WILDFIRE BURN SUSCEPTIBILITY TO NON-NATIVE PLANT INVASIONS IN BLACK SPRUCE FORESTS OF INTERIOR ALASKA

By

Katie Lin Villano

RECOMMENDED: ____________________________________

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Advisory Committee Chair

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Chair, Department of Biology and Wildlife

APPROVED: ____________________________________
Dean, College of Natural Science and Mathematics

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Dean of the Graduate School

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Date

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A

THESIS

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By
Katie Lin Villano, B.A.

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ABSTRACT

As the climate changes, Alaska’s boreal forest faces the simultaneous threats of rising invasive plant abundances and increasing area burned by wildfire. Highly flammable and widespread black spruce forest represents a boreal habitat that may be increasingly susceptible to non-native plant invasion. In other biomes, non-native plant invasions are generally greatest in high severity burns that are only a few years old. The relationship between fire and non-native plant invasion has not been investigated in the northern boreal forest. To assess the invasibility of burned black spruce forests, I used burned field sites that spanned a gradient of burn severities, moisture levels, and burn ages. I conducted both field surveys and a greenhouse experiment using soil taken from burn sites. Contrary to generalizations from other biomes, I found soils from low severity burns and burns between 10 and 20 years old support greater invasive plant growth in black spruce forests than do high severity and more recent burns. In addition, regional differences between burn complexes outweighed burn severity and site moisture in determining the invasibility of burned black spruce sites. Finally, rebounding native vegetation appears to offer burned areas a level of resistance to invasive plant establishment.

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CHAPTER 1:

WILDFIRE, NON-NATIVE PLANT INVASIONS, AND THE BOREAL FOREST

GENERAL INTRODUCTION AND LITERATURE REVIEW

Introduction

Non-native plant invasions have seriously altered community structure and ecosystem functioning in habitats around the globe (Vitousek et al. 1997; Levine et al. 2003). Invasive species are among the top causes of losses in native biodiversity worldwide (Sala et al. 2000), and play a role in the imperilment of nearly half the extinct and endangered species in the U.S. (Wilcove et al. 1998). Non-native plant invasions can change ecosystem properties such as nutrient cycling (Vitousek and Walker 1989; Evans et al. 2001; Mack et al. 2001), hydrology (Busch and Smith 1995; Rickard and Vaughan 1988), and fire regimes (Whisenant 1990; D'Antonio and Vitousek 1992; Grigulis et al. 2005). Invasive plants have also been shown to cause positive feedbacks with soil microbial communities, changing soil biota in a way that promotes their own expansion (Klironomos 2002).

Boreal ecosystems comprise one third of the world's forested land (Shugart et al. 1992) and cover the second largest area of any terrestrial biome (Pielou 1988). Despite their size and global distribution, little is known about the susceptibility of boreal systems to invasion by non-native plants. The boreal biome has low biodiversity when compared to other biomes (Pielou 1988). Because each species has large ecosystem effects in boreal ecosystems (Chapin and Danell 2001), the extirpation of native species and changes in community structure due to non-native plant invasions could substantially impact these northern ecosystems. Due to the largely inaccessible nature of Alaska's boreal forest, monitoring and control must be prioritized in areas that are most susceptible to invasion

(Nijs et al. 2004) to prevent the potentially devastating impacts of invasive plants on intact boreal habitats.

Because of its wide distribution and dependence on natural disturbances, one potentially vulnerable boreal habitat is black spruce (*Picea mariana* Mill.) forest. Black spruce-dominated forest spans northern North America (Hultén 1968) and depends on lightning-ignited wildfire to reset successional processes (Agee 1999). In boreal ecosystems and across the globe, a warming climate has increased the number and extent of wildfires (Shlisky et al. 2007). While difficult to predict, the vulnerability of native plant communities to non-native plant invasions is often considered to be a function of disturbance (Hobbs and Huenneke 1992), resource availability (Davis et al. 2000), and community structure (Elton 1958; Levine and D’Antonio 1999; Shea and Chesson 2002). As summers have become drier and warmer, increasing fire disturbances in boreal systems could change all three of these factors. Fire could increase the susceptibility of boreal black spruce forests through an increase in the area disturbed, increased resource availability following a fire, and decreased competition from native plant communities (Harrod and Reichard 2001). If invasive plants establish after a fire, they could alter successional trajectories, future fire regimes, and cause positive feedbacks in the ecosystem to promote their own expansion (Harty 1986; Vitousek 1986; Hobbs and Huenneke 1992; D’Antonio and Vitousek 1992).

The goal of my thesis was to assess the susceptibility of burned black spruce forests to invasion by non-native plants. For my study system, I used the black spruce forests of interior Alaska, an area between the Alaska and Brooks Mountain Ranges that covers 60 million burnable hectares (Duffy 2006). In this chapter, I review the literature available on the interaction between invasive plants and wildfire. Due to the limited study of invasive plants in boreal ecosystems, I draw parallel examples from studies of other biomes and pose potential scenarios for post-fire susceptibility of boreal habitats in Alaska. In the literature review, I explore the following questions: 1) Is burned boreal forest more susceptible to non-native plant invasions than unburned forest? 2) Does burn severity influence boreal forest susceptibility to non-native plant invasion? 3) Does the time elapsed since fire influence boreal forest susceptibility to non-native plant invasion? In Chapter Two of this thesis, I address these three questions directly through complimentary field surveys and greenhouse experiments. In addition, I explore the influence of spatial scale on burn site invasibility and attempt to find general patterns in invasive plant response to burn site characteristics across taxa. Finally, in Chapter Three, I compare my results to the studies conducted in other ecosystems, discuss further directions for research, and use my results to identify potentially vulnerable burned black spruce areas for invasive plant management efforts.

Invasibility of Alaskan Boreal Systems in a Changing Climate

In the past, cold climate and limited human population were thought to restrict the movement of non-native plants into northern ecosystems (Shephard 2004). Climate largely controls the distribution of plants globally (Salisbury 1926; Woodward 1987), and the short growing season, cold winters, and large areas underlain by permafrost preclude many temperate species from establishing at high latitudes. However, successful non-native plant introductions are known to occur beyond species' expected climatic zones (Elven and Elvebakk 1996; Carlson and Shephard 2007). As both the climate warms and the levels of both anthropogenic and natural disturbance grow, boreal habitats are becoming increasingly susceptible to non-native plant invasions (Rose and Hermanutz 2004; Mandryk and Wein 2006; Carlson and Shephard 2007; Sumners and Archibold 2007). Callaghan and colleagues (1995) expressed the prevailing thought on the response of non-native plants to climate warming in boreal systems when they wrote, "In the sub-Arctic, subtle shifts in plant community composition with occasional losses of plant species are more likely than immigration of non-native species." More recently, however, the changes in sub-arctic climate have created an increasingly suitable environment for non-native plant species. In Alaska today, it is obvious that the spread of invasive plants is rapidly accelerating, with the number of recorded invasive plant populations more than doubling since 1941 (Carlson and Shephard 2007). Warmer winters (Chapman and Walsh 1993) and longer growing seasons (Myneni et al. 1997) are likely enabling the spread of non-native species that were previously unable to tolerate northern conditions.

While invasive plants have largely remained restricted to areas of human disturbance in Alaska (Shephard 2004; Alaska Exotic Plant Information Clearinghouse (AKEPIC) 2008; Conn et al. *in press*), in the past decade invasives have begun to move into natural disturbance areas (i.e., wildfire burn scars, glacial floodplains) and intact boreal plant communities (Wurtz et al. 2006; Cortés-Burns et al. 2007; Lapina et al. 2007). Warmer temperatures and changes in precipitation have also increased fire frequency, extent and severity in Alaska (Overpeck et al. 1997; Stocks et al. 2000; Bachelet et al. 2005; Alaska Fire Service (AFS) 2007). Increasing amounts of area burned by wildfire may present invasive plants a broadened avenue through which they can spread from human disturbance areas into boreal plant communities.

Is burned boreal forest more susceptible to non-native plant invasions than unburned forest?

Most types of ecosystems have been shown to be more susceptible to invasion after fire (Milberg and Lamont 1995; D’Antonio 2000; Maret and Wilson 2000; Asher et al. 2001; Keeley et al. 2003; Haskins and Gehring 2004; Dimitrakopoulos et al. 2005; Floyd et al. 2006; Zouhar et al. 2007). Reduced competition from native plants, exposed mineral soil, and increased nutrient availability in burned areas are commonly cited as the mechanisms underlying the differences between invasibility of burned and unburned sites (Asher et al. 2001; Keeley et al. 2003; Dimitrakopoulos et al. 2005; Floyd et al. 2006). Nearly all studies comparing invasion levels between burned and unburned sites are observational field studies, and, as a result, are incapable of controlling for propagule pressure or pre-fire non-native plant abundances. If a site is more resistant to invasion, more propagules are needed for a non-native to become established. Alternatively, if a site is less resistant to invasion, fewer propagules are needed for invasion (Zouhar et al. 2007). In fact, some field studies show no difference between levels of invasion in burned and unburned sites (Klinger et al. 2006). Recent field survey data in Alaska do not reveal any differences between invasion rates in burned and unburned areas (Cortés-Burns et al.

2007), but this is almost certainly due to the overall low levels of propagule pressure. No study has yet determined if burned areas in Alaska are more susceptible to invasion than unburned areas. Due to the relatively low levels of invasion in the state, an experimental approach is necessary to investigate if the trends in burned areas in other habitats hold true in boreal ecosystems.

Another factor that may influence the susceptibility of burned sites is the native community structure that develops after a fire. In experimental grassland communities, invader biomass and density in burned plots decreased as resident species richness increased (Dimitrakopoulos et al. 2005). Greater richness may increase the chances of including a key species that prevents invasion (sampling effect; Loreau and Hector 2001; Wardle 2001; Emery and Gross 2006), or may decrease available nutrients for invaders by fully utilizing available niche space (complementarity effect; Shea and Chesson 2002). Immediately after a fire in Alaska’s boreal forest, richness and diversity generally shift to the few species that are rapid regenerators (Viereck and Schandelmeier 1980; Johnstone et al. in press). This may open niche space for invasive plants and reduce the chances of being excluded by highly competitive key native species. Nearly all the research conducted on biotic resistance to non-native plant invasions has focused on the native vascular plant community structure (reviewed in Levine and D’Antonio 1999). The role of non-vascular plants in preventing invasions has remained unknown. In Alaska’s burned boreal and tundra ecosystems, quickly colonizing bryophyte species play a vital role in post-fire succession, permafrost development, and understory species composition

(Viereck and Schandelmeier 1980), and may be an important source of biotic resistance to non-native plant invasions.

In Alaska, the rapid changes in fire regime due to a warming climate may also favor invasive plant species. Wildfire disturbances in Alaska have increased dramatically in the past few decades (AFS 2007). In 2004 alone, 6.7 million acres of Alaska's boreal forest burned, making it the largest fire year in recorded history (Fitzgerald 2006). Historically, increased temperatures in Alaska have increased fire frequency, severity and extent (Nash and Johnson 1996; Overpeck et al. 1997; Stocks et al. 2000; Bachelet et al. 2005). With current warming trends, fire regime is predicted to change in a similar way in the future (Flannigan et al. 2001). Not only could larger fires increase the area of disturbed habitat for invasive plants, but shorter fire intervals could also favor invasive plant species because they reproduce rapidly and can quickly colonize burned areas.

Does burn severity influence boreal forest susceptibility to non-native plant invasion?

If burned boreal forest is more susceptible to invasive plant colonization than unburned forest, then black spruce habitats within Alaska's boreal forest may be a particularly vulnerable type of habitat. Highly flammable black spruce communities comprise the majority of the boreal forest in Alaska (Viereck et al. 1992). Black spruce has remained the stable successional climax community of much of boreal Alaska since the species arrived over 10,000 years ago (Viereck 1979), and its life history is closely linked to the fire cycle (Clark 1988).

The community structure of black spruce forests after a burn is largely determined by the severity, or amount of canopy, surface and organic layer biomass consumed during the fire (Schimmel and Granstrom 1996; Johnstone and Chapin 2006). In Alaska's black spruce forest a thick layer of moss, lichen and organic soil (duff), commonly up to 30 cm thick, typically overlays mineral soils and permafrost (Viereck et al. 1992). Among native boreal species, plants regenerate from seed at a higher rate in high severity sites (Schimmel and Granstrom 1996; Johnstone et al. *in press*), where patches of mineral soil are exposed. In low severity burns, much of the charred, dry duff remains, offering a less hospitable surface for germination and establishment (Johnstone and Chapin 2006). As such, one would anticipate invasive plants in black spruce forests to have greater colonization success in high-severity burn areas. This has been the case in the majority of studies conducted in other ecosystems in North America (Agee 1996; Turner et al. 1997; Crawford et al. 2001; Keeley et al. 2003; Hunter et al. 2006).

In theory, invasive plants should show greatest establishment rates in areas with the highest levels of disturbance and highest levels of available resources (Hobbs and Huenneke 1992; Huston 2004). This pattern is well documented in the literature (Turner et al. 1997; White et. al 1997; Keeley et al. 2003; Hunter et al. 2006), and has been documented in southern boreal ecosystems (Rose and Hermanutz 2004; Mandryk and Wein 2006). However, high disturbance, high resource conditions are also optimal for native colonizers, which may provide competitive barriers to invading non-native plants. Thus, sites with comparatively low levels of disturbance and low levels of available resources may also be highly invasible and offer invasives a refuge from intense competition (Tilman 1988; Grime 2001; MacDougall et al. 2006). For burned black spruce sites in Alaska, complex interactions between disturbance levels (i.e., burn severity) and resource availability (i.e., water availability, post-fire nutrient pulse, and pre-fire soil legacies) may make patterns of site invasibility unpredictable. In particular, the variable way fire influences the thick organic mat covering the forest floor may influence invasibility in ways undocumented in other biomes.

Does the time elapsed since fire influence boreal forest susceptibility to non-native plant invasion?

In western U.S. coniferous forests, the abundance of both native and non-native plants tend to increase the first few years after a burn (Turner et al. 1997; Crawford et al. 2001; Keeley et al. 2003), more so in high severity than low severity sites (Keeley et al. 2003). Beyond about five years, however, the number and abundance of non-native species tends to decrease with time since burn while the native vegetation continues to rebound (Klinger et al. 2006). On a longer time scale (beyond 20 years post-burn), the relationship between time elapsed since burn and non-native plant abundance disappears (Fornwalt et al. 2003). This pattern was documented in the southern boreal forest of Saskatchewan, where recently disturbed sites (<15 years since wildfire or logging) had greater non-native cover than mature sites (Sumners and Archibold 2007). However, this was not the case in the southern boreal forest of Alberta, where later successional coniferous stands had higher non-native plant cover than did earlier deciduous stands (Mandryk and Wien 2006). In other habitat types, the response of invasive plants to the time since fire is species specific, with some species more able to persist in the long-term than others (Ruggiero et al. 1991). Differences in non-native species identity and differences in propagule pressure may explain the seemingly contradictory results of these two southern boreal forest examples.

In Alaska, most of the invasive plant species are early successional and shade intolerant (AKEPIC 2005; Carlson et al. 2008). These characteristics would lead one to assume that, like the general pattern documented elsewhere, the invasibility of burned black spruce sites decreases with time since burning. Presumably, this trend would be due to canopy closure and increased competition from native plants. However, some non-native species (*Vicia cracca* L., *Caragana arborescens* Lam., *Crepis tectorum* L.) have been documented moving into closed canopy and mature forest systems (Cortés-Burns et al. 2007, Lapina et al. 2007, K. Villano *pers. obs.*). This suggests older burns may still be susceptible to non-native plant invasions. Again, no prior study in Alaska has investigated the role of time since fire in site susceptibility to invasion independently of propagule pressure. After the record breaking 2004 fire year, land managers received substantial financial support to monitor these burns for invasive plant spread. An experimental approach is necessary to determine if the most recent burns are, in fact, the most susceptible to non-native plant invasions, or if management priority should be directed to other burn characteristics.

Susceptibility of Burned Black Spruce Sites in Alaska

The literature from other ecosystem types suggest that burned areas are more susceptible to invasive plants, with high severity and recent burns being more susceptible to invasion by non-native plants than low severity and older burns. The unique interactions between the thick organic mat on the forest floor, native plant regeneration, soil properties and permafrost after fires in black spruce forests of Alaska call these generalizations into question. In the next chapter, I experimentally test these generalizations in Interior Alaska black spruce forests. In addition, I further explore the relationship between invasive plants and burn characteristics in Alaska’s boreal forest by addressing two additional questions: 1) Are invasive plant responses to burn severity or time elapsed since burning similar across taxa or species-specific? and 2) Do factors determining burn invasibility change with spatial scale? By experimentally approaching these generalizations and questions, my thesis presents a first step toward understanding the susceptibility of burned boreal forest in Alaska to non-native plant invasions.

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CHAPTER 2:

SUSCEPTIBILITY OF BLACK SPRUCE WILDFIRE BURNS TO NON-NATIVE PLANT INVASIONS IN INTERIOR ALASKA

Abstract

As climate changes, Alaska's boreal forest faces the simultaneous threats of increasing invasive plant abundances and increasing area burned by wildfire. Highly flammable and widespread black spruce forest represents a boreal habitat that may be increasingly susceptible to non-native plant invasion. To assess the invasibility of burned black spruce forests, I used burned field sites that spanned a gradient of burn severities, moisture levels, and burn ages. I conducted both field surveys and a greenhouse experiment using soil taken from my burn sites. I found that invasive focal species *Melilotus alba, Hieracium aurantiacum*, and *Bromus inermis* ssp. *inermis* grew better in soil from low severity burns and burns between 10 and 20 years old than in soil from high severity or recent burns. In addition, regional differences between burn complexes outweighed burn severity or burn age in determining the invasibility of burned black spruce sites. In both recent and older burns, re-establishing native ground cover vegetation appeared to offer burned areas a level of resistance to invasive plant establishment. I concluded that burned black spruce areas are susceptible to non-native plant invasions, and managers of natural lands should monitor burned areas with nearby non-native plant populations to reduce the potential of spread into Alaska's boreal forest.

Keywords Boreal forest, Fire, Invasive species, Disturbance, Climate change, *Bromus inermis* ssp. *inermis*, *Hieracium aurantiacum*, *Melilotus alba*

Introduction

The boreal forest remains one of the few ecosystems on earth where invasive plants have had relatively little impact. Low levels of human disturbance, short growing seasons, cold winters, and large areas dominated by permafrost have clearly precluded many temperate non-native species from establishing in boreal systems (Elliot-Fisk 2000; Shephard 2004; Carlson and Shephard 2007). However, successful non-native plant introductions are known to occur beyond species' expected climatic zones (Elven and Elvebakk 1996; Carlson and Shephard 2007). As climate has changed and human disturbance has increased in boreal Alaska, the spread of invasive plants has accelerated (c.f. Carlson and Shephard 2007). In the past decade, invasives have begun to move off the human footprint into naturally disturbed areas (i.e., wildfire burn scars, glacial floodplains) and intact boreal plant communities (Wurtz et al. 2006; Carlson and Shephard 2007; Cortés-Burns et al. 2007).

Burned black spruce (*Picea mariana*) forest represents one potentially vulnerable boreal habitat. Highly flammable black spruce communities compose 40% of Alaska's boreal forest (Van Cleve et al. 1983). Wildfire, primarily ignited by lightning strikes, is the most frequent disturbance in black spruce forest and is an integral part of re-setting successional processes (Van Cleve et al. 1983). In other biomes, areas burned by wildfire are more favorable to invasives than unburned areas (Vitousek 1986; Milberg and Lamont 1995; D'Antonio 2000; Maret and Wilson 2000; Asher et al. 2001; Keeley et al. 2003; Haskins and Gehring 2004; Dimitrakopoulos et al. 2005; Floyd et al. 2006).

Factors such as exposed mineral soil, increased nutrient availability, and reduced competition from native plants all combine to make conditions ideal for non-native seeds to germinate and flourish after a fire (Asher et al. 2001). If invasive species establish rapidly after a fire disturbance, they may prevent the establishment of native plants or out-compete the rebounding native vegetation (Vitousek 1986). Furthermore, an increase in invasive species, particularly grasses, may result in increased fire frequency, in turn, creating more disturbed habitat for invasive plants to spread (D'Antonio and Vitousek 1992; Mack et al. 2001; Brooks 2002; Grigulis et al. 2005).

Climate change is expected to increase the vulnerability of Alaska's boreal forest to non-native plant invasion directly by affecting temperature and growing season, and indirectly by affecting the fire regime. Warmer winters (Chapman and Walsh 1993) and longer growing seasons (Myneni et al. 1997) may facilitate the survival of a greater diversity and abundance of non-native species in Alaska. In addition, invasive plants tend to have higher reproductive output and better dispersal ability than functionally similar native plants, which may allow invasives to respond to the changes in Alaska's climate more rapidly than native boreal plant species. Warmer summer temperatures and decreased precipitation in Alaska have dramatically increased wildfire disturbances in the past few decades (Overpeck et al. 1997; Stocks et al. 2000; Bachelet et al. 2005; Alaska Fire Service (AFS) 2007), which may provide further advantages to invading non-native plant species. During the 2004 and 2005 fire seasons, 11.2 million acres of Alaska's boreal forest burned making them, respectively, the first and third largest fire years in recorded history (Fitzgerald 2006). Fire frequency, severity, and extent are predicted to continue to increase in the future (Flannigan et al. 2001). If burned areas in Alaska's boreal forest are more susceptible to invasion than undisturbed areas, as they are in other biomes, then the simultaneous threats of increasing wildfire and increasing non-native plant invasion pose serious consequences to the boreal forest in a changing climate.

Non-native plant invasions can seriously alter community structure and ecosystem functioning (Vitousek et al. 1997; Levine et al. 2003), resulting in loss of biodiversity (Pyšek and Pyšek 1995; Martin 1999) and changes in nutrient cycling (Vitousek and Walker 1989; Evans et al. 2001; Mack et al. 2001), hydrology (Busch and Smith 1995; Rickard and Vaughan 1988), and fire regimes (Whisenant 1990; D'Antonio and Vitousek 1992). To prevent these potential impacts in Alaska, land managers must be able to prioritize areas which are the most susceptible to invasion. Currently, Alaska's invasive plants largely occur on road corridors (Shephard 2004; Alaska Exotic Plant Information Clearinghouse (AKEPIC) 2008; Conn et al. *in press*). The low number of invasions into boreal forest habitats provides an opportunity for Alaska to control these plants, but also offers little power to predict which areas will be most vulnerable to invasive plants in the future.

In other ecosystems in North America, high severity burns (areas where fire has had a large effect on the ecosystem; Turner et al. 1997) are generally more susceptible to non-native plant invasions than areas burned less severely (Agee 1996; Turner et al. 1997; Crawford et al. 2001; Keeley et al. 2003; Hunter et al. 2006). In Alaska's black spruce forest a thick layer of moss, lichen and organic soil (duff), commonly up to 30 cm thick, typically overlays mineral soils and permafrost (Viereck et al. 1992). Unlike many other fire dependent systems, where burn severity is defined based on tree mortality and duff consumption (Turner et al. 1997), in boreal black spruce forests the proportion of the thick duff layer consumed best reflects the fire’s impact on the ecosystem (Kasischke and Johnstone 2005; Johnstone and Chapin 2006; Johnstone et al. in press). As a result, high severity burns are defined by the large percentages of the duff consumed during the fire (Kasischke and Johnstone 2005). Among native boreal species, plants regenerating from seeds tend to have higher establishment rates in high severity sites (Schimmel and Granstrom 1996; Johnstone et al. *in press*), where patches of mineral soil are exposed. In low severity burns, much of the charred, dry duff remains, offering a less hospitable surface for germination and establishment (Johnstone and Chapin 2006). Invasive seeds arriving at a low severity site should potentially suffer the same recruitment barrier as native seeds. In addition, the invasibility of Alaska’s burned black spruce forests should decrease with increasing time since fire due to the resurgence of native plants. This trend has been documented in western U.S. coniferous forests, where non-native species abundance and richness tend to decrease with increasing burn age (Agee and Huff 1987; Turner et al. 1997; Doyle et al. 1998; Klinger et al. 2006).

While at the site-level, severity, moisture, or burn age may influence a burned area’s susceptibility to invasion, the controls over burn site invasibility may change with spatial scale. Controls over habitat invasibility by non-native plants in other ecosystems differ at different scales (Stohlgren et al. 1999; Knight and Reich 2005), with recipient community structure playing a large role at smaller scales (Tilman 1997; Naeem et al. 2000; Kennedy et al. 2002) and climate and soil properties determining invasibility at larger scales (Stohlgren et al. 1999; Stohlgren et al. 2003). In black spruce communities of Alaska, species assemblages are influenced by different factors at different scales, with topographic position, soil texture, soil pH, paludification and fire history determining plant assemblages at a site level, and mineral soil pH overriding these factors at a regional scale (Hollingsworth et al. 2006). In the boreal forest of Newfoundland, Canada, proximity to anthropogenic disturbance was the best predictor of invasion by non-native plants at small scales, while mineral soil pH was the best predictor throughout the 1,805 km^2 Grose Mourne National Park (Rose and Hermanutz 2004). Similarly, differences in soil properties may outweigh the influence of burn severity or burn age on patterns of non-native plant invasion in black spruce forests at larger scales.

Large-scale management of invasive plants necessitates using broad trends across taxa to predict areas of conservation concern. In other habitats, predicting which areas were most susceptible to invasion has proven to be difficult, primarily because site invasibility tended to depend on the match between the invader and the environment (Nijs et al. 2004; Richardson and Pyšek 2006). For example, *Melilotus alba* Medik. (Fabaceae), *Hieracium aurantiacum* L. (Asteraceae), and *Bromus inermis* ssp. *inermis* Leyss. (Poaceae) represent three plant families that occur disproportionately among invasive taxa in Alaska (AKEPIC 2005, AKEPIC 2008). Though all three species are highly invasive in many parts of the state (Alaska Natural Heritage Program (ANHP) 2006), they each possess different functional traits and regeneration strategies. *Melilotus alba* is a short-lived nitrogen-fixer that produces over 20,000 seeds per individual (Turkington et al. 1978), which are easily scarified by fire (Heitlinger 1975) and persist in seedbanks for up to 81 years (Royer and Dickinson 1999). The perennial *H. aurantiacum* can colonize a burn from long distances with its hundreds of wind-dispersed seeds, and spreads rapidly using stolons (ANHP 2006, Carlson et al. 2008). This hawkweed tends to be found in well drained soils and thrives in nutrient poor, disturbed soils (ANHP 2006). *Bromus inermis* ssp. *inermis* (hereafter referred to as *B. inermis*) is a drought-tolerant perennial that regenerates tillers quickly after fire (Blankenspoor and May 1996; Willson and Stubbendieck 1997), forming a dense monotypic vegetation layer that may slow succession (Densmore et al. 2001) and change fuel properties. While differences in invasiveness traits among these species will likely influence their responses to different burn severities, site moisture levels, and burn ages, trends that emerge across taxa would be more useful to agencies attempting to prevent a suite of non-native plants from invading burned areas.

Understanding how burn characteristics, specifically edaphic factors and competition at the seedling stage, affect invasion potential is the first step in understanding the likelihood of widespread invasion across the boreal forest of Alaska. Therefore, the primary objective of my study was to experimentally determine factors that may influence burn susceptibility to non-native plants. In this paper I pose three primary questions: 1) Do burn severity, soil moisture and burn age of black spruce sites influence the likelihood of non-native plant establishment? 2) Do regional scale factors outweigh site level factors in determining vulnerability to invasion, or vice versa? and 3) Are invasive plant responses to burn site characteristics species-specific or general across taxa?

Methods

I used two complementary approaches to address my questions: a field survey of burned areas adjacent to roadways and a greenhouse experiment using soil cores taken from my field sites. The field survey provided an assessment of current patterns of non-native plant movement into burn areas. The greenhouse approach controlled for propagule pressure (a confounding factor in most field studies on invasibility) and prevented accidental introductions of invasives into the largely pristine burn sites. The surveys served as a comparison for my greenhouse study and provide a baseline for future field research. My greenhouse approach could not account for climatic variations or biotic interactions beyond competition from small plants, factors that may further limit or promote invasive growth in the field.

Study Area

In July 2006, I sampled burned black spruce stands within a 120,000 km^2 area located between the Alaska and Brooks Mountain Ranges (Fig. 1). All my sites were established prior to this study as a part of the Bonanza Creek Boreal (BNZ) Long Term Ecological Research (LTER) Program. My sites were located near major roadways throughout interior Alaska: the Steese, Taylor, Dalton, Alaska, and Richardson Highways. Both the Taylor and the Steese Highways experience low levels of traffic and primarily serve as access to wilderness areas and remote towns. The Dalton Highway experiences higher levels of traffic, primarily truck traffic, as it is the only road to the

North Slope oil fields and services the northern half of the Trans-Alaska Oil Pipeline. All three of these roadways are largely unpaved with some stretches of pavement. The Alaska Highway, which connects Alaska to Canada and the contiguous U.S., and the Richardson Highway, which connects Valdez to Fairbanks and services the southern half of the Trans-Alaska Oil Pipeline, have the highest levels of traffic and are entirely paved.

Experimental Design

I conducted two separate experimental manipulations: one which investigated site factors and regional influences that affect invasibility of sites that all burned within a single year (2004), and another which investigated the influence of the time elapsed since burning on site invasibility within a single region.

To understand local and regional factors that affected the susceptibility of areas burned in the year 2004, I surveyed and sampled sites located in three regions along the Steese, Taylor, and Dalton Highways. In these sites, I crossed burn severity with site moisture to create four different site types: low severity-high moisture, low severity-low moisture, high severity-high moisture, and high severity-low moisture. One site of each type was located in the Steese region, the Taylor region, and the Dalton region, making a total of 12 sites. To classify site burn severity, the percent mineral soil cover was visually estimated and the remaining organic soil (duff) depths was measured at eleven random points. Sites with >5% mineral soil exposed and with <7 cm mean remaining duff were considered high severity. To classify site moisture, sites were assigned a moisture class from 1 (xeric) - 6 (subhygric) based on soil texture, topography, and average percent moisture in mineral soil (as measured using a TDR probe at eleven random points). Sites with moisture classes 4 through 6 were considered high moisture, and tended to have fine soil texture, >30% mineral soil moisture, and be located in low lying areas. Sites with moisture classes 1 through 3 were considered low moisture, and tended to have coarse soil texture, <30% mineral soil moisture, and be located on slopes or ridges. Further details on the 2004 site classification protocols are available in Johnstone et al. (*in press*). To provide an unburned control, I established a site in a moist black spruce stand that had not burned since 1901 (105 years old; Fastie et al. 2003). This site was located in the Steese region within the BNZ LTER Caribou-Poker Creeks Research Watersheds (CPCRW).

To evaluate the influence of time elapsed since fire on site susceptibility to non-native plant colonization, I used a chronosequence of sites that burned in 1999 (7 years old), 1994 (12 years old), and 1987 (19 years old) located in a single region near the town of Delta Junction at the intersection of the Alaska and Richardson Highways. In these sites, I crossed the three burn ages with my two levels of burn severity to create six different site types. Site burn severity was assigned in the same manner as for the 2004 burn sites. Due to similarities in topography and soil texture, site moisture was not a factor in the chronosequence investigation. Detailed descriptions of the Delta Chronosequence sites are available in O'Neill et al. (2003) and Kasischke and Johnstone (2005).

All sites were less than 100m from roadsides. Sites consisted of 30 m x 30 m plots placed in relatively homogeneous areas with respect to fire severity and site moisture.

Field Survey

To assess current patterns of invasion in interior Alaska, I surveyed my 19 study sites for presence and abundance of non-native plant species both within the burns and along the nearest adjacent roadside. I used the Alaska Natural Heritage Project invasiveness rankings (ANHP 2006) to categorize the non-native plant species present at each site as “aggressive” (invasive) or as “non-aggressive” (non-invasive). Aggressive species had invasiveness rankings >50, while non-aggressive species rankings were <50. A rank of 0 indicates no perceived threat to natural ecological systems and no difficulties in controlling the species. A rank of 100 indicates extremely high threat of colonization, ecological damage, and an inability to control its spread. These rankings are based on literature records of species impacts, biological traits, dispersal ability, distribution, and feasibility of control in Alaska and similar habitats elsewhere (see Carlson et al. 2008).

I recorded the presence or absence of all aggressive and non-aggressive non-native plant species within the burned area of each site; this included the area within the 30 m x 30 m burn plot and burned area between the plot and the roadside. Roadside surveys consisted of two 1 m x 100 m belt transects parallel to the road: one belt centered 1 m from the road shoulder and another approximately 1m from the edge of the burned forest (Fig. 2). Within each belt transect, I visually estimated the cover of all aggressive and non-aggressive non-native species biomass. The strips of vegetation between the road and the forest differed in width between sites and regions. At sites where the distance between the road and the burned forest edge was less than 2 m, I surveyed only one belt transect centered 1m from the road edge.

To get a more thorough perspective of non-native plant distributions in interior Alaska burns and provide baseline data for continued monitoring of these sites, I recorded presence or absence of non-native plant species in 77 additional BNZ LTER sites that had burned in 2004. These sites had all been established by previous BNZ LTER researchers and were selected to represent a gradient of burn severity and moisture levels in the Steese, Taylor and Dalton regions. Site level data and metadata for soil, vegetation, and surface cover on these additional sites is available in the BNZ LTER database (J. Johnstone, http://www.lter.uaf.edu/data_b.cfm).

Field Measurements and Experimental Soil Sample Collection

Within each burn site, I established three randomly selected 30 m transects in a uniform compass direction with a minimum distance of 2 m between transects (Fig. 2). I took three intact soil cores (7 cm diameter x 22 cm depth) every 5 m along the transects using a soil corer inserted at the soil surface and inserted them into cylindrical pots of similar dimensions. Pots had a tapered bottom, which I filled with rockwool to better fit the soil core and prevent mineral soil from escaping. I used each of the three cores at each sampling point in my greenhouse experiment to grow one of three different invasive plant species. There were no established populations of my three focal invasive species at these sampling points. Additional field measurements at each sampling point included soil compaction (measured with a pocket penetrometer in kg cm^{-2} by pressing the piston 2 cm into the soil), and the horizon thicknesses of live moss, upper duff (fibric soil or Oi/Oe horizons) and lower duff (humic soil or Oa horizons) (measured inside core holes) at each sampling point. Every 10 m along each transect an additional core was taken with a soil corer inserted at the soil surface to determine the bulk density and water holding capacity of the two different organic soil layers and the mineral soil (procedures below). From each site, a total of 54 cores were transported to the greenhouse to grow invasive plants (18 cores for each of my three focal species), and 9 cores per site were used to conduct soil analysis (Fig. 2).

Greenhouse Study

I conducted a greenhouse experiment to assess the invasibility of burn soils independent of propagule pressure, and to examine the influence of edaphic factors and small-scale plant interactions on three different invasive species. To do this, I sowed seeds of *Melilotus alba, Hieracium aurantiacum,* and *Bromus inermis* ssp. *inermis* on a core from each sampling point at each site. In soils from 2004 burns, I looked at the overall effects of burn severity, site moisture, and region on germination, survival, growth, and reproduction for each invasive species. In soils from the chronosequence burns, I measured germination, survival, growth, and reproduction in response to burn age and burn severity. In addition, I measured soil and small-scale vegetation characteristics to capture soil core variation within sites and better explain the influence each 2004 and chronosequence treatment had on invasive plant response variables.

I used two watering treatments in the greenhouse: cores from high moisture sites were arranged randomly in 0.6 m x 1.3 m trays with approximately 10 cm standing water and watered with an overhead boom every 1-2 days; cores from low moisture and chronosequence sites were watered on the same schedule with the overhead boom only. Four trays for the high moisture treatment and four blocks of randomly placed low moisture cores were staggered evenly along the greenhouse bench to account for potential positional effects.

To determine if burn site characteristics affect invasive plants in any general growth patterns across species, I selected three focal species, *M. alba, H. aurantiacum*, and *B. inermis*, to represent three problematic families of invasive plants in Alaska (see ANHP 2006). Seeds of *M. alba* and *B. inermis* were collected from naturalized populations just outside the Institute of Arctic Biology Greenhouse at the University of Alaska Fairbanks. *H. aurantiacum* seeds were purchased from Chiltern Seeds, UK, due to limited availability of seeds currently in interior Alaska. I scarified all *M. alba* seeds by hand using sandpaper to prepare them for germination.

I placed five seeds of *M. alba* or *B. inermis*, or seven seeds of *H. aurantiacum* on each core top for all sites and evaluated germination, survival (percent seeds germinating and surviving), and growth over 30 days. I assessed survival, growth and reproduction again after 90 days, and took final measurements after 150 days. A surviving invasive plant was considered reproductive if it was either flowering or reproducing asexually. I grew my seedlings in the University of Alaska Fairbanks Institute of Arctic Biology Greenhouse at a mean temperature of 22 °C with 20 hours of light per day, typical of the growing season in interior Alaska.

To quantify invasive plant response to the burn soil characteristics, I measured a variety of fitness variables throughout the growing season. I scored germination of *M.*

alba after 10 days. Due to longer time requirements for germination, I scored *B. inermis* and *H. aurantiacum* germination after 14 days. After 30 days, I randomly thinned plants to 1 invasive per pot (n=18 per species per site) for the remainder of the experiment. I calculated invasive plant survival after 90 days and then harvested half the plants. I dried the shoots of all harvested plants (n=9 per species per site) and the roots of a random subset of plants (n=3 per species per 2004 site, n=5 per species per chronosequence site) to a constant weight for biomass measurements. After 150 days, I determined survival, assessed proportion of reproductive survivors, and harvested both shoots and roots of all remaining plants (n=9 per species per site).

Additional measurements of soil properties, native vegetation, and surface cover were collected to help explain variation in response variables:

Soil properties- Using the nine additional cores collected from each field site, I determined the water holding capacity and bulk density of the upper duff, lower duff, and mineral soil horizons. To calculate water holding capacity (WHC) of each horizon, I divided field-moist cores into sections based on the field measurements of the horizon thickness. Each horizon section was homogenized in a tray, and then a sub-sample was placed in a pre-weighed and saturated filter paper inside a funnel. I saturated the soil with deionized water and let it drip. When the soil ceased dripping, I weighed it, dried it to a constant weight, and then reweighed. WHC is expressed in g H_2O g^{-1} dry soil. The remaining soil in the tray was put into a pre-weighed paper bag and dried. To determine horizon bulk density, I added the sub-sample dry mass back to the remaining section dry mass and divided by the volume of the core section (g cm^{-3}).

Native vegetation- For all cores with invasive plants sown in them, I determined native plant cover and richness by visually estimating percent cover of each species in a given core. I also recorded the heights of the tallest native vascular plant in each core. Native non-vascular and vascular biomass were determined for each core by clipping live shoots at the soil surface at the time of the two invasive plant harvests (90 or 150 days).

Surface cover- I visually estimated percent cover of exposed mineral soil, bare charred organic soil, live non-vascular plants, dead non-vascular plants, and leaf litter for each core. Lichen biomass and cover in unburned soil cores was included in the non-vascular measurements.

Statistical analyses

All statistical analyses were performed using SAS v.9.1 (SAS Institute, Cary, North Carolina). To analyze field survey data, I determined if the presence of non-native plants in burned field sites was influenced by burn severity, site moisture, or region using chi-square analysis. To test for differences in invasive plant responses between burned and unburned soil cores, I conducted ANOVA Tukey studentized range tests. To determine the influence of burn severity, moisture, region, and age on invasive plant growth parameters, I tested for differences in the response of each of the three focal invasive species in 2004 burn sites and chronosequence burn sites using analysis of variance (ANOVA). The explanatory variables for 2004 burn sites were burn severity, site moisture, and region; for chronosequence burn sites, the explanatory variables were burn age and burn severity. Response variables individually tested for each species included germination, survival at 30 days, biomass at 90 and 150 days, and reproduction. I used chi-square analysis to test differences in invasive survival at 90 and 150 days between burn severity, site moisture and burn age levels.

I tested for differences in soil properties, native vegetation, and surface cover between burn severity and site moisture categories, burn age and burn severity categories, or regions using ANOVA Tukey studentized range tests. I then used stepwise linear regression to determine which soil, vegetation, or cover variables best explained the variation in the response variables of my three focal species. Data were log-transformed or rank-transformed as necessary to meet model assumptions.

Results

Field Survey

Across all 2004 burn sites surveyed (n=89), non-native plant presence was significantly influenced by the region in which it was located ($X^{2}_{(3)} = 14.52$, $P = 0.002$). Aggressive non-native plants were found moving off the roadway into the burned forest at a greater rate along the Dalton Highway compared to the Steese and Taylor Highways (Fig. 3, Appendix 1). Non-native plant presence was not influenced by burn severity or moisture classification.

Within the 12 intensively sampled 2004 burn sites and 6 chronosequence sites, I found five non-native species: *Agropyron repens*, *Chenopodium album, Crepis tectorum, Melilotus alba,* and *Taraxacum officinale* ssp. *officinale*. Three of the six Delta Chronosequence sites had both aggressive and non-aggressive non-native plants in the burn and showed the greatest non-native abundance and richness of all areas surveyed (Appendix 1, 2). Three of the four intensively sampled sites in the Dalton region had non-native plants within the burn, while none of the intensively sampled sites in the Taylor or Steese regions had non-native plants (Appendix 2).

I found eleven non-native plant species established and reproducing along roadsides adjacent to my burn sites: *Agropyron repens, Bromus inermis ssp. inermis, Chenopodium album, Crepis tectorum, Lepidium densiflorum, Matricaria discoidea, Melilotus alba, Plantago major, Polygonum aviculare, Taraxacum officinale* ssp. *officinale, and Trifolium hybridum*. Mean non-native plant cover on the roadsides adjacent to my sites was highest along the Dalton Highway (69.6 ± 10.6 %), followed by the Taylor Highway (21.5 ± 10.8 %) and the Steese Highway (1.1 ± 0.5 %) (Fig. 3). Roadside cover of non-native plants near the Delta Chronosequence burns was also low, but this was due to intentional weed control efforts by both the Department of Transportation (L. Johnson, pers. comm.) and the nearby Ft. Greeley Army Base (J. Mason, pers. comm.).

Greenhouse Experiment

Burned vs. Unburned Soils

In the greenhouse, germination and survival rates were considerably greater in cores from burned sites (both 2004 and chronosequence burns) than from the unburned site (*P* <0.001 for germination and survival for all three species; Fig. 4). Mean germination rates on burned cores were highest for *M. alba* (70.6 ± 1.0 %), followed by

B. inermis (58.2 ± 3.1%), and *H. aurantiacum* (39.1 ± 1.2 %). Mean survival rates on burned cores, calculated as a proportion of original propagules surviving, were highest for *B. inermis* (52.2 ± 3.9%), followed by *H. aurantiacum* (26.0 ± 2.6%), and *M. alba* (11.5 ± 4.4 %). Germination for all three species was approximately 20% lower on unburned cores. Of the 92 germinating invasive individuals in unburned cores, only two seedlings survived the length of the growing season. One of these survivors was *B. inermis,* and the other was *H. aurantiacum*; however, both were extremely small (<0.02 g dry mass) and non-reproductive after 150 days.

2004 Burns: Burn Severity, Moisture, and Region

Burn severity and moisture levels had little effect on germination, survival, growth, and reproduction of *M. alba* and *H. aurantiacum* (Table 1, Figs. 4a and 5a). While *H. aurantiacum* total biomass was not influenced by burn severity (Fig. 5a), it allocated significantly higher biomass to roots when grown in cores from low severity burns than in cores from high severity burns (Table 1). The region the of burn site, however, influenced germination, biomass accumulation, and survival in *M. alba* and *H. aurantiacum* (Table 1). Percent germination of *M. alba* was greatest in soils from the Dalton region (Table 1). Biomass of *H. aurantiacum* was significantly lower in soils from the Steese region than in soil from the Dalton or Taylor regions (Table 1). Survival at 150 days was greatest in soils from the Dalton region for both species (*M. alba*- $X^2_{(2)} = 16.22$, $P = 0.003$; *H. aurantiacum*- $X^2_{(2)} = 10.80$, $P = 0.004$).

In contrast, *B. inermis* was affected by burn severity and moisture levels, as well as by region (Table 1). *B. inermis* grown in cores from low severity sites showed, on average, 11% lower survival than in cores from high severity sites (Fig. 4a; $X^2_{(1)}=3.97$, $P=0.05$), but had 36% more biomass (Fig. 5a; $P=0.04$). *B. inermis* also preferred high moisture cores to low moisture cores (Table 1, Fig. 5a): seeds had 8% higher germination, and surviving seedlings had twice as much final biomass, twice as many tillers, and a 27% reduction in allocation to root biomass in high moisture cores. *B. inermis* also showed differences in growth responses in soils from different regions (Table 1). *B. inermis* grown in Dalton and Taylor region soils did not differ, but both groups had approximately 75% greater biomass and 77% more tillers than *B. inermis* in the Steese soils.

Chronosequence Burns: Burn Age and Severity

Burn age influenced the germination, survival, biomass, root-to-shoot ratio, or reproduction of all three invasive species (Table 1, Fig. 4b). *M. alba* and *H. aurantiacum* both showed increased survival in the 12 year old (1994) burn compared to all other burn ages (Fig. 4b). The age of the burn significantly affected *M. alba* survival at 90 days ($X^2_{(2)}=9.94$, $P=0.007$) and 150 days ($X^2_{(2)}=9.09$, $P=0.01$), and *H. aurantiacum* at 90 days ($X^2_{(2)}=9.94$, $P=0.007$). Burn age had a significant influence on *B. inermis* survival in the first month ($F_{(2,\ 102)}=8.84$, $P=0.0003$), and all remaining plants survived to the end of the experiment (Fig. 4b).

For all three species there was a general pattern toward greater biomass in soils from older burns. Specifically, all three species had the greatest biomass in soils from the 12-year-old (1994) burn sites (Fig. 5b); however, this was only significant for *M. alba.* In two of the three species (*H. aurantiacum* and *B. inermis*), the invasives growing in 7 year old burn soils had less biomass than in the 12 or 19 year old burns (Fig. 5b).

Across age levels, all three species showed greater biomass in low severity cores than in high severity cores, though this was not significantly greater for *M. alba* (Table 1; *M. alba*- 50% larger, *H. aurantiacum*- 35% larger, *B. inermis*- 37% larger). Invasive vegetative reproduction was also higher in low severity cores (Table 1; *H. aurantiacum*- 70% more stolons, *B. inermis*- 46% more tillers). While the interaction between age and severity was only significant for *H. aurantiacum* and *B. inermis* biomass (Table 1), all three species showed the greatest biomass in soils from the 12 year old (1994) low severity burn, the second greatest biomass in the 19 year old (1999) low severity soils, and least biomass in the 7 year old (1999) high severity soils (Fig. 5b).

Soil, Vegetation, and Cover Influences on Invasibility

2004 Burns- Relative to high severity burns, cores taken from low severity burns tended to have lower soil compaction, greater remaining organic soil depth, greater organic soil water holding capacity and lower organic soil bulk density (Table 2). Vegetation type, biomass, and cover were also influenced by the burn severity and site moisture level. Specifically, non-vascular plant biomass and cover was greater in cores from high severity sites and native vascular plant biomass tended to be greater in cores from high moisture sites (Table 2). Native plant richness was greater in cores taken from high severity sites, and richness in cores taken from high severity, high moisture sites was not significantly different from that of cores from the unburned control site (Table 2). Between regions, there were few differences in organic or mineral soil variables; however, when compared to cores from sites in the Dalton or Taylor regions, cores from Steese region had significantly greater non-vascular biomass and cover, vascular cover, and native plant richness (Table 3).

Using multiple regression stepwise model selection analysis, I was able to explain 15% of the variation in total biomass of *M. alba* with the thickness of the lower duff alone (Table 4). Thickness of the lower duff was also a significant explanatory variable for *B. inermis*, where 31% of the variation in total biomass was explained by a combination of lower duff thickness, nonvascular biomass, bulk density of the mineral soil, and the maximum native vascular plant height (Table 4). Non-vascular biomass explained the most variation in total biomass for *H. aurantiacum,* and combined with native vascular height and bulk density of the lower duff, explained 33% of the variation in total biomass (Table 4).

Chronosequence Burns- As in the 2004 burn cores, soils taken from low severity chronosequence burns tended to have lower soil compaction, greater remaining organic soil depth, greater organic soil water holding capacity and lower organic soil bulk density than high severity burns (Table 5). While native vascular and non-vascular biomass varied little between sites, native plant richness was significantly higher in cores from the 1999 high severity site than in cores from any other site (Table 5).

Overall, the best multiple regression models found for invasives grown in chronosequence cores explained a greater proportion of the variation in invasive plant response variables than did the best models found for plants grown in 2004 burns (mean R^2 for models explaining total biomass: chronosequence =0.77, 2004 burns =0.26). Native vascular biomass was negatively correlated with final biomass in all three species and had the first or second largest partial R^2 in each model (Table 6). Similarly, native richness was negatively correlated with both *H. aurantiacum* and *B. inermis* biomass, and accounted for large proportions of the variability in the model (*H. aurantiacum* R^2= 0.37, *B. inermis* R^2=0.13). Both *M. alba* and *B. inermis* responded positively to water availability, with the water holding capacity of the mineral soil explaining 35% of the model variation in *M. alba* biomass, and the water holding capacity of the lower duff explaining approximately 20% of variability in both biomass and tiller production for *B. inermis* (Table 6).

Discussion

My experimental approach showed that there is high potential for invasion by non-native plants into black spruce burn areas, even though current non-native plant distribution in wildfire burn areas is low and restricted to areas where roadside populations occur. Rates of germination and survival for all three of my focal species were consistently higher in soils from burned sites compared to unburned soils. This greenhouse result was reflected in my field survey, where I observed flourishing reproductive *C. tectorum* populations in multiple burn sites and flowering *M. alba* spreading into burns from the roadside.

Current Patterns of Invasion in Burned Field Sites

Despite recent non-native plant control efforts on the roadsides, Delta Chronosequence sites showed the highest levels of aggressive non-natives present in native plant communities. Several factors may have increased the non-native abundances in these sites. First, the Delta Chronosequence sites are located near the junction of the Richardson and Alaska Highways, two of the largest highways in the state. These sites are also much closer to a human population center and agricultural areas than any of the sites on the Dalton, Steese or Taylor Highways. Second, these burns have been used for military training exercises, hunting, and long-term ecological research, which may have influenced non-native propagule influx to the sites through gear or equipment contaminated with non-native seeds. Finally, these older disturbances have had a substantially longer time for non-native introductions to occur and for seed banks to develop. For example, widespread *Crepis tectorum* occurrence and well developed seedbanks in the 1994 burn suggests that this species has already had a residence time of several years.

Data from my field survey are consistent with similar interior Alaska surveys of sites burned in 2004 (Cortés-Burns et al. 2007, J. Heys *pers. comm.*), where the highest levels of roadside non-native infestation and movement off the road corridor into native plant communities occurred in the Dalton region (Fig. 3). Despite the low levels of roadside non-native plant cover near my field sites on the Taylor and Steese regions, it is important to note that non-native plants are well documented to occur along the roadsides in many other portions of these highways (Cortés-Burns et al. 2007; Lapina et al. 2007; AKEPIC 2008). The Dalton Highway has the highest levels of traffic of any of the roads near my 2004 burn sites. The Dalton is the main support road for the North Slope oil fields and the Trans-Alaska Oil Pipeline. At one site *Crepis tectorum* appeared to be dispersing into the burn site from the adjacent Pipeline corridor rather than from the road. The greatest movement into burns appears to be occurring in areas of high propagule pressure where naturalized populations of non-native plants are established. In general, these areas correspond with areas of frequent human use and high levels of anthropogenic disturbance (Cortés-Burns et al. 2007). While my 2004 burn sites only showed non-native presence if an established population was nearby, the vast majority of sites remained free of non-native plants. The question remained, what caused some burn sites with established roadside non-native populations nearby to remain uninvaded? My greenhouse experiment addressed some possible mechanisms for resistance to invasion in these field sites.

Factors Influencing Invasibility

Burn Severity and Site Moisture

Contrary to the findings of studies in other ecosystems (Hunter et al. 2006; Keeley et al. 2003; Turner et al. 1997), my three focal invasive plant species did not show better establishment and growth in high severity burn soils. In fact, the one species that showed a significant burn severity effect in the ANOVA models (*B. inermis*) had greater biomass in low severity soils (Table 1). *B. inermis* also had increased germination, growth, and reproduction when water availability was high. My results for *B. inermis* are consistent with those from a study in tallgrass prairie communities that found this species tends to grow better in areas of higher water availability (Blankenspoor and May 1996). However, when faced with competition from native grasses after a fire, *B. inermis* tends to do better in low-moisture sites, where its higher drought tolerance allows it to dominate native vegetation (Blankenspoor and Larson 1994). Greater competitive ability may also allow *B. inermis* to perform well in low moisture black spruce burn sites in Alaska; however, my greenhouse experiment did not include competitive interactions between large plants.

While *M. alba* and *H. aurantiacum* did not respond to overarching severity and moisture categories, my multiple regression analysis shows that the biomass of all three of my focal species was influenced by soil and vegetation characteristics that reflect the complex interactions between burn severity and site moisture. Lower duff thickness explained the greatest amount of variation in both *M. alba* and *B. inermis* total biomass. Lower duff thickness reflects the amount of time between the most recent fire and the previous fire, the pre-fire species composition, decomposition rates, and environmental conditions, and the post-fire site characteristics (with greater thickness of this layer remaining in low severity, moist sites) (Kashischke and Johnstone 2005). These results suggest *M. alba* and *B. inermis* could have the greatest establishment success in sites where the lower duff layer is well developed before fire, and the fire consumes nearly all of the moss and upper duff layer while leaving a substantial amount of the lower duff layer intact which acts as a post-fire growth substrate. In fact, in one of my additional survey sites fitting this description, I documented the highest numbers of *M. alba* in any burn site, with over 30 reproductive individuals spreading into the burn.

In addition, non-vascular plant biomass played an important role in determining the final biomass of *H. auranitacum* and *B. inermis* (Table 4). The greater non-vascular biomass of liverworts (*Marchantia polymorpha*) and mosses (*Ceratadon purpureus* and *Polytrichum* spp.) biomass in high-severity sites (Table 2) appeared to reduce invasive plant growth. Though the ground cover species composition was different in the unburned site than in high severity sites, the impact of non-vascular plant (and lichen) biomass on invasive plants was similar. Thick layers of moss (*Hylocomium splendens*) and lichens (*Cladonia* spp.) overlaying unburned soils doubtlessly prevented all three of my focal species from surviving (Table 2, Fig. 4). A similar pattern was documented in Arctic tundra, where the abundant mosses decreased germination and establishment of a diverse array of native tundra plants (Gough 2006). It is highly likely that non-vascular plant abundance represents an important barrier to invasive plant colonization and spread in black spruce forest of interior Alaska.

Within a burn site of a particular severity and moisture classification, the soil surface exhibited some degree of microvariation (*pers. obs.*) most likely due to small scale differences in soil moisture or vegetation, micrtopography, and changes in weather during the fire. For example, within a low severity site, islands of unburned bryophytes often remain. In addition, small patches of higher severity burn with rapidly establishing *Ceratadon purpureus* or *Marchantia polymorpha* could occur within a low severity site.

In these microsites, my data suggest that establishment would be difficult for many invasive species. However, the proportion of bryophyte-free area was much greater in my low severity sites than in high severity or unburned sites (Appendix 2; Johnstone et al. *in press*), which my data suggest could contribute to the invasibility of these sites.

My analyses allow me to conclude that, in the greenhouse, low severity soils tend to lead to greater invasive plant growth than either unburned areas or those severely burned. However, my greenhouse experiment may overestimate the favorability of the low severity burns because it doesn't take into account additional environmental factors. The partially combusted, porous ground surface of low severity burns is prone to heat fluctuations and rapid drying (Johnstone and Chapin 2006), which means the timing and amount of precipitation would likely dictate germination and early invasive seedling survival. Another factor that did not exist in the greenhouse was the difference in soil temperature between high and low severity sites; soil temperatures were colder in my low severity sites due to the thicker layer of remaining organic material insulating the permafrost (Appendix 2; Kasischke and Johnstone 2005). However, it is quite likely that the barriers that are presented by low severity burns to native seed colonizers may not prevent invasive plant colonization. All three of my focal species are drought-resistant and cold-tolerant (Klebesadel 1992, 1993; USDA 2002) and occur in low moisture habitats throughout Alaska (AKEPIC 2008). In addition, I found reproductive invasive plants growing in low severity burns in my field survey, and the proportion of low severity sites with non-native plants present did not differ from that of high severity sites.

Burn Age

The highest survival, growth rates, and reproduction of invasives occurred in soils from the chronosequence burns (5-19 years old), which suggests that conditions in black spruce burns become more favorable over time. The increased invasive plant success with burn age in the first two decades following fire that I observed in my greenhouse study may be due to the increases in decomposition (O'Neill et al. 2003) and N-mineralization (Zhuang et al. 2003), and the associated changes in soil bacterial and fungal communities (Treseder et al. 2004) over time that have been documented in the Delta Chronosequence sites.

In the field, additional pressures from competition with native plants might limit the invasibility of these sites. Reduced light availability associated with higher canopy closure should presumably reduce invasive plant growth and field abundances, as most invasive plant species in Alaska are early successional species with limited shade tolerance (AKEPIC 2005). As burn age increased, the chronosequence sites showed increased leaf area index (Liu et al. 2005), increased above ground biomass (Zhuang et al. 2003), and decreased canopy openness (Appendix 2). My soil core cover data (Table 5) reflect the influence of canopy closure on native plant cover through time: both non-vascular and vascular plant cover decrease. In addition, vascular plant species richness and biomass accounted for large proportions of the variation in total invasive plant biomass (Table 6). In my greenhouse experiment, the reduced competition from understory plants combined with the absence of shade from dominant deciduous trees and shrubs doubtlessly allowed invasive plant biomass and reproduction to be greater than it would be in the field.

The length of time between fire and canopy closure has been cited as an important parameter for site invasibility (Keeley et al. 2003). The longer the time that has elapsed since fire, the more opportunities for introduction, and the longer potential residence time to build up seed banks that will emerge after the next disturbance. If this holds true in the boreal forest it suggests, once again, that low severity burns may be important avenues for invasive spread. While high severity burns in black spruce forests tend to develop into dense, closed canopy deciduous forests (if a seed source is available), low severity burns tend to regenerate into an open canopy black spruce forests (Johnstone and Chapin 2006). The greater light availability in low severity burns, even as time elapses, may provide ample opportunity for invasive colonization and seed bank establishment. I found some evidence of this in my field survey, where aggressive non-native plants occurred in 66% of my low severity chronosequence sites and only 33% of my high severity chronosequence sites (Appendix 1). Further, in the greenhouse, all three of my focal species grown in low severity soils taken from the chronosequence burns showed greater biomass (and number of flowers, crown buds, stolons, or tillers) than those grown in high severity soils (Fig. 4). While this result was not due to light availability, my multiple regression analysis suggests that reduced competition from native vascular plants in low severity sites may also influence the invasibility of these low severity sites (Tables 5 and 6). All three species also showed strong interactions between severity and age for a variety of response variables (Table 1). This suggests that burn severity and age have additive effects, with the most suitable soils for invasive plant growth and survival occurring in low severity burns that are between 10-20 years old.

Site vs. Regional Factors

My field survey and greenhouse data suggest that the influence of regional factors outweigh the influence of burn site characteristics on invasive plant growth, survival and reproduction in burned areas (Fig. 3, Table 1). Comparing the partial R^2 values for ANOVA response parameters, region explained 6.4 times more variation in *M. alba* germination than did severity or moisture levels combined (region $R^2 = 0.54$, severity + moisture $R^2 = 0.08$). Similarly, region explained 2.6 times more variation in *H. aurantiacum* biomass (region $R^2 = 0.33$, severity + moisture $R^2 = 0.13$), 1.5 times more variation in *B. inermis* biomass (region $R^2 = 0.41$, severity + moisture $R^2 = 0.28$), and 2.2 times more variation in *B. inermis* tiller production (region $R^2 = 0.48$, severity + moisture $R^2 = 0.22$), than did site severity and moisture levels combined.

In my field survey, burns in the Dalton region were more frequently invaded than burns in the Steese and Taylor regions and were the only burns with aggressive species (Fig. 3). Levels of invasion in my field sites were not influenced by burn severity or moisture. This result was likely due to the higher levels of propagule pressure from Dalton roadside populations (Fig. 3) and greater levels of traffic, road maintenance and human disturbance. In addition to greater propagule pressure along the Dalton Highway, my greenhouse study indicated all three of my focal species showed greater germination, survival, and biomass in soils from the Dalton region; however, this was only significantly greater than soils from the Steese region (Table 1). Furthermore, the region a core was taken from accounted for a greater proportion of the variation in *H. aurantiacum* and *B. inermis* biomass and reproduction than did differences in site severity and moisture levels (Table 1). Compared to the Dalton and Taylor regions, higher levels of non-vascular plant biomass and cover, vascular plant cover, and native plant richness in cores from Steese region likely aided in reducing the establishment of my focal invasive species (Tables 3 and 4).

Soil pH may also play a role in the greater field abundances of non-native plants along the Dalton highway. BNZ LTER data from the additional survey sites I used indicate that soil pH significantly differed between the three regions, with the Dalton having a higher mineral soil pH than the Steese and Taylor Highways (J. Johnstone, http://www.lter.uaf.edu/data_b.cfm). These results are consistent with the findings of Rose and Hermanutz (2004), who found increasing abundances of invasive plants in boreal forest sites with higher pH. However, pH cannot explain the greater biomass and reproduction of my focal species in the greenhouse, as pH did not differ between regions when comparing only sites from which I collected my soil cores (Appendix 2). In the field, the combined effects of higher propagule pressure, lower non-vascular plant cover, and a higher mineral soil pH may have made burns in the Dalton region more susceptible to invasion than burns in the Steese and Taylor regions.

Species-Specific Responses to Burn Characteristics and Trends Across Taxa

Several trends emerged in the responses of my focal species to burn characteristics. All three of my focal species performed better in soils from low severity burns, soils from burns that were 10-20 years old, and soils from burns in the Dalton region. At least two of the three species increased in biomass with decreasing competition from native plants and with increasing soil suitability (Tables 4 and 6). In the 2004 burn soils, the focal species tended to have increased biomass with the decreased non-vascular plant competition and increased lower-duff layer depths of low severity burn soils (Table 4). In the chronosequence experiment, the focal species tended to have greater biomass with the decreased vascular plant competition and increased soil water holding capacity of low severity and older burn soils (Table 6).

This is not to say, however, that all three species responded identically to all burn characteristics. Each particular species had a different pattern of fitness-related responses influenced by different burn characteristics (Table 1), and had a unique array of soil, vegetation and surface cover variables explaining each fitness response (Tables 4 and 6). For example, *M. alba* was less responsive to non-vascular plant competition in 2004 burns that the other two species (Table 4), and this was observed anecdotally in the field, where I found mature *M. alba* growing in *Ceratadon purpureus* in some of my sites. The differential response of my focal species to non-vascular plant competition may be due to differences in the morphology of these plants. *M. alba* has a tap-root and single stem, which would allow for less interaction with non-vascular plants than the fibrous-rooted, sprawling *H. aurantiacum* and *B. inermis*. Despite the nuanced responses of particular species, my data suggest certain burn types are more suitable than others to a variety of invasive plants. These generalizations of burn characteristics that influence site susceptibility to invasion can be useful to land managers attempting to prioritize monitoring and control efforts of all invasive species in Alaska’s burned black spruce forests.

Conclusions

As the climate changes, Alaska faces the simultaneous threats of increasing invasive plant abundances and increasing area burned by wildfire. This study indicates that these two increasing forces indeed make the boreal forest more susceptible to non-native plant invasions. I found invasive plants grow and reproduce better in burned soils compared to the unburned soils. This study presents a first step toward identifying wildfire burn characteristics that are likely to increase the susceptibility of boreal forest burn areas to non-native plant invasions. In black spruce forests, I found soils from low severity burns allow greater invasive plant growth, both in the first years after a fire and in the following two decades. Native vegetation rapidly re-establishing in high severity burn sites may provide a level of resistance to non-native plant invasion, while low severity sites may provide invasive plants a refuge from intense resource competition. In addition, I found that the soil suitability for invasive plant growth increases through time. With greater soil suitability and the increased probability of propagule arrival over time, burns between 10 and 20 years old are particularly vulnerable to invasion by non-native plants. Finally, regional differences in native plant regeneration, propagule pressure, and mineral soil pH outweigh the influence of site-level burn characteristics in determining the susceptibility of burned black spruce forest to non-native plant invasions. These results will aid Alaska land managers in effectively preventing the widespread invasion of non-native plants into burned areas. Further research, monitoring, and control efforts should be directed toward invasive plant in burned areas of the boreal forest, and these efforts should not be restricted to recently burned areas.

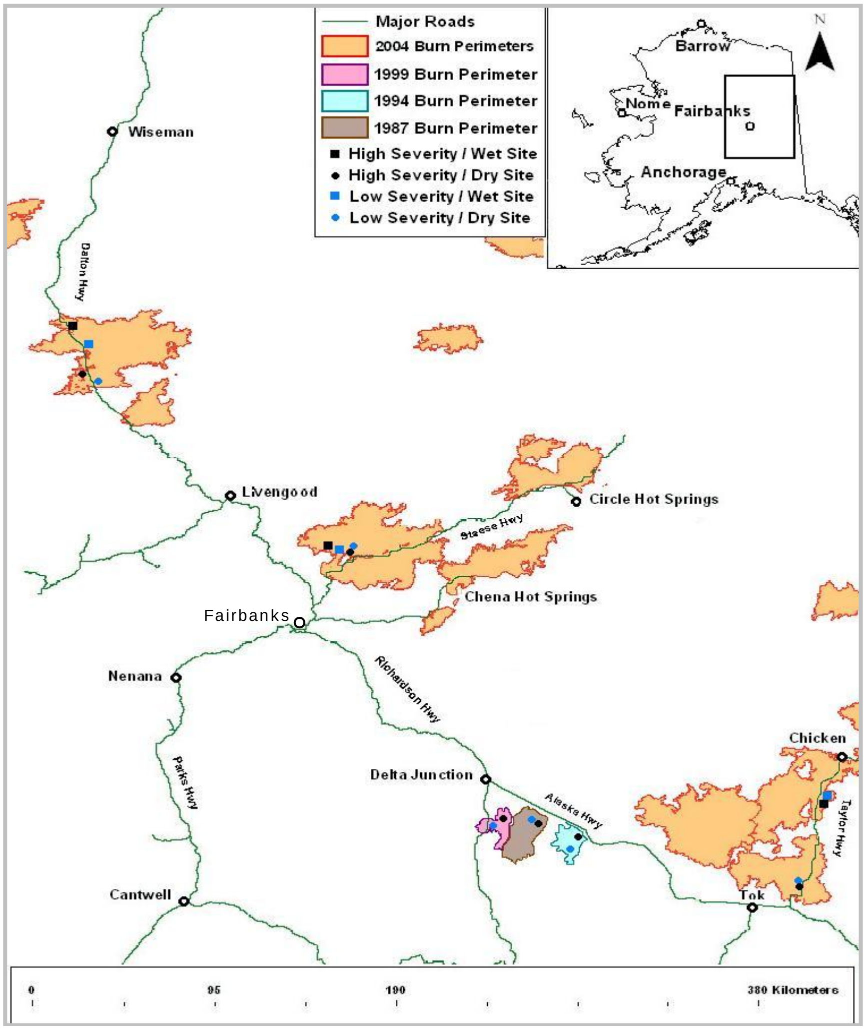

Figure 1. Map of interior Alaska, showing the location of study sites, perimeters of areas burned in 2004, 1999, 1994, and 1987, major roadways and towns.

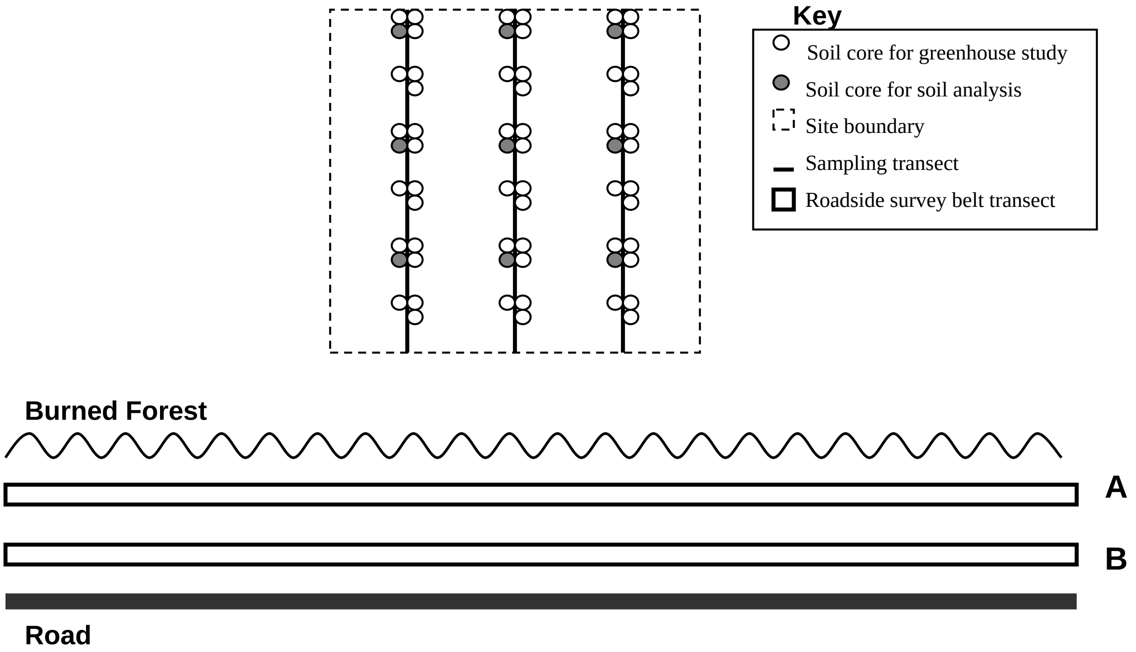

Figure 2. Site layout for field sampling and survey protocol. Three soil cores for greenhouse study were taken every 5 m along three 30 m transects. Additional cores for soil analysis were taken every 10 m. I conducted non-native plant surveys in the burn within the 30 m x 30 m plot and the area between the plot and the roadside. Surveys of roadside non-native plants were conducted in two 1 m x 100 m belt transects, one centered 1 m from the burned forest edge (A) and the other centered 1 m from the edge of the road (B). Distances between the road and the 30 m x 30 m plot varied between sites.

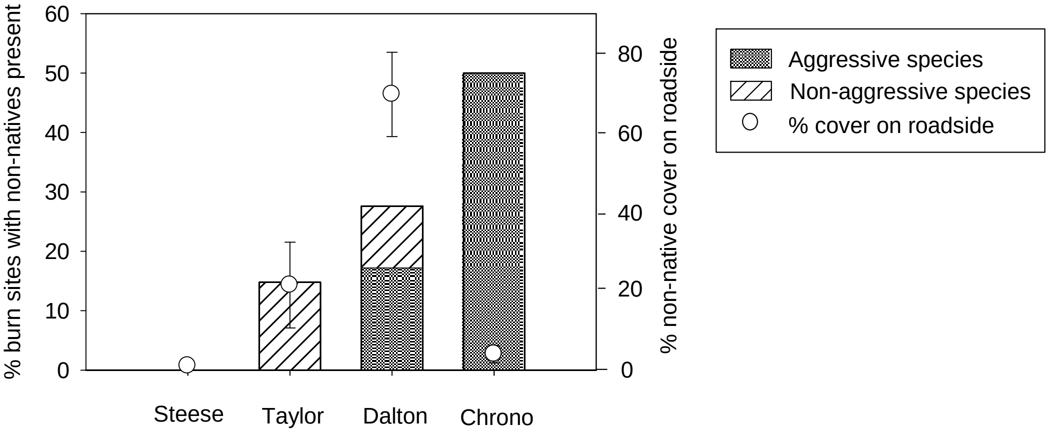

Figure 3. Percent burn sites with non-native plants present and percent cover of non-native plants on roadsides of different regions in interior Alaska, July 2006. Bars indicate percent burn sites surveyed with non-native plants found moving from roadsides into native vegetation in the Steese (n=33), Taylor (n=27) and Dalton (n=29) regions, and in the Delta Chronosequence burns ("Chrono"; n=6). Striped bar segments indicate percent of sites where only non-aggressive non-native species were present, while solid bar segments indicate only aggressive non-native species present or aggressive and non-aggressive species co-occurring. Open dots indicate mean percent non-native plant cover (± s.e.) from a subset of sites where I conducted roadside surveys in each region (Steese n=4, Taylor n=4, Dalton n=4, Chrono n=5). Only non-native plant cover data from the transect closest to the road were used in this figure.

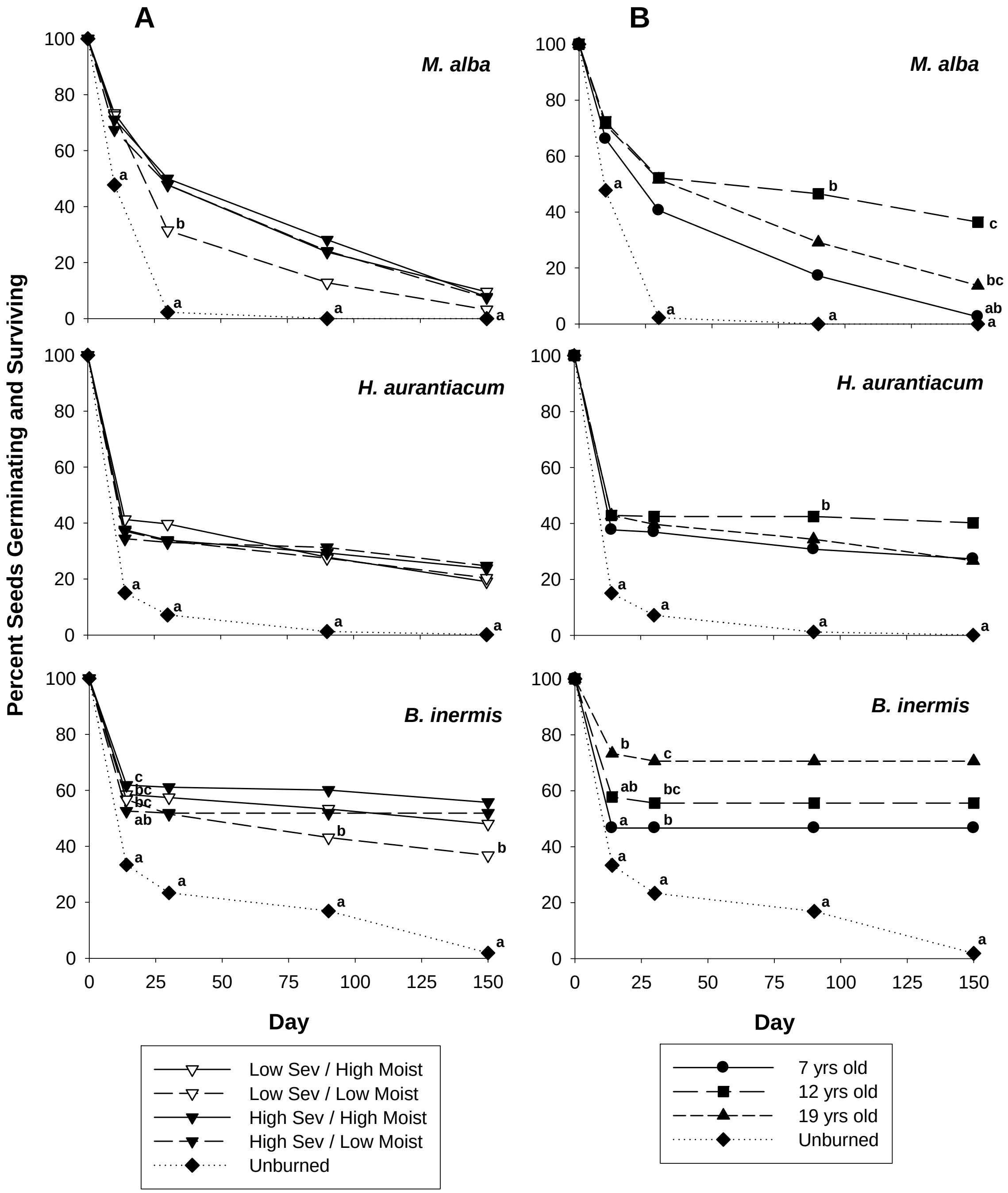

Figure 4. Percent of invasive plant seeds that germinated and survived in soil cores taken from four types of sites burned in 2004 (A) and from three ages of sites in the Delta Chronosequence (B). Germination was assessed on day 10 for *M. alba* and on day 14 for *H. aurantiacum* and *B. inermis*. Survival of all species was assessed on days 30, 90, and 150. Invasive plant germination and survival in the unburned, high moisture control soil cores (dotted line) is repeated on both 2004 graphs and Chronosequence graphs as a reference. Different lowercase letters indicate significant differences ($P<0.05$) in germination and survival between site types and ages at each date.

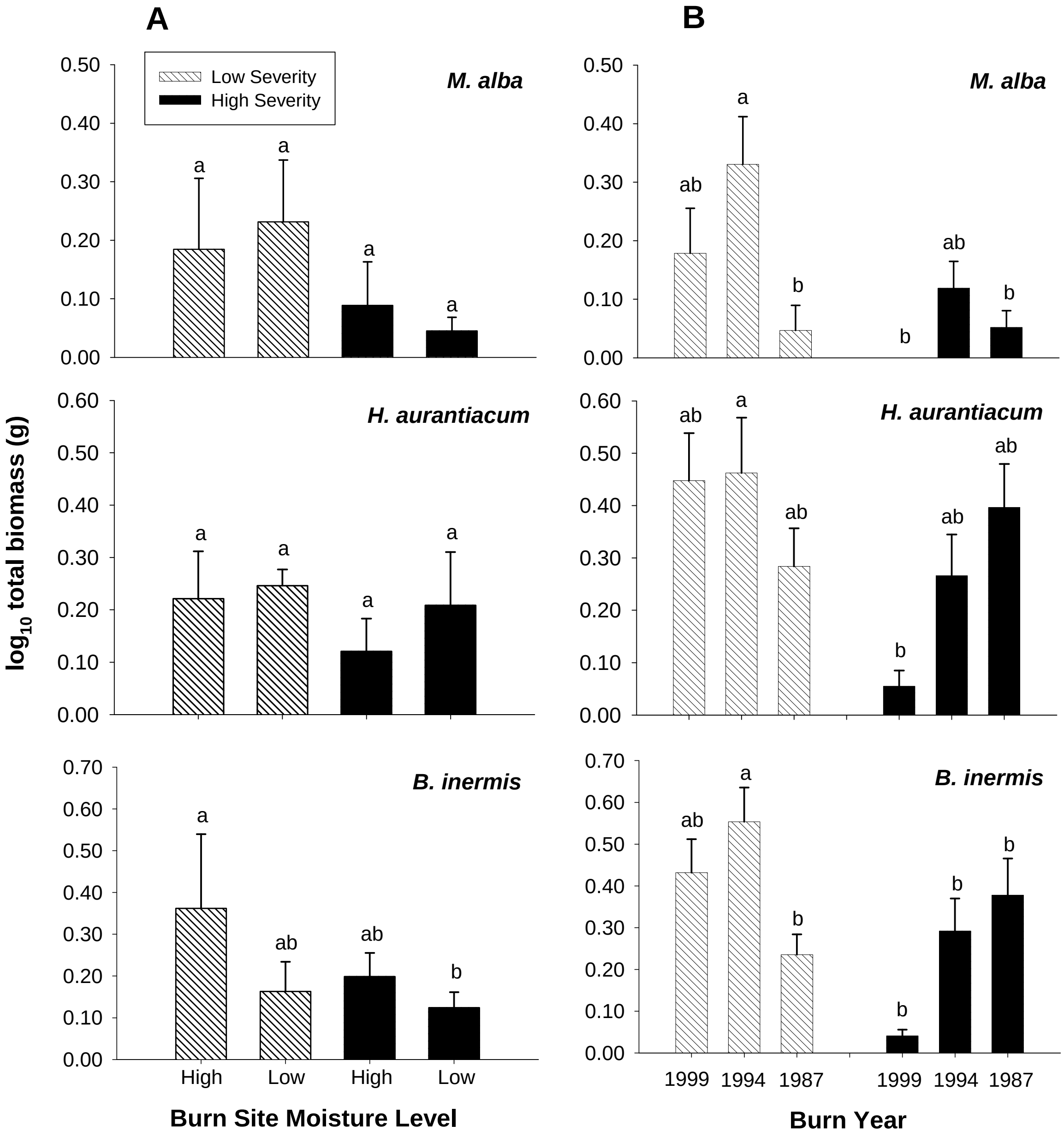

Figure 5. Mean $\log_{10}$ total biomass (± 1 se) of invasive plants grown for 150 days in soil cores taken from sites burned in 2004 (A) and from sites in the Delta Chronosequence (B). Low severity burn types are indicated by striped bars, and high severity burn types are indicated by solid bars. 2004 values represent the mean biomass across the three sampling regions. Different letters indicate significant differences (P<0.05) in total biomass between severity/moisture categories or age/severity categories.

Table 1. 2004 burn experiment and chronosequence experiment ANOVA F values for each explanatory variable (source of variation). Each invasive species was modeled separately with percent germination, final total biomass, root to shoot ratio, or reproductive capacity (*H. aurantiacum*- # of stolons; *B. inermis*- # tillers) as the response variable. *=*P*<0.05, **= *P* <0.01, ***= *P* <0.001

Experiment	**df**	***M. alba***			***H. aurantiacum***				***B. inermis***			
Source		%Germ	Biomass	R:S	%Germ	Biomass	R:S	Stolons	%Germ	Biomass	R:S	Tillers
2004 Burns												
Severity	1	1.02	2.18	0.02	1.53	2.48	**3.89***	0.36	2.75	**4.62***	0.21	0.27
Moisture	1	0.37	0.58	0.71	1.54	1.67	1.83	0.34	**5.21***	**8.40****	**4.22***	**5.02***
Region	2	**4.40****	0.37	0.66	1.43	**5.34****	0.46	1.78	0.42	**9.65*****	0.98	**15.94*****
S x M	1	0.16	1.41	0.01	0.57	0.52	1.71	0.07	**4.30***	1.74	**4.03***	0.29
M x R	2	0.16	0.03	0.91	1.44	**4.17***	1.06	2.26	**3.47***	**4.02***	1.71	**3.10***
S x R	2	0.70	3.29	0.32	0.21	0.70	**3.27***	0.69	0.58	2.89	**5.25****	0.61
S x M x R	2	2.08	.	1.16	1.77	2.31	1.67	0.23	**8.80*****	1.80	**7.10****	2.35
error df		204	21	21	204	64	64	64	204	82	82	85
Chronosequence Burns												
Age	2	0.67	**4.22***	**3.39***	0.59	0.89	**3.87***	0.3	**10.11*****	**3.11***	2.19	**3.49***
Severity	1	0.06	2.85	2.15	0.05	**4.97***	0.01	**10.86****	**14.48*****	**7.65****	1.21	**7.29****
A x S	2	**5.91****	3.15	1.97	1.25	**4.07***	2.14	**3.91***	0.55	**6.93****	**3.61***	1.48
error df		102	20	20	102	37	37	41	102	45	45	48

Table 2. Soil characteristics, native vegetation, and cover type for cores from an unburned control site and 2004 burn sites of different severity and moisture levels. All values are means with standard error in parentheses. Significant differences (*P*<0.05) between burn types (columns) for each variable are denoted by different letters. Soil water holding capacity (WHC) and soil bulk density (BD) are abbreviated.

Variable	Unburned	Low Severity		High Severity	
		High Moist	Low Moist	High Moist	Low Moist
Soil Characteristics					
soil compaction (kg/cm^2)	0.9 (0.1) a	2.7 (0.1) b	3.2 (0.7) b	3.9 (0.4) c	4.7 (0.04) d
residual organic soil depth (cm)	17.1 (1.9) a	13.8 (0.8) a	10.3 (2.1) b	4.5 (0.8) c	3.2 (1.7) c
WHC organic soil (g $H_2$0 / g soil)	6.57 (0.42) a	4.65 (0.16) b	3.11 (0.47) c	2.00 (0.88) d	1.03 (0.51) d
WHC mineral soil (g $H_2$0 / g soil)	0.75 (0.12) a	0.65 (0.12) a	0.84 (0.12) a	0.74 (0.10) a	0.70 (0.14) a
BD organic soil (g/cm^3)	0.15 (0.01) a	0.19 (0.04) a	0.26 (0.05) ab	0.36 (0.10) bc	0.48 (0.02) c
BD mineral (g/cm^3)	0.89 (0.08) a	1.01 (0.22) a	0.97 (0.18) a	0.87 (0.06) a	0.84 (0.07) a
Native Vegetation					
moss layer depth (cm)	4.1 (0.4) a	0.2 (0.0) b	0.3 (0.2) b	1.0 (0.2) c	0.4 (0.1) b
non-vascular biomass (g)	1.62 (0.16) a	0.84 (0.36) b	0.76 (0.48) b	1.74 (0.17) a	1.35 (0.11) a
native vascular biomass (g)	0.58 (0.17) a	0.50 (0.07) a	0.21 (0.09) b	0.44 (0.14) ab	0.22 (0.10) b
max. native vascular height (cm)	4.1 (0.4) a	2.5 (0.8) b	1.5 (0.4) c	3.4 (0.2) ab	2.8 (1.4) b
native plant richness (# spp.)	3.2 (0.2) a	1.9 (0.4) c	1.6 (0.6) c	3.4 (0.5) a	2.7 (1.0) b
Cover Type					
mineral soil cover (%)	0.0 (0.0) a	0.01 (0.0) a	1.3 (1.2) a	0.3 (0.3) a	5.2 (2.6) b
charred organic cover (%)	0.0 (0.0) a	40.8 (3.0) b	33.6 (0.6) bc	13.6 (5.3) d	31.7 (14.8) c
dead moss cover (%)	9.3 (2.2) a	10.0 (5.0) a	10.2 (4.3) a	5.4 (2.9) ab	1.8 (1.8) b
litter cover (%)	6.6 (1.0) a	19.2 (5.9) b	28.9 (4.9) c	19.3 (13.1) b	8.2 (5.1) a
non-vascular cover (%)	73.7 (3.6) a	24.0 (7.8) b	17.8 (8.7) b	59.0 (7.4) c	47.8 (13.3) d
native vascular cover (%)	7.8 (2.3) a	6.1 (1.7) ab	3.5 (1.8) b	10.2 (0.8) a	16.3 (9.2) c

Table 3. Soil characteristics, native vegetation and cover type for cores from 2004 burn sites in the Steese, Taylor, and Dalton regions. All values are means with standard error in parentheses. Significant differences (P<0.05) between burn types (columns) for each variable are denoted by different letters. Soil water holding capacity (WHC) and soil bulk density (BD) are abbreviated.

Variable	Steese	Taylor	Dalton
Soil Characteristics			
soil compaction	3.8 (0.4) ab	3.2 (0.6) b	4.0 (0.5) a
residual organic depth (cm)	6.6 (2.4) a	9.9 (2.3) b	7.3 (3.1) a
WHC organic soil (g H_20 / g soil)	2.88 (0.91) a	2.91 (0.63) a	2.30 (1.08) a
WHC mineral soil (g H_20 / g soil)	0.87 (0.05) a	0.68 (0.05) ab	0.65 (0.14) b
BD organic (g/cm^3)	0.30 (0.09) a	0.32 (0.05) a	0.35 (0.09) a
BD mineral (g/cm^3)	0.85 (0.15) a	1.07 (0.11) b	0.84 (0.06) a
Native Vegetation			
moss layer depth (cm)	0.5 (0.1) a	0.5 (0.3) a	0.4 (0.2) a
non-vascular biomass (g)	1.62 (0.13) a	0.85 (0.36) b	1.04 (0.32) b
native vascular biomass (g)	0.37 (0.08) a	0.41 (0.14) a	0.25 (0.08) a
max. native vascular height (cm)	3.0 (0.8) a	3.3 (0.4) a	1.2 (0.6) b
native plant richness (# spp.)	3.4 (0.5) a	1.9 (0.6) b	1.9 (0.4) b
Cover Type			
mineral soil cover (%)	2.7 (1.7) a	0.3 (0.2) b	2.1 (2.1) a
charred organic cover (%)	24.0 (6.2) a	31.0 (5.8) ab	34.8 (11.6) b
dead moss cover (%)	6.6 (4.5) ab	9.7 (2.3) a	4.2 (3.0) b
litter cover (%)	14.7 (3.9) a	18.6 (8.9) ab	23.4 (8.6) b
non-vascular cover (%)	47.6 (9.7) a	33.8 (16.9) b	29.9 (5.7) b
native vascular cover (%)	13.9 (6.3) a	8.6 (3.3) b	4.6 (1.8) c

Table 4. 2004 Burns: Variables selected by stepwise multiple regression for invasive plant dependent variables. Candidate independent variables are soil compaction, moss layer thickness, upper duff layer thickness, lower duff layer thickness, water holding capacity of the upper duff (WHCup), the lower duff (WHClow) , and the mineral soil (WHCmin), bulk density of the upper duff (BDup), the lower duff (BDlow), and the mineral soil (BDmin), mineral soil cover, charred organic cover, dead moss cover, litter cover, non-vascular plant cover, native vascular plant cover, native vascular plant height, native plant richness, non-vascular biomass, and native vascular plant biomass. Selection entry level and elimination level was *P* =0.05. † indicates data were $\log_{10}$ transformed and [a] indicates data were rank transformed to meet model assumptions. Model significance level: *=*P*<0.05, **=*P* <0.01, ***=*P* <0.001

Species	Dependent variable	n	Parameter	Parameter Estimate	Partial R^2	Model R^2
M. alba	% germination	216	No variable entered			
	total biomass †	29	lower duff thickness	0.04	0.146	**0.146***
	root:shoot	29	WHCmin	4.80	0.173	**0.173***
	% with shooting crown buds	29	No variable entered			
H. aurantiacum	% germination	216	non-vascular cover	-0.08	0.016	**0.016***
	total biomass †	76	non-vascular biomass	-0.13	0.182	**0.334***
			native vascular height	-0.02	0.099	
			BDlow	0.31	0.053	
	root:shoot [a]	76	native vascular height	-2.37	0.071	**0.071***
	# stolons	76	charred organic cover	0.03	0.129	**0.128****
B. inermis	% germination	216	soil compaction	-7.43	0.075	**0.124***
			native vascular cover	-0.36	0.027	
			WHCup	-2.16	0.022	
	total biomass †	94	lower duff thickness	0.02	0.136	**0.308***
			non-vascular biomass	-0.06	0.064	
			BDmin	0.33	0.068	
			native vascular height	-0.02	0.040	
	root:shoot	94	native vascular cover	0.02	0.180	**0.351***
			non-vascular biomass	-0.18	0.089	
			lower duff thickness	0.06	0.043	
			native richness	0.11	0.039	
	# tillers	97	native richness	-0.57	0.096	**0.137***
			BDmin	4.15	0.041	

Table 5. Soil characteristics, native vegetation and cover type for cores from the Delta Chronosequence high and low severity sites burned in 1999, 1994, and 1987. All values are means with standard error in parentheses. Significant differences (*P*<0.05) between burn types (columns) for each variable are denoted by different letters. Soil water holding capacity (WHC) and soil bulk density (BD) are abbreviated.

Variable	Low Severity			High Severity		
	1999	1994	1987	1999	1994	1987
Soil Characteristics						
soil compaction (kg/cm^2)	2.7 (0.2) a	3.9 (0.2) b	2.9 (0.2) a	4.9 (0.1) c	4.7 (0.1) c	4.4 (0.2) bc
residual organic soil depth (cm)	9.6 (0.7) a	10.7 (0.8) a	10.8 (0.9) a	3.0 (0.3) b	2.7 (0.4) b	4.5 (0.6) b
WHC organic soil (g H_20 / g soil)	2.90 (0.14) a	4.10 (0.23) b	2.80 (0.18) a	1.50 (0.29) cd	0.91 (0.16) d	2.26 (0.19) ac
WHC mineral soil (g H_20 / g soil)	0.84 (0.17) a	1.70 (0.28) b	0.77 (0.05) a	0.82 (0.07) a	0.73 (0.04) a	0.77 (0.06) a
BD organic soil (g/cm^3)	0.22 (0.01) a	0.20 (0.01) a	0.19 (0.01) a	0.46 (0.04) b	0.62 (0.05) c	0.39 (0.03) b
BD mineral (g/cm^3)	0.84 (0.08) a	0.70 (0.15) a	0.8 (0.05) a	0.76 (0.04) a	0.68 (0.04) a	0.90 (0.09) a
Native Vegetation						
moss layer depth (cm)	1.0 (0.2) ab	0.9 (0.1) ab	2.0 (0.4) c	0.6 (0.1) a	1.3 (0.2) abc	1.5 (0.2) bc
non-vascular biomass (g)	1.57 (0.14) ab	1.32 (0.14) a	1.85 (0.25) ab	2.10 (0.21) b	1.64 (0.10) ab	1.10 (0.23) a
native vascular biomass (g)	0.53 (0.10) a	0.59 (0.11) a	0.51 (0.12) a	0.50 (0.07) a	0.76 (0.12) a	0.61 (0.09) a
max. native vascular height (cm)	4.0 (0.5) a	3.2 (0.4) ab	3.4 (0.2) ab	2.2 (0.2) b	2.3 (0.3) b	2.7 (0.3) ab
native plant richness (# spp.)	3.0 (0.2) a	3.3 (0.2) a	3.2 (0.2) a	4.5 (0.1) b	3.0 (0.2) a	3.0 (0.1) a
Cover Type						
mineral soil cover (%)	0.0 (0.0) a	0.7 (0.3) a	0.9 (0.8) a	0.0 (0.0) a	6.4 (2.7) b	0.0 (0.0) a
charred organic cover (%)	14.8 (2.6) bc	23.6 (2.6) ab	33.5 (3.8) a	17.7 (2.2) b	3.7 (0.8) c	29.0 (3.5) a
dead moss cover (%)	8.0 (2.0) ab	10.9 (2.2) a	12.3 (3.0) a	0.3 (0.1) b	9.4 (1.4) a	8.6 (2.0) a
litter cover (%)	22.4 (3.2) a	10.8 (1.3) b	16.0 (1.8) ab	8.0 (1.1) b	6.9 (0.8) b	37.6 (4.2) c
non-vascular cover (%)	49.6 (4.0) a	53.5 (3.2) ab	33.4 (3.5) c	66.4 (3.3) bd	71.3 (3.1) d	21.6 (2.4) c
native vascular cover (%)	12.9 (1.9) ab	9.4 (1.8) abc	5.0 (1.0) c	15.8 (1.7) a	6.7 (1.8) bc	7.6 (1.6) bc

Table 6. Chronosequence Burns: Variables selected by stepwise multiple regression for invasive plant dependent variables. Candidate independent variables are soil compaction, moss layer thickness, upper duff layer thickness, lower duff layer thickness, water holding capacity of the upper duff (WHCup), the lower duff (WHClow) , and the mineral soil (WHCmin), bulk density of the upper duff (BDup), the lower duff (BDlow), and the mineral soil (BDmin), mineral soil cover, charred organic cover, dead moss cover, litter cover, non-vascular plant cover, native vascular plant cover, native vascular plant height, native plant richness, non-vascular biomass, and native vascular plant biomass. Selection entry level and elimination level was *P* =0.05. † indicates data were $\log_{10}$ transformed and [a] indicates data were rank transformed to meet model assumptions. Model significance level: *=*P*<0.05, **=*P* <0.01, ***=*P* <0.001

Species	Dependent variable	n	Parameter	Parameter Estimate	Partial R^2	Model R^2
M. alba	% germination	108	native vascular height	-1.89	0.052	**0.052***
	total biomass †	25	WHCmin	0.28	0.353	**0.847***
			native vascular biomass	-0.11	0.290	
			native vascular height	-0.05	0.099	
			native vascular cover	0.01	0.067	
			litter cover	-0.01	0.038	
	root:shoot	25	no variable entered			
	% with shooting crown buds	25	no variable entered			
H. aurantiacum	% germination	108	charred organic cover	0.38	0.112	**0.112*****
	total biomass †	43	native richness	-0.10	0.369	**0.727***
			native vascular biomass	-0.24	0.130	
			litter cover	0.01	0.133	
			native vascular cover	-0.01	0.063	
			WHCmin	0.13	0.033	
	root:shoot [a]	43	WHCmin	-0.47	0.092	**0.092***
	# stolons	47	BDlow	-9.80	0.260	**0.361***
			native vascular height	-0.26	0.101	
B. inermis	% germination	108	non-vascular cover	-0.33	0.146	**0.218****
			upper duff thickness	2.85	0.072	
	total biomass †	51	native vascular biomass	-0.29	0.314	**0.736***
			WHClow	0.21	0.201	
			native richness	-0.05	0.129	
			moss layer thickness	0.07	0.033	
			non-vascular cover	0.01	0.033	
			non-vascular biomass	-0.04	0.026	
	root:shoot	51	BDup	3.00	0.321	**0.383***
			non-vascular biomass	-0.48	0.062	
	# tillers	54	WHClow	2.62	0.206	**0.428****
			native vascular biomass	-2.04	0.063	
			native vascular height	0.96	0.072	
			native vascular cover	-0.11	0.087	

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CHAPTER 3:

GENERAL CONCLUSIONS

COMPARISON TO STUDIES OF OTHER ECOSYSTEMS, FURTHER DIRECTIONS, AND IMPLICATIONS

Comparison of Thesis Research to Studies of Other Ecosystems

In other ecosystems, general patterns have emerged between post-fire site conditions and levels of non-native plant invasions (Zouhar et al. 2007). As discussed in Chapter One, most studies have shown that burned areas are more easily invaded by non-native plants than unburned areas (Milberg and Lamont 1995; D'Antonio 2000; Maret and Wilson 2000; Keeley et al. 2003; Haskins and Gehring 2004; Dimitrakopoulos et al. 2005; Floyd et al. 2006). Further, severely burned areas in other systems are more susceptible to invasive plant colonization than less severely burned areas (Agee 1996; Turner et al. 1997; Keeley et al. 2003; Hunter et al. 2006). In addition, most ecosystems decrease in invasibility with increasing time since the fire after about five years (Agee and Huff 1987; Turner et al. 1997; Turner et al. 2003; Klinger et al. 2006). My thesis experiments, however, show that generalizations on the relationship between fire and invasive plants derived from other habitats may be inappropriate for describing this relationship in Alaskan black spruce systems.

Similar to the trend in other habitats, I found that invasive plants grow and reproduce better in burned soils compared to the unburned ones. While there were species-specific responses to a variety of burn characteristics for my three focal invasives, the general trends that emerged across the species were not consistent with the trends found in other biomes. The burned black spruce sites that had soils best supporting invasive plant growth and reproduction were lower in burn severity and were older than predicted by the generalizations from other habitats. The rapidly establishing native vegetation (bryophytes in the most recent burns, and vascular plants in burns between 5 and 20 years old) in high severity burn sites may provide a level of ecosystem resistance to non-native plant invasion. Low severity burn sites may offer invasive plants a refuge from intense competition from native plants. In addition, I found that the soil suitability for invasive plant growth increased through time. With greater soil suitability and the increased probability of propagule arrival over time, boreal black spruce burns between 10 and 20 years old are likely particularly vulnerable to invasion by non-native plants.

It is unclear how severity and burn age might interact to influence site invasibility in the long term. For example, my greenhouse study was incapable of testing the influence of permafrost resurgence or canopy closure after a fire in invasive plant success. The influence of permafrost may affect low severity sites more rapidly than high severity sites, with uncombusted organic material providing greater insulation to permafrost in low severity sites (Yoshikawa et al. 2003; Kasischke and Johnstone 2005). Invasive plant abundances in low severity burns may be reduced by increases in permafrost under the insulative remaining organic layer. In high severity burns, the influence of canopy closure would likely influence high severity sites more rapidly than low severity sites, with broadleaf trees emerging more readily in high severity sites (Johnstone and Chapin 2006). Further study is necessary to determine how severity and burn age might interact throughout black spruce forest succession to influence invasive plant establishment.

Even if non-native plant presence does decrease as permafrost redevelops in low severity sites, or as canopy closes in high severity sites, invasive species that had any chance to establish and reproduce in any site have a high probability of emerging again after the next disturbance. For example, *Melilotus alba* can produce over 20,000 seeds per individual that remain viable in the seed bank for up to 81 years (Royer and Dickinson 1999). Fire has been documented to aid the establishment of *M. alba* in grasslands, as it simultaneously scarifies the seeds and creates new openings for establishment (Heitlinger 1975). If even a patchy seed bank is left intact after a fire, *M. alba* can easily re-establish (Cole 1991) and out-compete native boreal vegetation (Spellman 2008), possibly delaying or shifting natural succession. Legacies of previous invasions in burns may be an even more important consideration if fire return interval in interior Alaska shortens as predicted (Flannigan et al. 2001). Increased fire frequency has been well documented in many ecosystems to favor some invasive plants (especially annual grasses) and completely alter long-term community structure and function (Brooks et al. 2004).

Regional factors may play a larger role than burn severity or burn age in determining the susceptibility of burned black spruce sites. Data from my 2004 burns experiment suggest that the combined effects of higher propagule pressure and lower non-vascular plant abundances may have made the burns in the Dalton region more susceptible to invasion than the Taylor or Steese regions. Conversely, low propagule pressure and relatively high native plant abundance in the Steese region likely increase the resistance of burns in this area to invasion. Moreover, region accounted for larger proportions of variability in the fitness-related responses of all three focal invasive species than did burn severity or site moisture level. In addition, a higher mineral soil pH in the Dalton region may help explain why roadside populations in the field were highest and why non-native plant movement from roadways into burned areas was greatest in the Dalton region. Beyond proximity to human disturbances, soil pH was the most important factor in explaining large scale non-native plant distributions in Newfoundland boreal forest (Rose and Hermanutz 2004). Further research in needed to determine the specific biotic and abiotic factors that have made the Dalton region more susceptible to non-native plant establishment.

Directions for Further Study

My thesis presents the first study in the northern boreal forest that investigates specific factors that influence the susceptibility of burned boreal forest to non-native plant invasions. In the context of a changing fire regime (Stocks et al. 2000) and an accelerating spread of non-native plant species throughout the state (Carlson and Shephard 2007), immediate further research and timely publication will be necessary to prevent further spread of invasives into Alaska’s intact native plant communities. Continued field study and greenhouse manipulations will offer greatly needed insight into the complex interactions between fire and invasive plants in boreal ecosystems. Foremost, researchers must gather intensive, long-term field survey data that include vegetation and edaphic characteristics of both invaded and uninvaded burn sites from a wide range of burn ages. In interior Alaska, preliminary surveys (Gronquist 2005; Cortés-Burns et al. 2007; Lapina et al. 2007; J. Heys *pers. comm.)* and the establishment of long-term monitoring points in anthropogenically disturbed sites near burned areas (Cortés-Burns et al. 2007) and in undisturbed sites that have been studied both in their pre- and post-fire conditions (Hollingsworth et al. 2006; Johnstone et al. *in press*) have been good first steps. In further greenhouse studies, useful additions to the experiments conducted in my thesis would be to include more invasive species, more site factors, a wider range of burn ages from different regions, and variety of unburned forest sites.

My thesis was unable to address many biotic and abiotic interactions that may reduce or facilitate the spread of invasive plants in the field. Several burning questions on these interactions remain: How does the timing of native and non-native propagule arrival after a fire influence invasion success? Do other tropic levels, such as herbivores, soil biota, and pathogens affect the spread of invasive plants in burned areas? Will invasive plants impact boreal forest communities over the long term, and if so, which communities will suffer the greatest consequences?

The greenhouse results from this thesis suggest that increased presence of native vegetation, particularly bryophytes in the most recent burns, reduces invasive seedling establishment and growth. The timing of propagule arrival to any given microsite within a burn will doubtlessly influence this effect in the field setting. If the bryophytes are fully established in a burn before the invasive seed arrives, my greenhouse experiment showed that the non-native plant establishment and growth will be reduced. However, if invasive plant seeds arrive at the site or invasive seedlings emerge rapidly from a seed bank before the colonizing mosses and liverworts arrive, the invasive plant will likely be little affected by the bryophytes. The later scenario will likely become more common as invasive plant abundances and fire frequency, severity, and extent continue to increase in interior Alaska. It is important to note that not all of my focal species were limited by bryophyte biomass and cover. In cores from sites burned in 2004, *M. alba* was less influenced by non-vascular abundance than *H. aurantiacum* or *B. inermis,* suggesting non-vascular plants will represent an important barrier to colonization by some invasive species but not others. Further research is needed to disentangle the order of native and non-native propagule arrival, invasiveness traits of specific non-native species, and burn site invasibility.

While my thesis did not directly address the influence of other trophic levels, my data and the literature from other ecosystems suggest soil biota and herbivores may play a key role in determining the invasibility of burned sites in Alaska. Plant-soil feedbacks and the match between the invader and the microbial community have been documented as key factors promoting the invasiveness of non-native plants (Klironomos 2002, Callaway et al. 2004; Levine et al. 2006; Vinton et al. 2006). My field observations and greenhouse data hint that such a mechanism may be operating in some of my black spruce sites. The sites burned in 1994 had surprisingly high non-native species richness and abundance in the field, and in the greenhouse invasive plants grown in soil from this burn achieved the highest biomass. In the 12 years since the fire, it is not inconceivable that the non-natives have begun to change the soil communities to favor themselves. In addition, the Chronosequence burns may be the most suited for invasion by non-native legumes, as it was the only site I sampled with native legumes present (*Oxytropis* spp., *Astragalus* spp., and *Lupinus arcticus*), and perhaps the only sites with the appropriate *Rhizobia* spp. bacteria to assist non-native legumes in nitrogen fixation. The lack or presence of herbivores may also influence non-native plant abundances in burn sites. For example, high severity burns create excellent habitat for moose forage (MacCracken and

Viereck 1990). Moose browse can decrease canopy cover in early stages of succession (McInnes et al. 1992), which could benefit the more shade intolerant invasive plants. Further, moose footprints have been documented in Eastern Canadian boreal systems to open disturbed microsites ideal for invasive plant establishment (Rose and Hermanutz 2004). More research is needed to investigate the role of other trophic levels in facilitating or hindering non-native plant invasions in Alaska's boreal forests.

While invasive plants are known to alter biodiversity (Pyšek and Pyšek 1995; Martin 1999), nutrient cycling (Vitousek and Walker 1989; Evans et al. 2001; Mack et al. 2001), hydrology (Busch and Smith 1995; Rickard and Vaughan 1988), and fire regimes (Whisenant 1990; D'Antonio and Vitousek 1992) in other biomes, very little is known about the impacts of invasive plant species in boreal ecosystems. In Alaska, only one study has been conducted to date on the impacts of an invasive plant on boreal plant communities (Spellman 2008). In that study, *M. alba* was reported to decrease the recruitment of native plant seedlings in early-successional floodplain communities (Spellman 2008). *Melilotus alba* and other invasive species may competitively displace native seedlings or alter ecosystem processes in early-successional post-fire communities as well.

In general, the impacts of an invasive plant population can be described as a combination of the total area occupied, the abundance, and some measure of the effect on the habitat per plant (Parker et al. 1999). The greatest per capita impacts often occur when the invasive plant performs an entirely novel function within the native community (Simberloff 1991; Ruesink et al. 1995; Parker et al. 1999), such as an invasive nitrogen fixer in an area with nitrogen poor soil (Vitousek and Walker 1989). In boreal black spruce forests, few short-lived legumes or species with vine growth forms exist. Non-native short lived legumes such as *M. alba* and legumous vines such as *Vicia cracca* are likely to fill new functional roles in the community and have high per capita impacts. The greatest abundance related impacts tend to occur under high disturbance, high nutrient conditions where invasives can rapidly reproduce, achieve high densities, and spread (Huston 2004). My thesis experiments showed that areas disturbed by fire are vulnerable to non-native plant establishment; however, it is still unknown which types of burns will be able to support the highest densities of invasive plants. Furthermore, the effects of fire on soil nutrient levels in both high and low severity boreal forest burns are highly variable (Viereck and Schandelmeier 1980; Van Cleve and Dyrness 1985; Certini 2005; Smithwick et al. 2005). It remains uncertain whether invasive plants will have different impacts in boreal forest burned at different severities. An understanding of invasive plant impacts on burned boreal forest is vital for Alaska to prioritize management in areas where invasives are most likely to cause the greatest consequences to community structure and ecosystem function.

Management Implications

The burn characteristics that I found to influence site susceptibility to invasion can be useful to land managers attempting to prioritize monitoring and control efforts for a variety of invasive species in Alaska's burned black spruce forests. My greenhouse experiments suggest that soil from low severity and older burns best support the growth of three very different invasive plant species. However, we need further research to confirm that these factors will influence burn site susceptibility to invasive plants in the field. For now, monitoring and eradication efforts in Alaska should focus on areas where invasives have been found moving into burns and on areas near heavy roadside infestations. My greenhouse study and field survey provide solid support that managers should focus their plans on burn complexes in regions with the highest amounts of unvegetated ground cover and highest levels of invasive propagule pressure such as the Dalton burns.

All generalizations about the invasibility of burned boreal forest be it from literature from other ecosystems, or from my study, need to be scrutinized carefully. Variations in the pre-fire vegetation composition, the post-fire permafrost and moisture regime, and the degree of non-native propagule pressure and seed bank development all provide ample opportunity for generalizations to misinform management decisions. Nothing can serve land managers better than long-term, detailed study of their specific management areas.

In a recent synthesis of post-fire non-native plant invasions across North America, three management practices were recommended to limit the spread of invasives into burned lands: 1) prioritize the control of species that are known to invade burned areas in your region, 2) prevent new invasions through early detection and control of species likely to spread into burned areas, and 3) monitor burned areas long-term and reduce invasions through adaptive management (Zouhar et al. 2007). Thus, beyond identifying site factors that influence burn site’s vulnerability to invasions, it is important to identify the particularly problematic non-native species for interior Alaska. Applying my thesis results to these recommended practices, the following approaches might be taken to protect our largely intact boreal habitats:

1) Prioritize the control of *Melilotus alba* and *Crepis tectorum*, near and in burned areas of interior Alaska.

In my field survey, I found both *M. alba* and *Crepis tectorum* in burned sites in the Dalton region. *Crepis tectorum* also occurred in sites in the Delta Chronosequence burns. In addition, *M. alba* has moved into burns along the Parks Highway near the town of Nenana (*pers. obs.*). *Melilotus alba* seedlings were able to establish in a wide range of burn soils in my greenhouse experiment. Two other species have been documented by other survey efforts (Cortés-Burns et al. 2007; S. Seefeldt *pers. comm.*) moving into burned areas in interior Alaska: *Hieracium umbellatum* and *Vicia cracca*. All four of these invasive species should be priorities for control efforts. Specific recommendations of control methods for existing populations of these species can be found in Cortés-Burns et al. (2007).

2) Prevent movement of *Hieracium aurantiacum* and *Bromus inermis* ssp. *inermis*, into burned areas of interior Alaska.

While *Hieracium aurantiacum* and *Bromus inermis* ssp. *inermis* have not yet been documented in burn areas, my greenhouse trials suggest these two species will have little difficulty colonizing wildfire scars. The widespread *B. inermis* ssp. *inermis* populations near burned areas in interior Alaska should be an issue of concern. While *H. aurantiacum* has not yet been documented in interior Alaska, early detection of its arrival and immediate response will be the key to preventing this species from spreading into burned boreal forest. *Caragana aborescens*, *Trifolium hybridum*, and *Bromus tectorum* are additional species that have been found in anthropogenically disturbed areas near burns in interior Alaska (Cortés-Burns et al. 2007; Lapina et al. 2007). Because these species show high potential of colonizing burned areas, these populations should be monitored carefully and eradicated if possible. Detailed accounts of these and other species requiring prevention efforts are presented in Cortés-Burns et al. (2007) and Lapina et al. (2007).

3) Continue monitoring, investigating, and adaptively managing burned areas in interior Alaska for several decades.

My 19 sampled sites and 20 of my additional survey sites will continue to be monitored and studied by the Bonanza Creek Long Term Ecological Research Program for the next few decades. These sites will offer greater insight into invasion processes in boreal systems and a better understanding of changes in burn invasibility throughout post-fire succession. In addition, the Alaska Natural Heritage Program has established long term monitoring photo points for the Bureau of Land Management where non-native plant populations have been documented in or near burns in interior Alaska (Cortés-Burns et al. 2007).

A key component to the long-term management of burned lands threatened by non-native plant invasions will be the education of key user groups. Invasions in burned areas can be exacerbated by further disturbances, management practices, and human use. Wildfire fighters, hunters, backpackers and field researchers using these areas must be educated on their role in preventing the spread of invasive plants from the road corridors. Land users should clean equipment and gear of dirt, seeds, and plant material, and be cautious when moving from infested roadsides into burned areas. Excellent references for management of invasive plants after fire include Goodwin and Sheley (2001) and Goodwin et al. (2002).

The boreal forest of Alaska is in a period of rapid change (Chapin et al. 2006). A warming climate has increased the natural fire disturbances (Overpeck et al. 1997; Stocks et al. 2000; Bachelet et al. 2005; AFS 2007), and the spread of non-native plants in Alaska is accelerating (Carlson and Shephard 2007). My thesis presents the first data showing that burned areas in Alaska are susceptible to non-native plant invasions. I hope that this thesis can serve as a launching point for increased awareness and further study of this pressing issue for the conservation of Alaska’s boreal forests.

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APPENDICES

Appendix 1. Non-native plant species found in burns from the Delta Chronosequence ("Chrono"), Steese, Taylor, and Dalton Regions. X indicates at least one reproductive non-native plant individual present in the burn site. XX indicates > 30 *Melilotus alba* individuals or > 100 *Crepis tectorum* individuals present within the burn. Steese, Taylor, and Dalton sites are BNZ LTER sites that burned in the 2004 fire season and will continue to be monitored for the next several decades. All sites are located adjacent to roadways and no non-native species were documented moving more than 20 m off of the road into burned areas.

						Aggressive spp.			Non-aggressive spp.	
Region	Site Identifier	Severity	Moisture	Latitude (N)	Longitude (W)	*Melilotus alba*	*Crepis tectorum*	*Agropyron repens*	*Taraxacum officinale ssp. officinale*	*Chenopodium album*
Chrono	1999H	High	Low	63.92076	145.74817					
Chrono	1999L	Low	Low	63.84843	145.71292		x			
Chrono	1994H	High	Low	63.84354	145.04477		xx	x		x
Chrono	1994L	Low	Low	63.80168	145.10771		x		x	
Chrono	1987H	High	Low	63.91920	145.36954					
Chrono	1987L	Low	Low	63.92122	145.37677					
Steese	BF58	High	Low	65.28903	146.55050					
Steese	BF59	Mod	Low	65.28984	146.54885					
Steese	BF60	Low	High	65.28784	146.54786					
Steese	BF61	Low	High	65.34932	146.66884					
Steese	BF62	Low	Low	65.35095	146.67091					
Steese	BF63	Low	Low	65.35313	146.67369					
Steese	BF64	High	Low	65.29941	146.72077					
Steese	BF65	Low	Low	65.29726	146.72073					
Steese	BF66	Low	Low	65.29641	146.71733					
Steese	BF67	Low	Low	65.28422	146.72928					
Steese	BF68	Low	Low	65.28238	146.73662					
Steese	BF69	Low	Low	65.28307	146.73944					
Steese	BF70	Low	Low	65.11973	147.43453					
Steese	BF71	Low	Low	65.11955	147.42990					
Steese	BF72	Mod	Low	65.11642	147.42870					
Steese	BF73	Low	Low	65.11811	147.44866					
Steese	BF74	Mod	Low	65.11682	147.46775					
Steese	BF75	Mod	Low	65.12270	147.46526					
Steese	BF76	High	Low	65.12340	147.46543					
Steese	BF77	Low	High	65.12969	147.47369					
Steese	BF78	Mod	High	65.15297	147.48116					
Steese	BF79	High	High	65.15089	147.47612					
Steese	BF80	High	Low	65.15125	147.47288					
Steese	BF81	High	High	65.15034	147.47324					
Steese	BF82	High	Low	65.14845	147.47171					

Appendix 1. Continued

						Aggressive spp.			Non-aggressive spp.	
Region	Site Identifier	Severity	Moisture	Latitude (N)	Longitude (W)	*Melilotus alba*	*Crepis tectorum*	*Agropyron repens*	*Taraxacum officinale ssp. officinale*	*Chenopodium album*
Steese	BF83	Mod	Low	65.14803	147.47086					
Steese	BF84	Low	High	65.15299	147.47819					
Steese	BF85	Mod	Low	65.14273	147.46579					
Steese	BF86	Low	Low	65.14241	147.46490					
Steese	BF87	High	Low	65.14190	147.46555					
Steese	BF88	Low	Low	65.15116	147.34463					
Steese	BF89	Low	Low	65.15011	147.34393					
Steese	BF90	Low	High	65.15440	147.34118					
Taylor	TC01	Low	High	64.05748	142.02016					
Taylor	TC02	Low	Low	64.04594	142.05910					
Taylor	TC03	Low	High	64.03970	142.05803					
Taylor	TC04	Low	High	64.01855	142.08485					
Taylor	TC05	Mod	Low	64.02051	142.08615					
Taylor	TC06	Low	High	63.98127	142.15649					
Taylor	TC07	Low	High	63.97744	142.16344					
Taylor	TC08	Low	High	63.96040	142.16955					
Taylor	TC09	High	Low	63.85791	142.23307					
Taylor	TC10	Mod	High	63.84833	142.22066					
Taylor	TC11	Mod	Low	63.84807	142.21893					
Taylor	TC12	High	Low	63.82153	142.21451					
Taylor	TC13 (T)	Low	Low	63.65836	142.29002				x	
Taylor	TC14 (T)	Low	Low	63.63048	142.30823					
Taylor	TC15	Low	Low	63.62526	142.32314				x	
Taylor	TC16	Low	Low	63.58512	142.36101				x	
Taylor	TC17	Low	High	63.56311	142.37179					
Taylor	TC18	Low	Low	63.56230	142.37247					
Taylor	TC19	Low	Low	63.53854	142.38546					
Taylor	TC20	Low	Low	63.52627	142.39380					
Taylor	TC21	Mod	Low	63.50946	142.40588					
Taylor	TC22	NA	NA	63.49913	142.41549					
Taylor	TC23	Mod	Low	63.46035	142.46836					
Taylor	TC24	Low	Low	63.46201	142.47031					
Taylor	TC25	Low	High	63.42011	142.48094					
Taylor	TC26	Low	Low	63.52002	142.38803					
Taylor	TC27	Low	High	63.40473	142.46973					
Taylor	TC28	Mod	High	63.39563	142.49364				x	
Taylor	TC29	High	Low	63.38703	142.52448					

Appendix 1. Continued

						Aggressive spp.			Non-aggressive spp.	
Region	Site Identifier	Severity	Moisture	Latitude (N)	Longitude (W)	*Melilotus alba*	*Crepis tectorum*	*Agropyron repens*	*Taraxacum officinale ssp. officinale*	*Chenopodium album*
Dalton	DC30	High	Low	66.31539	150.40571					
Dalton	DC31	Mod	Low	66.31513	150.39724					
Dalton	DC32	Low	High	66.28175	150.35847				x	
Dalton	DC33	Low	High	66.26531	150.33485					
Dalton	DC34	Low	Low	66.20926	150.27006					
Dalton	DC35	Low	High	66.21316	150.26394					
Dalton	DC36	High	High	66.21495	150.25713					
Dalton	DC37	High	High	66.20773	150.23489					
Dalton	DC38	Mod	High	66.19255	150.21556					
Dalton	DC39	High	High	66.16861	150.20427					
Dalton	DC40	High	High	66.16364	150.20208				x	
Dalton	DC41	Mod	High	66.15536	150.18442	x				
Dalton	DC42	High	High	66.15127	150.18096					
Dalton	DC43	Low	High	66.14549	150.17627					
Dalton	DC44	Low	Low	66.14078	150.17241				x	
Dalton	DC45	High	Low	66.10999	150.15626					
Dalton	DC46	High	Low	66.10977	150.15785					
Dalton	DCAW14	Low	High	66.11552	150.16656	x x				
Dalton	DC47	Low	High	66.11999	150.16491					
Dalton	DC48	High	Low	66.10866	150.15695					
Dalton	DC49	Low	High	66.10515	150.15355	x				
Dalton	DC50	Low	High	66.08579	150.16491					
Dalton	DC51	High	Low	66.07446	150.16788					
Dalton	DC52	High	Low	66.07289	150.16743					
Dalton	DC53	High	Low	66.07199	150.16675					
Dalton	DC54	Low	Low	65.91048	149.78075		x x		x	
Dalton	DC55	High	Low	65.89613	149.75351					
Dalton	DC56	High	Low	65.89578	149.75385	x	x			x
Dalton	DC57	Low	Low	65.88307	149.71782					
Dalton	DC78	NA	NA	65.15296	147.48117					
Dalton	DC100	High	High	66.15178	150.18129					

Appendix 2. Site location, classification, non-native plant abundaces, soil characteristics, native plant characteristics, and surface cover data for each site sampled. Values that were replicated at each site are written as mean (± se). Native plant cover and biomass measurements are from the soil core tops used in the greenhouse experiment. NA indicates data not available. Soil water holding capacity (WHC) and bulk density (BD) are abbreviated.

Site Identifier	Region	Burn severity level	Site moisture level	Year of most recent fire	Latitude (N)	Longitude (W)	Elevation (m)	Roadside aggressive non-native % cover	Roadside non-aggressive non-native % cover	Roadside non-native plant richness	Aggressive non-native found in burn (Y/N)	Non-aggressive non-native found in burn (Y/N)	Burn non-native plant richness
Control	Steese	Unburned	High	1901	65.15241	147.48119	246	0.0	2.6	2	N	N	0
BF78	Steese	High	High	2004	65.15298	147.48117	240	0.0	0.9	3	N	N	0
BF87	Steese	High	Low	2004	65.14189	147.46556	235	0.0	0.3	1	N	N	0
BF84	Steese	Low	High	2004	65.15299	147.47819	240	0.0	0.6	2	N	N	0
BF86	Steese	Low	Low	2004	65.14240	147.46490	250	0.0	0.3	1	N	N	0
TC10	Taylor	High	High	2004	63.84834	142.22064	722	50.0	0.6	4	N	N	0
TC29	Taylor	High	Low	2004	63.38705	142.52443	628	25.0	0.0	2	N	N	0
TC8	Taylor	Low	High	2004	63.96044	142.16955	653	3.0	0.0	1	N	N	0
TC24	Taylor	Low	Low	2004	63.46201	142.47032	870	7.3	0.0	2	N	N	0
DC40	Dalton	High	High	2004	66.16364	150.20207	280	85.0	5.3	5	N	Y	1
DC51	Dalton	High	Low	2004	66.07446	150.16788	230	50.3	0.9	6	N	N	0
DC49	Dalton	Low	High	2004	66.10515	150.15355	220	85.0	0.6	3	Y	N	1
DC54	Dalton	Low	Low	2004	65.91047	149.78075	135	50.0	1.3	3	Y	Y	2
1999H	Chrono	High	Low	1999	63.92076	145.74817	468	0.3	0.6	3	N	N	0
1999L	Chrono	Low	Low	1999	63.84843	145.71292	524	0.0	0.0	0	Y	N	1
1994H	Chrono	High	Low	1994	63.84354	145.04477	424	5.3	4.9	7	Y	Y	4
1994L	Chrono	Low	Low	1994	63.80168	145.10771	467	0.6	8.0	4	Y	Y	3
1987H	Chrono	High	Low	1987	63.91920	145.36954	393	0.3	0.3	3	N	N	0
1987L	Chrono	Low	Low	1987	63.92122	145.37677	389	0.3	0.3	3	N	N	0

Appendix 2. Continued.

Site Identifier	Upper duff layer depth (cm)	Lower duff layer depth (cm)	WHC upper duff (g H_20 / g soil)	WHC lower duff (g H_20 / g soil)	WHC mineral (g H_20 / g soil)	BD upper duff (g / cm^3)	BD lower duff (g / cm^3)	BD mineral (g / cm^3)
Control	11.6 (1.9)	5.4 (0.5)	9.48 (0.68)	3.66 (0.34)	0.75 (0.12)	0.08 (0.01)	0.22 (0.03)	0.89 (0.08)
BF78	1.2 (0.5)	3.0 (0.3)	5.77 (0.82)	3.44 (1.38)	0.91 (0.11)	0.17 (0.03)	0.29 (0.09)	0.76 (0.05)
BF87	0.2 (0.2)	2.3 (0.5)	1.87 (0.00)	1.42 (0.13)	0.95 (0.13)	0.33 (0.00)	0.54 (0.08)	0.69 (0.09)
BF84	9.0 (2.3)	4.7 (0.4)	6.90 (1.78)	3.90 (0.80)	0.89 (0.07)	0.12 (0.02)	0.21 (0.02)	0.65 (0.05)
BF86	1.5 (0.5)	4.5 (0.3)	5.63 (1.08)	2.55 (0.30)	0.72 (0.19)	0.13 (0.02)	0.40 (0.05)	1.28 (0.20)
TC10	2.6 (0.6)	3.3 (0.3)	3.25 (0.51)	1.78 (0.31)	0.77 (0.21)	0.28 (0.06)	0.41 (0.05)	0.99 (0.12)
TC29	1.6 (0.5)	4.8 (0.8)	3.05 (0.28)	2.02 (0.38)	0.69 (0.11)	0.26 (0.04)	0.49 (0.09)	0.94 (0.07)
TC8	8.7 (0.7)	6.6 (0.9)	6.53 (0.69)	2.45 (0.38)	0.55 (0.07)	0.11 (0.04)	0.45 (0.20)	1.40 (0.13)
TC24	5.9 (0.5)	6.1 (0.5)	4.17 (0.17)	2.47 (0.22)	0.72 (0.17)	0.14 (0.02)	0.32 (0.03)	0.95 (0.16)
DC40	0.7 (0.2)	2.6 (0.2)	0.18 (0.00)	0.98 (0.05)	0.55 (0.07)	0.03 (0.00)	0.54 (0.04)	0.85 (0.09)
DC51	0.0 (0.0)	0.6 (0.2)	0.00 (0.00)	1.01 (0.07)	0.46 (0.08)	0.00 (0.00)	0.73 (0.14)	0.88 (0.05)
DC49	5.2 (0.8)	7.3 (0.6)	5.29 (0.79)	3.72 (0.35)	0.52 (0.07)	0.12 (0.02)	0.23 (0.04)	0.97 (0.10)
DC54	6.3 (1.5)	6.2 (0.4)	4.88 (0.35)	3.25 (0.26)	1.07 (0.13)	0.12 (0.02)	0.25 (0.04)	0.67 (0.07)
1999H	0.5 (0.2)	2.6 (0.3)	3.28 (0.53)	1.54 (0.17)	0.82 (0.07)	0.26 (0.09)	0.56 (0.07)	0.76 (0.04)
1999L	5.5 (0.5)	4.1 (0.5)	3.66 (0.21)	2.14 (0.12)	0.84 (0.17)	0.16 (0.01)	0.32 (0.02)	0.84 (0.08)
1994H	0.1 (0.1)	2.6 (0.3)	2.45 (0.00)	1.54 (0.08)	0.73 (0.04)	0.30 (0.00)	0.62 (0.05)	0.68 (0.04)
1994L	3.4 (0.6)	7.3 (0.5)	4.95 (0.30)	3.25 (0.23)	1.70 (0.28)	0.15 (0.01)	0.28 (0.03)	0.70 (0.15)
1987H	1.3 (0.3)	3.2 (0.4)	2.71 (0.30)	2.04 (0.15)	0.77 (0.06)	0.30 (0.03)	0.45 (0.04)	0.90 (0.09)
1987L	6.6 (0.5)	4.2 (0.6)	3.53 (0.29)	2.08 (0.16)	0.77 (0.05)	0.12 (0.01)	0.35 (0.03)	0.80 (0.05)

Appendix 2. Continued.

Site Identifier	Soil compaction (kg / cm^2)	Soil temperature at 10cm (^{o}C)	Mineral soil pH	Moss layer depth (cm)	Non-vascular plant biomass (g)	Native vascular biomass (g)	Max. native vascular height (cm)	Native plant richness (# spp.)
Control	0.9 (0.1)	14.6 (5.4)	NA	4.1 (0.4)	1.62 (0.16)	0.58 (0.17)	41. (0.4)	3.2 (0.2)
BF78	3.7 (0.2)	10.4 (0.3)	4.39	0.6 (0.1)	1.93 (0.20)	0.39 (0.15)	3.4 (0.5)	4.4 (0.3)
BF87	4.7 (0.1)	11.9 (0.2)	3.99	0.6 (0.1)	1.35 (0.11)	0.31 (0.08)	4.8 (0.4)	4.3 (0.2)
BF84	2.7 (0.2)	NA	4.53	0.3 (0.1)	1.49 (0.17)	0.59 (0.22)	2.5 (0.4)	2.7 (0.3)
BF86	4.0 (0.2)	13.1 (0.3)	4.61	0.5 (0.2)	1.72 (0.34)	0.19 (0.05)	1.3 (0.2)	2.4 (0.2)
TC10	3.4 (0.2)	9.4 (0.6)	5.44	1.4 (0.3)	1.39 (0.14)	0.69 (0.16)	3.7 (0.6)	3.0 (0.2)
TC29	4.6 (0.2)	9.7 (0.8)	5.73	0.6 (0.1)	1.54 (0.13)	0.31 (0.04)	3.6 (0.3)	3.0 (0.1)
TC8	2.9 (0.3)	4.7 (0.9)	6.28	0.1 (0.1)	0.27 (0.08)	0.55 (0.14)	3.9 (0.5)	1.4 (0.2)
TC24	1.8 (0.2)	6.5 (0.3)	4.93	0.0 (0.0)	0.20 (0.06)	0.07 (0.04)	2.3 (0.3)	0.4 (0.1)
DC40	4.7 (0.1)	14.5 (0.8)	7.32	1.0 (0.2)	1.89 (0.23)	0.23 (0.04)	2.9 (0.4)	2.9 (0.1)
DC51	4.8 (0.1)	14.3 (0.2)	4.12	0.1 (0.1)	1.16 (0.23)	0.02 (0.01)	0.1 (0.1)	0.8 (0.1)
DC49	2.6 (0.2)	3.9 (0.3)	5.08	0.2 (0.1)	0.75 (0.16)	0.38 (0.05)	1.0 (0.2)	1.7 (0.2)
DC54	3.9 (0.3)	8.3 (0.6)	5.17	0.4 (0.2)	0.37 (0.08)	0.38 (0.08)	1.0 (0.1)	2.0 (0.2)
1999H	4.9 (0.1)	13.3 (0.3)	NA	0.6 (0.1)	2.10 (0.21)	0.50 (0.07)	2.2 (0.2)	4.5 (0.1)
1999L	2.7 (0.2)	9.4 (0.3)	NA	1.0 (0.2)	1.57 (0.14)	0.53 (0.10)	4.0 (0.5)	3.0 (0.2)
1994H	4.7 (0.1)	11.7 (0.3)	NA	1.3 (0.2)	1.64 (0.10)	0.76 (0.12)	2.3 (0.3)	3.0 (0.2)
1994L	3.9 (0.2)	8.0 (0.5)	NA	0.9 (0.1)	1.32 (0.13)	0.59 (0.11)	3.2 (0.4)	3.3 (0.2)
1987H	4.4 (0.2)	10.3 (0.2)	NA	1.5 (0.2)	1.10 (0.23)	0.61 (0.09)	2.7 (0.3)	3.0 (0.1)
1987L	2.9 (0.2)	8.7 (0.3)	NA	2.0 (0.4)	1.85 (0.25)	0.51 (0.12)	3.4 (0.2)	3.2 (0.2)

Appendix 2. Continued.

Site Identifier	Non-vascular plant cover (%)	Native vascular cover (%)	Mineral soil cover (%)	Charred organic cover (%)	Dead moss cover (%)	Litter cover (%)	Canopy openness (%)
Control	73.7 (3.6)	7.8 (2.3)	0.0 (0.0)	0.0 (0.0)	9.2 (2.2)	6.6 (1.0)	91.93 (0.65)
BF78	72.0 (4.0)	10.5 (1.8)	0.0 (0.0)	13.9 (2.5)	4.9 (2.8)	8.1 (1.2)	100.00 (0.00)
BF87	54.1 (4.8)	32.3 (3.4)	7.1 (2.7)	12.7 (2.7)	0.0 (0.0)	18.5 (3.2)	99.39 (0.22)
BF84	34.1 (5.7)	8.7 (1.2)	0.0 (0.0)	36.6 (5.0)	19.8 (4.3)	8.2 (1.4)	94.44 (2.50)
BF86	30.2 (4.1)	3.9 (0.9)	3.7 (1.1)	32.8 (3.8)	1.8 (1.2)	23.9 (3.1)	92.80 (1.86)
TC10	58.5 (4.8)	11.3 (1.8)	0.9 (0.5)	22.7 (4.1)	10.5 (2.2)	4.5 (0.8)	99.65 (0.23)
TC29	67.1 (4.3)	15.8 (1.4)	0.2 (0.2)	21.6 (4.0)	5.3 (1.1)	2.7 (0.6)	100.00 (0.00)
TC8	8.6 (2.5)	6.8 (1.7)	0.0 (0.0)	46.5 (4.3)	7.1 (2.8)	28.6 (3.3)	93.75 (1.14)
TC24	1.1 (0.4)	0.4 (0.2)	0.2 (0.2)	33.2 (4.0)	15.9 (3.6)	38.8 (4.0)	94.62 (0.63)
DC40	46.3 (3.6)	8.8 (1.5)	0.0 (0.0)	4.3 (1.2)	0.6 (0.4)	45.3 (3.8)	100.00 (0.00)
DC51	22.2 (4.2)	0.6 (0.4)	8.4 (1.7)	60.7 (4.0)	0.0 (0.0)	3.5 (1.3)	92.10 (1.88)
DC49	29.2 (5.1)	2.8 (0.5)	0.0 (0.0)	39.4 (4.5)	3.2 (1.8)	20.8 (3.2)	92.10 (1.42)
DC54	22.0 (4.0)	6.4 (1.0)	0.0 (0.0)	34.8 (3.6)	12.8 (3.6)	24.1 (2.8)	90.28 (1.28)
1999H	66.4 (3.3)	15.8 (1.7)	0.0 (0.0)	17.7 (2.2)	0.3 (0.1)	8.0 (1.1)	96.61 (1.43)
1999L	49.6 (4.0)	12.9 (1.9)	0.0 (0.0)	14.8 (2.6)	8.0 (2.0)	22.4 (3.2)	93.32 (1.59)
1994H	71.3 (3.1)	6.7 (1.8)	6.4 (2.7)	3.7 (0.8)	9.4 (1.4)	6.9 (0.8)	91.41 (1.71)
1994L	53.5 (3.2)	9.4 (1.8)	0.7 (0.3)	23.6 (2.6)	10.9 (2.2)	10.8 (1.3)	99.22 (0.26)
1987H	21.6 (2.4)	7.6 (1.6)	0.0 (0.0)	29.0 (3.5)	8.6 (2.0)	37.6 (4.2)	70.83 (10.71)
1987L	33.4 (3.5)	5.0 (1.0)	0.9 (0.8)	33.5 (3.8)	12.3 (3.0)	16.0 (1.8)	96.01 (1.26)