving the shore westward at a rate of one meter per century (Hillaire-Marcel *et al.*, 1981). As ocean bottom emerges as new land through this process, more surface area for terrestrial plant colonization is made available, and allows for synchronous movement of upland vegetation seaward (Iris von & Bégin, 1993; Sayles & Mulrennan, 2010). Thus land emergence acts as a disturbance event, contributing to the changing distribution and abundance of vegetation in the James Bay area over a somewhat palpable time frame – that of a human life (Sayles & Mulrennan, 2010).

1.1.6.5 *Landscape Scale*

Variations in disturbance regimes also play a strong role in creating the patterns seen on landscapes; however, finer features of the environment, such as topography and soils, become important drivers of species' distribution and abundance

as well (Heinselman, 1973; Foster *et al.*, 1998). Forest composition is thought to be a reflection of interactions between species regeneration strategies and longevity along with the frequency and type of disturbance (Bergeron, 2000). Heinselman (1973) suggested that boreal forest dynamics are akin to 'shifting mosaics' in which the spatial location of recent burns and stands of various ages would shift, but each would be present within the greater area at some relatively constant frequency. From a fire perspective, it is these "large" fires that have the greatest influence on landscape architecture, however part of the reason fire burns the way it does at any given place and time is in part due to historic geomorphic processes operating over geologic time scales which help shape landforms, that in turn, affect fire behavior (Heinselman, 1973; Swanson, 1978; Foster *et al.*, 1998; Turner *et al.*, 2003). For example, topography's control over soil-vegetation interactions plays a strong role in structuring plant community composition and structure through slope's influence on moisture and drainage patterns, the relationship between aspect and solar insolation, and the influence of elevation on temperature. The suite of exposure conditions common to south facing slopes generally provide added opportunities for more frequent or more intense fires which are likely to create conditions conducive to aspen establishment. Topography also affects processes that influence land cover change, such as paludification, whose rates and productivity are related to topography through the influence of water retention on the growth of *Sphagnum* spp. (moss), and successive organic matter accumulation (Simard *et al.*, 2009).

1.1.6.6 Local Scale

Local patterns characterizing plant species distribution and abundance are often related to interspecific interactions including competition, predation, and facilitation. Competition is a mutually detrimental interaction between two individuals. Many organisms share similar requirements for essential resources such as light, water, soil nutrients, and physical space and inevitably end up competing for resources. If resources are limited, as is often the case, reduced growth, survival, and reproduction will occur in one or both organisms depending on their fitness. Some organisms make the local environment toxic for other species as a form of competition. Yamasaki *et al.* (1998) demonstrated that through this process of

allelopathy the boreal shrub *Kalmia angustifolia* inhibited the growth of black spruce in its vicinity, thus effectively competing for space. Predation can be defined as any interaction between two species in which one benefits and the other suffers. According to this definition, relationships between herbivores and their food plants are classified as predation. Facilitative interactions include a variety of relationships that provide benefit to one or more of the participating organisms (Stachowicz, 2001). These relationships can be characterized by their relative strength and the type of interaction. They appear to be most common in environments with relatively high physical disturbance, stress, or predation, where associated species can increase the fitness of other species incapable of surviving on their own (Hacker & Gaines, 1997). In terrestrial habitats, many plants facilitate other plants by ameliorating physical stress (Choler *et al.*, 2001; Arroyo *et al.*, 2003; Brooker *et al.*, 2008), altering substrate characteristics (Callaway *et al.*, 1991), increasing resource availability (Chapin *et al.*, 1994), or providing protection from herbivores (Hjältén *et al.*, 1993).

1.1.6.7 The individual - species traits, evolution, and adaptation

The laws of physics and chemistry delimit where particular species can exist due to individual tolerances and physiological limits (Levin, 1999). A species presence in a particular place in time is in some part a function of its evolutionary history and the traits it has evolved (Webb *et al.*, 2002). Disturbance and dispersal events may be important for a species becoming established, whereas biotic interactions, such as facilitation, competition, and predation, can eliminate a species presence shortly after initial establishment. However, it is a species' traits that reflect their inherent constraints (Chase, 2003). The filtering of species by their trait values either allows a species to establish in a particular community, or alternatively prevents them from establishing in that community (Lavorel & Garnier, 2002). Viewing traits as the building blocks of "a species" is an easy way to conceptualize the relations between traits and the environment. It is the set of blocks that defines the species and dictates where the species will fit into a particular environment. All of the blocks, or traits, have particular functions which directly or indirectly affect the fitness of the species. All of the blocks interact and work together at a multitude of levels over different time scales to determine where the species will be successful at any given time and space.

The biotic and abiotic resources available to any species success in any given locality at any particular time throughout its establishment vary. These processes interact to determine alternative trajectories and endpoints. For example, species that arrive early in community development can have a priority effect within a community and may facilitate or inhibit the future recruitment of later arriving species depending on biotic and abiotic resources (Samuels & Drake, 1997). Communities are composed of many species, interacting and evolving in response to one another (Haloin & Strauss, 2008). Interactions among species can drive evolution, adaptation, and speciation of community members. Conversely, evolutionary changes in community members can feed back to modify species interactions, community composition, and community as well as ecological dynamics (Haloin & Strauss, 2008).

1.1.7 Aspen stand scale studies

The majority of aspen stand studies in North America are conducted in the Intermountain West where aspen habitat is generally quite dissimilar to that of NE boreal forests (Shepperd & Fairweather, 1994; Peterson & Squiers, 1995b; Bartos & Campbell Jr, 1998; Kulakowski et al., 2004; Margolis et al., 2007). In Quebec, although a significant amount of research has been done in the southern boreal forest where aspen is found on fine textured soils, site conditions are considerably different in NW QC, and very few studies include aspen stands growing near their NDL. Existing published quantitative data characterizing aspen near its NDL is based on two stands and addresses only climate-related factors, whose values are derived from interpolated climate data in a territory with few weather stations (Huang et al., 2010; Lapointe-Garant et al., 2010).

The few studies that specifically address aspen stands in an environment comparable to NW Quebec were conducted in Alaska (Van Cleve & Viereck, 1981; Van Cleve et al., 1991; Johnstone & Kasischke, 2005). Alaskan studies suggest that a suite of variables including vegetation reproductive ecology, fire frequency, fire intensity, substrate, organic matter accumulation, and competing vegetation all play a role in aspen stand initiation, stand expansion, stand contraction, and ultimately stand death.

1.1.8   Aspen Ecology

Aspen reproduces both sexually from seed and asexually (vegetatively) through suckering, root collar sprouts and stump sprouts (Peterson & Peterson, 1992). Vegetative reproduction through suckering is most common despite aspen's prolific production of small seeds capable of rapid long-distance seed dispersal. Most of the aspen literature emphasizes that conditions for natural seedling development are so critical that stands of seedling origin are relatively infrequent (Zasada & Schier, 1973), suggesting that seed regeneration of aspen is potentially more important in the northern parts of its range, as in NW Quebec, because the relatively cold soil conditions are not conducive to suckering, however, supporting studies are lacking. Aspen seed germination is most limited by substrate and soil moisture (Peterson & Peterson, 1992; Causse, 2006). Mineral soil has often been cited as necessary for seed germination, yet Causse (2006) demonstrated that aspen also grows well on organic substrates colonized by polytrichum moss (*Polytrichum strictum*) in the southern boreal forest of QC.

Aspen produces abundant suckers following large disturbances such as fire that most often arise from roots 4-12 cm below the surface (Horton & Maini, 1964), and post-disturbance sucker density varies greatly in the first year following disturbance; as many as 200,000 stems per hectare have been reported (Steneker, 1976; Frey *et al.*, 2003). Burning is a stimulus to suckering for several reasons. First, the hormonal inhibition of sucker production imposed by live over-story aspen is removed if the fire kills the stems in the stand without injuring the roots, and second, the fire removes or decreases the thick organic layers of duff (Landhausser & Wein, 1993; Walther *et al.*, 2002; Chapin *et al.*, 2004; Johnstone & Chapin, 2006b; Greene *et al.*, 2007; Landhäusser *et al.*, 2010). The charred and darkened soil surfaces absorb more heat, resulting in higher soil temperatures that stimulate sucker formation through degradation of the auxins in the roots. In addition, the increased light resulting from fire's removal of the above-ground vegetation encourages the development of the shade intolerant aspen suckers (Schier *et al.*, 1985).

Despite aspen's prolific ability to reproduce vegetatively, stress tolerant conifers and ericaceous plants dominate boreal environments. Aspen is a nutrient

demanding species that accelerates nutrient cycling, decomposition, N mineralization and nitrification, and is associated with soils with little organic matter accumulation (Mitton & Grant, 1996). These conditions are not generally associated with boreal environments that are dominated by cool, nutrient-poor / slow-cycling, low pH, and thick surface organic soils that favor the conservative growth strategy of black spruce (Van Cleve *et al.*, 1991). However, in a patchy system like the boreal forest, where most plants are perennial, clonal, and disturbance-driven, it may prove difficult to substantiate such "generalizations". A species living at the edge of its tolerance may be in constant flux between the disadvantages that come with a marginal existence and the advantages that arise when surrounding vegetation fairs worse.

1.2   Thesis Roadmap

1.2.1   Thesis structure

The thesis comprises primarily three manuscripts (Chapters Two through Four) that will be submitted for publication review in peer-reviewed journals. Collectively, the three research manuscripts address a larger set of questions and objectives that are defined below, and again revisited in the context within the thesis sections and in the conclusions (Chapter 5). Tables, figures, and literature cited from each chapter and research paper are grouped together at the end of each chapter, similar to formatting guidelines for submission to scientific journals.

1.2.2   Research Questions and Objectives

The main objective of this thesis is to answer the question: *What factors govern the northern distributional limit (NDL) of aspen in the James Bay area of Quebec?* Indeed, it has been suggested that many factors may be responsible for the NDL of boreal tree species (i.e., climate, disturbance dynamics, physical barriers, soil and nutrient status, and competition) (Flannigan & Bergeron, 1998; Asselin *et al.*, 2003) and that the factors themselves operate over different spatial and temporal gradients (i.e., forest stand, landscape, region) (Allen & Hoekstra, 1990; Levin, 1992). To address the broad thesis objective, we used a multi-scale / multi-variate approach to interpret the different patterns of aspen distribution and abundance observed at

different spatial scales of organization, while keeping in context the historical legacies of the study area (i.e. glacial history, fire disturbance). We ask several questions in three distinct, but related thesis chapters. Each successive thesis chapter developed in part from insights gleaned from former chapters, and in turn, aids in the understanding of each chapter's general findings.

In Chapter 2 we ask: *What does the actual distribution and abundance of aspen in the James Bay area look like?*

- In particular, we were interested in characterizing and quantifying the biogeographic extent of aspen's distribution in the James Bay area where it nears its NDL. A range map of this detail was nonexistent, yet necessary for basic comparative / quantitative ecological and biogeographic studies, and thus needed to be built.

- In Chapter 2, our objectives were to: 1) construct a land cover map using a combination of field, GIS, and remote sensing techniques, 2) characterize the dominant regional scale pattern of aspen distribution and abundance, 3) test if there is a significant spatial relationship between the presence of aspen and important landscape features.

In Chapter 3 we ask: What is the growth response of aspen along a climatic gradient spanning 8° in latitude in the eastern Canadian boreal forest?

- Here, we were interested in exploring aspen's growth response to the gradual change in climate experienced as one moves from south-north throughout the boreal zone. Most often constraints to tree species growth imposed by precipitation decrease with increasing latitude, while those enforced by cooling temperatures become increasingly important (Woodward, 1987; Hofgaard *et al.*, 1999). This line of thinking naturally extended into historic and current ideas regarding the NDL of a species, which suggest tree growth rates necessarily decline as one approaches the NDL of a species (Woodward, 1987; Loehle, 1998). Furthermore, this assumption has become fundamental to many climatic envelope models forecasting future species distributions, and forest growth models, where

both assume a unimodal growth response to some measure of temperature (Schenk, 1996).

- The objective of this chapter was to test the prediction that aspen growth rates will necessarily decline with increasing latitude.

In Chapter 4 we ask: What drives the distribution and abundance of aspen at the landscape scale in an area supporting uncharacteristic abundance for a tree species nearing its NDL?

- Chapter 4 involves scaling up detailed tree-, species-, and stand-level data collected on field plots to characterize forest composition and structure at the landscape scale.

- The objectives of Chapter 4 included: 1) distinguishing the factors controlling plant community composition in aspen dominated stands from factors controlling other dominate vegetation in the study area, 2) explicitly investigating the factors controlling local levels of aspen abundance, and 3) testing specific hypotheses related to the northern distributional limits of aspen in QC (see Chapter 4 for detailed explanations of hypotheses).

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Linking Statement between Chapter 1 and Chapter 2

This chapter constitutes the first regional scale effort to quantify and characterize the distribution and abundance of aspen in the James Bay area of Quebec, and further relate the observed distribution and abundance patterns to important landscape features. We used a combination of remote sensing, GIS, and ground-based techniques to compensate for the low accessibility of the study area. Three Landsat Thematic Mapper images from 2010 and 2011 were used in conjunction with a robust collection of ground reference data developed from aerial photography, and four field seasons of vegetation sampling to quantify aspen abundance using point pattern analysis techniques. We then investigated potential explanations for the pattern of aspen distribution and abundance including aspen's relationship to local topography (aspect, slope, and elevation) and distance to open areas, roads, regulated waterways, settlements, utility lines, and streams and lakes.

2 Aspen near its northern range edge in Quebec: Is human activity more important than climate?

2.1 Abstract

Predictions of shifting tree species distributions in boreal forests require policy that is based on a sound understanding of the principal drivers of forest response to environmental change. This research characterizes the regional distribution and abundance of trembling aspen (*Populus tremuloides* Michx.) near its northern range limit in northwestern Quebec, Canada, using a combination of remote sensing, geographic information systems (GIS) analysis, and ground-based techniques. Although not regionally abundant, aspen is the main broadleaf tree species in this conifer dominated landscape. Regionally, the ~51,000 km^2 study area has few settlements or roads, and is without industrial activity that affects the land. Most of the region is inaccessible. We utilized Landsat Thematic Mapper images from 2010 and 2011, a robust collection of ground reference data developed from aerial photography, supported by field verification where access permitted – vegetation sampling, to construct a thematic map of 11 land cover classes. The map highlights the spatial distribution of aspen, which represents only 0.3% of the study area. Map validation indicated an overall mapping accuracy of 74%, while the aspen predicted class was assessed at over 77% accurate. The regional scale distribution of aspen stands ≥ 0.5 ha within the study area shows a highly clustered pattern that is inconsistent with a gradual northerly decline expected if climate was the dominant controlling factor. Instead, the pattern appears to reflect human disturbance, suggesting that human activity plays a greater role in controlling aspen distribution than climate. Forest management policies concerned with changing forest composition in these northern landscapes should not assume climate-driven change and should recognize the potentially important role of human activity in driving the abundance of broadleaf tree species.

2.2 Introduction

With growing evidence that climate change is substantially affecting forest processes, structure, and function, understanding the appropriate responses to such issues is increasingly critical, and rests on the ability to predict how different tree species will respond over the entire range of their distributions.

Populations of trees near their range edges generally consist of scattered individuals and stands with depressed vigour that are often more vulnerable to environmental stressors than those in the centre of their range (Hoffmann & Blows, 1994; Gaston, 2003, 2009). Contrary to this common pattern is trembling aspen (*Populus tremuloides* Michx.), which occurs in uncharacteristic abundance near the northern edge of its range limits in the area east of James Bay in Quebec (Parisien & Sirois, 2003). This unusual distribution presents an opportunity to investigate range-boundary related determinants of distribution and abundance for a Canadian tree species of significant economic and ecological importance using a broad scale spatial approach (Bartos, 2000; St. Clair et al., 2013).

Aspen is the most widely distributed tree species in North America, has been identified as a keystone species in many parts of its range, and is a major component of the conifer-dominated northern boreal forest of Quebec (Hustich, 1966; St. Clair et al., 2013). Aspen's broad ecological amplitude is attributed to its high genetic and phenotypic diversity (St. Clair et al., 2010). Aspen produces copious amounts of small tufted seeds that are capable of long distance dispersal by wind, a trait it shares with many invasive plant species (Landhäusser *et al.*, 2010). However, they have a short three-week window of opportunity to arrive at a suitably moist germination site or they die. Most of the aspen literature emphasizes that conditions for natural seedling development are so critical that stands of seedling origin are relatively infrequent. In contrast, Zasada et al. (1973) suggest that seed regeneration of aspen is potentially more important in northerly parts of its range because the relatively cold soil conditions are not conducive to suckering. Once established, aspen spreads by clonal growth and resprouts vigorously from roots if a stand is burned or cut (Maini & Cayford, 1968; Landhäusser *et al.*, 2010).

We have a general idea from Payette (1993) and others (Foster & King, 1986; Ritchie, 2004) that the main range of aspen in QC is located in the southern part of the boreal forest (~48°N latitude) with extensive stands occurring as far north as 52°N latitude, particularly around southern James Bay. Aspen's northern boundary approximates the 13° C July isotherm, nears the forest-tundra ecotone (Halliday & Brown, 1943; Hustich, 1966; Maini & Cayford, 1968), and has been observed as far north as the Little Whale River (56°N latitude) (Ritchie, 2004). Although this literature provides a coarse view of aspen's geographic extent in Quebec, there is no thorough documentation of aspen's distribution and abundance in the northern part of its range due to the remoteness and general inaccessibility of the region (Ritchie, 2004); the few roads that cross the territory are illustrated in Figure 1. In the Abitibi area south of James Bay, aspen is very abundant but abundance decreases to small patches and scattered individuals along the gravel shoulders of the James Bay Highway (JBH) within 20 km of Matagami (49°45'N latitude; JBH km 0). The few aspen seen in this area appear to occupy sites disturbed by road-building which first occurred in the region in the 1960's and 70's. The use of road networks by aspen to colonize new areas in a linear fashion has previously been documented by Fortin (2008) and Laquerre *et.al.* (2009). Moving farther north, where aspen stands are not evident in the surrounding viewshed, black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.) uplands, and bogs dominate for over 250 km. Approaching the Old Factory River (JBH km 464), the terrain changes from relatively flat to an area with large outcrops and rolling hills that support many extensive young aspen stands; in general, the regional topography is of low relief. These stands, regenerating from a major fire in 1989, are accompanied by small clusters of 75-85 year old (30-40 cm diameter at breast height) trees that survived the fire. The stands appear to be well-established, productive historical forests. They are not sparse peripheral populations, nor are they new populations that have established following construction of the highway in 1971 (Salisbury, 1986). The oldest aspen core collected and dated from the study area was 114 years old. We speculate that the large stands around Old Factory Lake are the continuation of forests established thousands of years ago and are an important local seed source. Aspen's inconsistency with generally

expected species distribution patterns raises questions about how species and their individual constituents are distributed at regional scales, and about the potential determinants of these patterns.

The most common and enduring explanation of geographical range limits is climate (Currie, 2001). Changes in climate alter the geographic distributions of many species, presumably because climate limits range expansions and can cause range contractions (Parmesan & Yohe, 2003; Gaston, 2009).

The assumption that climate is the driving factor shifting species range limits underpins the majority of attempts to predict the responses of species to global environmental change. This approach, often referred to as bioclimatic envelope modelling, correlates species' present distributions in terms of current environmental conditions, and then examines the consequences of various climate change scenarios based on the modelled links between climate and distribution (Gaston, 2003). Recently, a number of critiques have questioned the validity of this approach by pointing out that many factors other than climate play an important part in determining species' distributions; the assumption that species will have a uniform response to changing climate across their entire distribution is inaccurate (Gaston, 2003); and realistically, we lack comprehensive distribution descriptions for most species because it is only within the last few decades that sufficient technology is readily available to map and characterize large geographic areas in detail (Brown *et al.*, 1996). In the James Bay area of northern Quebec, much research has been directed towards understanding the current and historic range dynamics of common conifers at various spatial scales due to their dominance in the northern boreal forest. However, little investigation has been directed towards understanding the regional scale dynamics of broadleaf tree species, such as aspen, that are very present in the landscape despite nearing their northern distributional limits (NDL) (Payette, 1983; Gajewski et al., 1993; Ritchie, 2004). Considering that northern Canada is predicted to experience considerable warming and associated impacts, studies of aspen populations near their NDL may help inform modellers and decision-makers about the factors associated with successfully established northern populations of aspen, and how they, and other broadleaf tree species, might respond to climate change (Parmesan & Yohe, 2003;

Parmesan, 2006). In addition, the current merits and/or limitations of bioclimatic modelling approaches can be assessed with respect to aspen.

The specific objectives of this study were to (1) to spatially (geographically) model aspen ecosystems across the study area to develop a realistic description of aspen's current distribution near its northern range edge in NW QC and detect broad regional patterns consistent with the scale of the study design, (2) determine if a regional response of aspen to climate is detectable (does aspen abundance decrease systematically with increasing latitude?), and (3) determine if there are spatial correlations between aspen and landscape features capable of influencing its regional distribution, such as topography, human infrastructures (roads, dams, settlements), and 'open' areas (<33% vegetated) which in theory should include some safe spots for aspen establishment (i.e., post burn sites in early stages of recovery). Through land cover mapping using remote sensing and GIS techniques, we show that the distribution and abundance of aspen is not consistent with the expected gradual northerly decline and that there are stands throughout the study area established on north facing slopes, which together suggest climate is not the most limiting factor for these northern populations of aspen. We suggest that human disturbance may be an important control on current distribution, but does not explain some important aspects of the regional distribution of aspen.

2.3   Methods

2.3.1   Study area - James Bay Area

The James Bay Area, as defined by our study boundaries, occupies a ~51,000 km^2 area in the northern boreal zone of western Quebec from 79°00' W to 76°30' W longitude, and 51°10'N to 53°50'N latitude (Figure 2-1). The regional topography is generally of low relief but rolling hills and rock outcrops (250-350 m a.s.l.) are observed in the central-eastern part of the study area in the vicinity of Old Factory Lake (OFL; 52°48'N, 77°30'W) and near the northern extent of the study boundary. Situated in the Canadian Precambrian Shield, the underlying rock is granite and gneiss (Stockwell et al 1998), and the soils are typically podzolic on mesic sites with organic fibrisols in the poorly drained areas (Ritchie, 2004). Bedrock geology has a strong

influence over much of the landscape characteristics such as relief, surface roughness, drainage pattern, vegetation pattern, and soil development because large areas of the shield are exposed with little or no mantle of unconsolidated materials (Ritchie, 2004).

The forests of northern Quebec are dominated by conifers; however, there is a distinct broadleaf component. Black spruce is the most common species; jack pine is also very common, but often limited to well drained, inland sites; white spruce (*Picea glauca* (Moench) Voss) is typically confined to coastal areas and occasionally inland on stream banks and disturbed sites; balsam fir (*Abies balsamea* (L.) Mill.) is predominately found on sites with long fire intervals; and balsam poplar (*Populus balsamifera* L.) is sparse and mainly on alluvial sites (Parisien and Sirois 2003). Aspen, tamarack (*Larix laricina* (Du Roi) K. Koch), and paper birch (*Betula papyrifera* Marsh.) are also found in the study area – but typically in lower abundances (Ritchie, 2004).

The area is affected by cold, dry arctic air from the north during the winter and by warm, moist air originating from the south during the summer which yields long and cold winters, and short and warm summers. The mean annual temperature ranges from -1 to -3°C from south to north. In the south, the average growing season lasts 140 days with 1100 degree-days ≥ 5°C as compared to 120 days and 600 degree-days ≥ 5°C in the north (Environment Canada 2002). Total precipitation varies from 868 to 684 mm from south to north, with about one-third falling as snow (Hutchinson et al., 2009). It is important to note here that there is only one weather station (La Grande Rivière station) with enough weather data to obtain interpolated-based climate estimates (30 years or more) for the study area; most weather stations in the area have less than 10 years of weather data (Rapaic et al., 2012).

2.3.2 Ground reference data

At the spatial scale of the study we collected the appropriate data to address and detect potential drivers of regional scale patterns of aspen distribution and abundance in the defined study area. This study was designed to examine the coarse distribution of aspen on a very large landscape and studies addressing aspen site characteristics such as soil, age, and origin are finer grained studies requiring data

acquisition and processing outside the scope of this study. We created a land cover map of the region with the goal of separating aspen from non-aspen vegetation. Accomplishing this was challenging because boreal forest manifests as a patchy mosaic of heterogeneous vegetation, and it was difficult to find suitably large patches of homogenous vegetation that were detectable given the spatial resolution of our primary source data, Landsat Thematic Mapper imagery.

We reviewed the available vegetation and ecological mapping data and found that existing sources were not suitable for assessing aspen distribution and abundance in the James Bay Area. Because a substantial portion of the study area is above the northern limit for timber allocations (~ 51°N latitude) there has historically been little attempt to quantify or characterize the landscape (Comite sur la limite nordique des forets attribuables, 2000).

Field sampling took place during 2009 through 2012. We initially focused on areas in the vicinity of Old Factory Lake (52°45'N, 77°20'W) and along Old Factory River (52°44'N, 77°40'W to 52°36'N, 78°43'W) due to previous observations of abundant aspen in the area. Field work yielded vegetation cover data from ground estimates obtained using a Garmin Oregon 550 global positioning satellite receiver to determine geographical location. For the most part, field sites were predetermined based on visual analysis of aerial photographs and satellite imagery, so as to select areas of homogenous broadleaf forest cover that were reasonably unscathed by recent fires. Access to the landscape of the James Bay area is severely limited because it has few roads, so most of our ground reference plots are accumulated along roadways, rivers, reservoirs, and lakes where ready access was available.

Aerial photographs were obtained from Hydro Quebec for various portions of our study area that had photo coverage (Table 2-1). Photos were from different time periods (1989-2010), multiple resolutions (1:4,000 to 1:40,000), and both panchromatic and colour. Aerial photos were scanned and geo-rectified and used as a source for screen digitization of cover classes that are typically stable over the time-frame of the photos (water, rock, and shoreline) and for identifiable cover classes present in most recent photos (mixed conifer and aspen) and/or in areas where we were certain disturbance history was stable (i.e., around OFL).

We accessed suitable hilltop locations where we could obtain high-resolution panoramic photos of areas that included multiple vegetation cover types. These sites were identified using visual inspection of a digital elevation model (DEM) in tandem with a vector layer of roads in a GIS. High places near roads, mostly clear of vegetation yet surrounded by a diversity of land cover types, were targeted for the acquisition of high-resolution ground reference photography. Upon return from the field, the photographs were digitally combined, geo-located in Google Earth®, and hosted to an online web service (Photosynth®) where we were then able to extract vegetation cover class data co-located with the satellite imagery and georectified aerial photographs (Oetter et al., 2011). Seven hundred and seventy-four ground reference sites were digitized as polygons for association with satellite imagery.

2.3.3 Remotely sensed images and pre-processing

Landsat Thematic Mapper imagery was selected as the primary source imagery for land cover classification, both to take advantage of its regional scale and to exploit the spectral classification abilities of Landsat's mid-infrared bands (Cohen & Goward, 2004). A total of five separate path / row combinations were necessary to cover the entire study area, with the vast majority of the study area covered by path 19, rows 22-24 (Figure 2-1). During 2011-2012 there were only four satellite passage days on path 19 that yielded reasonably cloud-free images. Three of these dates were selected (May 11, 2010; July 14, 2010; and October 5, 2011) for the core of our image analysis focus (Table 2-2-2) to coincide with field data reconnaissance dates and the best cloud- and ice-free imagery while capturing much of the phenological change from a growing season. Standard terrain corrected images were obtained from the U. S. Geological Survey (Earth Explorer) as GeoTiff files, which were processed using ERDAS® Imagine software.

To take advantage of seasonal differences in imagery due to changes in vegetation among the three different imagery dates for the core scenes, we elected to apply atmospheric correction and radiometric normalization to the path 19 imagery. The COST method was used to calculate atmospheric corrected reflectance values (Skirvin, 2002), and the ridge method was applied to normalize the May and October

images to the July scene (Song, 2001). Normalized radiance images were transformed to tasselled cap images (Crist, 1985), and multi-date images were created using a layer stack procedure, to integrate the brightness, greenness, and wetness values for three different dates into a single image (Oetter et al., 2001). Additional combinations of two dates for the path 19 imagery were also created to allow for removal of clouds in each of the three scenes.

2.3.4 Image analysis

A four-step hierarchical process was used to classify the raw satellite imagery and produce a land cover classification of the study area. Initially, an unsupervised classification of the three-date tasselled cap image was used to identify and remove from analysis pixels representing perennial water. The remaining land pixels were then clustered with a supervised classification of the three-date tasselled cap image, using a maximum likelihood classifier (Lillesand et al., 2008) with a subset of the ground reference sites. A total of 455 reference polygons, divided into 20 separate land cover types, were linked to the 3-date image to produce eleven output cover types. Two-hundred and forty-two independent reference polygons were held back for validation, and used to assess the accuracy of each classification step.

For pixels that were covered by cloud or cloud shadow on any of the dates, a third clustering step was required, wherein those obscured pixels were clustered using cloud-free imagery from other dates. To determine obscured pixels, cloud/cloud shadow pixels were detected by visual inspection and polygons around each cloud/shadow were digitized. Within these areas of interest, a single-date unsupervised classification was performed to identify pixels with spectral properties of clouds or cloud shadow. Those pixels were then used to perform a supervised classification with a 2-date image (leaving out the image date with cloud present) as the source imagery. For the pixels that were obscured by cloud/cloud shadow in two of the three dates, a supervised classification was performed on the remaining cloud-free date.

In the fourth iteration of the classification, two single-date images from adjoining path/row scenes were clustered with a supervised classification approach to fill in parts of the study area that were not covered by the path 19 core images.

2.3.5 Map generation and error characterization

For the generation of our final map, we combined output classes from the four stages of image clustering to produce eleven distinct classes. The results of these classifications were combined into a single thematic image using a class-specific overlay process that allowed land cover classes to overwrite cloud and cloud shadow effects, in an effort to create a final image free of cloud and shadow classes. Independent ground reference polygons were then used to assess the accuracy of the overall classification by constructing an error matrix using the 242 testing plots that represented those classes.

2.3.6 Aspen in the James Bay Area

The thematic land cover map was used to identify and analyse predicted aspen stands throughout the study area. Aspen cover needed to be 80% or greater to achieve 'stand' designation. Adjacent aspen pixels (30 x 30 m resolution) at a minimum mapping unit of 0.5 ha were generalized into vector polygon stands, which for elongated clusters reduced the minimum vector area to 0.2 ha. These polygons were used to characterize the geographic distribution of aspen and the spatial association of aspen in relation to the latitude, topography, and potentially related landscape features.

Point pattern analysis was used to determine the tendency of aspen stands to exhibit a systematic pattern over an area as opposed to being randomly distributed. The three general patterns that emerge from this type of analysis are; random, uniform, or clustered. We used a quadrat analysis to examine and quantify the spatial arrangement of aspen stands in the study area. In this method (McGrew & Monroe 2000), a 10 x 10 km grid was created to cover the study area. Aspen stands within each grid cell were counted and compared to expected values from dispersed, random, and clustered predictions. A point-pattern analysis was also conducted, using the polygon centroid as the point coordinate, to examine the clustering tendency compared to a standard distance determined by the study area size.

The aspen stands were processed for their latitude and topographic setting, including elevation, slope and aspect. Vector GIS analysis tools in ESRI ArcMap® were used to extract location and topographic values, both for the generalized

polygons, and for the individual pixels, which were examined for relevant spatial associations.

Based on evidence that aspen thrive in specific mineral soils (Chapter 4), we analysed the spatial relationship between predicted aspen stands and a geological profile of the study area (Sharma, 1996). A presence-absence matrix of potassium-rich bedrock types was used to examine the spatial assembly of aspen stands throughout the study area.

Finally, a proximity analysis was conducted to measure the spatial association of the predicted aspen stand in relation to important landscape features. The distance from each stand was measured to the nearest settlements, roads, open areas (as determined from the land cover map), utility lines, natural streams and/or lakes, and regulated waterways (reservoirs and regulated rivers downstream from reservoirs). To describe the relationship between these features and the presence of aspen, we employed the Kolmogorov-Smirnov test for normal cumulative frequency distributions, with the expectation that non-normal distributions indicate a strong relationship between the landscape feature and the presence of aspen. The cumulative frequencies of aspen stand distances from features of interest were compared to a 'background' population distribution of a combination of all other forested areas.

2.4   Results

2.4.1   Image classification

The hierarchical classification yielded an 11-class thematic image of the James Bay study area (Table 2-3). The largest class by area was mixed conifer, followed by water, shrub, and wetland. Aspen, the main target class, covered 178 km^2, representing only 0.3% of the study area.

The classified image appropriately displays the complex ecological heterogeneity of the region (Figure 2-2). Extensive tracts of mixed conifer forest are broken by lowland bogs and wetlands, highland open and semi-open clearings, and large tracts of recently burned areas. Within the recent burns, open, semi-open, and shrub areas dominate the land cover, punctuated by bogs and mixed conifer forests.

The predicted aspen cover is clustered in particular areas that appear to be most associated with human activity.

2.4.2 Accuracy assessment

Based on comparison with an independent set of 242 ground reference polygons, the 11-class map had an overall accuracy of 74.0 % (Table 2-4). Our accuracy values were variable across cover types. Predictions of water, burn, bog, and mixed conifer classes were all validated at above 90% accuracy. The aspen predicted class was assessed at over 77% accurate.

The values reported above represent the producer's accuracy, a measure of the probability of a reference pixel being correctly classified. User accuracy values are also reported; these represent the probability that a pixel classified on the image actually represents that category on the ground (Congalton, 1991). In our case we achieved an 83% user's accuracy for aspen.

2.4.3 Aspen in the James Bay Area

"Aspen", as categorized above, covers 0.3% (17,821 ha) of the study area in variable spatial concentrations across the region. Spatial analysis of the aspen distribution suggests that the stands are highly clustered. The almost 200,000 individual 30 x 30 m pixels predicted as aspen were generalized into 3166 polygon stands with a minimum size of 0.5 ha. Isolated aspen pixels and connected pixels totalling less than the minimum size were eliminated from our locational analysis.

A quadrat analysis revealed that the spatial distribution of the aspen stands was highly clustered. Of the 473 grid cells (10 x 10 km), 363 cells contained fewer than the mean number of stands (6.8), and 205 cells contained no stands at all. Fourteen cells, clustered in particular areas (Figure 2-3), contained greater than 50 separate aspen stands. A chi-square statistical analysis of the distribution revealed a > 99.99% probability that the aspen stands are clustered (McGrew & Monroe 2000).

The centroid for each polygon stand was used to perform a nearest-neighbour analysis, which confirmed the highly clustered spatial pattern of aspen in the James Bay study area. The nearest neighbour distance for the aspen stand points was 736 m,

which is 37% of the calculated random nearest neighbour distance (2011 m). The Z-test statistic for the nearest neighbour analysis was calculated at 68.25, which indicates a > 99.99% probability that the aspen stands are significantly clustered.

To investigate potential explanations for the aspen clustering, we analysed the geographic setting of the polygon stands, including latitude, elevation, slope, and aspect. The latitude of the stands ranged throughout the study area, from 51.2° N to 53.9° N, with a mean value of 52.5° N. In the absence of climatic data necessary to map temperature and precipitation values for the study area, we used latitude as a proxy value for temperature, with the expectation that more northern locations would be subjected to slightly colder temperatures and longer periods of freezing. To allow comparisons, we divided the study area in to three roughly equivalent latitudinal ranges: South (51° 10' to 52° 00' N), Middle (52° 00' to 53° 00' N), and North (53° 00' to 53° 50' N). Almost half (49.8%) of the aspen analysis stands were located in the middle range (Table 2-5).

Aspen stands were found from sea level to a mean elevation of 165 m, with 69.3% of the stands found between 150 and 300 m (Table 2-6). Although the maximum elevation in the study area was ~350 m, it is important to keep in mind that most of the study area is of low elevation. Slope values ranged from flat to 22.2°, with 64.2% of stands found between 0 and 4° slope. Aspect values ranged throughout the entire azimuth spectrum, however we discovered a tendency for aspen stands to face south, with 64.5% of the stands directed toward the southeast, south, or southwest (Figure 2-4). This tendency was more pronounced in the north range of the study area, where 74.3% of the stands faced in a southerly direction, compared to 66.7% in the middle range, and 53.6% in the south range. Our attempt to correlate aspen presence with the variation in geological substrate across the study area was inconclusive as more detailed studies are needed.

Distance analysis revealed a strong relationship between the presence of aspen and distance to open areas, roads, settlements, utility lines, regulated waterways, and natural streams and lakes (Table 2-7). The closest distance from each aspen stand (polygon) to the nearest test feature was calculated for all 3166 stands, and converted to a cumulative frequency distribution (Figure 2-5). Clearly, aspen stands are found

more frequently close to open areas, roads, utility lines, and regulated waterways, respectively. Half of the aspen stands were located within 0.5 km of open areas, within 8.0 km of roads, within 8.5 km of utility lines, and within 13.0 km of regulated waterways, respectively (Figure 2-5). In the context of the James Bay area, "regulated waterways" refer to waterways impacted by the hydro-electric project in the study area, which includes several large reservoirs. Knowledge of the environmental effects of reservoir creation are well known and include non-natural fluctuations of water levels in areas down river of dams which can significantly lower flow rates and allow new vegetation to colonize former areas occupied by stream water (Baxter, 1979). A distance distribution from the same features was calculated for all the forested pixels in the study area at a scale of 120 x 120 m pixel size. The Kolmogorov-Smirnov two-sample test for normal distributions allowed us to compare the cumulative frequencies for aspen stand distance to a 'normal' background of the forested pixels in the study area. This test suggests that the spatial distribution of aspen is non-normal, with a propensity for aspen to congregate near open areas, roads, utility lines, and regulated waterways (Table 2-7).

2.5   Discussion

Our land cover mapping results are similar to other classifications of boreal forest that have performed accuracy assessments. For example, Johnson et al. (2003) achieved an accuracy of 77% when conducting a supervised classification to characterize woodland caribou habitat in British Columbia, Canada, and similarly Franklin & Moulton (1990) achieved an accuracy of 78% using a supervised classification to characterize habitat in southwest Yukon, Canada.

Northern land cover mapping presents many challenges not experienced in more southern environments due to its vast and remote coverage in Canada, leading to a lack of reference data and limited knowledge of northern land cover distribution and dynamics (Olthof et al. 2009). Many studies do not have enough ground reference data to perform adequate accuracy assessments (Wulder et al. 2006; Olthof et al. 2009) and thus do not instil confidence in their end products. Our results demonstrate that the

land cover map produced with the approaches applied in this study have a degree of accuracy suitable for use by resource managers and other end users.

Using the land cover map developed for the study, we show that the pattern of aspen distribution across the study area is patchy and that the north-south trend is not consistent with a climate-driven response. We expect a climate response pattern would show a gradual northerly decline across the study area. The distribution of stands relative to "open" area may arise from lower surface organic matter accumulation in these and surrounding areas, which would provide better establishment conditions for aspen. Open areas in this study include a combination of natural (i.e., recovering burned areas, low tidal flats, and rock) and anthropogenically modified areas (i.e., built structures, paved areas other than roads, and community dumps). Aspen was commonly observed growing in 'disturbed' areas during field data collection. However, further detailed studies exploring this relationship are needed to explicitly address how to identify suitable places for aspen establishment across the study area.

We found that 49.8% of the aspen stands in the study area were located at mid-latitude with respect to the study area (52° to 53° N latitude) (Table 2-5), rather than the majority of aspen stands occurring in the south where climate is generally more hospitable. This implies that a purely bioclimatic modelling approach to predicting species' responses to changing climate might not be sufficient to model change in the regional distribution of aspen. This comes as no surprise considering that lessons learned from the last two decades of ecological research strongly highlight how difficult it is to understand and interpret the spatial patterns generated by ecological processes (Levin, 1992; Tilman & Kareiva, 1997; Pastor et al., 1999). Not only do different patterns emerge depending on the scale of observation, but the underlying causes of these patterns also differ (Wiens, 1989; Levin, 1992). For example, a regional-scale study by Michaelian et al. (2011) showed that aspen responds strongly to drought in a southern portion of its range in Canada as evidenced by extreme stand dieback and mortality. In contrast, our study suggests that evidence for a dominant climate-driven response in northern Quebec is not strong; however, it is also not absent. We did find support for the microclimatic effects of aspect on aspen by showing that 64.5% of the stands face a southerly direction (Figure 2-4), which

suggests the microclimatic effect of warm slopes is important at smaller spatial scales relative to our study area; however, not the dominate driver at the spatial scale of this study. Our results showing a non-dominate role of climate on aspen distribution and abundance are generally consistent with two past studies that assessed aspen growth response to climate along latitudinal gradients in western Quebec. Huang et al. (2010) reported that of the four dominant boreal tree species they assessed, aspen was the least responsive to climate, and Whitbeck and Fyles (in prep.) found aspen's growth response to climate to be weak in general, and fairly similar across a ~8° latitudinal gradient. Scaling down to the landscape-level in Yellowstone National Park, USA, Turner et al. (2003) found that elevation largely explains variation in aspen seedling density. Together, these results suggest that we should be assessing how tree species ranges respond to climate and "change" in general with caution, due to the different factors affecting tree species in different parts of their range distribution. Understanding how, where, and which trees are most vulnerable to climate or other change is key to identifying viable options for future forest management policies and practices.

The pattern of aspen distribution and abundance that emerged from this project indicates that the highest levels of aspen abundance are in areas associated with human activity. While we cannot conclude that the landscape features in question have any direct influence on the presence of aspen nearby, the strong correlative relationships established through distance analysis do help us target some of the site conditions that may be contributing to the clustering of aspen stands in James Bay. Two readily identifiable areas appear related to land use changes associated with Hydro-Quebec hydroelectric projects. We found clustering of aspen along the Opinaca-Eastmain river complex in the middle of the study area, and along the La Grande River in the northern portion of the study area.

The pattern of aspen occupancy along regulated waterways suggests aspen may establish in response to the newly exposed mineral soils associated with the lower flows resulting from damming activities. Both river systems experienced dramatically reduced water levels when damned in the early 1980's. Subsequently mineral substrate

that was once underwater is now exposed and appears to provide quality establishment conditions for aspen.

Another cluster is found around the Namiscau community and the North Road. Here aspen presence also seems to be in concert with human disturbance associated with road building and disturbance associated with the human footprint in general. Although it was once thought that aspen reproduction by seed was a rare event (Barnes, 1966; Kemperman, 1977) an increasing number of studies are detecting seedling establishment, and proliferation, in response to both natural and anthropogenic disturbance (Kay, 1993; Romme *et al.*, 1997; Quinn & Wu, 2000; Turner et al., 2003; Landhäusser et al., 2010). For example, Landhäusser et al. (2010) tracked aspen moving up in elevation in the western Canadian Rockies in concert with forest harvesting practices that exposed mineral substrate. We observed aspen seedlings growing in the gravel substrate that lines the James Bay Road, even in areas with no aspen in the surrounding viewshed. Available substrate appears to be a critical component determining successful aspen colonization in the aforementioned cases and may be the key to explaining the two clusters of aspen in our study area that coincide with the disturbance associated with dammed rivers.

Given the apparently strong influence of human activity on aspen, and the increased level of human activity in the James Bay area, aspen is likely to increase in the landscape in coming decades. This presents an interesting contrast with western North America where the main management concern is the loss of aspen and its need for conservation for biodiversity and wildlife habitat (Michaelian et al., 2011). In the James Bay area increasing aspen cover is likely to increase mammal abundance to the benefit of subsistence and recreational hunters. The history of conflict over natural resources in this region, and the often strained relationships between the native Cree and the recreational hunters from "the south" generate circumstances in which complex management policies are likely to be required. Furthermore, this study demonstrates that it is very complicated to unravel the causal agents of species distribution and abundance patterns. At the scale of this study one would expect to detect a strong effect of climate, yet we did not. Thus many species distribution

models currently in use do not include important variables driving distributions because they are based solely on climatic factors (McGill, 2010).

2.6 Acknowledgements

2.7 References

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2.8   Tables

Table 2-1: Ground reference data – number of plots by source and scale.

Number of Plots	Source	Scale	Date
378	Field visits	Actual	2009-2011
244	Hydro Quebec aerial photos	1:4,000 to 1:40,000	1989-2010
152	Visual reference from SPOT, IKONOS, and TM satellite imagery	1 m to 30 m pixel	2006-2011

Table 2-2: Landsat Thematic Mapper satellite imagery – path, row, date, and cloud cover for each scene used

Path	Row	Date	Cloud Cover (%)
18	24	June 5, 2010	12.33
19	22	May 11, 2010	11.85
19	23	May 11, 2010	0.06
19	24	May 11, 2010	0.31
19	22	July 14, 2010	0.19
19	23	July 14, 2010	0.01
19	24	July 14, 2010	0.30
19	22	October 5, 2011	19.81
19	23	October 5, 2011	0.01
19	24	October 5, 2011	0.00
20	23	June 22, 2011	0.00

Table 2-3: Final land cover classes for the study area.

Cover	Area (km²)	Percent (%)
Water	9,799	19.1%
Open	1,950	3.8%
Burn	1,021	2.0%
Semi-open	632	1.2%
Shrub	9,143	17.9%
Bog	709	1.4%
Wetland	9,116	17.8%
Mixed forest	571	1.1%
Mixed conifer	17,922	35.0%
Mixed broadleaf	167	0.3%
Aspen	178	0.3%
Total:	51,208	100.0%

Table 2-4: Error matrix for supervised classification of the study area.

Predicted Class

	Water	Open	Burn	Semi-open	Shrub	Bog	Wetland	Mixed forest	Mixed conifer	Mixed broadleaf	Aspen	Total	User's Accuracy[1] (% correct)
Water	11											11	100%
Open		21		4	2							27	78%
Burn		3	7									10	70%
Semi-open		3		9	11							23	39%
Shrub				1	22		2		1	1	6	33	67%
Bog		2				1	6		2			11	9%
Wetland					3		33		1			37	89%
Mixed forest					1			2	1			4	50%
Mix. conifer					1		2	2	47			52	90%
Mix. broadleaf								2		2	1	5	40%
Aspen					1					4	24	29	83%
Total	11	29	7	14	41	1	43	6	52	7	31	242	
Producer's Accuracy[2] (% correct)	100%	72%	100%	64%	54%	100%	77%	33%	90%	28%	77%		

(Row label on left side, rotated: **Classification Data**)

[1] User's accuracy indicates the probability that an area on the ground will be classified correctly.

[2] Producer's accuracy indicates the probability that a unit from a classified map actually represents that category on the ground.

Table 2-5: Summary of aspen cover (stand and total area) by geoclimatic zones in study area, and % cover expected if aspen were evenly distributed across the study area. O%-E% indicates the difference in percentage.

Geoclimatic zones in study area	Zone Area (km^2)	% of total area	Aspen Stands (#)	% of stands within zone	O%-E%	Aspen Area (km^2)	%	O%-E%
South	15,100	29.6%	927	29.3%	-0.3%	19.5	27.8%	-1.8%
Middle	19,200	37.3%	1577	49.8%	12.5%	32.1	45.8%	8.5%
North	16,900	33.1%	662	20.9%	-12.2%	18.4	26.4%	-6.7%
Total:	51,200	100%	3166	100%		70	100%	

Table 2-6: Summary statistics for geotopographic characteristics of aspen stands.

	Latitude (°)	Area (ha)	Elev. (m)	Slope (°)	Aspect (°)
Minimum	51.2	0.2	0	0.0	-1.0
Maximum	53.9	104.9	328	22.2	355.2
Mean	52.5	2.2	165	3.6	183.3
Standard Deviation	0.7	4.8	77	2.7	75.9

Table 2-7: Summary statistics for distance analysis: testing goodness-of-fit for continuous distributions with the Kolmogorov-Smirnov test.

	Nearest Neighbor	Open	Road	Settlements	Utility Lines	Streams & Lakes	Regulated Waterways
Aspen							
Minimum Distance (km)	0.1	0.0	0.0	0.7	0.0	0.0	0.0
Maximum Distance (km)	17.8	6.3	44.8	134.9	54.2	2.5	83.5
Mean Distance (km)	0.7	0.7	9.7	57.0	11.6	0.4	17.0
Median Distance (km)	0.4	0.5	4.5	54.9	8.4	0.3	13.2
N (aspen)	3,166	3,166	3,166	3,166	3,166	3,166	3,166
Background Forest							
Mean Distance (km)	-	1.4	15.1	49.3	15.9	0.5	22.8
Median Distance (km)	-	1.1	12.8	43.8	12.8	0.3	18.9
N (background)	-	1,190	24,852	10,862	32,868	484	64,857
Two-tailed K-S test							
Kolmogorov-Smirnov D Statistic	-	0.27	0.21	0.10	0.21	0.03	0.17
P-value	-	0.000	0.000	0.000	0.000	0.435	0.000

2.9   Figures

Figure 2-1:   Location of the study area in northwestern Quebec; including
communities, roads, and major water bodies. Landsat Thematic Mapper
image boundaries are shown in dotted lines.
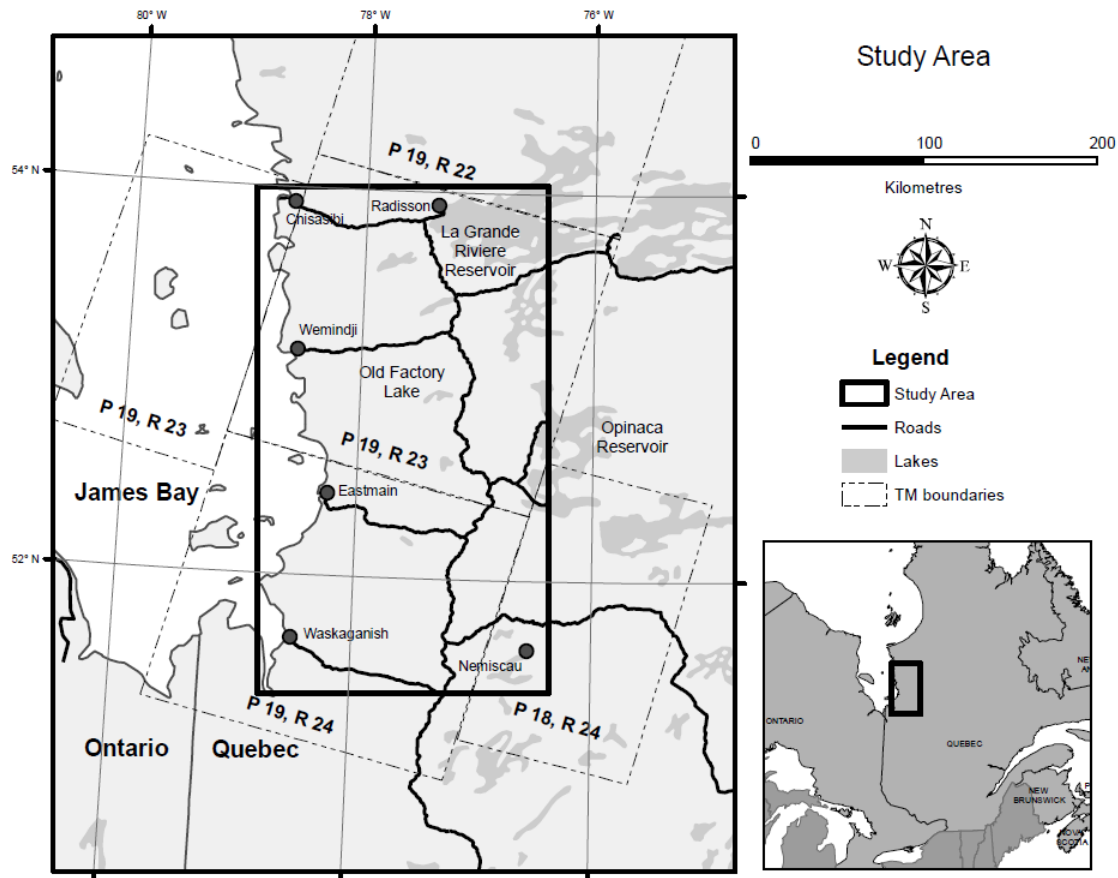
Figure 2-2:   The 11- class land cover map of the James Bay Area.

Inset maps highlight detail of land cover predictions: a) area around Lake Yasinski showing diverse area of conifer forest, shrub, and wetlands; b) Old Factory Lake vicinity showing an abundance of aspen; c) area around Eastmain River exhibiting recent burn and shrub recovery from previous burn.
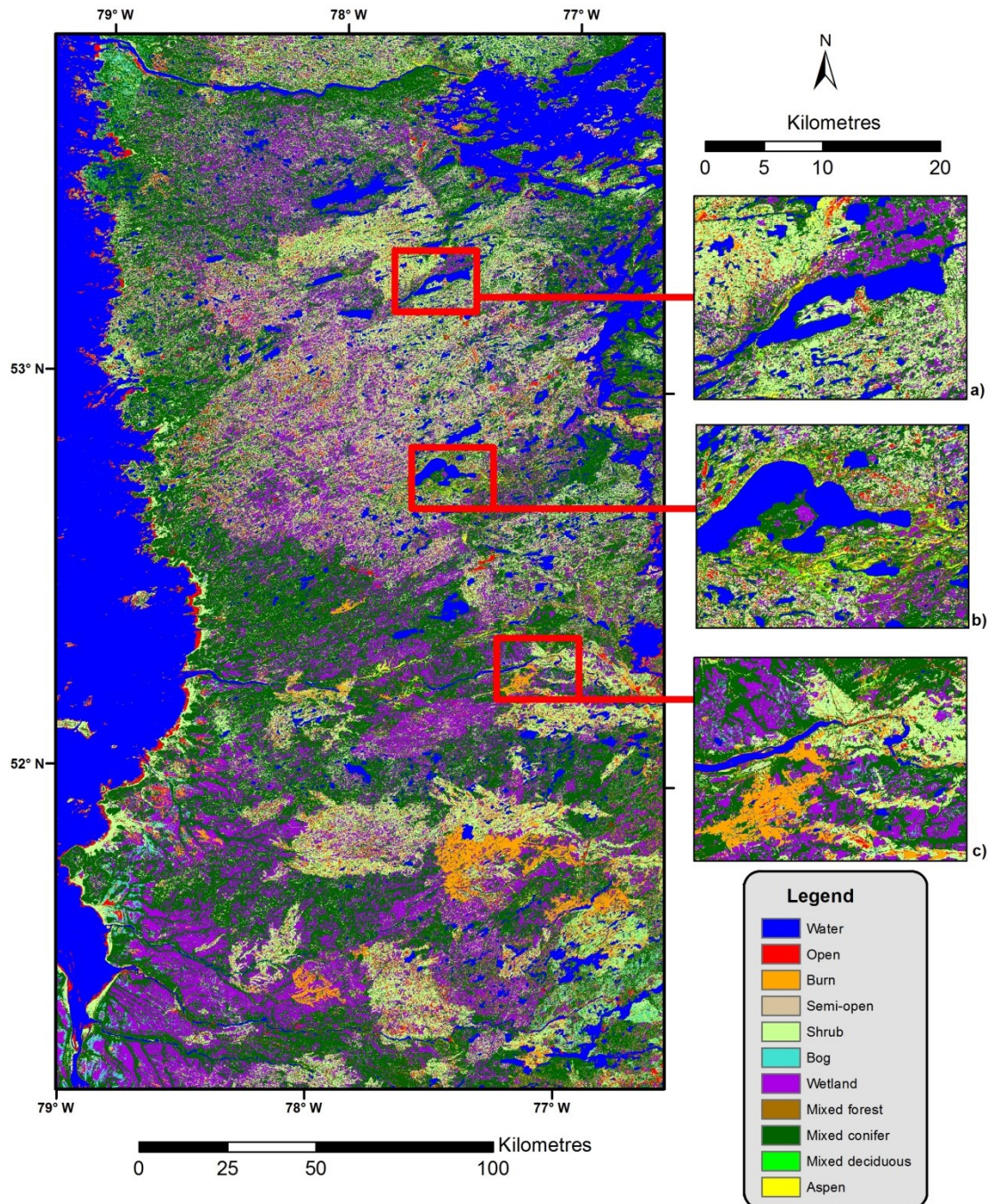
Figure 2-3: Quadrat Analysis: A set of 473 quadrats (100 km^2 each) superimposed on the study area to indicate the regional variation in aspen clustering.
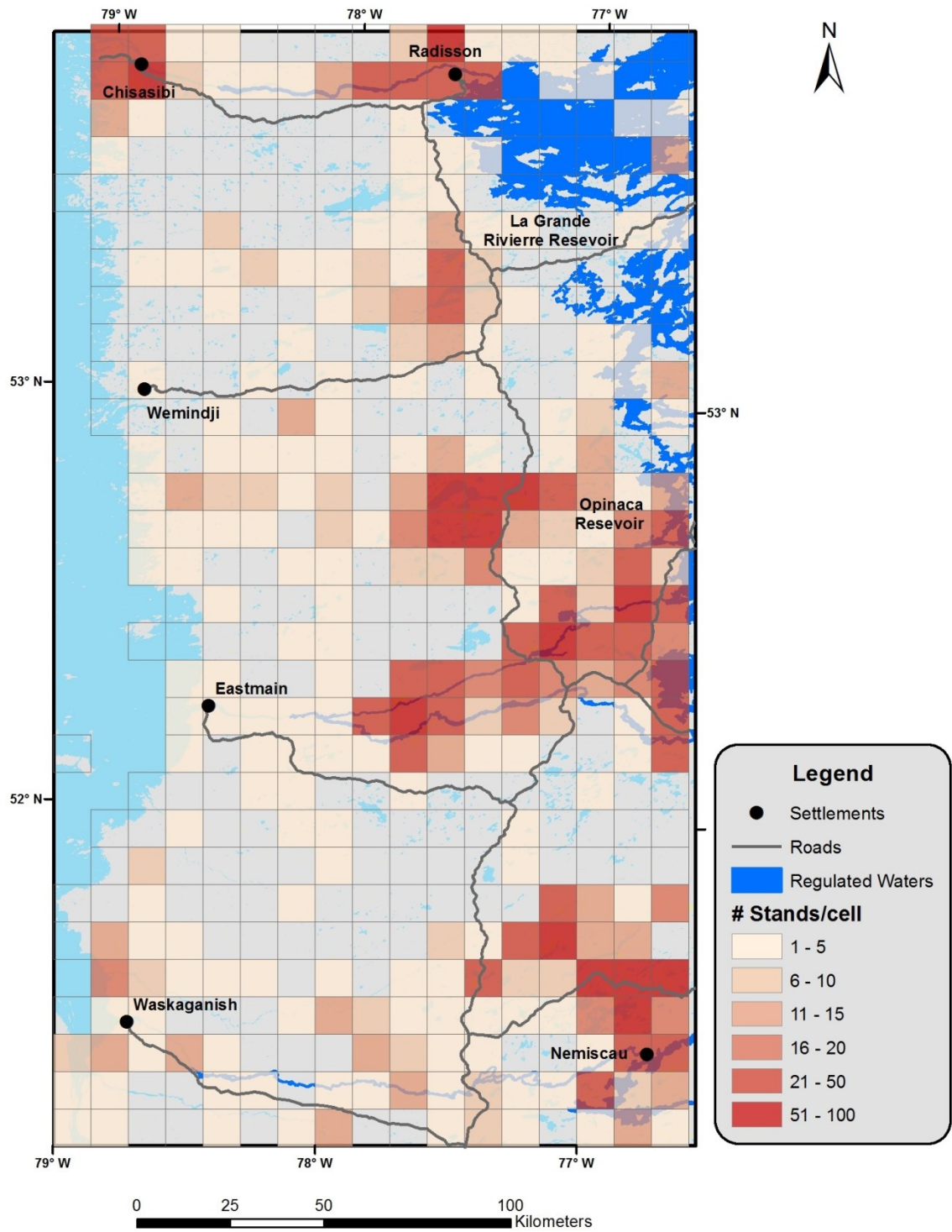
Figure 2-4: Frequency Distribution of Aspen Stands by Aspect. Flat means that all the pixels in a stand (polygon) have the same elevation value in the Digital Elevation Model (DEM).
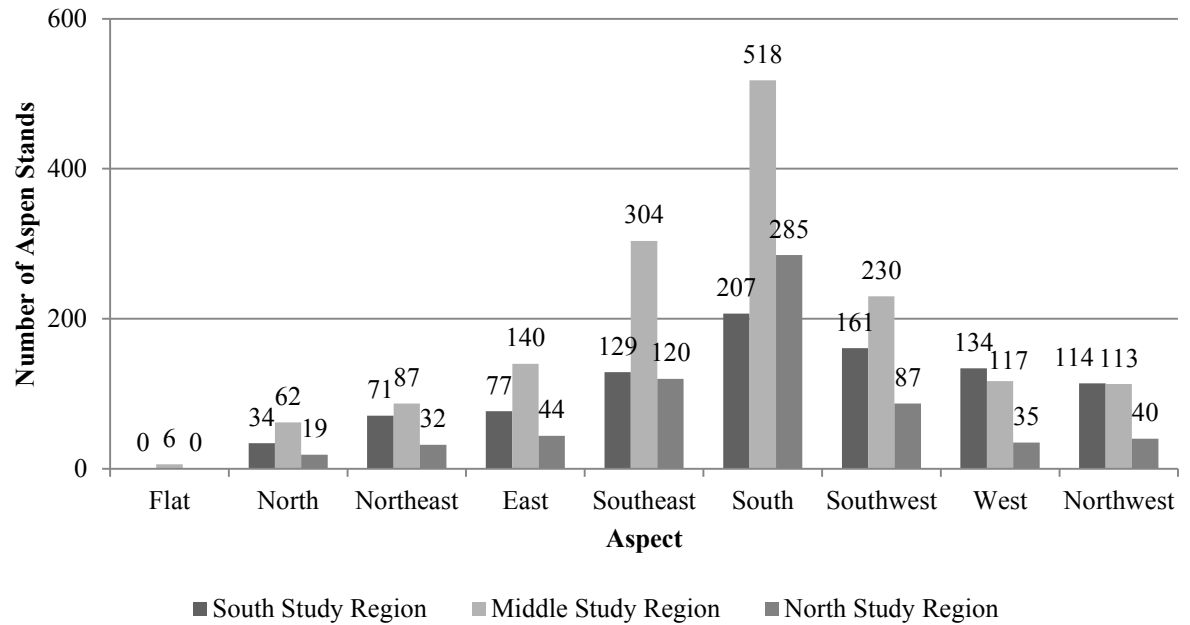
Figure 2-5:   Distance to Feature Histograms and Cumulative Fraction Plots for Six
               Selected Features: a) Open Areas, b) Roads, c) Settlements, d) Utility
               Lines, e) Water: Lakes and Streams, and f) Water: Regulated
               Waterways. Scales for the frequency counts vary, and the background
               frequency count has been normalized to that of the aspen in each graph.
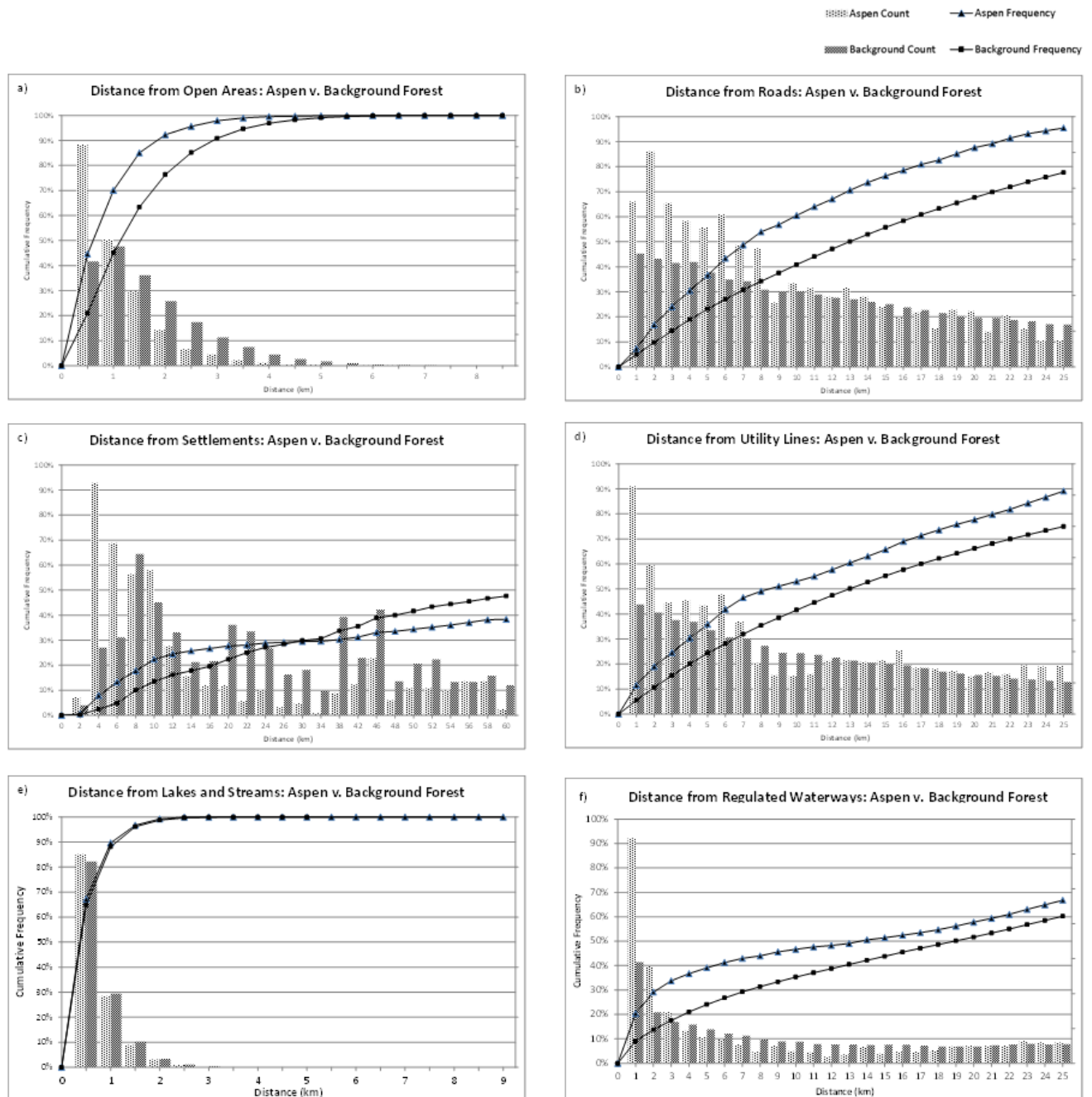
Linking Statement between Chapter 2 and Chapter 3

In **Chapter 2** we constructed a land cover map of the James Bay Area ($\sim$51,000 km^2) using a combination of field, GIS analysis, and remote sensing techniques in order to characterize and quantify the current biogeographic extent of aspen in the area. We then tested to see if there were significant spatial relationships between the presence of aspen and important landscape features. We determined the spatial distribution of aspen is non-normal, with a propensity for aspen to congregate near open areas, roads, utility lines and regulated waterways. We also discovered a strong tendency for aspen stands to face south, with 64.5% of the stands directed toward the southeast, south, or southwest. One of the predictions that resulted from this study is that aspen's NDL is not restricted by the poor growing conditions associated with northern climates.

In **Chapter 3** we evaluate aspen growth rates along a north-south latitudinal gradient from 46 to 54°N latitude to determine if broad change in climatic conditions causes aspen growth rates to decline as its NDL is approached.

3 Aspen growth response to change in environment along a latitudinal gradient in the eastern Canadian boreal forest

3.1 Abstract

The accelerating rates of environmental change occurring in northern boreal forests is expected to alter individual tree species growth rates in different ways, and in turn, may contribute to changes in boreal forest structure and composition. Understanding the growth responses of different species to changing environmental conditions is critical for accurate predictions of future forest assemblages. The objective of this study was to investigate the growth response of a common boreal tree species, *Populus tremuloides* Michx. (trembling aspen), to a wide range of natural climatic conditions in the context of changing climate. We predicted that aspen growth rates would decrease with increasing latitude in response to the increasingly poor climate associated with moving northward. A field study was conducted to determine the variation in growth rates of aspen saplings along a north-south latitudinal gradient from 46 to 54°N latitude. Cross sections of a representative sample of aspen saplings (2-3 individuals) growing at 71 different road-side sites were collected along the study transect. Regression analysis was used to determine the relationships between latitude and sapling average annual height and diameter growth rates in the SPSS package, followed by the fitting of linear and quadratic models using curve estimation, and finally, model comparison using an F-test. We observed a relatively weak relationship between aspen height growth and latitude ($R^2 = 0.17$, $p < 0.01$) and found aspen's growth response to change in environmental fairly similar across the ~8° latitudinal study transect. This study suggests that aspen does not respond strongly to change in climate associated with change in latitude, and highlights the need for more in depth species specific research to understand the vulnerability of individual boreal tree species to changing climatic conditions.

3.2   Introduction

Climate is one of the main factors influencing the growth and distribution of many tree species, and a deeper understanding of its role in governing forest dynamics is increasingly important so that forest managers can respond appropriately to the rapid pace of 21st century climate change (Johnston, 2009). There is a general expectation that tree species will track warming climate by shifting their ranges to higher latitudes or elevations, where warming is predicted to be most severe (Parmesan & Yohe, 2003; IPCC, 2007; Chen *et al.*, 2011). Such anticipation often rests on the assumption that all tree species will respond uniformly to the multiple, complex, and non-linear ecosystem adjustments that take place as climate changes (Johnston, 2009). Similarly the main modelling efforts directed at forecasting change in forest growth rates and the impact of climate change on plant demography operate on assumptions that generally fail to account for the diverse nature and behavior of individual species. For example, many forest growth models are based on a unimodal growth response to a measure of temperature such as heat sum or growing degree days (Loehle & LeBlanc, 1996). Similarly, the bioclimatic modelling framework used to predict the impacts of climate change on tree species' distributions is based on the relationship between a species' current distributions and some measure of climate – mainly some facet of temperature and/or precipitation (Heikkinen *et al.*, 2006). The lack of accounting for the varied responses of individual species to climate change is, and will continue, to complicate predictions surrounding the fate of forests, and what the corresponding appropriate management strategies should entail (Ordonez, 2013). A key issue and knowledge gap involves understanding how individual boreal tree species will respond to the ongoing changes in temperature (Johnston, 2009).

An extensive scientific literature dating, back to the work of Grinnell in the early 1900s, centers on the effects of climate on species distributions (Grinnell, 1917). The primary determinants of the distribution of global vegetation are temperature and precipitation, which together govern the availability of nutrients, water, and plant photosynthetic rates (Currie & Paquin, 1987). In the early 1970's, MacArthur proposed that latitude is responsible for the balance between abiotic and biotic factors controlling tree species' distributions, with northern distributional limits reflecting the

physiological constraints of species as imposed by temperature, and southern distributional limits representing the outcome of inter-species' competition (MacArthur, 1972). Existing ecological literature supports both the underlying hypothesis that temperature is the main factor controlling tree growth and distribution in northern regions (Mikola, 1962; Currie & Paquin, 1987; Briffa *et al.*, 1990), as well as the dominate importance of other factors in explaining the growth and distributional patterns of some species (Bonan & Sirois, 1992; Payette, 1993; Asselin *et al.*, 2003). These mixed results highlight a critical issue for current and future forest management strategies that are based on the expectation that different tree species respond uniformly to change in temperature.

Several recent studies have used complex dendroclimatological based modelling approaches to identify and/or predict the individual growth responses of important high latitude tree species to change in climate (Huang *et al.*, 2010; Lapointe-Garant *et al.*, 2010; Lloyd *et al.*, 2013). Collectively, there is evidence for species-specific growth responses to climate change, with some species being more or less affected (Huang *et al.*, 2010). In addition, there is documentation of intra-specific variation in species' growth response to climate across individual species' geographic range distributions (Anyomi *et al.*, 2012). However, a critical feature of plant growth seldom factored into such studies is the inherent variations in soil properties that are known to occur across small to large geographic expanses (Chapin III *et al.*, 1991). To date, there have been no direct empirical field tests documenting the impact of increasingly poor climate, as associated with moving north in latitude, on tree growth rates that account for soil variability. Understanding the growth response of different tree species to change in climate across broad spatial gradients, while accounting for soil variability, which itself varies with climate, is critical for accurate predictions of the impacts of climate change on forest structure and composition (Lafleur *et al.*, 2010).

Populus tremuloides Michx. (trembling aspen) is the most widely distributed tree in North America, a major tree species of the Canadian boreal forests, and a focal tree of related research agendas (Huang *et al.*, 2010; Lapointe-Garant *et al.*, 2010; Huang *et al.*, 2013). Its ability to establish across a diverse range of habitats and

environmental extremes demonstrates its adaptive capabilities as a species (Landhäusser *et al.*, 2010). However, in portions of its geographic range, such as the western Canadian Rockies, aspen is reported to be in sharp decline in response to changing environmental conditions (Hogg *et al.*, 2008). Dissimilarly, in other parts of its geographic distribution, ecologists have documented aspen stands undergoing range expansion (Landhäusser *et al.*, 2010) or steady occupancy. Aspen is a common pioneer species in disturbed areas such as roadsides. The occurrence of aspen growing in a relatively uniform roadside-gravel-substrate across a broad latitudinal gradient in western Quebec presented a unique opportunity to test the importance of climatic controls over aspen growth rates, while controlling for soil conditions. If we know how aspen growth responds to a wide range of climatic conditions, when soil conditions are held constant, we can better assess aspen's adaptive ability to keep pace with recent and future climate change. The response of this species may inform our understanding of other early successional tree species. Thus, our research objective was to test the hypothesis that aspen growth rates will decline significantly from south to north across a broad latitudinal gradient. To do this we determined growth rates for similarly sized/aged aspen saplings, growing in similar soil conditions, along a ~8° latitudinal gradient that represents a wide range of natural climatic conditions in northern Quebec. Our results demonstrate that the relationship between aspen growth and change in climate is weak at the scale of the study. Aspen growth rates not only appear to be quite similar across a broad latitudinal gradient, but some of the areas where aspen growth is above average are the northernmost sites.

3.3   Materials and Methods

3.3.1   Study area

The study area is located in western Quebec along a north-south latitudinal gradient (Figure 3-1). The southern extent is at approximately 46 °N latitude near Grand Remous which is situated within the boreal shield ecozone. The northern extent, near Radisson, lies within the taiga shield ecozone at approximately 54°N latitude. The area is affected by cold, dry arctic airstreams during the winter and by warm, moist Pacific airstreams during the summer (Ritchie, 2004). The climate

normals for 1971-2000 showed a decrease in mean annual temperature (from 3.3 to -3.1 °C), total annual precipitation (from 1,015 to 684 mm), and growing degree days (>5°C) (from 1,607 to 862) from the southernmost meteorological station (Mont Laurier, 46 °34'N, 75°33'W) to the northernmost station (La Grande Riviere, 53°38'N, 77°42'W) (Environment-Canada, 2002).

The vegetation transition zone between the mixed forests (both broadleaf and conifer) and the conifer-dominated boreal forests occurs at approximately 49°N (Bergeron *et al.*, 2004). The forested zones surrounding study site locations are dominated by conifer species including black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), larch (*Larix laricina* (Du Roi) K. Koch), and balsam fir (*Abies balsamea* (L.) Mill.), however, aspen, balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.) stands are encountered infrequently (Ritchie, 2004). The topography along the gradient is typically flat with a few hills and rock outcrops (up to 250 m a.s.l); the most notable are those that occur in the vicinity of Old Factory Lake (52°48'N, 77°30'W).

3.3.2 Ethics statement

This project was conducted on public land on which no specific permission for field work is required and no formal process is available. The project was developed in consultation with the First Nation of Wemindji. The approval of funding included a formal assessment of environmental impact according to the guidelines of the Natural Sciences and Engineering Research Council of Canada. The research involved no species-at-risk, and no animal or human subjects.

3.3.3 Site selection

To determine if aspen growth rates were consistent with a climatic signal we sampled young aspen saplings at 71 different road-side sites, with a ~15 km interval between them, along a north-south latitudinal gradient from 46 to 54°N latitude. Variation in soil and site conditions was controlled by sampling only aspen growing on road cuts and roadside gravel pits. This gave a consistently coarse textured and low organic matter growth substrate with a relatively consistent set of drainage conditions

and management disturbance regime in all sampling sites. The aspen saplings sampled were growing alone to avoid the potential effects of competition from other trees. Using this sampling strategy, saplings sampled were not subject to the effects of variation in accompanying vegetation, soil or site disturbance history of the natural sites adjacent to the road, and thus had the best possibility of expressing response to the climate gradient.

3.3.4   Tree selection criteria, measurements and sampling

At each sampling location we sampled, on average, three aspen saplings with diameters between 2 and 8 cm, cut at 30 cm from the ground. Saplings were growing in full sun, and had no apparent damage to the canopy or trunk. To eliminate the effects of inter-tree competition we sampled saplings growing singly in the gravel-based substrate, and as far away from other vegetation as possible. We measured sapling diameter and height to obtain multiple measures of individual growth rates.

3.3.5   Sample preparation

Samples were oven dried at 65°C. Top surfaces were sanded with three successive, increasingly finer, grits of sand paper using a band sander. Rings were counted under a binocular microscope; each sample was aged 3 times along different radii and the average age was recorded. Sample surface diameter was measured in two locations perpendicular to each other, averaged, and recorded. Growth rates were determined as height over age and diameter over age.

3.3.6   Sample data set for analysis

Ideally, all trees sampled would have been of the same age to control for variation in growth rate with age. Since we could not determine an accurate age in the field, we used diameter as a proxy for age, harvesting saplings 2-8 cm in diameter. Once the samples were dried and aged, we culled the data set to retain only saplings between 3 and 6 cm in diameter, and between 8 and 18 years of age. We recognize that these selection criteria, while reducing bias due to variation in age, may have eliminated very fast or very slow growing individuals thereby influencing the results.

However, we consider the range of ages chosen to be an appropriate balance between these effects that will allow detection of a trend across the latitudinal gradient.

3.3.7 Sites and height growth-climate relationship

Data were averaged for each site, for all parameters (height, diameter, annual height growth rate, annual diameter growth rate, and age), to control for within-site variation. Relationships between climate (change in latitude) and sapling average annual height growth, and average annual diameter growth were examined using regression analysis in SPSS (version 19.0.0) (SPSS, 2010). Subsequent fitting of linear and quadratic models was done using the curve estimation procedure in SPSS (SPSS, 2010), and was followed by an F-test which compared models and determined significance. Fifty-two sites were used in this analysis. Nineteen of the original 71 sites did not include trees that fell into our final criteria for diameter and age and were thus excluded.

3.4 Results

3.4.1 Latitude and climate

In this study, we use latitude as a surrogate for climate. In general we would expect the climatic variable temperature to decrease with latitude, and for the distribution of plant species to respond to this gradient (Woodward, 1987). In addition, we expected precipitation to decrease with increasing latitude; however, based on the common ecological literature describing the critical constraints plants face at their northern and southern distributional limits respectively, we expected temperature to be more of a limiting factor for aspen growing near its northern range limits than precipitation. Regional and continental climate patterns (i.e., regional influence of James Bay on temperature regimes) could have modified the relationships we expected to see, but the transect we used in this study suggests otherwise, as there is a very clear and linear relationship to both temperature ($R^2 = 0.95$, $p = 0.02$) and precipitation ($R^2 = 0.97$, $p = 0.01$) (Figure 3-2). This may be because the road transect is far enough inland (~100 km) for such an effect to be minimal.

3.4.2 Aspen growth in relation to latitude

Aspen growth rates were similar over seven degrees of latitude for both height and diameter (Figure 3-3 and Figure 3-4). We see a slight decrease in growth rates from beginning to mid-transect (46° to ~50°), followed by a brief leveling out, or no change in growth rates as we move north in latitude (~51°), and end with a slight increase in growth rates (~51.5°+). Interestingly, some of the fastest growing trees are at the northern most sites.

The linear relationship between aspen annual height growth and latitude was significant but weak ($R^2 = 0.108$; $p < 0.05$; $R^2_{adj} = 0.09$). A quadratic model provided a better fit for the data ($R^2 = 0.206$; $p \leq 0.01$; $R^2_{adj}=.174$) than the linear model ($p < 0.01$). Although the relationship between aspen diameter growth and latitude is similar in form to the trend observed with height growth, it was not statistically significant. There were no other significant relationships between other measured variables and latitude.

3.5 Discussion

Through investigation of growth rates of established saplings across a broad latitudinal gradient we have demonstrated that climate is not the critical factor limiting aspen growth rate in the northern part of its range in western Quebec. While we recognize other aspects of aspen biology, such as flowering, seed production and seedling germination and survival will also influence aspen distribution, our results are consistent with the pattern of aspen occurrence in the area, which also suggests a relative independence from climatic influence. This is a critical finding because the assumption that climate is the driving factor of changing species distributions underpins most attempts to predict the responses of species to climate change (Pearson & Dawson, 2003). Here, we see that once seedlings establish, there is little effect of climate on growth.

The majority of work on the implications of climate change for tree species' geographic ranges has consisted of modelling present distributions in terms of current environmental conditions, and then examining the consequences of various climate change scenarios based on the modeled links between climate and distribution (Loehle

& LeBlanc, 1996; Pearson & Dawson, 2003). These models are not designed to take into account other abiotic and biotic factors known to affect tree species distributions such as disturbance, physical barriers to dispersal, soil properties, competition, herbivory, and parasitism (Gaston, 2003; Hollingsworth *et al.*, 2006; Johnstone & Chapin, 2006). Our findings suggest non-climatic factors have a strong influence over aspen growth, relative to climatic factors, and need to be explored to explain the controls over aspen growing near the northern edge of its range in the boreal forest of western Quebec.

Non-climatic factors have been shown to explain the northern limits of several boreal species in different geographic locations. For example, investigations by Lloyd et al. (2007) into the controls over the northern range limit of black spruce in Alaska found that the interaction between fire and substrate determined the species' northern range limit; Asselin et al. (2003) found that fire frequency and size explains the northern distributional limit of jack pine in northern Quebec; and Bergeron & Brisson (1990) found that large and intense fires limit the northern distribution of *Pinus resinosa* Ait. (red pine) in northwestern Quebec. More recently Landhausser et al. (2010) found that aspen is expanding its range upslope in the Canadian Rocky Mountains of Alberta along forest logging roads that bear newly exposed mineral soils.

In northern Quebec, aspen has demonstrated the capacity to establish by seed in the gravel substrate lining the roads, which is similar to the above scenario in Alberta (Landhäusser *et al.*, 2010). In both cases aspen is occupying substrate exposed by human disturbance which suggests aspen's northern range limits in Quebec may reflect a general lack of suitable, and available, substrate for establishment. Given that in natural conditions aspen is known as an aggressive pioneer species that comes in after fire burns away organic matter and exposes mineral substrate, it seems quite reasonable that anthropogenic disturbance yielding the same substrate exposure would have similar results – more aspen. Further investigation into how human activity, in the form of road construction, may be changing seedling establishment conditions for aspen in northern Quebec may provide important insight into aspen's future distribution and abundance in northern Quebec.

In conclusion this study has demonstrated a weak relationship between climate and growth of aspen over ~8° of latitude. This implies that predictions of change of growth and distribution of this species need to be based on response to other variables in addition to climate. The presence of aspen in disturbed roadside areas suggest that factors that control the availability of suitable substrate and other site conditions may be more important than climate in determining the expansion of this species in northern regions. This study suggests that further reflection on the relative importance of climate in predicting patterns of growth and distribution of other species is warranted.

3.6 References

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3.7 Figures

Figure 3-1: Map showing the study area in the eastern Canadian boreal forest. The dotted bracket between Grand-Remous and Radisson indicates the extent of the field study transect. Major cities, communities, roads, and major water bodies are labelled for reference and context. Map data: Google.
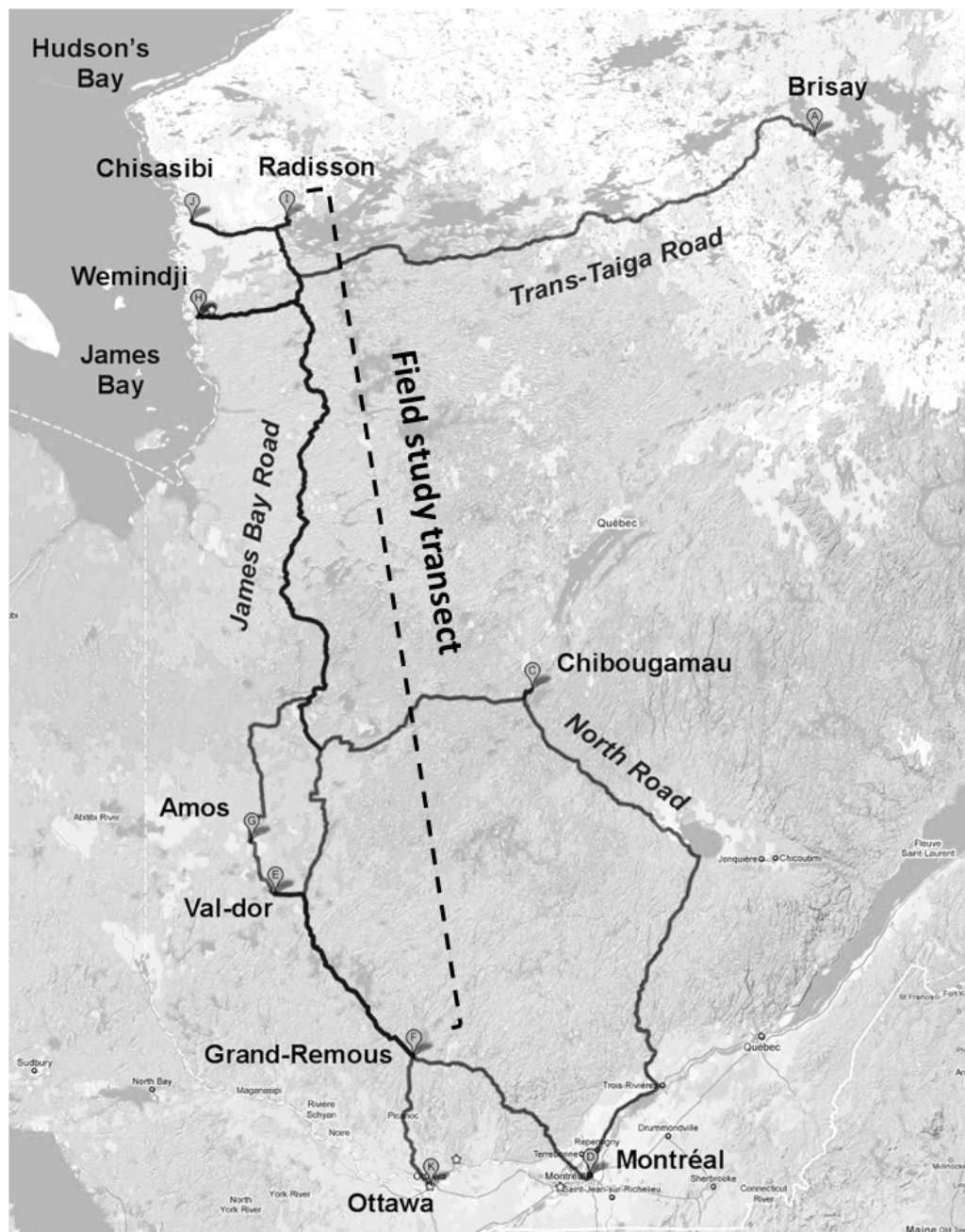
Figure 3-2:   Mean annual temperature and mean annual total precipitation. Data
               from 1971-2000 and recorded from the four weather stations (shown on
               x-axis) located along a latitudinal gradient from 46 to 54° N in the
               eastern Canadian boreal forest (Environment-Canada, 2002).
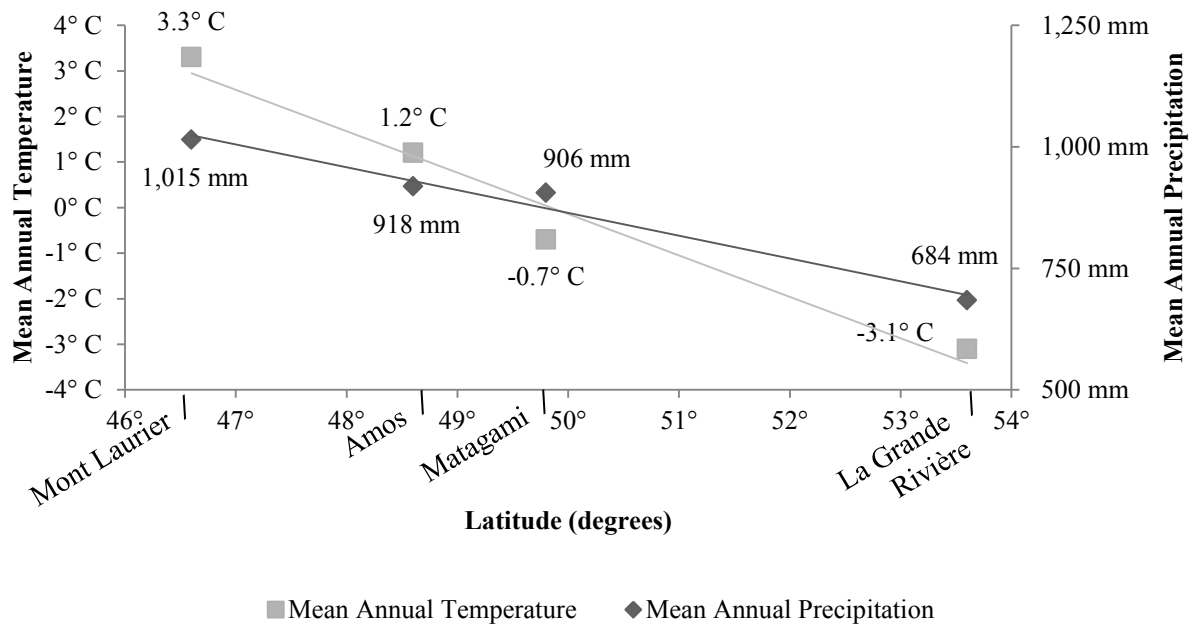
Figure 3-3:   Aspen annual height growth in cm for 52 sites across ~8° of latitude.

Average Height Growth Per Year by Latitude

$R^2_{adj} = 0.174$
$p < 0.01$

Y-axis: Height Growth per Year (cm)
X-axis: Latitude (degrees)
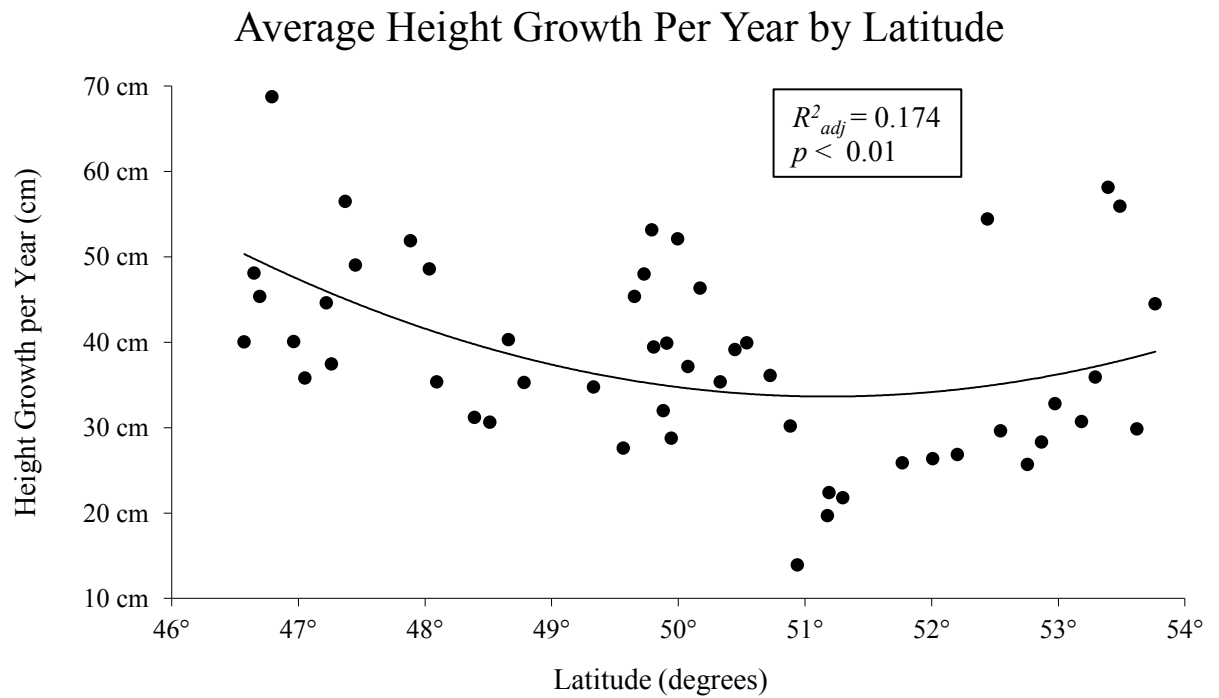
Figure 3-4:   Aspen annual diameter growth in mm for 52 sites across ~8 degrees of
latitude. Although there is no relationship between diameter growth and
latitude, a trend line has been added to the data to highlight the similar
pattern identified between aspen annual height growth and latitude.

Average Diameter Growth Per Year by Latitude

R^2_{adj} = -0.004
P > 0.05
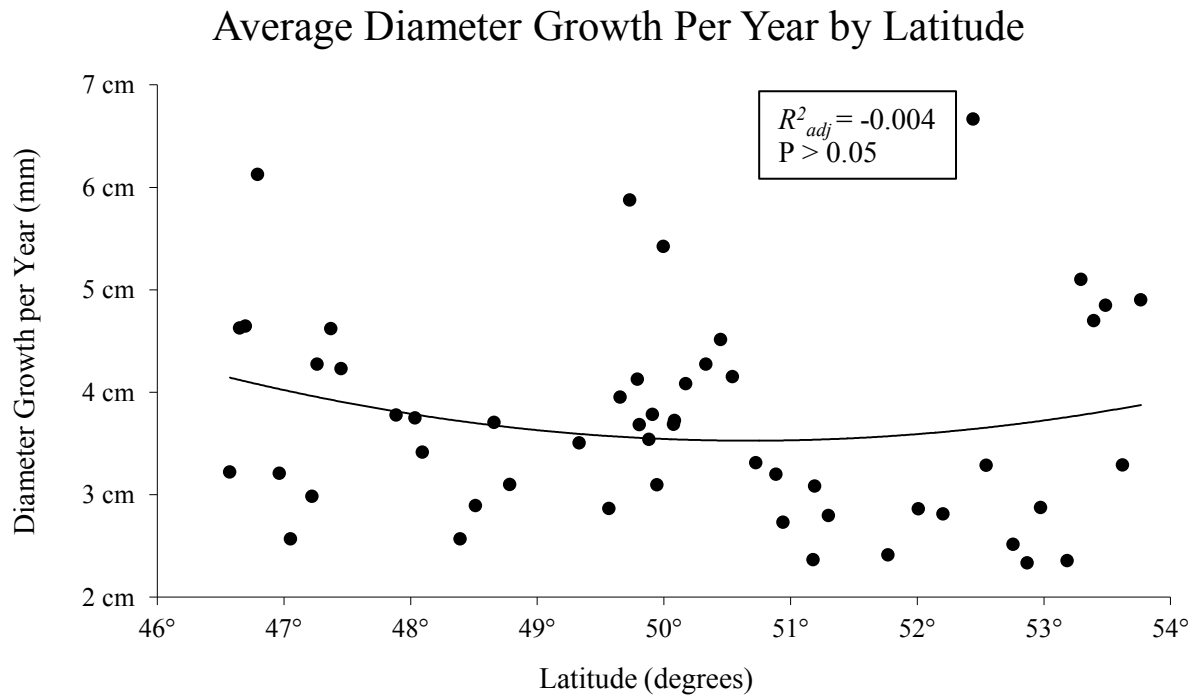
Linking statement between Chapter 3 and Chapter 4

The results of **Chapter 3** showed that aspen growth rates are not strongly correlated with the natural climatic conditions that change with increasing latitude, and that aspen growth rates are fairly similar across the broad latitudinal gradient. This study suggests that the climate – growth relationship is not the most important factor controlling aspen's NDL because, if it were, we would expect a more gradual decline in growth rates with increasing latitude, or perhaps a sharp decline at some latitude if there was a threshold effect. Instead, some of the best aspen growth rates are seen at the most northern sites. A similar pattern of aspen growth near its NDL in Saskatchewan was observed by Maini and Cayford (1968). However, because species abundance and distribution are known to be influenced by multiple and interacting factors that operate over varying spatial and temporal scales, a more detailed study of the influence of a wide range of factors on aspen's distribution and abundance was carried out at the landscape scale and reported in **Chapter 4**.

Chapter 4 addressed the need for an ecological analysis of aspen at the landscape scale to further understand the factors constraining and/or facilitating its growth near its NDL. The objectives of chapter 4 included: 1) distinguishing the factors controlling plant community composition in aspen dominated stands from factors controlling other dominate vegetation on the landscape, 2) explicitly investigating the factors controlling local levels of aspen abundance, and 3) testing specific hypotheses related to the northern distributional limits of aspen in QC.

4 Ecological Analyses of Trembling Aspen and associated vegetation near Aspen's Northern Distributional Limit

4.1 Abstract

Climate, disturbance, topography, and soils drive many patterns of boreal tree species distribution and abundance at the landscape scale, but our understanding of the factors that constrain or facilitate individual species success at different parts of their distributions is still limited. With the uncertainty surrounding climate change and how to accurately model the impacts it will have on tree species distributions and community structure and function, it is most critical to understand what factors affect individual tree species at the edges of their distributional limits, where impacts are predicted to be the greatest. Within this context, we took a hierarchical approach to assess the relative influences of environmental conditions and fire-cycle related disturbance on aspen and associated vegetation in northwestern Quebec, where aspen nears its northern distributional limit (NDL). First, we characterize forest composition at the landscape scale by scaling up detailed species and stand level data collected on field plots. We follow with an investigation of the relationships between predictor variables describing site conditions (i.e., spatial, topographic, soil, and disturbance as reflected by spatial variation in the fire cycle) and associated variation in species' abundance. Lastly, we identify significant factors associated with variation in aspen abundance across the study area. We found gradients related to soil moisture, soil fertility, and aspect best characterized forest composition and structure across the study area, while aspen abundance in particular was associated with soils high in K, and inland areas associated with frequent fire events. Our findings demonstrate the importance of looking "beyond" climate factors to explain aspen's distribution patterns.

4.2 Introduction

The most common and enduring explanation of global and continental species' range limits is climate (Woodward, 1987). The hypothesized role of climate underpins current predictions for North American tree species' range shifts in response to anthropogenic-driven climate change, and directly informs policy developed to mitigate the negative repercussions of such change (Johnston, 2009). Many ecologists believe that if species' can migrate northward and upward in elevation they can track changing climate as growing conditions, and habitat, become more tolerable at northern distributional limits (NDL), and increasingly inhospitable at southern distributional limits (SDL) (McKenney *et al.*, 2007). A growing point of contention is that most of these predictions are based on bioclimatic envelope models that grossly simplify the complex nature of species-environment relationships (Beaumont *et al.*, 2007). This approach uses species' known distributions and current environmental conditions to examine the consequences of various climate change scenarios based on the modelled links between climate and distributions (Gaston, 2003). This method, although powerful, does not necessarily take into account the large body of ecological literature that documents the numerous other factors known to affect tree species distributions, such as historical legacies (i.e., geologic history and landscape evolution), disturbance (i.e., fire, insects, and disease), and species' interactions (i.e., competition, facilitation, herbivory) (Gaston, 2003). Developing appropriate land management and long-term conservation plans for forest areas responding to climate change and associated impacts is increasingly critical, and rests on the ability to meaningfully predict how tree species will respond to changes in climate across their distributions, particularly where they meet range limits (Johnston, 2009).

A wide range of climate-related mechanisms limit tree species distributions at various spatial scales operating over different, but integrative temporal scales (Fettig *et al.*, 2013); however, temperature-related factors are considered the main determinants setting NDL, and moisture-related factors are believed to control SDL (Woodward, 1987). Accordingly, many empirical studies on tree species range limits have been able to show direct climatic limitations to species' establishment and reproduction (Hobbie & Chapin, 1998). Yet, other studies have pointed to alternate

explanations for range limits including physical barriers to dispersal, disturbance, soil properties, competition, herbivory, parasitism, and lack of essential resources or mutualisms (Iverson *et al.*, 2008). Common patterns associated with tree species growing near their NDL are scattered individuals appearing stunted in growth, or stands with depressed vigour. These trees tend to be more vulnerable to environmental stress than those growing near the center of their range because they are already considered to be growing in sub-optimal conditions (Renner *et al.*, 2006).

Ritchie (2004) documented the central abundance of Quebec's aspen around the southern part of the boreal forest (~48°N latitude) and noted stands occur up to ~52°N latitude, roughly indicating its NDL. In accordance with the assumed environmental stress associated with a species growing near its NDL, one would expect individuals and/ or stands to exhibit the degenerative characteristics described above; however, these generalities were not observed for aspen found growing near their NDL in this study.

East of James Bay, Quebec, around Old Factory Lake (OFL; 52°48'N, 77°24'W), aspen is found growing vigorously and in greater abundances than expected for a species growing near its NDL. Published quantitative data characterizing aspen stands growing near their NDL are far from comprehensive; together, the available data is based on two stands and addresses only climate-related factors whose values are derived from interpolated climate data (Huang *et al.*, 2010; Lapointe-Garant *et al.*, 2010). The fact that there is only one weather station (La Grande Rivière station) with enough weather data to obtain interpolated-based climate estimates (30 years or more) for these northern sites (Rapaic *et al.*, 2012) suggests there is a need for studies using alternative methodologies. Improved understanding of what controls tree species distributional limits is needed for the development of better predictive models to forecast future species range shifts in response to climatic uncertainty (Johnston, 2009). Two factors that limit current accurate model predictions are: 1) incomplete knowledge of individual tree species ecology around their NDL, and 2) exclusion of non-climatic factors known to affect species' northern distributional limits (Gaston, 2003).

The apparent inconsistency of aspen's distribution in northern Quebec relative to expected species distribution patterns provided an opportunity to develop a better understanding of the controlling factors that drive forests growing near their NDL. Here we examine the factors that determine the occurrence of aspen in and around its NDL in Quebec. Specifically, we test for the influence of multiple potential predictor variables using a regression approach, followed by model evaluation using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). Specific predictors including spatial (i.e., latitude, longitude, and elevation), topographic (i.e., slope and aspect) and soil (thickness of LFH, depth of mineral horizon, soil texture, soil pH, and soil fertility) variables are used to explore predictions related to the NDL of aspen in Quebec and to identify factors associated with the maintenance of these populations. Specific predictions explored in this study include: (1) site conditions that promote aspen dominance near its NDL are different than the site conditions that promote commonly abundant boreal species like black spruce; (2) aspen abundance is positively correlated with fire disturbance events; (3) aspen abundance is positively correlated with warm aspect slopes; (4) aspen abundance is positively correlated with coarse grained substrates; and (5) aspen abundance is positively correlated with soil potassium.

4.3   Materials and Methods

4.3.1   Study area – Old Factory Lake Watershed, Quebec, Canada

The Old Factory Lake Watershed (OFLW; Figure 4-1) is located in the James Bay Area of Quebec in the northern boreal forest zone. Old Factory Lake is at the head of the watershed and drains westward via the ~ 90 km Old Factory River way that connects to James Bay. The area's sub-arctic climate is characterized by long and cold winters, and short and warm summers. The mean annual temperature is -3°C, with the coldest month being January and the warmest month being July. The average growing season includes 862 degree-days $\geq$ 5°C and the mean annual precipitation is 684 mm, with about one-third falling as snow (Canada, 2013).

The OFLW system lies in Precambrian Canadian shield with bedrock consisting mostly of granite and gneiss; both are felsic and composed mainly of

feldspar (specifically orthoclase and microcline) and silica (Stockwell *et al.*, 1968). Here, feldspar is known for its high concentrations of potassium (K) (Goad & Cerny, 1981). Soils dominating the study area include: dystric brunisols; organic mesisols and humisols; and gleysols (ESWG, 1996). Bedrock geology has a strong influence over many landscape characteristics such as relief, surface roughness, drainage pattern, vegetation pattern, and soil development due to large areas of exposed rock with little or no mantle of unconsolidated materials (Ritchie, 2004).

The terrain surrounding the OFLW includes rolling hills with large rock outcrops (up to 250 m a.s.l.) that have some of the highest relief in the greater James Bay Area (Parisien & Sirois, 2003). These hills are full of aspen stands regenerating from a fire in 1989 intermixed with small clusters of 75-85 year old (30-40 cm diameter at breast height) individuals that survived the fire. From a landscape perspective the OFLW consists of mixed conifer species assemblages broken by lowland bogs and wetlands, upland open and semi-open clearings, hill sides with broadleaf cover, and recently burned areas. Within the recent burns, open, semi-open, and shrub areas dominate (Whitbeck *et al.*, 2012). The role of fire in structuring the boreal forest's physical and biological attributes through its effects on plant succession, ecosystem processes, landscape structure, and biological diversity is well known. Plant community development is limited by the length of the fire cycle which is reflected across boreal zones as patchy mosaics of heterogeneous vegetation (Weber & Flannigan, 1997).

4.3.2   Sampling design and data collection

A principal objective of this study was to distinguish the factors controlling plant community composition in aspen dominated stands from factors controlling other dominate vegetation in the study area. Species and environmental data were collected between 4 July and 13 August 2010 at 158 plots, within 15 aspen stands and their respective adjacent non-aspen stands, to measure plant community composition and a suite of environmental factors relevant to aspen growth habits (see Table 4-1 for list of environmental factors).

At each of the 15 sites, sampling points were established along transects running from a non-aspen stand to the center of an aspen stand to characterize change in vegetation and the environment (Ter Braak & Prentice, 1988). Transects were aligned with the longest axis of each aspen stand. Transect length, total number of sample points, number of sample points in aspen vs. non-aspen stands, and distance between sample points varied with the size and location of aspen stands.

Geographic coordinates were recorded using a Garmin Oregon 550 GPS unit at each sample point. Circular plots (78.5 m^2) were established at each location and cover-abundance was estimated of all vascular and non-vascular species using the Domin scale: 1 = one or two individuals; 2 = sparsely distributed; 3 = frequent but low cover (<5%); 4 = 5-19%; 5 = 20-25%; 6 = 26-33%; 7 = 34-50%; 8 = 51-75%; 9 = 76-90%; 10 = 91-100% (Kent & Coker, 1992). Plant species were recorded following the nomenclature of Gleason and Cronquist (1991) for vascular plants, Anderson et al. (1990) for mosses, and Brodo et al. (2001) for lichens. Site values for slope, aspect, and elevation were extracted from the USGS Global Land Survey Digital Elevation Model (USGS, 2008).

To sample the soil environment at each plot, a soil pit (between 20 and 30 cm deep) was excavated near plot center after documenting cover estimates. Soil profiles were characterized by horizon thickness, color, structure, and texture. Two soil samples, one at the surface and one from the mineral horizon (when present) were collected for further nutrient and pH analysis.

4.3.3   Laboratory analyses methodology

Soils were sorted to remove large (>0.5 cm diam.) woody debris, air dried, crushed, passed through a 2mm sieve, and weighed. We used a combination electrode (Accumet AR10) to measure organic and mineral soil pH in deionized water (1:10 and 1:2, soil: water, respectively). The major cations, Ca, Mg, K, and P and Al were extracted using the Mehlich III method; organic soil:solution ratios 1:25, and mineral soil: solution ratios 1:10. Levels of major cations and Al in extracts were determined using a Perkin-Elmer 2380 Atomic Absorption Spectrophotometer, and available P was determined using a Lachat Quickchem automated chemical analysis system.

4.3.4 Treatment of data prior to statistical analysis

Closely related species that were consistently difficult to separate in the field were combined at the generic level, i.e., *Salix* (willow) and *Poaceae* (grass). Vegetation data recorded using Domin Categories was transformed to single percent cover values, for 61 species, using the Domin 2.6 function to facilitate the direct comparison of data, and adjust the scaling to approximately linear for use in numerical analyses. Following, the Hellinger transformation was applied to the 61 species set of percent cover data using the *deocostand* function of the vegan package in R version 2.15.1 prior to ordination analyses. The Hellinger transformation is well suited for redundancy analysis (RDA) of species abundance data for numerous reasons, including; conversion of species' percent cover data to respective relative abundances; giving less weight to abundant species; and preventing problems associated with Euclidean distance - where the distance between two sites sharing no species can be smaller than that between two sites sharing species (Legendre & Gallagher, 2001).

All environmental predictor variables, excluding aspect, latitude, and longitude, were standardized to zero mean and unit variance. Due to the circular nature of the variable "aspect", it was transformed using trigonometric functions as per Roberts (1986) into two separate variables, "northness" and "eastness" using the *cos* and *sin* functions in R (R-Core-Team, 2012).

4.3.5 Synthesis of data - statistical analyses

4.3.5.1 Vegetation – environment relationships – RDA

To investigate the relationship between environmental variables and vegetation assemblages we used RDA. A 'global' RDA was computed as per Borcard et al. (2011) using the Hellinger transformed species' matrix as response variables, and all predictor variables, excluding transect (predictor variables summarized in Table 4-1). Transect was excluded from this and following RDA analyses because we accounted for the effects of spatial variability in our data by using geographic coordinates. Permutation tests of RDA results were conducted followed by a test of the canonical axes (Borcard *et al.*, 2011).

Significant predictor variables included in regression models were selected using forward selection with a double stopping criterion using the *forward.sel* function of the vegan package in R (Oksanen *et al.*, 2012). Forward selection is used to construct parsimonious statistical models where predictor variables are added to a model, one at a time, and assessed as to whether they significantly improve model fit (Borcard *et al.*, 2011). Inclusion of a variable in the model indicates that it met the double stopping criterion inclusion threshold of $p < 0.05$ and that the adjusted coefficient of multiple determination (R^2_{adj}) of the current model was of a lesser value than the 'global' model.

We partitioned the variance in the final selected model to identify the unique and shared contributions of significant subsets of predictors using the *varpart* function in *vegan*. Predictors were grouped into three different subsets based on the 'nature' of the variable: soil, site topography, and spatial location (Borcard *et al.*, 2011).

4.3.5.2 Aspen-environment relationship – multiple linear regression

Two phases of variable selection were done to reduce multicollinearity between variables before generating a set of *a priori* candidate models. Phase 1 was completed after careful consideration of aspen biology, and history and ecology of the study area; exploration of the relationships between measured predictor variables and species' relative abundances using RDA; and investigation of pairwise relationships among predictor variables with Pearson's r and Kendall's τ (Borcard *et al.*, 2011). To avoid biasing our regression analyses through the use of collinear variables we used surrogate or representative variables when appropriate. For example, the base cations (Ca, Mg, and K) were highly correlated with each other and thus it was necessary to choose one as a general indicator to represent base cation concentration. Potassium was a reasonable choice because we wanted to address a specific prediction about its local impact on aspen abundance, and also because it was the base cation least correlated with other environmental predictors in the data set (see Appendix2). We excluded elevation as a predictor due to its high correlation with longitude ($r = 0.91$, $p < 0.001$), previous findings that longitudinal differences in forest cover are linked to spatial variation in the fire regime around our study area (Parisien & Sirois, 2003), and

our intention of evaluating the relationship between aspen and the local fire regime, using longitude as a proxy for the local fire regime.

Following phase 1, forward selection was used to reduce the number of predictor variables due to the impracticality of investigating all distinct sub models, and our focus on identifying the most parsimonious model; the *forward.sel* function was applied to a multiple linear regression model using aspen relative abundance as the response variable and the 'full' set of predictor variables (see Table 4-1).

We acknowledged the importance of random variation in space and time by modelling with random effects, which are used to quantify the variation among units (i.e., sites). To account for possible temporal and spatial variation in the data imposed by the study design, we used aspen relative abundance as a function of the forward selected predictors to compare the fit of a linear regression model (*gls* function; nlme package; R (Pinheiro *et al.*, 2013)), to the fit of a linear mixed effects model with transect included as a random effect (using the *lmer* function in the lme4 package of R (Bates *et al.*, 2012)). Because both models were estimated with REML, the likelihood ratio test could be applied to see whether including the random effect improved the model.

The candidate model set was constructed using all possible combinations of the forward selected variables, the 'full' model that included all variables considered (pre-forward selection), and a model containing intercept only. The strength of evidence for each model was based on the second-order Akaike Information Criterion (AICc) (Burnham & Anderson, 2002). Each model was ranked based on ΔAICc and AICc weight calculations. We evaluated model performance by comparing R^2_{adj} values. The effect size of individual predictor variables was assessed by computing model-averaged parameter estimates with unconditional standard errors and confidence intervals with the AICcmodavg package in R (Mazerolle, 2013).

4.4   Results

4.4.1   Vegetation – environment relationships – RDA

Using RDA, we were able to account for 23.4% of the variance in community composition in the OFLW study area. Using variance partitioning, we identified 3.5 %

associated with spatial structure, 5.3% with topography, and 8% with soil. The remaining 6.6% of the "explained" variance was shared among predictor variables.

4.4.2 Aspen – environment relationships – multiple linear regressions

4.4.2.1 Variable selection

Initial variable selection yielded the 'full' set of predictors which included: longitude (Long), Eastness, slope (Sl), thickness of LFH layer (LFH), depth of soil in A horizon (Depth_A), percent of sand in soil (Sand), average pH of mineral and organic soils (Avg_pH), average amount of K in mineral and organic soils (Avg_K), and average amount of Al in mineral and organic soils (Avg_Al) (Table 4-1). Avg_K was a correlate variable for Mg, Ca, and the cation exchange capacity. We selected Avg_K and Long as significant predictors to use in model building and comparison based on forward selection applied to a linear regression model of aspen abundance as a function of the 'full' set of predictor variables.

4.4.2.2 Model comparison using a likelihood ratio test (Λ)

Using the likelihood ratio test we determined that the mixed-effects modelling approach that included transect as a random effect did not improve model fit ($\Lambda = 2.24$; $df = 1$; $p = 0.134$), and thus regression using the linear model structure without a random effect was used for all subsequent analyses.

4.4.2.3 Candidate model set

Using the significant predictors identified by forward selection, we used all possible variable combinations to build and compare models to describe the relative abundance of aspen (Table 4-2). Aspen abundance was best described by a single model (Avg_K + Long) which accounted for 97% of the AICc weight with an $R^2adj = 0.16$ (Table 4-2). Calculating the "evidence ratio" showed that this model is 49 times more likely than the next likely candidate model. Model-averaged parameter estimates, unconditional standard errors, and confidence intervals computed from the full set of candidate models are shown in Table 4-3.

4.4.3 Discussion

Through scaling up detailed tree-, species-, and stand-level data collected on field plots we characterized forest composition and structure at the landscape scale, and identified specific factors associated with variation in aspen abundance across the OFLW. We demonstrate that fire disturbance and soil K are important landscape level determinants of aspen distribution and abundance near its NDL in Quebec. The finding that spatial variation in the fire cycle (as inferred by the variable longitude) impacts aspen abundance supports previous research findings that longitudinal change in vegetation (i.e., parallel to James Bay) is primarily associated with change in the fire regime, and more specifically the fire cycle (Parisien and Sirois 2003). This discussion expands on the five predictions explored to account for the unique patterns of aspen occurrence near its NDL.

4.4.3.1 *Prediction 1: The factors that promote aspen dominance near NDL are different than the factors that promote commonly abundant boreal species like black spruce.*

Both aspen and black spruce are common boreal species with significant overlap in their North American distributions, yet the two tree species have different life strategies, and are generally associated with habitats differing in soil fertility, temperature, and moisture (Van Cleve *et al.*, 1986). Aspen is an early successional species that grows fast, is nutrient demanding, and accelerates nutrient cycling, decomposition, N mineralization and nitrification. It is also associated with base cation-rich soils that are high pH, and thin organic forest floors (Alban *et al.*, 1978; Cote *et al.*, 2000). As a pioneering shade intolerant species, aspen is often found growing well in open areas that are relatively dry (Mitton & Grant, 1996). These conditions are not generally associated with boreal environments that are dominated by cool, nutrient poor soils, slow-cycling, low pH, and thick surface organic layers that favour the conservative growth strategy of black spruce (Van Cleve *et al.*, 1991). Given the different ecological profiles of the two species presented here, and field observations of abundant aspen around OFL, we predicted that different factors would be correlated with landscape patches dominated by these species.

4.4.3.2 *Prediction 2: Aspen abundance is positively correlated with increased fire disturbance events*

Aspen is a long-lived clonal tree species that is well adapted to disturbance as demonstrated by its common occurrence on burnt, cutover, or otherwise disturbed forest areas (Maini & Cayford, 1968). Natural disturbances, such as fire that remove organic layers, create conducive seedbeds for aspen establishment, and will also allow for local re-establishment of aspen through vegetative reproduction if the pre-fire vegetation community included aspen (Turner *et al.*, 2003).

In 1980, Gérardin reported that longitude influences vegetation assemblages along the entire length of James Bay. Parisien and Sirois (2003) hypothesized and tested the idea that the observed longitudinal change in vegetation was associated with spatially explicit variation in the fire cycle. They were able to demonstrate that there is a significant shortening in the fire cycle along a coast – inland (longitudinal) gradient, and that particular species were spatially constrained by how frequently fire burned in any given area. For example, white spruce is not well adapted to frequent fire in comparison to jack pine, and is thus confined to the coast where fire is infrequent, while jack pine is confined to inland areas with a shorter fire cycle (Parisien & Sirois (2003). Their study was conducted around Chisasibi, Quebec, ~ 80 km north of the study area we used for the current study.

Our study investigated the relationship between aspen abundance and disturbance, as manifested by the fire cycle. We used the variable longitude as a surrogate for the fire cycle, in accord with Parisian & Sirois (2003), to determine if aspen is associated with sites that burn more frequently. We predicted aspen abundance would be positively correlated with sites further inland where shorter fire cycles prevail. Our results are consistent with this prediction, as aspen showed a pattern of increasing abundance with increasing distance from the coast, as demonstrated by the change in the variable longitude.

The increased fire frequency, characteristic of inland sites, theoretically should provide more opportunities for the creation of seedbeds conducive to aspen establishment through the burning off of organic matter and the subsequent exposure of mineral soil. However, the intensity of any given fire is also a critical factor. If fire provides sufficient heat to fully consume a particular area of forest floor, mineral soils

will be exposed and aspen may establish if the timing is right and seed is available. Alternatively, in a case where an already established aspen stand experiences a low intensity fire, opportunity for increased aspen abundance exists due to aspen's prolific suckering and sprouting response to fire. Parent trees may be killed in such a fire, but leave behind high belowground carbohydrate reserves in root systems and trunks, from which new aspen grow - in this case, fire intensity needs be low enough to not eradicate root systems, but not too low or paludification is a potential outcome (Paré *et al.*, 2001).

The spatial variability associated with the fire cycle helps explain aspen's greater inland versus coast occurrence. The general idea of fire creating 'space' for aspen to establish suggests that a critical factor preventing aspen from expanding beyond its NDL may be the absence of suitable substrate, rather than just purely a direct climatic limitation. Landhäusser et al. (2010) demonstrated aspen's upslope range expansion in the Rocky Mountains in response to disturbance caused by forest harvesting activities. Landhäusser et al. (2010) also point out that aspen, and common invasive species, share a number of life history traits including: small seeds carried by air and water, allowing for long distance dispersal and prolific vegetative reproduction.

4.4.3.3 Prediction 3: Aspen abundance is positively correlated with warm slopes

Sloping terrain is known to create unique patterns of microclimate variation that allow forest stands, and individual species, to establish and persist hundreds of kilometers beyond their core distributions (Chapin III & Matson, 2011). A common pattern among plants of the northern hemisphere is that as they approach their NDL, they become increasingly restricted to south-facing aspects which provide warmer and drier microclimates (Renner *et al.*, 2006). These slopes allow for enhanced plant productivity, soil nutrient turnover, decomposition, and other ecosystem processes. They are also more likely to experience more frequent or more intense fire activity which are likely to create conditions conducive to aspen establishment or regeneration. In contrast, analogous slopes found in more southern climates are prone to increased drought which has the opposite effect on plant productivity and general health (Chapin

III & Matson, 2011). Previous aspen studies support this general pattern. In the boreal zones of Canada and Alaska aspen grows best on warm-aspect slopes (Chen *et al.*, 2002), while studies conducted in the western and central areas of the United States and Canada found aspen productivity to be greatest on cool-aspect exposures (Shepperd, 1986). Thus, we predicted that aspen abundance would be positively correlated with warm aspect slopes. Interestingly, we were unable to affirm this prediction as our analyses demonstrated that there was no significant relationship between aspen abundance and warmer slopes at the scale of the study. In addition, as indicated earlier, the RDA suggests a positive relationship between aspen and northness, which is contrary to the expected pattern. From the landscape level vantage point a positive effect of warm aspect slopes on aspen abundance was not detectable and the prediction was rejected. The observation of northness correlated with aspen abundance in the RDA suggest that factors other than a simple effect of warm south facing slopes are active in this landscape. These results suggest that the landscape level distribution and abundance of aspen growing in the OFLW is controlled more strongly by non-climatic factors, or that other conditions 'favorable' to aspen are locally present to compensate for the cool growing conditions in the north. In general, these results seem inconsistent with a species strongly restricted by climatic conditions near its NDL.

4.4.3.4 *Prediction 4: Aspen abundance is positively correlated with coarse grained substrates*

Aspen, being the most widely distributed broadleaf tree in North America, naturally occurs on a wide range of soils and sites (Perala, 1990); however, through much of its range, it shows a preference for well-drained soils - consistent with coarse rather than fine-grained substrate (Mitton & Grant, 1996). Despite nearing its NDL, aspen are abundant around OFL which suggests local site conditions are favorable for aspen establishment and persistence. From studies in paleogeography and landscape evolution we know that the current James Bay area reflects a history of deglaciation events, proglacial lakes, and inundation by waters of the ancient Tyrell Sea (Hillaire-Marcel *et al.*, 1981). The local geological interpretation of the OFL hills is that they emerged after release from the weight of the Laurentide ice sheet. Coarse beach sands

settled out along the hillsides whereas fine, poorly drained sediments accumulated in basins and bays which today are largely bogs (Pendea *et al.*, 2010). Given the local geomorphology of the study area and aspen's observed preference for well drained soils, we hypothesized that aspen may be locally restricted to the coarse textured, post –glacial sand deposits that could provide adequate drainage in a region where poorly drained soils dominate. The observed distribution of aspen in this study failed to substantiate this prediction because aspen was found growing on a variety of substrates throughout the study area. It was found colonizing fissures in dry rock outcrops with little to no mineral soil as well as waterlogged peaty-clay soils. Furthermore, study results showed little correlation between aspen abundance and a topography / soil drainage gradient (RDA1; Figure 4-2). These results also seem inconsistent with a species restricted by climatic conditions near it's NDL, as several tree species identified as subject to climatic limitations near their NDL occupy specific habitat to counter the effects of poor climate (i.e., black spruce, larch, and balsam poplar) (Payette, 1993). It may be that aspen's current distribution is not in sync with current climate and it will continue to expand northward when appropriate environmental conditions are present, such as in the wake of large disturbances that expose mineral substrate.

4.4.3.5 *Prediction 5: Aspen abundance is positively correlated with soil potassium*

In the James Bay region, a bedrock 'exposure' gradient of high to low follows a north-south trajectory, with highest exposure occurring north of the 52th parallel, and lowest exposure occurring south of the 49th parallel (Ciesielski, 1998). This exposed bedrock in the north is generally acidic and low in Ca and Mg but high in K (Hocq, 1994). As in other northern environments, the rock is expected to be subject to severe physical weathering processes associated with seasonal freeze-thaw events in conjunction with normal chemical weathering (Chapin III & Matson, 2011). The exposed granitic ridges that top the hills around OFL illustrate the high exposure end of this gradient. The composition of these landforms includes high amounts of K-rich pink feldspar (Personal communication, Youcef Larbi, Chief Geologist, Cree Mineral Exploration Board). Given that parent material fundamentally determines the nutrient

capital of a site (Stone & Gibson, 1975), that the prevalent role of mineral weathering in introducing K inputs to ecosystems, aspen's known affinity for base-cations, the low amounts of Ca and Mg in shield substrate; and the coincidental hill-slopes covered with aspen, we predicted that aspen abundance is positively associated with soil K. The study results indicate that local variation in soil K is significantly related to aspen abundance and thus supports the prediction (Table 4-1). Therefore, the chemical properties of the rocks in the north, and particularly around OFL, appear to play a conspicuous role in determining the local distribution and abundance of aspen, through their function as a source of K. These results further highlight the important role soil K can play in structuring northern plant communities.

4.4.4   Understanding the distribution of aspen near its NDL

This study reveals the importance of soil K to aspen growing near its NDL in Quebec and supports previous research demonstrating the clear relationship between plant community composition and structure and the fire cycle (Parisien & Sirois, 2003). The results of this study demonstrate that the factors controlling species range limits are more complex than simply climate. If climate was the major factor determining the landscape level distribution and abundance of aspen growing near its NDL, the distribution of aspen would be expected to be consistent with a climatic signal, such as a significant relationship between aspen abundance and warm-facing slopes (prediction 3) or the restriction of aspen to particular habitat (prediction 4) as documented for other tree species near their NDL (Payette, 1993). This is not to say that climate does not contribute at all to observed patterns of aspen occurrence and abundance near its NDL, but rather that other factors appear to be stronger determinants of aspen's success at the landscape scale, such as the strong link identified between aspen abundance and soil K availability. In addition, perhaps aspen's ability to establish under the poor climate of north facing locations may be enhanced by localized soil fertility conditions. Our findings highlight some limitations of the bioclimatic envelope modelling approach when finer scale spatial factors may also determine local species range limits. Even at regional scales where the climate signal may be more pronounced, the spatial distribution of soils and parent material

arising from patterns in bedrock and surficial geology may play an important role and constrain the importance of climate. This study suggests that climate-based models may be improved by including relevant soil fertility information, and factors associated with local disturbance regimes.

Ultimately, the controlling factors that drive forest composition near NDLs need further investigation because species' vary in their response to both abiotic and biotic factors. All of these relationships must be considered to develop strong models capable of predicting the effects of climate change on forest systems and individual species.

4.5   Acknowledgements

4.6   References

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4.7   Tables

Table 4-1: Summary of Predictor variables (Data) used in: RDA = Redundancy analysis, MLR = Multiple linear regression; and LMM = Linear mixed model; ANOVA = Analysis of variance model comparison

	Data	Code	Source	Description	Why chosen	Analysis	Ref.
Spatial	Latitude	Lat	Field	Recorded with Garmin Oregon 550 global positioning satellite receiver.	• To account for spatial structure in data • Indirect measure of regional climate	RDA; MLR	(Tilman & Kareiva, 1997; de Blois *et al.*, 2002)
	Longitude	Long	Field	Recorded with Garmin Oregon 550 global positioning satellite receiver. Note values of longitude are negative west of the Prime Meridian and thus throughout the study area.	• To account for spatial structure in data • Indirect measure of regional climate • Predicted longitudinal change in vegetation across study area is mainly associated with the fire regime	RDA; MLR	(Tilman & Kareiva, 1997; de Blois *et al.*, 2002; Parisien & Sirois, 2003)
	Elevation	Elev	DEM	Recorded with Garmin Oregon 550 global positioning satellite receiver.	• Indirect measure of regional climate	RDA; MLR	(Tilman & Kareiva, 1997; Chen *et al.*, 2002; de Blois *et al.*, 2002)
	Transect	Transect	Field	Measured with 50 meter field tape.	• To test if there was a significant effect of including transect in models	MLR; LMM; ANOVA	(Austin, 1985; Ter Braak & Prentice, 1988; Chen *et al.*, 2002)
Topography	Slope	Sl	DEM	A measure of the % change in elevation per unit distance travelled.	• Predicted that aspen abundance will be greatest on warm-aspect slopes in boreal climates of Canada	RDA; MLR	(Chen *et al.*, 2002)
	Northness	northness	DEM	Northness quantifies the degree to which an aspect is north; i.e., northness for an angle of 360° is 1, for 90° is zero, and 180° is -1.	• Predicted that aspen abundance will be greatest on warm-aspect slopes in boreal climates of Canada	RDA	(Zar, 1999; Chen *et al.*, 2002)
	Eastness	eastness	DEM	Eastness quantifies the degree to which an aspect is east.	• Predicted that aspen abundance will be greatest on warm-aspect slopes in boreal climates of Canada	RDA; MLR	(Zar, 1999; Chen *et al.*, 2002)
Soil environment	LFH	LFH	Field	Organic horizon at the surface of the soil profile.	• Predicted aspen is restricted to areas where organic material has been removed by fire	RDA; MLR	(Weber *et al.*, 1987; Miyanishi & Johnson, 2002; Chen *et al.*, 2009)
	A.horizon	Depth_A	Field	Consists of one or more mineral horizons of maximum organic accumulation; or surface or subsurface horizons that are lighter in color than the underlying horizon - the horizon of maximum biological activity.	• Predicted aspen is restricted to areas where organic material has been removed by fire	RDA; MLR	(Staff, 1951; Weber *et al.*, 1987; Bergeron *et al.*, 2004; Chen *et al.*, 2009)

Data	Code	Source	Description	Why chosen	Analysis	Ref.
% Clay	Clay	Field	Determined using USDA soil texturing field flow chart	• Predicted that aspen will be less abundant in soils with high clay content	RDA	(Pare *et al.*, 2001; Chen *et al.*, 2002)
% Sand	Sand	Field	Determined using USDA soil texturing field flow chart	• Predicted that aspen will be most abundant on sites that are well drained and aerated	RDA; MLR	(Pare *et al.*, 2001; Chen *et al.*, 2002)
Avg. soil pH	Avg_pH	Field / Lab	Forest floor and mineral soil were sampled and analysed to determine pH using a combination electrode (Accumet AR10)	• Predicted a positive relationship between aspen abundance and pH; used as a proxy for Ca and Mg due to their high correlation.	RDA; MLR	(Legare *et al.*, 2005; Pinno *et al.*, 2009)
Avg. soil Al	Avg_Al	Field / Lab	Forest floor and mineral soil were sampled and analysed to obtain average concentration of extractable Al (mg/g) in combined horizons	• Predicted a positive relationship between aspen abundance and nutrient richness (particularly base cations)	RDA	(Alban *et al.*, 1978; Tran & Simard, 1993; Brais *et al.*, 1995; Chen *et al.*, 1998; Pare *et al.*, 2001; Pinno *et al.*, 2009)
Avg. soil Ca	Avg_Ca	Field / Lab	Forest floor and mineral soil were sampled and analysed to obtain average concentration of extractable Ca (mg/g) in combined horizons	• Predicted a positive relationship between aspen abundance and nutrient richness (particularly base cations)	RDA	(Alban *et al.*, 1978; Tran & Simard, 1993; Brais *et al.*, 1995; Chen *et al.*, 1998; Pare *et al.*, 2001; Pinno *et al.*, 2009)
Avg. soil K	Avg_K	Field / Lab	Forest floor and mineral soil were sampled and analysed to obtain average concentration of extractable K (mg/g) in combined horizons	• Predicted a positive relationship between aspen abundance and nutrient richness (particularly base cations)	RDA; MLR	(Alban *et al.*, 1978; Tran & Simard, 1993; Brais *et al.*, 1995; Chen *et al.*, 1998; Pare *et al.*, 2001; Pinno *et al.*, 2009)
Avg. soil Mg	Avg_Mg	Field / Lab	Forest floor and mineral soil were sampled and analysed to obtain average concentration of extractable Mg (mg/g) in combined horizons	• Predicted a positive relationship between aspen abundance and nutrient richness (particularly base cations)	RDA	(Alban *et al.*, 1978; Tran & Simard, 1993; Brais *et al.*, 1995; Chen *et al.*, 1998; Pare *et al.*, 2001; Pinno *et al.*, 2009)
Avg. soil P	Avg_P	Field / Lab	Forest floor and mineral soil were sampled and analysed to obtain average concentration of extractable P (mg/g) in combined horizons	• Predicted a positive relationship between aspen abundance and nutrient richness (particularly base cations)	RDA	(Alban *et al.*, 1978; Tran & Simard, 1993; Brais *et al.*, 1995; Chen *et al.*, 1998; Pare *et al.*, 2001; Pinno *et al.*, 2009)

Table 4-2: Summary of Rankings of candidate models from multiple linear regressions assessing aspen abundance related to environmental variables. K = number of parameters, w_i = Akaike weight, C_{wi} = Cumulative Akaike weight, R^2 = coefficient of determination, R^2_{adj} = adjusted R^2

Model	K	AICc	ΔAICc	w_i	C_{Wi}	R^2	R^2_{adj}
% aspen ~ Avg_K + Long	4	8.44	0.00	0.97	0.97	0.17	0.16
% aspen ~ Avg_K	3	16.23	7.78	0.02	0.99	0.11	0.10
% aspen ~ Long + eastness + Sl + LFH +Depth_ A + Sand + Avg_pH + Avg_K + Avg_Al	11	17.64	9.20	0.01	1.00	0.21	0.15
% aspen ~ Long	3	26.58	18.13	0.00	1.00	0.03	0.03
Intercept only	2	28.90	20.46	0.00	1.00	-	-

Models are ranked from most (**ΔAICc = 0**) to least plausible; k is the number of estimated parameters included in the model.

Table 4-3: Model-averaged parameter estimates, unconditional standard errors, and unconditional confidence intervals computed from the full set of candidate models of the effects of environmental factors on aspen abundance in the northern boreal forest of northwestern Quebec, Canada. See **Table 4-1** for model code descriptions. Parameter estimates in bold are considered statistically significant (i.e., confidence intervals do not overlap with 0).

Parameter	Estimate	Unconditional SE	Unconditional CI	
Long	**0.23**	0.07	**0.09**	**0.37**
eastness	0.01	0.02	-0.03	0.05
Slope	0.02	0.03	-0.04	0.07
LFH	-0.02	0.03	-0.07	0.03
Depth_A	**0.04**	0.02	**0.00**	**0.09**
Sand	0.00	0.03	-0.05	0.06
Avg_pH	-0.01	0.02	-0.06	0.03
Avg_K	**0.10**	0.02	**0.06**	**0.14**
Avg_Al	0.03	0.03	-0.03	0.08

4.8   Figures

Figure 4-1:   Location of the study area in northwestern Quebec. Major settlements
are identified with dark circles and major water bodies are labeled.
Note that near Old Factory Lake some survey sites (triangles) are not
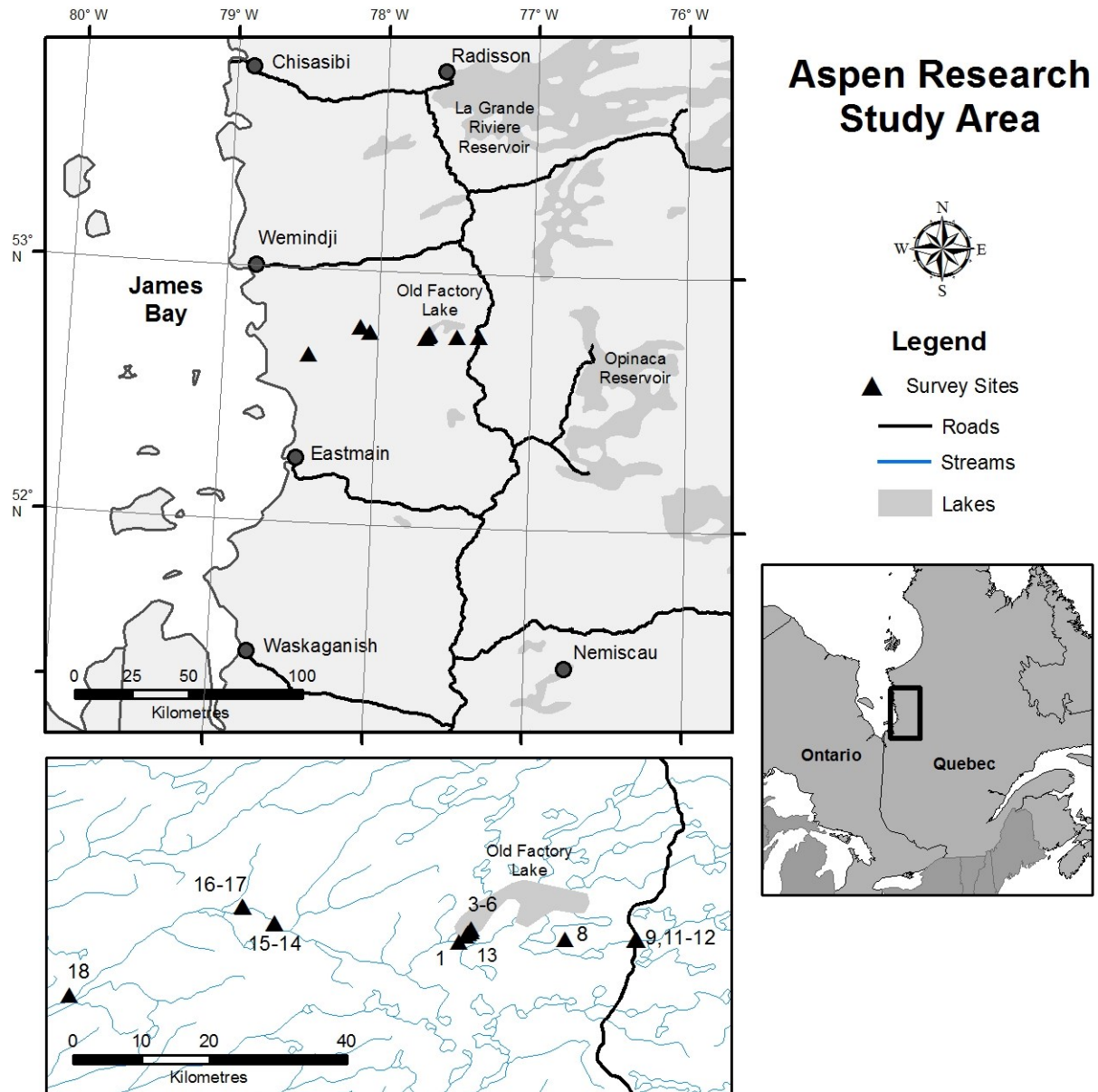visible because of triangle overlap.

Figure 4-2:   Parsimonious redundancy analysis (RDA) triplot, plant species relative abundance data constrained by 12 predictor variables with P < 0.05 (see Table 4-1 for summary of variables). Percent variation in species relative abundance explained by the selected model is 23.1% (R^2_{adj}). Percent variation explained by axis 1 = 10.0% and axis 2 = 6.0%.
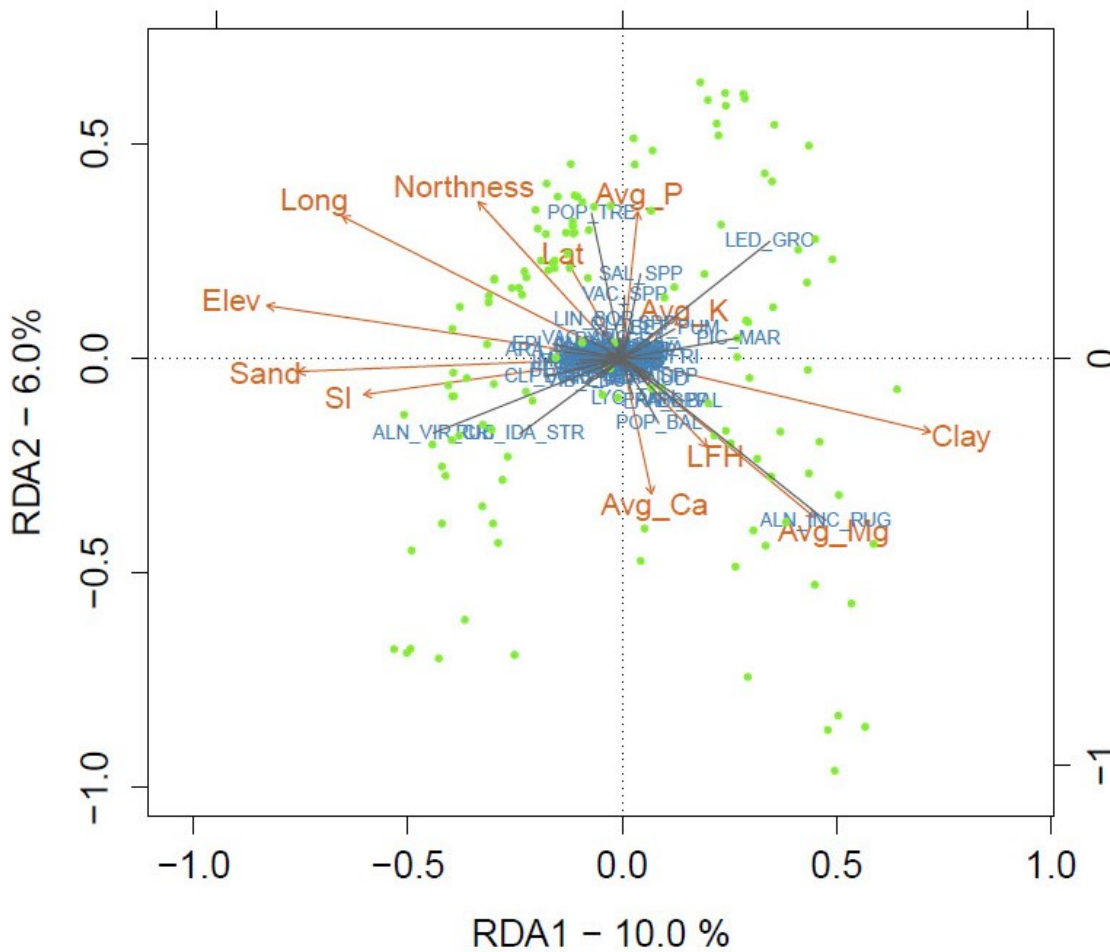
4.9   Appendix 1

Table 4-4:   Study species

Acronym	Species	Form	Common Name
ABI_BAL	*Abies balsamea*	*Tree*	*balsam fir*
ACT_RUB	*Actaea rubra*	*Herb*	*red baneberry*
ALN_INC_RUG	*Alnus incana ssp. rugosa*	*Shrub*	*speckled alder*
ALN_VIR_CRI	*Alnus viridis ssp. crispa*	*Shrub*	*mountain alder*
AME_SPP	*Amelanchier spp.*	*Shrub*	*serviceberry*
ARA_NUD	*Aralia nudicaulis*	*Herb*	*wild sarsaparilla*
ARC_UVA	*Arctostaphylos uva-ursi*	*Shrub*	*kinnikinnick or bearberry*
BET_PAP	*Betula papyrifera*	*Tree*	*white birch*
BET_PUM	*Betula pumila*	*Shrub*	*dwarf birch*
CLA_SPP	*Cladina spp.*	*Lichen*	*Reindeer lichen*
CLI_BOR	*Clintonia borealis*	*Herb*	*bluebead*
COP_TRI	*Coptis trifolia*	*Herb*	*threeleaf goldthread*
COR_CAN	*Cornus canadensis*	*Herb*	*bunchberry*
COR_STO	*Cornus stolonifera*	*Shrub*	*redosier dogwood*
DRY_SPP	*Dryas spp.*	*Herb*	*mountain-avens*
EPI_ANG	*Epilobium angustifolium*	*Herb*	*fireweed*
EQU_SPP	*Equisetum spp.*	*Herb*	*horse tail*
FRA_SPP	*Fragaria spp.*	*Herb*	*strawberry*
GAL_SPP	*Galium spp.*	*Herb*	*bedstraw*
GYM_DRY	*Gymnocarpium*	*Fern*	*oakfern*
HUP_LUC	*Huperzia lucidula*	*Herb/subshrub*	*shining clubmoss*
KAL_ANG	*Kalmia angustifolia*	*Herb*	*sheep laurel*
LAR_LAR	*Larix laricina*	*Tree*	*Tamarack*
LED_GRO	*Rhododendron groenlandicum*	*Shrub*	*Labrador tea*
LIN_BOR	*Linnaeae borealis*	*Herb*	*twinflower*
LYC_ANN	*Lycopodium annotinum*	*Herb/subshrub*	*stiff clubmoss*
LYC_COM	*Lycopodium complanatum*	*Herb/subshrub*	*groundcedar*
LYC_DEN	*Lycopodium dendroideum*	*Herb/subshrub*	*tree groundpine*
LYC_DIG	*Lycopodium digitatum*	*Herb/subshrub*	*fan clubmoss*
LYC_OBS	*Lycopodium obscurum*	*Herb/subshrub*	*rare clubmoss*
MAI_CAN	*Maianthemum canadense*	*Herb*	*Canada mayflower*
MEL_LIN	*Melampyrum lineare*	*Herb*	*narrowleaf cowwheat*
MER_PAN	*Mertensia paniculata*	*Herb*	*tall bluebells*
MIT_NUD	*Mitella nuda*	*Herb*	*naked miterwort*
ORT_SEC	*Orthilia secunda*	*Herb/subshrub*	*sidebells wintergreen*
PET_FRI	*Petasites frigidus*	*Herb*	*arctic sweet coltsfoot*
PIC_MAR	*Picea mariana*	*Tree*	*black spruce*

Acronym	Species	Form	Common Name
PIN_BAN	*Pinus banksiana*	*Tree*	*Jack pine*
POA_SPP.	*Poa spp.*	*Grass*	*bluegrass*
POL_COM	*Polytrichum commune*	*Moss*	*common haircap moss*
POL_JUN	*Polytrichum juniperinum*	*Moss*	*juniper haircap*
POP_BAL	*Populus balsamifera*	*Tree*	*balsam poplar*
POP_TRE	*Populus tremuloides*	*Tree*	*quaking aspen*
PRU_PEN	*Prunus pensylvanica*	*Tree*	*pin cherry*
PRU_SER	*Prunus serotina*	*Tree*	*black cherry*
PYR_ASA	*Pyrola asarifolia*	*Herb/subshrub*	*liverleaf wintergreen*
PYR_GRA	*Pyrola grandiflora*	*Herb/subshrub*	*largeflowered wintergreen*
RIB_GLA	*Ribes glandulosum*	*Herb*	*skunk currant*
RIB_LAC	*Ribes lacustre*	*Shrub*	*prickly currant*
RIB_TRI	*Ribes triste*	*Shrub*	*red currant*
RUB_IDA_STR	*Rubus idaeus var. strigosus*	*Shrub*	*wild red rasberry*
SAL_SPP	*Salix spp.*	*Shrub*	*willow*
SOR_DEC	*Sorbus decora*	*Tree*	*northern mountain ash*
SPH_SPP	*Sphagnum spp.*	*Moss*	*moss*
TRI_BOR	*Trientalis borealis*	*Herb*	*starflower*
VAC_ANG	*Vaccinium angustifolium*	*Shrub*	*early low blueberry*
VAC_SPP	*Vaccinium spp.*	*Shrub*	*blueberry*
VIB_ACE	*Viburnum acerifolium*	*Shrub*	*maple viburnum*
VIB_ALN	*Viburnum alnifolium*	*Shrub*	*hobblebush*
VIB_EDU	*Viburnum edule*	*Shrub*	*squashberry*
VIO_SPP	*Viola spp.*	*Herb*	*violet*

4.10 Appendix 2

Table 4-5: Pearson's correlation coefficients describing relationships between predictor variables.

	Elev	Sl	LFH	Depth_A	Clay	Sand	Avg_pH	Avg_P	Avg_K	Avg_Al	Avg_Ca	Avg_Mg	Eastness	Northness	Lat	Long
Sl	0.54 ***	1.00	-0.03	0.14	-0.37 ***	0.36 ***	0.01	0.06	-0.06	-0.11	0.10	-0.15	-0.10	-0.04	0.27 **	0.52 ***
LFH	0.41 ***	0.03	1.00	0.08	0.32 ***	-0.26 **	-0.21 *	-0.02	0.15	0.08	0.10	0.28 **	-0.01	-0.13	-0.04	-0.40 ***
D_A	0.18 *	0.14	0.08	1.00	0.12	-0.05	0.16	0.06	0.16	-0.14	0.19 *	0.05	0.05	0.06	-0.13	-0.22 *
Clay	0.68 ***	0.37 ***	0.32 ***	0.12	1.00	-0.90 ***	-0.12	0.18 *	0.32	0.31 ***	0.07	0.47	0.11	-0.20 *	0.24 **	-0.60 ***
Sand	0.60 ***	0.36 ***	-0.26 **	-0.05	-0.90 ***	1.00	0.09	-0.16	-0.24 **	-0.34 ***	-0.07	-0.40 ***	-0.07	0.18 *	-0.25 **	0.46 ***
Avg_pH	0.03	0.01	-0.21 *	0.16	-0.12	0.09	1.00	0.05	0.06	-0.18 *	0.42 ***	0.07	0.17	-0.02	-0.18 *	0.03
Avg_P	0.06	0.06	-0.02	0.06	0.18 **	-0.16	0.05	1.00	0.45 ***	0.12	0.08	0.08	-0.21 *	0.11	0.22 *	-0.10
Avg_K	0.22 *	0.06	0.15	0.16	0.32 ***	-0.24 **	0.06	0.45 ***	1.00	-0.24 **	0.47 ***	0.66 ***	0.1	-0.05	0.19 *	-0.21 *
Avg_Al	0.25 **	0.11	0.08	-0.14	0.31 ***	-0.34 ***	-0.18 *	0.12	-0.24 **	1.00	-0.37 ***	-0.17	0.14	-0.15	0.12	-0.22 *
Avg_Ca	0.12	0.10	0.10	0.19 *	0.07	-0.07	0.42 ***	0.08	0.47 ***	-0.37 ***	1.00	0.53 ***	0.13	-0.15	-0.12	-0.07
Avg_Mg	0.50 ***	0.15	0.28 **	0.05	0.47 ***	-0.40 ***	0.07	0.08	0.66 ***	-0.17	0.53 ***	1.00	0.24 **	-0.36 ***	0.02	-0.43
East	0.10	0.10	-0.01	0.05	0.11	-0.07	0.17	-0.21 *	0.10	0.14	0.13	0.24 **	1.00	-0.30 ***	-0.16	-0.16
North	0.27 **	0.04	-0.13	0.06	-0.20 *	0.18 *	-0.02	0.11	-0.05	-0.15	-0.15	-0.36 ***	-0.30 ***	1.00	0.07	0.26 **
Lat	0.32 ***	0.27 **	-0.04	-0.13	0.24 **	-0.25 **	-0.18	0.22 *	0.19 *	0.12	-0.12	0.02	-0.16	0.07	1.00	0.41 ***
Long	0.91 ***	0.52 ***	-0.40 ***	-0.22 *	-0.60 ***	0.46 ***	0.03 *	-0.10	-0.21 *	-0.22 *	-0.07	-0.43 ***	-0.16	0.26 **	0.41 ***	1.00

Significance of correlations is indicated as follows: *p<0.05, **p<0.01 and ***p<0.001

5 Summary and Final Conclusions

Chapter 1 provides a review of the range limit literature and presents context for the working predictions I used to examine aspen's range dynamics in northwestern QC. Each successive data chapter (Chapter 2 – 4) aimed to: improve our understanding of aspen range dynamics through evaluation of one or more research predictions (or models) related to patterns of aspen occurrence or growth; reject or accept specific predictions; and generate new predictions. In Chapter 2 we examine patterns of aspen distribution and abundance in the James Bay area using a combination of field, GIS, and remote sensing techniques, and follow with investigations into the potential range limiting controls associated with the findings. Chapter 3 examines the influence of a wide range of climatic conditions on the growth of young aspen saplings across a broad latitudinal gradient in northwestern QC. Chapter 4 uses a combination of ordination and regression modelling techniques to distinguish the factors controlling plant community composition in aspen dominated stands from factors controlling other dominate vegetation in the study area that are commonly found near aspen stands, and specifically account for the factors controlling aspen abundance. In this final section of the dissertation, I review the preface of each data chapter, review the main objectives, present the findings, highlight the relationships among them, and describe any other value added features of the chapter. Then, I describe the contextual significance of the combined findings to understanding aspen's range in northwestern QC.

Chapter 2 was the first step towards an integrated hierarchical approach to understanding aspen range dynamics in the northern boreal forest of Canada because without documentation and knowledge of its current distribution there is no baseline for accurate comparative and quantitative studies now and/or in the future. In chapter 2, we represent aspen's range in the James Bay Area of QC by building a land cover map (~51,000 km^2) using Landsat Thematic Mapper images from 2010 and 2011, a robust collection of ground reference data developed from aerial photography, and four field seasons of vegetation sampling. Following, we quantify aspen abundance using quadrat analysis.

The specific objectives of this study were to (1) provide a more accurate description of aspen distribution and abundance around its northern range edge in NW QC, (2) determine if we can detect a regional response of aspen to climate (does aspen abundance decrease systematically with increasing latitude?), (3) determine if there are spatial correlations between aspen and landscape features capable of influencing its regional distribution, such as topography, human infrastructures (roads, dams, settlements), and 'open' areas (<33% vegetated) which in theory should include safe spots for aspen establishment. We found that the distribution of aspen stands within the study area clearly show a clustered pattern with concentrations of aspen stands in particular areas. This pattern is inconsistent with the expected pattern of greater aspen abundance in the south, followed by an incremental decrease in abundance with increasing latitude; such a pattern would have demonstrated a strong climatic response of aspen to the deteriorating climatic conditions associated with moving poleward. Furthermore, we demonstrated that aspen could establish on north facing slopes over the entire study area which reinforces the idea that climate is not the strongest control over aspen's distribution in the study area. Instead, we found that the pattern of aspen distribution at the regional scale of this study correlates well with anthropogenic driven disturbance. These findings suggest that the regional distribution of aspen in the James Bay area is likely to change with continued and increased human disturbance.

In addition to general results, this second chapter is 'methodologically' unique for several reasons. First, the dataset used to construct the land cover map of the James Bay area presented in this thesis was specifically developed for this thesis, and designed to be used in testing predictions related to aspen's distribution within the ~51,000 km^2 study area. Most regional-scale quantitative biogeographic research relies on data combined from existing literature or other sources, such as biological surveys and museum specimens. The use of such data is known to be problematic because most often the data were not collected under a shared protocol, or with a shared objective related to characterizing a species' range. Thus complications with respect to the precision, accuracy, and interpretation of the data are known to be abundant (Brown *et al.*, 1996).

Second, during the process of creating the land cover map for this thesis, we developed and applied a novel method for rapid extraction of land cover classification

data in remote areas. The process of mapping northern land cover is known to present many challenges not experienced when mapping more southern environments due to the vast and isolated nature of the north (few roads, few settlements, costly travel etc...). This has led to a lack of reference data and limited knowledge of northern land cover distribution and dynamics (Olthof *et al.*, 2009). Most of the published studies on northern land cover mapping did not have enough ground reference data to perform adequate accuracy assessments of their final mapped products (Wulder *et al.*, 2006), which does not instill confidence in land managers and other map users who need to make important decisions about societal resources based in part on available land cover maps. Working in a remote area such as northern QC revealed a pressing need to develop a time-sensitive method for field acquisition of ground reference data to use in the land cover classification process without the added expense of returning to the field site. The method developed in this thesis for rapid acquisition of ground reference data incorporates GPS systems with high resolution ground photography to allow analysts to create geo-referenced data points in a research lab setting (as opposed to the field) which can be used to develop and validate land cover classifications.

Chapter 3 examines aspen growth rates across a broad range of climatic conditions. Tree growth is related to reproductive effort and success (Werren, 1979), and thus understanding environmental limitations on growth provides a basis for characterizing general tree performance. The north-south pattern of aspen distribution detected in chapter 2 appears inconsistent with the expected pattern of a tree species responding strongly to varied climatic conditions. Chapter 3 specifically addresses the general prediction that climate (specifically temperature) limits tree growth near species' northern distributional limits. I found that the relationship between aspen height growth and change in climate is weak ($R^2 = 0.17$, p < 0.01), and similarly the relationship between aspen diameter growth and climate is not significant. Furthermore aspen's growth response to change in latitude was fairly similar across the study transect despite the wide range of associated climatic conditions. This study demonstrates that climate is not the critical factor limiting aspen growth rate in the northern part of its range in western Quebec. This is a critical finding because the assumption that climate is the driving factor of changing species distributions

underpins most attempts to predict the responses of species to climate change, and in Chapter 3 we see once seedlings establish, there is little effect of climate on growth. These findings highlight the need for more in depth species specific research on determinants of range limits, and the subsequent factors most appropriate for use in predictive modelling of future tree species' distributions.

Chapter 4 involves scaling up detailed tree-, species-, and stand-level data collected on field plots to characterize forest composition and structure for an area where aspen occurs in uncharacteristic abundance near its northern range limit in QC. The objectives of chapter 4 included: 1) distinguishing the factors controlling plant community composition in aspen dominated stands from factors controlling other dominate vegetation in the study area, 2) explicitly investigating the factors controlling local levels of aspen abundance, and 3) testing specific hypotheses related to the northern distributional limits of aspen in QC. I found gradients related to soil moisture and soil fertility best characterized forest composition and structure across the study area, capturing 16 out of the 23.4% of the explained variance in species composition, while aspen abundance in particular was associated with soils high in K, and inland areas where fire events are more frequent than those on the coast. Understanding the direct impacts of environmental gradients on natural aspen populations occurring near their NDL is a first step toward integrating individual and population level dynamics.

The results of chapter 4 demonstrate the importance of looking "beyond" climate factors to explain aspen's distribution patterns (Beauregard & de Blois, in press). This is not to argue that climate does not contribute at all to observed patterns of aspen occurrence and abundance near its NDL in QC, but rather evidence supporting the direct influence of climatic factors was not detected, and other factors appear to be stronger determinants of aspen's local success (i.e., the strong link identified between aspen abundance and soil K availability). Based on these results, a natural extrapolation to future research would be to examine substrate and soil fertility across the broader James Bay study area to see whether the regional patterns of aspen distribution reflects the regional patterns in these variables, perhaps driven by geological history. These findings highlight some limitations of the bioclimatic envelope modelling approach when medium-to-fine-scale ecosystem properties, such

as disturbance and soil fertility have strong influences over tree species range limits. This study suggests that proper investigation of non-climatic factors influencing species' distributions is necessary to advance the field of ecological forecasting under climate change.

Finally, although this thesis focused on the influence of abiotic factors on aspen distribution and abundance patterns, a deeper understanding of such patterns can likely be achieved through investigations into biotic interactions, such as facilitation, competition, and herbivory. Just as individual species' distributions and abundances are expected to shift with ongoing climate change, so are the strength and direction of inter-species relationships. These species' dynamics provide the mechanisms by which communities and biomes respond to global change. At the same time, biomes and communities may constrain the nature of the species' response. For example, some plant species may not be able to shift their range distribution without their associated mutualist pollinators (Davis & Zabinski, 1992). Understanding how variation in climate can influence the structure and dynamics of natural communities across different scales of ecological organization is necessary to accurately predict how climate change will affect different inter-species relationships, and in turn, their impact on community structure and function.

5.1   References

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