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The effects of underplanted white spruce on understory environment and vegetation in aspen-dominated stands of the western boreal forest

by

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ABSTRACT

In the boreal forest of Alberta, Canada, underplanting white spruce (*Picea glauca*) in aspen (*Populus tremuloides*) forests attempts to address concerns about “unmixing the mixedwoods”. Important ecological differences exist between mixedwood, broadleaf and conifer forests. I studied changes in understory environment and vegetation of underplanted stands, and examined how changes related to distance from individual spruce. No changes were observed 4-5 and 10 years after underplanting. Forest floor pH and microbial nitrogen increased within one meter of 15 year old spruce. By 48 years after underplanting, litter and FH depths, soil sulphur, and forest floor pH increased; soil temperature, light, vegetation cover, total and herb richness and Shannon’s Diversity Index decreased. These effects had limited spatial extent, occurring only within 1-2 meters from the spruce. If the overstory aspen are harvested, the underplanted white spruce may have greater influence on the understory environment and vegetation in the subsequent regenerating stands.

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CHAPTER 1: GENERAL INTRODUCTION

Comparison of Broadleaf, Mixedwood and Conifer Stands of the Boreal Forest

The boreal forest extends across the subarctic latitudes of North America, Scandinavia and Russia, composing almost 25% of the world's closed canopy forest (Natural Resources Canada, 2009). In Canada the boreal forest covers 35% of the landmass, representing 77% of the total forested land (Natural Resources Canada, 2009). The main conifer species in the Canadian boreal forest are white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* var. *latifolia*), balsam fir (*Abies balsamea* (L.) Mill.) and tamarack (*Larix laricina* (Du Roi) K. Koch.). The main broadleaf species in the Canadian boreal forest are trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.).

The southern boreal forest, which extends through the Yukon, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario and Quebec, is dominated by mixedwoods of varying composition (Macdonald et al., 2010). The composition is influenced by the topography and soils, moisture and nutrient regimes, and the regeneration processes and successional pathways following disturbance (Chen and Popadiouk, 2002; Park et al., 2005; Peters et al., 2005; Peters et al., 2006). On mesic sites in the Mixedwood Section of the western boreal forest, aspen and white spruce are the most dominant tree species (Rowe, 1972). The successional development of these mixedwoods is generally perceived as a gradual transition from aspen to white spruce. The timing and density of white spruce regeneration, which are a product of the combined interactions of timing relative to mast years, distance to seed source, fire severity and competitive influences, can lead to several possible other successional pathways, reflected in the mosaic of the landscape (Chen and Popadiouk, 2002; Peters et al., 2005; Peters et al., 2006). White spruce can establish immediately after a fire and remain suppressed in the understory of an aspen stand until aspen undergo self-thinning and the canopy begins to open up, increasing light transmittance to the understory and causing increased white spruce growth (Peters et al., 2006). A smaller proportion of white spruce can germinate on nurse logs in the understory of these aspen stands once the canopy opens (Peters et al., 2006).

The understory plant community of a forest is influenced by canopy composition and cover through competition for resources, and direct effects on the understory environmental and edaphic conditions; thus understory plant communities are a reflection of the site, canopy and successional development (Macdonald and Fenniak, 2007). In natural mixedwoods there are important ecological differences in understory environment and vegetation related to the canopy tree species. The boreal mixedwood landscape is a mosaic of stands that are comprised of patches of forest of varying composition and the understory correspondingly varies among these. The understory plant community of conifer patches within boreal mixedwood stands are characterized by shade-tolerant and evergreen species and low abundances of shade intolerant species, while broadleaf patches are characterized by a higher abundance of grasses and shade intolerant species (Chávez and Macdonald, 2010). Mixedwood stands have a more species-rich flora than broadleaf or conifer-dominated stands due to different canopy species providing more heterogeneous understory conditions (Saetre et al., 1997). A greater diversity of microhabitats in the understory of mixedwoods allows for more understory plant species associated with each canopy type, not understory plant species unique to mixedwoods (Cavard et al., 2011). Mixedwoods also host a higher diversity of both birds (Hobson and Bayne, 2000) and arthropods (Work et al., 2004; Buddle et al., 2006). Mixedwoods have many more potential ecological and economical benefits, including increased timber productivity, shelter from nurse trees, reduced pest attack and increased wind stability (Man and Lieffers, 1999).

In the following two subsections the differences between broadleaf, mixedwood and conifer stands and patches will be discussed in terms of the forest canopy and understory light transmittance, and the forest floor and soils. The main points that will be illustrated are as follows. Lower light transmittance in conifer stands compared to broadleaf stands largely influences plant development in the understory. Differences in litter quality between conifers and broadleaf trees result in differences in soil pH and rates of nutrient cycling between these two types of stands. Mixedwoods provide a more heterogeneous understory than broadleaf or conifer stands, but in many respects mixedwoods are more similar to conifer than broadleaf stands. Later in this chapter the second section will discuss the current state of knowledge on the use of underplanting to create mixedwood stands. Underplanting has been used to add white spruce to the landbase for economic purposes since the 1960s, but it was not until recently that forest managers, faced with maintaining diverse forest values and ecosystem services, have considered underplanting for both its potential forest productivity and biodiversity values. Finally, the outline and objectives of this thesis will be presented.

Forest Canopy and Understory Light Transmittance

The forest canopy influences understory light transmittance; both the quantity and quality of light transmitted is important to understory plant growth. Plants depend on photosynthetically active radiation, the spectrum of the wave band between 380 and 710 nm, for photosynthesis but other bands of the spectrum are also important to the thermal qualities of the understory environment (Lieffers et al., 1999). Unlike broadleaf trees, which lose their leaves in the autumn, conifer trees (with the exception of tamarack) retain their needles year-round, reducing early spring and late autumn light levels in the understory. Because of its occurrence at high latitudes, the boreal forest has long winters with very low solar elevations and short summers with relatively low maximum solar elevations (Lieffers et al., 1999). Periods of leaf-off in early spring (April and early May) and in autumn (late September and October) in broadleaf stands are important to understory evergreen species, including white spruce, because these species are able to photosynthesize during these periods (Lieffers et al., 1999).

Shade-tolerant tree species transmit less light than shade-intolerant species (Canham et al., 1994; Messier et al., 1998). Aspen, white birch and jack pine transmit a significantly higher percentage of Photosynthetic Photon Flux Density than is transmitted in shade-tolerant conifer stands and mixedwood stands when measured above the understory vegetation (Messier et al., 1998). Light transmitted through the canopy decreases with increased abundance of spruce in the overstory (Lieffers and Stadt, 1994; Constabel and Lieffers, 1996), with a single white spruce transmitting half to one-tenth the amount of light as an aspen with similar stem size (Constabel and Lieffers, 1996). During the summer, light transmission through the canopy of old mixedwood forests ranges from 14-32% (Constabel and Lieffers, 1996) compared to the 6-10% transmission range through the canopy measured in spruce-dominated stands (Lieffers and Stadt, 1994). Light transmission through the canopy of aspen stands (both young and old) have the greatest difference from mixedwood stands in the spring and autumn because of the leaf-off period of the aspen; this difference is greater in spring than in autumn because of higher solar elevation in the spring (Constabel and Lieffers, 1996).

A comparison of old mixedwood stands to young and old aspen stands indicated that, although there are larger amounts of light transmitted through the canopies of aspen stands, the amount of light transmitted to the forest floor is approximately the same because the amount of understory vegetation increased with increased light transmittance through the canopy (Constabel and Lieffers, 1996). Comeau et al. (2009) also showed this relationship between light transmittance and understory vegetation. Shrub and herb layers can be almost absent when a dense overstory of conifers is present because of low understory light levels (Rowe, 1956; De Grandpré et al., 1993).

Forest Floor and Soils

The forest canopy can affect the understory temperature and influence the amount of precipitation received as throughfall or stemflow. The species of trees present in the canopy of a forest are highly influential on the forest floor and soil properties through their litter characteristics and resource utilization (Beatty, 1984; Saetre et al., 1997, van Pelt and Franklin, 2000; van Oijen et al., 2005). Replacement of broadleaf species with conifer species has the potential to induce changes in soil chemical properties (pH, cation exchange capacity, N availability, nitrification and soil biological activities), and in the boreal forest, succession from broadleaf-dominated to conifer-dominated stands is thought to reduce soil nutrient availability (Paré and Bergeron, 1996).

Broadleaf-dominated stands can have greater litter depths than mixedwood and conifer-dominated stands (Macdonald and Fenniak, 2007) because broadleaf tree species shed their leaves annually, unlike the majority of conifer species. However, white spruce-dominated stands have thicker forest floors than aspen-dominated stands (Hannam et al., 2004; Hannam et al., 2006). Lower soil temperatures in conifer stands, and higher C:N ratios and more compounds that inhibit decomposition and microbial activity in conifer litter cause aspen leaves decompose faster than white spruce needles (Man and Lieffers, 1999).

Soil pH in conifer-dominated stands is lower than in broadleaf-dominated stands (Ste-Marie and Paré, 1999; Légaré et al., 2001; Hannam et al., 2004). The difference in soil pH between broadleaf-dominated stands and conifer-dominated stands is the result of different types of litter and acidification of the forest soil from the decomposition of conifer needles (Fisher et al., 2000).

Broadleaf-dominated stands and patches have warmer soils than both mixedwood and conifer-dominated stands and patches (Macdonald and Fenniak, 2007; Chávez and Macdonald, 2010). Although the differences in soil temperatures between forest types can be small (less than 1°C), soil temperature was significantly related to understory plant community composition in broadleaf-dominated, mixedwood and conifer-dominated stands (Macdonald and Fenniak, 2007). Soil moisture was greater in broadleaf-dominated and mixedwood patches than in conifer-dominated patches (Chávez and Macdonald, 2010).

Soil microbial communities differ between broadleaf-dominated stands and conifer-dominated stands because of differences in litter quality, soil pH and soil temperatures. Hannam et al. (2006) found that aspen-dominated stands had soils with higher rates of microbial respiration than soils from white spruce-dominated stands even at the same pH. Microbial biomass (measured by phospholipid fatty acid (PLFA) concentrations) was higher in the forest floor of aspen-dominated stands than in the forest floor of either mixedwoods or white-spruce dominated stands (Hannam et al., 2006). A greater proportion of PLFAs associated with actinomycetes and a higher mol% of 16:1ω5, a PLFA associated with gram negative bacteria and arbuscular mycorrhizal fungi, were found in aspen-dominated stands than white-spruce dominated stands (Hannam et al., 2006). Hannam et al. (2006) also found five out of the six PLFAs with high indicator values were present only in the white spruce-dominated and mixedwood stands rather than broadleaf stands, suggesting that conifer trees have a much stronger influence on the soil microbial communities than broadleaf trees.

Although conifer trees immobilize nutrients at a higher rate than deciduous trees (Légaré et al., 2001), white spruce and aspen are able to reduce some aspects of competition through their differences in soil resource utilization (Man and Lieffers, 1999). Understory plant species associated with aspen stands are able to make use of greater amounts of soil nutrients in aspen stands, particularly calcium (Légaré et al., 2001). Not all soil nutrients exhibit clear differences between the soils of broadleaf-dominated stands and conifer-dominated stands, but instead are species specific; the concentration of exchangeable calcium in the soil is highest in aspen stands and lower in spruce-fir and pine stands, but the exchangeable calcium in the soil of birch stands is not different from that of spruce-fir stands (Légaré et al., 2001). Other nutrients, such as soil nitrate and phosphate, do not differ between aspen, birch and spruce-fir stands but are different in pine stands (Légaré et al., 2001). Soil nitrogen has been shown to be greater in broadleaf stands than in mixedwood and conifer stands in some studies (Hannam et al., 2004; Macdonald and Fenniak, 2007), but others have shown no difference in total soil nitrogen levels between broadleaf and conifer stands (Ste-Marie and Paré, 1999). Rates of nitrogen, carbon and phosphorus mineralization are generally higher in broadleaf stands (Hannam et al., 2006). Organic layer phosphorous concentrations were greater in broadleaf stands than in conifer stands but there was no difference in mineral soil phosphorous concentrations (Macdonald and Fenniak, 2007). Forest floor total carbon was greater in white spruce stands than in aspen stands (Hannam et al., 2004). The larger amount of carbon in the forest floor of white spruce stands than of aspen can be attributed to the differences in rooting pattern between them; the lateral roots of aspen are mainly concentrated in the mineral soil while the lateral roots of white spruce are mainly concentrated in the forest floor, hence carbon in the fine roots of the white spruce may account for the higher carbon in the forest floor of conifer stands (Hannam et al., 2004).

Establishing Mixedwood Stands Through Underplanting

Underplanting allows for the creation of mixedwoods, and potentially the mixedwood ecosystems described in the first section of this chapter, in areas where they do not exist, whether due to regeneration difficulties or from removal of seed sources. Underplanting is an attempt to mimic the most general model of natural boreal succession in which stands begin after disturbance with the establishment of shade-intolerant pioneer broadleaf species, then shade-tolerant conifers in the understory, and finally the gradual transition to a conifer stand by taller and longer living white spruce (Lieffers et al., 1996). Underplanting generally involves planting a shade-tolerant species (e.g., white spruce) beneath a shade-intolerant species (e.g., aspen) without removal of the overstory canopy. There are benefits provided to the underplanted species (i.e., nurse crop effects). Once the underplanted species has grown large enough to be easily seen during harvesting operations so these trees are not damaged and have grown large enough to avoid being outcompeted by regenerating vegetation (approximately 20 years after planting), the overstory trees are harvested. In the case of aspen, regeneration then occurs from suckering, and the quicker growing and shorter lived aspen grow along with the white spruce, creating a mixedwood forest. The second harvest occurs when this white spruce/aspen mixedwood reaches maturity.

Underplanting in Canada was first introduced in the 1960s (Duffy, 1963; Lees, 1963; Wang and Horton, 1968; Dyck, 1994). Underplanting white spruce in aspen-dominated forest in the boreal mixedwood region of Alberta was introduced to add a commercially valued species to a forest landbase that was not considered economically valuable. Throughout the 1970s and 1980s, underplanting trials were still conducted (Sutton, 1986) but clearcutting and replanting became common practice. In Alberta silvicultural operations and regeneration rules tended to lead to the establishment of relatively pure stands of aspen and white spruce (Man and Lieffers, 1999; Lieffers and Grover, 2004; Lieffers et al., 2008). Strict regeneration standards and legal requirements ("Free-to-Grow" standards), the increased expense of planting mixedwoods, and the tenuring of land to forestry companies which either processed hardwood or softwood lumber resulted in pressure which helped to unmix the mixedwoods. It was not until the 1990s that underplanting trials were reintroduced (DeLong, 1997; DeLong, 2000; Stewart et al., 2000; Comeau et al., 2004). Underplanting was reintroduced as an ecologically-based forest management option because of concerns about forest management reducing boreal mixedwood, and single species management reducing biodiversity and changing natural forest processes (Man and Lieffers, 1999). Underplanting white spruce in aspen-dominated stands attempts to address issues of single species management, competing interests on the landbase, white spruce regeneration difficulties after clearcutting and a public demand for more ecologically based silvicultural systems, based on a model of natural tree species succession (DeLong, 1997; DeLong, 2002). Underplanting remains a relatively uncommon practice by forestry companies because, under current regulations, companies do not receive credit for underplanted trees until the overstory canopy is harvested, resulting in companies carrying the cost of planting for up to 20 years (Gitte Grover, personal communication).

Underplanting is not always done using this ‘conifer under broadleaf’ model. Underplanting conifer in conifer-dominated stands has also been used to improve or diversify the gene pool and to add more desirable species to stands that have been subjected to selective cutting and high grading for hundreds of years (Glen, 1993). Underplanting of broadleaf species in broadleaf-dominated stands also occurs (e.g., with *Quercus* spp.) but due to the shade intolerant nature of these species, this mostly occurs in shelterwood harvest systems (Dey and Parker, 1997; Povak et al., 2008). Underplanting of conifer species has also been done in mixedwood stands where all overstory conifers have been harvested, removing any potential seed source (Guldin and Heath, 2001).

Site Selection and Planting

To try to ensure successful establishment and survival, as well as the best possible growth rates of underplanted white spruce, it is important that proper consideration be given to site selection, site preparation and planting. Proper site selection can ensure high seedling survival without expensive site preparations. Delong (1997) recommended that when underplanting aspen stands, the aspen should be between 30 and 60 years old. This is because stands younger than age

30 have not undergone self thinning and stands older than age 60 will not provide adequate time for white spruce growth before removal of the overstory aspen canopy needs to occur (DeLong, 1997). Younger stands which require thinning are more expensive to underplant and therefore are less desirable sites because increases in white spruce growth following thinning are not enough to justify the expense (DeLong, 1997; Comeau et al., 2009). Light levels in aspen stands are at their lowest when aspen are 10-25 years old and then begin to increase with age as canopy gaps develop (Lieffers et al., 2002).

Ideal stands to underplant are those with an aspen density of less than 1200 stems per hectare and a basal area of less than $35 m^2 ha^{-1}$ (DeLong, 1997) but underplanted white spruce have been shown to successfully establish in stands with higher aspen densities and basal areas (Comeau et al., 2009). White spruce can survive under low light levels (as low as 8% transmittance according to Leiffers and Stadt (1994)) but underplanting in aspen stands that are starting to open up will result in better growth of white spruce. Stands with too low of canopy cover may be a problem though since increased light in the understory also increases abundance of other potentially competing vegetation. Mesic to submesic sites should be underplanted to reduce competition from understory vegetation, in particular *Calamagrostis canadensis,* which is typically greater on moister sites (DeLong, 1997). Planting should occur early in the spring so that the underplanted white spruce can take advantage of increased light levels before aspen leaf out (DeLong, 1997). The overstory canopy provides protection to underplanted seedlings on sites with frost pockets prone to summer frost (DeLong, 1997). Underplanting schedules should take hare population cycles into consideration, avoiding planting during peak populations in favor of planting when the populations decrease in order to reduce browsing, and not underplanting stands with heavy vegetation cover or near recently disturbed areas, which are good hare browsing areas (DeLong, 1997).

Underplanted White Spruce Growth

Results from underplanting studies conducted during the 1960s and 1990s showed promising results for white spruce establishment under aspen canopies. Survival rates of up to 98% on scarified strips and 96% on non-scarified sites within the first three to four years after planting (Stewart et al., 2000) indicated a potential for high stocking in underplanted stands. Similar survival rates between scarified and non-scarified sites indicated that underplanting can also establish white spruce without the requirement of expensive site preparation or the risk of damage to aspen roots. Growth of understory white spruce has the potential to be suppressed because of low light levels in the understory, but at 40% transmittance height increment was equivalent to that observed in 100% light conditions (Lieffers and Stadt, 1994). With increased light transmittance, the number of buds, diameter of the leader, and height to diameter ratio also increased (Lieffers and Stadt, 1994). Growth of the underplanted white spruce seedlings was reasonably stable initially compared to white spruce planted in clearcuts, where growth started slowly but then increased exponentially

(DeLong, 2000). Like scarification and thinning, fertilization prior to underplanting is not warranted. A study of the effects of fertilization three years before planting showed fertilization negatively influenced white spruce growth for the first five years after planting due to increased competition from surrounding vegetation (Comeau et al., 2004) but no effect, either negative or positive, on height or growth rate 10 years after underplanting (Comeau et al., 2009).

Underplanting can still be an important silvicultural option which removes regeneration delays after clearcutting. Removal of the aspen overstory after the white spruce has grown to the recommended heights for overstory removal (approximately 20 years) greatly increases white spruce growth. The release growth in diameter of white spruce was greater than for height growth; this is attributed to increased light, growing space, and soil nutrients and moisture (Man and Greenway, 2004). It is also possible for white spruce to have a weak response to overstory removal, but this was most strongly associated with small trees (Man and Greenway, 2004), highlighting the importance of following white spruce height guidelines for overstory aspen removal. The weak response to release in small trees can be the result of shock from changes in the growth environment, damage to the white spruce from harvesting, or increased competition from understory vegetation which develops due to the increased light levels (Man and Greenway, 2004).

Benfits of Underplanting

Benefits of underplanting exist in many areas, including benefits to the health and survival of underplanted trees, and potential yield benefits from growing species in mixtures. White spruce grown under an aspen canopy benefit from the protection of aspen, which acts as a nurse crop. There are several advantages of underplanting white spruce beneath an aspen canopy in comparison to white spruce grown in clearcuts. Underplanting reduces over-winter injury by maintaining snow cover over white spruce seedlings and reduces summer frost injury through moderation of night time minimum temperatures (DeLong, 1997). In addition to protecting white spruce from the environment, underplanting also protects white spruce from insects, such as white pine weevil, diseases, such as root rot infestations, and competing vegetation (as long as there is sufficient overstory canopy remaining) (DeLong, 1997). Other biological benefits include increased diversity and habitat creation. Underplanted white spruce may provide increased thermal cover for ungulates as trees grow larger (DeLong, 1997). Society may also find benefit in underplanting through the aesthetics of continual maintenance of tree cover on the landscape as opposed to clearcutting (DeLong, 1997).

A difference in resource utilization exists between aspen and white spruce mixedwoods through the partitioning of above-ground (light) and below-ground (nutrient and water) resources by physical separation of the canopies and roots, a shade tolerance separation and a phenological separation, thereby decreasing competition between the two species (Man and Lieffers, 1999). Also, the presence of aspen has the potential to improve litter decomposition and nutrient cycling, thus benefitting white spruce growth (Man and Lieffers, 1999). If white spruce establish in a stand at the same time as aspen, the white spruce can sustain damage to the leader as they start growing through the lower branches of the aspen canopy. Underplanting in older aspen stands is beneficial to white spruce by still allowing all the benefits of the aspen nurse crop without damage from leader whipping (Lieffers and Grover, 2004).

There has been speculation and research into the productivity of mixedwoods compared to pure stands. If mixedwoods are more productive and have better yields this could make the concept of underplanting more appealing. Many examples showing greater productivity in mixedwoods than in pure stands come from substitutive plantation experimental designs, although many of the studies lack statistical testing and initial density control (Man and Lieffers, 1999). Comparison of mixedwood productivity to pure stand productivity has also been done using the growth of natural stands under similar conditions, by comparing yield tables and by modelling (Man and Lieffers, 1999). In Ontario mixedwoods have been said to have an average growth rate that is one third higher than the combined average of all forest types (Penner, 2008). A study by Greene et al. (2002), modelling silviculture alternatives for conifer regeneration, indicated that relying on advanced regeneration or underplanting are the cheapest alternatives for attaining full or partial conifer stocking, and that conventional plantations (with the exception of full conifer stocking when there is little advanced regeneration and herbicides can be used) are more expensive.

Thesis Objectives and Outline

Based on observed differences between broadleaf, mixedwood and conifer trees, patches and stands of the boreal forest, I hypothesized white spruce may act as an ecosystem engineer when introduced into aspen-dominated stands, changing the understory environment and below-ground processes, and subsequently the understory vegetation. An ecosystem engineer "directly or indirectly modulate[s] the availability of resources to other species, by causing physical state changes in biotic or abiotic materials", and in so doing modifies, maintains and creates habitats (Jones et al., 1994). Ecosystem engineers can influence the local microclimate (Wright and Jones, 2006), and create and maintain patches (Jones et al., 1994). If the addition of white spruce to aspen-dominated stands results in changes to the understory environment (through changes in light transmission, litter quality and quantity, etc.), it is possible that the understory vegetation may change from that of an aspen-dominated stand to one more closely resembling that of a mixedwood patch around the white spruce. If it is possible to create mixedwood forest ecosystems (in a broader ecological sense), and not just "mixedwoods" pertaining strictly to the tree species/timber prospective, underplanting will have the possibility to address and integrate two important issues facing forest managers – stand productivity and biodiversity/ecological values. The objectives of my study were addressed by the following questions:

1. Does underplanting white spruce in aspen-dominated stands change the understory environment, and subsequently the understory vegetation?
2. If changes are observed:

   a) at what age are changes first observed?

   b) are the changes greater close to the base of the underplanted tree and less pronounced as distance outward from the base of the tree increases?

   c) does the spatial extent of the effects increase with time passed since underplanting?

I studied these objectives in two groups of underplanted stands: a group of stands studied 4, 5, 10 and 15 years after underplanting (young), and a group of stands studied 48 years after underplanting (old). I also looked at the size and growth of these underplanted white spruce to put these trees in context to other underplanting studies and open-grown white spruce. Results from the young stands are presented in Chapter 2 and results from the old stands are presented in Chapter 3. General conclusions and management implications of the research are provided in Chapter 4.

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CHAPTER 2:

EFFECTS OF UNDERPLANTED WHITE SPRUCE ON UNDERSTORY VEGETATION AND ENVIRONMENT 4-15 YEARS AFTER UNDERPLANTING

Introduction

Underplanting white spruce in aspen-dominated stands originated in the 1960s as a way to add a commercially valued species to a forest landbase that was not considered economically valuable. As aspen became more commercially valued underplanting evolved as a silvicultural tool that could optimize fibre yield by growing the two species together (Man and Lieffers, 1999). Previous studies have looked at growth of underplanted white spruce in aspen stands (DeLong, 1997; Comeau et al., 2004; Comeau et al., 2009). These previous underplanting studies have shown that, while white spruce can successfully establish when underplanted in aspen stands, growth rates of underplanted white spruce are lower than open-grown white spruce. Lieffers and Stadt (1994) showed that at 40% transmittance height increment of understory spruce was equivalent to that observed in 100% light conditions.

Important ecological differences exist in the understory between natural broadleaf, mixedwood and conifer stands and patches (as discussed in detail in Chapter 1). A greater diversity of microhabitats in the understory associated with different species present in the canopy allow for greater species biodiversity in these mixedwoods (Cavard et al., 2011). Although studies have been conducted looking at the survival and growth of white spruce underplanted in aspen-dominated stands (DeLong, 2000; Comeau et al., 2004; Comeau et al., 2009), there have been no studies of the effects of underplanting on other ecological properties. It is desirable to know whether mixedwood stands created by underplanting white spruce have similar ecological properties (e.g. increased biodiversity) to natural mixedwoods. We know from other studies that conifer trees exert particular influence on the forest environment and are associated with particular ecological effects on soils, understory environment and plant communities. Thus there is interest in seeing if such effects are exerted when white spruce are underplanted and the spatial extent of such effects.

Studies comparing natural mixedwood to broadleaf and conifer stands have focused on mixedwood stands in which the white spruce are old enough to have grown up into the main overstory canopy. In these natural mixedwood stands it is unknown how old or how large the white spruce are before the understory starts to differ from a broadleaf-dominated stand. By studying stands of various aged underplanted white spruce, a relationship between tree age and influence on the forest environment can be determined.

In this chapter I compare understory environmental variables and vegetation composition between areas underplanted with white spruce 4-5, 10 and 15 years prior to sampling with non-underplanted areas in aspen-dominated stands. The objectives of this study were to i) determine if underplanting white spruce changes the understory environment and vegetation, and if so, ii) how these changes varied with distance from the underplanted spruce, and iii) at what age underplanted white spruce change the understory environment and vegetation. The main purpose of studying such young underplanted stands was to determine at what age the white spruce start to have an effect on the understory environment. At the same time, I could examine whether there were effects which could be attributed simply to the act of planting.

Methods

Study Area

This study was conducted in the Central Mixedwoods Ecological Subregion (Strong, 1992) near Calling Lake (55°N, 113°W, 598 m above sea level) and Lac La Biche (55°N, 112°W, 574m above sea level), Alberta, Canada. The area is characterized by a boreal climate with short summers and long winters; the mean May-August temperature is 13.5°C and the mean November-February temperature is -13.2°C (Strong, 1992). The mean annual precipitation is 397 mm (Strong, 1992), over 75% of which occurs as rainfall during summer (Environment Canada, 2011). Soils on upland mesic sites are usually Gray Luvisols on moderately well-drained, medium-textured moraine and lacustrine parent material, derived from mostly sedimentary rocks weathered in situ or translocated by glacial activity (Kocaoglu, 1975; Kocaoglu and Bennet, 1983).

Site Selection and Study Design

Research was conducted in nine mature aspen-dominated stands that were underplanted with white spruce: three stands underplanted in 1994 located on the west side of Calling Lake, and three stands underplanted in 1999, two stands underplanted in 2004 and one stand underplanted in 2005 near Lac La Biche (Figure 2.1; Appendix 1). The two stands underplanted in 2004 and the one stand underplanted in 2005 were treated as one age class.

Underplanting of these stands was conducted by Alberta-Pacific Forest Industries. The underplanted stands were mature (>80 years old), upland aspen-dominated stands, in which the aspen canopies were beginning to open up. Sites received no mechanical site preparation before planting. The planting densities of white spruce in stands underplanted in 1994 were around 630 stems per hectare. The planting densities of stands underplanted between 1999 and 2005 ranged from 1334 to 1440 stems per hectare. The soils and ecosites differed slightly between stands (Appendix 2). Stands selected for this study had very little to no slope, and had areas that were left unplanted, in which reference aspen plots were established.

I established plots in these stands during the summer of 2009. The study was conducted 4-5, 10 and 15 years after underplanting (the underplanted white spruce were 1-2 years old at the time of planting so the true tree ages would be range from 5-7 to 16-17 years old). To address my first objective of determining if underplanting white spruce changed the understory environment and vegetation, 2x1 m plots were established in both underplanted area (spruce plots) and non-underplanted area (aspen plots) of each of the nine stands. Aspen plots were selected to avoid large amounts of downed wood, edges created by linear features such as seismic lines, the direct base of any broadleaf trees, and slopes and depressions unrepresentative of the condition of the majority of the stand. These aspen plots were essentially placed in areas that would have been underplanted with white spruce if the entire stand had of been underplanted. Plots were placed at least 15 m apart. Five aspen plots were established in each of the 1994, 1999 and 2005 underplanted stands. In the 2004 stands seven aspen plots were established in one of the stands and eight aspen plots were established in the second stand. A combined total of 50 aspen plots were sampled in all nine stands.

To address whether changes in environment and vegetation varied with distance from the underplanted spruce, the spruce plots were established contiguously (0-1 m and 1-2 m from the base) at underplanted white spruce trees. Figure 2.2 shows the layout of the plots within a stand. I established spruce plots at five trees in each of the 1994, 1999 and 2005 underplanted stands, and at seven trees in one of the 2004 stands and eight trees in the other 2004 stand. A combined total of 50 spruce trees and 100 spruce plots were sampled in all nine stands. Spruce trees were only included in the study if the distance to the next underplanted tree was at least twice as far as the contiguous plots distance (i.e., 4 m). The same set of criteria were used as described for the set up of aspen plots (avoiding large amounts of downed wood, edges created by linear features such as seismic lines, the direct base of any broadleaf trees, and slopes and depressions unrepresentative of the condition of the majority of the stand).

Data Collection

Vegetation

Within each of the 150 2x1 m plots, I recorded percent cover of each species of forb, shrub, grass and moss. Percent cover estimates were recorded within 0.25% for estimates up to 20%, within 0.5% for estimates up to 40%, and within 2.5% for estimates above 40%. For species with percent cover values between 0-0.25%, percent cover was recorded as <0.25%; these were later changed to 0.01% for data analysis. Vegetation surveys were conducted between July 9 and August 10, 2009. Nomenclature followed Moss (1983).

I measured the height, stem diameter at 5 cm and crown radius (in the direction of the plots) of each white spruce at which plots were established. I also measured diameter at breast height (dbh) when the tree was above 1.3 m.

Soil Moisture and Temperature

I measured soil moisture and temperature once during the summer. Soil moisture was measured between July 24 and August 8, 2009. Soil moisture measurements were taken at a 5 cm depth in the mineral soil with a ML2x ThetaProbe soil moisture sensor attached to a HH2 moisture meter (Delta-T Devices, Cambridge, UK), at least two days after a major rain event. Soil temperature was measured between July 24 and August 24, 2009. Soil temperature measurements were taken with a 450ATT digital soil thermocouple thermometer (Omega, Laval, PQ, Canada) at 5 cm and 10 cm depths in the mineral soil. Since a single point measurement was taken, this was done between 12h00-16h00 MST to obtain the peak soil temperature (Stathers and Spittlehouse, 1990). Soil moisture measurements were not taken in the stands with 4-5 year old underplanted white spruce because of equipment failure. Both soil moisture and temperature measurements were taken in three spots in each of the 150 2x1 m plots and averaged at the plot level. Measurements were evenly spaced across the two meter width of the plot.

Litter and Organic Layer

Litter and organic layer (combined F and H layers) depths were measured in August 2009. Once again, three measurements were taken in each of the 150 2x1 m plots and averaged at the plot level. Measurements were taken at the same locations as the soil moisture and temperature readings.

Decomposition

In each of the plots decomposition was measured using five 15 cm diameter Whatman No. 1 cellulose filter papers enclosed in mesh bags of 1.5 mm x 1.5 mm mesh size. I initially dried a subset of the filter papers in a 70°C drying oven for 48 hours and then weighed them to determine the average weight of a filter paper before being placed in the ground. I placed the decomposition bags at the interface between the forest floor and mineral soil. The decomposition bags were placed in the field at the end of June/beginning of July 2009 and removed at the end of August 2009. After removal from the forest floor, the decomposition bags were dried at 70°C for 48 hours, weighed and then the percent loss of the cellulose filter paper calculated.

Soil Nutrients

Soil nutrients were measured using Plant Root Simulator^{TM} (PRS^{TM}) probes (Western Ag. Innovations Inc., Saskatoon, SK, Canada), which contained ion-exchange membranes. The PRS^{TM}-probes were installed vertically in the mineral soil of the plots with the top of the membrane at the mineral-organic horizon interface. I installed the PRS^{TM}-probes at the end of June/beginning of July 2009 and removed them at the end of August 2009 (at the same time as the decomposition bags). Three anion and three cation probes were installed in each plot, with the pairs of PRS^{TM}-probes being evenly spaced across the two meter width of the plot. The PRS^{TM}-probes were analyzed for NO_3^--N, NH_4^+-N, P, K, S, Ca, Mg, Al, Fe, Mn, Cu, Zn, B, Pb and Cd by Western Ag Innovations Inc.

Forest Floor pH

At the end of August 2010, I collected FH-layer forest floor samples from each of the 45 2x1 m plots in the stands with 15 year old underplanted white spruce.

From each plot three subsamples of FH-layer forest floor were collected to the depth of the mineral soil surface. The three subsamples were collected near where soil moisture and temperature, and litter and FH layer measurements were taken, and aggregated for the plot. I then sieved samples to 2 mm. Samples were stored at 4°C until analyzed. All samples were analyzed within a few days of collection. Forest floor pH was measured potentiometrically using a 1:4 soil to 0.01 M $CaCl_2$ ratio (Kalra and Maynard 1991).

Forest Floor Microbial Biomass

The sieved forest floor samples I collected from the stands with 15 year old underplanted white spruce were also analyzed for microbial biomass carbon and nitrogen content using the chloroform fumigation procedure (Brooks et al., 1985; Vance et al., 1987). I divided each sample into five subsamples for the different analyses. Two subsamples of five grams of fresh forest floor from each sample were fumigated for 24 hours, and then extracted with 50 ml of 0.5M K_2SO_4. Another two subsamples of five grams were immediately extracted without being fumigated. A fifth subsample was weighed, then dried in a 107°C drying oven for 48 hours, and reweighed to determine moisture content. All extractions were completed within three weeks of the samples being collected. The extracts were stored at -20°C until submitted to the Natural Resources Analytical Laboratory at the University of Alberta for analysis of non-purgeable organic carbon (NPOC) and total nitrogen (TN). I calculated microbial biomass carbon and nitrogen from the difference between the fumigated and unfumigated subsamples. Final measurements were expressed on a dry weight basis. Because comparisons were made within a stand of the same forest floor substrate and no comparisons were made between different soil types, no correction factor was used (Leckie et al., 2004).

Data Analysis

Cover values for vegetation were summed across all species in a plot to calculate total percent cover and for each 2m^2 plot I calculated the following: total richness, shrub richness, herb richess, Shannon's Diversity Index (Shannon and Weaver 1949), and Simpson's Diversity Index (Simpson 1949). Shannon's Diversity Index takes into account both species richness and evenness, while Simpson's Diversity Index places less weight on rare species than Shannon's. Whittaker's beta diversity measure (Whittaker, 1972) was used to calculate species turnover among plot types (0-1 m from spruce, 1-2 m from spruce, aspen) within a stand:

$$\beta_w = (\gamma/\alpha) - 1$$

where γ is total species richness per stand and α is mean species richness per plot type.

To determine the influences of underplanting and of plot location in relation to distance from the underplanted tree on the understory environmental variables and vegetation, mixed-model analyses of variance (ANOVAs; PROC MIXED in SAS v. 9.2; SAS Institute, 2008) were used to test decomposition, soil moisture and temperature, litter and FH layer depths, soil nutrients, forest floor pH, forest floor microbial biomass, total percent vegetation cover, total species richness, shrub richness, herb richness, and Shannon's, Simpson's and Whittaker's diversity indices. Before I performed ANOVAs, residuals of the data were tested for normality (Kolmogorov-Smirnov) and homogeneity of variance (Levene's test), and I transformed data when necessary to conform to these assumptions. Two sets of ANOVAs were run to address the following two questions:

1) Do the understory environmental and vegetation variables differ between the underplanted areas and the non-underplanted areas of the stands?

2) Do the understory environmental and vegetation variables differ in relation to distance from underplanted white spruce?

In the ANOVAs comparing the underplanted to the non-underplanted areas (non-blocked ANOVAs) the stand was the experimental unit and plots within a stand were treated as subsamples:

$$\mu = L_i + S_j + R_k(L_i*S_j) + \varepsilon$$

where L is the plot location (i = 1-2, fixed), S is the stand (j = 1-3, random), $R(S*L)$ is the replicate within a plot location and stand (k = 1-10, random), and ε is the experimental error. Non-blocked ANOVAs were performed comparing all three plot locations (0-1 m from spruce, 1-2 m from spruce and aspen) without blocking the spruce plots at the common underplanted tree. This was done to compare the underplanted plots (0-1 m and 1-2 m combined) to the non-underplanted plot (aspen).

ANOVAs were also conducted to examine the influence of distance from an underplanted white spruce tree – in which case only the underplanted plot locations were used. A blocked ANOVA was used in which the white spruce tree was the block with the plots representing the treatment effect of the two distances from the underplanted tree:

$$\mu = L_i + S_j + T_l\,(S_j) + \varepsilon$$

where *L* is the plot location (i = 1-2, fixed), *S* is the stand (j = 1-3, random), *T(S)* is the tree nested within the stand (l = 1-5, random), and ε is the experimental error. Both non-blocked and blocked ANOVAs were performed making comparisons within an underplanted age class (with stands underplanted in 2004 and 2005 being considered the same age class) instead of including age of the underplanted white spruce as a covariate and analyzing for differences between stands of different aged underplanted white spruce. I did this because the type of ecosites underplanted varied quite a bit between years underplanted, but tended to be more similar for stands underplanted within the same year.

To determine the influences of underplanting and of plot location in relation to distance from the underplanted tree on the understory vegetation composition, permutational multivariate analyses of variances (PERMANOVA) were performed using PC-ORD (v. 5.10; McCune and Mefford, 2006; Anderson, 2001), as data were not normally distributed. The PERMANOVAs were run using the understory vegetation species data with a Sørenson (Bray-Curtis) distance measure and 4,999 unrestricted permutations of the raw data. All PERMANOVAs were performed on each of the three ages of white spruce separately. Like the ANOVAs, separate PERMANOVAs were run to address two questions:

1) Does the understory vegetation composition differ between the underplanted areas and the non-underplanted areas of the stands?

2) Does the understory vegetation composition differ in relation to distance from underplanted white spruce?

In the PERMANOVAs used to compare the underplanted to the non-underplanted areas, one-way PERMANOVAs were performed with replicates within plot location as the grouping variable. PERMANOVA cannot be used to analyze unbalanced data sets. Because of this, the two underplanted plot locations were not combined into a single underplanted group and compared against the non-underplanted aspen plots as was done with the ANOVAs. Instead each underplanted plot location (0-1 m and 1-2 m from the spruce) was compared to the non-underplanted aspen plots separately.

To compare the understory vegetation composition in relation to the distance from the underplanted white spruce, a randomized complete block PERMANOVA was performed treating the spruce tree as the block and with the plots representing the treatment effect of the two distances from the underplanted tree.

To examine variation in understory vegetation species composition at the three different plot locations nonmetric multidimensional scaling (NMS) ordinations were performed, using PC-ORD (v. 5.10; McCune and Mefford, 2006) with a Sørenson (Bray-Curtis) distance measure. NMS allows the patterns in species composition to be visualized, while the Sørenson distance measure of community similarity is suitable for ecological data. NMS ordinations were run for each of the three ages groups (15, 10 and 4-5 year old underplanted white spruce) separately and included all plots (0-1 and 1-2 m from spruce, and aspen). For each NMS I first completed 100 runs with real data and 100 runs with randomized data, starting with a six-dimensional solution and stepping down to a one-dimensional solution. Plots of stress versus iteration were used to assess stability of the solution (stability criterion=0.00001). Optimal number of dimensions (n=3) and best starting configurations were determined from the preliminary runs and then final NMS ordinations were performed using these.

Results

The 4-5 year old white spruce had a mean height of 62.7 (± 2.8) cm, mean crown radius of 19.2 (± 1.3) cm and mean stem diameter of 0.7 (± 0.05) cm. The 10 year old spruce had a mean height of 116.6 (± 6.5) cm, mean crown radius of

37.9 (± 2.3) cm and mean stem diameter of 1.3 (± 0.1) cm. The 15 year old white spruce had a mean height of 162.8 (± 10.2) cm, mean crown radius of 52.6 (± 2.9) cm and mean stem diameter of 2.3 (± 0.2) cm (Figure 2.3).

None of the non-blocked ANOVAs, which compared the environmental and vegetation variables between underplanted and non-underplanted plots in the stands with 4-5, 10 and 15 years, were significant (Table 2.1). In the blocked ANOVAs, which compared the environmental and vegetation variables between distances from the underplanted spruce, the only significant differences between the two distances from the spruce trees were in the forest floor pH (p=0.006) and the microbial biomass nitrogen (p=0.040) in the 15 year old underplanted stands (Table 2.2). Both the forest floor pH and microbial biomass nitrogen were higher in the plots 0-1 m from the base of the spruce (pH=5.61, microbial biomass nitrogen=5.18 mg N/g dry forest floor) than in the plots 1-2 m from the spruce (pH=5.39, microbial biomass nitrogen=4.49 mg N/g dry forest floor).

Results from one-way PERMANOVAs showed that plot location (underplanted versus non-underplanted; Table 2.2) did not have a significant effect (significance level of α=0.05) on understory plant species composition in any of the underplanted age groups. Results from randomized complete block PERMANOVAs showed that distance from the underplanted white spruce (0-1 m versus 1-2 m; Table 2.3) did not have a significant effect (significance level of α=0.05) on understory plant species composition in the 10 and 15 year old underplanted stands. There was, however, a significant difference (p=0.0240) between the plots 0-1 m and 1-2 m from the base of spruce in the 4-5 year old underplanted stands (Table 2.3). Visual examination of the NMS ordinations did not indicate any differences in the understory plant species composition between plot locations for any of the underplanted age classes (Figure 2.4, Figure 2.5, Figure 2.6).

Discussion

The sizes of the underplanted white spruce in these stands were comparable to that observed of underplanted white spruce of the same age in other studies. The mean height of 62.7 cm for the five year old underplanted spruce was similar to the mean heights (61.3 cm, 68.7 cm) of five year old underplanted spruce from trials in northeastern British Columbia (Comeau et al., 2004). At 10 years old, the underplanted white spruce in the northeastern B.C. trials varied more in mean height between trials than when the trees were five years younger, with mean height of the trials being 99.0 cm and 125.4 cm (Comeau et al., 2009). The mean height of the 10 year old underplanted spruce I studied fell within this range (116.6 cm). The mean root collar diameters of trees in the northeastern B.C. trials were 0.79 cm and 0.90 cm at five years old (Comeau et al., 2004), and 1.39 cm and 1.81 cm at 10 years old (Comeau et al., 2009). Although I measured stem diameter 5 cm above the ground instead of at the root collar, the mean stem diameters of the five year old spruce (0.7 cm) and 10 year old spruce (1.3 cm) in my study were similar to the mean root collar diameters in Comeau's studies.

In the study in northeastern B.C., mean height growth increment, based on measuring inter-whorl distances, was 10.6 cm/year for one of the trials at age five (Comeau et al., 2004) and 10.8 cm/year by age 10 (Comeau et al., 2009). I did not measure inter-whorl distances to calculate growth rates. If I assume that the white spruce planting stock had an initial height of 20-25 cm then the height growth increment for the first five years can be assumed to be between 7.5 and 10.7 cm/year. This upper range is comparable to growth rates observed for the underplanted white spruce trees in northeastern B.C., and this range falls within the range of 5-12 cm/yr during the first five years observed by DeLong (2000). If I take the difference in height between the five and 10 year old spruce in my study and average the height growth over five years, assuming similar site and growing conditions, and initial stock height, then growth rates by 10 years can be assumed to be close to 11 cm/year. Comeau et al. (2004) found initial stock height to be highly significant in explaining height growth but did not find site to be a significant explanatory factor. An 11 cm/yr height growth rate is similar to that observed by Comeau et al. (2009). If I take the difference in height between the 15 and 10 year old spruce in my study and average the height growth over five years, assuming similar site and growing conditions, and initial stock height, then growth rates by 15 years can be assumed to be just over 9 cm/year. Alternatively, if I take the difference in height between the 15 and five year old spruce in my study and average the height growth over 10 years, assuming similar site and growing conditions, and initial stock height, then growth rates over this period for the 15 year old white spruce can be assumed to be around 10 cm/year.

The growth rates of the underplanted white spruce observed by Comeau et al. (2004, 2009) were considerably lower than the 40 cm/yr height growth rates observed by Boateng et al. (2006) in a study of open grown white spruce at approximately 10 years old in the same area. White spruce grown in a clearcut without receiving any mechanical site preparation or chemical treatments had heights of 50, 92, 171 and 241 cm at age 5, 8, 12 and 14, respectively (Boateng et al., 2006). The ground level stem diameters of those trees were 0.76, 1.22, 2.56 and 3.58 cm at age 5, 8, 12 and 14, respectively (Boateng et al., 2006). The height at age five was less than the height of the five year old spruce I studied and the stem diameters were comparable. These open grown spruce had greater heights and diameters than the 10 and 15 year old spruce I studied. An increase in the growth rates of the underplanted white spruce could be expected with release from the aspen overstory due to increased resource availability (Man and Greenway, 2004).

Studies comparing natural stands and patches of broadleaf, mixedwood and conifer have found differences in terms of soil temperature, moisture, pH and nutrients; litter depth; forest floor microbial communities; and understory vegetation diversity, richness and cover (Hannam et al., 2004; Hannam et al., 2006; Macdonald and Fenniak, 2007; Chávez and Macdonald, 2010). However, very few of these differences were observed in the underplanted stands I studied. This is most likely due to the age of the underplanted white spruce, and not of the potential of white spruce to act as an ecosystem engineer in these stands. Previous studies comparing the differences related to canopy composition were conducted in mixedwood stands in which the white spruce had grown up into the mature aspen canopy. These full grown white spruce would have a greater influence on light levels and shed a greater amount of litter, having a greater influence on the understory environmental conditions. In addition, these full grown white spruce would have been present in the stands for a longer, having a possible cumulative effect over time.

Differences were observed in understory plant species composition between plots 0-1m and 1-2 m from the base of underplanted white spruce in 4-5 year old stands but not in 10 and 15 year old stands, which was unexpected. These results from the randomized complete block PERMANOVAs were not visually evident in NMS ordinations of plant species composition. Significant differences would not observed between the 0-1 m and 1-2 m plots in the 10 and 15 year old stands if the understory plant species composition in both unplanted plots had similar changes from the aspen plots; results from the one-way PERMANOVAs (Table 2.2) and the NMS ordinations (Figure 2.5 and Figure 2.6) did not indicate this. It was possible that differences observed only in the 4-5 year old stands were a legacy of disturbance from the original underplanting.

Differences in pH and total nitrogen microbial biomass of the forest floor between plot locations at the base of the underplanted white spruce and 1-2 m from the tree by 16 years after underplanting (forest floor analysis conducted one year after the rest of the study), indicate that white spruce do have an influence on the below-ground processes in these stands. The exact age at which these effects begin to occur is unknown though, as I did not do these analyses in the five and 10 year old stands. Soil moisture and temperature were only measured as single point measurements. It is possible that if diurnal or seasonal measurements were taken, differences may be observed. Light levels were not studied in these young underplanted stands but, based on the small heights and crown radii of the trees, it is likely there is little impact to understory light levels and any potential decreases in light would be limited to a small area right at the base of the spruce. As the underplanted white spruce grow larger, reducing light levels and shedding more litter, and more time elapses, it is possible more changes will be observed in these stands. This theory is addressed further in Chapter 3.

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Figure 2.1: Map showing study site locations. Stands with 4-15 year old underplanted white spruce were studied in Calling Lake and Lac La Biche, Alberta (Chapter 2) and stands with 48 year old underplanted white spruce were studied in Edson, Alberta (Chapter 3). (Map source: http://www.edzimkulu.org/who_we_are/edmonton.html)

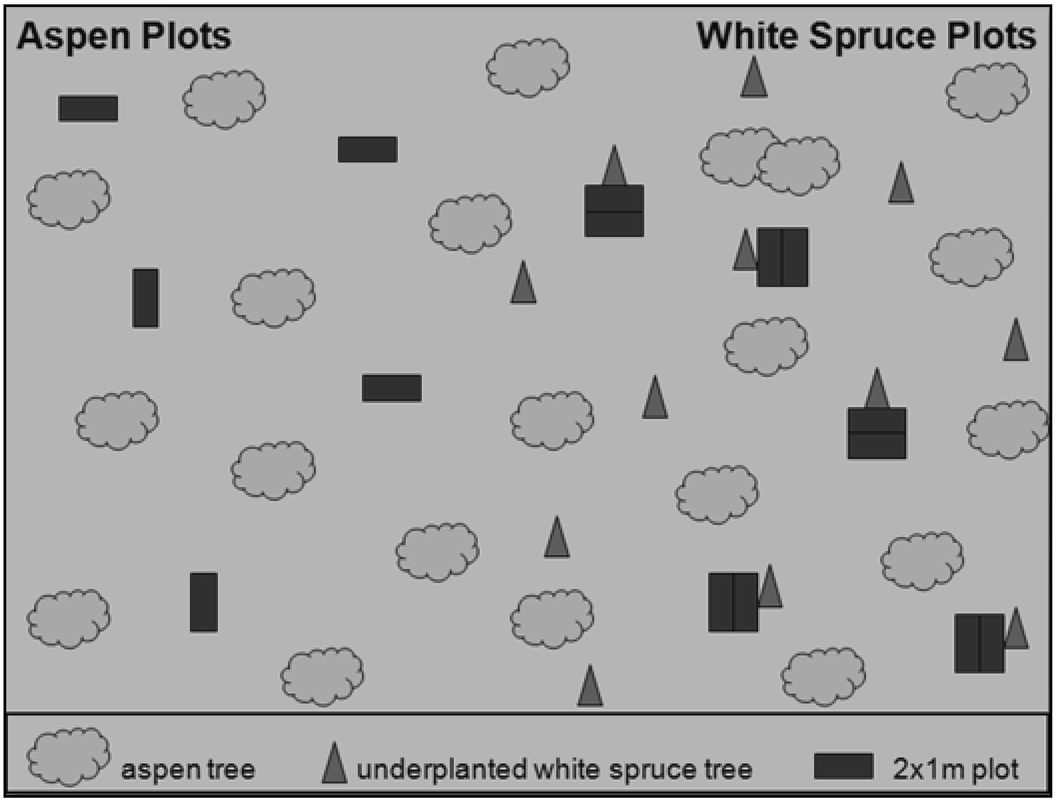

Figure 2.2: Example of plot layout within each stand. Note that within each stand of 5 year old underplanted white spruce, plots were established at 7-8 trees and an equivalent number of aspen plots were also established. Tree densities and graphics are not to scale.

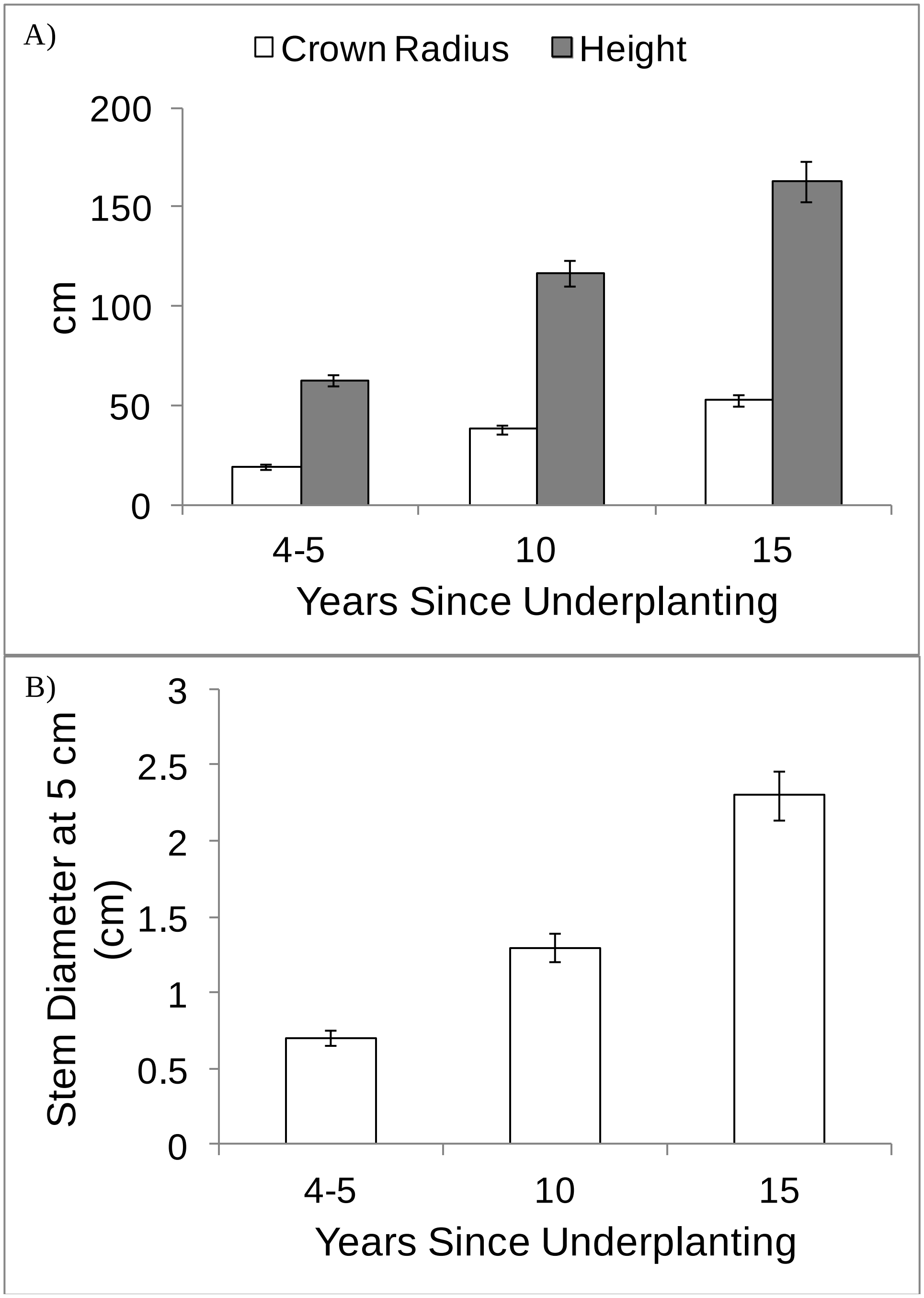

Figure 2.3: Mean crown radius and height (A) and mean stem diameter at 5 cm (B) of underplanted white spruce by years since planting. Bars represent standard error of the mean.

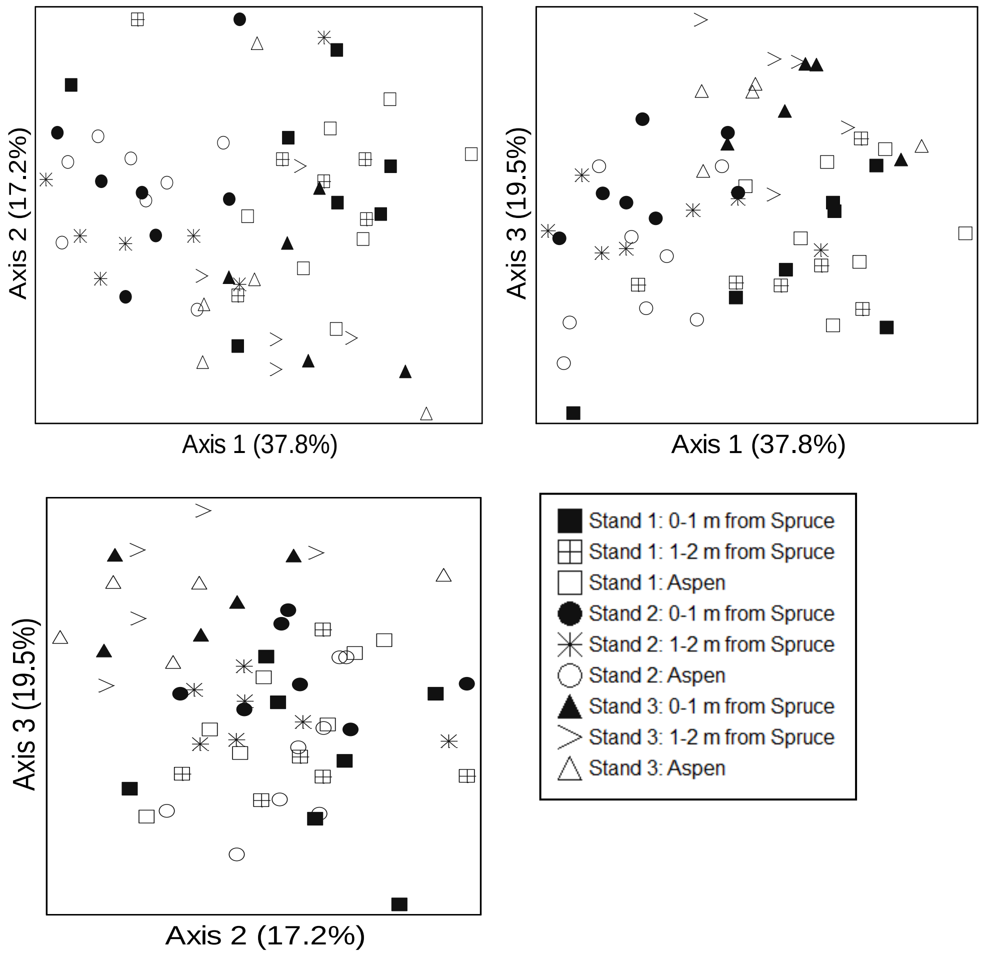

Figure 2.4: Results of a three-dimensional nonmetric multidimensional scaling (NMS) ordination of understory plant species in stands with 4-5 year old underplanted white spruce. The Sørenson distance measure was used. The percent of variation explained by each axis presented in parentheses. Stress=17.675.

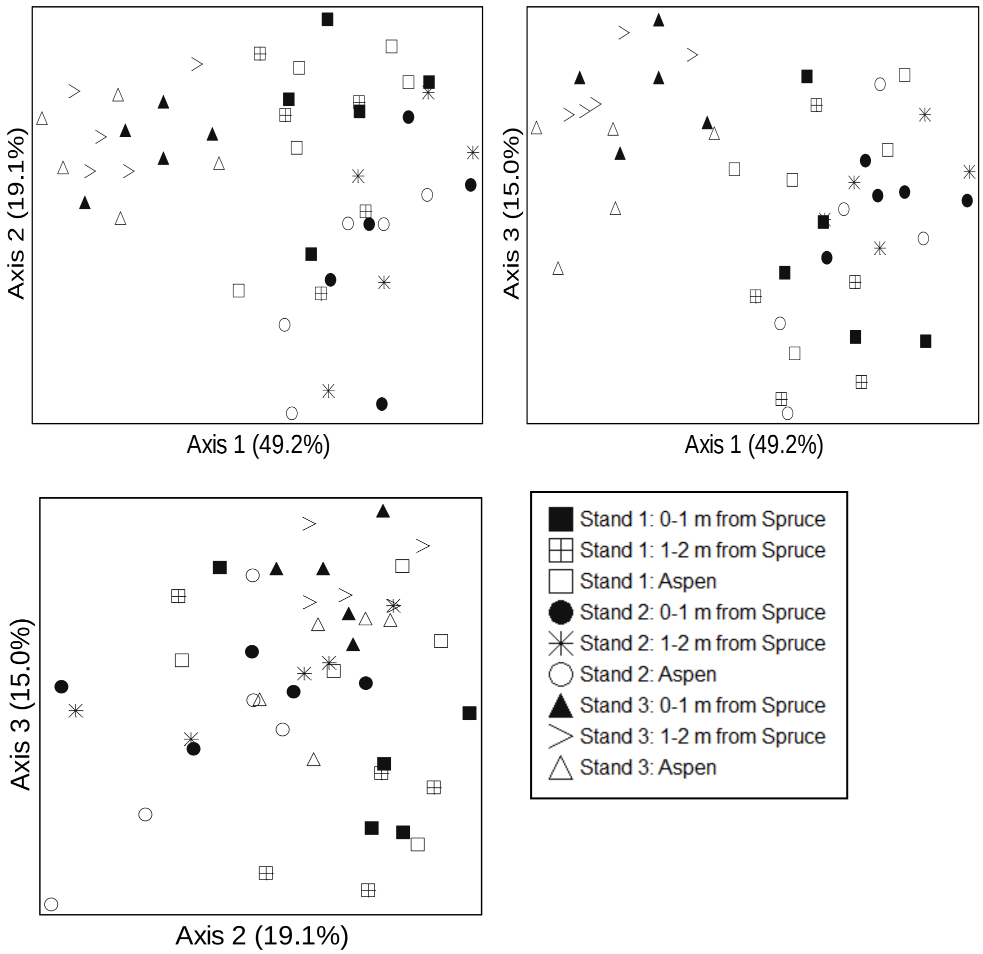

Figure 2.5: Results of a three dimensional nonmetric multidimensional scaling (NMS) ordination of understory plant species in stands with 10 year old underplanted white spruce. The Sørenson distance measure was used. The percent of variation explained by each axis presented in parentheses. Stress=13.849.

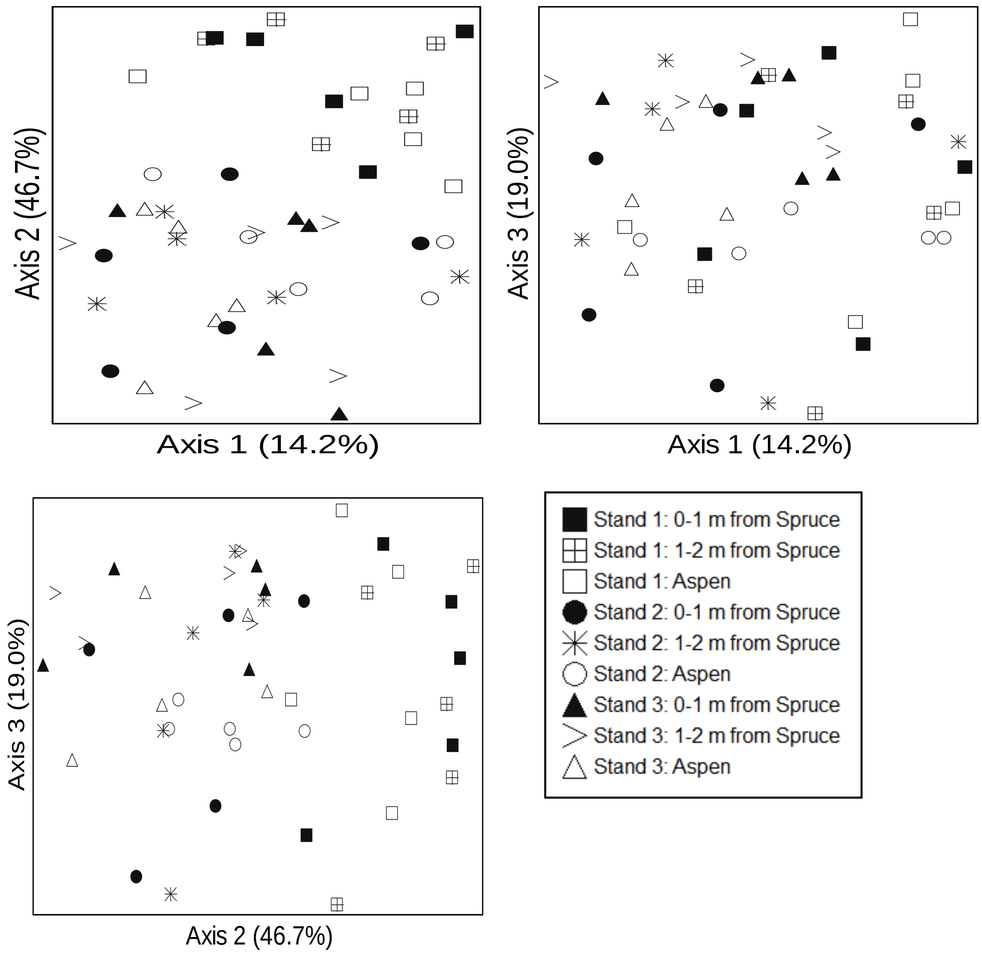

Figure 2.6: Results of a three-dimensional nonmetric multidimensional scaling (NMS) ordination of understory plant species in stands with 15 year old underplanted white spruce. The Sørenson distance measure was used. The percent of variation explained by each axis presented in parentheses. Stress=15.200.

Table 2.1: Least square mean values of (A) environmental variables and (B) vegetation/diversity measures (95% confidence intervals in brackets). P-values of non-blocked and blocked ANOVAs are presented*. Significant p-values in bold.

	Years Since Underplanting	0-1 m from Spruce	1-2 m from Spruce	Aspen	P-value (non-blocked)	P-value (blocked)
(A)						
Decomposition (% loss of cellulose)	4-5	48.77 *(21.50-76.05)*	38.04 *(10.57-65.51)*	47.41 *(20.13-74.69)*	0.432	0.113
	10	54.58 *(36.23-72.93)*	47.02 *(28.67-65.37)*	27.29 *(8.94-45.64)*	0.093	0.458
	15	39.73 *(16.30-63.17)*	48.98 *(25.54-72.41)*	32.71 *(9.28-56.15)*	0.329	0.363
Soil Moisture (m^3m^{-3})	4-5	0.10 *(0.08-0.12)*	0.10 *(0.08-0.12)*	0.10 *(0.08-0.12)*	0.996	0.960
	10	0.14 *(0.09-0.18)*	0.13 *(0.09-0.18)*	0.13 *(0.08-0.18)*	0.813	0.995
	15	0.18 *(0.11-0.26)*	0.20 *(0.12-0.27)*	0.20 *(0.13-0.27)*	0.552	0.333
Litter Depth (cm)	4-5	1.87 *(1.60-2.13)*	1.78 *(1.52-2.05)*	1.87 *(1.60-2.13)*	0.790	0.544
	10	2.21 *(1.75-2.67)*	2.09 *(1.63-2.55)*	2.34 *(1.88-2.81)*	0.595	0.194
	15	1.71 *(1.30-2.12)*	1.60 *(1.19-2.01)*	1.69 *(1.28-2.10)*	0.856	0.116
FH Depth (cm)	4-5	5.06 *(4.21-5.91)*	5.38 *(4.53-6.23)*	5.89 *(5.04-6.74)*	0.266	0.544
	10	7.96 *(5.91-10.00)*	6.63 *(4.59-8.86)*	7.04 *(5.00-9.09)*	0.407	0.070
	15	7.24 *(4.02-*	7.53 *(4.31-*	7.24 *(4.02-*	0.867	0.621

		10.47)	*10.76)*	*10.47)*		
Soil Temperature (°C) at 5 cm	10	11.61 *(11.27-11.96)*	11.58 *(11.24-11.93)*	11.55 *(11.21-11.90)*	0.929	0.860
	15	12.42 *(11.62-13.21)*	12.31 *(11.52-13.10)*	12.32 *(11.53-13.11)*	0.818	0.612
Soil Temperature (°C) at 10 cm	10	11.31 *(11.04-11.58)*	11.18 *(10.91-11.46)*	11.27 *(11.00-11.54)*	0.667	0.381
	15	11.95 *(11.19-12.71)*	11.94 *(11.18-12.70)*	11.89 *(11.13-12.65)*	0.910	0.949
Total N (mg/10 cm^2)	4-5	6.74 *(4.46-9.02)*	7.42 *(5.23-9.60)*	6.80 *(4.62-8.99)*	0.811	0.577
	10	6.87 *(2.72-11.02)*	6.69 *(2.54-10.85)*	7.35 *(3.20-11.51)*	0.908	0.919
	15	4.83 *(2.85-6.80)*	5.92 *(3.94-7.90)*	6.47 *(4.49-8.44)*	0.332	0.324
NO_3^--N (mg/10 cm^2)	4-5	4.59 *(0.06-9.13)*	2.65 *(0-7.18)*	2.42 *(0-6.95)*	0.549	0.429
	10	3.77 *(0-7.67)*	3.73 *(0-7.64)*	4.21 *(0.30-8.11)*	0.923	0.980
	15	2.27 *(1.03-3.50)*	2.35 *(1.12-3.59)*	3.24 *(2.00-4.47)*	0.332	0.896
NH_4^+-N (mg/10 cm^2)	4-5	4.42 *(2.41-6.43)*	4.71 *(2.73-6.69)*	4.38 *(2.40-6.37)*	0.940	0.750
	10	3.10 *(2.06-4.14)*	2.96 *(1.92-4.00)*	3.15 *(2.10-4.19)*	0.936	0.803
	15	2.56 *(0.91-4.21)*	3.57 *(1.92-5.22)*	3.23 *(1.58-4.88)*	0.532	0.171

Ca (mg/10 cm^2)	4-5	1526.70 *(910.33-2143.07)*	1477.26 *(860.89-2093.63)*	1528.57 *(912.20-2144.94)*	0.805	0.562
	10	1581.55 *(992.41-2170.68)*	1519.99 *(930.85-2109.12)*	1403.92 *(814.78-1993.06)*	0.228	0.499
	15	1556.79 *(957.45-2156.13)*	1579.73 *(980.39-2179.07)*	1447.19 *(847.85-2046.53)*	0.515	0.824
Mg (mg/10 cm^2)	4-5	308.00 *(149.50-466.50)*	309.77 *(151.27-468.27)*	307.45 *(148.95-465.95)*	0.991	0.917
	10	332.56 *(48.41-616.71)*	307.05 *(22.90-591.20)*	331.80 *(47.65-615.95)*	0.750	0.340
	15	191.11 *(141.16-241.05)*	184.60 *(134.66-234.54)*	191.84 *(141.90-241.78)*	0.832	0.587
P (mg/10 cm^2)	4-5	20.29 *(14.18-26.41)*	19.69 *(13.57-25.81)*	18.59 *(12.47-24.71)*	0.847	0.824
	10	24.23 *(16.78-31.68)*	21.43 *(13.98-28.88)*	18.37 *(10.92-25.82)*	0.392	0.528
	15	22.18 *(6.82-37.54)*	23.63 *(8.27-38.98)*	22.62 *(7.26-37.98)*	0.948	0.750
K (mg/10 cm^2)	4-5	363.52 *(63.72-663.31)*	408.59 *(108.80-708.39)*	378.85 *(79.05-678.64)*	0.763	0.444
	10	217.97 *(123.04-312.91)*	161.96 *(67.02-256.90)*	246.57 *(151.64-341.51)*	0.311	0.091
	15	308.39 *(166.57-450.20)*	289.98 *(148.16-431.80)*	313.56 *(171.74-455.38)*	0.933	0.570
Forest Floor pH	15	5.61 *(5.05-6.16)*	5.39 *(4.83-5.94)*	5.40 *(4.84-5.96)*	0.513	**0.006**
Microbial Biomass	15	22.44 *(16.85-*	18.73 *(13.13-*	20.27 *(14.68-*	0.490	0.129

NPOC (mg C/ g dry FF)		*28.04)*	*24.32)*	*25.87)*		
Microbial Biomass TN (mg N/ g dry FF)	15	5.18 *(4.10-6.27)*	4.25 *(3.17-5.34)*	4.49 *(3.41-5.57)*	0.320	**0.040**

(B)

Total Cover (%)	4-5	84.13 *(73.20-95.06)*	83.04 *(72.12-93.97)*	85.88 *(74.95-96.81)*	0.880	0.795
	10	69.37 *(56.06-82.68)*	69.83 *(56.52-83.14)*	74.83 *(61.52-88.14)*	0.467	0.911
	15	78.05 *(58.79-97.31)*	72.30 *(53.04-91.56)*	87.30 *(68.04-106.56)*	0.135	0.373
Total Richess/Plot (# species/ 2 m^2)	4-5	20.74 *(18.98-22.51)*	21.08 *(19.31-22.85)*	22.29 *(20.52-24.06)*	0.294	0.556
	10	19.67 *(17.23-22.10)*	19.67 *(17.23-22.10)*	18.20 *(15.76-20.64)*	0.466	1.000
	15	17.00 *(12.62-21.38)*	17.53 *(13.15-21.91)*	18.20 *(13.82-22.58)*	0.437	0.530
Shrub Richness/Plot (# species/ 2 m^2)	4-5	3.69 *(2.30-5.09)*	3.49 *(2.10-4.89)*	4.14 *(2.75-5.54)*	0.359	0.580
	10	3.53 *(1.57-5.49)*	3.40 *(1.44-5.36)*	3.00 *(1.04-4.96)*	0.489	0.762
	15	2.73 *(1.50-3.96)*	2.67 *(1.44-3.90)*	3.27 *(2.04-4.50)*	0.286	0.846

Herb Richness/Plot (# species/ 2 m^2)	4-5	11.65 *(10.58-12.71)*	12.13 *(11.07-13.20)*	11.94 *(10.88-13.01)*	0.692	0.252
	10	11.67 *(10.06-13.28)*	11.80 *(10.19-13.41)*	11.13 *(9.52-12.74)*	0.712	0.861
	15	10.13 *(6.47-13.80)*	10.60 *(6.93-14.27)*	11.20 *(7.53-14.87)*	0.309	0.501
Shannon's Diversity Index	4-5	2.49 *(2.30-2.68)*	2.56 *(2.37-2.75)*	2.58 *(2.39-2.77)*	0.327	0.211
	10	2.36 *(2.15-2.57)*	2.41 *(2.20-2.62)*	2.31 *(2.10-2.52)*	0.573	0.589
	15	2.36 *(2.11-2.61)*	2.34 *(2.09-2.59)*	2.43 *(2.18-2.68)*	0.358	0.697
Simpson's Diversity Index	4-5	0.90 *(0.86-0.94)*	0.90 *(0.87-0.94)*	0.90 *(0.87-0.94)*	0.708	0.470
	10	0.88 *(0.84-0.92)*	0.88 *(0.84-0.93)*	0.87 *(0.82-0.91)*	0.585	0.905
	15	0.89 *(0.86-0.92)*	0.88 *(0.85-0.92)*	0.89 *(0.86-0.92)*	0.781	0.704
Whittaker's β Diversity Index	4-5	0.26 *(0.20-0.36)*	0.28 *(0.17-0.34)*	0.20 *(0.12-0.29)*	0.056	-
	10	0.24 *(0.01-0.46)*	0.25 *(0.02-0.47)*	0.31 *(0.09-0.53)*	0.802	-
	15	0.24 *(0.11-0.36)*	0.26 *(0.13-0.38)*	0.29 *(0.16-0.41)*	0.636	-

* For the non-blocked ANOVAs all three plot locations (0-1 m from spruce, 1-2 m from spruce and aspen) were included in the analysis, treating stand as the experimental unit and plots within a stand as subsamples. The non-blocked ANOVAs were performed to test for differences between underplanted areas and non-underplanted areas of the stands. For the blocked ANOVAs only plots 0-1 m and 1-2 m from the spruce were analyzed and were blocked at the underplanted

white spruce tree with plots representing the treatment effect of the two distances from the underplanted tree. Blocked ANOVAs were performed to test for differences related to distance from the underplanted white spruce.

Table 2.2: Results from one-way PERMANOVAs comparing understory plant species composition between (A) 0-1 m from spruce plots and aspen plots, and (B) 1-2 m from spruce plots and aspen plots for each age of underplanted white spruce.

	Years Since Underplanting	DF	SS	MS	F-value	P-value
(A) 0-1 m vs Aspen						
	4-5					
Plot Location		1	0.14222	0.14222	1.0022	0.4376
Residual		28	3.9733	0.14190		
Total		29	4.1155			
	10					
Plot Location		1	0.18977	0.18977	1.0051	0.4018
Residual		28	5.2868	0.18881		
Total		29	5.4766			
	15					
Plot Location		1	0.11509	0.11509	0.77588	0.6634
Residual		28	4.1535	0.14834		
Total		29	4.2686			
(B) 1-2 m vs Aspen						
	4-5					
Plot Location		1	0.10549	0.10549	0.75012	0.7026
Residual		28	3.9375	0.14063		
Total		29	4.0430			
	10					
Plot Location		1	0.17405	0.17405	0.88374	0.4986
Residual		28	5.5145	0.19695		
Total		29	5.6885			
	15					
Plot Location		1	0.15230	0.15230	1.0153	0.4156
Residual		28	4.2002	0.15001		
Total		29	4.3525			

Table 2.3: Results of a randomized complete block PERMANOVA comparing understory plant species composition in relation to the distance from the underplanted white spruce for each age of underplanted white spruce. Significant p-value (α=0.05) is in bold.

	Years Since Underplanting	DF	SS	MS	F-value	P-value
	4-5					
Spruce Tree		14	3.3107	0.23648	4.9676	0.0002
Plot Location		1	0.10020	0.10020	2.1047	**0.0240**
Residual		14	0.66646	0.476E-01	4.0774	
Total		29				
	10					
Spruce Tree		14	4.8628	0.34734	9.3566	0.0002
Plot Location		1	0.287E-01	0.287E-01	0.77350	0.6458
Residual		14	0.51972	0.3712E-01		
Total		29	5.4112			
	15					
Spruce Tree		14	4.0621	0.29015	8.0697	0.0002
Plot Location		1	0.309E-01	0.309E-01	0.86085	0.5920
Residual		14	0.50338	0.359E-01		
Total		29	4.5964			

CHAPTER 3:

EFFECTS OF UNDERPLANTED WHITE SPRUCE ON UNDERSTORY VEGETATION AND ENVIRONMENT 48 YEARS AFTER UNDERPLANTING

Introduction

In Chapter 2 I examined the potential of 'young' underplanted white spruce (4-15 years old) to influence the understory environmental conditions and vegetation in the forest understory. By 15 years after underplanting, changes were limited to the forest floor, with both pH and microbial total nitrogen content increased within one meter of the underplanted white spruce when compared to plots 1-2 m from the tree. No differences were observed in the soils or understory vegetation of these stands. In Chapter 3 I expand upon the research conducted in Chapter 2. A literature search of comparisons between natural mixedwoods and broadleaf stands (see Chapter 1) showed more differences in understory environmental variables than I observed in these young underplanted stands and also showed differences in the understory vegetation. The goal of this chapter was to determine if older underplanted stands showed more differences in terms of understory environment and vegetation between unplanted and underplanted areas and as a function of distance from the underplanted spruce than were seen in younger underplanted stands.

While one of the main ecological focuses of present-day underplanting is attempting to emulate a natural pattern of boreal succession, this focus only became more prevalent in the 1990s. During the 1960s when trials of underplanting white spruce in aspen stands began in western Canada, the focus was on adding a commercially valued species to an aspen landbase - that was not considered economically valuable - with as little effort and cost as possible. The stands studied in this chapter were part of trials conducted by the Federal Forest Research Branch and the Alberta Forest Management Branch to explore this management approach. Trials such as these were abandoned during the 1970s and 1980s in favor of single-species management, therefore there was a large gap in the age of trials of underplanted white spruce that were available to be studied.

In this chapter I compare the understory environment and vegetation between areas underplanted with white spruce and non-underplanted areas in aspen-dominated stands that were underplanted 48 years prior (because trees were initially grown in a nursery, true tree age was 49-50 years old). The primary objectives of this study were: i) to determine if underplanting changed the understory environmental conditions (i.e., forest floor, soil and light properties) and the understory vegetation 48 years after underplanting; and ii) if changes occurred, how these changes varied with distance from underplanted white spruce.

Methods

Study Area

Research for this study was conducted in the Lower Foothills Natural Subregion of West-central Alberta, Canada near Edson (53°N, 116°W, 927 m above sea level) (Figure 2.1). The area is characterized by a subhumid and continental climate with short, mild summers and long, cold winters. The mean May-August temperature is 12.5°C and the mean November-February temperature is -9.6°C (Environment Canada, 2011). The mean annual precipitation is 562 mm, about 70% of which occurs as rainfall during summer (Environment Canada, 2011). In the Edson area, about 70% of the soils have developed on till deposits of Continental and Cordilleran origin, with the rest having developed on lacustrine, alluvial, aeolian and residual parent material (Macyk et al., 1973). Due to a wide variation in parent materials, topography and climate, soil profiles are variable but generally include Gray Luvisolic soils with smaller amounts of Brunisols and Podzols (Macyk et al., 1973).

Site Selection and Study Design

Research was conducted in three aspen-dominated stands (Marlboro, Sundance Creek and Swanson Road) which were underplanted with white spruce in 1962 by the Federal Forest Research Branch and the Alberta Forest Management Branch (Duffy, 1963; Appendix 1). Underplanted stands were aspen-dominated, with the aspen ranging from 64 to 73 years old at the time of planting. Sites received no mechanical site preparation before planting. Within each stand a one hectare block was underplanted. This one hectare block was subdivided into nine compartments. These nine compartments were planted using one of the following spacing treatments: 9’x9’, 12’x12’ or 15’x15’, with each spacing treatment replicated three times. See Duffy (1963) for more details about the original study setup and plot layout design. As part of the continued monitoring of these stands, one 11.28 m radius permanent sampling plot had been established at the center of each of the nine compartments within the one hectare underplanting block.

The Marlboro stand was on a landform comprised of glacial fluvial and reworked till material, and had a moderate understory ground cover at the time of underplanting (as reported by Duffy, 1963). The Sundance Creek stand was on a glacial fluvial landform and had a light understory ground cover at the time of underplanting (Duffy, 1963). Scattered white spruce (51 years old, just over 20 m in height) were present in the Sundance Creek stand before underplanting. The Swanson Road stand was on a stony till landform and had a heavy understory ground cover at the time of underplanting (Duffy, 1963). All three stands had minimal slope.

I established plots in these stands during the summer of 2010. At this time the underplanted white spruce were 48 years old. To determine if underplanting white spruce changed the understory environment and vegetation, 2x1 m plots were established in both the underplanted area (spruce plots) and the non-underplanted area (aspen plots) of each stand. Two of the stands had areas that were left unplanted, in which I established reference (aspen forest) plots. In the Swanson Road stand there was no area left unplanted in which reference plots could be established. Instead, the reference aspen plots were placed within the stand in areas where white spruce seedlings had not established. Reference plots were established in these aspen patches when the area without white spruce had a diameter greater than twice the height of the surrounding underplanted white spruce trees. Aspen plots were selected to avoid large amounts of downed wood, edges created by disturbance such as cutlines and a gravel pit, the direct base of any broadleaf trees, and slopes and depressions unrepresentative of the condition of the majority of the stand. These aspen plots were essentially placed in areas that would have been underplanted with white spruce if the entire stand had of been underplanted. Ten aspen plots were established in each stand.

To address whether changes in environmental variables and vegetation varied with distance from the underplanted spruce, the spruce plots were established contiguously (0-1, 1-2, 2-3 and 3-4 m from the base) at underplanted white spruce trees (Figure 3.1). Spruce plots were established at ten trees in each stand. A combined total of 30 spruce trees and 120 spruce plots were sampled in all three stands. Plots were established at spruce trees where the distance to the next underplanted tree was at least twice as far as the contiguous plots distance (i.e., at least 8 m). I only established plots at spruce trees in the 12’x12’ and 15’x15’ spacing compartments because the dense spacing in the 9’x9’ made it too difficult to find areas with at least 8 m between spruce trees. Cardinal direction was not considered when determining direction of the plots outward from the base of the white spruce because all stands were relatively flat upland sites with little slope. The same set of criteria used to set up the spruce plots was used to set up the aspen plots (avoiding large amounts of downed wood, edges created by linear features, the direct base of any broadleaf trees, and slopes and depressions unrepresentative of the condition of the majority of the stand).

Data Collection

Data collection in these stands with 48 year old underplanted white spruce was conducted similarly to that done in the stands with 4-15 year old underplanted white spruce (Chapter 2), with the following notable exception: photosynthetically active radiation (PAR) measurements were taken at a subset of these plots but were not measured in the young underplanted stands.

Vegetation

Within each of the 150 2x1 m plots, I recorded the percent cover of each species of vascular plants and bryophytes. Percent cover estimates were recorded within 0.25% for estimates up to 20%, within 0.5% for estimates up to 40%, and within 2.5% for estimates above 40%. For species with percent cover between 0-0.25%, percent cover was recorded as <0.25%; these were later changed to 0.01% for data analysis. Vegetation surveys were conducted between July 12-30, 2010.

Nomenclature followed Moss (1983).

Height, diameter at breast height (dbh) and crown radius (in the direction of the plots) were measured for each white spruce at which spruce plots were established. To characterize the overstory of the stands, I re-sampled the 11.28 m radius permanent sampling plots that were established as part of the original underplanting study. All trees and snags occurring within these plots were measured for height and dbh, and species and condition were recorded. I only measured the permanent sampling plots located within the 12’x12’ and 15’x15’ compartments because these were the compartments where I established 2x1 m plots. Each stand contained three plots within the 15’x15’ spruce spacing and three plots within the 12’x12’ spruce spacing. I established three additional plots within the aspen areas of each of the stands, with the exception of the Sundance Creek stand where only two plots were established because of limited space. These plots were established to compare stand characteristics in the unplanted areas to stand characteristics of the underplanted areas measured in the permanent sampling plots.

Soil Moisture and Temperature

I measured soil moisture and temperature once during the summer. Soil moisture measurements were taken between July 27 and August 3, 2010. Moisture measurements were taken at a 5 cm depth in the mineral soil with a ML2x ThetaProbe soil moisture sensor attached to a HH2 moisture meter (Delta-T

Devices, Cambridge, UK), at least two days after a major rain event. Soil temperature measurements were taken between July 15-27, 2010. Temperature measurements were taken with a 450ATT digital soil thermocouple thermometer (Omega, Laval, PQ, Canada) at 5, 10 and 15 cm depths in the mineral soil. Since a spot measurement was taken, this was done between 12h00-16h00 MST to obtain the peak soil temperature (Stathers and Spittlehouse, 1990). Two soil moisture and two soil temperature measurements were taken in each of the 150 2x1 m plots. Measurements were evenly spaced across the two meter width of the plot, with the moisture and temperature measurements being taken at the same locations. Measurements were averaged at the plot level to give a single soil moisture value and a single soil temperature value for each plot.

Litter and Organic Layer

Litter and organic layer (combined F and H layers) depths were measured at the beginning of August 2010. Two measurements were taken in each of the 150 2x1 m plots and averaged at the plot level. Measurements were taken at the same locations as the soil moisture and temperature readings.

Decomposition

Decomposition in each of the plots were measured using five 15 cm diameter Whatman No. 1 cellulose filter papers enclosed in mesh bags of 1.5 mm x 1.5 mm mesh size. I placed the decomposition bags at the interface between the forest floor and mineral soil. Initially I dried a subset of the filter papers in a

70°C drying oven for 48 hours and then weighed them to determine the average weight of a filter paper before being placed in the ground. The decomposition bags were placed in the field during the middle of June 2010 and removed at the end of August 2010. After removal, the decomposition bags were dried at 70°C for 48 hours, weighed and then the percent loss of the cellulose filter paper determined.

Soil Nutrients

Soil nutrients were measured using Plant Root Simulator^{TM} (PRS^{TM}) probes (Western Ag. Innovations Inc., Saskatoon, SK, Canada), which contained ion-exchange membranes. The PRS^{TM}-probes were installed vertically in the mineral soil of plots with the top of the membrane at the mineral-organic horizon interface. I installed the PRS^{TM}-probes during the middle of June 2010 and removed them at the end of August 2010. Three anion and three cation probes were installed in each plot, and analyzed for NO_3^--N, NH_4^+-N, P, K, S, Ca, Mg, Al, Fe, Mn, Cu, Zn, B, Pb and Cd. Analysis of the PRS^{TM}-probes was conducted by Western Ag Innovations Inc.

Photosynthetically Active Radiation

Measures of photosynethically active radiation (PAR) were taken with a ceptometer (Decagon AccuPAR v3.3 and Sunfleck PAR Ceptometer Model SF-80) during July and August 2010. Within each stand I took measurements at 6-7 of the 10 white spruce trees where 2x1 m plots were established and at an equivalent number of aspen plots. I did not include every tree and plot due to time constraints. Measurements were taken at ground level, 0.5 m and 1.3 m over 0.5 m intervals outward from the base of the white spruce, and at the same three heights at the center and opposite sides of the aspen plots. Measurements of full light were also taken in openings. Because measurements were taken under variable sky conditions, and not under ideal uniformly overcast days, all measurements were taken three times a day (morning: ~07h30-10h30 MST, midday: ~10h30-14h00 MST, and afternoon: ~14h00-16h30 MST), once a week for three weeks and averaged. Final PAR values were expressed as a percentage of full light. The measurements could not be taken during the final week in the Marlboro stand because of equipment failure.

Forest Floor pH

I collected FH-layer forest floor samples from each of the 150 2x1 m plots at the end of August 2010. From each plot three subsamples of FH-layer forest floor were collected to the depth of the mineral soil surface and aggregated for the plot. Samples were sieved to 2 mm and stored at 4°C until analyzed. All samples were analyzed within a few days of collection. The pH was measured potentiometrically using a 1:4 soil to 0.01 M $CaCl_2$ ratio (Kalra and Maynard, 1991).

Forest Floor Microbial Biomass

Sieved forest floor samples collected at the end of August 2010 were also analyzed for microbial carbon and nitrogen content using the chloroform fumigation procedure (Brooks et al., 1985; Vance et al., 1987). I divided each of the 150 samples into five subsamples for different parts of the analysis. Two subsamples of five grams of fresh forest floor from each sample were fumigated for 24 hours and then extracted with 50 ml of 0.5M K_2SO_4. Another two subsamples were immediately extracted without being fumigated. A fifth subsample was weighed, then dried at 107°C for 48 hours, and reweighed. All extractions were completed within three weeks of the samples being collected. The extracts were stored at -20°C until submitted to the Natural Resources Analytical Laboratory at the University of Alberta for analysis of non-purgeable organic carbon (NPOC) and total nitrogen (TN). I calculated microbial biomass carbon and nitrogen from the difference between the fumigated and unfumigated subsamples. Because comparisons were made within a stand of the same forest floor substrate and no comparisons were made between different soil types, no correction factor was used (Leckie et al., 2004). Final measurements were expressed on a dry weight basis.

Data Analysis

Cover values for vegetation species were summed to calculate total percent cover for each plot. I also calculated the following for each 2m^2 plot: total richness, shrub richness, herb richess, Shannon's Diversity Index (Shannon and

Weaver, 1949), and Simspon's Diversity Index (Simpson, 1949). Shannon's Diversity Index takes into account both species richness and evenness, while Simpson's Diversity Index places less weight on rare species than Shannon's. Whittaker's beta diversity measure (Whittaker, 1972) was used to calculate species turnover among plot locations (0-1, 1-2, 2-3 and 3-4 m from spruce, and aspen) within a stand:

$$\beta_w = (\gamma/\alpha) - 1$$

where γ is total species richness per stand and α is mean species richness per plot location.

To determine the influence of underplanting and plot location in relation to distance from the underplanted tree on the understory environment and vegetation, I performed mixed-model analyses of variance (ANOVAs; PROC MIXED in SAS v. 9.2; SAS Institute, 2008), testing the following variables: soil temperature and moisture; litter and FH depth; decomposition; soil nutrients; PAR; soil pH; soil microbial biomass; total, shrub and herb cover; total, shrub and herb richness; and Shannon's, Simpson's and Whittaker's Diversity. Before ANOVAs were performed, I tested residuals of the data for normality (Kolgorov-Smirnov) and homogeneity of variance (Levene's test), and transformed data where appropriate to meet assumptions. Two sets of ANOVAs were run to address the following two questions:

1) Do the understory environmental and vegetation variables differ between the underplanted areas and the non-underplanted areas of the

stands?

2) Do the understory environmental and vegetation variables differ in relation to distance from underplanted white spruce?

In the ANOVAs comparing the underplanted to the non-underplanted areas (non-blocked ANOVA) the stand was the experimental unit and plot within a stand were treated as subsamples:

$$\mu = L_i + S_j + R_k(L_i{*}S_j) + \varepsilon$$

where *L* is the plot location (*i* = 1-2, fixed), *S* is the stand (*j* = 1-3, random), *R(S*L)* is the replicate within a plot location and stand (*k* = 1-40, random), and ε is the experimental error. Non-blocked ANOVAs were performed comparing all five plot locations (0-1, 1-2, 2-3 and 3-4 m from spruce, and aspen) without blocking the spruce plots at the common underplanted tree. This was done to compare the underplanted plots (0-1, 1-2, 2-3 and 3-4 m combined) to the non-underplanted plot (aspen).

ANOVAs were also conducted to examine the influence of distance from a underplanted white spruce tree – in which case only the underplanted plot locations were used. A blocked ANOVA was used in which the white spruce tree was the block with the plots representing the treatment effect of the four distances from the underplanted tree:

$$\mu = L_i + S_j + T_l\,(S_j) + \varepsilon$$

where *L* is the plot location (*i* = 1-5, fixed), *S* is the stand (*j* = 1-3, random), *T(S)* is the tree nested within the stand (l = 1-10, random), and ε is the experimental error.

Blocked ANOVAs were performed to increase statistical power while non-blocked ANOVAs were performed to allow for comparison between the underplanted and non-underplanted areas. For significant (α=0.05) differences in the blocked ANOVAs, I conducted pairwise contrasts between each of the first three plot locations and the plot location furthest from the base of the spruce (i.e., 0-1 m vs 3-4 m, 1-2 m vs 3-4 m and 2-3 m vs 3-4 m) using a Bonferroni corrected significance of α=0.0167 to account for mulitple comparisons.

To examine variation in understory vegetation species composition at the different plot locations I performed nonmetric multidimensional scaling (NMS) ordinations using PC-ORD (v. 5.10; McCune and Mefford, 2006) with a Sørenson (Bray-Curtis) distance measure. NMS allows the patterns in species composition to be visualized, while the Sørenson distance measure of community similarity is suitable for ecological data. NMS ordinations were performed for each of three stands separately and included all plots (0-1, 1-2, 2-3 and 3-4 m from spruce, and aspen). For each NMS I initially completed 100 runs with real data and 100 runs with randomized data, starting with a six-dimensional solution and stepping down to a one-dimensional solution. Plots of stress versus iteration were used to assess stability of the solution (stability criterion=0.00001). Optimal number of dimensions (n=3) and best starting configurations were determined from the preliminary runs and then final NMS ordinations were performed using these.

To determine the influences of underplanting and of plot location in relation to distance from the underplanted tree on the understory vegetation composition, permutational multivariate analyses of variances (PERMANOVA) were performed using PC-ORD (v. 5.10; McCune and Mefford, 2006; Anderson, 2001), as data were not normally distributed. The PERMANOVAs were run using the understory vegetation species data with a Sørenson (Bray-Curtis) distance measure and 4,999 unrestricted permutations of the raw data. Like the ANOVAs, separate PERMANOVAs were run to address two questions:

1) Does the understory vegetation composition differ between the underplanted areas and the non-underplanted areas of the stands?

2) Does the understory vegetation composition differ in relation to distance from underplanted white spruce?

In the PERMANOVAs used to compare the underplanted to the non-underplanted areas, one-way PERMANOVAs were performed with replicates within plot location as the grouping variable. PERMANOVA cannot be used to analyze unbalanced data sets. Because of this, the four underplanted plot locations were not combined into a single underplanted group and compared against the non-underplanted aspen plots as was done with the ANOVAs.

Instead each underplanted plot location (0-1, 1-2, 2-3 and 3-4 m from the spruce) was compared to the non-underplanted aspen plots separately (α=0.05).

To compare the understory vegetation composition in relation to the distance from the underplanted white spruce, a randomized complete block PERMANOVA was performed treating the spruce tree as the block and with the plots representing the treatment effect of the four distances from the underplanted tree. For a significant (α=0.05) difference in the blocked PERMANOVA, I conducted contrasts between each of the first three plot locations and the plot location furthest from the base of the spruce (i.e., 0-1 m vs 3-4 m, 1-2 m vs 3-4 m and 2-3 m vs 3-4 m) using a Bonferroni corrected significance of α=0.0167 to account for mulitple comparisons.

To examine the relationship between the environmental variables and the understory species composition at different plot locations, distance-based redundancy analysis (db-RDA) was used. Distance-based redundancy analysis is a type of constrained ordination in which principal coordinates of a matrix of ecological distances are obtained from a Principal Coordinate Analysis (PCoA) and then used as the species data in a redundancy analysis (Legendre and Anderson, 1999). The principal coordinates are Euclidean distances and therefore can be analyzed with linear models. With a db-RDA there is no assumption of normality. I performed two db-RDAs using a Bray-Curtis distance ("capscale" function in "vegan" package in R, Oksanen et al., 2010). The first db-RDA included the species composition data from all 150 plots and all environmental data except for the PAR measurements. The second db-RDA included only the species and environmental data for the 100 plots at which PAR measurements were taken. For each db-RDA a preliminary run was conducted to see which environmental variables were significant (α=0.05). Axes were also tested for significance (α=0.05). Final runs were then performed using only significant axes and environmental variables.

Indicator species analysis (Dufrêne and Legendre, 1997) was used to detect whether the abundance and frequency of any of the understory vegetation species within each stand were strongly correlated with non-underplanted versus underplanted areas, or were correlated with plot location in relation to the underplanted spruce. Indicator species analysis was performed using PC-ORD (v. 5.10; McCune and Mefford, 2006). Analyses were performed (for each of the three stands separately) comparing the non-underplanted aspen reference to all underplanted plot locations combined and then comparing among distances from the underplanted white spruce. Indicator species analysis provided an indicator value for each species based on the fidelity and exclusivity of the species to a single, predetermined group (i.e., underplanted or non-underplanted or plot location distances from the underplanted white spruce). Indicator values of 20 or greater and $p<0.05$ were considered to be of ecological importance.

Results

The Edson stands were aspen-dominated with some balsam poplar and very small amounts of paper birch, lodgepole pine, black spruce and white spruce natural regeneration (Table 3.1). Because natural mortality was causing the main aspen canopies to open up, young aspen were regenerating in the understory, with more aspen regeneration in non-underplanted areas than in underplanted areas (Table 3.1). By 48 years after underplanting the mean stand height of white spruce ranged from 11.5 m to 13.4 m, the mean stand dbh ranged from 160.3 mm to 191.5 mm, and the mean stand crown radius ranged from 210.9 cm to 221.3 cm (Figure 3.2).

There were significant differences in environmental variables, and vegetation measures and diversity between underplanted and non-underplanted plots, and among underplanted plot locations at varying distances from the spruce (Table 3.2). When underplanted plots were compared to non-underplanted plots in the non-blocked ANOVAs, significant differences were observed in the litter and FH depths; soil temperature at 5 cm, 10 cm and 15 cm; soil sulphur; forest floor pH; PAR at 0.5 m and 1.3 m; total, shrub and herb cover; total and herb richness; and Shannon's Diversity Index. Soil sulphur, forest floor pH, and litter and FH depth increased in the underplanted areas while all other variables decreased.

When underplanted plot locations were compared at varying distances from white spruce in the blocked ANOVAs significant differences were observed for the following variables: litter and FH depths; soil temperature at 10 cm and 15 cm; soil sulphur; forest floor pH; PAR at 0.5 m and 1.3 m; total shrub and herb cover; total and herb richness; and Shannon's Diversity Index. The FH depth, soil sulphur and forest floor pH were higher in the plots 0-1 m from the base of white spruce than in the plots 3-4 m from the base of spruce. Litter depth was higher in the plots 0-1 m and 1-2 m from the base of spruce than in the plots 3-4 m from the base of spruce. Herb and total cover, herb and total richness, soil temperature at 10 cm and 15 cm, Shannon's Diversity Index were lower in the plots 0-1 m from the base of spruce than in the plots 3-4 m from the base of spruce. PAR measurements at 0.5 cm and 1.3 m, and shrub cover were lower in plots 0-1 m and 1-2 m from the base of spruce than in the plots 3-4 m from the base of spruce.

Soil potassium, microbial biomass nitrogen content, shrub richness and Simpson's Diversity Index were not found to be significantly different between underplanted and non-underplanted plots (unblocked ANOVAs). There were, however, signifance differences in these variables among different distances from the base of underplanted white spruce. Shrub richness and Simpson's Diversity Index were lower in the plots 0-1 m from the base of spruce than in the plots 3-4 m from the base of spruce. Despite significance differences in soil potassium ($p=0.047$) and microbial biomass nitrogen content ($p=0.034$) in the blocked ANOVAs, subsequent contrasts with a Bonferroni corrected α for the multiple comparisons showed no significant differences in plot distances from the base of spruce.

Visual examination of the NMS ordinations for the three stands indicated a separation of understory plant species composition in plots located 0-1 m from spruce trees from aspen plots and plots 2-3 and 3-4 m from spruce (Figure 3.3, Figure 3.4, Figure 3.5). The plots 2-3 m and 3-4 m out from spruce and aspen plots did not separate out from one another in the NMS ordinations, indicating no differences among the understory plant communities in these plots. The plots 1-2 m from spruce started to separate out from the plots 2-3 m and 3-4 m out from spruce, which indicated some differences starting to occur. The plots 1-2 m from spruce did not separate out as far as some of the 0-1 m plots, indicating that, while there were some changes in the 1-2 m plots, these changes were not as great as in the 0-1 m plots. A high amount of variation was explained by the three-dimensional solutions on the NMS ordinations (75.6-84.3% of total variation). The difference in understory plant species composition visualized between plot locations was confirmed statistically by the PERMANOVAs (Table 3.3 and Table 3.4). Comparison of understory plant species composition between underplanted plot locations and aspen plots showed the plots at 0-1 m ($p=0.0002$) and the plots at 1-2 m ($p=0.0024$) to be significantly different than aspen plots (Table 3.3). A comparison of understory plant species composition based on distance from the underplanted white spruce indicated species compositon differed between the plots at 0-1 m and 3-4 m ($p=0.0002$; Table 3.4).

Results from the two db-RDAs showed several environmental variables to be significantly correlated with understory species composition. The environmental variables found to be significantly correlated with understory species composition depended on whether or not PAR was included in the analysis. Litter and FH depth, mineral soil sulphur, magnesium and calcium, soil moisture, decomposition, microbial biomass nitrogen, and soil temperature at 5 cm were all significantly correlated with understory species composition regardless of whether or not PAR was included in the analysis (Figure 3.6 and Figure 3.7). When PAR was not included in the analysis, forest floor pH and soil temperature at 10 cm were also significantly correlated to the understory species composition (Figure 3.6). When PAR was included in the analysis, PAR at ground level and 50 cm, as well as soil temperature at 15 cm and iron were significantly correlated with the understory species composition (Figure 3.7). As with the NMS ordinations, the plots 0-1 m from the base of underplanted white spruce showed quite a bit of separation from the aspen plots. The some of the plots 1-2 m from the base of underplanted white spruce showed separation from aspen plots while other plots 1-2 m from spruce were intermixed with the aspen plots. The plots 1-2 m from spruce did not separate out as far as some of the plots 0-1 m from spruce. Environmental vectors in the db-RDAs indicated that litter and FH depths, and mineral soil sulphur were higher in the plots 0-1 m from the base of underplanted spruce (Figure 3.6 and Figure 3.7) while PAR at 50 cm was higher in the aspen plots and plots 2-4 m from underplanted spruce (Figure 3.7). Including PAR in the db-RDA increased the variance explained by the first and second axes from 11.2% to 17.7%.

Results of the Indicator Species Analysis showed a total of four indicator species for underplanted plots when compared to the reference aspen forest, with only one or two species being indicators in each stand (Table 3.5). *Viola renifolia* was the only indicator of underplanted plots for more than one stand. There were a total of 15 indicator species for the reference aspen plots, with 5-8 indicator species for each stand (Table 3.5). *Vicia americana* was an indicator of aspen plots in all three stands. *Symphoricarpos albus* and *Orthilia secunda* were indicators of aspen plots in two stands. The rest of the aspen indicator species were stand specific. Six species were shown to be indicators of the plot locations at varying distances from the underplanted white spruce (Table 3.6). *Pleurozium schreberi* was the only indicator of the plots 0-1 m from the base of spruce and was only an indicator in the Swanson Road stand. No species were indicators of the plots 1-2 m from the base of the spruce. Indicators of the plots 2-3 m from the base of spruce were only observed in the Marlboro stand, where two indicator species were present. Indicators of the plots 3-4 m from spruce were observed in all three stands, with 1-2 indicator species per stand, and only *Linnaea boreali*s observed in more than one stand.

Discussion

Results from this study suggest that white spruce are able to act as ecosystem engineers when underplanted in aspen-dominated boreal stands, changing understory environmental variables and vegetation. The capacity of white spruce to exert influence as an ecosystem engineer is limited to within the first one or two meters from the base of the underplanted white spruce. This study extended upon the previous work done comparing broadleaf and mixedwood stands and patches (Macdonald and Fenniak, 2007; Chávez and Macdonald, 2010) by making these comparisons at an even finer scale and by spatially relating differences to individual trees. Most changes observed were as would be predicted based on the studies of differences between natural broadleaf and mixedwood stands and patches. By studying stands underplanted with white spruce and the adjacent areas of the stands left unplanted, changes can be related directly to the addition of white spruce to the stand – and not to natural environmental differences between stand types or changes in stand dynamics over time and with succession.

The 48 year old underplanted white spruce demonstrated good height and diameter growth. Using a site index curve for white spruce in the Lower Foothills natural subregion (Wang and Huang, 2000) and an age at breast height of 32-33, the site index for the three stands was in the 16-20 class, indicating very productive sites – particularly for spruce which were not open-grown. The white spruce reached breast height at 15-16 years old (Dan McIsaac, personal communication). The high productivities in these Edson stands were observed even though the overstory aspen were never harvested and the white spruce remained below the canopy. The growth of these spruce may have benefitted from the aspen reaching overmaturity (112-121 years old), with canopy break up leading to increased light levels in the understory.

A number of differences in the understory environmental variables and vegetation between the underplanted and reference areas, and among distances from the underplanted white spruce were similar to differences observed in previous studies of natural broadleaf, mixedwood and conifer stands and patches. Conifer and mixedwood stands and patches have been shown to have cooler soil temperatures than broadleaf stands and patches (Macdonald and Fenniak, 2007; Chávez and Macdonald, 2010). In this study plots 0-1 m and 1-2 m from the base of the white spruce had cooler soil temperature than the plots 3-4 m from the base of the white spruce. I did not find any differences in soil moisture based on plot location. Chávez and Macdonald (2010) did not find any differences in soil moisture between broadleaf and mixedwood patches but they did observe drier soils in conifer patches than in either mixedwood or broadleaf patches. Hannam et al. (2005) found the opposite trend, with soil moisture higher in white spruce stands than in aspen stands.

Some differences observed in this study were different than expected based on the literature and some differences observed in the literature were not observed in this study. Macdonald and Fenniak (2007) observed greater litter depths in broadleaf stands than in both mixedwood and conifer stands. Chávez and

Macdonald (2010) did not find any differences in the depths of litter and organic layers between broadleaf, mixedwood and conifer patches. In this study I found the litter depth in the underplanted plots to be greater than in the non-underplanted aspen plots. Litter depths were also greater in the plots 0-1 m and 1-2 m from the base of white spruce compared to the plots 3-4 m away. I also found the FH layer to be greater in the plots 0-1 m from the base of spruce compared to the plots 3-4 m away. The greater litter depths observed by Macdonald and Fenniak (2007) in the broadleaf stands were due to the annual shedding of leaves. The greater litter depths I observed with underplanted spruce were due to the accumulation of needles, which do not decompose as quickly as leaves.

Forest floor pH was found to be higher in plots 0-1 m from the base of underplanted white spruce than in plots 3-4 m from the base of spruce. This observation was opposite to what was expected based on previous research (Ste-Marie and Paré, 1999; Légaré et al., 2001; Hannam et al., 2004). Differences in pH between broadleaf-dominated stands and conifer-dominated stands were expected because of acidification associated with decomposition of the conifer needles (Fisher et al., 2000). This difference in forest floor pH was small (0.47) but was probably still biologically significant because a similar trend was observed in the stands with 15 year old underplanted white spruce. In those stands forest floor pH was 0.22 higher in the plots 0-1 m from the base of spruce than in plots 1-2 m from the base of spruce. Forest floor and soil processes involve many complex interactions. I only studied a few forest floor and soil properties. I did not study the microbial communities in fine detail and I did not study any ectomycorrhizal relationships. It is possible that something more complex occurred to increase the forest floor pH when a decrease was predicted based on previous studies.

Macdonald and Fenniak (2007) found mineral soil nitrogen to be higher in broadleaf stands than in mixedwoods and Chávez and Macdonald (2010) found mineral soil magnesium to be higher in broadleaf patches than in mixedwoods. Neither mineral soil nitrogen or magnesium differed with the addition of underplanted white spruce to the stands in this study. However, I observed differences in mineral soil sulphur that these previous studies did not examine. Mineral soil sulphur concentrations were three times higher 0-1 m from the base of the spruce than in plots 3-4 m from the base of the spruce. This increase in sulphur can be attributed to the throughfall chemistry. The water chemistry of throughfall is influenced by two primary mechanisms: washing off of dry deposition, and canopy exchange through leaching of tree nutrients and absorption of ions from precipitation (Parker, 1983). Canopy exchange of sulphur is minimal (Pajuste et al., 2006) so the washing off of dry atmospheric sulphur deposition is the more likely source of the increased mineral soil sulphur. The increase in sulphur at the base of underplanted white spruce trees is primarily the result of throughfall and not stemflow. The morphology of conifers makes stemflow less important than throughfall (Houle et al., 1999). Pajuste et al. (2006) found sulphur deposition to be higher under coniferous canopies than in bulk deposition. They attributed this increase to atmospheric deposition which was the result of human activity. The atmospheric sulphur deposition may be higher in the Edson area than in some boreal areas due to high industrial activity. I studied plots directly at the base of white spruce but did not set up any plots directly at the base of aspen trees. It is possible that increased mineral soil sulphur concentrations would be observed under aspen as well but the concentrations would probably not be as high. Rothe et al. (2002) found the throughfall deposition of sulphur compounds to be twice as high in stands of Norway spruce (*Picea abies* K.) than in stands of European beech (*Fagus sylvatica* L.). Norway spruce have a higher leaf area index than European beech and also retain their needles throughout the year, causing more sulphur deposition to be washed off by throughfall (Rothe et al., 2002). Needles are also more efficient at collecting aerosols than most leaves (Blood et al., 1989).

It is probable that lower vegetation cover under underplanted white spruce trees was a result of decreased light passing through the white spruce crowns. Total vegetation cover and herb cover were lower in the plots 0-1 m from the base of the spruce and shrub cover was lower in the plots 0-1 m and 1-2 m from the base of spruce compared to plots not underneath the crown (3-4 m from the base of the spruce). This corresponded with lower PAR levels at 0.5 m and 1.3 m meter heights in the plots 0-1 m and 1-2 m from the base of spruce compared to in the plots 3-4 m from the base of spruce. No differences in PAR levels at ground level were observed between the plots. Constabel and Lieffers (1996) found light transmission on the forest floor to be equally low in all forest types they studied despite differences in light transmission through the forest canopies. They suspected that this increased light transmitted through the canopy stimulated shrub and herb layer growth, attenuating more understory light and making light levels on the forest floor as low as in dense canopy stands (Constabel and Lieffers, 1996). Macdonald and Fenniak (2007) found shrub cover to be higher in broadleaf stands than in conifer stands but they found no differences between broadleaf and mixedwood stands.

Both Shannon's and Simpson's Diversity Indices were lower in plots within the first meter from the base of white spruce than in the plots 3-4 m from spruce. Shannon's Diversity Index was also lower when comparing underplanted plots to non-underplanted aspen plots. These observations are similar to the trend of decreased Shannon's Diversity Index with increased presence of white spruce in the canopy found by Macdonald and Fenniak (2007). Macdonald and Fenniak (2007) found beta diversity to be greater in mixedwoods than in broadleaf stands. I did not find a difference in beta diversity from the addition of underplanted white spruce compared to non-underplanted areas. Shrub and herb richness were higher in broadleaf stands than in conifer stands but there were no differences between broadleaf and mixedwood stands (Macdonald and Fenniak, 2007). I found decreases in both herb and shrub richness within the first meter from the base of spruce compared to 3-4 m away and I found herb richness to be lower in underplanted plots than in non-underplanted aspen plots. These decreases in richness indicated that species were being lost from the areas of the stands where underplanting occurred and at higher rates closer to the base of underplanted white spruce. The declines in richness also signify that the declines in diversity were not due to a decline just in evenness.

Results of the Indicator Species Analysis were similar to the other findings of this study, in that changes in the understory were limited to within the first one or two meters from the base of underplanted spruce. There were 15 indicator species for the aspen plots and four species as indicators of underplanted plots. This is similar to results found by Macdonald and Fenniak (2007) who found 13 species to be indicators of broadleaf stands, two species indicating mixedwoods and four species indicating conifer stands, and similar to results found by Chávez and Macdonald (2010) who found 15 indicator species for broadleaf patches, two for mixedwood and two for conifer patches. Three species Chávez and Macdonald (2010) found to be indicators of broadleaf patches (*Achillea millefolium*, *Amelanchier alnifolia* and *Vicia americana)* were indicators of non-underplanted aspen plots. I found *Pleurozium schreberi* to be a very strong indicator of underplanted plots in the Sundance Creek stand and of plots 0-1 m from the base of the spruce in the Swanson Road stand. *Pleurozium schreberi* is a very shade tolerant forest floor moss which commonly occurs in late successional stage conifer forests across the boreal forest (Royer and Dickinson, 2007). Four of the species which were indicators of plots 2-3 m and 3-4 m from the base of spruce (*Epilobium angustifolium*, *Fragaria virginiana*, *Lathyrus ochroleucus*, *Pyrola asarifolia*) were found to be indicators of broadleaf stands by Macdonald and Fenniak (2007). By comparing the abundance and frequency values, it appeared that the results of the Indicator Species Analysis were mostly due to changes in the abundance of species at different plot locations and not due to different species being present at the different plot locations. This was similar to previous studies which found most understory vascular plant species to be shared among different forest types, with varying abundances based on forest type (Macdonald and Fenniak, 2007; Chávez and Macdonald, 2010).

Differences in the understory environmental variables and vegetation within underplanted areas only occurred within the first two meters from the base of underplanted white spruce trees, with the majority of the changes only observed within the first meter. These areas where changes occurred were directly under the crowns of the white spruce (210.9-221.3 cm mean radii), and therefore were exposed to the greatest influence of the canopy through litter deposition, shading, and throughfall. Litter depths were greatest and PAR was lowest within the first two meters from the base of the trees. Zinke (1962) showed a single *Pinus contorta* (lodgepole pine) to have an influence on the soil roughly proportional to the crown area projection on the soil surface area, with maximum influence being under the canopy and decreasing influence outward from the tree. This study spatially related soil pH, nitrogen, exchangeable bases and exchange capacity to the distance from the base of the tree; pH was lowest near the base and increased outward while nitrogen was also lowest near the base but increased to a maximum at four to six feet from the tree and then either increased or decreased at further distances based on the surrounding vegetation (Zinke, 1962).

As the underplanted white spruce crowns grow larger in future, it is likely that differences will be observed further from the base of the trees. If the changes are related to light levels then some differences could potentially be observed further out than directly under the crown due to shading effects. However, changes in the understory due to the effects of litter deposition will be limited to under the spruce canopy. The combined effects of both litter and light would make changes most pronounced under the tree crown. It is also possible that there is a synergistic effect or threshold at some spacing, or even a combined effect of spacing and white spruce height. From personal observation of the 9'x9' underplanted compartments (which were not studied), this higher density planting may be more effective in changing the understory environment and vegetation than the 12'x12' and 15'x15' spacing. The compartments with 9'x9' spacing were much darker, had lower understory vegetation cover and had greater litter depths than the compartments with greater spacing.

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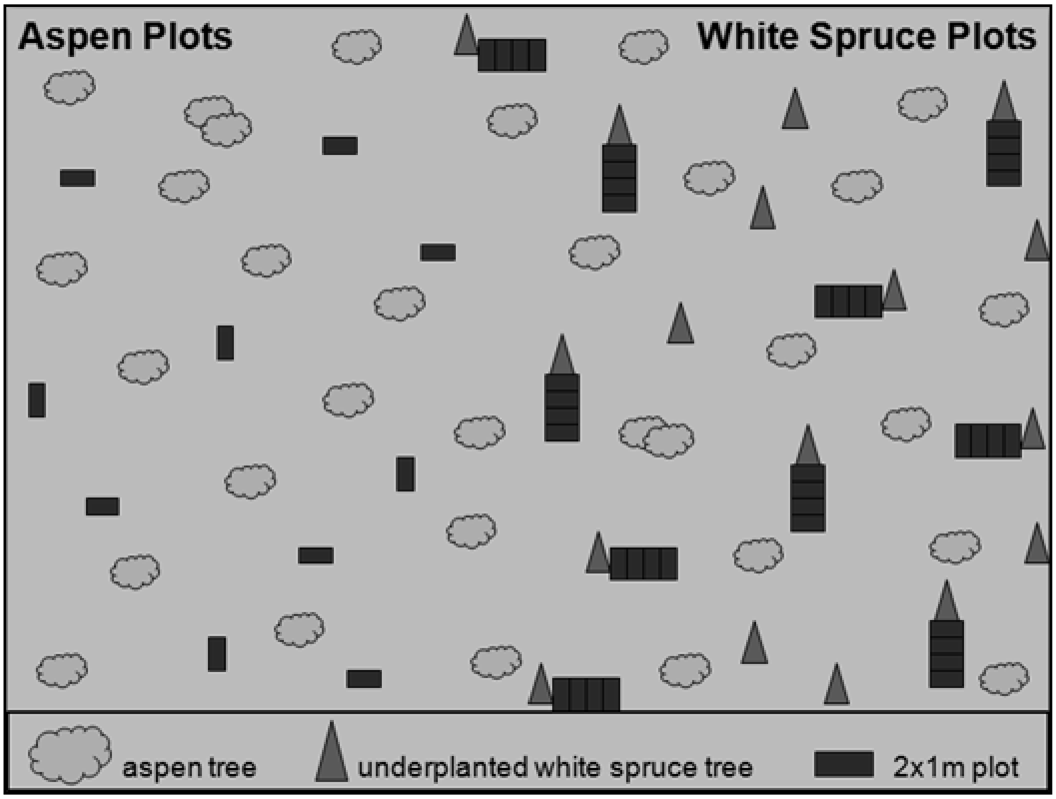

Figure 3.1: Example of plot layout within each stand. Note that for the Swanson Road stand aspen plots were located within the underplanted block in large patches where the underplanted white spruce seedlings did not survive. Tree densities and graphics are not to scale.

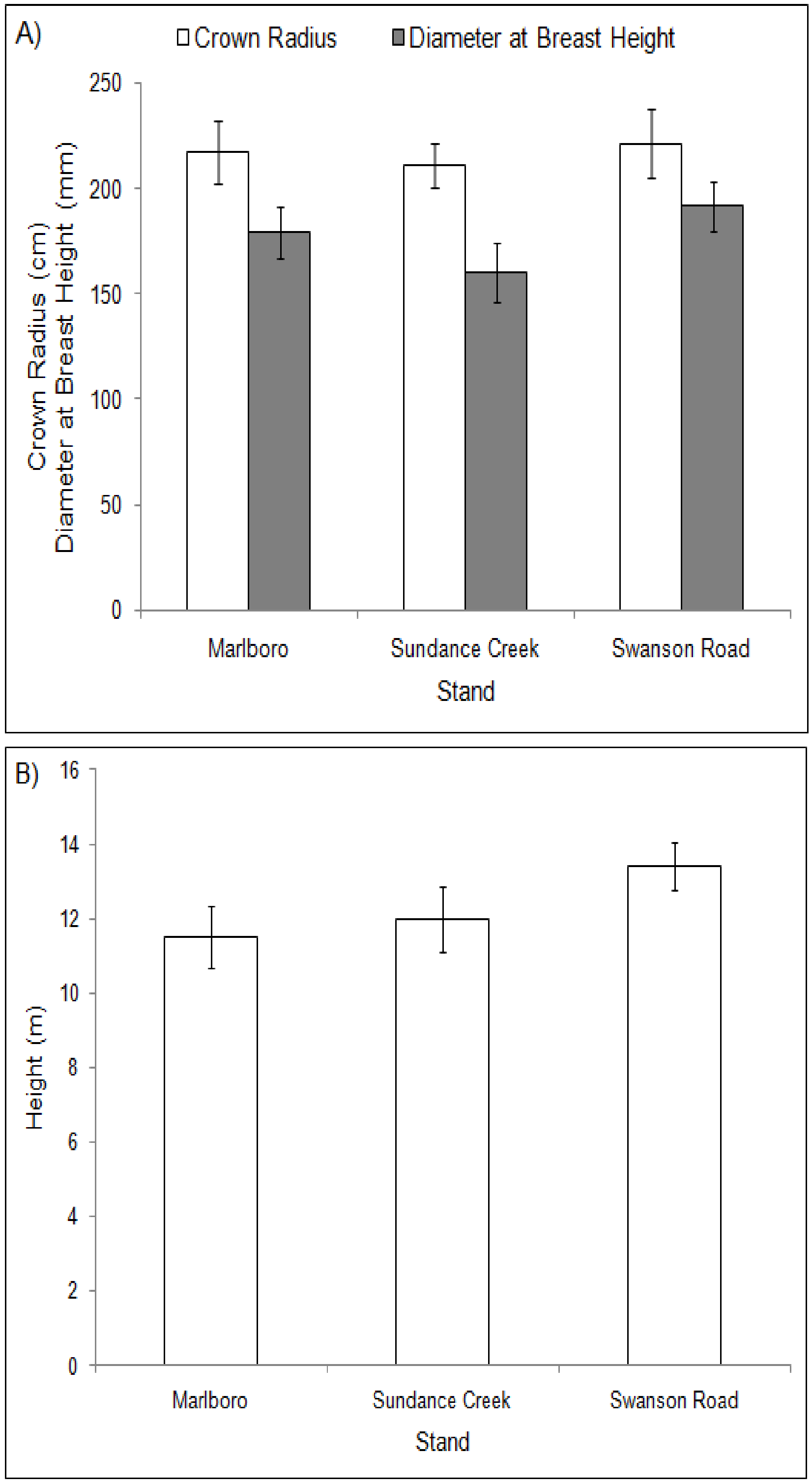

Figure 3.2: Mean crown radius and diameter at breast height (A) and mean height (B) of 48 year of underplanted white spruce by stand. Bars represent standard error of the mean.

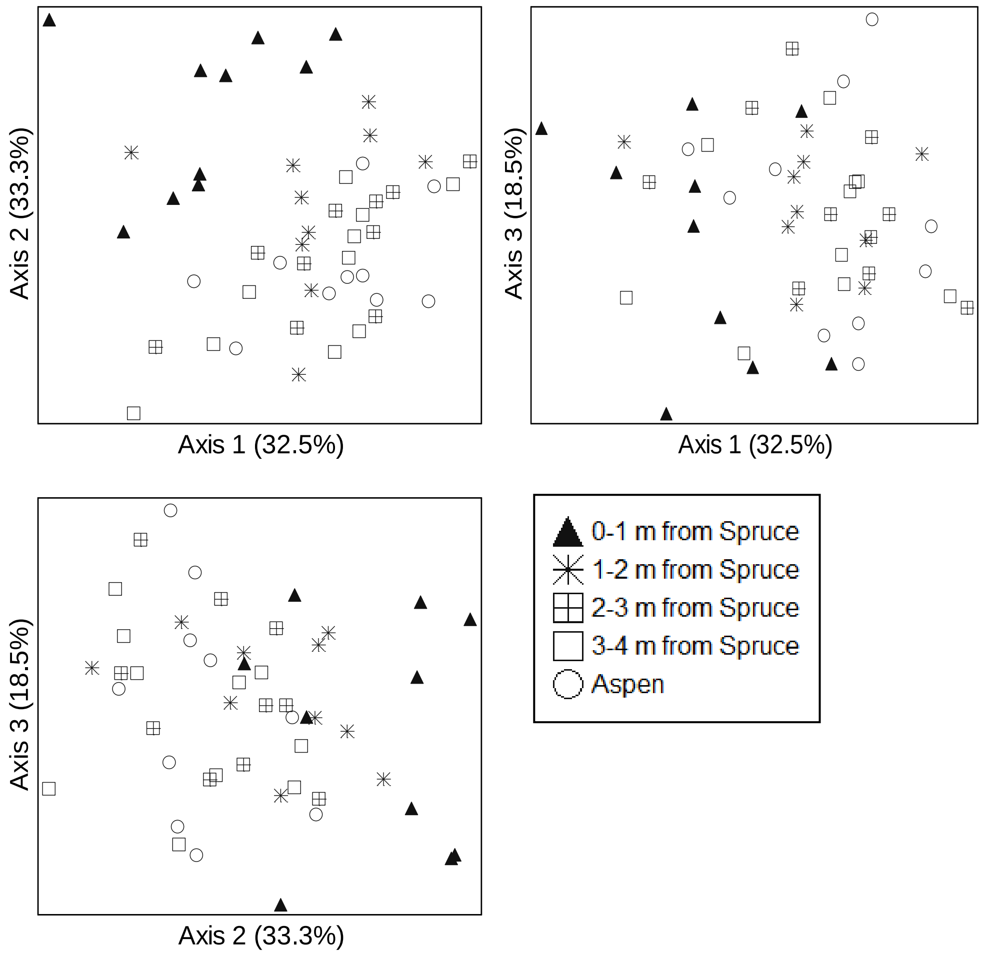

Figure 3.3: Results of a three-dimensional nonmetric multidimensional scaling (NMS) ordination of understory plant species in the Marlboro stand. The Sørenson distance measure was used. The percent of variation explained by each axis presented in parentheses. Stress=14.870.

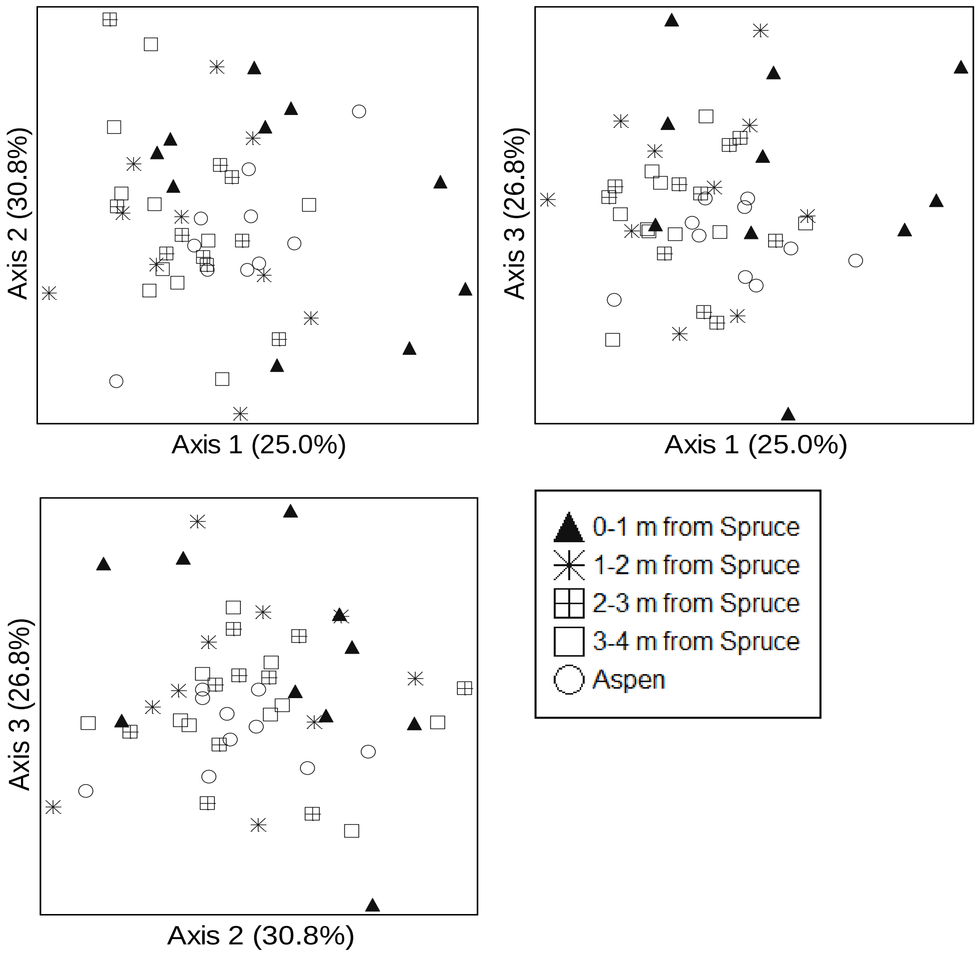

Figure 3.4: Results of a three-dimensional nonmetric multidimensional scaling (NMS) ordination of understory plant species in the Sundance Creek stand. The Sørenson distance measure was used. The percent of variation explained by each axis presented in parentheses. Stress=15.575.

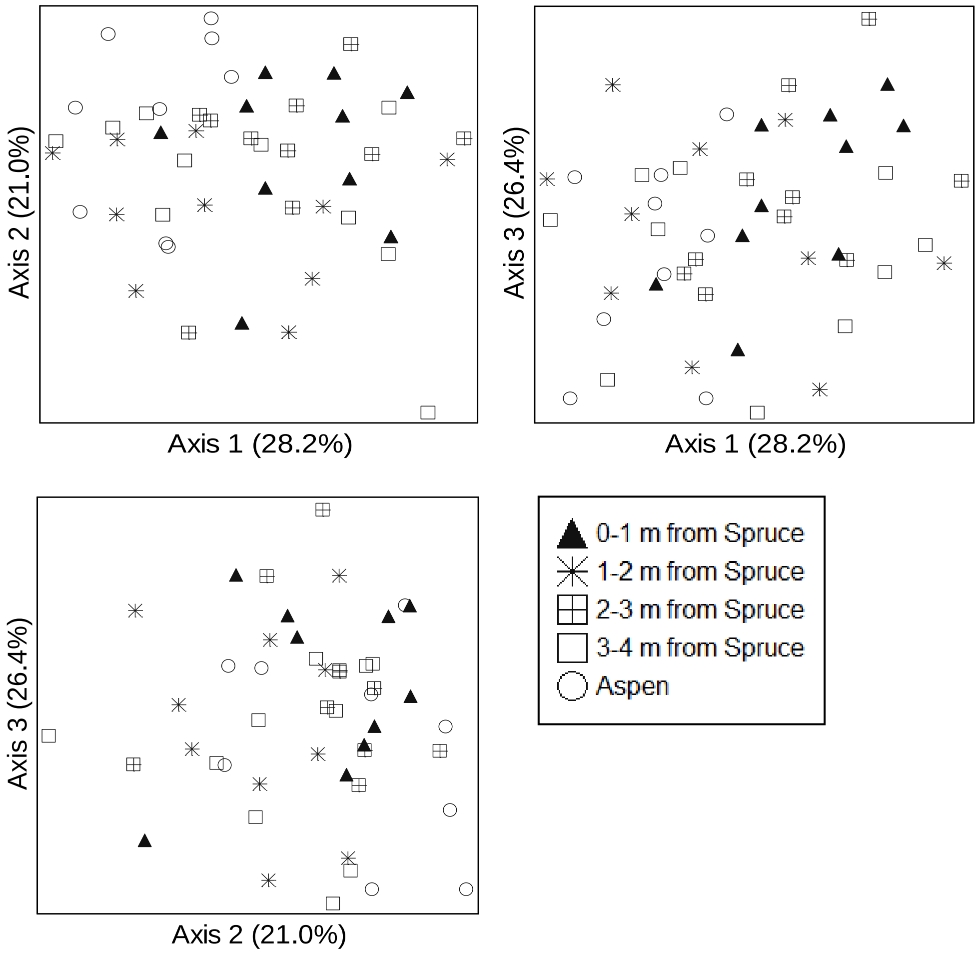

Figure 3.5: Results of a three-dimensional nonmetric multidimensional scaling (NMS) ordination of understory plant species in the Swanson Road stand. The Sørenson distance measure was used. The percent of variation explained by each axis presented in parentheses. Stress=17.608.

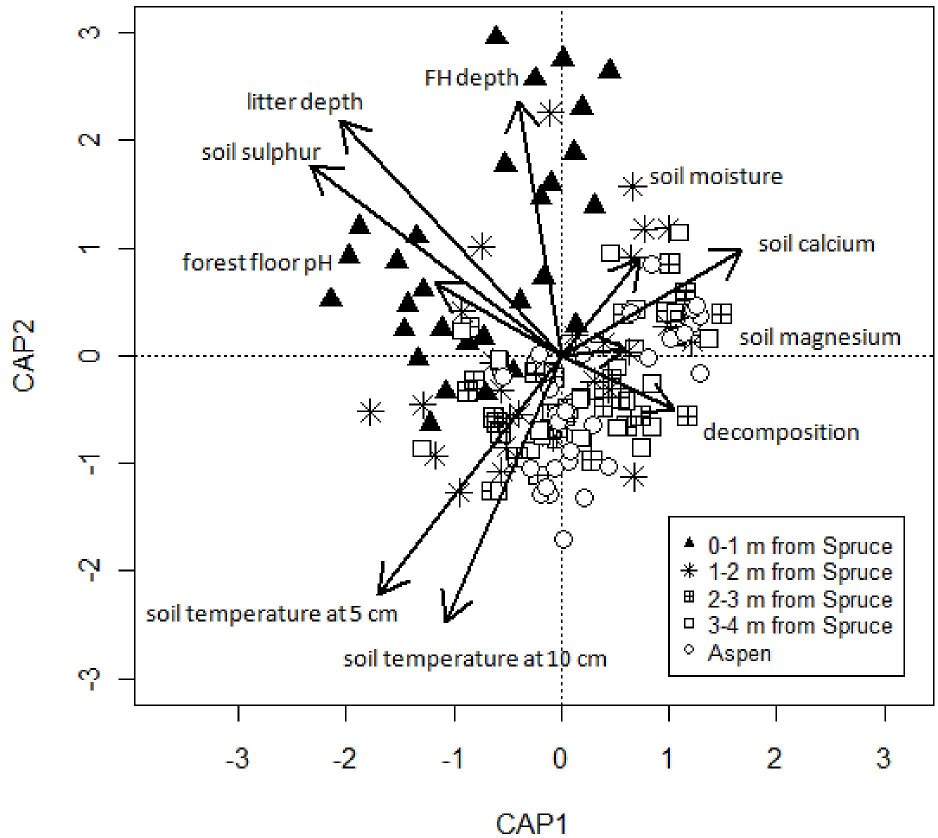

Figure 3.6: Results of distance-based redundancy analysis (db-RDA) for all stands showing significant environmental variables. The Bray-Curtis distance measure was used. All 150 plots were included in the analysis. PAR was not included as a variable in this analysis. Axis 1 explained 7.1% of the variation in the understory species data. Axis 2 explained 4.1% of the variation in the understory species data.

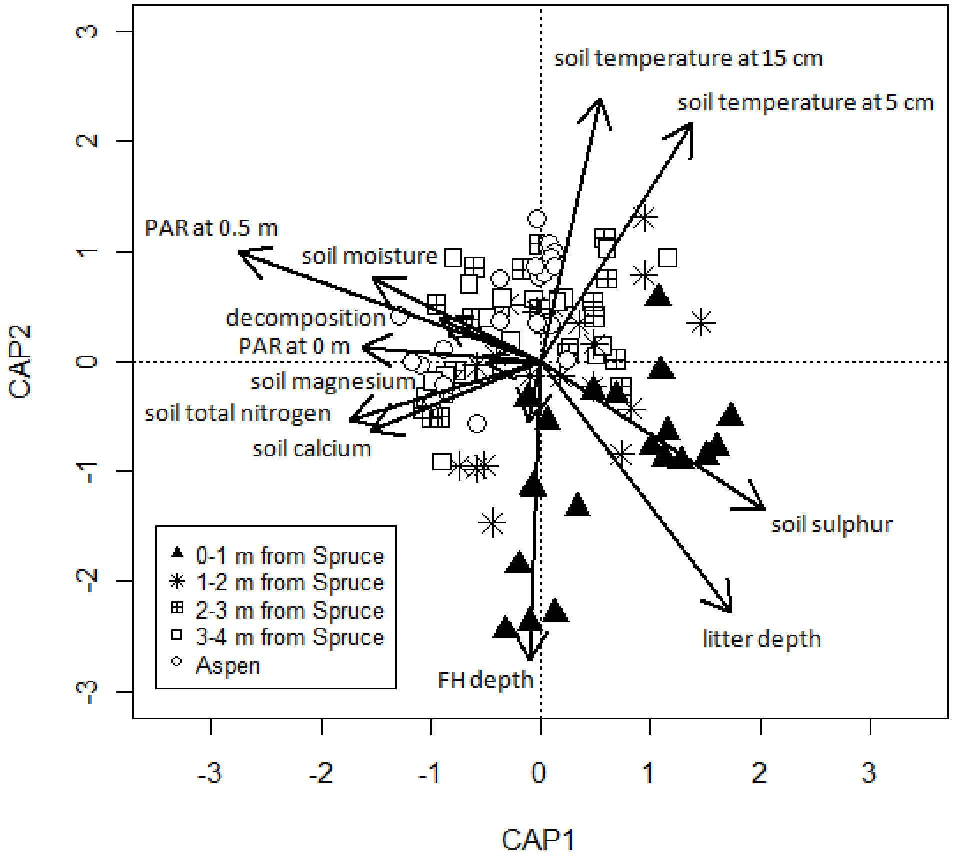

Figure 3.7: Results of distance-based redundancy analysis (db-RDA) for all stands showing significant environmental variables. The Bray-Curtis distance measure was used and in this case PAR was included as an environmental variable. Only the 100 plots at which PAR measurements were taken were included in the analysis. Axis 1explained 11.6% of the variation in the understory species data. Axis 2 explained 6.1% of the variation in the understory species data.

Table 3.1: Mean stems per hectare, mean height (m) and mean diameter at breast height (dbh; mm) of tree species in the 11.28 m radius tree plots in both the unplanted reference areas and the underplanted areas. The numbers in parentheses represent the standard errors of the means.

	Stems per Hectare	Height (m)	DBH (mm)
MARLBORO			
Aspen (>10 m)			
Unplanted Reference	433.3	23.4 (± 0.5)	294.3 (± 10.1)
Underplanted	416.7	22.3 (± 0.8)	270.9 (± 19.7)
Aspen (<10 m)			
Unplanted Reference	1500.0	1.9 (± 0.1)	12.3 (± 6.5)
Underplanted	75.0	6.1 (± 0.8)	59.5 (± 10.3)
Balsam Poplar (>10 m)			
Unplanted Reference	83.3	16.7 (± 2.6)	213.4 (± 14.6)
Underplanted	58.3	13 (± 0.7)	135.4 (± 17.2)
Balsam Poplar (<10 m)			
Unplanted Reference	158.3	3.5 (± 0.5)	24.7 (± 5.7)
Underplanted	50.0	6.5 (± 1.0)	64.9 (± 13.2)
Paper Birch			
Unplanted Reference	0	-	-
Underplanted	20.8	4.4 (± 1.2)	50.0 (± 18.1)
Lodgepole Pine			
Unplanted Reference	16.7	19.2 (± 4.6)	219.0 (± 87.0)
Underplanted	0	-	-
Black Spruce			
Unplanted Reference	0	-	-
Underplanted	4.2	17.7*	202.0*
White Spruce (natural regeneration)			
Unplanted Reference	25.0	3.0 (± 1.6)	37.5 (± 9.0)
Underplanted	29.7	3.5 (± 0.2)	40.5 (± 5.2)

*There was no standard error of the mean because there was only one tree of that species present.

Table 3.2: Least square mean values of (A) environmental variables and (B) vegetation/diversity measures (95% confidence interval in brackets). P-values of ANOVAs non-blocked and blocked ANOVAs are presented°. Significant p-values (α=0.05) are in bold. For the blocked ANOVAs, contrasts which indicated spruce plot locations significantly different from the 3-4 m from spruce plots (Bonferroni corrected α of 0.0167) are denoted by asterisks.

	0-1 m from Spruce	1-2 m from Spruce	2-3 m from Spruce	3-4 m from Spruce	Aspen	P-value (non-blocked)	P-value (blocked)
(A)							
Decomposition (% loss of cellulose)	39.16 *(20.88-57.44)*	55.02 *(36.74-73.30)*	53.16 *(34.88-71.44)*	53.82 *(35.54-72.10)*	51.11 *(32.83-69.39)*	0.633	0.163
Soil Moisture (m^3m^{-3})	0.09 *(0.06-0.12)*	0.09 *(0.06-0.12)*	0.10 *(0.07-0.13)*	0.10 *(0.07-0.13)*	0.11 *(0.09-0.14)*	0.671	0.804
Litter Depth (cm)	3.37* *(3.11-3.62)*	2.18* *(1.92-2.43)*	1.83 *(1.58-2.09)*	1.60 *(1.35-1.85)*	1.64 (1.39-1.89)	**<0.001**	**<0.001**
FH Depth (cm)	7.87* *(7.14-8.59)*	6.05 *(5.32-6.78)*	5.77 *(5.04-6.49)*	5.26 *(4.53-5.99)*	6.12 *(5.39-6.84)*	**0.001**	**<0.001**
Soil Temperature (°C) at 5 cm	11.47 *(10.89-12.06)*	11.63 *(11.04-12.21)*	11.68 *(11.10-12.27)*	11.77 *(11.18-12.35)*	12.04 *(11.46-12.63)*	**0.021**	0.160
Soil Temperature (°C) at 10 cm	10.85* *(10.40-11.30)*	11.08 *(10.62-11.53)*	11.20 *(10.75-11.65)*	11.27 *(10.82-11.72)*	11.49 *(11.04-11.94)*	**0.005**	**0.002**
Soil Temperature (°C) at 15 cm	10.57* *(10.17-10.96)*	10.78 *(10.38-11.17)*	10.96 *(10.56-11.35)*	11.01 *(10.61-11.41)*	11.22 *(10.82-11.61)*	**0.004**	**0.001**
Total N (mg/10 cm^2)	3.94 *(1.39-6.49)*	5.35 *(2.80-7.90)*	3.99 *(1.44-6.54)*	3.80 *(1.25-6.35)*	5.77 *(3.22-8.32)*	0.618	0.092
NO_3^--N (mg/10 cm^2)	1.83 *(1.06-2.60)*	2.67 *(1.90-3.44)*	1.78 *(1.01-2.55)*	2.07 *(1.30-2.84)*	1.96 *(1.19-2.73)*	0.399	0.217

NH_4^+-N (mg/10 cm^2)	2.11 *(0-4.56)*	2.68 *(0.23-5.13)*	2.21 *(0-4.66)*	1.73 *(0-4.18)*	3.81 *(1.35-6.26)*	0.694	0.421
Ca (mg/10 cm^2)	1047.7 *(749.5-1346.0)*	1099.7 *(801.4-1397.9)*	1183.5 *(885.3-1481.8)*	1132.7 *(834.5-1431.0)*	1332.5 *(1034.2-1630.7)*	0.214	0.474
Mg (mg/10 cm^2)	179.80 *(156.47-203.14)*	185.25 *(161.92-208.59)*	199.20 *(175.87-222.54)*	196.41 *(173.08-219.75)*	193.36 *(170.02-216.69)*	0.532	0.356
P (mg/10 cm^2)	13.01 *(9.52-16.50)*	12.81 *(9.32-16.30)*	13.73 *(10.24-17.22)*	12.23 *(8.74-15.72)*	10.66 *(7.17-14.15)*	0.433	0.853
K (mg/10cm^2)	372.50 *(296.75-448.25)*	372.77 *(297.02-448.52)*	272.83 *(197.08-348.58)*	308.33 *(232.58-384.08)*	274.34 *(198.59-350.09)*	0.112	**0.047**
S (mg/10 cm^2)	51.66* *(42.82-60.49)*	27.11 *(18.28-35.95)*	22.22 *(13.38-31.05)*	16.15 *(7.32-24.99)*	14.58 *(5.75-23.42)*	**0.001**	**<0.001**
Mn (mg/10 cm^2)	9.84 *(5.82-13.86)*	9.33 *(5.31-13.35)*	11.16 *(7.15-15.18)*	8.95 *(4.93-12.97)*	6.81 *(2.80-10.83)*	0.412	0.783
Zn (mg/10 cm^2)	0.67 *(0.23-1.11)*	1.06 *(0.62-1.50)*	0.75 *(0.31-1.19)*	0.75 *(0.31-1.19)*	0.57 *(0.13-1.01)*	0.350	0.329
Al (mg/10 cm^2)	14.03 *(5.39-22.68)*	16.57 *(7.93-25.22)*	18.98 *(10.33-27.62)*	16.49 *(7.85-25.13)*	14.41 *(5.76-23.05)*	0.297	0.274
Fe (mg/10 cm^2)	6.52 *(4.76-8.27)*	6.80 *(5.04-8.56)*	5.91 *(4.15-7.67)*	5.49 *(3.73-7.24)*	4.64 *(2.88-6.39)*	0.256	0.491
Forest Floor pH	5.74* *(5.37-6.12)*	5.47 *(5.10-5.85)*	5.23 *(4.85-5.60)*	5.27 *(4.89-5.64)*	5.50 *(5.12-5.87)*	**0.012**	**<0.001**

Microbial Biomass NPOC (mg C/g dry FF)	15.14 *(10.35-19.93)*	19.58 *(14.91-24.26)*	20.52 *(15.84-25.19)*	21.11 *(16.43-25.78)*	19.60 *(14.92-24.27)*	0.258	0.074
Microbial Biomass TN (mg N/g dry FF)	3.77 *(2.64-4.91)*	4.71 *(3.58-5.84)*	4.19 *(3.06-5.32)*	4.11 *(2.98-5.24)*	4.19 *(3.06-5.32)*	0.220	**0.034**
PAR at 0 m (% full light)	5.02 *(1.14-8.90)*	5.56 *(1.68-9.43)*	6.02 *(2.14-9.90)*	6.93 *(3.05-10.81)*	8.13 *(4.25-12.01)*	0.234	0.348
PAR at 0.5 m (% full light)	9.71* *(0-20.98)*	14.35* *(3.08-25.62)*	19.27 *(8.00-30.54)*	21.84 *(10.57-33.11)*	32.50 *(21.23-43.76)*	**<0.001**	**<0.001**
PAR at 1.3 m (% full light)	8.61* *(0-19.90)*	15.25* *(3.96-26.54)*	21.87 *(10.58-33.17)*	24.43 *(13.14-35.72)*	37.51 *(26.21-48.80)*	**<0.001**	**<0.001**

(B)

Total Cover (%)	48.51* *(39.94-57.09)*	74.87 *(66.29-83.45)*	81.85 *(73.27-90.43)*	81.82 *(73.24-90.40)*	87.46 *(78.89-96.04)*	**<0.001**	**<0.001**
Shrub Cover (%)	12.07* *(7.05-17.08)*	15.34* *(10.32-20.36)*	19.72 *(14.69-24.73)*	21.24 *(16.22-26.26)*	21.53 *(16.51-26.55)*	**0.010**	**<0.001**
Herb Cover (%)	33.11* *(24.02-42.20)*	55.20 *(46.11-64.29)*	56.57 *(47.48-65.66)*	54.69 *(45.60-63.78)*	57.63 *(48.54-66.73)*	**0.001**	**<0.001**
Total Richess/Plot (# species/2 m^2)	18.07* *(16.43-19.71)*	20.23 *(18.59-21.87)*	21.53 *(19.89-23.17)*	21.67 *(20.03-23.31)*	21.60 *(19.96-23.24)*	**0.009**	**<0.001**
Shrub Richness/Plot (# species/2 m^2)	3.03* *(1.92-4.15)*	3.60 *(2.49-4.71)*	3.70 *(2.59-4.81)*	4.00 *(2.89-5.11)*	4.10 *(2.99-5.21)*	0.171	**0.020**

Herb Richness/Plot (# species/2 m^2)	12.17* *(10.45-13.89)*	13.27 *(11.55-14.99)*	14.07 *(12.35-15.79)*	13.60 *(11.88-15.32)*	14.33 *(12.61-16.05)*	**0.007**	**<0.001**
Shannon's Diversity Index	2.35* *(2.28-2.43)*	2.45 *(2.37-2.53)*	2.56 *(2.48-2.63)*	2.55 *(2.47-2.63)*	2.60 *(2.52-2.68)*	**0.005**	**<0.001**
Simpson's Diversity Index	0.88* *(0.87-0.90)*	0.89 *(0.88-0.90)*	0.91 *(0.89-0.92)*	0.91 *(0.89-0.92)*	0.91 *(0.90-0.92)*	0.055	**0.016**
Whittaker's β Diversity Index	0.47 *(0.31-0.64)*	0.34 *(0.18-0.51)*	0.21 *(0.05-0.38)*	0.22 *(0.05-0.39)*	0.35 *(0.19-0.52)*	0.170	-

°For the non-blocked ANOVAs all five plot locations (0-1, 1-2, 2-3 and 3-4 m from spruce, and aspen) were included in the analysis, treating stand as the experimental unit and plots within a stand as subsamples. The non-blocked ANOVAs were performed to test for differences between underplanted areas and non-underplanted areas of the stands. For the blocked ANOVAs only the spruce plots (0-1, 1-2, 2-3 and 3-4 m from the spruce) were analyzed and were blocked at the underplanted white spruce tree with plots representing the treatment effect of the two distances from the underplanted tree. Blocked ANOVAs were performed to test for differences related to distance from the underplanted white spruce.

Table 3.3: Results from one-way PERMANOVAs comparing understory plant species composition between (A) 0-1 m from spruce plots and aspen plots, (B) 1-2 m from spruce plots and aspen plots, (C) 2-3 m from spruce plots and aspen plots, and (D) 3-4 m from spruce plots and aspen. Significant p-values are in bold (α=0.05).

	DF	SS	MS	F-value	P-value
(A) 0-1 m vs Aspen					
Plot Location	1	1.2644	1.2644	8.6171	**0.0002**
Residual	58	8.5104	0.14673		
Total	59	9.7748			
(B) 1-2 m vs Aspen					
Plot Location	1	0.33936	0.33936	2.5540	**0.0024**
Residual	58	7.7067	0.13287		
Total	59	8.0461			
(C) 2-3 m vs Aspen					
Plot Location	1	0.16002	0.16002	1.3091	0.1762
Residual	58	7.0897	0.12224		
Total	59	7.2497			
(D) 3-4 m vs Aspen					
Plot Location	1	0.17753	0.17753	1.4013	0.1304
Residual	58	7.3479	0.12669		
Total	59	7.5255			

Table 3.4: Results of a (A) randomized complete block PERMANOVA comparing understory plant species composition in relation to the distance from the underplanted white spruce (α=0.05) and (B) contrasts of spruce plot locations (0-1 m, 1-2 m and 2-3 m) from the 3-4 m from spruce plot locations (Bonferroni corrected α of 0.0167). Significant p-values are in bold.

(A)	**DF**	**SS**	**MS**	**F-value**	**P-value**
Spruce Tree	29	10.619	0.36618	6.8282	**0.0002**
Plot Location	3	1.5257	0.50855	9.4832	**0.0002**
Residual	87	4.6655	0.53627E-01		
Total	119	16.810			

(B)	**t-value**	**P-value**
0-1 m vs 3-4 m	2.6387	**0.0002**
1-2 m vs 3-4 m	1.3552	0.0352
2-3 m vs 3-4 m	0.41756	0.9982

Table 3.5: Results of Indicator Species Analysis for understory vegetation communities run of underplanted and non-underplanted areas (for each of the three stands separately). Given are species which were significant indicators for the (A) underplanted areas and (B) aspen (non-underplanted) areas. Listed are all indicator species which were significant at p<0.05 and with indicator values≥20. Indicator values (IV) are given for both locations.

		IV		
		Underplanted	**Aspen**	**P-value**
(A)	**Underplanted**			
Marlboro	*Maianthemum canadense*	**64**	17	0.038
Sundance Creek	*Pleurozium schreberi*	**45**	0	0.036
	Viola renifolia	**62**	16	0.025
Swanson Road	*Aralia nudicaulis*	**62**	35	0.021
	Viola renifolia	**66**	31	0.005
(B)	**Aspen/Non-underplanted**			
Marlboro	*Achillea millefolium*	5	**50**	0.012
	Amelanchier alnifolia	1	**56**	0.001
	Equisetum arvense	0	**20**	0.033
	Ledum groenlandicum	0	**20**	0.039
	Oryzopsis asperiflia	21	**73**	0.002
	Symphoricarpos albus	14	**53**	0.016
	Trientalis borealis	0	**50**	<0.001
	Vicia americana	17	**65**	0.013
Sundance Creek	*Castilleja miniata*	1	**36**	0.013
	Populus tremuloides	9	**67**	<0.001
	Pyrola asarifolia	28	**72**	0.001
	Orthilia secunda	0	**78**	<0.001
	Vicia americana	12	**68**	0.003
Swanson Road	*Arnica cordifolia*	33	**66**	0.011
	Disporum nudicaulis	0	**20**	0.034
	Galium boreale	11	**49**	0.027
	Orthilia secunda	0	**69**	0.001
	Symphoricarpos albus	0	**20**	0.037
	Vicia americana	11	**63**	0.007

Table 3.6: Results of Indicator Species Analysis for understory vegetation communities based on distance from the underplanted white spruce: (A) 0-1 m (B) 2-3 m and (C) 3-4 m from the underplanted white spruce (for each of the three stands separately). Listed are all indicator species which were significant at $p<0.05$ and with indicator values≥20. Indicator values (IV) are given for all locations. There were no significant indicator species for the location 1-2 m from underplanted white spruce plot location.

		IV				
		0-1	**1-2**	**2-3**	**3-4**	**P-value**
(A)	**0-1 m From Spruce**					
Swanson Road	*Pleurozium schreberi*	**61**	3	0	1	0.001
(B)	**2-3 m From Spruce**					
Marlboro	*Epilobium angustifolium*	11	27	**34**	28	0.027
	Fragaria virginiana	10	28	**33**	24	0.039
(C)	**3-4 m From Spruce**					
Marlboro	*Lathyrus ochroleucus*	5	24	29	**37**	0.039
Sundance Creek	*Linnaea borealis*	10	20	31	**39**	0.024
	Pyrola asarifolia	11	19	32	**38**	0.019
Swanson Road	*Linnaea borealis*	7	13	34	**41**	0.028

CHAPTER 4:

GENERAL CONCLUSIONS AND IMPLICATIONS OF RESEARCH

Summary and Conclusions

In Canada the boreal mixedwood forest, in which the canopy is dominated by varying mixtures of broadleaf and conifer trees, is the most widespread forest type (Rowe, 1972). However, in Alberta silvicultural operations and regeneration rules may be leading to the establishment of relatively pure stands (Lieffers and Beck, 1994; Lieffers et al., 1996, Man and Lieffers, 1999, Lieffers et al., 2008). More recently concern has risen over single species management reducing biodiversity and changing natural forest processes (Macdougall, 1988; DesGranges and Rondeau, 1993a; DesGranges and Rondeau, 1993b; Stelfox, 1995; Baker et al., 1996; Man and Lieffers, 1999). Underplanting white spruce in aspen-dominated stands was originally introduced in the 1960s to add a commercially valued species to a forest landbase that was not considered economically valuable. This practice was reintroduced in the 1990s as an ecologically-based management option. Underplanting was seen as an alternative to single species management which could address issues of competing interests on the landbase, difficulties in regenerating white spruce after clearcutting, and a public demand for more ecologically based silvicultural systems (Man and Lieffers, 1999). While some studies had been conducted looking at the survival and growth of white spruce underplanted in aspen-dominated stands, the impact of this practice on the understory environment and vegetation has not been previously studied. In natural boreal stands differences exist in understory environmental variables and vegetation composition, richness and diversity related to canopy composition, with mixedwoods being more similar to conifer-dominated than broadleaf-dominated forests. The objectives of this study were to determine if underplanted white spruce was an ecosystem engineer and if there was potential to use underplanting to establish mixedwoods in a broader ecological sense. The questions addressed were:

1. Does underplanting white spruce in aspen-dominated stands change the understory environment and subsequently the understory vegetation?
2. If changes were observed:

   a) at what age are changes first observed?

   b) are the changes greater close to the base of the underplanted tree and less pronounced as distance outward from the base of the tree increases?

   c) does the spatial extent of the effects increase with time passed since underplanting?

Changes in the understory were slow to occur around underplanted white spruce. No differences were observed between underplanted and non-underplanted areas or at different distances from the spruce by 10 years after underplanting. By 15 years after underplanting, forest floor pH and microbial biomass nitrogen were higher in plots 0-1 m from the base of the spruce than in plots 1-2 m from the base of the underplanted white spruce. These changes may have occurred earlier than 15 years after underplanting. Because the forest floor pH and microbial biomass were not studied in the 4-5 and 10 year old underplanted stands, the exact time it takes for these changes to begin is uncertain.

By 48 years after underplanting, there were many more differences observed in the understory environmental variables and vegetation, however these changes were limited to within the first one or two meters from the base of the underplanted white spruce. The FH depth, soil sulphur and forest floor pH were higher in the plots 0-1 m from the base of the spruce than in the plots 3-4 m from the base of the spruce. Litter depth was higher in the plots 0-1 m and 1-2 m from the base of the spruce than in the plots 3-4 m from the base of the spruce. Herb and total cover, richness (herb, shrub and total), soil temperature at 10 cm and 15 cm, and Shannon's and Simpson's Diversity Indices were lower in the plots 0-1 m from the base of the spruce than in the plots 3-4 m from the base of the spruce. PAR measurements at 0.5 cm and 1.3 m, and shrub cover were lower in the plots 0-1 m and 1-2 m from the base of the spruce than in the plots 3-4 m from the base of the spruce.

White spruce acted as an ecosystem engineer when underplanted in aspen-dominated stands but in a limited capacity. The lack of early changes in the understory indicated differences observed in the older stands were from the white spruce and not from disturbances caused in the understory during planting. By 15 years after underplanting changes began to appear in the forest floor and by 48 years after underplanting there were additional changes in the soils and understory vegetation. Because of a lack of underplanted stands established in the 1970s and 1980s, there was a large gap in the age sequence of stands studied. When most of these differences start to appear is uncertain but based on how limited the changes were 48 years after underplanting, it seems it takes a long period of time. In the 15 year old underplanted stands, changes in the forest floor were limited to within the first one meter from the base of the spruce and by 48 years after underplanting, although more changes had occurred, most changes were still limited to one meter from the base of the spruce. Differences in light and litter depths within two meters of the base of the white spruce by 48 years after underplanting indicated that as the white spruce canopy grew it had more influence on the understory.

The overstory aspen canopy was not harvested in the 48 year old underplanted stands. Underplanting guidelines recommend harvesting the aspen from underplanted stands when the spruce are approximately 20 years old (DeLong, 1997). It is possible the underplanted white spruce would have a greater effect on understory environment and vegetation in the subsequent stand that regenerates after harvesting. Within the areas of the stands left unplanted in these 48 year old underplanted stands, aspen regeneration was higher than in the underplanted areas. This probably occurred because the overstory aspen were beginning to die, causing openings in the canopy which increased light in the understory and promoted suckering. Suckering was probably more suppressed in underplanted areas of the stands despite openings in the aspen canopy because of light interception from the white spruce crowns and competition for other resources from the white spruce. After harvesting, white spruce would decrease the amount of regenerating aspen and be the major influence on light levels.

The size of white spruce in this study were comparable to the size of underplanted white spruce of the same ages in previous underplanting studies. By 4-5 years of age, the mean spruce height of 62.7 (± 2.8) cm was comparable to a previous study of 5 year old underplanted white spruce by Comeau et al. (2004). The estimated height growth increment of 6 cm/yr fell into the range observed within the first five years by DeLong (2000). The 10 year old underplanted spruce had mean height of 116.6 (± 6.5) cm, which was comparable to the height of the underplanted white spruce studied by Comeau et al. (2009) when the trees were remeasured at age 10. The 48 year old underplanted white spruce had a site index class of 16-20 which indicated high productivity.

Implications of Research

The results of this research indicate there may be a trade-off between the timber productivity of spruce and the ecological goals of underplanting when the overstory aspen are left unharvested. Of the eight stands that were originally underplanted as part of the 1963 study, there were significant differences in dbh between the different spacing treatments in five stands and significant differences in height between the different spacing treatments in four stands (Dan MacIsaac, personal communication). Stand attributes were shown to be more important to white spruce dbh and height growth than physical site conditions (Dan MacIsaac, personal communication). Because of this, planting density was recommended to be less than 1,000 stems/hectare to avoid potential intraspecific shading and competition, and to maximize growth (Dan MacIsaac, personal communication). Results from my study show that by underplanting at even-spaced low densities (12'x12' and 15'x15' spacing) there would be some changes in the understory environmental variables and vegetation but these changes would be limited to a small distance from the base of the underplanted spruce.

When white spruce naturally recruit into the understory of an aspen stand, the spacing is highly variable. There are areas with a few scattered white spruce and other areas where white spruce are highly aggregated in patches. It is these arrangements that make the understory of mixedwoods stands highly heterogeneous (Chávez and Macdonald, 2010). Patches of white spruce would create larger areas in which the white spruce exert a stronger influence on understory light levels and litter deposition, and therefore have a greater influence on the understory vegetation compared to a single white spruce scattered throughout a stand. Influences on the understory might be observed earlier in patches than around single trees. If the main goal of underplanting is white spruce establishment and trying to obtain growth rates as high as possible for an understory environment then white spruce should be evenly spaced and farther away from one another. If the main goal of underplanting is attempting to establish a mixedwood ecosystem and the overstory aspen are not going to be harvested then the white spruce should be planted with variable spacing which attempts to mimic natural patterns.

The understory of underplanted mixedwoods may never be completely comparable to that of natural mixedwoods which develop post-fire. These created mixedwoods are influenced by the biological legacies of the pre-underplanted aspen stands (seed banks, vegetation competition, soil nutrients, microbial communities, etc.). With underplanting, white spruce are planted into a plant community that is already well developed and there is little chance for new species to come in. Underplanting may just serve to filter the plant communities that already exist pre-planting.

Future Research

The effects of evenly spaced underplanted white spruce on understory environmental variables and vegetation were explored in this study. Results indicated that there may be a trade-off between the spruce timber productivity and the ecological goals of underplanting if the aspen canopy remains unharvested. To understand if spruce timber productivity and ecological goals of underplanting can be balanced when the aspen canopy remains, more underplanting trials may be required. Underplanting white spruce in various spacing arrangements and patch sizes, and then studying both the tree growth and the understory environmental conditions and vegetation would provide more insight into how to best balance competing goals of underplanting. More research into natural mixedwood patches (e.g., Chávez and Macdonald, 2010) could provide insight into possible ways to model underplanting layouts. By studying natural patches of white spruce of various sizes and densities within mixedwood stands, it may be possible to determine if there is a threshold patch size/density to have desired ecological effects. Studies could be conducted comparing the understory environment and vegetation in stands with underplanted white spruce to stands with natural white spruce regeneration in the understory which are the same age as underplanted white spruce. This would allow for direct comparison of the influences of underplanted white spruce to what naturally occurs in mixedwood stands.

The cost of underplanting in layouts other than even-spaced planting would be infeasible at operational levels for forestry companies. The compartments in the Edson stands underplanted at 9'x9' spacing could be studied to see if any desired ecological effects are observed. From personal observation, the understory light levels and the amount of understory vegetation differed considerably between the 9'x9' spacing, and the 12'x12' and 15'x15' spacing.

The understory environment and vegetation should be studied in underplanted stands after the overstory aspen are harvested. From this it could be determined if the underplanted white spruce have more influence on the subsequent regenerating stand than the spatially limited influence the spruce had when in the understory. If more influence is observed after harvesting, it is possible that underplanting, as currently prescribed with even spacing and low density, could balance both timber productivity and the ecological goals of underplanting.

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Appendix 1: Stand Locations

Year Underplanted	Age of White Spruce When Sampled	Stand	Latitude	Longitude
1962	48	Marlboro	N 53°35'57"	W 116°48'11"
1962	48	Sundance Creek	N 53°34'30"	W 116°44'36"
1962	48	Swanson Road	N 53°34'37"	W 116°44'41"
1994	15	Calling Lake #1	N 55°15'17"	W 113°29'02"
1994	15	Calling Lake #2	N 55°15'14"	W 113°30'03"
1994	15	Calling Lake #3	N 55°15'12"	W 113°30'36"
1999	10	Shaw Lake	N 54°46'45"	W 111°42'00"
1999	10	Touchwood	N 54°50'24"	W 111°41'20"
1999	10	K Road	N 55°03'35"	W 111°53'02"
2004	5	Piche Road #1	N 54°58'11"	W 111°38'55"
2004	5	Piche Road #2	N 54°57'42"	W 111°38'10"
2005	4	K Road	N 55°03'25"	W 111°53'44"

Appendix 2: Ecosites and Soil Textures

Year Underplanted	Age of White Spruce When Sampled	Stand	Ecosite	Soil Texture
1994	15	Calling Lk #1	BM-d1.4/SM4	silty clay loam
1994	15	Calling Lk #2	BM-d1.4/SM4	silty clay loam
1994	15	Calling Lk #3	BM-d1.4/SM3 BM-d1.6/SM3	silt loam
1999	10	Shaw Lk	BM-d1.6/SM4	silty clay loam
1999	10	Touchwood	BM-d1.2/SM4 BM-d1.6/SM4 BM-d1.8/SM4	silty clay loam
1999	10	K Rd	BM-d1.3/SM4	silty clay loam
2004	5	Piche Rd #1	BM-d1.5/SM4	sandy clay loam
2004	5	Piche Rd #2	BM-d1.6/SM4	silty clay loam
2005	4	K Rd	BM-d1.6/SM4	sandy clay loam