QUANTIFYING VARIABILITY IN THE ALASKAN BLACK SPRUCE ECOSYSTEM: LINKING VEGETATION, CARBON, AND FIRE HISTORY

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fullfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By
Teresa Nettleton Hollingsworth, B.A., M.Sc.

Fairbanks, Alaska
December 2004

QUANTIFYING VARIABILITY IN THE ALASKAN BLACK SPRUCE ECOSYSTEM: LINKING VEGETATION, CARBON, AND FIRE HISTORY

By

Teresa Nettleton Hollingsworth

RECOMMENDED:

Leslie A Viereck

Darrell Verbyla

Marilyn Walker
Advisory Committee Co-chair

F Stuart Chapin III
Advisory Commitee Co-chair

Chair, Department of Biology and Wildlife

APPROVED: Joan Braddock
Dean, College of Natural Science and Mathematics

Dean of the Graduate School

December 17, 2004
Date

ABSTRACT

The boreal forest is the largest terrestrial ecosystem in North America, one of the least disturbed by humans, and most disturbed by fire. This combination makes it an ideal system to explore the environmental controls over species composition, the relative importance of abiotic factors and floristic composition in governing ecosystem processes, and the importance of legacy effects at a large regional spatial scale. In the boreal region of interior Alaska, *Picea mariana* (black spruce) is the predominant tree species and spans a wide range of habitats, including north-facing slopes with permafrost, lowland bogs, and high dry ridge-tops. This research uses a combination of site description and analysis from both locally near Fairbanks (54) and across a large region and number of sites (146) to answer questions about the regional variability and biodiversity of the black spruce forest type. Based on the relationships between species composition and environmental factors, topography and elevation were the most important gradients explaining species composition locally in the Fairbanks region, and mineral soil pH was the overriding environmental gradient across interior Alaska. To describe the floristic variability, I separated the black spruce forest type into three floristically-based community types and five community subtypes. Variability in ecosystem properties among black spruce stands was as large as that documented previously among all forest types in the central interior of Alaska. The variability in plant community composition was at least as effective as environmental or abiotic factors and stand characteristics as a predictor of soil C pools in the black spruce forest type of interior Alaska. The variability in species composition at the community subtype-level was related to a combination of environmental factors and fire history. Together, these results provide a foundation for future work in black spruce ecosystems of interior Alaska, and contribute to our understanding of the regional variability and biodiversity of the black spruce forest type.

TABLE OF CONTENTS

CHAPTER 3: PREDICTING ECOSYSTEM PROPERTIES WITH COMMUNITY COMPOSITION 61

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

ACKNOWLEDGEMENTS

I gratefully acknowledge financial support for this research from the following sources: NSF support to UAF Bonanza Creek LTER (grant numbers 9870217 and 0080609), the USDA Forest Service Pacific Northwest Station support directly to me, and through a cooperative agreement with UAF (PNW01-JV11261592-231), a student research grant from the Center of Global Change and Arctic System Research at the University of Alaska Fairbanks, the UAF Austin Cooley Talent Grant, and a NASA/MSU Professional Enhancement Award.

This research would not have been possible without the support of my co-advisors, Marilyn Walker and F.S. (Terry) Chapin III. Marilyn gave me the support to start a PhD, and Terry gave me support to finish it. In addition, my graduate committee, Roger Ruess, David Valentine, David Verblya, and Leslie Viereck provided excellent input into research design, analysis, and previous drafts of this dissertation. Most importantly, my committee challenged me to think critically about my research and never stop asking questions. I feel truly fortunate to have worked with all of them. I am especially grateful to Les, for coming out of retirement to support me; your vegetation research over the years inspires me.

Field and laboratory assistance was provided by Lorien Nettleton (best brother ever), Kimberley (Kimbo) Maher, Matt (my southern boy) Cave, Tina (Sweetpea) Buxbaum, the Forest Frag chicks, Sketr Miller, Lyndsey Rose, Jennifer Arseneau, Julie Crawford, Amy Carroll, and Aurora Parsons (the best hire I ever made). I am grateful for the good company, the hard work, and the friendship.

When I began this research, I was overwhelmed by the enthusiasm and willingness for collaboration so many people extended to me. I thank, Eric Kasischke, and Edmond C. Packee, Tom Malone, and Carolyn Rosner of the Forest Growth and Yield program at UAF for providing helpful insight into the selection of sites (as well as

the use of their sites), Vladamir Romanovsky for providing soil and air temperature data, Olga Ofonina and Misha Zherbenko for verification of nonvascular specimens, Carolyn Parker, Allan Batten and Les Viereck for help in the verification of vascular specimens, Andi Lloyd for guidance in coring and aging trees, Ted Schuur for training me in the methods of soil collection and analysis, and Chris Fastie for opening my eyes to the influence of fire on the landscape.

For all research, I took the lead role in design, implementation, and synthesis. Both Marilyn Walker, and F.S. Chapin III contributed in an advisory capacity, and therefore are co-authors on all manuscripts. Aurora Parsons helped with Braun-Blanquet analysis, graphics and statistics, for which she is a co-author on the chapter 2 manuscript. E.A.G (Ted) Schuur analyzed soils for C and N for which he is a co-author on the chapter 3 manuscript.

I would like to acknowledge all my family, friends, and colleagues who helped me to believe in myself and made this experience worthwhile, fun, and educational. In particular, my mom Linda Toth, my dad Michael Nettleton, my brother and sister-in-law Lorien Nettleton and Robin Degrassi, Vera Alexander, Teri Viereck, Kim Stone, Amy Richey, Jerrod Warrington, Beth Ayen, Catharine Thompson (my comrade and confidant in the hardest part of the battle, finishing), Donie Bret-Harte, Isla Myers-Smith, Jason Vogel, and Nan Werdin. Finally, thank you to my husband Jamie Hollingsworth, for all the emotional support, love, tenderness, and hugs over the years. I would be nowhere without you.

This dissertation to dedicated to the memory of my grandfathers, Dr. John D. Nettleton and Edward (Poppy) Whatley. You taught me to cherish the outdoors, love the ones you're with, appreciate football, and pursue my dreams. I miss you both.

CHAPTER 1: INTRODUCTION

What is a plant community?

The simplest definition of a plant community is the species that occur in a particular area. Barbour et al. (1987) define a plant community as "a general term that can be applied to vegetation types of any size or longevity", and Kent and Coker (1992) define a plant community as "groups of plant species populations which are found growing together". Within the last two decades, plant community ecologists have come to recognize that this species/area-based definition does not incorporate the self-organization that generates communities (Kauffman 1995). Instead of a list of species, a community is the complex non-linear interaction among the species themselves, the species and their environment, and the genes and environment manifested across multiple temporal and spatial scales (Allen and Hoekstra 1992).

This emerging definition of plant communities has directed current research in plant community ecology towards topics such as the nature of community assemblage, the community as an emerging property of an ecosystem, and the contribution of current abiotic conditions versus past legacies in shaping long-term community patterns. Here, I examine black spruce communities in interior Alaska to answer questions about plant community dynamics and in particular:

1) How are black spruce plant community patterns shaped and how does this change across temporal and spatial scales?

2) What is the relationship between black spruce community patterns and black spruce ecosystem processes?

3) How does the legacy of fire shape the composition and distribution of mature

black spruce communities across the landscape?

Influence of glacial and climate history

Interior Alaska escaped the repeated glaciations of the Quaternary (Pewe et al. 1965), and served as a glacial refugium for many plants during this time (Hultén 1968). It is clear, however, that most of interior Alaska was not hospitable for boreal taxa during the full glacial conditions of the Pleistocene either due to the extreme aridity and cold air temperature of the region, or frequent light ground fires that kept the vegetation more deciduous in nature (Lloyd et al. in press). There are two opposing hypotheses on the fate of boreal taxa during this time. Some suggest that most boreal taxa, including the *Picea* species, were driven to the south or east of the ice sheets (Ritchie and MacDonald 1986) or to localized glacial refugia in Canada (Gamache et al. 2003, Jaramillo-Correa et al. 2004). Others suggest there was local persistence of trees, including *Picea*, on the Bering Land Bridge during the last glacial maxima (Brubaker et al. 2004), which explains the early appearances of tree and shrub taxa in western Alaska.

Black spruce (*Picea mariana*[Mill.] B.S.P.) is one of the most abundant conifers of northern North America, spanning the continent from Newfoundland and Maine in the southeast to Alaska in the northwest (Viereck and Johnston 1990). Yet, it has only recently colonized central Alaska (Ritchie 1982, Anderson et al. 1989, Swanson 2003, Jaramillo-Correa et al. 2004). It is believed that white spruce (*Picea glauca* [Moench] Voss) spread back into interior Alaska during the early Holocene, approximately 9,000-10,000 years BP, via multiple migration routes (Edwards and Brubaker 1986, Ritchie and

MacDonald 1986, Keenan and Cwynar 1992). Either a climatic shift to a moister, cooler climate (Barber 2002) or an increase in fire frequency (Lloyd et al. in press) caused the explosion of black spruce on the landscape approximately 6,500 to 7,000 years BP, as seen from an increase in black spruce pollen (Edwards and Brubaker 1986, Hu and Brubaker 1993).

Black spruce as a model for understanding community change

One of the most important contributions community ecologists can make in the coming decade is to quantify potential changes in communities with changes in climate. Community ecologists are in a unique position of understanding the species, the patterns they form, the environment in which these communities exist, and the reasons for these distributions. The black spruce ecosystem in interior Alaska presents a unique opportunity to study a dominant forest type that exhibits large phenotypic plasticity (Brubaker 1986) and occupies a large range of environmental conditions across a large region, relatively undisturbed by humans. Unlike the boreal forest of eastern Canada (Foster 1984), the floristic composition and distribution of black spruce forests in interior Alaska has remained relatively stable for the past 5,000 years, since its arrival. The Bering Sea isolates Alaska from Eurasia, the mountains of the Alaska Range to the south and the Brooks Range to the north restrict large-scale shifts in vegetation, and the extreme environmental conditions prevent large migrations of new species from the south Chapin et al. in press). The most important influences on species composition are, therefore, current abiotic conditions and large-scale disturbances such as fire. The influence of fire has created a mosaic of vegetation types in different stages of succession across the landscape (Van Cleve et al. 1991).

In this thesis I develop and test a conceptual model that describes the relationship between vegetation, environment, and disturbance in plant communities. Many community ecologists have ignored disturbance and treated community patterns as the result of the linkage between vegetation, abiotic properties or state factors such as drainage, moisture, parent material, glacial history and topography, and ecosystem processes such as nutrient cycling (e.g. Binkley et al. 1995, Chapin et al. 1996, Hobbie et al. 2000, Hobbie et al. 2002). This link between vegetation and environment is exemplified in arctic tundra (Figure 1.1, left), where these interactions have developed over geologic time and correspond to patterns of landscape age (Walker and Everett 1991) and large-scale disturbance is rare. There is large overlap in vascular and nonvascular species composition between arctic tundra and boreal forest. Consequently, if abiotic factors are sufficient to explain community patterns, abiotic variables should provide an adequate description of community patterns in the boreal forest, with little additional explanatory power coming from an understanding of disturbance history.

However, when large-scale disturbances, such as fire, are introduced into a system like the boreal forest, the strong links between vegetation, abiotic factors, and ecosystem processes might be changed (Figure 1.1, right), making it more difficult to predict a single factor based on either of the other two. The weakening of this linkage could be a result of both the direct effects fire has on the vegetation, and the indirect effects it has on the environment. For example, fire can promote the presence of fire dependent species or affect soil moisture properties. I use this conceptual model as a framework for emphasizing the effects of disturbance legacies -- in this case fire-- and environment in developing a floristic classification of the Alaskan boreal forest. In this thesis I focus on black spruce communities because of their dominance on the landscape; however, this framework could be useful for all tree-dominated vegetation types in the Alaskan boreal forest and could apply to a variety of disturbance types such as herbivory, logging, and flooding.

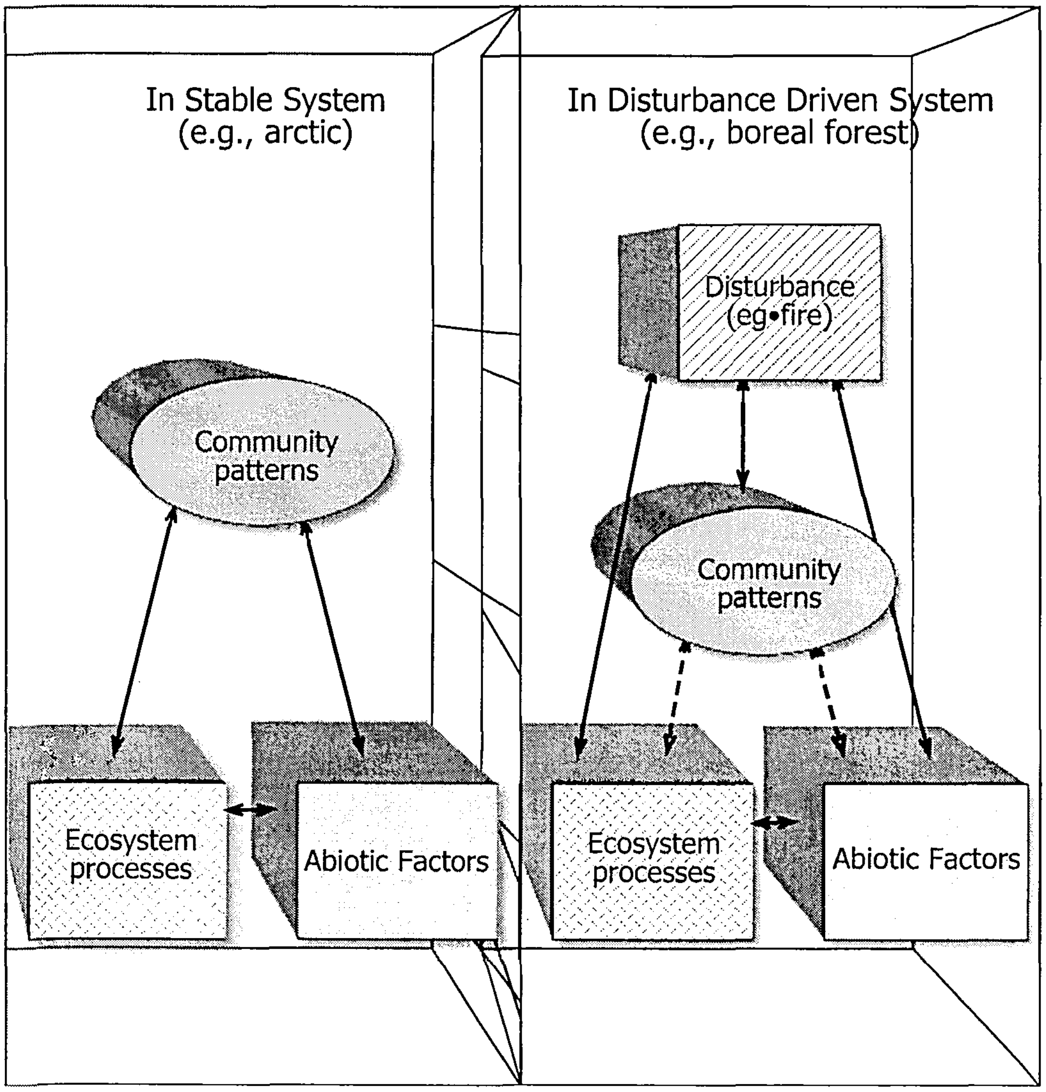

Figure 1.1. Conceptual model of the role of disturbance in the patterns of mature vegetation composition of the boreal forest of interior Alaska. In a stable system, such as the arctic, the relationship between vegetation patterns, hydrology of the system and abiotic factors such as climate and topography, are strongly linked, and vegetation patterns can be predicted based on a knowledge of the physical environment. However, in the disturbance driven boreal forest, fire acts as a factor to weaken or change the links between vegetation and the physical environment, thus making prediction of vegetation patterns based on environmental variables alone less accurate.

References

Allen, T. F., H., and T. W. Hoekstra. 1992. Toward a Unified Ecology. Complexity in Ecological Systems. Columbia University Press, New York.

Anderson, P. M., P. J. Bartlein, L. B. Brubaker, K. Gajewski, and J. C. Ritchie. 1989. Modern analogues of late-Quaternary pollen spectra from the western interior of North America. Journal of Biogeography 16:573-596.

Barber, V. A. 2002. Millennial to annual scale paleoclimatic change in central Alaska during the late Quaternary interpreted from lake sediments and tree rings. Ph.D Dissertation. University of Alaska Fairbanks, Fairbanks.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. Terrestrial Plant Ecology, Second edition. The Benjamin/Cummings Publishing Company, Inc, Menlo Park.

Binkley, D., F. Suarez, and C. Rhoades. 1995. Parent material depth controls ecosystem composition and function on a riverside terrace in northwestern Alaska. Ecoscience 2:377-381.

Brubaker, L. B. 1986. Response of tree populations to climatic change. Vegetatio 67:119-130.

Brubaker, L. B., P. M. Anderson, M. E. Edwards, and A. V. Lozhkin. 2004. Beringia as a glacial refugium for boreal trees and shrubs: New perspectives from mapped pollen data. Journal of Biogeography 31:1-16.

Chapin III, F. S., M. S. Bret-Harte, S. E. Hobbie, and H. Zhong. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science 7:347-358.

Chapin III, F. S., T. Hollingsworth, D. F. Murray, L. A. Viereck, and M. D. Walker. in press. Chapter 6. Floristic Diversity and Distribution in Alaska's Boreal Forest. in M. Oswood and F. S. Chapin III, editors. Alaska's Changing Boreal Forest. Oxford University Press, Oxford.

Edwards, M. E., and L. B. Brubaker. 1986. Late Quaternary vegetation history of the Fishhook Bend area, Porcupine River, Alaska. Canadian Journal of Earth Science 23:1765-1773.

Foster, D. R. 1984. Phytosociological description of the forest vegetation of southeastern Labrador. Canadian Journal of Botany 62:899-906.

Gamache, I., J. P. Jaramillo-Correa, S. Payette, and J. Bousquet. 2003. Diverging patterns of mitochondrial and nuclear DNA diversity in subarctic black spruce: imprint of a founder effect associated with postglacial colonization. Molecular Ecology 12:891-901.

Hobbie, S. E., K. J. Nadelhoffer, and P. Hogberg. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant and Soil 242:163-170.

Hobbie, S. E., J. P. Schimel, S. Trumbore, and J. R. Randerson. 2000. Controls over carbon storage and turnover in high-latitude soils. Global Change Biology 6:196-210.

Hu, F. S., and L. B. Brubaker. 1993. A 12 000 year record of vegetation change and soil development from Wien Lake, central Alaska. Canadian Journal of Botany 71:1133-1142.

Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford.

Jaramillo-Correa, J. P., J. Beaulieu, and J. Bousquet. 2004. Variation in mitochondrial DNA reveals multiple glacial refugia in black spruce (Picea mariana), a transcontinental North American conifer. Molecular Ecology 13:2735-2747.

Kauffman, S. 1995. At Home in the Universe. The search for Laws of Self-Organization and Complexity. Oxford University Press, New York.

Keenan, T. J., and L. C. Cwynar. 1992. Late quaternary history of black spruce and grasslands in southwest Yukon Territory. Canadian Journal of Botany 70:1336-1345.

Kent, M., and P. Coker. 1992. Vegetation Description and Analysis. A Practical Approach. John Wiley & Sons, Chichester.

Lloyd, A. H., M. E. Edwards, B. P. Finney, J. A. Lynch, V. A. Barber, and N. H. Bigelow. in press. Chapter 5. Development of the Boreal Forest. in M. Oswood and F. S. Chapin III, editors. Alaska's Changing Boreal forest. Oxford University Press, Oxford.

Pewe, T. L., D. Hopkins, M., and J. L. Giddings. 1965. The Quaternary Geology and Archaeology of Alaska. Pages 355-374 in H. E. J. Wright and D. G. Frey, editors. The Quaternary of the United States A review volume for the VII Congress of the International Association for Quaternary Research. Princeton University Press, Princeton.

Ritchie, J. C. 1982. The Modern and Late-Quaternary Vegetation of the Doll Creek area,

CHAPTER 2: SCALE DEPENDENT PATTERNS OF PLANT SPECIES COMPOSITION

"The atom is a pattern, and the molecule is a pattern, and the crystal is a pattern; but the stone, although it is made up of these patterns, is just a mere confusion"
-Aldous Huxley

---

*Manuscript title: Scale dependent controls over species composition in black spruce communities. Authors: T.N. Hollingsworth, M.D. Walker, F.S. Chapin III, and A. Parsons. Prepared for submission in Canadian Journal of Forest Research

Abstract

The boreal forest is the second largest terrestrial biome, yet it contains one of the lowest plant species diversities, making it an ideal system in which to study the environmental controls over species composition at large spatial scales. In the boreal region of interior Alaska, *Picea mariana* (black spruce) is the predominant tree species and spans a wide range of habitats, including north-facing slopes with permafrost, lowland bogs, and high dry ridge-tops. I described the floristic composition of 146 relatively homogenous black spruce stands based on information on all vascular and nonvascular plant species and their Braun-Blanquét cover estimates. I collected additional information on soil characteristics, forest structure, and physical characteristics of each stand and related species composition to environmental parameters using the Nonmetric Multidimensional Scaling ordination technique. I performed MANOVAs to compare species richness to pH and topographic position. Finally, I analyzed and classified the relevés using the Braun-Blanquét table sorting method.

I separated black spruce stands into three black spruce community types and five subtypes based on their floristic composition. The relationship of community composition to environmental gradients depended on both spatial and temporal scales. Topography and elevation were the most important gradients explaining species composition in the Fairbanks region. At the regional scale of interior Alaska, mineral soil pH became the overriding environmental gradient. Based on this research, I conclude that community composition of mature black spruce forests in interior Alaska is not a simple consequence of soil moisture/temperature gradients or based on age of the stand.

Instead, the interaction of landscape and fire history, soil pH, paludification, permafrost, and topographic position all contribute to a substantial degree of floristic diversity, which varied significantly along both acidity and topographic gradients.

Introduction

In the last decade, it has become increasingly clear that species' distribution along environmental gradients is scale-dependent (Allen and Hoekstra 1990, Levin 1992, Gould and Walker 1999). Many community and landscape studies have linked species responses to environmental gradients at small spatial or temporal scales (Viereck 1983b, Tilman 1993, Tilman et al. 1996, Arft et al. 1999, Raisa 1999) or at large spatial and temporal scales (Foster and King 1984, Currie and Paquin 1987, Latham and Ricklefs 1993, Bridge and Johnson 2000), yet few studies have investigated community patterns across multiple scales of space and time.

Soil temperature and moisture, which are controlled primarily by topography and successional status, have been described by many as the primary drivers of plant community composition in the boreal forest of interior Alaska (Skre et al. 1983, Van Cleve 1983, Yarie 1983, Van Cleve et al. 1990). In other parts of Alaska, however, other environmental factors are thought to regulate community composition. For example, large-scale community patterns in the Alaskan Arctic, to the north of the boreal forest, are related primarily to soil pH as it corresponds to landscape age (Walker and Everett 1991, Walker et al. 1994a). Although the species composition of the boreal forest understory broadly overlaps with the arctic tundra to the north, the interaction between mineral soil pH and Alaskan boreal community composition has never been studied. This raises questions about whether boreal forest and tundra are controlled by fundamentally different environmental gradients or whether the controls over community composition in the boreal forest might be regionally variable and therefore scale-dependent.

The boreal forest covers approximately 6.7 million km^2 across North America and Eurasia (Scott 1995) making it the second largest terrestrial biome on earth (Whittaker 1975). Although the boreal forest is the largest biome in North America, its plant diversity is one of the lowest, causing the vegetation to seem homogeneous or simple in its patterns (Drury 1956). This apparent simplicity may facilitate the recognition of key underlying determinants of community composition. The most widespread forest type in the Alaskan boreal forest is dominated by black spruce [*Picea mariana* (Mill.) B.S.P] (Viereck et al. 1992), which covers approximately 44% of the landscape (Van Cleve et al. 1983). Black spruce communities are particularly important in the context of global change in part because of the large amount of carbon stored in their soils, the prevalence of permafrost, and the tight link between black spruce and fire (Bonan and Shugart 1989).

Existing classifications of Alaskan boreal forest communities have been based on a combination of physiognomic and floristic data, with physiognomy being a primary element of the classification (Viereck et al. 1992, Brown and Smith 2000). However, many ecosystem processes, such as nutrient cycling, soil carbon storage, and fire regime, are more tightly associated with species composition than with stand structure (Flanagan and Van Cleve 1983, Driscoll et al. 1999, Bisbee et al. 2001). Therefore, previous vegetation classification of the boreal region of Alaska may be insensitive to key relationships between species distribution and the environment that have important functional consequences. Despite the extensive distribution and range of topographic conditions occupied by black spruce forests, there have been no detailed floristic surveys of this ecosystem type in boreal Alaska—the first step towards an understanding of the relationships between black spruce vegetation communities and the environment across the region.

This paper has three objectives: first, to examine the vegetation distribution within and among black spruce communities as it relates to environmental gradients within the Fairbanks region and across the entire interior of Alaska; second, to examine alpha, beta, and gamma diversity across important environmental gradients; and finally, to classify the black spruce communities of interior Alaska into communities and subtypes using a phytosociological approach to generate the first floristic-based classification of these communities.

Study area

The study area is bounded by the Alaska Range (~63°N) to the south, the Brooks Range (~67°N) to the north, where black spruce reaches its northern limit, the Dalton Highway (~ 150°W) to the west, and the Alaskan/Canadian border (~142°W) to the east (Figure 2.1). This 25,000 km^2 area is an intermontane plateau dissected by the Yukon, Tanana, and Kuskokwim River valleys (Hultén 1968). It is characterized by isolated mountain ranges, large areas of gently sloping uplands, flat lowlands, and braided rivers with broad floodplains (Van Cleve et al. 1983).

Interior Alaska is an area of discontinuous permafrost, with approximately 75-80 percent of the ground underlain by permanently frozen ground with some south-facing slopes and major river floodplains being the main exceptions (Osterkamp and Romanovsky 1999). Permafrost temperatures range from -0.5°C to –2°C, and the ground is covered with snow and ice for six to nine months of the year (Slaughter and Benson 1986). The region has a continental climate, with extreme temperatures ranging from –70°C to +35°C. Annual precipitation averages under 300 mm, of which about 35% falls as snow (Hinzman et al. in press).

Most of interior Alaska was ice-free during the repeated glaciations of the Quaternary. However, there are large Quaternary glacial deposits along the Yukon River valley. In addition, Illinoian glaciers were present at the northern edge of the study area along the southern slopes of the Brooks Range, and Illinoian and Pre-Illinoian glaciers were present at the southern edge of the study area, along the northern flanks of the Alaska Range. Periglacial processes were active during the entire Pleistocene and even as even during the Little Ice Age (~1350-~1900), so that modern-day lowlands are characterized by classical periglacial features including permafrost, ice wedges, and Aeolian activity (Pewe et al. 1965).

In this region soils show relatively little morphological development. Ninety-seven percent of the mapped areas of interior Alaska are Inceptisols, Entisols, Histosols, or Gelisols (Rieger et al. 1979, Ahrens et al. 2004). Throughout the region, silt-loam upland soils have developed from loess that was laid down during the last glacial maximum and from underlying schist bedrock with the loess caps becoming thinner farther away from loess sources. Floodplain soils have developed in sandy or silt-textured alluvium, mostly of glacial origin (Rieger et al. 1963).

Methods

Field sampling

I sampled black spruce communities at three scales: (1) along a climate transect that spanned the entire region (CT), (2) within a near-climatically uniform 100 X 100 km area around Fairbanks (FB), and (3) along toposequences within watersheds scattered across the region. I sampled 54 black spruce sites within a 10,000 km^2 area around Fairbanks during the summer of 2000, then expanded the sampling during the summers of 2001 and 2002 to include an additional 92 sites along the climate transect ranging from the Alaskan/Canadian border to the foothills of the Brooks Range (Figure 2.1). Sites were chosen based on their proximity to roads or river systems because of the inaccessibility of other areas. A modification of the centralized replicate sampling procedure was employed, and I subjectively chose plot locations in areas of homogenous vegetation that were dominated by a black spruce overstory (Mueller-Dombois and Ellenberg 1974). Where possible, I selected sites along a toposequence (summit, shoulder, sideslope, toeslope, and valley bottom). Many additional sites were selected because they were previously established by the Forest Growth and Yield Program at the University of Alaska Fairbanks (UAF) Agricultural and Forestry Experiment Station.

I conducted a relevé at each sites, defined as a vegetation sample or stand that included a list of all plant species present, both vascular and nonvascular, and an estimate of percent cover of each species using the Braun-Blanquét cover-abundance scale (Braun-Blanquét 1965, Mueller-Dombois and Ellenberg 1974). All relevés were at least 2,500 m^2 in size, and most were greater than 6,400 m^2. I sampled each species encountered at each site to verify species identity. Dr. Mikhail Zhurbenko and Dr. Olga Afonina of the Komarov Botanical Institute, St. Petersburg, Russia verified lichen and bryophyte specimens, respectively. Dr. Leslie Viereck verified the *Salix* species, and all other vascular specimens were verified with UAF herbarium specimens. Voucher specimens were placed in the Bonanza Creek Long Term Ecological Research (LTER) herbarium located at the University of Alaska Fairbanks.

While at each site I dug a soil pit to a depth of 1 m or to frozen ground, whichever came first. I described soil texture by hand texturing the uppermost mineral horizon using the protocol of Schoeneberger et al. (2002), measured *in situ* pH of the uppermost mineral horizon using an Oaklon pH meter, the depths of the Oi, Oe, and Oa horizons, and the depth to bedrock or frozen soil. Sites were revisited in September or October of the same year to measure maximum thaw depth. Soil samples were collected from the uppermost mineral horizon, at approximately 10-15 cm, and percent soil moisture and bulk density were determined following the methods of Walker et al. (1994b). Mineral soils were sieved, dried at 50° C, and then sent to the UAF Palmer Research Station for determination of mineral pH, concentrations of NH_4, NO_3, P, K, C, N, total exchangeable cations, cation exchange capacity, texture (sand, silt, and clay), and loss on ignition.

At each site I measured or estimated the following: site moisture through a visual assessment of moisture at a site and soil moisture based on the amount of water that could be squeezed out of the soil in the field, and the appearance of gleyed or mottling soils above 15 cm (Komarkova 1983); a disturbance scalar including fire [presence of charcoal in the soils, fire scars, and standing burnt trees], herbivores, humans, and other; latitude and longitude using a Trimble Geoexplorer 3 GPS unit; physical characteristics of the site including slope, aspect, elevation, slope position, parent material, and geomorphology; microtopography; and a gross water flux category: minerotrophic, with noticeable running water through site, ombrotrophic, with noticeable standing water at site, or no water present.

I cored five to ten of the largest trees in each stand, as close to the base of the tree as possible, to estimate the age of the oldest trees and inferring the time since last fire. Rings were counted with a microscope and visually cross-dated (Sweetnam and Sutherland 1985). If the pith was missed during coring, the distance to pith was estimated by fitting a circle template to the innermost curved ring, or by subtracting core length from the radius at core height (A Lloyd, personal communication). The number of years to the pith was then estimated empirically from age-diameter relationships based on trees in which the pith was obtained. The number of years the tree took to grow to the cored height was estimated by a regression equation that was developed for black spruce growing on the Kenai Peninsula, Alaska, and relates seedling height to age (Devolder 1999). These ages were analyzed in ten-year age classes to account for errors in those estimates. Finally, fire scars and charred, burned trees were noted, and charcoal was collected when found.

I employed the Point Centered Quarter Method (PCQ) (Mueller-Dombois and Ellenberg 1974) at five randomly selected points in each site to quantify density (trees per hectare), basal area, and average height/dbh of trees in the stand. In addition, I measured tree height and tree diameter at breast height (DBH) of the four trees closest to each of the five points. To ensure the precision of my estimated density, I performed a power analysis using actual density figures from over 150 black spruce sites in interior Alaska (E.C. Packee, unpublished). Using this method, my estimates were quite comparable (±5%) to true densities taken at five of my sites (C. Rosner, personal communication).

Ordination

I used Nonmetric Multidimensional Scaling (NMDS) with the program PC-ORD 4.25 (Mather 1976, Kruskal and Wish 1978, McCune and Mefford 1999) to analyze and detect the main patterns in the relationships between species composition and various environmental variables. NMDS is an ordination technique well suited for data that are nonnormal, or occur along arbitrary or discontinuous scales, and is considered by some to be the most effective ordination method for ecological community data (McCune and Grace 2002). NMDS searches iteratively for the best positions of n entities on k dimensions (axes) that minimize the stress of the k-dimensional configuration. The calculations are based on an n x n distance matrix calculated from the original n x p-dimensional data matrix where n is each site and p is each species and the value is the abundance of each species within each site. "Stress" is the measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original data matrix and the reduced k-dimensional ordination space, in other words, the inverse measure of fit (McCune 1993). Ordinations were performed on the subset of floristic data collected in the Fairbanks Region (FB) and for all data obtained from Interior Alaska (IA).

I used the Sorensen distance measure with randomly starting configurations, using ten runs of real data and twenty runs of randomized data, the latter to provide the basis for a Monte Carlo test of significance at each dimension, or axis. Dimensionality (i.e., the number of axes) was assessed by comparing the final stress values among the best solutions, with one best solution for each dimensionality. PC-ORD selects the highest dimensionality that minimizes stress. There were two dimensions for the FB ordination and three dimensions in the IA ordination.

Environmental variables were correlated to the NMDS axes using Kendall rank correlations and related to the ordination with a biplot diagram that indicates both the direction and magnitude of the strongest environmental variables in the ordination space.

Species diversity

I examined plant diversity at three scales: *alpha diversity* or the diversity within a community, *beta diversity*, or the degree of differentiation among communities, and *gamma diversity*, or the overall landscape or regional diversity. The pool of species available ultimately limits alpha diversity, while the number of different "habitats" available limits beta diversity. I looked at species richness, the number of species, within individual sites (alpha diversity), within the communities I define (beta diversity), and for all my samples pooled across the landscape of my study region (gamma diversity). Previous work in interior Alaska suggested that both species composition and diversity change along topographic gradient of soil temperature and moisture (Dyrness 1982, Van Cleve et al. 1982, Yarie 1983). After I performed ordinations, it became clear that, at the landscape scale, mineral soil pH was also highly correlated with species composition;

I therefore analyzed species richness along gradients in soil pH (hereafter "acidity") and topography. I used multi-variate analysis of variance (MANOVA) (SAS version 8.1 PROCGLM) to analyze the relationship of species richness to topographic position and acidity. The independent variables in the analysis were the categorical variables of acidity, i.e. acidic ≤ 5.5 or nonacidic>5.5 as defined by Walker and Everett (1991) and topographic position (summit, shoulder, sideslope, toeslope, valley bottom, and lowland), with the dependent variables being total species richness, vascular species richness, moss species richness, and lichen species richness. I assessed significant differences between the categories post hoc using the Fisher's PLSD and Tukey tests.

Vegetation classification

Vegetation was classified using the Braun-Blanquét sorted-table method (Braun-Blanquét 1965) and the specific protocol of Daniels (1982) for recognizing diagnostic and constant species. Diagnostic species are defined as species with high constancy (occurrence) and abundance within a given community, and low constancy and abundance in all other community types, while constant species are those that occur throughout all the community types. The sorted relevés are summarized in a synoptic table (Appendix. 2.1 a, b, c, d). Columns indicate relevé size, elevation, cover, and species richness for each relevé. The final columns for each subtype indicate the averages for each of the header rows and the frequency of each species, expressed as a percentage of the number of relevés in that subtype. The rows list all of the species found in the community, divided into diagnostic taxa for each subtype, non-diagnostic taxa that occur predominantly in each subtype, species restricted to the subtype, constant taxa, non-diagnostic species occurring throughout, and single occurrence species. If a species was non-diagnostic, and the frequency difference between subtypes was ten percent or more, the species was listed as occurring predominantly in one subtype. The species were sorted within each grouping by order of abundance within that subtype, with the exception of the constant taxa, which are sorted by total abundance within the community.

Within each relevé, the presence of a species is shown as the Braun-Blanquét cover estimate scale indicator, with r = rare, + = common but less than 1%, 1a = 1-2%, 1b = 3-5%, 2a = 6-10%, 2b = 11-25%, 3 = 25-50%, 4 = 51-75%, and 5 = 76-100%. Subtypes are surrounded by a black box, with a dashed line indicating notable absences of "wet" species in the drier relevés in that community. Communities are named first by the most abundant species, *Picea mariana* in all cases, followed by one or two of the diagnostic species most indicative of that community. Subtypes are named for the most abundant or important diagnostic species.

Results

Ordinations

Local patterns: Two major gradients capture 61% of the variance in species composition in the Fairbanks Region (FB). The first two dimensions (axes) represent 24% and 37% of the variance in species composition, respectively. The NMDS technique does not partition the amount of variance explained among axes; rather a post hoc test shows how well each axis represents the amount of variance in the original data (species composition). Therefore, the strongest environmental gradient (as defined by the Kendall correlation between each axis and the environmental variables) detected was related to Axis 1, but the strongest community gradient was on Axis 2, meaning that the species turnover rate was higher along Axis 2. It is important to remember that the environmental variables that I measured are only part of what structures the community (B. McCune, personal communication).

The strongest environmental gradient corresponds to a paludification gradient and the second major gradient corresponds to a topographic gradient (Figure 2.2). Higher dimensions add little explanatory power. Axis 1, a paludification gradient, is positively correlated with attributes of poorly drained organic lowlands, i.e. percent carbon, percent nitrogen, cation exchange capacity, loss on ignition, percent moisture, and depth of the Oi horizon (Table 2.1). The first axis also correlates negatively with attributes of better drained sites, including pH, percent tree cover, percent dead tree, average tree height of the stand, and tree density (Figure 2.2, Table 2.1). The second axis of the ordination separates uplands (summits, shoulders and sideslopes) from lowlands (toeslopes, valley bottoms, and lowlands) (Figure 2.2). This axis correlates positively with attributes of uplands, including slope and elevation, and negatively with attributes typical of lowland bogs, including pH, Ca, Mg, Na, and percent graminoids (Table 2.1).

Regional patterns: The axes that captured variance in species composition at the scale of interior Alaska (IA) differed from those in the Fairbanks region (Figure 2.3). Three axes capture 81% of the variance in species composition for all sites across interior Alaska, 20%, 24%, and 35% respectively. The strongest environmental gradient corresponds to an acidity gradient along Axis 1, Axis 2 corresponds to a topography/soil drainage gradient, and Axis 3 represents a productivity gradient. The strength of Axis 3 results in the strong pH gradient being represented on a diagonal through the ordination space. I present only Axis 1 versus Axis 2 (Figure 2.3).

Axis 1, a complex soil acidity gradient, correlates negatively with laboratory pH, *in situ* pH, Ca, Mg, Na, deciduous shrub cover, evergreen shrub cover, and seedling cover (Table 2.2). It is positively correlated with slope, which is also related to mineral soil pH. The second axis corresponds to a site topographic and drainage gradient, which is most likely a combination of the two important axes in the FB ordination. This axis correlates negatively with variables associated poorly-drained sites such as Ca, Mg, laboratory pH, Na, moss cover, water content, and stand density and positively with elevation and percent lichens. Axis 3 likely represents a productivity gradient, possibly associated with time since last disturbance, and is correlated with Oa thickness and stand structural characteristics, such as average dbh of stand, average height of stand, and stand density. The third axis is negatively correlated with attributes related to soil organic matter accumulation, such as percent K, C, and N, Na, percent clay, and seedlings (Table 2.2).

Regional patterns of species richness and diversity

I recorded a total of 275 species in the course of this study: 146 vascular, 67 bryophytes, and 62 lichens (Table 2.3). I encountered six tree species which is the entire tree flora of the region, 38 shrubs, and 102 forbs. Of the three black spruce community types, the treeline type had the highest alpha diversity and the lowest beta and gamma diversity, indicating that diversity occurred at a finer scale in the treeline community type. The acidic black spruce community type had the lowest alpha diversity, and the nonacidic black spruce community had the highest gamma diversity (Table 2.3).

Results from the MANOVA show a significant effect of pH class (F = 6.901, P = 0.0002 for both categories) and of topographic position (F = 3.53, P = < 0. 001) on total species richness, but no significant interaction between pH and topographic position. The univariate tests also show no significant interaction between pH and topographic position for any of the dependent variables (total species richness, vascular species richness, moss species richness, and lichen species richness). Univariate tests reveal that the uplands had significantly greater lichen richness, and lowlands had significantly greater moss richness (F = 4.99, P = 0. 0003 and F = 4.90, P = 0.0004 respectively) (Figure 2.4c, d). Univariate tests also show that acidic sites had significantly more moss species and nonacidic sites significantly more vascular species (F = 10.31, P = 0.0017 and F = 7.594, P = 0.0067) (Figure 2.5b, c).

Regional vegetation classification

I describe three black spruce community types and five subtypes that incorporate the range of vegetation dominated by black spruce in interior Alaska (Table 2.4, Appendix 2.1). Diagnostic species are listed for each community type, as well as diagnostic species for each subtype within the communities. It is important to note that diagnostic species for each subtype are only differential among the subtypes within that community and therefore may overlap with other subtypes in a different community type. Communities and subtypes are therefore defined by a group of species that occur together, not just by the presence or absence of particular species. In the descriptions below numbers (1,2,3) indicate communities, and letters (a, b) indicate subtypes.

1. Acidic Black Spruce/Lichen forest (*Picea mariana*/*Cetraria islandica*):

The acidic black spruce/lichen forest is dominated by black spruce, fruticose lichens, and many species of mosses. This community type occurs in both uplands and lowlands of interior Alaska and in areas of low mineral soil pH (< 5.5) and is usually associated with steep slopes or no slope; and is rarely found in sites of moderate slopes. Diagnostic species include (in order of increasing constancy – how restricted they are to a particular community); vasculars (v), lichens (l), and mosses (m)): *Cetraria islandica* (l), *Polytrichum commune* (m), *Lycopodium annotinum* (v), *Spiraea beauverdiana* (v), *Cladonia sulphurina* (l), and *Cladonia deformis* (l). Within this community type, there is one subtype that is restricted to wet acidic conditions and has clearly delineated diagnostic species. Dry sites within this community type exist, but has no recognizable set of diagnostic species and lacked the diagnostic wet species.

a) Wet Acidic Black Spruce muskeg (*Picea mariana*/*Ledum decumbens*/*Sphagnum girgensohnii*): This is an open black spruce subtype that occurs on low-nutrient soils and often occurs in lowland areas of shallow permafrost. Black spruce trees are often stunted, and the subtype tends to be dominated by shrubs (*Ledum decumbens*, *Betula nana*, *Oxycoccus microcarpus*, and *Rubus chamaemorus*), sedges (*Eriophorum vaginatum* and *Carex bigelowii*), and acidic *Sphagna* (*Sphagnum girgensohnii*, *Sphagnum rubellum*, and *Sphagnum magellanicum*). Other diagnostic species of this subtype are *Aulacomnium* *palustre* (m), *Aulacomnium turgidum* (m) and *Polygonum alaskanum* (v).

2. Nonacidic Black spruce/Rose/Horsetail forest (*Picea mariana/Rosa acicularis/Equisetum sps*):

This community is dominated more by vascular species (especially 3 different *Equisetum* species) than the acidic black spruce forest, with the occasional presence of *Picea glauca* (white spruce). This community occurs in both uplands and lowlands although more often in the lowlands, with a tendency toward well-drained flatlands or slight slopes. Diagnostic species in order of increasing constancy include: *Rosa acicularis* (v), *Equisetum scirpoides* (v), *Arctostaphylos rubra* (v), *Mertensia paniculata* (v), *Pyrola secunda* (v), *Tomenthypnum nitens (m), Picea glauca* (v), *Sausserea angustifolia* (v), *Equisetum arvense* (v), and *Sphagnum warnstorfii* (m). Within this community type, there are two subtypes defined by the moisture status of the site.

a) Wet Nonacidic Black Spruce/Larch fen (*Picea mariana/Larix laricina/Chamaedaphne calyculata*): This subtype is restricted to the lowlands and is usually co-dominated by larch. Due to recent larch sawfly outbreaks in interior Alaska (Holsten et al. 2001), many of these larch are now dead. This subtype occurs in areas with minerotrophic conditions, which indicate a fen rather than a bog. Shallow permafrost can also be present in this subtype, but permafrost conditions are more variable than in the wet acidic subtype. Trees in this subtype can have the same stunted appearance as in the wet acidic black spruce subtype, as well as some of the same diagnostic species, such as *Betula nana* (v), *Rubus chamaemorus* (v), and *Eriophorum vaginatum* (v). Therefore these particular species should not be used as sole indicators of community type. They are more an indication of site moisture status than of acidity. It is the combination of nonacidic diagnostic species with the wet diagnostic species that is the indicator of this subtype.

b) Dry Nonacidic Black Spruce forest (*Picea mariana/Cladina stellaris-Peltigera malacea*): This subtype occurs in xeric conditions, mostly in the uplands. Like the acidic black spruce forest, lichens dominate it, yet the lichen species are different. In addition to the nonacidic diagnostic species, this subtype can be recognized by the presence of *Equisetum pratense* (v), *Cladina stellaris* (l), *Peltigera malacea* (l), and *Cornus canadensis* (v).

3. Treeline Black spruce woodland (*Picea mariana/Tolfielda pusilla/Cetraria laevigata*):

Although white spruce is usually associated with treeline in interior Alaska, black spruce does occur at altitudinal and occasionally latitudinal treeline, sometimes co-dominating with white spruce or as the only dominant tree. Therefore, I describe a third community type with two subtypes. The treeline black spruce woodland tends to occur at higher elevations, on steeper slopes, and in much more xeric conditions than the two previous black spruce communities. Diagnostic species that are typical of treeline areas include: *Ledum decumbens* (v), *Tolfieldia pusilla* (v), *Cetraria islandica ssp. crispiformis* (l), *Pedicularis labradorica* (v), *Cladonia uncialis* (l), *Dicranum flexicaule* (m), *Stereocaulon tomentosum* (l), and *Polygonum bistorta* (v). Within this community type, there are two subtypes that are indicative of latitudinal treeline versus altitudinal treeline.

a) Elevational Acidic Treeline woodland (*Picea mariana/Loiseleuria procumbens/ Cetraria nivalis*): This subtype occurs at high elevation (500 m and above) and tends to be quite acidic. It therefore has many of the diagnostic species of the acidic black spruce forest such as *Polytrichum commune* (m), *Lycopodium annotium* (v), and *Spiraea beauverdiana* (v), and there are many diagnostic species fairly distinct to this subtype including *Cetraria nivalis* (l), *Anemone narcissiflora* (v), and *Salix brachycarpa* (v) and many *Cladonia spp.* including *Cladonia deformis* (l), *Cladina rangiferina* (l), and *Cladonia gracilis* (l).

b) Latitudinal nonacidic treeline (*Picea mariana/Salix reticulata/Dryas octopetala*): This subtype occurs at lower elevations (< 350 m) than the elevational treeline subtype and is typical of all northern treeline sites. It has a more distinct species group than any other black spruce type. It has many species in common with moist nonacidic tundra (Walker and Everett 1991). Diagnostic species include: *Tomenthypnum nitens* (m), *Potentilla fruticosa* (v), *Saussurea angustifolia* (v), *Andromeda polifolia* (v), *Equisetum arvense* (v), and *Equisetum scirpoides* (v), which occur in other nonacidic black spruce community types, as well as *Dryas octopetala* (v), *Salix reticulata* (v), *Carex coccina* (v), *Parnassia palustris* (v), *Plantanthera obtusata* (v), *Ranunculus lapponicus* (v), and *Spiranthes romanzoffiana* (v) which are mostly restricted to northern treeline sites.

Regional stand structural characteristics

The three black spruce community types that I defined based on floristics differ substantially in stand structure and environmental characteristics (Table 2.5). Average tree density of the treeline black spruce sites is only about 25% of the other two black spruce types, which was associated with shorter, younger trees and a thinner organic mat. The nonacidic black spruce community differs most strikingly from the acidic black spruce community in having higher basal area (due to both greater density and dbh), taller trees, and deeper active layer (Table 2.5). One of the most interesting results is that some of the structural and physical characteristics (e.g. density, basal area, maximum active layer, and maximum microtopography) are quite variable across the full range of sites and exhibit a large range of variability within each vegetation type. Thus, prediction of community type based on these variables alone is, thus, fairly difficult.

Discussion

Scale-dependent patterns

This study revealed the importance of scale, both spatial and temporal, in determining the patterns and controls over community composition in interior Alaska. Black spruce communities vary not only on the spatial scale represented, i.e., local versus regional, but also according to their age. For example, weathering of parent material, which happens on the time scale of landscape development (1000+y), and time since fire disturbance, which happens on shorter successional timescale (~100 y), both contribute to the patterns observed in mature black spruce forests in interior Alaska. I therefore discuss two spatial scales (local versus regional), and within those spatial scales I examine temporal patterns (landscape age versus succession).

Local patterns: Within the Fairbanks Region (FB) topography created the environmental gradient that explained the most variation in composition and structure of black spruce stands. These topographic gradients in species composition correlate with gradients in soil moisture, soil temperature, and soil pH (Figure 2.2 and Table 2.1). All of the acidic black spruce sites occurred in the uplands regardless of parent material (loess versus schist). This suggests that within the Fairbanks uplands topography of a site is more important than the nature of parent material as an independent control over floristic composition. However, all of the alluvium sites around Fairbanks were nonacidic black spruce communities, suggesting that soil pH as related to soil drainage, soil moisture, or some other consequence of this topographic position could be controlling species composition in the floodplains of the Fairbanks region.

1) Landscape development patterns- Within the uplands surrounding Fairbanks, topography affects soil-vegetation interactions through several mechanisms. Slope affects redistribution of moisture, which in turn affects soil properties, causing valley-bottom sites to become wetter over time as a result of paludification, i.e., the formation of peatlands (Birkeland 1999). Paludification leads to restricted drainage, acidification, and the introduction of *Sphagnum* mosses, which in turn increase the acidity of the soil and contribute to cooler soil temperatures and permafrost development (Jorgenson 1984). The presence of permafrost in the boreal forest can accelerate the chemically driven paludification process. In paludified landscapes, variation in hydrology and permafrost can either lead to ombrotrophic communities, where most of the water derives from precipitation and is highly acidic, or to minerotrophic communities in areas of groundwater upwelling where soils are more influenced by groundwater. This hydrologic contrast is one of the driving factors that gives rise to the acidic and nonacidic black spruce community types that I described in the uplands of the Fairbanks region, and is especially important in the formation of the “wet acidic black spruce muskeg” (Table

2.4). Topographic control over permafrost is, therefore, the most important driver in the structure and floristic composition of black spruce systems in the Fairbanks region.

2) Successional patterns- Previous work in both uplands and lowlands around Fairbanks has suggested that succession after disturbance either fire or flooding, is a major driver of species compositional change (e.g. Viereck 1973, Van Cleve et al. 1991, Mann et al. 1995). The lack of significance of stand age influencing species composition in my analysis was therefore surprising. There are at least two potential explanations: either successional trajectories after fire are highly variable, leading to differing vegetation communities of the same age, or the floristic composition of communities is determined within the first decades after fire. Johnstone et al. (2004) showed that successional trajectories of dominant trees in central Alaska and the Yukon are determined within 10-20 years after a fire. My work suggests that the trajectories of not only the dominant tree species, but also potentially entire community assemblages, could be determined relatively soon after fire.

Given that community composition of black spruce forests in the Fairbanks region appears to be relatively insensitive to stand age (Figure 2.2, Table 2.2), what are the mechanisms that give rise to the consistent patterns of community composition within topography and paludification gradients? I suggest that two complementary forces are at work at the successional time-scale: (1) After low-severity fires, vascular plants and mosses that were present before the fire rapidly sprout from surviving below-ground stems and from unburned patches (Zasada et al. 1992), so legacies of late successional vegetation patterns present before the fire govern the community composition in early succession. (2) After high severity fires, initial seedling replacements and community composition are probably sensitive to topographic variations in soil moisture and the chemistry and pH of mineral soils, and this initial species composition then persists through succession. In addition, an ultimate mechanism that might control fire severity is topography: cold wet sites occurring in the lowlands of the Fairbanks region are less likely to have severe burns and thus more likely to have legacies of late successional species.

Regional patterns: When the spatial scale of my study was expanded to include a larger extent of interior Alaska, the roles of topography, soil moisture, and soil temperature became secondary to the overwhelming influence of mineral soil pH (Figure 2.2, Table 2.3). This result is interesting for several reasons. First, it is now clear that earlier descriptions of Alaskan black spruce forest types (e.g., Van Cleve et al. 1983), which were concentrated in the Fairbanks region, did not incorporate the full range of regional variability in species composition and potentially ecosystem processes. Overall, the black spruce sites I sampled in the Fairbanks region were more acidic than areas to both the north and the south. In addition, I found none of the treeline community type in the Fairbanks region. This may be due to a combination of the bedrock of the Fairbanks region and human influence. The bedrock in much of the Fairbanks uplands is metamorphic rock of the Yukon-Tanana crystalline complex. The Yukon-Tanana schist extends about 50 km north and west of Fairbanks, 100 km south of Fairbanks, and almost 300 km to the east (Connor and O'Haire 1988). The Yukon-Tanana schist is the ultimate source of the gold in the Fairbanks mining district; mining brought extensive fires and logging to this area (Roesales 1997). Mining and human-caused anthropogenic fires, coupled with the Precambrian schist bedrock, could, therefore, contribute to the small number of nonacidic sites and subsequent decrease in species diversity of these uplands. As mentioned earlier, most of the nonacidic black spruce sites in the Fairbanks region occur on the Tanana River alluvium, which was scoured by glaciers from high pH bedrock in the Alaska Range. This distinct difference in community distribution between the uplands and floodplains does not represent the patterns of black spruce community types found across all interior Alaska (Figure 2.3). My study extent was limited by accessibility, and it is highly probable that including an even larger area of Alaska would result in additional communities and subtypes.

1) Landscape development patterns- Although the relationship between pH and vegetation communities has been explored in other systems to the north (e.g. Walker and Everett 1991) and south (e.g. Glaser et al. 1990), to my knowledge this is the first description of a prominent pH effect in the boreal forests of Alaska. Although community and ecosystem ecologists have acknowledged the influence of pH on vegetation composition in interior Alaska, the patterns of pH observed there were thought to be a product of vegetation that results from patterns associated with topography, paludification, and stand age (Van Cleve et al. 1983). At the regional scale, however, pH appeared to exert a strong primary effect on floristic composition that was independent of topographic controls and unrelated to stand age (Figure 2.3, Table 2.2). Thus, this study, sheds new light on the environmental gradients controlling floristic variability at the regional scale in interior Alaska.

Total species richness showed no significant trends along topographic or pH gradients (Figures 2.4 and 2.5). However, there was a significant relationship between topography and nonvascular species richness as well as a significant relationship between acidity and vascular and moss diversity. Lichen richness is greater in the uplands, whereas moss richness is greater in the lowlands. Vascular richness is greater in nonacidic sites, and moss richness is greater in acidic sites. Nonvascular species composition and diversity are often lumped into one or two functional groups, yet it is clear that the diversity and composition of both lichens and mosses are integral in determining black spruce community patterns and consequently ecosystem processes. For example, some *Sphagnum* mosses have a strong acidifying effect and are less decomposable than other mosses, leading to more rapid accumulation of soil organic matter and a lower pH (Kuhry and Nicholson 1993). Foliose and some fruticose lichens such as *Stereocaulon* fix nitrogen and are important contributors to the nitrogen economy of black spruce forests (Billington and Alexander 1983), whereas non-nitrogen-fixing lichens are important winter forage for caribou (Klein 1982).

2) Successional patterns- Biologically, the influence of mineral soil pH in permafrost-dominated terrain seems counter intuitive, because roots are concentrated in the organic horizon rather than in mineral soil. However, the importance of fire to the black spruce ecosystem is well documented (Rowe and Scotter 1973, Viereck 1973, Dyrness and Norum 1983, Viereck 1983a, Bergeron et al. 1998, Johnson et al. 1998, Brown and Smith 2000), and some species are rooted in mineral soil (Kummerow et al. 1983). Immediately after a severe fire, some species colonize directly on mineral soil,

utilizing nutrients mineralized by the fire and those provided by the mineral soil. If successional trajectories of floristic composition are determined in the first 10-30 years after fire (Johnstone et al. 2004), then variations in mineral soil pH could influence community composition long after mineral soils are directly accessed by most plant species. In addition, because pH results from a longer history than the age of the current stand, mineral soil pH may influence long-term vegetation patterns. It is still unclear why mineral soil pH is so variable throughout interior Alaska. However, it seems likely that site drainage, deposition of loess, organics derived from dead roots or the surface organic mat, fire history of the site, and geologic and glacial history of the site could all contribute to the variability in soil pH and consequently plant community patterns. Anecdotally, my ordinations included two sites that were younger than 50 years. One site burned in 1963, and the other site burned within the last 10 years. Neither site contributed strongly to the overall regional variability in species composition, and, other than lacking mature black spruce, both were similar in species composition to other black spruce sites visited.

Classification implications

This work provides the first extensive phytosociological analysis of Alaskan black spruce forests and therefore constitutes the first step in including Alaska into a circumboreal forest classification. The floristic differences between the black spruce communities that I describe for Alaska and those described previously in Canada (e.g. La Roi 1967, La Roi and Stringer 1975, Orloci and Stanek 1979, Foster 1984, La Roi 1991, Timoney et al. 1993, Peinado et al. 1998, Rivas-Martinez et al. 1999) reflect substantial differences in environment, fire regime, and biogeographic history. The continental climate of interior Alaska contrasts with the more maritime climate of Eastern Canada. Much of interior Alaska has never been glaciated, whereas most of Canada was (Larsen 1980). In addition, Alaskan black spruce ecosystems are thought to be relatively young, with black spruce entering the floral record approximately 5,000 years ago (Keenan and Cwynar 1992, Lynch et al. 2002). Finally, differences in disturbance regimes and substrate might contribute to the differences in species composition and consequently community classifications.

Viereck et al. (1992) provided the most widely used classification of black spruce in interior Alaska. The Alaskan Vegetation Classification describes seven black spruce community types with four broad classes: closed needleleaf forest, open needleleaf forest, needleleaf woodland canopy, and dwarf tree scrub woodland, all based on stand structure characteristics, such as tree size and density. In my study I found no significant correlations between stand density and species composition at the spatial scale of interior Alaska (Table 2.2 and Figure 2.3), indicating that floristic and physiognomic approaches lead to quite different community classifications. The floristic approach is particularly useful in predicting those ecosystem processes that are strongly affected by the understory species composition. These processes include thermal insulation of permafrost, nutrient cycling, fire regime, herbivory, and pollination (Walker et al. 1994b, Walker 2000, Chapin and Danell 2001). The physiognomic approach may be a better predictor of processes such as productivity and energy exchange that are dominated by the tree canopy (Chapin et al. 1996).

Conclusions

This comprehensive analysis of the community composition and structure of Alaskan boreal black spruce forests demonstrates not only a surprising amount of floristic diversity, particularly of nonvascular species, but also large variations in stand structure and complexity. The patterns of floristic composition that I observed suggest a spatially complex mosaic (Bergeron et al. 1998) that develops in response to a hierarchy of environmental controls, including regional variation in pH, local variation in paludification, and fine-scale topographic variation in drainage. In addition, community composition in the stands that I studied, mostly >50 yr post-fire, was more sensitive to stage of landscape development, i.e., degree of paludification, than to successional age. Other studies in younger stands (<30 yr post-fire) have shown substantial change in species composition in the initial years after fire (Viereck 1973, Van Cleve et al. 1991), suggesting a hierarchy of temporal as well as spatial controls.

Perhaps the most pressing questions left unresolved are in regard to soil mineral pH, which was the strongest environmental gradient at the regional scale. What are the controls over mineral soil pH in interior Alaska? Is soil mineral pH specifically determining community composition, or is it a covariate of another driving variable? It is clear, however, that further work is required to disentangle effects of fire and glacial history, soil drainage, and other factors on the regional variation in black spruce community composition.

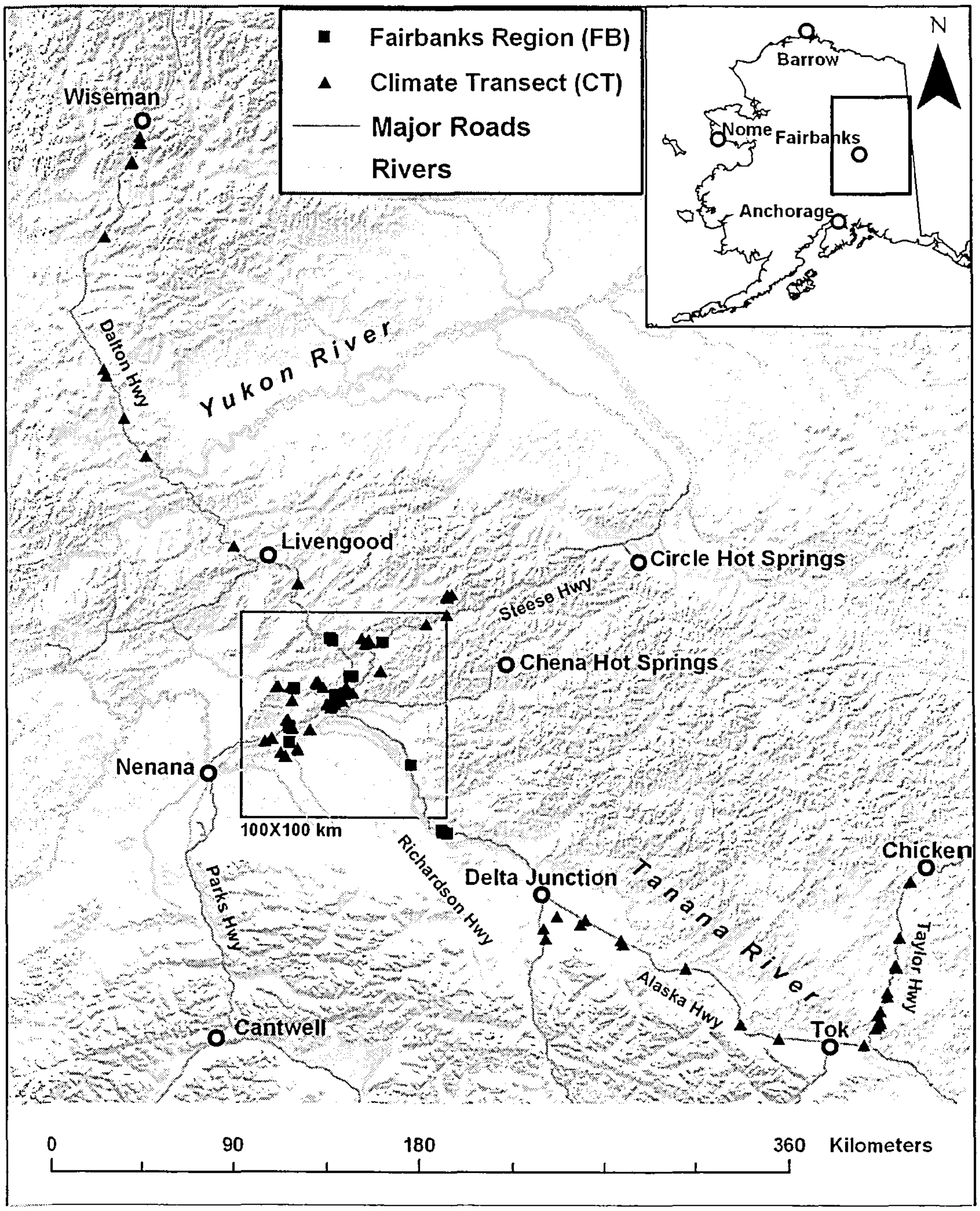

Figure 2.1. Location and extent of the study area within Alaska (inset) showing the topography of the region, sites within the Fairbanks Region (100 x 100 km grid), and along the Climate Transect.

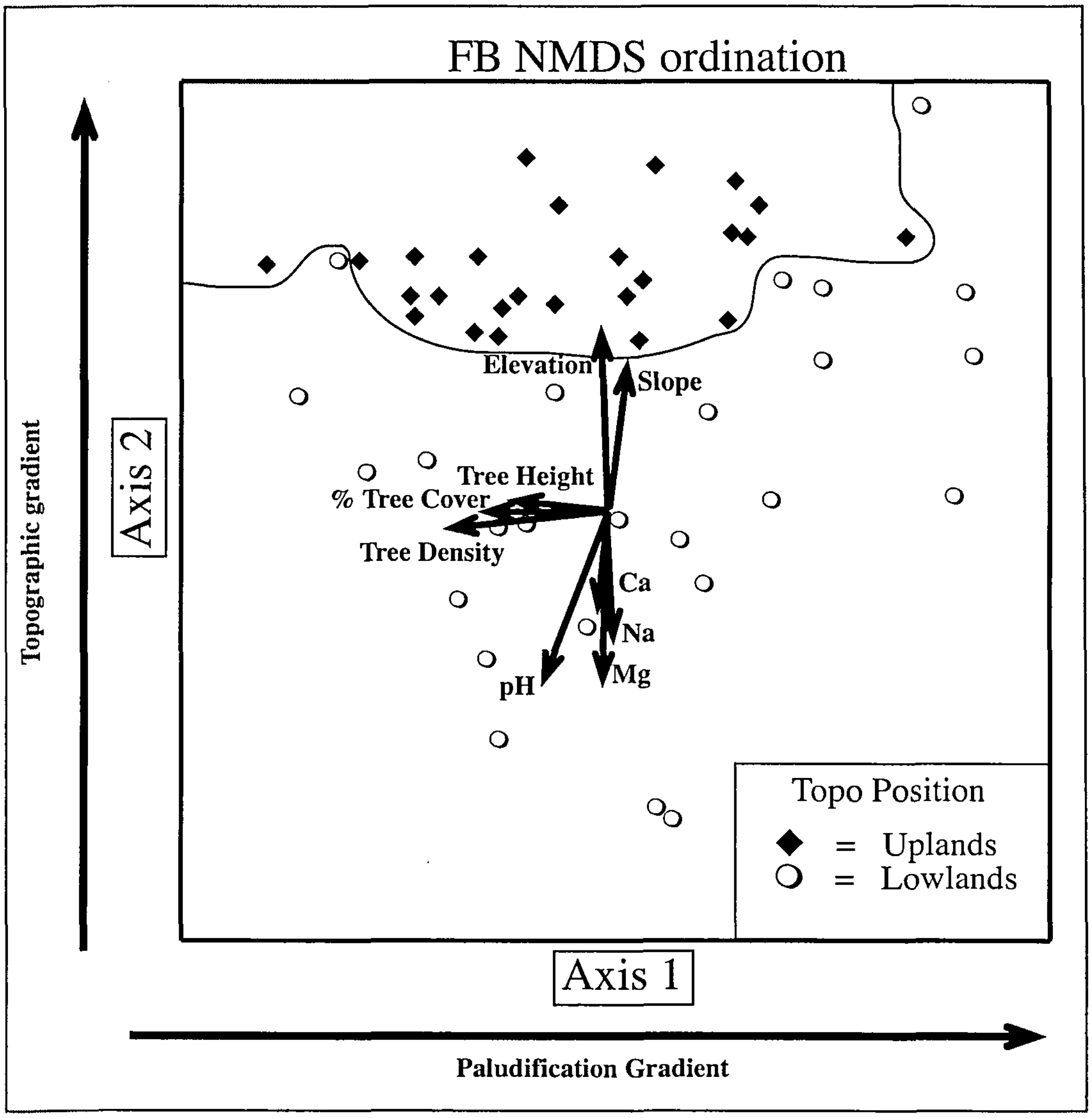

Figure 2.2. The FB ordination grouped by topographic position, where summits, shoulders, and sideslopes indicate "uplands" and toeslopes, valley bottoms, and lowlands indicate "lowlands". An isoline was drawn to better emphasize the groupings. A biplot diagram shows vectors indicating the most correlated environmental variables, where length and direction represent magnitude and direction of correlation, respectively.

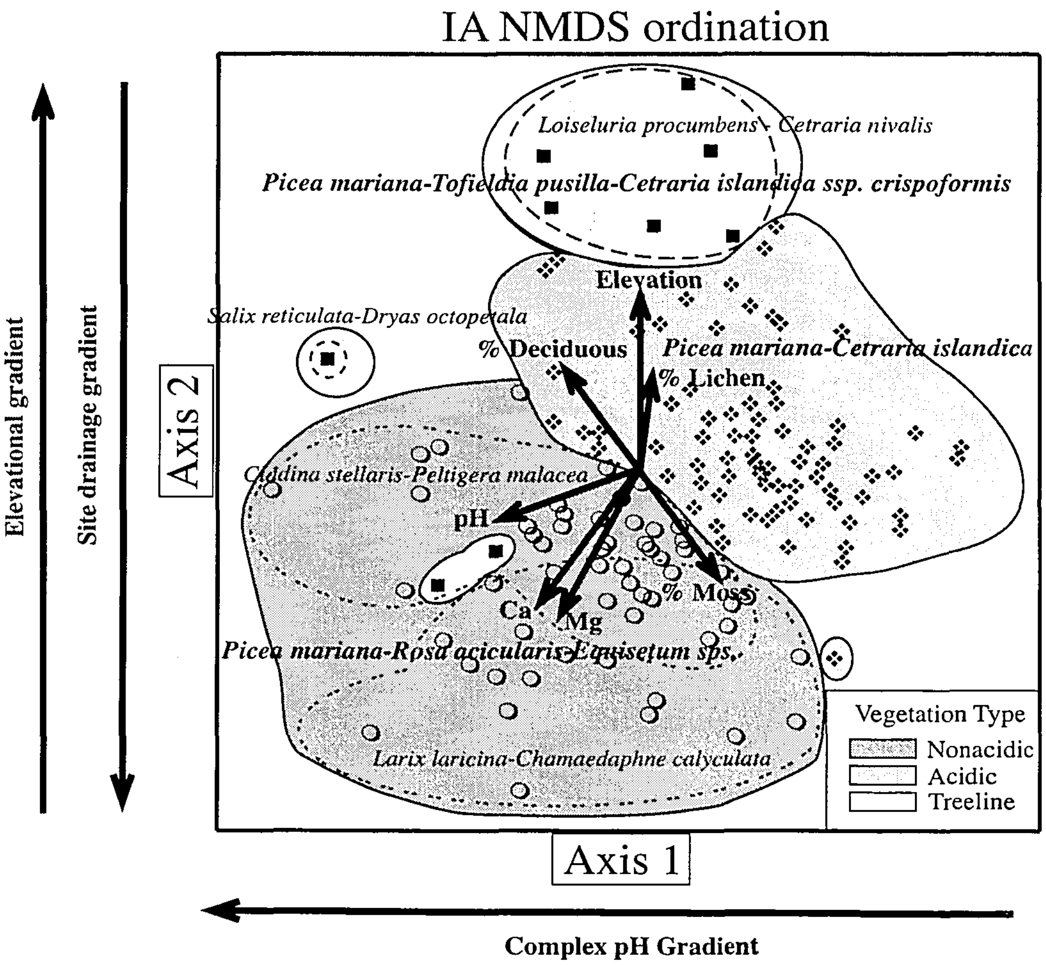

Figure 2.3. The IA ordination grouped by vegetation type as defined by the classification. Community types are named on the ordination, and dashed lines within each community type represent subtypes. However, there is much overlap between the subtypes in each community, so subtypes are not named. A biplot diagram indicates the strongest correlations.

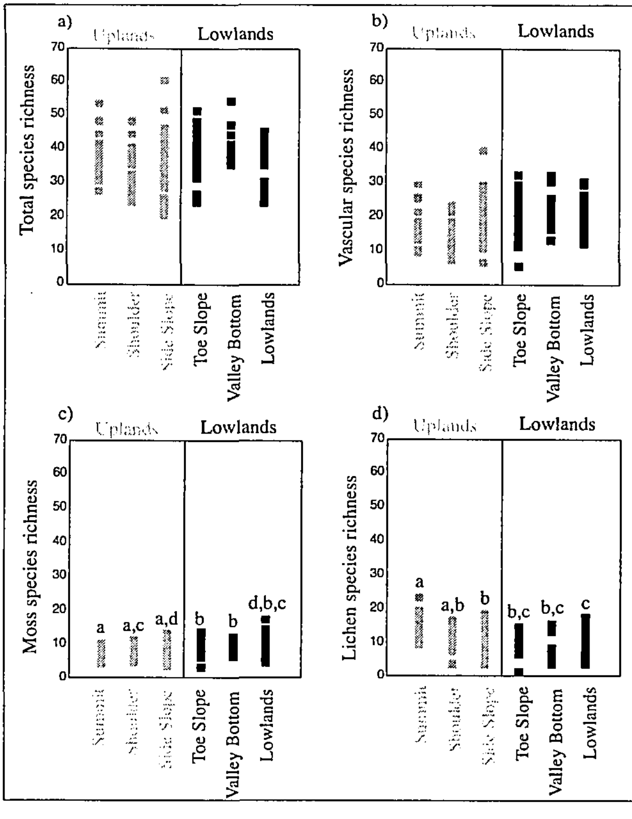

Figure 2.4. Species richness across the entire study region, separated by topographic position where letters (a, b, c, d) indicate ANOVA groupings. a) Total species richness, b) vascular species richness, c) moss species richness, and d) lichen species richness.

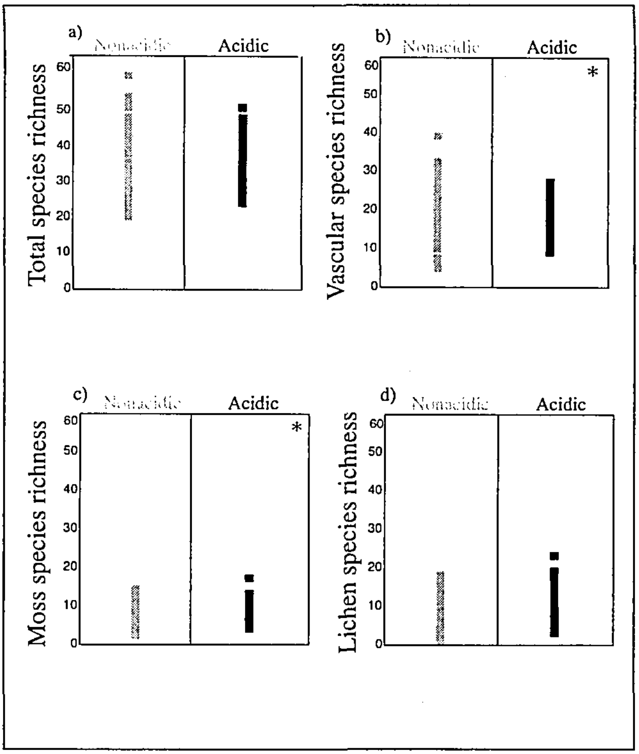

Figure 2.5. Species richness across the entire study region, separated by acidity where * indicates significance. a) Total species richness, b) vascular species richness, c) moss species richness, d) lichen species richness.

Table 2.1. The Kendall correlations of environmental variables and site characteristics and NMDS Axis 1 and Axis 2 for the Fairbanks Region (FB) ordination. Significant correlations are bold. Variables with no signficance ($P > 0.05$) with either axis are not presented.

Environmental Variable	**Axis 1 Paludification gradient**	**Axis 2 Topographic gradient**
% slope	0.125	**0.478**
Elevation	-0.062	**0.373**
pH of mineral	**-0.300**	**-0.529**
%C	**0.323**	0.044
%N	**0.414**	0.083
CEC	**0.287**	-0.060
Ca	-0.048	**-0.336**
Mg	-0.104	**-0.420**
Na	-0.076	**-0.279**
LOI	**0.286**	-0.058
% moisture	**0.272**	-0.001
in situ pH	0.038	**-0.301**
Oi (cm)	**0.283**	0.129
%tree	**-0.470**	-0.054
%deciduous shrubs	**0.287**	-0.205
%gramminoids	0.005	**-0.298**
%dead trees	**-0.342**	-0.149
%water	0.108	**-0.413**
ave hgt of stand	**-0.315**	0.011
density of stand	**-0.299**	-0.029

Table 2.2. The Kendall correlations of environmental variables and site characteristics and NMDS Axis 1, Axis 2, and Axis 3 for the Interior of Alaska (IA) ordination. Significant correlations are bold. Variables with no significance ($P > 0.05$) with any axis are not presented.

Environmental Variable	Axis 1 pH gradient	Axis 2 Drainage gradient	Axis 3 Productivity gradient
% slope	**0.273**	0.233	-0.045
Elevation	0.017	**0.491**	-0.096
pH of mineral	**-0.477**	**-0.323**	-0.202
%P	0.031	-0.098	0.22
%K	-0.057	-0.107	**-0.367**
%C	0.168	-0.084	**-0.424**
%N	0.116	-0.039	**-0.25**
Ca	**-0.371**	**-0.446**	0.036
Mg	**-0.333**	**-0.427**	-0.058
Na	**-0.258**	**-0.285**	**-0.305**
%clay	-0.079	0.151	**-0.298**
in situ pH	**-0.413**	-0.088	-0.069
Oa (cm)	-0.053	-0.166	**0.488**
%deciduous shrubs	**-0.302**	0.213	-0.096
%evergreen shrubs	**-0.347**	-0.067	-0.246
%seedlings	-0.219	-0.153	**-0.259**
%moss	0.13	**-0.328**	-0.129
%lichens	-0.056	**0.343**	**0.32**
%water	-0.001	**-0.252**	-0.233
ave dbh of stand	-0.047	0.078	**0.268**
ave height of stand	0.029	-0.05	**0.406**
density of stand	-0.011	**-0.254**	**0.277**

Table 2.3. The diversity (alpha, beta, gamma), richness, and number of sites (N) within each community and subtype and across the entire study region. Although there are 72 Acidic sites, 28 did not fall into a recognizable subtype.

	Diversity Measure			
	N	**alpha**	**beta**	**gamma**
Treeline	9	47	3	161
Acidic	6	46	3	115
Nonacidic	3	49	2	93
Nonacidic	61	41	5	220
Wet	23	42	4	177
Dry	38	38	5	184
Acidic	72	38	5	191
Wet	44	40	4	162

Total vascular	146
trees	6
shrubs	38
forbs	102
Total moss	67
Total lichens	62
Total species	275

Table 2.4. Black Spruce community names and habitat characteristics in interior Alaska, all of which fall within the Braun-Blanquét class Linnaeo americanae-Piceetea marianae. Community subtypes are also named.

Class (underline), community **(bold)**, subtype	Habitat characteristics
Linnaeo americanae-Piceetea marianae	
Picea mariana/Cetraria islandica	acidic (pH<5.5, average pH 5), tendency towards either steep or flat slope, average elevation 493m, mostly side slopes.
Ledum decumbens/Sphagnum girginsohhnii	acidic (pH<5.5, average pH 4.7), mesic
Picea mariana/Rosa acicularis/Equisetum sps.	nonacidic (pH>5.5, average pH 6.1), tendency towards well-drained flatlands to slight slope, average elevation 290m, mostly
Larix laricina/Chamadaphne calyculata	slightly nonacidic , mesic site conditions
Cladina stellaris-Peltigera malacea	slightly nonacidic, xeric site conditions
Picea mariana/Tofieldia pusilla/Cetraria laevigata	Treeline, mostly uplands and tendency for steeper slopes, more xeric than above.
Loiseluria procumbens/Cetraria nivalis	Elevational Treeline (500m and above), acidic (pH<5.5, average
Salix reticulata/Dryas octopetala	Latitudinal Treeline (between 329m and 350m), nonacidic pH (average pH 7.6).

Table 2.5. Stand structural characteristics for each black spruce community type. Mean values are ± one standard error. Range (maximum and minimum) over all three community types are also presented.

	Non acidic vegetation type	Acidic vegetation type	Treeline vegetation type	Overall minimum	Overall maximum
Tree characteristics					
Density of stand (trees/ha)	5133.74 ± 516.07	4153.24 ± 472.15	1158.71 ± 266.40	88.66	23668.64
Stand age	142 ± 9	150 ± 6	88 ± 15	~10	408
Height of trees (m)	4.8 ± 0.03	4.12 ± 0.15	3.03 ± 0.26	1.81	16
Basal area of stand (m^2/ha)	13.38 ± 1.19	10.11 ± 1.08	3.77 ± 1.16	0.14	42.5
Dbh of trees (cm)	5.51 ± 0.03	5.03 ± 0.19	5.13 ± 0.66	1.53	18.27
Ground characteristics					
Live moss thickness (cm)	4.4 ± 0.3	4.75±0.29	4.2 ± 1.0	0.5	13
Oi depth (cm)	5.2 ± 0.4	5.73±0.44	3.5 ± 0.8	0	18
Oe depth (cm)	7.4 ± 0.5	6.6 ± 0.4	3.7 ± 0.6	1	21
Oa depth (cm)	7.5 ±0.6	6.3 ± 0.5	4.7 ± 0.8	0.5	23
Physical characteristics					
Mean active layer depth (cm)	55.1 ± 0.3	50.3 ± 0.2	51.3 ± 0.7	23	>130
Max microtopography (cm)	27.0 ± 2	27.6 ±1.7	27.2 ± 3.8	5	110

References

Ahrens, R. J., J. G. Bockheim, and C. Ping. 2004. The Gelisol order in Soil Taxonomy. Pages 2-10 *in* J. Kimble, editor. Cryosols: Permafrost-affected soils. Springer-Verlag, New York.

Allen, T. F. H., and T. W. Hoekstra. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. Journal of Vegetation Science **1**:5-12.

Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jonsdottir, K. Laine, E. Levesque, G. M. Marion, U. Molau, P. Molgaard, U. Nordenhall, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenstrom, M. Stenstrom, O. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. Ecological Monographs **69**:491-511.

Bergeron, Y., O. Engelmark, B. Harvey, H. Morin, and L. Sirois. 1998. Key issues in disturbance dynamics in boreal forests: Introduction. Journal of Vegetation Science **9**:464-467.

Billington, M. M., and V. Alexander. 1983. Site-to-site variations in nitrogenase activity in a subarctic black spruce forest. Canadian Journal of Forest Research **13**:782-788.

Birkeland, P. W. 1999. Soils and Geomorphology. Oxford University Press, New York.

Bisbee, K. E., S. T. Gower, and J. M. Norman. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia **129**:261-270.

Braun-Blanquét, J. 1965. Plant sociology: The Study of Plant Communities. Hafner, London.

Bridge, S. R. J., and E. A. Johnson. 2000. Geomorphic principles of terrain organization and vegetation gradients. Journal of Vegetation Science **11**:57-70.

Brown, J. K., and J. K. Smith. 2000. Wildland fire in ecosystems: Effects of fire on flora. General Technical Report RMRS-42 vol 2, USDA Forest Service, Rocky Mountain Research Station.

Chapin III, F. S., M. S. Bret-Harte, S. E. Hobbie, and H. Zhong. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science **7**:347-358.

Chapin III, F. S., and K. Danell. 2001. Boreal Forest. *in* F. S. Chapin III, O. E. Sala, and E. Huber-Sannwald, editors. Ecological Studies 152. Biodiversity in a changing climate. Springer, New York.

Connor, C., and D. O'Haire. 1988. Roadside Geology of Alaska. Mountain Press Publishing Company, Missoula.

Currie, D. J., and V. Paquin. 1987. Large-scale biogeographical patterns of species richness in trees. Nature **329**:326.

Daniels, F. J. A. 1982. Vegetation of the angmagssalik District, Southeast Greenland IV-Shrubs, dwarf shrubs, and terricolous lichens. Medd. Gronl. Bioscience **10**:1-78.

Devolder, A. 1999. Fire and climate history of black spruce forests, Kenai National Wildlife Refuge, Alaska. M.S. Northern Arizona University, Flagstaff.

Driscoll, K. G., J. M. Arocena, and H. B. Massicotte. 1999. Post-fire soil nitrogen content and vegetation composition in sub-boreal spruce forest in B.C. central interior. Forest Ecology and Management **121**:227-237.

Drury, W. H. 1956. Bog Flats and physiographic processes in the upper Kuskokwim river region, Alaska. contrib. gray herbarium No CLXXVIII, Harvard University, Cambridge.

Dyrness, C. T. 1982. Control of Depth to Permafrost and Soil Temperature by the Forest Floor in Black Spruce/Feathermoss Communities. USDA, Forest Service. Pacific Northwest Forest and Range Experiment Stations.

Dyrness, C. T., and R. A. Norum. 1983. The effect of experimental fires on black spruce floors in interior Alaska. Canadian Journal of Forest Research **13**:879-893.

Flanagan, P. W., and K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Canadian Journal of Forest Research **13**:795-817.

Foster, D. R. 1984. Phytosociological description of the forest vegetation of southeastern Labrador. Canadian Journal of Botany **62**:899-906.

Foster, D. R., and G. A. King. 1984. Landscape features, vegetation and developmental history of a patterned fen in southeastern Labrador, Canada. Journal of Ecology **72**:115-143.

Glaser, P. H., J. A. Janssens, and D. I. Siegel. 1990. The Response of Vegetation to Chemical and Hydrological Gradients in the Lost River Peatland, Northern Minnesota. Journal of Ecology **78**:1021-1048.

Gould, W. A., and M. D. Walker. 1999. Plant communities and landscape diversity along an Arctic River. Journal of Vegetation Science **10**:537-548.

Hinzman, L., L. A. Viereck, P. Adams, V. E. Romanovsky, and K. Yoshikawa. in press. Climatic and permafrost dynamics in the Alaskan boreal forest. *in* M. Oswood and F. S. Chapin III, editors. Alaska's Changing Boreal Forest. Oxford University Press, Oxford.

Holsten, E., P. Hennon, L. Trummer, and M. Schultz. 2001. Insects and Diseases of Alaskan Forets. R10-TP-87, USDA Forest Service, Alaska Region.

Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford.

Johnson, E. A., K. Miyanishi, and J. M. H. Weir. 1998. Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. Journal of Vegetation Science **9**:603-610.

Johnstone, J. F., F. S. Chapin III, J. Foote, K. Kemmett, K. Price, and L. A. Viereck.

2004. Decadal observations of tree regeneration following fire in boreal forests. Canadian Journal of Forest Research **34**:267-273.

Jorgenson, T. 1984. The response of vegetation to landscape evolution on glacial till near Toolik Lake, Alaska. Pages 134-141 *in* Proceedings of an International Symposium, Society of American Foresters Regional Technical Conference, Fairbanks, AK.

Keenan, T. J., and L. C. Cwynar. 1992. Late quaternary history of black spruce and grasslands in southwest Yukon Territory. Canadian Journal of Botany **70**:1336-1345.

Klein, D. R. 1982. Fire, lichens, and caribou. Journal of Range Management **35**:390-395.

Komarkova, V. 1983. Environmental data for 235 plots in the Gunnison and Uncompahgre National Forests. Contract number 28-K2-234, Rocky Mountain Forest and Range Experiment Station.

Kruskal, J. B., and M. Wish. 1978. Multidimensional Scaling. Sage Publications, Beverly Hills.

Kuhry, P., and B. J. Nicholson. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Canadian Journal of Botany **71**:10-22.

Kummerow, J., B. A. Ellis, S. Kummerow, and F. S. Chapin III. 1983. Spring growth of shoots and roots in shrubs of an Alaskan muskeg. American Journal of Botany **70**:1509-1515.

La Roi, G. H. 1967. Ecological Studies in the Boreal Spruce-Fir Forests of the North American Taiga. I. Analysis of the Vascular Flora. Ecological Monographs **37**:229-253.

La Roi, G. H. 1991. Classification and ordination of southern boreal forests from the Hondo-Slave Lake area of central Alberta. Canadian Journal of Botany **70**:614-628.

La Roi, G. H., and M. H. L. Stringer. 1975. Ecological studies in the boreal spruce-fir forests of the North American taiga. II. Analysis of the bryophyte flora. Canadian Journal of Botany **54**:619-643.

Larsen, J. A. 1980. The Boreal Ecosystem. Academic Publishing, New York.

Latham, E., and R. E. Ricklefs. 1993. Global patterns of tree species richness in moist forests: Energy-diversity theory does not account for variation in species richness. Oikos **67**:325-333.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology **73**:1943-1967.

Lynch, J. A., J. S. Clark, N. H. Bigelow, M. E. Edwards, and B. P. Finney. 2002. Geographical and temporal variations in fire history in boreal ecosystems of Alaska. Journal of Geophysical Research **Atmospheres 108(D1)**:8152.

Mann, D. H., C. L. Fastie, E. L. Rowland, and N. H. Bigelow. 1995. Spruce succession, disturbance, and geomorphology on the Tanana River floodplain, Alaska.

Ecoscience **2**:184-199.

Mather, P. M. 1976. Computional methods of multivariate analysis in physical geography. Wiley & Sons, London.

McCune, B. 1993. Gradients of epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. Bryologist **96**:405-411.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4.25. MjM Software Design, Gleneden Beach.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Orloci, L., and W. Stanek. 1979. Vegetation survey of the Alaska Highway, Yukon Territory: Types and gradients. Vegetatio **41**:1-56.

Osterkamp, T. E., and V. E. Romanovsky. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost and Periglacial Processes **10**:17-37.

Peinado, M., J. L. Aguirre, and M. de la Cruz. 1998. A phytosociological survey of the boreal forest (Vaccinio-Piceetea) in North America. Plant Ecology **137**:151-202.

Pewe, T. L., D. Hopkins, M., and J. L. Giddings. 1965. The Quaternary Geology and Archaeology of Alaska. Pages 355-374 *in* H. E. J. Wright and D. G. Frey, editors.

The Quaternary of the United States A review volume for the VII Congress of the International Association for Quaternary Research. Princeton University Press, Princeton.

Raisa, M. 1999. Response patterns of *Vaccinium myrtillus* and *V. vitis-idaea* along nutrient gradients in boreal forest. Journal of Vegetation Science **10**:17-26.

Rieger, S., J. A. Dement, and D. Sanders. 1963. Soil survey, Fairbanks area, Alaska. US Soil Conservation Society, Fairbanks.

Rieger, S., D. B. Schoephorster, and C. E. Furbush. 1979. Exploratory Soil Survey of Alaska. US Soil Conservation Service, Washington, D.C.

Rivas-Martinez, S., D. Sanchez-Mata, and M. Costa. 1999. North American boreal and western temperate forest vegetation. Itinera Geobotanica **12**:5-316.

Roesales, J. S. 1997. Disturbance history in the Tanana River Basin of Alaska: Management option. MS Thesis. University of Alaska Fairbanks, Fairbanks.

Rowe, J. S., and G. W. Scotter. 1973. Fire in the Boreal Forest. Quaternary Research **3**:444-464.

Schoeneberger, P. J., D. A. Wysocki, E. C. Benham, and W. D. Broderson, editors. 2002. Field Book for Describing and Sampling Soils, Version 2.0. Natural Resources Conservation Service, National Soil Survey Center, Lincoln.

Scott, A. J. 1995. Canada's vegetation: a world perspective. McGill-Queen's University Press, Montreal.

Skre, O., W. C. Oechel, and P. M. Miller. 1983. Moss leaf water content and solar radiations at the moss surface in a mature black spruce forest in central Alaska. Canadian Journal of Forest Research **13**:860-868.

Slaughter, C. W., and C. S. Benson. 1986. Proceedings, Cold Regions Hydrology. Pages 101-109 *in* D. L. Kane, editor. American Water Resources Association, Bethesda, USA.

Sweetnam, T., and E. K. Sutherland. 1985. Using dendrochronology to measure the growth of defoliated trees. Agricultural Handbook No. 639, USDA Forest Service.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? Ecology **74**:2179-2191.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

Timoney, K. P., G. H. La Roi, S. C. Zoltai, and A. L. Robinson. 1993. Vegetation communities and plant distributions and their relationships with parent materials in the forest-tundra of northwestern Canada. Ecography **16**:174-188.

Van Cleve, K. 1983. Introduction and overview of a multidisciplinary research project: the structure and function of a black spruce (*Picea mariana*) forest in relation to other fire-affected taiga ecosystems. Canadian Journal of Forest Research **13**:695-702.

Van Cleve, K., F. S. Chapin III, C. T. Dyrness, and L. A. Viereck. 1991. Element cycling in taiga forest: State-factor control. Bioscience **41**:78-88.

Van Cleve, K., C. T. Dyrness, L. A. Viereck, J. F. Fox, F. S. Chapin III, and W. C. Oechel. 1983. Taiga ecosystems in interior Alaska. Bioscience **33**:39-44.

Van Cleve, K., W. C. Oechel, and J. L. Hom. 1990. Response of black spruce ecosystems to soil temperature modification in interior Alaska. Canadian Journal of Forest Research **20**:1530-1535.

Van Cleve, K., L. A. Viereck, and C. T. Dyrness. 1982. Dynamics of a black spruce ecosystem in comparison to other forest types: a multi-disciplinary study in interior Alaska. Pages 148-166 *in* Resources and dynamics of the boreal zone. Association of Canadian Universities for northern studies, Thunder Bay, On.

Viereck, L. A. 1973. Wildfire in the taiga of Alaska. Journal of Quaternary Research **3**:465-495.

Viereck, L. A. 1983a. The effects of fire in Black Spruce ecosystems of Alaska and Northern Canada. Pages 201-219 *in* R. W. Wein and D. A. MacLean, editors. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, Ltd.

Viereck, L. A. 1983b. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Canadian Journal of Forest Research **13**:703-720.

Viereck, L. A., C. T. Dyrness, A. R. Batten, and K. J. Wenzlick. 1992. Alaska Vegetation Classification. General Technical Report PNW-GTR-286 USDA Forest Service Pacific Northwest Research Station.

Walker, D. A. 2000. Hierarchical subdivsion of arctic tundra. Global Change Biology **6**:19-34.

Walker, D. A., and K. R. Everett. 1991. Loess ecosystems of northern Alaska: Regional gradient and toposequence at Prudhoe Bay. Ecological Monographs **61**:437-464.

Walker, M. D., F. J. A. Daniels, and E. van der Maarel. 1994a. Circumpolar arctic vegetation- Introduction and perspective. Journal of Vegetation Science **5**:758-764.

Walker, M. D., D. A. Walker, and N. A. Auerbach. 1994b. Plant Communities of a tussock tundra landscape in the Brooks Range foothills, Alaska. Journal of Vegetation Science **5**:843-866.

Whittaker, R. J. 1975. Communities and ecosystems. Macmillan, New York.

Yarie, J. 1983. Environmental and successional relationships of the forest communities of the Porcupine River drainage, interior Alaska. Canadian Journal of Forest Research **13**:721-728.

Zasada, J. C., T. L. Sharik, and M. Nygren. 1992. The reproductive process in boreal forest trees. Pages 85-125 *in* H. H. Shugart, R. Leemans, and G. B. Bonan, editors. A System Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge.

CHAPTER 3: PREDICTING ECOSYSTEM PROPERTIES WITH COMMUNITY COMPOSITION

"Form follows function-that has been misunderstood. Form and function should be one..."

-Frank Lloyd Wright

---

*Manuscript title: The role of plant community composition as a predictor of regional soil carbon storage in the boreal black spruce ecosystem. Authors: T.N. Hollingsworth, E.A.G. Schuur, F.S. Chapin III, and M.D. Walker. Prepared for submission to Ecological Applications

Abstract

The boreal forest is the largest terrestrial ecosystem in North America and is one of the least disturbed by humans. This combination makes it an ideal system in which to explore the relative importance of abiotic factors and floristic composition in governing ecosystem properties on a regional scale. In this chapter I examine the relationship between floristic composition and ecosystem parameters such as soil carbon pools, C/N of live black spruce needles, and normalized basal area increment (NBAI) of trees in black spruce communities, the most widespread forest type in the boreal forest of Alaska. Variability in ecosystem properties among black spruce stands was as large as that documented in previous studies among all forest types in the central interior of Alaska (eight-fold range in normalized basal area increment, and five-fold range in mineral soil carbon and nitrogen pools). Acidic sites ($pH < 5.5$) had significantly more carbon in the organic soil than did nonacidic ($pH > 5.5$) sites, but did not differ in any other measured ecosystem parameter. Plant community composition was at least as effective as environmental or abiotic factors and stand characteristics as a predictor of soil C pools in black spruce ecosystems of the boreal forest of Alaska. I conclude that among the community properties analyzed, the presence of key species, overall species composition, and diversity of certain functional types (i.e. *Sphagnum* species), are most tightly linked to carbon sequestration in the black spruce forest type.

Introduction

Species composition and diversity strongly influence ecosystem processes such as nutrient cycling, productivity, decomposition rate, and trophic dynamics, particularly if the traits of one or few species have strong ecosystem effects (Vitousek and Hooper 1993, Tilman et al. 1996, Hooper and Vitousek 1997, Chapin et al. 2000, Diaz et al. 2004). In general, the dominant plant species account for most of these ecosystem effects because they account for most of the biotic pools and fluxes (Chapin et al. 1996, 1997, Hooper et al. 2000). Thus, biogeochemical models that incorporate biotic diversity do so only at the level of biomes (e.g. needle-leafed evergreen forests versus deciduous forests), or by incorporating two to four major functional types within a biome, such as mosses, lichens, evergreen, and deciduous shrubs. There is little information on the extent to which variation in the diversity of small-statured or sub-dominant plants either reflect or influence forest ecosystem processes at the regional or landscape scale, although some studies have looked at the effect of sub-dominants on ecosystem processes (e.g. Chapin 1983, Epstein et al. 1999, Diaz et al. 2004, Thompson et al. 2004). In this chapter I ask whether knowledge of understory species composition and diversity improves the prediction of a key ecosystem property, soil carbon (C) storage, relative to predictions based only on environment and stand structure alone. I addressed this question in black spruce forests across the region of interior Alaska.

The boreal forest is an excellent system in which to improve our knowledge of the links between plant community patterns and ecosystem processes in three respects: first, as the second largest terrestrial biome on Earth (Whittaker 1975), it covers an extensive part of North America, most of which has not been modified by human activity; second, it is important in the context of global change because of its large stock of soil C, its potential for methane release, and the speculation that it may be a missing sink for atmospheric CO_2 (Zimov et al. 1997, Gower et al. 2001); finally, the boreal forest is comprised of only a few tree species and has lower vascular plant diversity than the biomes to its north or south. Chapin and Danell (2001) suggested that its low species diversity causes community and ecosystem processes to be more sensitive to landscape-scale variations in community types than to broad latitudinal patterns of climate. A particularly important aspect of the boreal forest is the large proportion of reactive soil organic matter contained in its organic and surface mineral soil, which could be released given changes in climate or fire frequency (Bonan and Shugart 1989). Therefore, understanding the link between species composition and soil carbon processes in this biome is especially important.

Black spruce-dominated communities cover over 40% of the interior Alaska region (Van Cleve et al. 1983a) across a broad variety of environmental conditions. the black spruce ecosystem plays a critical role in the global carbon (C) cycle because it contains more C per unit area than other major boreal ecosystems in North America. Up to 87% of the C is found in the soil. High C contents at or near the soil surfaces make the black spruce ecosystem extremely susceptible to release under a warming climate (Gower et al. 1997). Previous research in the black spruce ecosystem of boreal Alaska focused on the relationship between soil C dynamics and nutrient cycling (Heilman 1968, Chapin 1983, Van Cleve et al. 1983b, Van Cleve et al. 1991, Bonan and Van Cleve 1992, Hobbie et al. 2002), fine root production (Ruess et al. 1996, Ruess et al. 2003, Vogel et al. in press), stand productivity (Bonan and Van Cleve 1992), and abiotic factors (Flanagan and Van Cleve 1983, Van Cleve and Dyrness 1983, Van Cleve et al. 1990). From these and other studies in Canada (e.g. Harden et al. 1997, Bisbee et al. 2001, Dioumaeva et al. 2003), we know that soil temperature and moisture, presence and depth of permafrost, age since disturbance, and litter quality control soil C in black spruce forests. However, there has been little research on the relationship between soil C patterns and plant community characteristics in black spruce forests.

There are substantial differences in C pools and fluxes among Canadian black spruce communities that differ in dominant moss species and stand structural characteristics, such as stand density (Harden et al. 1997, O'Connell et al. 2003a, b), but we know little about how variability in floristic composition and functional diversity affects C allocation and storage. There is evidence that the black spruce communities of interior Alaska vary substantially in plant community composition (Viereck 1973, Dyrness and Grigal 1979; Chapter 2).

A recent classification of black spruce communities revealed that floristics vary most strongly with changes in mineral soil pH and soil moisture regime (Chapter 2). The Acidic Black Spruce/Lichen Forest is dominated by fruticose lichens and many species of mosses and has a moist to wet subtype, whereas the Nonacidic Black Spruce/Rose/Horsetail Forest is characterized by greater vascular plant diversity, especially various species of *Equisetum*, and has both a wet and dry subtype distinguished by different species (Chapter 2). This floristic classification provides a framework for understanding the relationship of species composition and diversity to ecosystem properties, such as soil carbon, across the boreal region of Alaska.

The objectives of this chapter are to link plant community structure to ecosystem processes and to incorporate plant community characteristics such as diversity and composition into a conceptual model of regional soil C storage in black spruce soils. To accomplish this, I first describe the regional variation in tree growth/aboveground tree productivity, C/N ratio of live needles, and soil C of black spruce communities. I then link community patterns of species composition and diversity and environmental variables to patterns in these ecosystem properties. Finally, I delineate black spruce communities based on community type and reexamine the relationship of community type to patterns of soil C.

Methods

Study site

Interior Alaska is a region of discontinuous permafrost with approximately 75-80% of the ground underlain by a permanently frozen layer (Osterkamp and Romanovsky 1999). Mean annual permafrost temperatures range from -0.5°C to –2°C (Slaughter and Benson 1986). The climate is extremely continental, with temperatures ranging from –70°C to +35°C. Annual precipitation is low, averaging 286 mm a year, of which about 35 percent falls as snow (Hinzman et al. in press). Soils show relatively minor morphological development, and most of the soils are classified as Inceptisols, Entisols, Histosols, or Gelisols (Rieger et al. 1979, Ahrens et al. 2004).

Field sampling

I studied 32 sites along a climate/latitudinal transect from the Alaska Range (Latitude ~63°N) to the Brooks Range (Latitude ~67°N) covering approximately 25,000 km^2 (Figure 3.1) in order to include a wide range of variability in both community structure and function. Sampling was conducted in four distinct geographic study areas: the northern interior, the central interior, the southern interior, and southeastern interior.

Sites were selected within 1 km of road access because of the inaccessibility of other areas. The 32 sites are a subset of a larger study that documented the regional variability in black spruce plant community composition (Chapter 2), wherein methods of sampling species composition and environmental variables are described. At each site I measured latitude and longitude using a Trimble Geoexplorer 3 GPS unit and physical characteristics of the site including slope, aspect, elevation, topography, parent material, and geomorphology.

I subjectively chose site locations in areas of homogenous vegetation that were dominated by a black spruce overstory, and at each site I sampled vegetation using the relevé method. My relevés included a list of all vascular and nonvascular plant species present and an estimate of percent cover of each species using the Braun-Blanquét cover-abundance scale (Braun-Blanquét 1965, Mueller-Dombois and Ellenberg 1974). All relevés were at least 2500 m^2 in area, and most were greater than 6400 m^2.

I cored five to ten of the largest black spruce trees in each site as close to the base of the tree as possible in order to estimate the age of the oldest trees and tree growth rates. I employed the Point Centered Quarter Method (PCQ) (Mueller-Dombois and Ellenberg

1974) randomly at five points in each site to quantify density and basal area.

At each site I dug a soil pit to a depth of 1 m or to frozen ground, whichever came first, measured the depths of the Oi (recognizable organic litter layer), Oe (unrecognizable litter layer), and Oa (humified organic matter) horizons, and the depth to bedrock or frozen soil. One soil sample per site was collected from the uppermost mineral horizon, and percent soil moisture and bulk density were determined following the methods of Walker et al. (1994). Although soil moisture can change depending on rain events, I observed regional-scale variation in soil moisture that was not strongly linked to storm events. Soils were air dried, sieved, and sent to the UAF Palmer Research Station for determination of mineral pH.

Sites were revisited in September or October of the same year to measure maximum thaw depth and to collect needles and soil for the analysis of soil and needle C and nitrogen (N). I clipped live needles, both new growth and the previous year's growth, from 10-20 trees randomly selected in each site. Three random locations were picked within each site, and in each the organic layer was carefully removed and its thickness measured. Mineral soil was then sampled volumetrically with a Giddings soil corer to a minimum depth of 15 cm at all sampling locations. Frequently, rocks or ice prevented consistent sampling of deeper soils; however, a large proportion of the total reactive soil organic matter pool is contained in the organic and surface mineral soil.

Laboratory analyses

Soil cores were separated in the field into organic and mineral horizons (n = 3 cores per site). In the laboratory, I further separated the organic horizons (Oi, Oe, and Oa), and the mineral soil into the top 5 cm and a 5-15 cm layer. Subsamples from each horizon were dried, ground, and acidified to remove carbonates. Soil C and N were then measured using a Cotech C/N ratio analyzer (Valencia, CA). I used these data together with the horizon bulk density and thickness to calculate total organic C and N density per unit area down to 15 cm mineral soil. I calculated C and N pools for total soil, organic soil, and mineral soil, since organic soil may be more directly related to vegetation properties in contrast to mineral soil C and N pools that can also reflect surface properties of soil minerals.

I separated new needle growth and the previous year's growth from a composite sample of 10-20 cohorts of needles per site. After drying the needles at 25° C for 48 hours, needles were ground to a fine powder and analyzed for C and N content using the methods outlined above. All sampled needles within each annual cohort were composited, giving one C/N ratio value per cohort of needles for each site. To assess the analytical quality of my C and N needle data, I ran three subsamples from 10 sites and found no significant difference in C or N values within any particular site.

Analysis of tree age, growth rates, and aboveground tree productivity

Annual growth rings were counted with a microscope and visually cross-dated (Sweetnam and Sutherland 1985). If the pith was missed during coring, the distance to pith was estimated by fitting a circular template to the innermost curved ring, or by subtracting core length from the radius at core height. The number of years to the pith was then estimated empirically from age-diameter relationships based on trees in which the pith was obtained. The number of years the tree took to grow to the cored height was estimated by a regression equation that relates seedling height to age of black spruce trees on the Kenai Peninsula, Alaska (Devolder 1999). These ages were analyzed in ten-year age classes to account for errors in those estimates.

Growth rate increment (ring width) was measured using an Acu-Rite Linear encoder and a microscope. The encoder measures growth to a precision of one micron. The data were recorded by a Quick Check QC-1000 and exported to the MeasureJX software program. If the pith was present in the core, all rings from the inner edge of the outer bark to the pith were measured. If distance to pith could not be estimated, the core was not used.

The last 11 years of growth were used to estimate an average area per ring – basal area increment (BAI) - for that core following the method of Atkins et al. (1998). First, a radius was calculated by adding growth rate increments from the pith to the beginning of the last 11 years of growth. An area for this inner circle or "inner area" was then calculated based on this radius. For each of the 11 rings remaining, starting with the oldest ring, a new radius was calculated based on the growth rate increment for that ring. Then, a new area for the inner circle plus the additional ring was calculated, and then the inner ring area was subtracted to leave only the area for the ring in question. This new growth was the basal area increment (BAI) for that ring. In order to compare growth rates for many sites, this NBAI value is then normalized to the inner area (Normalized BAI (NBAI) = BAI for that year divided by inner area up to previous year, expressed as a % of the inner area). NBAI for the last 11 years' growth was then averaged for each tree, and then for the site. NBAI is used as an index of productivity because it gives an estimate of the recent aboveground tree productivity of a stand.

Statistical analyses

I ran multiple independent sample t-tests (equal variance not assumed) to test for differences in means of NBAI, C/N ratio and soil C between acidic and nonacidic black spruce communities. For purposes of all statistical analyses, latitudinal treeline sites, that is, those at the northern limit of black spruce, were grouped with the nonacidic sites because they share some of the same species and occur on high pH substrates (Chapter 2). Pearson correlation coefficients were used to correlate C/N ratio of soil and needles, NBAI, soil N (g N m^{-2}), and soil C (kg C m^{-2}). I ran ordinary least square regressions to explore the relationships between stand age and NBAI (independent variables) and total soil C (dependent variable).

Nonmetric multi-dimensional scaling (NMDS) ordinations were run using the program PC-ORD 4.25 (McCune and Mefford 1999) in order to detect the main patterns in species composition, based on a combination of both presence and abundance of each species. These produced ordination axis scores for each site (Chapter 2), and these scores were then used as a measure of species composition for future analyses. I ran a backwards stepwise multiple regression to explore the correlations between plant community and ecosystem patterns, abiotic variables, and soil C pools. I used the best subset regression method (removal $p = 0.10$), including non-redundant variables.

I report only the best-fit model (i.e. highest amount of variance explained and the most significant), and I report both the R^2 and the adjusted R^2. I used the beta values (regression coefficients standardized by converting to Z scores) to assess the relative importance of each variable to the regression model. Beta values (β) indicate the portion of variance in a dependent variable that can be attributed directly to an independent variable, and are often termed "path coefficients" (Mitchell 1993). Descriptive statistics were run on dependent variables to test for normality, and I used Pearson correlation coefficients and high a variance inflation factor (VIF) (VIF >10) to look for multicollinearity among independent variables. The dependent variables were total soil C, soil C in the organic soil, and soil C in the mineral soil (kg C m^{-2}). All independent variables used in the multiple regression are listed in Table 3.1. All t-tests, correlations, and regression analyses were performed in SPSS version 11.0.2.

Results

Regional variability in ecosystem function

There was a wide range of values for different ecosystem parameters among the 32 black spruce study sites that I sampled. Normalized basal area increment (NBAI, an index of aboveground tree productivity) varied eight-fold across the sites (0.004 - 0.027, mean = 0.012 ± 0.001 %), C/N ratio of first year needles varied three-fold (23.5 - 64.3, mean = 48.5 ± 1.5), soil C pools varied five-fold (4.4 - 24.7, mean = 10.8 ± 0.73 kg C m^{-2}), and soil N pools varied ten-fold (172.0 - 1237.9, mean = 475.5 ± 34.0 g N m^{-2}; Figure 3.2, Appendix 3.1). Across all sites, total soil N and total soil C were highly correlated ($r = .936$, $p = .0001$) (Table 3.2), so total soil N was not used in the multiple regression analysis. Soil C/N, an index of organic matter quality, was moderately correlated with total soil C pools ($r = 0.42$, $p = 0.022$) (Table 3.2), but not significantly correlated with either the organic or mineral layer C pool (data not shown). NBAI was a weak predictor of total soil C ($r^2=0.134$, $p = 0.030$) among these relatively mature stands (44 - 295 yr). There was no significant relationship between stand age and total C content (Figure 3.3).

Most of the variation in ecosystem parameters reflected variation within, rather than among, geographic study areas (Figure 3.2). This is shown by the lower variance among sites than within study areas and by the lack of significant difference in the means of the ecosystem parameters measured among my different study areas. All of the four study regions included acidic and nonacidic communities, making it unlikely that differences in ecosystem processes between these community types were inadvertent consequences of regional variation in climate. By definition, only the northernmost region had latitudinal treeline sites (Figure 3.2). These results suggest that my cross-site comparisons of different study areas provide a useful basis for examining controls over regional variation in ecosystem processes.

Acidic and nonacidic black spruce community types did not differ significantly in NBAI, needle C/N ratio, or total soil C pools using independent sample t-tests. However, there was significantly more C in the organic layer of acidic than nonacidic black spruce community types ($t = -2.35$, $p = 0.027$)(Figure 3.4).

Predictors of regional soil C pools

Total soil C pools (combined organic and mineral soil) for all sites: Plant community composition was at least as important as abiotic or stand characteristics in predicting total soil C, when all sites were considered. *Sphagnum* diversity, Axis 1 of the NMDS ordination (floristic composition related to soil acidity), and Axis 2 (floristic composition related to soil moisture) were significant predictors of total soil C (Table 3.3). Soil mineral pH was the only abiotic variable, and stand age and NBAI, an estimate of recent productivity, were the only stand variables that were significant predictors of total soil C. The regression model explained 59% of the total variance in total soil C across all sites (F value = 5.47, p = 0.001), with the majority of this variance being explained by Axis 1 (β = -0.75) and pH (β = -0.62).

C in the organic soil for all sites: Within the soil organic layer across all sites, C amounts were associated with lower aboveground production of black spruce trees, wetter sites occurring in slightly sloping or lowland areas. No plant community composition traits were good predictors of soil C in the organic soil (Table 3.3). The multiple regression model explained 44% of the overall variance in soil C in the organic layer across all sites (F value = 5.10, p = 0.004), with aspect (β = 0.48), and NBAI (β = -0.43) explaining the most variance.

C in the mineral soil for all sites: Within the soil mineral layers across all sites, C amounts were associated with acidic, steep slopes, slower aboveground tree growth, and higher vascular and moss species richness (Table 3.3). The multiple regression model explained 41% of the total variance in the C of the mineral soil across all sites (F value = 3.84, p = 0.007), with aspect (β = -0.73) and Axis 1 (β = -0.57) explaining the most variance. Slope had an opposing effect on predicting soil C in the organic and mineral horizons, whereas NBAI showed a consistent negative correlation with organic, mineral, and total soil C.

Predictors of soil C pools within communities

Because plant community composition (NMDS Axis 1) associated with mineral soil pH acidity was such a strong predictor of total soil C across all sites (Table 3.3), I evaluated the controls over soil C in acidic and nonacidic community types separately.

The acidic black spruce community

Total soil C pools (organic plus mineral soil): Within the acidic black spruce community, larger total soil C pools were associated with greater C/N ratio of the needles, suggesting that controls over decomposition (i.e., C/N ratio reflecting litter quality) are an important control over soil C pool size (Table 3.3). Variation in C/N ratio of live needles explained 36% of the overall variance in total soil C in the acidic black spruce community variation (F value = 6.71, $\beta = 0.60$) (Figure 3.5).

C in the organic soil: Larger C amounts in the organic layer were associated with lower moss richness, higher C/N ratio of the live needles, and lower Axis 3 values, floristic composition associated with productivity (Table 3.3). These variables together explained 77% of the variation in C storage in the organic layer (F value = 12.02, p = 0.001), with Axis 3 ($\beta = -0.79$) and moss richness ($\beta = -0.76$) contributing greatly to the variability. This suggests a strong relationship between moss richness, soil acidity, and soil carbon amounts.

C in the mineral soil: Larger C amounts in the mineral soil were associated with sites on steeper slopes and higher C/N ratio of the live needles of this type (Table 3.3).

The regression model explained 36% of the overall variation in C pools in the mineral soil (F value = 4.62, p = 0.035), with slope contributing more to the model (β = 0.51). Live needle C/N ratio correlated positively with soil C pools in both the organic and mineral horizons and total soil C content on an area basis in the acidic community.

The nonacidic black spruce community

Total soil C pools (organic and mineral soil): Within the nonacidic community type, larger total soil C pools were associated with younger, relatively moist sites with high *Sphagnum* richness and lower rates of aboveground tree production (Table 3.3). The model explained 81% of the variation in soil (F value = 11.32, p = 0.001) with the largest contributions by soil moisture (β = 0.55) and *Sphagnum* richness (β =0.46).

C in the organic soil: Larger C amounts were associated with lower aboveground tree production and higher *Sphagnum* richness in this type. These variables explained 51% of the total variance in soil C in the organic layer (F value = 6.72, p = 0.010), and NBAI contributed the most to the overall variance (β = -0.49).

C in the mineral soil: In the mineral soils of the nonacidic community type, higher total soil C was associated with wet, young, lowland or flat sites with a shallow active layer (Table 3.3). The regression model explained 78% of the total variance observed (F value = 10.74, p = 0.001), with active layer depth (β = -0.49) contributing the most to the model.

Discussion and conclusions

Regional variability in the black spruce ecosystem in interior Alaska

I found greater variation in recent aboveground tree productivity (NBAI) and soil C among sites within a study area than among study areas within the region of interior Alaska (Figure 3.2). This suggests that my within-site sampling (n = 3) was generally adequate to assess the ecosystem characteristics within a site at a regional scale, and that some factors other than regional variations in climate or parent material were important drivers of variation in ecosystem processes. Some of this variation likely represents the strong topographic control on ecosystem structure and function that is repeated at the landscape scale throughout the boreal zone, which potentially accounts for a large amount of the variability in structure and function in the black spruce ecosystem. This topographic control reflects differences in soil temperature and associated differences in active layer and forest floor chemistry, which are known to drive ecosystem dynamics in the region (Dyrness 1982, Van Cleve et al. 1990, Bonan and Van Cleve 1992).

The low variability in soil C among the northeastern interior sites may be a consequence of their sandy soils and relatively uniform soil moisture (Appendix 3.1). Soil texture often influences soil drainage (Van Veen and Kuikman 1990) which in turn has a substantial effect on decomposition in black spruce forests (Trumbore and Harden 1998). This study area included sites on a variety of topographic positions, ranging from summit to valley bottom, and aspects, north and south facing slopes, but its soils were uniformly higher in sand content and drainage class and lower in soil moisture than other study areas (Chapter 2).

The ecosystem property that differed most predictably among my study sites was the C content (volume per area) of the organic horizon, which was significantly larger in acidic than in non-acidic sites (Figure 3.4). There was no difference in the C pools of mineral soils among all sites, and total soil C pool was only marginally greater ($p = 0.055$) in acidic than in nonacidic sites. These observations suggest that regional and landscape variations in soil acidity are strongly linked to carbon accumulation in the organic horizon and therefore total soil C pools of black spruce ecosystems. The relationship between plant community composition and ecosystem structure and function may result from the vegetation responding to the same underlying factors, such as forest floor chemistry, or reflect the influence of the vegetation on the ecosystem (Vitousek 1982, Wedin and Tilman 1990, Aber and Melillo 2001). The lack of a difference in NBAI between acidic and nonacidic sites suggests that acidity is affecting decomposition more than aboveground tree production.

The five-fold range in mineral soil C pools (2.4 - 13.3 kg C m^{-2}) that I observed among black spruce ecosystems across interior Alaska was larger than the range of values in mineral soil reported across a range of black spruce forest stands within the Fairbanks study area (4.1 - 10.4 kg C m^{-2}) and almost as great as the range of values reported across five different forest types within the Fairbanks study area (3.0 - 18.1 kg C m^{-2}) (Van Cleve et al. 1983b). This extreme variability was also observed for mineral soil N pools (110 - 554 g N m^{-2} as compared to 190 - 406 g N m^{-2}) and mineral soil C/N (13 - 29 as compared to 11 in birch stands to 30 in black spruce stands) (Figure 3.2, Appendix 3.1) (Van Cleve et al. 1983b). In addition, stand species richness varied almost two-fold (from 29-45 species) and stand density varied twenty-fold (639 – 13,212 trees/ha), which are larger ranges of values than those reported across a range of successional stands in the Fairbanks area (261 – 4,730 trees/ha) (Appendix 3.1) (Viereck 1983). These results clearly indicate that regional variation in forest structure and function within the black spruce ecosystem is as great as among-ecosystem variation within a landscape or study area. These patterns are seen in the black spruce ecosystem in particular, as opposed to other conifers or hardwoods in boreal Alaska, because of the wide range in environmental conditions in which black spruce can survive and grow (Viereck and Johnston 1990). This study, however, did not measure stand NPP across all of interior Alaska, which is a critical next step to understanding the overall regional variability in black spruce ecosystem function.

Predicting regional variation in soil C pools

The wide range in aboveground tree production, forest structure, and soil C and N pools among sites within a given ecosystem type provides a powerful framework for evaluating effects of climate, parent material, time, and vegetation on ecosystems, as shown by Vitousek (2004) for *Metrosideros* forests of Hawaii. I use a similar framework to address whether community composition of the understory of black spruce forests improves our ability to predict soil C pools of mature forests stands. By holding the species composition of the overstory (black spruce) constant, I increase my chances of detecting the relationships between understory species composition and soil C because variation in understory is not confounded by differences in overstory. If, in fact, the interactions between sub-dominant functional groups and the environment are driving forest processes, this has large implications for regional extrapolation and modeling, based purely on the remotely sensed distributions of overstory dominants (e.g. McGuire et al. 2002).

Plant community composition was at least as effective as environmental or abiotic and stand characteristics in predicting soil C pools among 32 sites across interior Alaska (Table 3.3). Axis 1 of the NMDS ordination (floristic composition related to soil acidity) was the most significant predictor of total soil C, and half of the variables that contributed significantly to the multiple regression predicting total soil C pool were floristic in nature: Axis 1, Axis 2, and *Sphagnum* richness. Community floristic variables were equally important when considering variation in the mineral horizon (Axis 1, vascular richness, and moss richness). However abiotic factors such as slope and aspect were more significant than floristics in predicting soil C in the organic layer. Across all sites, young, acidic stands with high *Sphagnum* richness had the largest pools of total soil C (Table 3.3). Axis 2, which describes the floristic variation associated with the topographic variation in soil moisture and paludification (the accumulation of *Sphagnum* mosses and the subsequent accumulation of peat in the uplands over time) was the other major floristic predictor of soil C pools. Soil moisture alone was not a significant predictor of total soil C pools, although it was significantly negatively correlated with organic soil C pool (Table 3.3). In the boreal forest, high soil moisture can produce anaerobic conditions, which slows decomposition. This contrasts with most drier ecosystem types where moisture enhances decomposition.

There are at least three potential factors that may contribute to the role of vegetation (and associated litter) on soil C storage in boreal and arctic systems (Flanagan and Van Cleve 1983, Neff and Hooper 2002): 1) variation in plant litter chemistry and deposition associated with changes in vegetation; 2) vegetation/environment covariation; and 3) differences in microbial communities across vegetation types. I examine the first two factors within the context of understory black spruce communities in interior Alaska.

The difference in plant chemistry between *Sphagnum* species and other non-vascular and vascular species underlies its importance in predicting regional level patterns in soil C. *Sphagnum* diversity is usually highest in acidic sites, whereas other mosses and vascular plants tend to be more diverse on less acidic sites (Chapter 2, Appendix 3.1). *Sphagnum* is more effective than other mosses or vascular plants in soil insulation, moisture retention, and acidification, and has very poorly decomposable litter, all factors that reduce decomposition rate and contribute to soil C accumulation (Heilman 1968, Skre and Oechel 1979, Foster and King 1984, Kuhry and Nicholson 1993, Anderson et al. 1995, Vitt 2000). Because of these strong ecosystem effects, *Sphagnum* species are often grouped as a distinct functional type for purposes of assessing vegetation effects on ecosystem processes (e.g. Chapin et al. 1996, Thompson et al. 2004). In addition, an increase in *Sphagnum* diversity could reflect fire history of a stand (both ground severity and time since fire), which in turn would relate to differences in carbon accumulation (Harden et al. 2000).

It is not surprising that soil moisture, aspect, active thaw depth, and other abiotic factors appear as important predictors throughout my regression models, as these factors have been shown to influence carbon storage on the regional scale in boreal forests as well as other systems (Van Cleve et al. 1983b, Liski and Westman 1997, Harden et al. 2000, Vogel et al. in press). The unique contribution of these results is that ordination axes, which represent differences in species composition among sites and are correlated to environmental variables, also appear to have a direct effect on soil C.

Relationships between abiotic and stand characteristics and soil C pools provide insight into the potential mechanisms controlling soil C accumulation in boreal black spruce forests. For example, the consistent negative correlation between aboveground tree productivity and soil C pools (organic, mineral, and total soil C) suggests that factors controlling decomposition were more important than factors controlling production as causes of regional variation in soil C pools. In turn, thick organic mats may constrain productivity. This result also supports the suggestion that black spruce sites may accumulate carbon only to the age of 80-100 years (younger than most of these stands) (Harden et al. 1998). Older black spruce stands, thought to be large carbon sinks, could be releasing carbon from the soil (Ruess et al. 2003). The exact role of these older black spruce stands in the regional and global carbon budget should, therefore, be examined further.

The lack of relationship between stand density and soil C pools (across all sites) has practical significance because it suggests that some remotely sensible aspects of stand structure, like density, are not necessarily good predictors of soil C pools across interior Alaska. Previous community classifications, such as the Alaska Vegetation Classification (Viereck et al. 1992), delineated black spruce communities first based on stand density, and many process-based studies have used structure as a proxy of productivity and age (as a stand gets older, it gets less productive and more open in stature) (e.g. Van Cleve et al. 1991). However, these results, coupled with previous work looking more specifically at community structure (Chapter 2), suggest that on the regional scale of interior Alaska, density is not a good indicator of stand-level composition and some processes. These results are similar to those of Litton et al. (2004), who suggested that C allocation patterns in a post-fire lodgepole pine ecosystem are independent of tree density; however the lodgepole pine ecosystem is moisture-limited, which contrasts strongly with my study.

Based on the correlations that I determined, I present the following conceptual model to describe important processes driving soil C accumulation in black spruce forests at the regional scale (Figure 3.6). Although many of the mechanisms described have been proposed by others (e.g., Van Cleve et al. 1991); my contribution is the addition of soil acidity and floristic composition (particularly *Sphagnum* richness) to existing models, and the degree to which these relationships hold across the landscape. Soil temperature, volume of thawed soil, and moisture have been described as the primary environmental drivers of decomposition rate and soil C accumulation (Van Cleve *et al.* 1981, Van Cleve *et al.* 1983b, Vogel *et al.* in press) at the regional scale. However, soil moisture and acidity also promote floristic changes, especially the accumulation of an abundance and diversity of *Sphagnum* mosses (as measured by ordination axes scores and *Sphagnum* richness, respectively) (Chapter 2), which increase acidity, further reinforce the changes in soil moisture, temperature, and thaw depth, and cause a decline in litter quality

(Katz 1926, Kuhry and Nicholson 1993, Sundberg and Rydin 2002). Together these changes reduce decomposition rate and increase accumulation of soil C, strengthening the feedback loops that promote *Sphagnum* accumulation and reduced decomposition. Nitrogen available to support plant growth is reduced both by its sequestration in soil organic matter and by the high acidity that leaches cations beneath the rooting zone (Marschner 1995). This reduction in nutrient supply reduces tree growth. The resulting decline in carbon inputs to soil is insufficient to offset the large reduction in decomposition, so soil carbon accumulates. These interlocking feedbacks are eventually interrupted by fire, which depending on the severity, can combust much of the *Sphagnum* and soil organic matter (Harden et al. 2000, Kasischke et al. 2000) until succession initiates the feedback loops described above.

Prediction of soil C pools within community types

Overall species composition, as measured by the NMDS ordination scores for each site, was not a significant predictor of soil C pools either within acidic or nonacidic community types. Instead, measures of species richness, such as vascular, moss, and *Sphagnum* became important. This is a logical consequence of the reduction in variation of overall species composition within, compared to among, communities. However, site ordination scores do reflect both species presence and species abundance, so it is somewhat surprising that the differences in abundance of species within a community type, as represented by the ordination scores, were not correlated with soil C pools. It suggests that within a given black spruce plant community type the presence of particular species, and not abundance of that species, is most tightly linked to variation in soil C.

When only acidic communities were considered, moss richness and Axis 3, a floristic index of a productivity gradient (Chapter 2), became the most significant predictors of total soil C. In addition, live needle C/N ratio, which made no significant contribution to the model of total soil C storage across all sites, contributed most significantly to explaining all soil C pools (organic, mineral, and total). The reason for the appearance of C/N ratio as a predictor of soil C in acidic sites is unclear, but may relate to low N availability in sites with high soil C, leading to reduced tissue N (high leaf C/N ratio) among acidic sites, where C storage is most pronounced.

When only nonacidic sites were considered *Sphagnum* richness was a highly significant predictor of soil C pools. In addition, active layer appeared for the first time as a significant predictor of soil C pools. The importance of active layer depth could relate to the dramatic difference in species composition between the two subtypes within the Nonacidic Black spruce/Rose/Equisetum spp community (Chapter 2). The nonacidic wet subtype has permafrost and a variety of nonacidic mosses, including some species of nonacidic *Sphagnums*, and potentially is accumulating soil C at a much higher rate than the drier nonacidic subtype.

Conclusions

My results demonstrate that community composition is at least as effective a predictor of soil C pools as are the abiotic and biological properties that are typically used in models to simulate soil C dynamics across the interior Alaskan region. In particular, it appears that the presence of key species and diversity of certain functional types, such as *Sphagnum*, rather than abundance or overall species richness, are good predictors of black spruce ecosystem function.

This suggests that (1) many of the impacts of abiotic variables are mediated by variation in the biotic diversity and composition of the community, (2) biotic diversity and composition are important integrative variables that capture the complex feedback dynamics governing biogeochemical cycling, and/or (3) variation in biotic diversity and composition reflect the long-term physical nature of a site. The intrinsic link between vegetation and the environment make it difficult to disentangle these three alternatives, but there is likely to be truth in all three interpretations. The rich literature on plant functional types and the diversity-function relationship indicates that variation in floristic composition should affect most ecosystem processes, including soil C storage (Diaz et al. 2004, Hooper et al. in press). Conversely, variations in soil C storage will likely alter nutrient availability and other ecosystem properties in ways that alter the competitive balance among species and therefore floristic composition. I therefore suggest that inclusion of vegetation composition in studies of ecosystem processes such as carbon balance may provide insights that are overlooked when only physical and biogeochemical properties or biome types are considered.

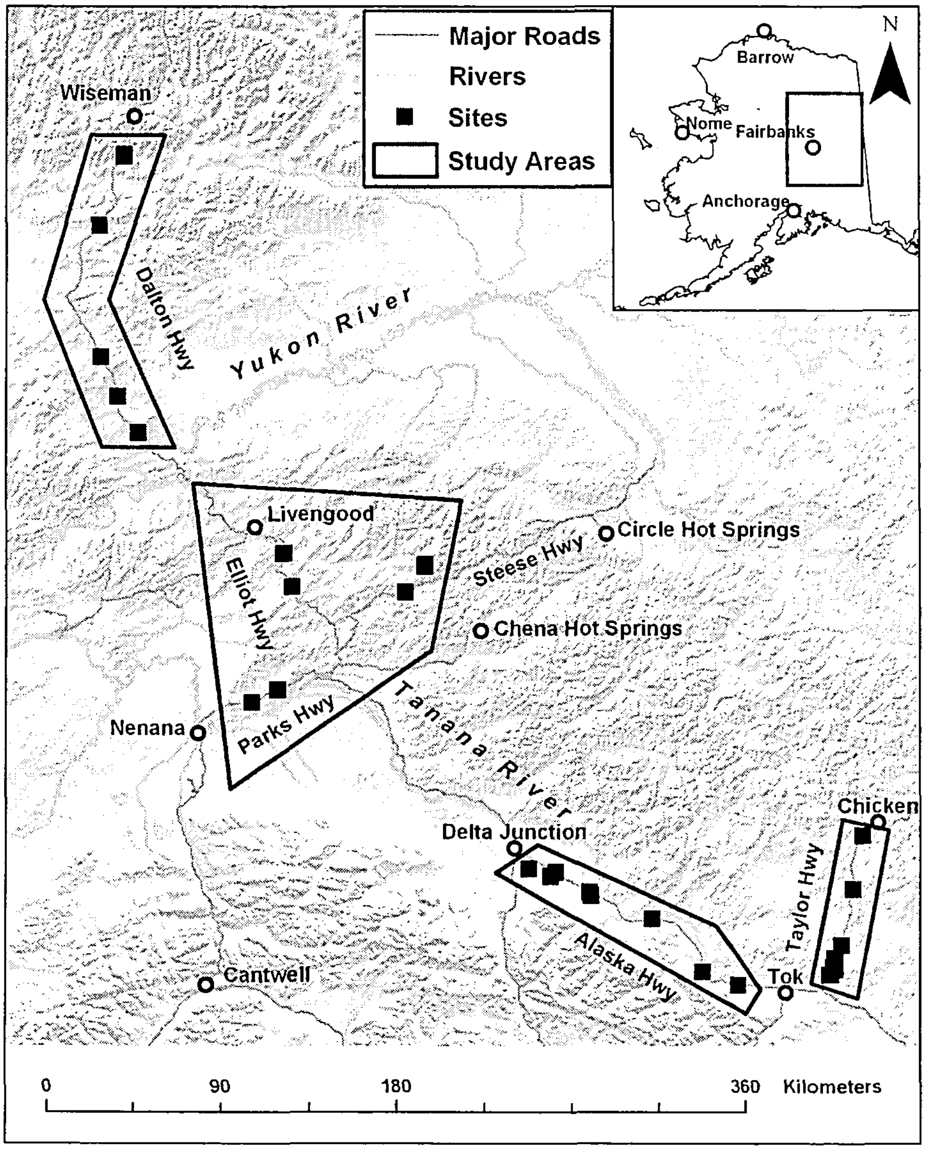

Figure 3.1. A map of interior Alaska, showing the 32 study sites. Sites are grouped within the study areas. The study areas from west to east are: Northern Interior, Central Interior, Southern Interior, and Southeastern Interior.

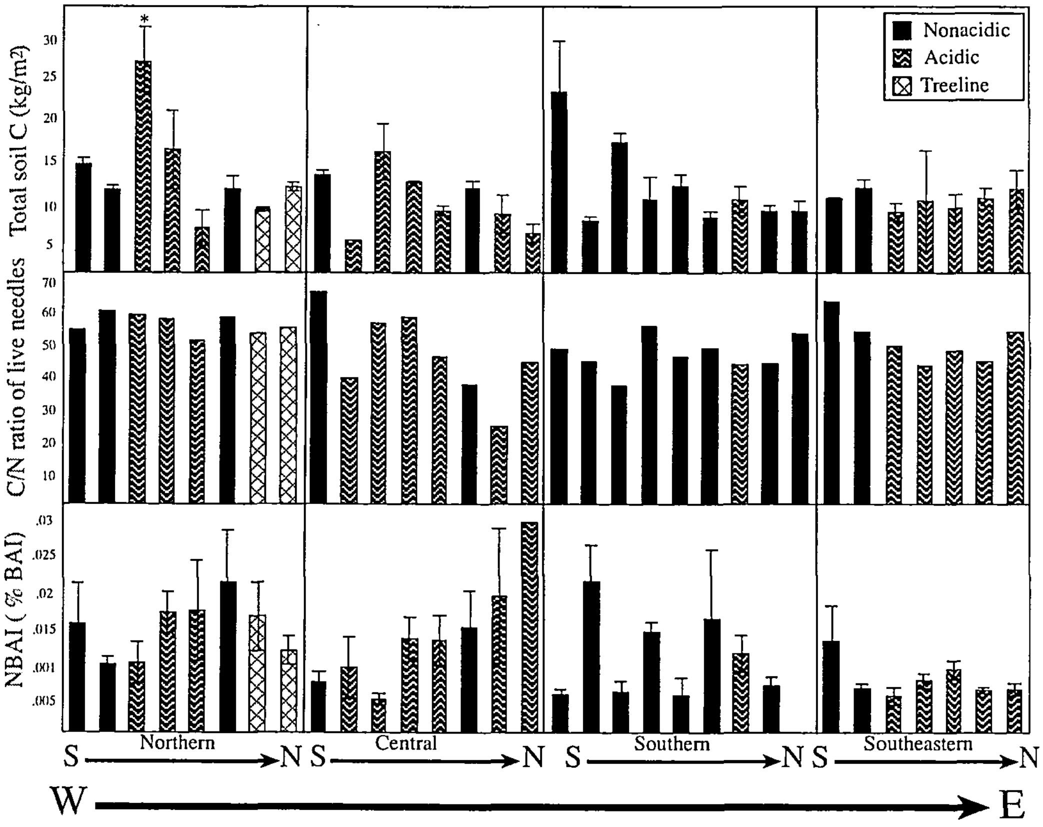

Figure 3.2. The regional variability in total soil carbon (kg/m^2, mean, ± SE) C/N of live needles, and NBAI (%, mean ± SE) Sites are grouped by study area (east to west) and within each region are grouped south to north. Community types are depicted by different shading. All study areas include both the nonacidic and acidic community type, only the Northcentral Interior includes the Treeline community type. (*) Mineral soil carbon was estimated using % C and bulk density from a small soil sample instead of the soil core. This was because we could not reach the mineral soil due to permafrost when we were coring.

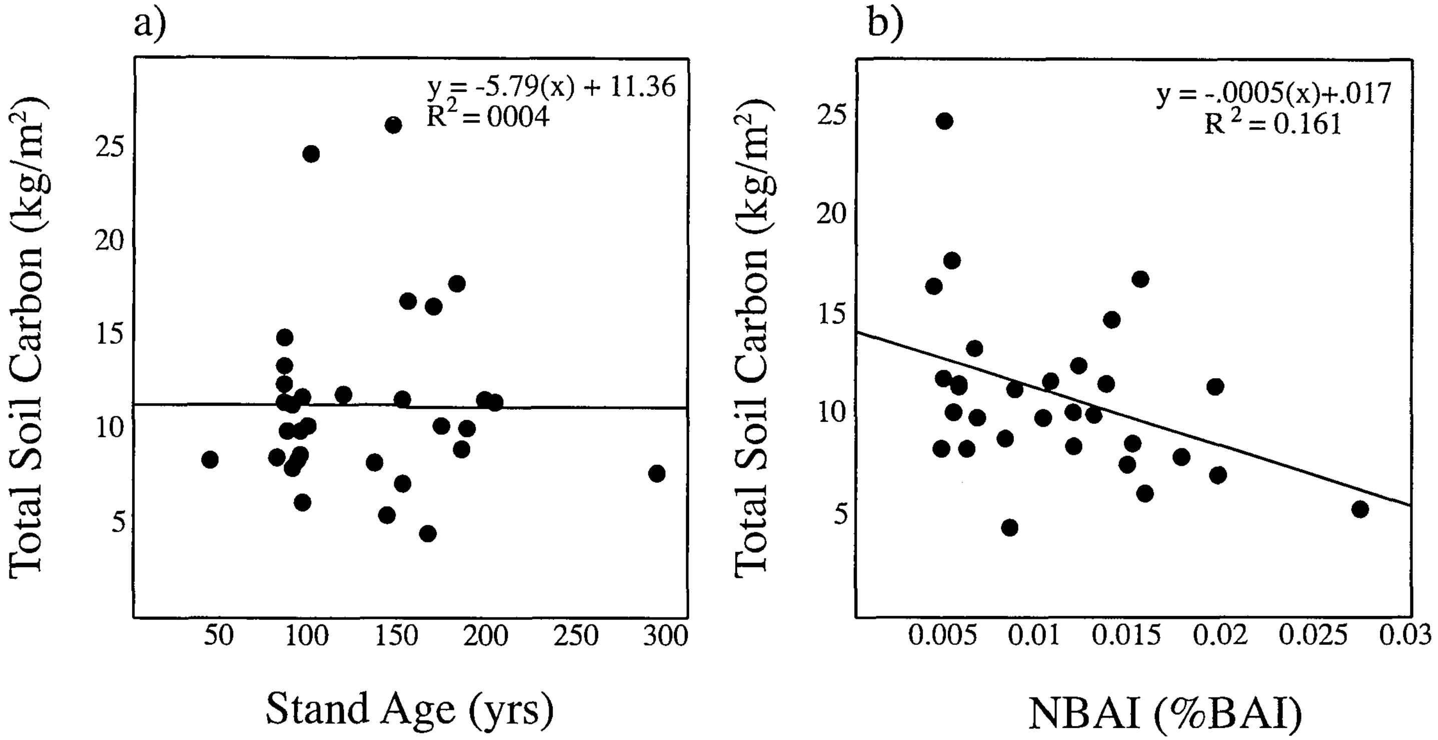

Figure 3.3. Regression line showing the relationship between total soil carbon (kg/m^2) and a) stand age (yrs), b) NBAI (%) across all sites. There was no significant relationship between total soil carbon and stand age, however there was a slight significant relationship ($p = 0.03$) between total soil carbon and NBAI.

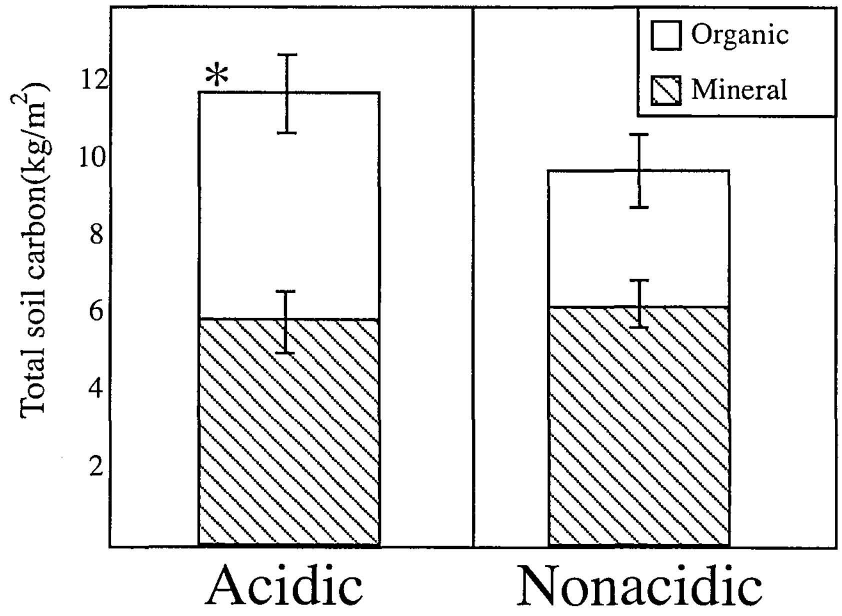

Figure 3.4. Total soil carbon (kg/m^2) differentiated by organic layer and mineral layer. The carbon in the organic layer is significantly different between the acidic and nonacidic sites.

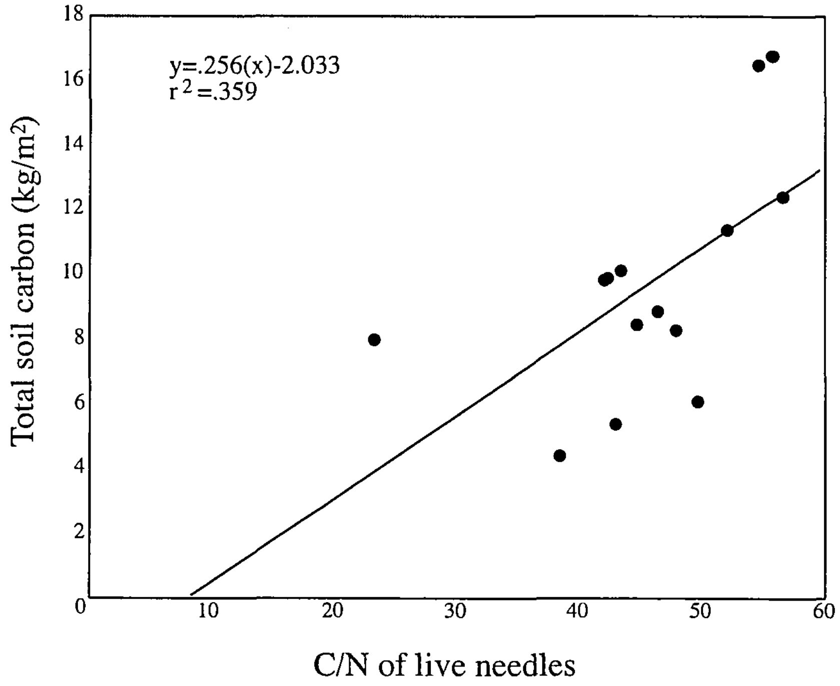

Figure 3.5. Regression line showing the relationship between total soil carbon (kg/m^2) and C/N ratio of the live needles in acidic sites. The C/N ratio alone explains 40% of the total variance in total soil carbon ($p = 0.005$). The causal nature of this relationship is uncertain. It is possible that high organic carbon accumulation restricts N availability and starves the trees of N, resulting in a high leaf C/N ratio.

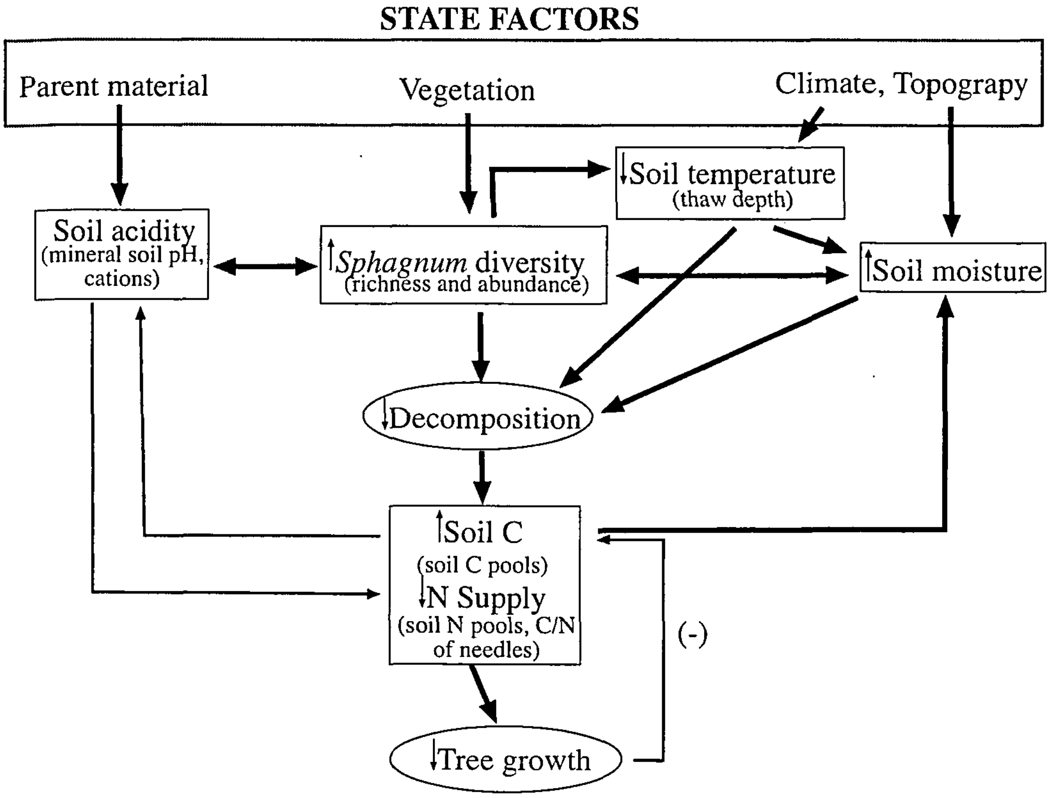

Figure 3.6. Conceptual model of regional soil C accumulation in black spruce communities of interior Alaska. Stronger effects are indicated by thicker lines, and negative correlations are indicated by (-). Squares indicate the primary environmental drivers of soil C accumulation with measured variables in parentheses (), circles indicate processes.

Table 3.1. Independent variables used in multiple regression analysis, where the dependent variables were total soil carbon, total carbon in the organic soil, and total carbon in the mineral soil.

Plant community characteristics	Abiotic characteristics	Stand/tree characteristics
NMDS Axis 1	Elevation (m)	NBAI
NMDS Axis 2	Slope (°)	Density of stand (trees/ha)
NMDS Axis 3	Aspect (°)	Stand age
Vascular richness	Thaw depth (m)	Age of oldest tree*
Lichen richness	Mineral soil pH	C/N ratio of live needles
Moss richness	Soil moisture	
Sphagnum richness	Soil texture	

*Age of oldest tree sometimes differed from stand age if the stand had multiple cohorts.

Table 3.2. Pearson correlation coefficients for NBAI, C/N ratio of needles and soil, total soil nitrogen, and total soil carbon. NBAI is negatively correlated with soil carbon, soil C/N ratio is positively correlated with soil carbon, and total soil n is highly positively correlated with soil carbon.

	Total Soil C (kg/m^2)
NBAI (%NBAI)	-0.401*
Needle C/N ratio	0.241
Soil C/N ratio	0.423*
Total Soil N (g/m^2)	0.936**

* Correlation is significant at the 0.05 level (2-tailed)
**Correlation is significant at the .01 level (2-tailed)

Table 3.3. Multiple regressions for three soil carbon components for all sites across interior Alaska. Model presented explains the most variance, all coefficients are significant at ≤0.05. Community indices are in bold (n = 32, 13, and 15 for all sites, acidic, and nonacidic, respectively).

Dependent variable	r^2/adjusted r^2	Predicting variables	Coefficient	Beta	Pvalue
ALL SITES					
Total soil carbon	.588/.481	Constant	31.021		0.0001
		Axis 1	-7.533	-0.746	0.002
		pH	-2.943	-0.62	0.011
		NBAI	-377.619	-0.516	0.003
		Axis2	-3.896	-0.471	0.01
		***Sphagnum* richness**	1.085	0.419	0.006
		Stand age	-0.02	-0.329	0.043
Soil carbon in the organic	.440/.354	Constant	4.941		0.024
		Aspect	0.001	0.478	0.007
		NBAI	-291.241	-0.425	0.009
		Slope	-0.586	-0.42	0.018
		Soil moisture	0.110	0.368	0.021
Soil carbon in the mineral	0.550/.407	Constant	6.546		0.073
		Aspect	0.013	-0.732	0.002
		Axis 1	-3.236	-0.572	0.019
		Slope	0.447	0.538	0.012
		pH	-1.349	-0.508	0.041
		Moss richness	0.476	0.514	0.003
		Vascular richness	0.221	0.440	0.033
		NBAI	-160.683	-0.392	0.028
ACIDIC SITES					
Total soil carbon	.359/.305	Constant	-2.033		0.042
		C/N of live needles	0.256	0.599	0.005
Soil carbon in the organic	.766/.702	Constant	2.659		0.494
		Axis 3	-6.617	-0.793	0.001
		Moss richness	-1.279	-0.759	0.001
		C/N of live needles	0.321	0.497	0.007
Soil carbon in the mineral	.456/.358	Constant	-2.088		0.559
		Slope	0.424	0.505	0.044
		C/N of live needles	0.149	0.454	0.066
NONACIDIC SITES					
Total soil carbon	.805/.733	Constant	8.983		0.005
		Soil moisture	0.183	0.549	0.002
		***Sphagnum* richness**	1.687	0.459	0.006
		NBAI	-297.561	-0.347	0.028
		Stand age	-0.180	-0.248	0.099
Soil carbon in the organic	.708/.562	Constant	9.041		0.002
		NBAI	-396.775	-0.496	0.025
		***Sphagnum* richness**	1.506	0.464	0.034
Soil carbon in the mineral	.782/.709	Constant	7.967		0.0001
		Active layer	-0.032	-0.493	0.005
		Slope	-0.454	-0.459	0.012
		Soil moisture	0.063	0.444	0.015
		Stand age	-0.011	-0.367	0.024

References

Aber, J. D., and J. M. Melillo. 2001. Terrestrial Ecosystems, 2nd edition. Harcourt-Academic Press, San Diego.

Ahrens, R. J., J. G. Bockheim, and C. Ping. 2004. The Gelisol order in Soil Taxonomy. Pages 2-10 *in* J. Kimble, editor. Cryosols: Permafrost-affected soils. Springer-Verlag, New York.

Anderson, D. S., R. B. Davis, and J. A. Janssens. 1995. Relationships of bryophytes and lichens to environmental gradients in Maine peatlands. Vegetatio **120**:147-159.

Atkins, S., S. Bosak, A. Heinz, J. Seldon, N. Matson, and A. St. John. 1998. Methods of ecosystem analysis: Dendrochronology (AKA Tree rings) on Totoket MT, North Brandford, CT. *in*. http://www.yale.edu/fes519b/totoket/treering/treerings_results.html.

Bisbee, K. E., S. T. Gower, and J. M. Norman. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia **129**:261-270.

Bonan, G. B., and H. H. Shugart. 1989. Environmental Factors and Ecological Processes in Boreal Forests. Annual Review of Ecology and systematics **20**:1-28.

Bonan, G. B., and K. Van Cleve. 1992. Soil temperature, nitrogen mineralization, and carbon source-sink relationships in boreal forests. Canadian Journal of Forest Research **22**:629-639.

Braun-Blanquét, J. 1965. Plant sociology: The Study of Plant Communities. Hafner, London.

Chapin III, F. S. 1983. Nitrogen and phosphorus nutrition and nutrient cycling by evergreen and deciduous understory shrubs in an Alaskan black spruce forest. Canadian Journal of Forest Research **13**:773-781.

Chapin III, F. S., M. S. Bret-Harte, S. E. Hobbie, and H. Zhong. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science **7**:347-358.

Chapin III, F. S., and K. Danell. 2001. Boreal Forest. *in* F. S. Chapin III, O. E. Sala, and E. Huber-Sannwald, editors. Ecological Studies 152. Biodiversity in a changing climate. Springer, New York.

Chapin III, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, E. S. Osvaldo, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science **277**:500-504.

Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, T. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature **405**:234-242.

Devolder, A. 1999. Fire and climate history of black spruce forests, Kenai National Wildlife Refuge, Alaska. M.S. Northern Arizona University, Flagstaff.

Diaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Marti, J. P. Grime, F. Zarrinkamar, Y. Asri, S. R. Band, S. Basconcelo, P. Castro-Diez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Perez-Harguindeguy, M. C. Perez-Rontome, F. A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny,

V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martinez, A. Romo-Diez, S. Shaw, B. Siavash, P. Villar-Salvador, and M. R. Zak. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science **15**:295-304.

Dioumaeva, I., S. Trumbore, E. A. G. Schuur, M. L. Goulden, M. Litvak, and A. Hirsch. 2003. Decomposition of peat from upland boreal forest: Temperature dependence and sources of respired carbon. Journal of Geophysical Research **108**:8222-8234.

Dyrness, C. T. 1982. Control of Depth to Permafrost and Soil Temperature by the Forest Floor in Black Spruce/Feathermoss Communities. USDA, Forest Service. Pacific Northwest Forest and Range Experiment Stations.

Dyrness, C. T., and D. F. Grigal. 1979. Vegetation-soil relationships along a spruce forest transect in interior Alaska. Canadian Journal of Botany **57**:2644-2656.

Epstein, H. D., M. D. Walker, F. S. I. Chapin, and A. M. Starfield. 1999. A transient nutrient-based model of arctic plant community response to climatic warming. Ecological Monographs.

Flanagan, P. W., and K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Canadian Journal of Forest Research **13**:795-817.

Foster, D. R., and G. A. King. 1984. Landscape features, vegetation and developmental history of a patterned fen in south-eastern Labrador, Canada. Journal of Ecology **72**:115-143.

Gower, S. T., O. Krankina, R. J. Olson, M. J. Apps, S. Linder, and C. Wang. 2001. Net

Primary Production and carbon allocation patterns of boreal forest ecosystems. Ecological Applications **11**:1395-1411.

Gower, S. T., J. Vogel, T. K. Stow, J. M. Norman, C. J. Kucharik, and S. J. Steele. 1997. Carbon distribution and aboveground net primary production of upland and lowland boreal forests in Saskatchewan and Manitoba. Journal of Geophysical Research **102**:029-041.

Harden, J., K. P. O'Neill, S. Trumbore, H. Veldhuis, and B. J. Stock. 1998. Moss and soil contribution to the annual net carbon flux in a mature boreal forest. Journal of Geophysical Research **102**:28805-28816.

Harden, J., K. P. O'Neill, S. E. Trumbore, H. Veldhuis, and B. F. Stocks. 1997. Accumulation and turnover of carbon in soils of the BOREAS NSA: 2 Soil contribution to annual net C flux in a maturing spruce-moss forest (OBS NSA). Journal of Geophysical Research **102**:805-816.

Harden, J., S. Trumbore, B. J. Stock, A. Hirsh, S. T. Gower, K. P. O'Neill, and E. Kasischke. 2000. The role of fire in the boreal carbon budget. Global Change Biology **6**:174-184.

Heilman, P. E. 1968. Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. Ecology **49**:331-336.

Hinzman, L., L. A. Viereck, P. Adams, V. E. Romanovsky, and K. Yoshikawa. in press. Climatic and permafrost dynamics in the Alaskan boreal forest. *in* M. Oswood and F. S. Chapin III, editors. Alaska's Changing Boreal Forest. Oxford University Press, Oxford.

Hobbie, S. E., K. J. Nadelhoffer, and P. Hogberg. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant and Soil **242**:163-170.

Hooper, D. U., D. G. Bignell, V. K. Brown, L. Brussard, J. M. Dangerfield, D. H. Wall, D. A. Wardle, D. C. Coleman, K. E. Giller, P. Lavelle, W. H. Putlen, D. Ruiter, J. Rusek, W. L. Silver, T. M. Tiedje, and V. Wolters. 2000. Aboveground and belowground biodiversity in terrestrial ecosystems: Pattern, mechanisms, and feedbacks. Bioscience **50**:1049-1061.

Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. in press. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge and needs for future research. Ecological Applications.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science **277**:1302-1305.

Kasischke, E., K. P. O'Neill, N. H. F. French, and B.-C. L.L. 2000. Controls on patterns of biomass burning in Alaskan boreal forest. *in* E. Kasischke and B. J. Stock, editors. Fire, Climate Change, and Carbon Cycling in the North American Boreal Forest. Springer-Verlag, New York, NY.

Katz, N. J. 1926. *Sphagnum* bogs of central Russia: Phytosociology, ecology and succesion. Journal of Ecology **14**:177-202.

Kuhry, P., and B. J. Nicholson. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Canadian Journal of Botany **71**:10-22.

Liski, J., and C. J. Westman. 1997. Carbon storage in forest soil in Finland 1. Effect of thermoclimate. Biogeochemistry **36**:239-260.

Litton, C. M., M. G. Ryan, and D. H. Knight. 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. Ecological Applications **14**:460-475.

Marschner, H. 1995. Mineral Nutrition of Plants, second edition. Academic Press, London.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4.25. MjM Software Design, Gleneden Beach.

McGuire, A. D., C. Wirth, M. J. Apps, J. Beringer, J. Clein, H. Epstein, D. W. Kicklighter, J. S. Bhatti, F. S. Chapin III, B. de Groot, D. Efremov, W. Euguster, M. Fukuda, T. gower, L. Hinzman, B. Huntley, G. J. Jia, E. Kasischke, J. Melillo, V. E. Romanovsky, A. Shvidenko, E. Vaganov, and D. A. Walker. 2002. Environmental variation, vegetation distribution, carbon dynamics and water/energy exchange at high latitudes. Journal of Vegetation Science **13**:301-314.

Mitchell, R. J. 1993. Path analysis: Pollination. Pages 211-231 *in* S. M. Scheiner and J. Gurevitch, editors. Design and Analysis of Ecological Experiments. Chapman & Hall, New York.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Neff, J. C., and D. U. Hooper. 2002. Climate and Vegetation controls over soil organic matter dynamics. Global Change Biology **8**:872-884.

O'Connell, K. E. B., S. T. Gower, and J. M. Norman. 2003a. Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities. Ecosystems **6**:236-247.

O'Connell, K. E. B., S. T. Gower, and J. M. Norman. 2003b. Net ecosystem production of two contrasting boreal black spruce forest communities. Ecosystems **6**:248-260.

Osterkamp, T. E., and V. E. Romanovsky. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost and Periglacial Processes **10**:17-37.

Rieger, S., D. B. Schoephorster, and C. E. Furbush. 1979. Exploratory Soil Survey of Alaska. US Soil Conservation Service, Washington, D.C.

Ruess, R. W., R. L. Hendrick, A. J. Burton, K. S. Pregitzer, B. Sveinbjornsson, M. F. Allen, and G. E. Maurer. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecological Monographs **73**:643-662.

Ruess, R. W., K. Van Cleve, J. Yarie, and L. A. Viereck. 1996. Comparative estimates of fine root production in successional taiga forests in the Alaska interior. Canadian Journal of Forest Research **26**:1326-1336.

Skre, O., and W. C. Oechel. 1979. Moss production in a black spruce *Picea mariana* forest with permafrost near Fairbanks, Alaska, with two permafrost-free stands. Holarctic ecology **2**:249-254.

Slaughter, C. W., and C. S. Benson. 1986. Proceedings, Cold Regions Hydrology. Pages

101-109 *in* D. L. Kane, editor. American Water Resources Association, Bethesda, USA.

Sundberg, S., and H. Rydin. 2002. Habitat requirements for establishment of *Sphagnum* from spores. Journal of Ecology **90**:268-278.

Sweetnam, T., and E. K. Sutherland. 1985. Using dendrochronology to measure the growth of defoliated trees. Agricultural Handbook No. 639, USDA Forest Service.

Thompson, C., J. Beringer, F. S. Chapin III, and A. D. McGuire. 2004. Structural complexity and land-surface energy exchange along a gradient from arctic tundra to boreal forest. Journal of Vegetation Science **15**:397-406.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

Trumbore, S., and J. Harden. 1998. Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study. Journal of Geophysical Research **102**:28817-28830.

Van Cleve, K., F. S. Chapin III, C. T. Dyrness, and L. A. Viereck. 1991. Element cycling in taiga forest: State-factor control. Bioscience **41**:78-88.

Van Cleve, K., and C. T. Dyrness. 1983. Effects of forest-floor disturbance on soil-solution nutrient composition in a black spruce ecosystem. Canadian Journal of Forest Research **13**:894-902.

Van Cleve, K., C. T. Dyrness, L. A. Viereck, J. F. Fox, F. S. Chapin III, and W. C. Oechel. 1983a. Taiga ecosystems in interior Alaska. Bioscience **33**:39-44.

Van Cleve, K., W. C. Oechel, and J. L. Hom. 1990. Response of black spruce ecosystems to soil temperature modification in interior Alaska. Canadian Journal of Forest Research **20**:1530-1535.

Van Cleve, K., L. Oliver, and R. Schlentner. 1983b. Productivity and nutrient cycling in the taiga forest ecosystem. Canadian Journal of Forest Research **13**:747-766.

Van Veen, J. A., and P. J. Kuikman. 1990. Soil structure aspects of decomposition of organic matter by micro-organisms. Biogeochemistry **11**:213-233.

Viereck, L. A. 1973. Wildfire in the taiga of Alaska. Journal of Quaternary Research **3**:465-495.

Viereck, L. A. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Canadian Journal of Forest Research **13**:703-720.

Viereck, L. A., C. T. Dyrness, A. R. Batten, and K. J. Wenzlick. 1992. Alaska Vegetation Classification. General Technical Report PNW-GTR-286 USDA Forest Service Pacific Northwest Research Station.

Viereck, L. A., and W. F. Johnston. 1990. *Picea mariana* (Mill.) B.S.P. black spruce. Pages 227-237 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Forest Service, U.S. Department of Agriculture, Washington D.C.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. The American Naturalist **119**:552-572.

Vitousek, P. M. 2004. Nutrient cycling and Limitation: Hawai'i as a model system. Princeton University Press, Princeton.

Vitousek, P. M., and D. U. Hooper. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. *in* D. Schulze and H. A. Mooney, editors. Biological Diversity and Ecosystem Function. Springer-Verlag, Berlin.

Vitt, D. H. 2000. Peatlands: Ecosystems dominated by bryophytes. Pages 312-343 *in* A. J. Shaw and B. Goffinet, editors. The Biology of Bryophytes. Cambridge University Press, Cambridge.

Vogel, J., D. Valentine, and R. W. Ruess. in press. Soil and root respiration in mature Alaskan black spruce that vary in soil organic matter decomposition rates. Canadian Journal of Forest Research.

Walker, M. D., D. A. Walker, and N. A. Auerbach. 1994. Plant Communities of a tussock tundra landscape in the Brooks Range foothills, Alaska. Journal of Vegetation Science **5**:843-866.

Wedin, D., and D. Tilman. 1990. Species effects on nitrogen cycling: A test with perennial grasses. Oecologia **84**:433-441.

Whittaker, R. J. 1975. Communities and ecosystems. Macmillan, New York.

Zimov, S. A., T. V. Voropaev, I. P. Semiletov, S. P. Davidov, S. F. Prosiannikov, F. S. Chapin III, M. C. Chapin, S. Trumbore, and S. Tyler. 1997. North Siberian Lakes: A methane source fueled by Pleistocene carbon. Science **277**:800-802.

Appendix 3.1.

Ecosystem parameters measured for 36 black spruce sites as well as a selection of site variables.

Table A.1. Site, stand, and soil properties for each site. Data are means ± standard error.

	Site characteristics				Stand/tree characteristics					Soil characteristics			
Site	veg class	elevation (m)	slope (°)	aspect (°)	site index (BAI) (%)	density trees/ha	stand age (yr)	Recruit-ment	C/N ratio needles	thaw depth (cm)	min soil pH	total N (g/m2)	total C kg.m2)
TKN0102	acidic	426	5	90	0.0084 ± 0.0040	1683	167 --	1	38.5	78 ± 7	4.24	172 -- --	4.4 -- --
TKN0103	acidic	400	9	20	0.0043 ± 0.0007	980	170 --	1	54.8	68 ± 4	3.95	548 ± 75	16.5 ± 3.8
TKN0104	acidic	872	1	184	0.0274 --	895	144 --	1	43.0	>120 --	4.11	311 ± 58	5.3 ± 1.2
TKN0105	acidic	716	7	188	0.0178 ± 0.0088	1634	90 --	1	23.5	>120 --	5.65	383 ± 120	7.9 ± 2.6
TKN0122	acidic	410	0	0	0.0103 ± 0.0024	5653	87 ± 3	2	42.5	>120 --	5.95	398 ± 66	9.8 ± 1.8
TKN0137	acidic	485	0	0	0.0120 ± 0.0033	4474	82 ± 4	3	44.9	55 ± 2	5.24	355 ± 20	8.4 ± 0.6
TKN0139	acidic	270	5	54	0.0122 ± 0.0029	6664	86 ± 2	2	56.7	52 ± 2	4.71	542 ± 36	12.4 ± 0.1
TKN0140	acidic	385	0	0	0.0159 ± 0.0065	1646	96 ± 6	2	49.7	63 ± 2	4.83	320 ± 57	6.1 ± 2.4
TKN0144	acidic	382	0	0	0.0156 ± 0.0027	5407	155 --	1	56.0	58 ± 6	4.91	634 ± 158	16.8 ± 5.4
TKN0149	acidic	717	8	120	0.0057 ± 0.0008	3629	204 --	1	52.2	55 ± 3	5.07	545 ± 194	11.4 ± 2.7
TKN0150	acidic	775	3	84	0.0055 ± 0.0004	1680	174 --	1	43.4	51 ± 4	5.65	439 ± 69	10.1 ± 1.4
TKN0152	acidic	876	0	0	0.0067 ± 0.0010	2153	95 ± 2	2	42.1	88 ± 6	5.70	406 ± 237	9.8 ± 6.8
TKN0153	acidic	815	1	64	0.0082 ± 0.0012	8190	186 ± 7	2	46.5	79 ± 4	6.59	415 ± 82	8.8 ± 1.9
TKN0154	acidic	802	6	332	0.0047 ± 0.0011	2685	137 ± 1	3	48.1	44 ± 2	5.44	422 ± 58	8.2 ± 1.2
TKN0107	nonacidic	327	0	0	0.0137 ± 0.0047	1494	74 ± 5	3	36.2	54 ± 2	6.02	522 ± 29	11.5 ± 1.0
TKN0116	nonacidic	473	0	0	0.0049 ± 0.0007	3052	100 ± 14	3	47.1	47 ± 3	5.64	1238 ± 330	24.7 ± 7.0
TKN0117	nonacidic	480	0	0	0.0197 ± 0.0047	2799	152 ± 5	2	43.4	109 ± 6	6.50	323 ± 13	7.0 ± 0.6
TKN0118	nonacidic	448	2	303	0.0053 ± 0.0014	4189	182 ± 3	2	36.0	61 ± 2	6.17	750 ± 25	17.8 ± 1.3
TKN0119	nonacidic	429	0	0	0.0148 ± 0.0090	3775	295 ± 13	3	47.3	54 ± 2	5.54	300 ± 21	7.5 ± 0.7
TKN0120	nonacidic	430	0	0	0.0131 ± 0.0012	2590	188 ± 2	3	54.2	44 ± 1	5.83	397 ± 142	9.9 ± 3.2
TKN0121	nonacidic	430	0	0	0.0049 ± 0.0022	13212	119 ± 4	2	44.8	All rock hits	5.34	384 ± 24	11.7 ± 1.7
TKN0123	nonacidic	380	0	0	0.0061 ± 0.0011	3981	93 ± 1	2	42.7	91 ± 5	5.67	333 ± 27	8.3 ± 0.8
TKN0125	nonacidic	425	0	0	-- --	4328	44 ** --	2	51.7	106 ± 5	6.22	384 ± 35	8.3 ± 1.4
TKN0133	nonacidic	218	0	0	0.0065 ± 0.0014	5447	86 ± 2	2	64.3	46 ± 1	5.94	557 ± 16	13.3 ± 0.6
TKN0141	nonacidic	374	2	290	0.0196 ± 0.0068	639	86 ± 4	2	56.6	60 ± 3	6.72	523 ± 134	11.3 ± 1.8
TKN0146	nonacidic	224	1	364	0.0088 ± 0.0011	9246	90 ± 2	2	58.5	51 ± 4	6.19	529 ± 34	11.2 ± 0.6
TKN0147	nonacidic	190	0	0	0.0141 ± 0.0054	6249	86 ± 5	2	53.0	44 ± 1	6.13	684 ± 63	14.8 ± 0.8
TKN0155	nonacidic	807	5	340	0.0057 ± 0.0006	3882	198 * --	3	52.3	47 ± 2	5.54	513 ± 3	11.5 ± 1.2
TKN0157	nonacidic	645	4	114	0.0119 ± 0.0046	4535	99 ± 3	3	61.2	70 ± 6	6.72	355 ± 1	10.1 ± 0.1
TKN0142	treeline	336	5	348	0.0151 ± 0.0045	1240	95 ± 6	3	51.7	73 ± 6	7.92	434 ± 36	8.5 ± 0.3
TKN0143	treeline	329	2	264	0.0107 ± 0.0019	2215	97 ± 3	2	53.4	46 ± 1	7.01	625 ± 55	11.6 ± 0.6

*only one tree count in this cohort, plus one much older tree counted but not included here.

**only one tree count available

CHAPTER 4: LEGACY EFFECTS VERSUS STATE FACTOR CONTROLS ON COMMUNITY COMPOSITION

"...For what is the present after all but a growth out of the past?"
-Walt Whitman

---

*Manuscript title: Alternative stable states following fire in Alaska's boreal black spruce communities: Wildfire legacy effects versus state factor controls. Authors: T.N. Hollingsworth, F.S. Chapin III, and M.D. Walker. Prepared for submission to American Naturalist.

Abstract

Landscape patterns of community assemblages reflect both the relationship between vegetation and environment as well as legacies of previous disturbances. In the boreal forest, fire is a key regulator of both the structure and functioning of forest communities, yet the composition of mature late-successional communities is assumed to reflect only environmental influences and to be independent of fire history. Here, I quantify fire history in 141 mature black spruce stands across a region of interior Alaska. I relate fire history, both the severity and time since disturbance, to the species composition of these stands using ordination techniques. Finally, I use discriminant function analysis to partition the extent to which knowledge of fire history improves our ability to predict black spruce communities and community subtypes across the landscape. Although fire history did not significantly predict communities, it did significantly predict community subtypes. The results suggest that fire has a lasting effect on the vegetation composition of mature black spruce stands, and it contributes to the presence of alternative stables states of these black spruce stands in interior Alaska. Based on my results, I present five mechanisms in which alternative stable states after fire are possible.

Introduction

The vegetation composition of a region is often viewed as a relatively stable configuration that conforms to environmental gradients (Whittaker 1967, Peet 1985). This view is based on the assumption that there is a single stable state for each point in the environmental matrix. However, alternative community states could exist in a particular environment if there was either (1) a difference in starting conditions such as initial species densities or the order in which species are introduced (Drake 1991) or (2) a disturbance generates large changes in the relative abundance of species (Petraitis and Latham 1999). These events can produce alternative states, even when the species are drawn from a single regional pool (Law and Morton 1996). Although supported by theory, the existence of alternative stable states is rarely tested in field studies because of the large sample size required to partition the variance in species composition attributable to current environmental conditions versus differences in starting conditions or changes in species densities. In addition, differences in initial conditions are difficult to document in late-successional stands. Here, a comparative approach is used to quantify the legacy effects of past fire disturbance versus current abiotic controls in predicting mature black spruce community composition throughout interior Alaska.

The boreal forest covers approximately 6.7 million km^2 across North America and Eurasia (Scott 1995), making it the second largest terrestrial biome (Whittaker 1975). Fire is the dominant agent of disturbance in the boreal forest and strongly influences landscape patterns of community structure and composition by determining the spatial distribution of early and late successional stands (La Roi 1967, Shafi and Yarranton

1973, Foster 1985, Payette 1992, Arseneault 2001, Johnstone et al. 2004). In other systems, disturbances such as agriculture can create biotic and abiotic legacies that determine the composition and functioning of late-successional stands (Foster and Motzkin 1998). Biotic legacies refer to types, quantities, and patterns or organisms and biotic structures that persist after a disturbance, sometimes referred to as "residuals" whereas abiotic legacies are physical modifications of the environment that may result from a disturbance (Turner and Dale 1998).

The structure and composition of late-successional stands in the Alaskan boreal forest are usually thought to be determined by abiotic state factors such as topography, climate, time, and parent material (Van Cleve et al. 1991). However, the role of fire disturbance in creating legacy effects on composition of late-successional stands has never been tested in the boreal forest of Alaska. Of particular interest is whether fires of different severities might generate alternative stable states in mature late-successional forests.

Fire leads to predictable patterns of community composition across repeated disturbance cycles when prefire vegetation strongly determines postfire community composition (Frelich and Reich 1999). This occurs if variation in the successional trajectories is closely linked to initial patterns of recruitment and recovery (Viereck 1973, Johnstone et al. 2004), and strong environmental effects on vegetation cause a return to pre-fire composition (Dix and Swan 1970, Mann and Plug 1999). A return to prefire community composition seems likely in the boreal forest, the northern limit of forest biomes, where the environment and vegetation relationships are strong and diversity of vascular plants is low. However, most studies on successional trajectories in the boreal forest have concentrated on either short-term fire effects (less than 50 years) or the effects at a broad vegetation scale, i.e., forest type. Sampling a large number (141) of mature black spruce stands (>60 years old) across a large, environmentally diverse region, that of interior Alaska, enables an examination of the long-lasting effects of fire (abiotic and biotic legacies) on black spruce vegetation.

Within the Alaskan boreal forest, black spruce is the most widespread forest type (Viereck et al. 1992), covering over 40% of boreal Alaska (Van Cleve 1983). Black spruce communities change in species composition across a large range of environmental conditions (Viereck 1973, Dyrness and Grigal 1979) and are well adapted to fire disturbance. The chemical make-up of black spruce makes them highly flammable (Viereck 1973). Black spruce forests also tend to be associated with either a thick organic mat that can continue to burn throughout the growing season or a highly flammable moss or lichen layer. Following fire, black spruce reestablishes quickly by seed released from semi-serotinous cones (Viereck 1973), and species such as *Eriophorum spp.* and *Salix spp.* regenerate quickly from suckering roots (Chapin et al. 2004).

The floristics of these communities vary most strongly with mineral soil pH and soil moisture/topography (Chapter 2) leading to a classification separating two community types related to pH and three subtypes related to topography/soil moisture regime. The Acidic Black Spruce/Lichen Forest is dominated by fruticose lichens and many species of mosses and has a wet subtype (Acidic wet bogs). The

Nonacidic Black Spruce/Rose/Horsetail Forest is characterized by high vascular plant diversity, especially various species of *Equisetum*, and has both a wet and dry subtype (Nonacidic wet fens and Nonacidic dry forest). The Treeline Black Spruce Woodland was identified based on presence of common tundra vascular and nonvascular plants. These floristic patterns suggest that environmental factors exert a strong influence on the floristic composition of mature black spruce stands in boreal Alaska. The influence of fire disturbance on floristic composition of these mature black spruce communities has not been tested, however, because traditional techniques in vegetation science emphasize the relationship between vegetation and the environment, and assume that legacy effects are negligible.

The purpose of this study is to address the following questions: 1) Is it possible to quantify fire history, in terms of severity and time since fire, in mature black spruce communities in interior Alaska? 2) What is the role of fire legacy in determining the floristic composition of mature black spruce communities and subtypes? 3) Under what circumstances is the role of fire legacy more important than environment in determining community composition?

Methods

Field sampling

The study region extended from the Alaska Range (Latitude 63°N) to the Brooks Range (Latitude 67°N) covering approximately 25,000 km^2 (Figure 4.1). Interior Alaska is a region of discontinuous permafrost with approximately 75-80% of the ground underlain by permafrost (Osterkamp and Romanovsky 1999). The mean annual permafrost temperature ranges from -0.5°C to –2°C, and the ground is covered with snow and ice for six to nine months of the year (Slaughter and Benson 1986). This region has a continental climate with extreme temperatures ranging from –70°C to +35°C. Annual precipitation is low (30mm), of which about 35% falls as snow (Hinzman et al. in press). Soils show relatively minor morphological development and most are classified as Inceptisols, Entisols, Histosols, or Gelisols (Rieger et al. 1979, Ahrens et al. 2004).

I sampled 141 mature black spruce stands to examine fire history. These sites included nine treeline sites, 60 nonacidic sites (pH > 5.5), and 72 acidic sites (pH < 5.5), all selected to span the regional variability in black spruce plant community composition (Chapter 2). I subjectively chose plot locations in areas of homogenous vegetation that were dominated by a black spruce overstory using a modification of the centralized replicate sampling procedure (Mueller-Dombois and Ellenberg 1974). At each site I sampled vegetation using the relevé method (Braun-Blanquét 1965, Mueller-Dombois and Ellenberg 1974). My relevés included a list of all vascular and nonvascular plant species present and an estimate of percent cover of each species using the Braun-Blanquét cover-abundance scale (Chapter 2). All relevés were at least 2500 m^2 in size, and most were greater than 6400 m^2.

At each site I estimated latitude and longitude using a Trimble Geoexplorer 3 GPS unit, physical characteristics of the site including slope, aspect, elevation, topography, parent material, and geomorphology, site moisture through visual assessment of moisture at a site), soil moisture based on a scalar based on the amount of water that could be squeezed out of the soil in the field, disturbance (a scalar including fire [presence of charcoal, fire scars, and standing burnt trees], herbivores, humans, and other), and gross water flux in three categories: minerotrophic (noticeable running water through site), ombrotrophic (noticeable standing water at site), or no water present. I dug a soil pit to a depth of 100 cm or to frozen ground, whichever came first, measured the depths of the Oi, Oe, and Oa horizons, and the depth to bedrock or frozen soil. Soil samples were collected from the uppermost mineral horizon, and percent soil moisture and bulk density were determined. Soils were sieved and then sent to the UAF Palmer Research Station for determination of mineral pH, KCL-extractable NH_4 and NO_3, total C,N, P, K, and other major cations, cation exchange capacity, soil texture, and loss on ignition. Sites were revisited in September or October of the same year to measure maximum thaw depth. All abiotic or environmental data were related to the species composition of black spruce communities using multivariate ordination techniques (Chapter 2).

To estimate the age of the oldest trees in the stand I cored five to ten of the largest trees in each stand as close to the base of the tree as possible. I also recorded the dbh of each tree. To estimate stand age, which could be different than the age of the oldest tree in the stand, I recorded the number of size cohorts in each stand and the proportion of the total tree cover represented by each cohort. If the largest trees in the stand did not constitute the dominant cover class, I also cored five trees in the dominant cover class. Black spruce seedlings were counted as their own cohort, as were white spruce trees.

Black spruce cores were aged by counting annual growth rings with a microscope and visually cross-dated (Sweetnam and Sutherland 1985). If the pith was missed during coring, the distance to pith was estimated by fitting a circle template to the innermost curved ring, or by subtracting core length from the radius at core height. The number of years to the pith was then estimated empirically from age-diameter relationships based on trees in which the pith was obtained. The number of years the tree took to grow to the cored height (as close to the ground as possible) was estimated by a regression equation relating seedling height to age of black spruce trees on the Kenai Peninsula, Alaska (Devolder 1999). These ages were analyzed in ten-year age classes to account for errors in those estimates.

Quantifying fire history

The large number of stands sampled precluded a thorough documentation of fire history in each stand, where all the trees in the stand are aged. Therefore, my aim was to collect or visually assess variables in the field that could be used to more easily quantify fire history of each stand. I used the age of the trees cored to estimate the time since major recruitment, and the recruitment pattern and the even-agedness of each stand. Time since major recruitment was then used as a "time since disturbance" variable, assuming that a major recruitment was initiated by a fire. Based on the age of the tree cores, I observed three prominent patterns: 1) even-aged stands in which all trees cored were within ten years of each other, and in which time since fire was defined as the average age for all trees cored; 2) multi-cohort stands in which two or more distinct age cohorts were identified in which time since fire was defined as the age of the most abundant cohort; and 3) constant-recruitment stands in which the age of trees decreased in a uniform pattern in which time since fire was defined as the age of the oldest tree cored.

I counted the number of fire-scarred trees and measured the height of the fire scar on each tree. I also counted the number of charred burned standing (CBS) trees, dead standing trees that were severely burned in a previous fire. These counts were taken in a 50 x 50 m subplot in the middle of the 100 x 100 m relevé plot. The numbers of fire scared trees and CBS trees were then converted to an index based on the amount of each that occurred at each site (Table 4.1). I developed a tree crown fire severity index based on the number of fire scarred trees and the number of CBS trees in a stand (Table 4.1). A high density of live trees with fire scars represents a low-severity crown fire, whereas a high density of CBS trees represent a high-severity crown fire. In sites with a large number of CBS trees and fire scar trees, I assumed a severe crown fire that was patchy in nature (C. Fastie, personal communication).

Finally, charcoal in my soil pit was visually assessed by the depth and horizon in which it occurred and by the amount, which I assessed as 0-3, where 0 = no charcoal found in the soil, 1-2 = broken or partial layers of varying amounts, and 3 = a full layer of charcoal observed (Table 4.1). Soil horizons are described as Oi (histic organic recognizable litter layer), Oe (hemic organic unrecognizable litter layer), Oa (sapric humified organic matter), and mineral soil (Fanning and Fanning 1989). I created a ground fire severity index based on a combination of the amount and placement of charcoal in the soil (Table 4.1). Previous research indicated no significant relationship between age of stand and organic depth (Chapter 3) in a subset of these sites. Therefore, I interpreted the placement of charcoal to be more related to the amount of organic matter consumed (severity) rather than an indication of the time since fire. In addition, the more charcoal I found, the more severe I classified the ground fire (Table 4.1).

Statistical methods

Nonmetric multi-dimensional scaling (NMDS) ordinations were run to detect the main patterns in species composition, and ordination axes values (Axis 1 and Axis 2) were obtained for each site (Chapter 2) (PC-ORD 4.25) (McCune and Mefford 1999). These data were then used as a measure of species composition for future analyses. Unless specified, all other statistical analyses were performed in SPSS version 11.0.2.

I used a variety of statistical methods to explore the relationships between vegetation community data and fire history estimates. Descriptives were run to test for normality of all variables and to explore the variability in stand age of my sites. All continuous data (number of CBS trees and fire scarred trees, time since fire, and depth of charcoal) had relatively normal distributions. I tested correlations between my fire history variables (time since fire, crown severity, and ground severity) and Axis 1 and Axis 2 for all sites (n=141) with parametric 2-tailed Pearson correlation coefficients.

I ran independent sample t-tests (equal variance not assumed) to test for significant differences in time since fire between even-aged and non even-aged stands. I was interested in whether crown fire severity predicted even-agedness and ran a logistical regression (dependent variable = even-agedness [0=even-aged, 1=non even-aged], independent variables = crown fire severity variables [number of CBS trees and fire scars]).

After determining that the fire history variables were significantly correlated with ordination axes, I asked the question: how well do these fire-history variables improve my ability to predict my pre-defined black spruce communities? To answer this question I used Discriminant Function Analysis (DFA) to predict black spruce community and community subtype membership based on abiotic factors alone, and fire history alone. I excluded treeline sites from these analyses because I was interested in the differences in fire history between acidic versus nonacidic sites, and wet versus dry sites. DFA is an eigenanlysis technique that maximally separates a fixed number of predefined groups (McCune 1993). Due to the required assumptions of DFA (linearity, homogenous within-group variances, normality, and prior probabilities) it is rarely used as an ordination technique to describe the relationship of sites with differing species composition. However, I chose this technique because the vegetation communities were pre-defined based on a Braun-Blanquét classification, the within-group variances were similar, there was relatively equal distribution of sites among groups, and I was interested the relationship between environmental variables and my predefined communities (Karels et al. 2004).

DFA was used to predict the occurrence of a) the Acidic wet subtype (n = 43), b) the Acidic non-wet sites (n = 28). The latter lacked a set of diagnostic species, but had few or none of the acidic wet subtype diagnostic species. To simplify interpretation, these sites are referred to as a subtype, c) the Nonacidic wet subtype (n = 23), and d) the Nonacidic dry subtype (n = 36). Based on my NMDS ordination axes and correlations with environmental variables (Chapter 2, Table 2.2), mineral soil pH was the abiotic variable most strongly correlated with Axis 1, and elevation was the abiotic variable most strongly correlated with Axis 2 (Chapter 2). I therefore ran DFA with two different models. Model 1 used abiotic factors (pH and elevation) to predict black spruce community and community subtype membership, and Model 2 used fire history variables (time since fire, even-agedness of stand, and tree and ground severity) to predict community and community subtype membership. Because I was interested in how well a given model predicted subtype, and not which variables contributed the most to the model, all variables were entered simultaneously.

Kappa analysis determines if an error matrix generated by a classification scheme is significantly different than random (Congalton 1991). A Kappa coefficient and the resulting Z statistic were computed for each error matrix of my DFA classification. Kappa analysis was performed in SAS Version 8.01.

Results

Quantifying fire history

Time since fire: I compared the age of the oldest trees cored, and the time since fire with paired t-tests (Table 4.2). In the Treeline community types the mean of the age of the oldest tree did not differ significantly from time since fire. However, in both the Acidic and Nonacidic communities, and across all sites, the mean of the oldest tree was significantly older than the time since the most recent fire (P value = 0.0001; Table 4.2), most likely because it was not burned in the last fire, indicating that within these communities the age of the oldest tree in a stand is not a good predictor of the time since most recent disturbance. Therefore, in subsequent analyses I use only time since fire or major tree recruitment to represent age of stand.

Of the 141 stands sampled, 30% resulted from stand-replacing fires those having a single cohort, 47% had multiple cohorts, and 22% had relatively continuous recruitment without distinct cohort classes (Table 4.2). In all multi-cohort stands the most abundant cohort was never the oldest (data not shown). Within all three black spruce communities, multi-cohort stands were more abundant than either stand-replacing or continual recruitment stands. Within the Acidic wet subtype, however, stand replacement was the most prevalent recruitment type (Table 4.2). Even-agedness could also be an indicator of crown fire severity, however a logistical regression showed no significant correlation between the number of CBS trees, or fire scars and even-agedness of a stand ($r^2 = 0.042$, $P = 0.113$). This suggests that even-agedness is a better indicator of patchiness of burn than of burn severity. Only 30% of the mature black spruce stands I visited were even-aged (Table 4.2). The large number of multi-cohort stands could suggest that many black spruce stands do not result from stand-replacing fires, but this could be a function of the sampling area (50 X 50 m^2).

I further separated stands into single-cohort or multiple-cohort stands based on even-agedness, and examined the distribution of age (i.e., time since fire) (Figure 4.2). Time since the most recent fire varied ten-fold from 32 years to 312 years with a mean of 126 ± 4 years (mean ± standard error). Time since fire in single-cohort stands varied nine-fold, from 33 years old to 268 years old, with a mean age of 115 ± 5. Multi-cohort stands had a significantly less time since fire than even-aged stands (t value = 3.065 P =

0.003) and showed less variation (from 69 to 311 with a mean age of 143 ± 7). Time since fire showed a bimodal distribution with peaks at 80-100 years and 180-200 years (Figure 4.2). The second peak is mainly multi-cohort stands, suggesting that it could take a stand with surviving trees a century before it burns again, and points to a potential 100 year fire return interval in mature black spruce of boreal Alaska.

Severity of disturbance: Based on our data (i.e., time since last fire, tree crown severity, and ground severity), fire history was significantly correlated with species composition of mature black spruce stands (Table 4.3). Across all sites, crown severity was significantly negatively correlated with Axis 1 ($r = -0.33$) indicating that high crown severity was associated with species composition typical of nonacidic sites (Table 4.2, 4.3). Ground severity was positively correlated with Axis 2 ($r = 0.18$) indicating that low ground severity was associated with species composition typical of wetter sites, typically valley bottoms and lowlands and therefore lower in elevation (Table 4.2, 4.3). Time since fire was negatively correlated with Axis 2 ($r = -0.22$) indicating that fewer wet upland black spruce sites experienced fire most recently (Table 4.2, 4.3).

Fire history predictions of black spruce community types

I used DFA to determine if abiotic factors and/or fire history significantly predicted community types of mature black spruce stands. For both models there was one discriminant function (canonical correlation = 0.75 and 0.093, respectively) and only the abiotic factor model significantly discriminated among community type ($P < 0.001$ and 0.570, respectively; Table 4.4). DFA correctly classified 85% of the sites with the abiotic factors, and 53% with fire history variables (data not shown). This suggests that fire history does not explain a large amount of the variability in floristic composition when comparing black spruce communities.

Fire history predictions of black spruce community subtypes

For both the abiotic and fire history models the first discriminant function accounted for most of the variation (canonical correlation = 0.79 and 0.27, respectively) and both models significantly discriminated among community subtypes (Acidic wet, Acidic non-wet, Nonacidic wet, Nonacidic dry) (P = 0.002, 0.0001, 0.003, respectively; Table 4.4). The abiotic model had a second function that was significant in discriminating the community subtypes, but it contributed very little to the overall variation in the data (4%). Overall, DFA correctly classified the community subtypes 58% based on abiotic factors and 34% based on abiotic and fire variables (n=130) (Table 4.5). Prediction of the Nonacidic wet subtype increased 18% when the fire history model was used instead of an abiotic model, indicating a strong link between fire history and community composition for this subtype. The fire history model correctly classified the Acidic non-wet, the Acidic wet, and the Nonacidic wet subtype more often than expected (17% more, 1% more, and 35% more) (Table 4.5). To determine whether classifications were significantly different than random, I performed a Kappa analysis on the error matrices of my classifications. Both error matrices were significantly different than random (Z statistics 8.4 and 2.8, respectively) (Table 4.6).

In what community types is fire history the most important?

Fire history variables contributed significantly to my prediction of subtypes rather than community types. Therefore, I separated my sites based on community type (Nonacidic versus Acidic) and repeated the DFA on each community type separately based on abiotic factors alone, fire history alone, and age of oldest tree in the stand. I included the age of oldest tree to evaluate the importance of paludification in predicting the Acidic wet subtype. Paludification is the formation of peatlands caused by the redistribution of moisture over time which in turn causes wetter and more acidic valley bottoms (Birkeland 1999), and is one of the main processes thought to lead to wet acidic black spruce sites (Van Cleve et al. 1991). Based on earlier results which showed that wetter sites tend to experience less severe fires (Table 4.2, Figure 4.3), I determined that the age of oldest tree would be more suitable as a surrogate than "time since fire" for this change in vegetation over time caused by paludification.

Within the Nonacidic community type, DFA classified the sites into their correct subtype 58% with stand age (8% more than expected), 54% with abiotic factors alone (4% more than expected), and 62% with fire history alone (12% more than expected) (Table 4.7). This suggests fire history could be a better overall predictor of species composition within the nonacidic black spruce community type than are abiotic factors. Although none of three models based on stand age, abiotic, and fire history, significantly discriminated between the Nonacidic wet and dry subtypes ($P = 0.214$, 0.843, 0.100, respectively), fire history was the closest to significant (Table 4.7).

Within the acidic community type, DFA correctly classified each subtype 69% accurately with stand age alone (19% more than expected), 73% accurately with abiotic factors alone (23% more than expected), and 78% accurately with fire history alone (28% more than expected) (Table 4.7). All three models (stand age, abiotic, and fire history) significantly discriminated between the Acidic wet and Acidic non-wet subtypes (P = 0.002, 0.0001, and 0.003, respectively; Table 4.7). Kappa analysis verified all three models were significantly different than random (Z statistics 3.8, 3.3, 4.7, respectively) with the highest significance found using fire history model (Table 4.6). This indicates that the paludification process, as represented by the age of oldest trees in a stand, is a significant process in the formation of the wet acidic subtype. Secondly, fire history could be more important than abiotic factors in separating Acidic subtypes.

Discussion

How does fire create alternative stable states of black spruce?

My results show that differences in species composition between Acidic and Nonacidic communities are driven primarily by state factors such as glacial history, site drainage, parent material, and topography, which control mineral soil pH and moisture (Table 4.4). Fire history contributes little information to the differences in species composition between Acidic and Nonacidic communities (Table 4.4). This suggests that an Acidic or Nonacidic black spruce stand, given enough time, will return to the same community type after a fire. In contrast, my results show that fire history exerts a strong influence on both the establishment of subtypes within these two major communities and shifts in species compositions within these subtypes (Table 4.5, 4.7), suggesting fire can act to create alternative stable states under otherwise similar environmental conditions.

I present a heuristic model to explain how these multiple stable states might be created or maintained. I suggest five pathways to multiple stable states, depending on fire severity: three pathways that promote the persistence of a prefire state, and two that lead to a switch in state (Figure 4.4).

(1) Low Ground Severity/High Legacy Mechanism (Figure 4.4-MechanismA):

Low ground fire severity coupled with effective reestablishment of prefire vegetation cause regeneration of prefire vegetation. These factors co-occur in the Nonacidic wet subtype and both of the dry subtypes. Low ground severity fires always lead to regeneration of the same prefire community subtype, because the understory species survive fire and regenerate vegetatively, with no long-term change in species composition (Figure 4.4; Frelich and Reich 1999, Mann and Plug 1999, Johnstone 2003). This mechanism occurs most frequently in the Nonacidic wet fen subtype, which has the longest time since fire (Table 4.2) and showed little evidence of severe ground fires due to high soil moisture (Figure 4.3). The high pH and associated species composition of this subtype could also indicate an increase in nutrient availability (as contrasted with Acidic wet sites), which could account for the observed increase in seedling or tree recruitment (Table 4.3, Figure 4.3).

(2) High Ground Severity/High Recruitment Mechanism (Figure 4.4-Mechanism B):

This mechanism is specific to dry subtypes where dry soils and shallow organic depths contribute to the greater likelihood of a severe ground fire (Table 4.2, Table 4.3, Figure 4.3). Severe ground fires lead to high seedling recruitment and establishment by the pre-fire species. Consequently, the dry subtype is maintained after fire.

(3) Strong Species-Effect Mechanism (Figure 4.4 - Mechanism C):

The acidic chemical properties of some *Sphagnum* species create a feedback between *Sphagnum* and their local environment that has been hypothesized to generate alternative states (Peterson 1984). *Sphagnum* can occur in acidic substrates, and some *Sphagnum* are known to excrete acids lowering the pH and overall acidity of the soil, thereby promoting the self-replacement of *Sphagnum* and reducing the likelihood of invasion by other acidiphilous species (Figure 4.4) (Sousa and Connell 1985). Acidic wet bogs also have a long fire interval. The nutrient-poor, acidic conditions and associated species composition cause larger organic mat and carbon accumulation (Chapter 3), which in turn decreases seedling or tree recruitment and establishment (Table 4.3, Figure 4.3). Viereck and Johnston (1990) suggested that post-fire black spruce stands tend to be both even-aged and multi-cohort and continuous recruitment stands are more prevalent in bogs or anywhere that the average interval between fires is greater than 200 years. In contrast, my results show that the fire return interval in even-aged stands is less than multi-cohort stands (Figure 4.2), and Acidic wet bogs show a higher number of even-aged stands, in contrast to the Nonacidic wet fens which show a higher number of multi-cohort stands (Table 4.3), suggesting a higher fire return interval in these sites. My results suggest that as these Acidic wet sites age, they become more acidic and wet, and the probability of a stand replacing fire decreases (Figure 4.3; Kuhry 1994). This conclusion is also supported by evidence that stand age is a good predictor between Acidic wet and non-wet sites (Table 4.7). The interactions between the paludification process, stand age, and fire history control the species composition of this subtype.

(4) High Ground Severity/Shift in Environment Mechanism (Figure 4.4 - Mechanism D):

Given the likelihood for prefire conditions to persist after a fire, how does a change in state occur? This is most likely when a severe ground fire changes the starting conditions or abiotic factors, and/or the relative abundances of the residuals enough to shift a wet subtype to a dry subtype. This occurs in both Acidic and Nonacidic communities (Figure 4.4). For example, my results show a strong relationship between fire history and the Nonacidic wet fen subtype (Table 4.5, 4.7, Figure 4.3). Given a high severity ground fire, a Nonacidic wet fen could potentially flip to a Nonacidic dry forest after fire-induced changes in site drainage causing changes in the biochemistry and nutrient cycling at a site (i.e. Szumigalski and Bayley 1996, Thormann and Bayley 1997, Turetsky et al. 2000). The severe fire removes the moss layer, which provides new areas for recruitment, increasing the potential for a change in the community subtype to a Nonacidic dry forest. Similarly, an Acidic wet subtype could flip to an Acidic Non-wet state if the ground fire was severe enough to consume the *Sphagnum* and disrupt the *Sphagnum*/environment feedback.

(5) High Severity/New Tree Species Mechanism (Figure 4.4-Mechanism E):

If a new dominant tree, for example white spruce or aspen, established after fire, this could cause a complete shift to another ecosystem. This is most likely to occur if high crown severity reduces seed input from black spruce and/or if high ground severity or environmental change from climate warming favors the establishment of a different dominant tree species. For example, permafrost is already shallow in the dry subtypes relative to the wet subtypes (Chapter 2), and severe fires will increase the active layer of a site due to less insulation and the blackened surface (Viereck et al. in preparation). Therefore, it is unlikely that fire would promote a change in state from a dry to a wet black spruce subtype, where permafrost is usually thicker (Chapter 2). In contrast, these conditions might instead favor establishment of white spruce or aspen. These results are consistent with previous research indicating that regeneration and recruitment vary depending on the severity of the fire (i.e. Johnson 1981, Sirois 1993, Greene et al. 1999, Cater and Chapin 2000). For example, lodgepole pine is migrating northward in Canada, just east of the Alaskan border, where pine replaces spruce after severe fire at the northern limits of its current range (Johnstone and Chapin 2003). Litter accumulation by lodgepole pine alters understory composition and promotes frequent fire, causing a permanent change in ecosystem state.

The role of fire in shaping the current treeline vegetation communities

White spruce dominates treeline in boreal Alaska; even though treeline areas are not as productive or dry as “typical” white spruce stands and treeline sites are ecologically more similar to areas dominated by black spruce (Viereck et al. 1992, Lloyd and Fastie 2003). The domination of treeline by white spruce could be due to the earlier migration of white spruce into Alaska after the last glaciation (Edwards and Brubaker

1986), maintained by the lower frequency of lightning strikes in higher elevation/treeline areas as compared to other areas of the boreal forest (Dissing and Verbyla 2003). My results indicate that fire is a strong factor in promoting the establishment of black spruce at treeline. Firstly, treeline black spruce sites have the youngest trees and the shortest time since most recent disturbance (Table 4.3, Figure 4.3). Secondly, black spruce treeline sites showed the highest ground severity, suggesting that severe ground fires at treeline created favorable seedbed conditions for black spruce to establish. These results have large implications in a changing climate because fire could increase in treeline areas, causing shifts in dominant tree species and associated community composition.

The fire return interval in mature black spruce stands across the region of interior Alaska

The bimodal distribution of stand ages (i.e. time since most recent fire) and the high proportion of multi-cohort stands in the second peak of 180-200 years (Figure 4.2) are also observed in forest inventory data for all the forest types in interior Alaska (Crimp et al. 1997). This indicates a much longer fire return interval than previously observed in the Porcupine River Drainage of northeastern Alaska (Yarie 1981). My results are comparable to those of Fastie et al. (2002) near Fairbanks. These authors suggest a 100 to >250 year interval between fires in upland forest in interior Alaska over the last 200 to 300 years. The peak in stand ages at 100 years correlates with the gold rush in interior Alaska and associated logging and burning (Lloyd et al. in press). My data suggest that, in the absence of broad-scale human intervention, stand-replacing fires happen when black spruce sites are relatively young (less than 100 years), but as more time passes, the probability of a stand replacing fire decreases. This decrease could be due in part to the tendency of acidic sites to become wetter over time, or the accumulation of species such as mosses. My study area encompassed a large region with climate and topographical variation known to contribute to differences in fire regime. For example, the fire return interval increases from the east to the west of interior Alaska due to an increase in moisture (T.S. Rupp, personal communication). My results represent regional averages in fire return interval and the relationship between prefire species composition and fire severity at that spatial scale. It would be interesting to further analyze the relationship between regional fire return intervals, fire severity, prefire species composition in the context of the mechanisms and subtypes presented above in regions with different fire regimes.

Concluding remarks

This study evaluates the biotic effects of fire on the species composition of mature black spruce plant communities. I suggest adaptations to fire in species typical of black spruce ecosystems create legacy effects, which are reflected in the species composition of mature black spruce stands. Crown severity, ground severity, and time since fire each distinctly affected the long-term patterns of vegetation, and these effects were distinct from the influences of state factors. At large spatial scales, fire behavior and intensity are driven by macroscale climatic events (Duffy et al. submitted). However, at the scale of forest stands, differences in fire severity and behavior are more likely to be determined by the relationship between vegetation and the environment (Foster et al. 1998).

Prefire vegetation affects the severity of a fire, which in turn has a legacy effect on the regeneration of a site, and this legacy is reflected in the current species composition of mature black spruce stands in Alaska. The results presented here are significant not only in the face of a changing climate and fire cycle, but also in the context of modeling landscape and regional dynamics in boreal Alaska.

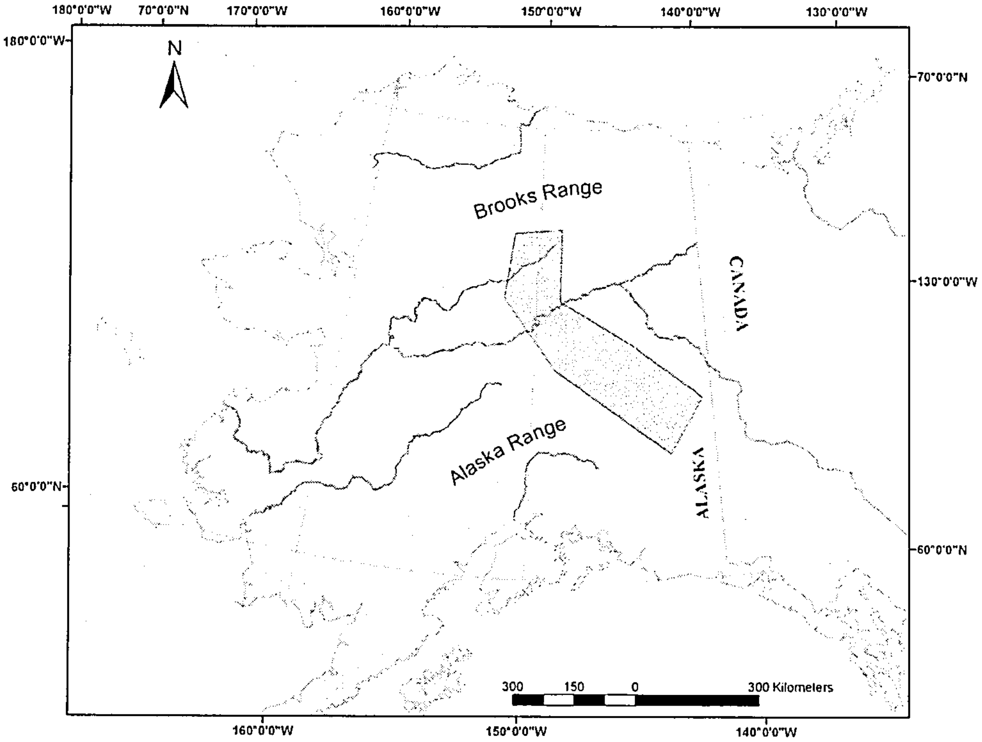

Figure 4.1. Map of the study region, bounded by the Alaskan Range to the north and the Brooks Range to the south. This large region is over 25,000 km^2.

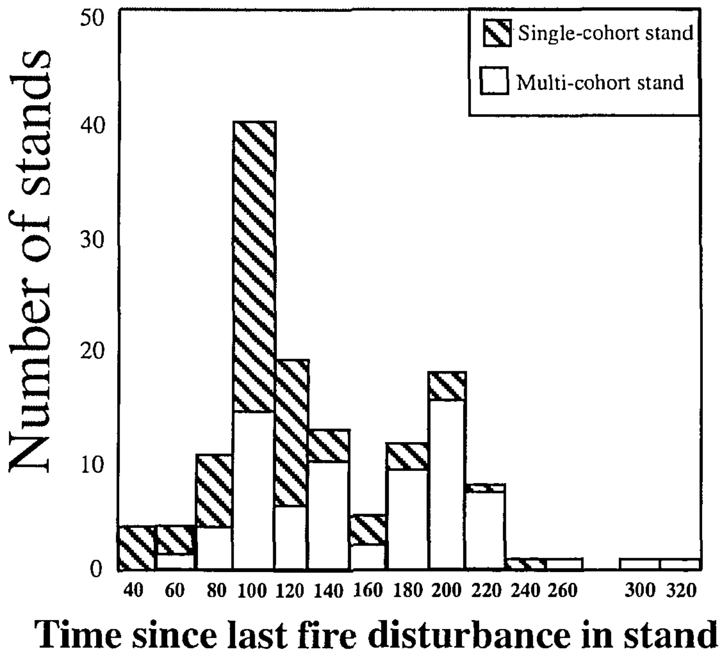

Figure 4.2. Age of 5-10 largest trees cored from each stand (n = 141), as represented by time since fire, and separated into single-cohort stands and multi-cohort stands.

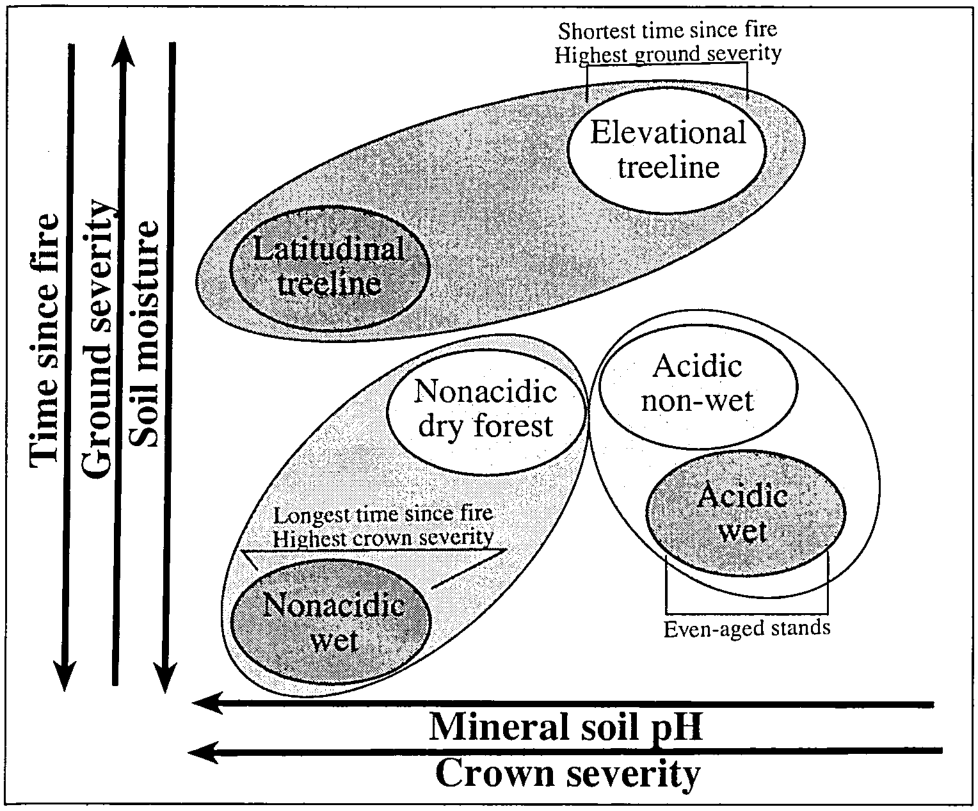

Figure 4.3. Conceptual diagram depicting theoretical distribution of black spruce communities and subtypes along the most important environmental gradients, modified from Figure 2.3. Fire history variables (severity and time since fire) are also shown based on correlations between species composition and fire history variables.

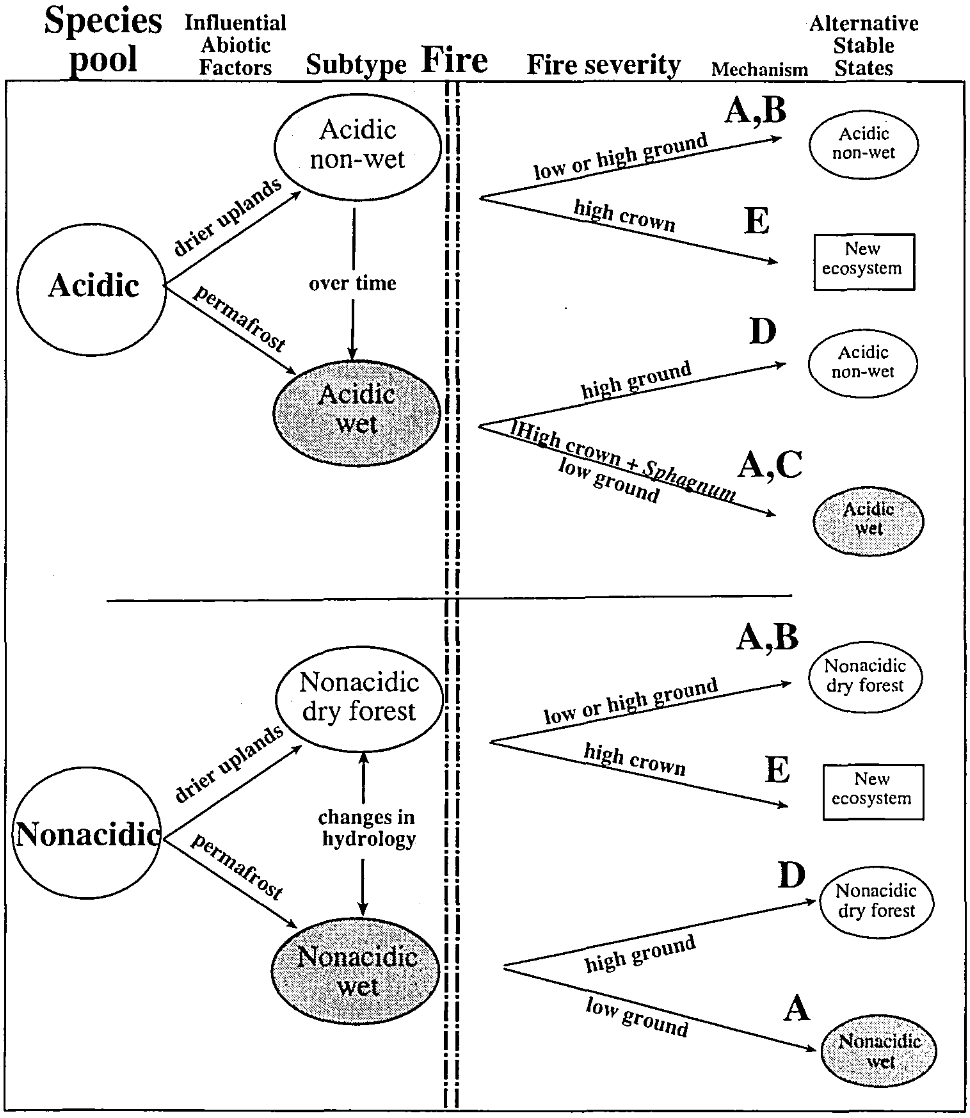

Figure 4.4. Heuristic model describing the relationship between fire, and alternative stable states of black spruce communities. Black spruce species pools are separated by differences in abiotic factors (i.e. parent material, glacial history, and site drainage), which are reflected in the mineral soil pH of each site. Over geologic time, nonacidic sites will tend to become more acidic, but at any given point in time, these communities are distinct in species composition. There are influential abiotic factors such as topography and presence of permafrost, which determine a smaller set of species within each community type. It is possible for these subtypes to exist in similar environmental conditions depending on the fire history of a site. Circles represent black spruce states and squares represent non-black spruce states.

Table 4.1. The variables used to assess fire severity (crown and ground) of mature black spruce communities.

Fire scar density	CBS tree density	**Crown severity index**	Where charcoal found	Amount of charcoal index[a]	**Ground severity index**
< 5	0	**1**	Oe, Oi horizon	1	**1**
> 4	0	**1.5**	Oi horizon	2	**1**
1 - 4	1 - 10	**1.5**	Oa horizon	1	**1.5**
0	11 - 20	**2**	Oe horizon	2	**1.5**
> 5	< 10	**2**	Oi horizon	3	**1.5**
> 10	11 - 20	**2.5**	Mineral horizon	1	**2**
-	> 20	**3**	Oa horizon	2	**2**
			Oe horizon	3	**2**
			Mineral horizon	2	**2.5**
			Oa horizon	3	**2.5**
			Mineral horizon	3	**3**

[a] 0 = no charcoal present; 1 = small amount in organic or mineral; 2 = large amount or full layer in organic; 3 = large amount or full layer right above mineral

Table 4.2. Variables separated by subtype and community, with means and standard errors if applicable.

	Acidic Black Spruce community			Nonacidic Black Spruce community			Treeline community		
	Wet	**Non-wet**	**Total**	**Wet**	**Dry**	**Total**	**elevational**	**latitudinal**	**total**
Even-aged (freq)	20	5	25	5	13	18	0	0	0
Multi-cohorted (freq)	11	17	28	12	20	32	5	1	6
Constant recruitment (freq)	13	6	19	5	5	10	1	2	3
Age of oldest tree (mean ± SE)	166 ± 8	125 ± 10	150 ± 7	155 ± 18	132 ± 10	141 ± 9	63 ± 5	138 ± 22	88 ± 14
*Time since fire (mean ± SE)	134 ± 8	119 ± 9	128 ± 6	138 ± 13	124 ± 8	130 ± 7	64 ± 10	122 ± 16	83 ± 12
*pH (mean ± SE)	4.8 ± .07	5.4 ± .09	5.0 ± .07	6.0 ± .09	6.0 ± .06	6.1 ± .07	5.2 ± .20	7.6 ± .30	6.0 ± .43
*elevation (mean ± SE)	477 ± 32	516 ± 29	492 ± 22	290 ± 45	290 ± 29	290 ± 25	722 ± 45	338 ± 6	594 ± 70
*ground severity (mean ± SE)	1.02 ± .2	0.86 ± .2	0.96 ± .1	0.50 ± .1	1.01 ± .2	0.82 ± .1	0.83 ± .4	1.00 ± .6	.89 ± .3
*crown severity (mean ± SE)	.77 ± .1	1.27 ± .1	0.97 ± .1	0.89 ± .2	1.08 ± .2	1.01 ± .1	0.50 ± .2	1.83 ± .2	.94 ± .3

* variables used as predictors of community and subtype in the DFA model

Table 4.3. Pearson correlations between fire history variables and NMDS Axis 1, Axis 2, and Axis 3 (measures of species composition) for all sites (n=140).

NMDS Axis	Crown severity	Ground severity	Time since disturbance
Axis 1	-0.326**	-0.088	0.090
Axis 2	0.046	0.176*	-0.222**

** correlation is significant at the .01 level

* correlation is significant at the .05 level

Table 4.4. Test of discriminant functions for community subtype of abiotic and fire history models.

Model ran	Test function	% variance	Cananical correlation	Wilks lambda	Chi-squared	P value
Community type						
Abiotic factors	1	100	0.754	0.432	106.63	0.0001
fire history	1	100	0.093	0.991	1.13	0.57
Subtype						
Abiotic factors	1	96.3	0.790	0.353	131.35	0.0001
	2	3.7	0.246	0.940	7.85	0.0200
fire history	1	74.1	0.274	0.899	13.61	0.034
	2	25.9	0.167	0.972	3.60	0.1650

Table 4.5. Correct classification rates by DFA of community subtype for both models. The expected values are based on equal probability of occurrence.

Community subtype	Sample size	expected %	Correct % Abiotic	Correct % fire history
Acidic non-wet	28	22	57	39
Acidic wet	43	33	72	34
Nonacidic dry	36	28	56	19
Nonacidic wet	23	18	35	53
Total	130	25	58	34

Table 4.6. The Individual error matrix Kappa analysis results.

Error matrix	Kappa coefficient	Z statistic	Pvalue
no treeline abiotic	0.43	8.41	0.0001
no treeline fire history	0.13	2.81	0.0025
Acidic community abiotic	0.45	3.81	0.0001
Acidic community stand age	0.38	3.28	0.0010
Acidic community fire history	0.55	4.73	0.0001

* Kappa analysis was only run on signficant DFA models

Table 4.7. Test of discriminant functions and correct classification rates by DFA for the nonacidic and acidic black spruce communities for my three models. The expected values are based on equal probability of occurrence.

Community	Model	Sample size	Canonical correlation	Wilks lambda	Chi-squared	P value	Wet expected %	Wet correct %	Dry expected %	Dry correct %	Total epected %	Total correct %
NONACIDIC												
	Stand age only	60	0.163	0.974	1.543	0.2140	38	48	62	65	50	58
	Abiotic	59	0.078	0.994	0.343	0.8430	39	56	61	67	50	54
	Fire history	60	0.392	0.847	9.235	0.1000	38	74	62	54	50	62
ACIDIC												
	Stand age only	72	0.356	0.873	9.441	0.0020	39	71	61	68	50	69
	Abiotic	71	0.550	0.698	24.493	0.0001	40	71	60	74	50	73
	Fire history	72	0.486	0.764	18.205	0.0030	39	82	61	75	50	78

References

Ahrens, R. J., J. G. Bockheim, and C. Ping. 2004. The Gelisol order in Soil Taxonomy. Pages 2-10 *in* J. Kimble, editor. Cryosols: Permafrost-affected soils. Springer-Verlag, New York.

Arseneault, D. 2001. Impact of fire behaviour on postfire forest development in a homogeneous boreal landscape. Canadian Journal of Forest Research **31**:1367-1374.

Birkeland, P. W. 1999. Soils and Geomorphology. Oxford University Press, New York.

Braun-Blanquét, J. 1965. Plant sociology: The Study of Plant Communities. Hafner, London.

Cater, T. C., and F. S. Chapin III. 2000. Differential species effects of competition and microenvironment on boreal tree seedling establishment after fire. Ecology **81**:1086-1099.

Chapin III, F. S., T. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. A. Zimov. 2004. Global change and the boreal forest: Thresholds, shifting states or gradual change? Ambio **33**:361-365.

Congalton, R. G. 1991. A review of assessing the accuracy of classifications of remotely sensed data. Remote sensing of the environment **37**:35-46.

Crimp, P. M., S. J. Phillips, and G. T. Worum. 1997. Timber resources on state forestry lands in the Tanana Valley. Alaska Department of Natural Resources, Division of Forestry, Fairbanks.

Devolder, A. 1999. Fire and climate history of black spruce forests, Kenai National

Wildlife Refuge, Alaska. M.S. Northern Arizona University, Flagstaff.

Dissing, D., and D. Verbyla. 2003. Spatial patterns of lightning strikes in interior Alaska and their relations to elevation and vegetation. Canadian Journal of Forest Research **33**:770-782.

Dix, R. L., and J. M. A. Swan. 1970. The roles of disturbance and succession in upland forests at Candle Lake, Saskatchewan. Canadian Journal of Botany **49**:657-676.

Drake, J. A. 1991. Community assembly mechanisms and the structure of an experimental species assemblage. The American Naturalist **137**:1-26.

Duffy, P. A., J. E. Walsh, J. M. Graham, D. H. Mann, and T. S. Rupp. submitted. Impacts of the east Pacific teleconnection on Alaskan fire climate. Climatic change.

Dyrness, C. T., and D. F. Grigal. 1979. Vegetation-soil relationships along a spruce forest transect in interior Alaska. Canadian Journal of Botany **57**:2644-2656.

Edwards, M. E., and L. B. Brubaker. 1986. Late Quaternary vegetation history of the Fishhook Bend area, Porcupine River, Alaska. Canadian Journal of Earth Science **23**:1765-1773.

Fanning, D. S., and M. C. B. Fanning. 1989. Soil Morphology, Genesis, and Classification. John Wiley & Sons, New York, NY.

Fastie, C. L., A. H. Lloyd, and P. Doak. 2002. Fire history and post-fire development in an upland watershed of interior Alaska. Journal of Geophysical Research **108**:8150,doi:1029/2001JD000570.

Foster, D. R. 1985. Vegetation development following fire in black spruce-feather moss forests of south-eastern Labrador, Canada. Journal of Ecology **73**:517-534.

Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems **1**:497-510.

Foster, D. R., and G. Motzkin. 1998. Ecology and conservation in the cultural landscape of New England: Lessons from nature's history. Northeastern Naturalist **5**:111-126.

Frelich, L. E., and P. B. Reich. 1999. Neighboring effects, disturbance severity, and community stability in forests. Ecosystems **2**:151-166.

Greene, d. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research **29**:824-839.

Hinzman, L., L. A. Viereck, P. Adams, V. E. Romanovsky, and K. Yoshikawa. in press. Climatic and permafrost dynamics in the Alaskan boreal forest. *in* M. Oswood and F. S. Chapin III, editors. Alaska's Changing Boreal Forest. Oxford University Press, Oxford.

Johnson, E. A. 1981. Vegetation organization and dynamics of lichen woodland communities in Northwest Territories, Canada. Ecology **62**:200-215.

Johnstone, J. F. 2003. Fire and successional trajectories in boreal forest: implications for response to a changing climate. Doctor of Philosophy. University of Alaska Fairbanks, Fairbanks, Alaska.

Johnstone, J. F., and F. S. Chapin III. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Global Change Biology **9**:1401-1409.

Johnstone, J. F., F. S. Chapin III, J. Foote, K. Kemmett, K. Price, and L. A. Viereck. 2004. Decadal observations of tree regeneration following fire in boreal forests. Canadian Journal of Forest Research **34**:267-273.

Karels, T. J., A. Bryant, and D. S. Hik. 2004. Comparison of discriminant function and classification tree analyses for age classification of marmots. Oikos **105**:575-587.

Kuhry, P. 1994. The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada. Journal of Ecology **82**:899-910.

La Roi, G. H. 1967. Ecological Studies in the Boreal Spruce-Fir Forests of the North American Taiga. I. Analysis of the Vascular Flora. Ecological Monographs **37**:229-253.

Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. Ecology **77**:762-775.

Lloyd, A. H., M. E. Edwards, B. P. Finney, J. A. Lynch, V. A. Barber, and N. H. Bigelow. in press. Chapter 5. Development of the Boreal Forest. *in* M. Oswood and F. S. Chapin III, editors. Alaska's Changing Boreal forest. Oxford University Press, Oxford.

Lloyd, A. H., and C. L. Fastie. 2003. Recent changes in treeline forest distribution and structure in interior Alaska. Ecoscience **10**:176-185.

Mann, D. H., and L. J. Plug. 1999. Vegetation and soil development at an upland taiga site, Alaska. Ecoscience **6**:272-285.

McCune, B. 1993. Gradients of epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. Bryologist **96**:405-411.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4.25. MjM Software Design, Gleneden Beach.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Osterkamp, T. E., and V. E. Romanovsky. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost and Periglacial Processes **10**:17-37.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. Pages 144-169 *in* H. H. Shugart, R. Leemans, and G. B. Bonan, editors. A System Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge.

Peet, R. K. 1985. Plant Community Ecology: Papers in honor of Robert H. Whittaker. Junk, The Hague.

Peterson, C. H. 1984. Does a rigourous criterion for environmental identity preclude the existence of multiple stable points? The American Naturalist **124**:127-133.

Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. Ecology **80**:429-442.

Rieger, S., D. B. Schoephorster, and C. E. Furbush. 1979. Exploratory Soil Survey of Alaska. US Soil Conservation Service, Washington, D.C.

Scott, A. J. 1995. Canada's vegetation: a world perspective. McGill-Queen's University Press, Montreal.

Shafi, M. I., and G. A. Yarranton. 1973. Vegetational heterogeneity during secondary (postfire) succession. Canadian Journal of Botany **51**:73-90.

Sirois, L. 1993. Impact of fire on *Picea mariana* and *Pinus banksiana* seedlings in subarctic lichen woodlands. Journal of Vegetation Science **4**:795-802.

Slaughter, C. W., and C. S. Benson. 1986. Proceedings, Cold Regions Hydrology. Pages 101-109 *in* D. L. Kane, editor. American Water Resources Association, Bethesda, USA.

Sousa, W. P., and J. H. Connell. 1985. Further comments on the evidence for multiple stable points in natural communities. The American Naturalist **125**:612-615.

Sweetnam, T., and E. K. Sutherland. 1985. Using dendrochronology to measure the growth of defoliated trees. Agricultural Handbook No. 639, USDA Forest Service.

Szumigalski, A. R., and S. E. Bayley. 1996. Net above-ground primary production along a bog-rich fen gradient in central Alberta, Canada. Wetlands **16**:467-476.

Thormann, M. N., and S. E. Bayley. 1997. Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. Ecoscience **4**:374-384.

Turetsky, M., R. K. Wieder, C. J. Williams, and D. H. Vitt. 2000. Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. Ecoscience **7**:379-392.

Turner, M. G., and V. H. Dale. 1998. Comparing large, infrequent disturbances: What have we learned? Ecosystems **1**:493-496.

Van Cleve, K. 1983. Introduction and overview of a multidisciplinary research project: the structure and function of a black spruce (*Picea mariana*) forest in relation to other fire-affected taiga ecosystems. Canadian Journal of Forest Research **13**:695-

702.

Van Cleve, K., F. S. Chapin III, C. T. Dyrness, and L. A. Viereck. 1991. Element cycling in taiga forest: State-factor control. Bioscience **41**:78-88.

Viereck, L. A. 1973. Wildfire in the taiga of Alaska. Journal of Quaternary Research **3**:465-495.

Viereck, L. A., C. T. Dyrness, A. R. Batten, and K. J. Wenzlick. 1992. Alaska Vegetation Classification. General Technical Report PNW-GTR-286 USDA Forest Service Pacific Northwest Research Station.

Viereck, L. A., and W. F. Johnston. 1990. *Picea mariana* (Mill.) B.S.P. black spruce. Pages 227-237 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Forest Service, U.S. Department of Agriculture, Washington D.C.

Whittaker, R. J. 1967. Gradient analysis of vegetation. Biological Review **42**:207-264.

Whittaker, R. J. 1975. Communities and ecosystems. Macmillan, New York.

Yarie, J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. Canadian Journal of Forest Research **11**:554-562.

CHAPTER 5: CONCLUSIONS

The future direction of community ecology

We are entering a new era in community ecology when research is based on how the species composition and interactions between species, both past and present, contribute to the apparent self-organization of a community at multiple scales (Allen and Hoekstra 1992, Kauffman 1995). The boreal forest is the second largest terrestrial biome (Whittaker 1975) and one of the least disturbed by human activities (Schneider and Apps 1995). Within boreal Alaska, the black spruce ecosystem occupies over 40% of the landscape (Van Cleve 1983) across a wide range of environmental conditions, often in areas of low productivity and high carbon storage. Quantifying and understanding the underlying factors contributing to variation in this forest type is important not only for understanding boreal forests, but also for studying theoretical questions about community assembly.

Black spruce community composition and patterns are scale-dependent (Chapter 2). Variation in species composition within a 100 x 100 km area around Fairbanks was related to changes in paludification and soil moisture, whereas across the entire region of interior Alaska variation in species composition was most highly correlated with changes in mineral soil pH. Based on species composition, I recognized and described three communities of black spruce within this broad region; The Nonacidic Black Spruce Forest, the Acidic Black Spruce Forest, and the Treeline Black Spruce Woodland and five subtypes (Wet Acidic Black Spruce Muskeg, Wet Nonacidic Black Spruce Fen, Dry Nonacidic Black Spruce Forest, Elevational Treeline Black Spruce Woodland, and Latitudinal Treeline Black Spruce Woodland) (Chapter 2). This is the first study to demonstrate the correlation between black spruce species composition and mineral soil pH and to present a floristically-based classification of black spruce stands within this region. I hypothesize that both long-term geologic processes such as formation of parent material and its modification by glacial history, and short-term successional changes, such as site paludification and fire history, contribute to the differences in soil pH and consequently in species composition.

The black spruce ecosystem is considered to be one of the most sensitive to changes in climate, due in part to the large amounts of carbon stored in the soils (O'Connell et al. 2003). However, I present evidence that the variability in soil carbon storage within the black spruce forest type is as great as variation previously described across four major forest types in the Fairbanks area (Chapter 3; Van Cleve et al. 1983, Viereck 1983). Across the region, species composition was at least as good a predictor of soil carbon pools as were abiotic factors such as soil moisture and topography (Chapter 3). In particular, *Sphagnum* richness was a good predictor of soil carbon amounts. *Sphagnum* species not only occur in areas where environmental conditions reduce decomposition rate, particularly in cold wet sites (Bisbee et al. 2001), but also have low decomposability and promote acidic conditions that further retard decomposition (Kuhry and Nicholson 1993).

Fire is considered the most important disturbance shaping the patterns of North American boreal forests (Bonan and Shugart 1989), and it is hypothesized that fire disturbance can generate alternative stable states through changes in species density or starting conditions (Petraitis and Latham 1999). Results from Chapter 4 suggest the role of fire in shaping mature black spruce stands is an extremely important factor determining differences in species composition within the subtypes of a particular black spruce community. I propose five mechanisms to account for the alternative stable states seen in the black spruce subtypes-- three that maintain pre-fire conditions, and two that promote the switch to an alternative stable state between fires.

A framework to predict the stability, resilience, and resistance

Black spruce communities in boreal Alaska have been described as the final stage in linear succession after fire and flooding (Van Cleve et al. 1991). The other dominant forest types in boreal Alaska, such as white spruce and aspen, have been viewed as alternative stable states that occur predictably at different points along environmental gradients. These dominant tree types define the position of each site along a successional trajectory after disturbance. Communities within these forest types have been considered continua of species distributions along environmental gradients (Chapin et al. 2004) in spite of the spatially and temporally patchy nature of disturbance across the landscape. Work presented in this thesis (Chapter 2, 3) demonstrates considerable variability in community composition and ecosystem properties within the black spruce ecosystem. This variability represents the potential for alternative stable community states, which encompass different states of structure and function, arising from differences in initial site conditions or species' density (Chapter 4).

Since current theories account for stability of ecosystem types, for example black or white spruce, but not for stability of communities within an ecosystem, we need a new framework that takes into account the predictable patterns of variability that we observed among black spruce community types. Resilience theory (Gunderson and Holling 2002) provides a hierarchical framework to expand our understanding of the characteristics of stability and change in black spruce ecosystems after fire in boreal Alaska. Our results indicate that across all sites the addition of fire history variables, which quantify the legacy of fire, did not increase our ability to predict community types, but did increase our ability to predict subtypes both among and within communities (Chapter 4).

Implicit in resilience theory is the existence of multiple stable states (Holling 1973, Holling and Gunderson 2002), because resilience is defined as the maximum amount of pulse disturbance, such as fire, a system can withstand without flipping to another state. In other words, resilience is the recovery of a system from perturbation up to some threshold, beyond which it changes to an alternative stable state. Resistance, on the other hand, is defined as the ability of a system to resist change in the face of a slow, steady disturbance. Both the resilience and resistance of a system determine its overall stability; a stable system exhibits both high resistance and resilience (May 1973, Pfisterer and Schmid 2002). Within this framework I examine the magnitude of change or threshold (e.g. high or low) needed to flip a system to an alternative state, the ability of the system to resist changes in structure and function in the face of perturbation, and the overall stability of the system within the context of the black spruce ecosystem, communities, and subtypes.

I present a conceptual hierarchical model of the resilience, resistance, and stability at three scales of decreasing species richness (ecosystem, community and subtype) for black spruce in boreal Alaska (Figure 5.1). This model implies a spatial and temporal hierarchy in the sense that within interior Alaska, the black spruce ecosystem occupies a greater range of environmental conditions than does a single black spruce community type, which in turn occupies a greater range of environmental conditions than each subtype. In addition, over time two processes, succession and paludification, (Chapter 2), contribute to the resilience of a certain state in the face of disturbance.

At the largest spatial scale, the black spruce ecosystem is highly stable because of its high variability in structure and function observed across the boreal forest of Alaska (Chapter 2, 3). This allows a wide range of responses to environmental perturbation, without altering the identity of the dominant tree species (Lawton and Brown 1993). The black spruce ecosystem appears to have been a stable component of interior Alaskan forests for the last 5000 years (Lynch et al. 2002). Highly predictable black spruce regeneration after fire from semi-serotinous cones contributes to the likelihood that black spruce ecosystem will remain dominated by black spruce after fire (Chapin et al. 2004). Therefore, it is highly resilient to change and it would take a large magnitude of disturbance to change black spruce ecosystem to anything but black spruce, taking into account potential succession after fire through other forest types and eventually back to black spruce. Given a severe fire, black spruce could theoretically flip to another ecosystem type such as aspen; however, the probability of a site staying aspen over longer successional time-scales, such as those that we address with our analysis of late-successional communities, is low unless there is a large change in temperature, fire regime, or other abiotic factors that alter the local species pool (Johnstone and Chapin

2003).

When the scale of analysis shifts to community types there is a decrease in the stability of the system (Figure 5.1). Each community type occupies a smaller range along the main environmental gradients (pH and paludification). This decreases the variability seen in structure and function within each community. The lower species richness within each community, as compared to the black spruce ecosystem as a whole, may decrease the resilience of the system at the community level relative the ecosystem level (Lawton and Brown 1993). Finally, when observing black spruce subtypes, the threshold of change decreases as well as the resistance to change is much lower, leading to lower stability (Figure 5.1). This reflects the result of relatively small range of environmental conditions that each subtype occupies and the capacity of fire to alter conditions enough that a given stand may shift from one subtype to another (Chapter 4).

Future directions

Research presented here quantified variability in both the composition and functioning of the black spruce ecosystem across interior Alaska. This has large implications for modeling the boreal forest's resistance to changes in climate and its resilience in the face of changes in fire frequency. We still do not understand the relative importance of both the direct effects (i.e., effects on species) and indirect effects (i.e., effects on the initial state), and the actual magnitude of disturbance needed to cause a flip to alternative stable states. To answer these questions, long-term monitoring of burned sites in which we know the pre-fire vegetation and site characteristics is essential.

In the summer of 2004, we gained a unique opportunity for further study.

Wildfire burned a record 6.7 million acres across the interior of Alaska, of which a large portion was black spruce (http://fire.ak.blm.gov). These fires burned almost one third of the 146 study sites used in this dissertation (Figure 5.2). With our in-depth description of pre-fire vegetation and stand characteristics, we can begin to answer questions about the relationship of pre-fire vegetation and post-fire recovery, providing an opportunity to test our proposed alternative stable state mechanisms. Therefore, the research presented in this dissertation will be an important component in future research in boreal forests of Alaska.

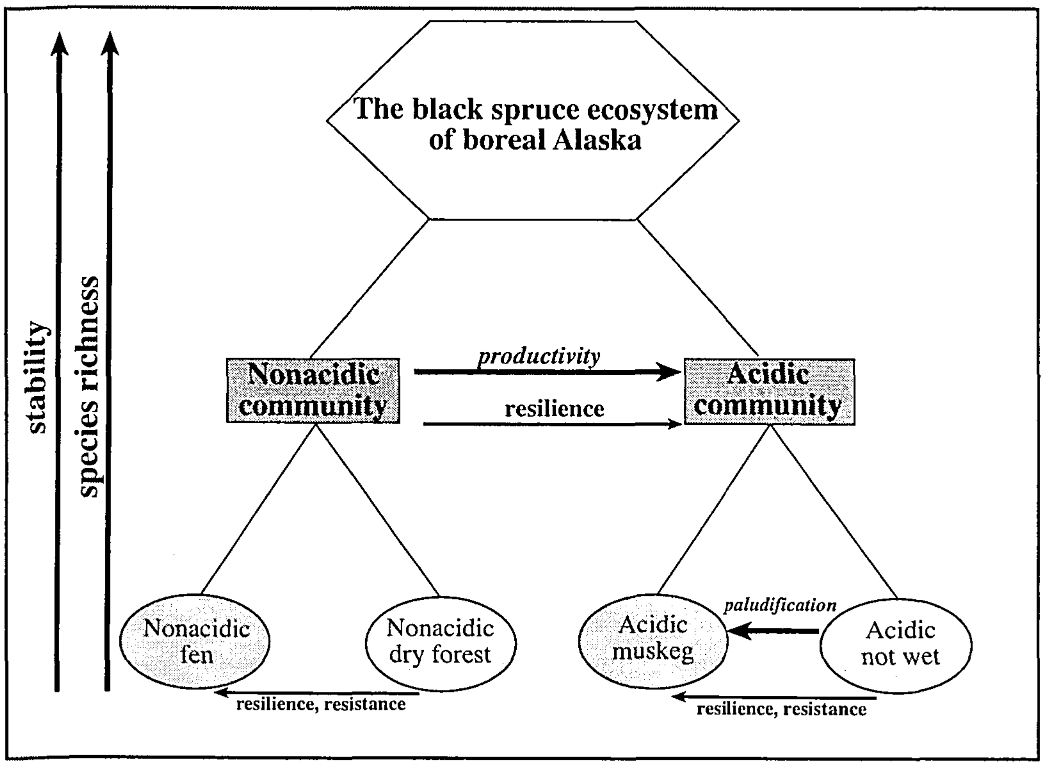

Figure 5.1. A framework for understanding the stability, resilience, and resistance in the Alaskan black spruce ecosystem. The proposed processes (italics) and patterns (bold) and are explored in depth in Chapters 2, 3, and 4.

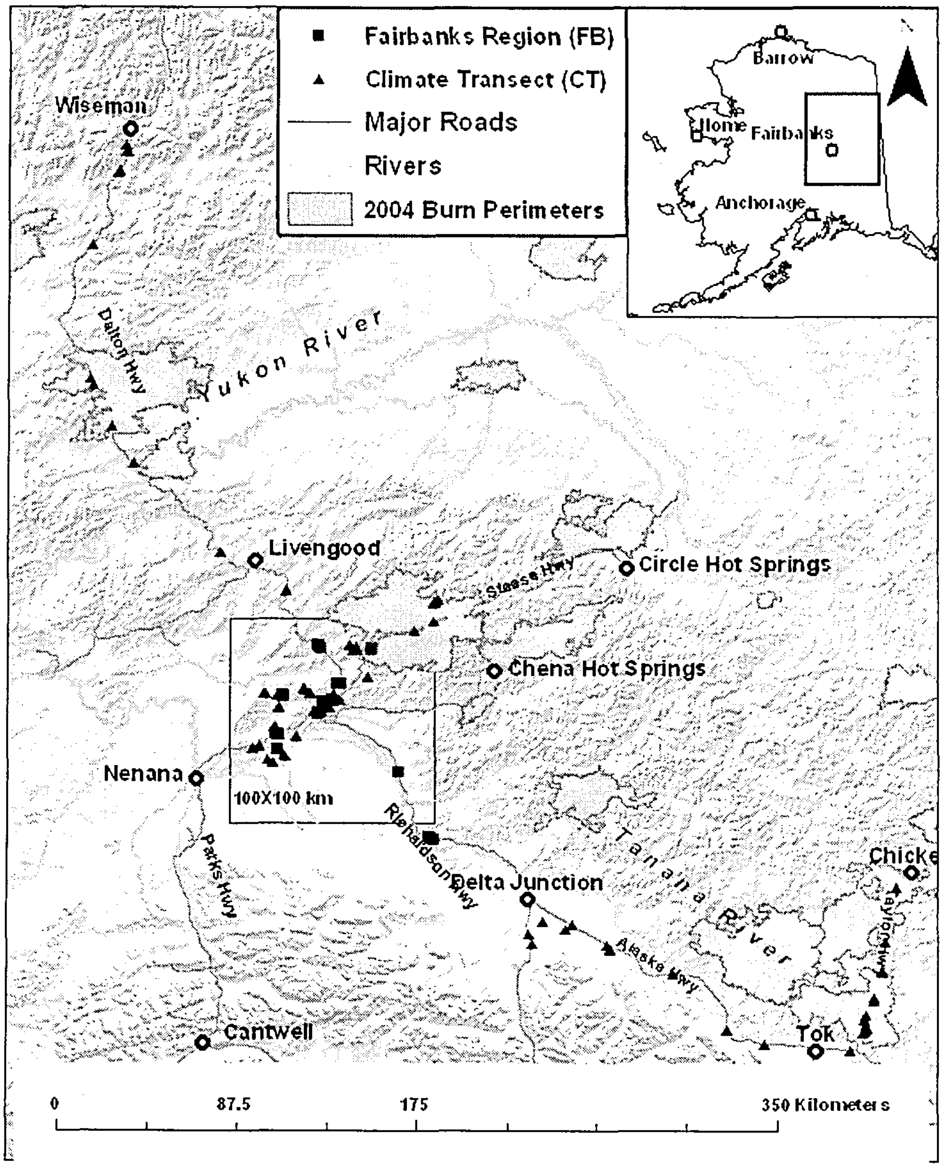

Figure 5.2. Map of 2004 burn perimeters with sites visited for work in this dissertation overlaid. Approximately 32 sites were burned in 2004.

References

Allen, T. F., H., and T. W. Hoekstra. 1992. Toward a Unified Ecology. Complexity in Ecological Systems. Columbia University Press, New York.

Bisbee, K. E., S. T. Gower, and J. M. Norman. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia **129**:261-270.

Bonan, G. B., and H. H. Shugart. 1989. Environmental Factors and Ecological Processes in Boreal Forests. Annual Review of Ecology and systematics **20**:1-28.

Chapin III, F. S., T. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. A. Zimov. 2004. Global change and the boreal forest: Thresholds, shifting states or gradual change? Ambio **33**:361-365.

Gunderson, L. H., and C. S. Holling. 2002. Panarchy. Island Press, Washington.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and systematics **4**:1-23.

Holling, C. S., and L. H. Gunderson. 2002. Resilience and adaptive change. Pages 25-62 *in* L. H. Gunderson and C. S. Holling, editors. Panarchy. Island Press, Washington.

Johnstone, J. F., and F. S. Chapin III. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Global Change Biology **9**:1401-1409.

Kauffman, S. 1995. At Home in the Universe. The search for Laws of Self-Organization and Complexity. Oxford University Press, New York.

Kuhry, P., and B. J. Nicholson. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Canadian Journal of Botany **71**:10-22.

Lawton, J. H., and V. K. Brown. 1993. Redundancy in ecosystems. *in* D. Schulze and H. A. Mooney, editors. Biodiversity and Ecosystem Function. Springer, Berlin.

Lynch, J. A., J. S. Clark, N. H. Bigelow, M. E. Edwards, and B. P. Finney. 2002. Geographical and temporal variations in fire history in boreal ecosystems of Alaska. Journal of Geophysical Research **Atmospheres 108(D1)**:8152.

May, R. M. 1973. Stability and Complexity in Model Ecosystem, Second edition. Princeton University Press, Princeton.

O'Connell, K. E. B., S. T. Gower, and J. M. Norman. 2003. Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities. Ecosystems **6**:236-247.

Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. Ecology **80**:429-442.

Pfisterer, A. B., and B. Schmid. 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. Nature **416**:84-86.

Schneider, S. H., and M. J. Apps. 1995. Foreward and Preface. Pages ix-xiv *in* M. J. Apps, D. T. Price, and J. Wisneiwski, editors. Boreal forests and global change. Kluwer Acadmeic Publishers, Dordrecht.

Van Cleve, K. 1983. Introduction and overview of a multidisciplinary research project: the structure and function of a black spruce (*Picea mariana*) forest in relation to other fire-affected taiga ecosystems. Canadian Journal of Forest Research **13**:695-

702.

Van Cleve, K., F. S. Chapin III, C. T. Dyrness, and L. A. Viereck. 1991. Element cycling in taiga forest: State-factor control. Bioscience **41**:78-88.

Van Cleve, K., L. Oliver, and R. Schlentner. 1983. Productivity and nutrient cycling in the taiga forest ecosystem. Canadian Journal of Forest Research **13**:747-766.

Viereck, L. A. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Canadian Journal of Forest Research **13**:703-720.

Whittaker, R. J. 1975. Communities and ecosystems. Macmillan, New York.