Natural regeneration in the boreal forest: seedling establishment and success in western North American and European boreal forests

by

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Abstract

As the costs and ecological implications of intensive forest management rise, alternative management strategies that minimize intervention become more desirable options, particularly natural regeneration. Two locations were studied: the boreal mixedwoods of western North America (Alberta) and the European middle boreal (Eastern Finland). In Alberta, the impact of different substrates and surrounding vegetation on *Picea glauca* seedlings were evaluated in the four years following harvesting. Substrate had a significant impact on seedling success; thin organics and scarified substrates were best at supporting establishment, while thick organic substrates were poor. In Eastern Finland, regeneration was studied 11 years partial retention harvesting and prescribed burning were applied. Pioneer species benefitted from prescribed burning; variable retention at the levels studied did not affect the growth of these species. In both cases, natural regeneration is a viable management alternative, but standards must be inclusive of mixed species and increased time for establishment.

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I. Introduction

Natural regeneration – ecology of tree species

For millennia before the advent of forest management and modern silvicultural methods, natural regeneration sustained forest ecosystems. Tree species have developed adaptations for regeneration and modern forestry can take advantage of these. However, planting is often favoured over natural regeneration as it guarantees managers more control of species composition and density and offers potential growth benefits for the future stand (Ackzell 1993, Comeau et al. 2005). The efficacy of silviculture models based on an investment in artificial reforestation is being questioned as the cost of reforestation rises and the forestry community becomes more aware of the ecological consequences of intensive management. Natural regeneration provides a more cost-effective alternative based on pre-existing ecological systems that can be successfully included as part of a silviculture strategy (Lieffers et al. 1996, Wurtz & Zasada 2001, Comeau et al. 2005, Martin-DeMoor et al. 2010, Solarik et al. 2010).

In both the northern European and western North American boreal forests, most tree species are well adapted to regenerate after disturbance – namely fire – and the regeneration ecology of each species shows evidence of this adaptation. Some of the clearest examples can be found in pine (*Pinus* spp) species – jack pine (*Pinus banksiana*) in North America and Scots pine (*Pinus sylvestris*) in Europe – although broadleaf species (*Betula* spp. and *Populus* spp.) and *Picea* spp also regenerate in these conditions quite well.

Scots Pine in Europe and jack pine in North America are widely described as species adapted to a fire-dominated natural disturbance regime. Although neither species is well adapted to survive severe fire, both have ecological and regeneration strategies to quickly colonize after large disturbances (Carey 1993, Sullivan 1993, Kuuluvainen & Rouvinen 2000). Notably, jack pine has serotinous cones specifically designed to open in high temperatures (Carey 1993). While Scots pine does not share this characteristic, most seeds originate from the well-protected cones in trees remaining after the fire or from nearby stands (Sullivan 1993). Seedlings of these tree species establish best on exposed mineral soil sites with high light conditions, like those found after a disturbance (Carey 1993, Sullivan 1993)

European trembling aspen (*Populus tremula)* in Europe and trembling aspen (*Populus tremuloides)* in North America are both adapted to rapidly colonize after a disturbance, particularly low-severity fires. On a local scale, their dominant regeneration strategy is to produce dense stands of ramets that grow rapidly from expansive root systems after a loss of apical dominance when the parent tree is killed (Bärring 1988, Howard 1996, Myking et al. 2011). While this strategy of vegetative reproduction can be quite successful after harvesting, it does not work in the case of severe fires or disturbance where underground root structures are destroyed. In this case, regeneration by seed on the recently burned site is another strategy that allows aspen to invade recently disturbed areas (Bärring 1988, Howard 1996). Mature aspen produces millions of tiny seeds that are capable of travelling great distances in the wind (Bärring 1988, Howard 1996). While these seeds face very high mortality rates, a recently exposed area with little or no other vegetation can provide excellent conditions for germination in the right climate and the surviving seedlings grow quickly (Bärring 1988, Howard 1996).

In European forests, silver birch (*Betula pendula*) and downy birch (*Betula pubescens*) are pioneer species and both employ a similar sexual regeneration strategy to the aspens, i.e., production of large quantities of tiny seeds that require ample light and moisture to successfully establish. Exposed mineral soil following disturbance can be an ideal substrate (Atkinson 1992, Nilsson et al. 2002, Hynynen et al. 2010). Once established, seedlings are able to tolerate poor soil conditions and grow very rapidly (Atkinson 1992, Nilsson et al. 2002, Hynynen et al. 2010). Although these species are capable of vegetative reproduction via stump sprouts, this is not the predominant regeneration strategy.

While the previously discussed species clearly have adaptations to regenerate following disturbance, particularly fire, spruce (*Picea* spp.) are not often described as species relying on disturbance for regeneration. Norway spruce (*Picea abies)* in Europe and white spruce (*Picea glauca*) in North America tend to be more climax species and share very similar characteristics in terms of regeneration ecology. However, recent research has shown that stands dominated by white spruce have mostly originated following fire (Kemball et al. 2006, Gärtner et al. 2011) and Norway spruce seedlings also benefit from mineral or thin organic substrates (de Chantal et al 2003*b*, Kuuluvainen & Kalmari 2003) suggesting that these tree species also can take advantage of soil disturbance to some extent for successful regeneration.

DISTURBANCE AND FOREST REGENERATION

Historically, the European boreal was dominated by a cycle of either low or moderate severity fires (Kuuluvainen & Rouvinen 2000), similar to fire-dominated disturbance regime present in western boreal forests of North America (Wurtz & Zasada 2001, Brassard & Chen 2006). These fires result in a mosaic-like distribution of substrates across the disturbed area that varies depending on the substrate and environmental conditions (Wurtz & Zasada 2001, Johnstone & Chapin 2006, Kemball et al. 2006, Greene et al. 2007). Boreal tree species have adapted to this disturbance regime over generations; however, this cycle of fire based disturbance has changed – particularly in Europe where fire has been practically eliminated from the forested landscape (Östlund et al. 1997) – and natural regeneration must occur under new and different conditions. Due to fire suppression, forest disturbance in the European boreal is now primarily a result of intensive management activities where openings are created by harvesting (Fries et al.

1997, Östlund et al. 1997). This shift is also occurring in Canada where forest fire suppression has increased over the past century and forest management activities have affected greater areas of the landscape, although vast forest areas still burn annually. In both Europe and North America, planting is often used to reforest harvested areas.

Planting is often the preferred regeneration method as it allows managers to confidently meet objectives for species composition, stocking, and rapid growth. Although this varies slightly by species, planting is the primary means of regenerating white spruce (Greene et al. 1999, Gärtner et al. 2011), Norway spruce and Scots pine (Mielikäinen & Hynynen 2003). Spruce are widely planted to achieve target densities; natural regeneration is considered unreliable due to limited seed sources and a lack of suitable microsites (Hagner 1965, Greene et al. 1999, Mielikäinen & Hynynen 2003, Gärtner et al. 2011). While planting offers this same advantage for pines, a greater benefit for these species is the superior height and growth planted seedlings have over neighbouring vegetation (Ackzell 1993, Comeau et al. 2005), as small seedlings are poor competitors in thick vegetation (Nilsson et al. 2006). Similarly, silver birch may be planted for superior growth and wood quality, but it is more commonly established through natural regeneration (Yrjölä 2002, Hynynen et al. 2010).

Natural regeneration is already being used operationally as a regeneration method for several boreal tree species, but its use is relatively limited even though it holds some distinct economic and ecological advantages. By using natural regeneration – an established natural system – the cost of planting is not incurred thereby reducing reforestation costs (Lieffers et al. 1996). Instead, reforestations costs would likely be in the form of site preparation before or stand tending after the regeneration establishes (Comeau et al. 2005); these costs, however, are often incurred in planted stands as well. Natural regeneration in the boreal is likely to be composed of a greater diversity of species than a plantation. It is important to consider that this mixture may have a greater overall yield than a monoculture at the time of harvest (Mielikäinen & Hynynen 2003, Comeau et al. 2005). Beyond these economic advantages, the diverse species composition that is often found in naturally regenerated stands is ecologically beneficial and maintains the patterns and processes of natural systems (Lieffers et al. 1996), which in turn has benefits for wildlife and has other ecological values (Bergeron et al. 2014). In order for these benefits to be seen for forest operations, managers must accept some of the challenges associated with natural regeneration: it is less predictable (Gärtner et al. 2011) and will have delayed establishment when compared to planted stands (Lieffers et al. 1996).

In order to encourage natural regeneration to establish quickly and reliably, it is critical that managers consider the substrates available after disturbance and their suitability to support the germination and establishment of seedlings. Appropriate seedbeds are essential to ensure that seeds are able to germinate and establish successfully on a site (DeLong et al. 1997, Greene et al. 1999, Peters et al. 2005, Bergeron et al. 2014). In order to increase the availability of high-quality substrates after harvesting, site preparation (DeLong et al. 1997, Wurtz & Zasada 2001, Kuuluvainen & Kalmari 2003, Nilsson et al. 2006, Gärtner et al. 2011) or prescribed burning (Greene et al. 2007) may be used to reduce or remove thick organic soil layers. If we are to increase the amount of natural regeneration as part of our silvicultural strategy, we need to better understand the nature of where and how this regeneration is successful in harvested forests and the role substrates play in this.

Contents

The first study was established in the broadleaf-dominated boreal mixedwoods of Alberta, Canada. Here, white spruce regeneration is being found in harvested areas where few seed sources are present – deciduous-dominated forests – suggesting that substrates present on these sites are successfully supporting the establishment of seedlings from the few seeds that are present. However, there is very little known about the quality and availability of seedbeds for white spruce in these harvested areas. The current practice of artificial regeneration of white spruce in this region has reduced the need to understand the opportunities for natural regeneration; however, the economical and ecological benefits of natural regeneration are making it more attractive to forest managers and there is a need to better understand the factors supporting this. The objectives of this study were to:

- assess the availability of intact substrates after harvesting in the broadleaf-dominated boreal mixedwood forest,
- assess the viability of these substrates for natural white spruce germination, and
- quantify the effects of surrounding vegetation on the survival and growth of white spruce seedlings

The second study took place in the boreal forests of Eastern Finland where human intervention has shaped the forest landscape for centuries. In recent decades, forest management has intensified to maximize the amount of wood products produced from the land and as a result, critical forest habitats – especially deadwood – have been lost (Hyvärinen et al. 2006, Gustafsson et al. 2012, Lindenmayer et al. 2012). Novel forest management practices – aimed at emulating natural disturbance patterns and processes – to increase deadwood features on the landscape are being tested to determine their impact on local biodiversity and threatened species. This landscape-level experiment included harvesting four different retention levels on ca. 4 ha stands; half the replicates were treated with prescribed burning and half were not. However, in order for these to be practical forest management alternatives, the natural regeneration resulting from the practices must be successful in terms of tree density and quality. This study investigated the success of regeneration of four different tree species ten years after treatments were applied.

The objectives of this study were to:

- test if novel forest management practices (prescribed burning combined with green-tree retention) have a significant effect on the regeneration quantity and quality of four native tree species, and
- assess if natural regeneration following treatments meets government-recommended standards for forest regeneration.

II. What substrates best support white spruce regeneration in the Western boreal mixedwood forest?

INTRODUCTION

BACKGROUND

Suitable substrates and density of seed rain have been described as the most important factors in determining white spruce germination rates, in both intact forests (Nienstadt & Zasada 1990, DeLong et al. 1997) and in recently burned stands (Greene et al. 1999, Charron & Greene 2002, Peters et al. 2005, Greene et al. 2007). While seed production depends on the masting nature of white spruce – controlled by climate and site conditions (Gärtner et al. 2011) – the effect of seedbed types in harvested areas on the germination and establishment of white spruce seedlings is not as clearly understood (however, see Wang & Kemball 2005) and is the focus of this study. As the cost of reforestation continues to grow relative to the value of the wood harvested, natural regeneration becomes an important economical alternative (Gärtner et al. 2011), so it is very important to understand the factors influencing incidental natural regeneration of these conifers.

Following harvesting, regeneration of white spruce in the boreal mixedwood is primarily done through planting seedlings because natural regeneration is less predictable and success cannot be guaranteed (Greene et al. 1999, Gärtner et al. 2011). As planting is expensive it must hold distinct benefits over natural regeneration. The advantages of planting established white spruce seedlings appear to be three-fold: their numbers and spatial distribution are dependable, shovels can drive their root systems through inhospitable substrates to reach mineral soil at the time of planting and therefore they get a head start in life. There is growing evidence, however, that natural regeneration for white spruce may be a successful cost-effective strategy, in the right conditions (Wurtz & Zasada 2001, Martin-DeMoor et al. 2010, Solarik et al. 2010). The question remains, however, what are the specific microsites most successful for germination of these naturally regenerated spruce – often called incidental conifers in the re-establishment of these forests.

Effect of substrate

Deciduous-dominated mixedwoods can apparently support good regeneration of white spruce, despite relatively few seed-producing spruce trees nearby (Solarik et al. 2010). It would therefore seem that microsite availability may be a more important limiting factor than previously understood for determining the amount of white spruce natural regeneration in these boreal mixedwood forests. There is already some evidence suggesting that the substrates available in coniferous-dominated mixedwoods – feather mosses and needle litter (Wurtz & Zasada 2001) – provide poorer conditions for seedling germination and establishment than substrates in burned deciduous-dominated forests (Greene et al. 1999) where feather mosses are less abundant (Wang & Kemball 2005). We aim to investigate the availability and suitability of these substrates in harvested sites in order to better understand the conditions that allow white spruce regeneration in these deciduous-dominated boreal mixedwoods. Our research includes new aspects of site assessment by including original broadleaf forest floor soon after harvest before being covered in thick layers of litter in the years following harvest; the result of this may be surprising as substrates have not been previously investigated in these conditions. If we find that the harvested deciduous-leading mixedwoods are dominated by leaf LFH and we find it to be a desirable substrate, it will then be clear that given an adequate seed source, there is great potential for white spruce natural regeneration in these stands.

It is generally acknowledged that sites with thin layers of litter and duff are better substrates for white spruce germination and establishment than those with a thick, intact layer of coarse organic material (DeLong et al. 1997, Greene et al. 1999, Wang & Kemball 2005, Greene et al. 2007, Gärtner et al. 2011). Harvesting leaves these surface organics more or less intact compared to the fire, the typical natural disturbance. Thus, in the absence of site preparation in harvested areas, little natural regeneration is expected due to slash, feather mosses and organic layers, especially on aspen-dominated sites, which have thick layers of leaf litter added each year, which can also increase overwinter mortality by smothering or crushing small seedlings (Greene et al. 1999, Wang & Kemball 2005). Despite these problems, regeneration of white spruce at good densities can occur on undisturbed forest floor after logging (Wurtz & Zasada 2001, Martin-DeMoor et al. 2010). This is further supported by the natural occurrence of white spruce seedlings found in regeneration surveys of deciduous leading cut blocks without planting of spruce (Weyerhaeuser, personal communication). We believe that these incidental conifers are no coincidence.

Substrate qualities

Across the spectrum of the boreal mixedwood the forest floor can be categorized into broad substrate categories: leaf litter and needle LFH, mosses, rotten wood and mineral soil. Immediately following disturbance, mineral soil and thin humus layers provide the best seedbeds, while decayed logs provide the best opportunities for seedlings in an intact forest (Brassard & Chen 2006, Gärtner et al. 2011). As the resources in white spruce seeds are low, germinants must quickly develop a root that gives them access to a relatively stable water source (Greene et al. 1999, Gärtner et al. 2011). In general, good microsites are relatively warm, have low soil strength, low quantities of competing vegetation and do not accumulate litter (DeLong et al. 1997); elevated seedbeds best provide these conditions (Wang & Kemball 2005, Gärtner et al. 2011).

<u>Leaf litter and LFH</u>

Leaf litter and coarse surface organics are some of the most widely available substrates for germination, although they are also thought to be some of the poorest (DeLong et al. 1997, Greene et al. 1999, Wurtz & Zasada 2001, Wang & Kemball 2005, Greene et al. 2007). The small seeds of white spruce can fall deep into the loose layers where germinants are unable to reach a light source and subsequently die (Gärtner et al. 2011). In deciduous-dominated forests if seeds are able to germinate, multiple layers of broadleaf litterfall can decrease overwinter-survival (DeLong et al. 1997). These surface organics tend to be very porous and are prone to rapid desiccation in dry periods making them unstable to deliver moisture to germinants (Greene et al. 1999, Wang & Kemball 2005, Greene et al. 2007), which may be further worsened by exposure following harvesting. Harvesting operations will mostly compress leaf and needle LFH layers and may expose some mineral soil where turning or skidding of logs moves the LFH layer (Wurtz & Zasada 2001), but will not consume the materials -as they would be in a fire - to expose the favourable mineral soil and well-decomposed organic substrates (Greene et al. 2007).

<u>Feather mosses</u>

Feather mosses are most common in coniferous-dominated forests; they do occur in deciduous-dominated mixedwoods, but are very rare, as aspen leaf litter smothers the moss and the phenolic compounds of aspen leaves kill mosses (Startsev et al. 2008). These moss-dominated layers – including their lower decomposing organic horizons – can average 10 cm to 30 cm in depth and are generally considered to be lethal seedbeds for white spruce seeds both because of their porous structure and the fact that the moss may grow faster than a spruce germinant (Wurtz & Zasada 2001, Johnstone & Chapin

2006, Gärtner et al 2011). Like litter layers, seeds can fall deep into thick feather mosses where germinants are unable to reach a light source or roots are unable to quickly penetrate below the mosses to reach a stable moisture source (Nienstadt & Zasada 1990, Nilsson et al. 1996, Gärtner et al. 2011). There is evidence that *Pleurozium schreberi* (Brid.) Mitt. restricts the germination of seeds not only through physical limitations, but also chemical interference by acting as a nutrient barrier – intercepting nutrients from canopy throughfall – preventing successful seedling establishment (Nilsson et al. 1996). Feather mosses usually die after harvest due to increased exposure – direct sunlight and moisture fluctuations – causing the chemical and nutrient barrier of feather mosses that dominate the forest floor to temporarily shut down (Nilsson et al. 1996, Wurtz & Zasada 2001). However, the dead moss persists as loose surface organic matter for several years, leaving an unsuitable substrate for white spruce recruitment from seed.

Rotten Wood

The most important substrate for white spruce seedling recruitment in intact deciduous dominated mixedwoods is rotten logs (DeLong et al. 1997). They represent the third most common substrate in pre-harvest sites and are the favoured substrates for natural regeneration in those conditions (DeLong et al. 1997). There are many factors that influence the amount of downed and decaying wood available including the disturbance regime, time since disturbance, climate, tree species and site productivity (Brassard & Chen 2006). The success of recruitment on rotten logs is dependent on their elevation above the surrounding forest floor and vegetation so that leaf litter is shed and also that the log is in an advanced state of decay where roots can easily penetrate to deeper layers (DeLong et al. 1997, Brassard & Chen 2006, Gärtner et al. 2011). However, rotten logs that are usually hospitable to seedlings while intact might be broken up by logging equipment or risk desiccating rapidly due to their porous nature (Wang & Kemball 2005, Johnstone & Chapin 2006). Additionally, logging deposits an added layer of new woody material created from the delimbing and skidding of harvested trees that occupies microsites and decreases the soil temperature (Landhäusser 2009). These slash loads decompose within a few years and never act as suitable seedbeds as large snags would (Brassard & Chen 2006).

Exposed mineral soil

Exposed mineral soil is perhaps the most rare yet the most favourable for the recruitment of white spruce seedlings in intact forests (Wurtz & Zasada 2001, Wang & Kemball 2005, Gärtner et al. 2011). This substrate is able to provide stable moisture conditions on the surface (Wang & Kemball 2005, Kemball et al. 2006) through capillary action from lower horizons allowing it to support drought-sensitive white spruce seedlings and germinants (Greene et al. 1999, Gärtner et al. 2011). The creation of exposed mineral soil in intact boreal mixedwood forests depends on specific events such as tree tip-up or animal burrowing (DeLong et al. 1997). During harvesting these relatively rare substrates are susceptible to infilling by the mixing of organic matter and logging debris. Thus, the likelihood of harvesting preserving exposed mineral soils is low, but equipment and logging operations can also disturb the forest floor causing some mixing of the organic layers and even exposure of mineral soil (Wurtz & Zasada 2001, Martin-DeMoor et al. 2010, Gärtner et al. 2011), thereby giving some opportunity for white spruce seedlings to establish. Solarik et al. (2010) found that skidding trails clearly increased the density of white spruce regeneration on harvested sites with partial retention.

Competition

In addition to substrate qualities, competing vegetation influences the quality of the microsite for regeneration by influencing light and moisture conditions. Open conditions following harvesting tend to benefit invasive early successional species that compete with seedlings (Brassard & Chen

2006). One of the biggest concerns is that surrounding vegetation can crush seedlings, especially when weighed down with snow (Martin-DeMoor et al. 2010). Especially high densities of grasses (e.g. *Calamagrostis* sp.), herbs (e.g. *Epilobium angustifolium*) and *Populus tremuloides* regeneration can have a negative effect on white spruce seedlings (Wurtz & Zasada 2001, Martin-DeMoor et al. 2010, Solarik et al. 2010, Gärtner et al. 2011). However, white spruce is generally shade-tolerant (Wang & Kemball 2005) and seedlings are able to adapt to somewhat shaded conditions (Feng et al. 2006, Gärtner et al. 2011). Understorey vegetation may even offer benefits to seedlings by increasing surface humidity and providing some shelter (Wang & Kemball 2005). Given the potential for both positive and negative effects of surrounding vegetation on the growth and survival of white spruce seedlings we wanted to explore this issue further.

OBJECTIVES

The objective of this study is to assess the viability of different post-harvest germination substrates in the boreal mixedwood forest in terms of availability and suitability to host white spruce germinants when there is an abundant supply of natural seed. We hope to clearly demonstrate which substrates – accounting for both quantity and quality – play a key role in white spruce natural regeneration.

In this study we will determine where and when white spruce is naturally regenerated in harvested areas in two aspects: substrate and neighbouring vegetation. This is done by assessing substrate availability and suitability for white spruce establishment and quantifying the effects of competing vegetation on growth and mortality of white spruce seedlings. As a result, we will be able to better understand the dynamics of white spruce recruitment in harvested areas so that we may inform future management decisions concerning the natural regeneration of white spruce in the boreal mixedwood.

METHODS

OVERVIEW OF EXPERIMENTS

The research presented herein is comprised of three components designed to investigate the establishment, survival and growth of white spruce seedlings in the boreal mixedwood forests of Alberta. Part I focussed on the germination success of seeds artificially distributed on natural and prepared microsites. Part II investigated natural regeneration (germination and early survival) as affected by microsite type and part III focussed on the subsequent success of these seedlings as affected by competing vegetation.

Forests on the study sites were boreal mixedwoods dominated by either trembling aspen (*Populus tremuloides* (Michx.)) or white spruce (*Picea glauca* (Moench) Voss); other tree species included balsam poplar (*Populus balsamifera* Linn) and white birch (*Betula papyrifera* Marshall). The sites were classified as upland mesic (Natural Regions Committee 2006) and soils were generally relatively moist and rich. Soils on the sites were classified as orthic grey luvisols on a parent material of morainal glacial till. The study region, overall, is dry (450 – 550 mm annual precipitation, of which ~ 70% is rain) with cool short summers (average May to August temperature 11 – 13 °C).

ARTIFICIAL SEEDING AND FIRST-YEAR SUCCESS

Study site and sampling design

Part I of the study took place in several different management areas in the Peace River region ((56°N 116°W) that were either broadleaf (trembling aspen) or coniferous (white spruce) dominated. These areas were harvested in the winter of 2005/2006 following a white spruce masting event in the late summer of 2005. Following harvesting, site preparation using a ripper-plough was completed on coniferous sites in the winter of 2006/2007. Broadleaf sites had no-site preparation activities completed on them;

however, harvesting machinery and activities caused some disturbance and mineral soil exposure.

Transects were laid out in May of 2007 following site preparation. On coniferous sites five transects were established with 10 points marked using stakes every 50m for the entire 450m transect length (Figure 2- 1). Broadleaf sites had shorter transects as the length was restricted by the opening size; transects were 45m long and 10 points were marked using stakes every 5m (Figure 2- 1). Of the 10 stakes on each transect, eight were randomly selected and at each of these, the nearest example of each of several substrates (Figure 2- 1, Table 2- 1) was selected for seeding. The two remaining stakes were left unseeded as controls to determine natural regeneration rates (Figure 2- 1). The substrates that we sowed represent the range of available substrate types in the broadleaf forest and those naturally occurring in the harvested coniferous forest as well as those created by the site preparation. Site preparation was by ripper plough. The design was a randomized complete block where each stake was a block with one replicate of each substrate type. To assess availability of the different substrate types (Table 2- 1) the substrate was assessed every 1m along the entire length of all transects.

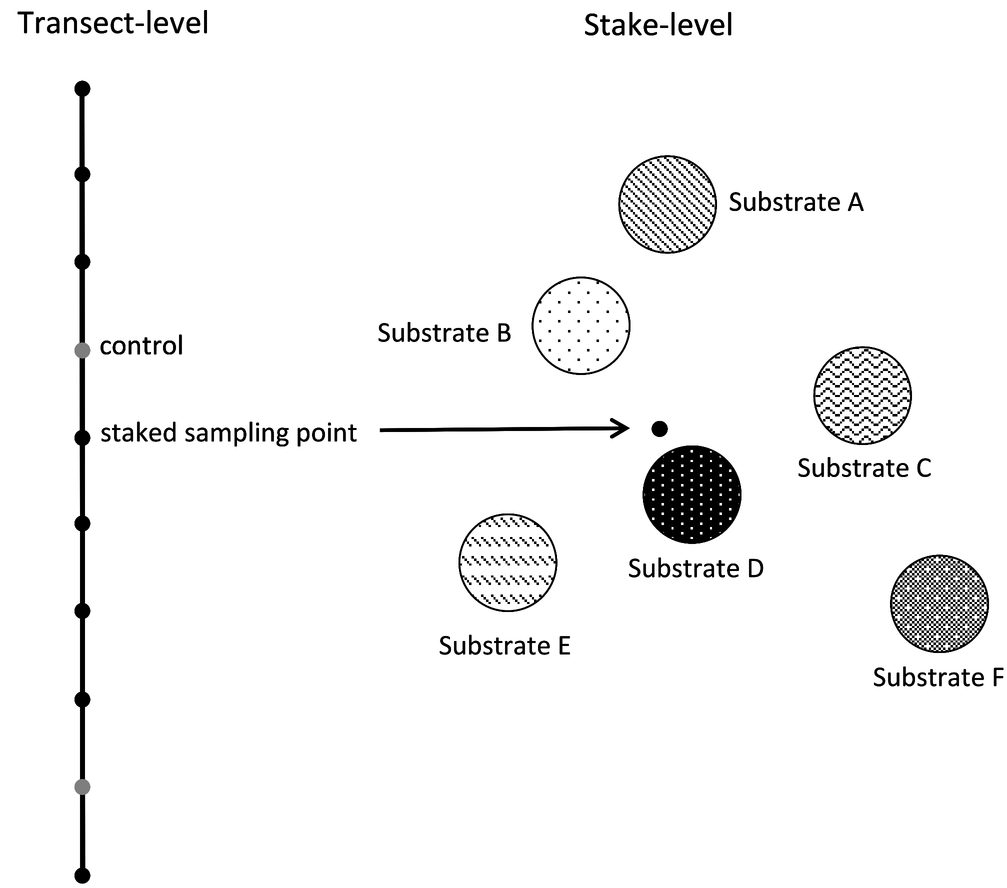

Figure 2- 1: Transect design (left) and seeding method design (right) for artificial seeding study. Transects were 450 m or 45 m long with 10 evenly spaced stakes. Two stakes on each transect were randomly selected as control sites (examples in grey). At the remaining eight stakes (examples in black), the example of each selected substrate (Table 2- 1) nearest to the stake was selected and a 20cm^2 area was seeded with 77 seeds on each.

Table 2- 1: Description of the defined substrate categories identified for artificial seeding grouped by pre-harvest forest composition in the Peace River region.

Site Type	Substrate	Description
broadleaf	mineral	Mineral soil exposed through the disturbance of the LFH layer during harvesting
	moss	Intact mosses >3cm depth from the pre-harvest forest (usually dying)
	rotten wood	Decaying wood that was dead and in the soft phase pre-harvest
	thin LFH	Leaf litter layer over a fine organic and humic layers with a total depth ≤ 5cm
	deep LFH	Leaf litter layer over fine organic and humic layers with a total depth > 5cm
	solid wood	Coarse woody debris created by harvesting (no seeds sown on this substrate)
Coniferous (no site preparation)	litter	Needle litter layer over fine humic layers
	moss	Intact feather moss > 3cm depth from the pre-harvest forest (usually dying)
Coniferous (site preparation-ripper plow)	trench	Cut depression with mineral soil exposed by site preparation
	mound	Overturned raised layer of loose mineral soil displaced from trench and deposited next to scarification track
	scalped	Bladed exposed flat mineral soil
	shelf	Flat area of broken up mineral soil higher than the scalp on the side of the trench
	FH	Needle litter scraped off leaving FH layer
	rotten wood	Decaying wood that was dead pre-harvest and scraped clean of debris by scarification
	slash	small woody material and organic matter created during harvesting (no seeds sown on this substrate)
	solid wood	Coarse woody material created by harvesting (no seeds sown on this substrate)

Seeds were not sown on substrates that were known to be completely unfavourable for establishment (slash pile, solid wood) but we did assess the availability of these substrates. The seeded area for each example of each microsites was small; 20cm^2 in order to ensure a uniform substrate. 77 seeds were distributed across this area. Seeds originated from a local population (seed zone 71 in Alberta) and were sourced from Smoky Lake Tree Improvement Centre. These were reported to be 78% viable; therefore, approximately 60 of the 77 seeds on each microsite could germinate.

In late August, four months following seeding, the number of live and dead recruits was recorded to determine the proportion of germination by substrate type. The germination potential of each prepared and natural microsite was then determined; the average germination success in the first growing season after seeding was calculated for each substrate.

Analyses

We examined the effect of substrate on germination percentages using an analysis of variance (PROC MIXED in SAS 9.3) with the model designed as follows: $Y_{ijk} = \mu + \tau_i + B_j + \varepsilon_{ijk}$, where Y_{ijk} is the germination percentage, τ_i is the substrate type (fixed effect), B_j is the block effect (stake, random effect) and ε_{ijk} is the residual error (sampling plots). Prior to these analyses, the data were transformed using $x' = \ln(x + 1)$ in order to meet assumptions of normality and homoscedasticity of the model residuals. An α-level of 0.05 was chosen for all our analyses.

SEEDLING ESTABLISHMENT FROM NATURAL SEEDING FOLLOWING A MAST SEED CROP

Study sites and sampling design

Part II of this study investigating the natural establishment of white spruce after harvesting of broadleaf dominated mixedwood stands took place in four regions of Alberta: Drayton Valley (53°N 115°W), Edson (53°N 116°W), Grand Prairie (54°N 118°W) and Peace River (56°N 116°W). In each region, transects to sample natural seedling establishment were laid out in multiple areas that were previously harvested; some large harvested openings had two transects established, but most only had one. Transects ranged in length between 45m and 250m depending on the size of the opening and 1m^2 quadrats were established every 5m or 10m depending on the total transect length. The total number of transects and plots established for this study are outlined in Table 2- 2.

Table 2- 2: Sample size for substrate preference study

Region	Boreal forest subregion	Years since harvest	Years since mast	No. of transects	No. of quadrats
Drayton Valley	Central Mixedwoods	4	2	15	348
Edson	Lower Foothills	4	2	6	109
Grande Prairie	Central Mixedwood	3	2	20	254
Peace River	Central Mixedwood	1	1	21	202

Drayton Valley and Edson sites were harvested in the summer of 2003 by Weyerhaeuser prior to the release of a mast seed crop in late summer and early fall. Thus, seeds dispersed from residual white spruce trees along the edge of the opening following harvest. Transects were laid out to quantify established natural white spruce seedlings in the spring of 2005 (two years following harvest) starting from seed sources along the opening edge and extending into the harvested area (Figure 2- 2). Along each transect, 1m^2 quadrats were established every 5m on transects less than 150m in length and every 10m for longer transects (Figure 2- 2).

Grande Prairie (harvested by Weyerhaeuser and Ainsworth) had a white spruce mast seed crop in the fall of 2003 and the areas were harvested in the winter of 2003/2004. Peace River (harvested by Daishowa-Marubeni International) had a mast crop in fall of 2005 and was harvested in the winter of 2005/2006. 45m transects were established in the openings in the spring of 2006 two years following harvest in Grand Prairie and one year following harvest in Peace River. This way, first year establishment and mortality could be sampled at Peace River sites in addition to the two-year data from other sites. 1m^2 quadrats were established every 5m along transects (Figure 2- 2).

Sampling of quadrats was similar at all sites. In each 1m^2 area, all white spruce seedlings were marked with a tagged flagged wire and their location relative to the plot centre was determined. Each seedling was assessed for total height, leader height and overall condition. The substrate type in which the seedling was rooted was recorded according to those listed in Table 2- 3. Substrate availability was assessed at each quadrat by noting the substrate (Table 2- 3) at the edge of the plot in the four cardinal directions (Figure 2- 2). The exception to this was in Peace River sites where substrate availability was sampled at 20 points surrounding each quadrat. Additionally, the vegetation and slash in the immediate area surrounding each seedling was recorded. If there were no seedlings present in a quadrat, only the substrate availability data were collected.

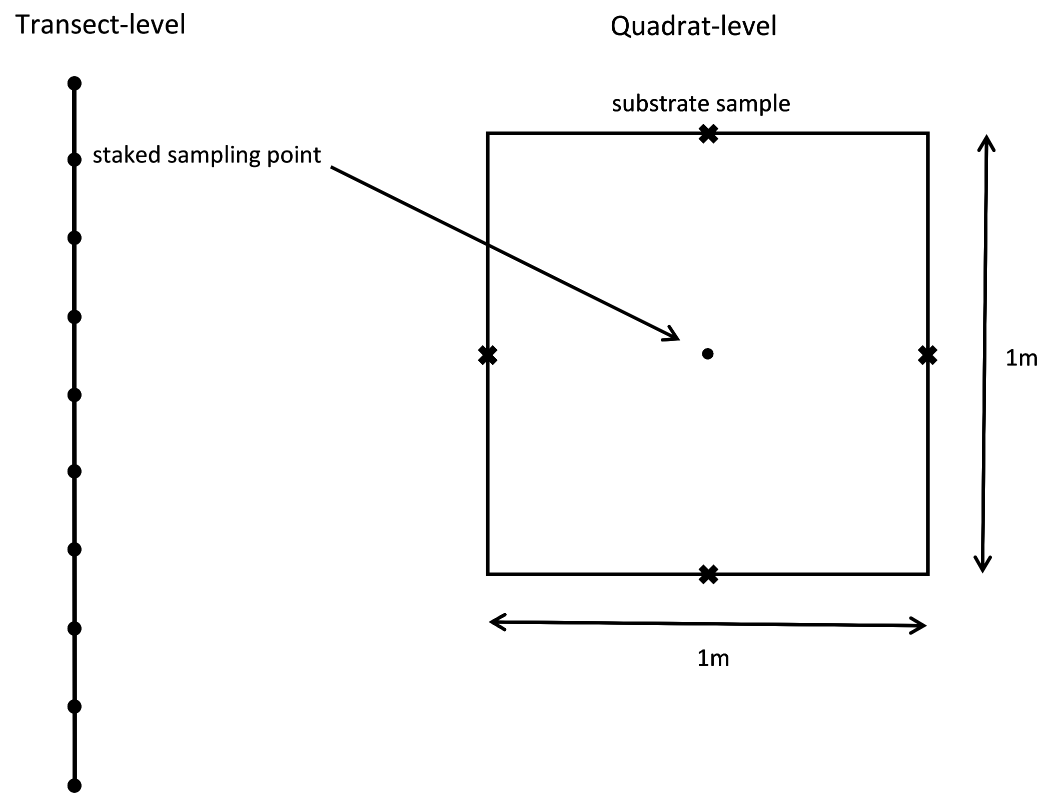

Figure 2- 2: Transect design (left) and quadrat design (right) for substrate sampling and survey of regeneration. Transects varied in length from 45m to 250m depending on the size of the opening and transects were evenly spaced every 5m or 10m along each transect depending on transect length. Substrate sampling was done at the edge of the quadrat (marked with "x") with the exception of Peace River. All white spruce seedlings and their surroundings within the quadrat were measured and recorded.

Table 2- 3: Description of the defined substrate categories for substrate preference/natural regeneration study

Substrate	Description
mineral	Mineral soil exposed through the removal of the LFH layer during harvesting
moss	Intact disturbance mosses > 3 cm deep
organic ≤ 5 cm	Leaf litter layer over a fine organic and humic layers with a total depth ≤ 5cm
organic > 5 cm	Leaf litter layer over fine organic and humic layers with a total depth > 5cm
rotten wood	Decaying wood that was dead and in the soft phase pre-harvest
solid wood	undecayed wood pre-existing harvesting or created by harvesting.

Analyses

Seedling and for the substrate availability counts were summarized by substrate and by region. The value of 1 was added to each count to ensure there were no zero counts during analyses. The count of seedlings in each substrate and the availability of each substrate were then used to quantify seedling substrate preferences in PROC CATMOD (SAS 9.3). Estimates calculated from the following models were used to quantify seedling preference for each substrate and region. The following model was used in analysis logit (seedling present) = intercept + influence of substrate + influence of region + substrate*region interaction. Quadrat was treated as the sampling unit and transect as a random variable in the analyses. In initial runs the interaction term was significant so we subsequently ran models for each region separately as follows: model logit (seedling present) = intercept **+** $ß_1X_1$ + $ß_2X_2$ etc. + where $ß_1$ is the influence of substrate1, $ß_2$ is the influence of substrate 2, etc.

MORTALITY AND GROWTH: THE EFFECTS OF SUBSTRATE AND COMPETITION

Study site and sampling design

Once established, the natural white spruce seedlings from part II were re-sampled in subsequent years to study their growth and mortality as well as the effects of substrate and competition on these factors; this formed part III of the study. Sites in Drayton Valley and Edson were re-sampled in 2006 and 2007 and Grande Prairie and Peace River sites were re-sampled in August 2007. The same seedlings were re-measured for total height, leader height and condition; substrates for each seedling were already recorded from the previous study. For the Peace River site only, seedlings were visited in spring 2007 and for each seedling we noted whether it was covered by leaf litter (no, partially covered, yes) and whether it was submerged in water (yes or no).

In addition to the re-measured transects, an herbicide treatment was applied to selected transects in the Grand Prairie region to remove a majority of the vegetative competition surrounding seedlings. 11 pairs of transects – 22 total – were established in 2005 and were 45m in length extending from the edge of the block to the centre (Figure 2- 3). One transect of each pair was sprayed with glyphosate in fall of 2005. The effectiveness of the herbicide treatment was determined in circular $10m^2$ plots every 5m along each transect (Figure 2- 3). Within each plot, all broadleaf stems of each species were recorded as healthy, slightly wounded, severely wounded or dead. This was re-measured and suckers were counted within the same areas in 2006.

Also in spring 2006, $4m^2$-sampling plots were established every 5m along the length of each transect (Figure 2- 3). White spruce seedlings within the plots that naturally established following the 2003 mast event were marked and their position was recorded relative to the transect. Seedling condition was noted and the total height as well as leader height of each seedling was measured. Vegetation surrounding the seedling (Table 2- 4) as well as presence of slash and rooting substrate were recorded for each seedling. Cover of the various types of overtopping vegetation was assessed as percent cover of a fixed area plot or by visualizing the cover in a 45° inverted cone over the seedling. Substrate availability was determined by recording the substrate present at points in each of the four cardinal directions on the plot edge. These measurements were repeated for each marked seedling along each transect in August 2007 to gain a better understanding of the survival and growth of spruce seedlings over multiple years in different conditions regarding competing vegetation.

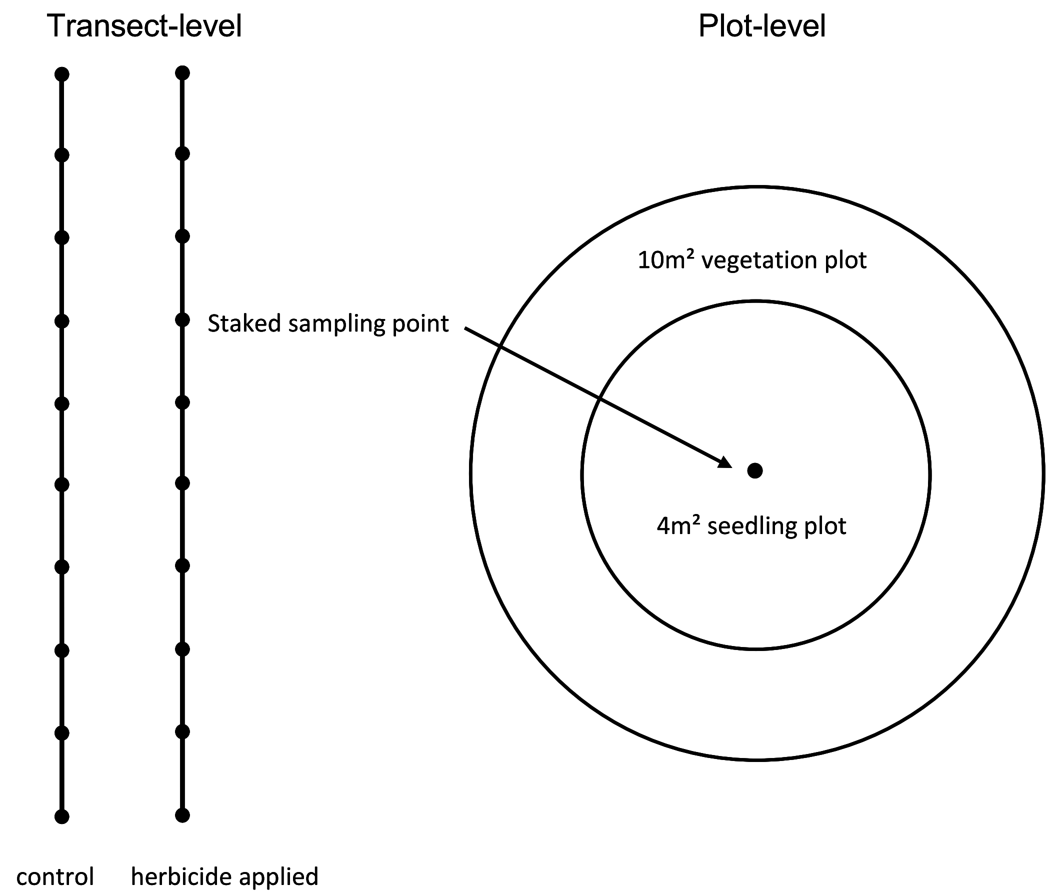

Figure 2- 3: Transect design (left) and sampling plot layout (right) for herbicide study in Grande Prairie. 22 transects 45m transects were laid out in 11 pairs; each pair of transects had one control transect with no herbicide applied and the other with a herbicide treatment applied. Sampling points were staked every 5m along transects and circular plots were done around each stake: 10m^2 plot for herbicide and vegetation cover, and 4m^2 plot for seedling growth and survival.

Table 2- 4: List and description of vegetation variables measured at all field sites.

Vegetation Variable	Description
number of saplings	Number of saplings >1.3m
cover of tall saplings	% cover saplings >1.3m
cover of saplings in cone	saplings vertical cone %
cover of short saplings	% cover saplings <1.3m
cover of tall forbs	% cover forbs >30cm
cover of forbs in cone	forbs vertical cone %
cover of short forbs	% cover forbs <30cm
cover of live grass	% cover live grasses
cover of live grass in cone	live grass vertical cone %
cover of all grass	live & dead grass % cover
cover of all grass in cone	live & dead grass vertical cone %
cover of all live vegetation	live total % cover
cover of all live vegetation in cone	live total vertical cone %
total of all cover	live & dead total % cover
total of all in cone	live & dead total vertical cone %

Analyses

Mixed model analyses of variance (proc mixed in SAS vers. 9.2) were used to compare vegetation between plots in which seedlings lived *versus* died. Seedling condition data were classified as either dead or live for these analyses. Each seedling was an individual sampling unit and transect was treated as a random factor in the analyses; each region was analysed separately. When there was a significant difference for a given vegetation variable we examined least-squares means (and standard errors) for plots with live *versus* dead seedlings to determine the direction of the difference. Model residuals were checked and no transformations were required to fulfill analysis assumptions.

We used categorical models (proc catmod in SAS version 9.2) to determine the influence of submergence and cover by leaf litter on seedling mortality at the Peace River site. An initial model was run, which showed that the interaction term between submergence and cover was not significant so for the final analysis we used the model without the interaction term. i.e., logit (seedling survival) = intercept + influence of submergence + influence of cover.

All analyses of seedling growth were done using R 2.15.1. The effect of surrounding vegetation on seedling growth in each region was first analyzed using mixed model ANOVA to determine significance of each measured vegetation variable (Table 2- 4) independently. The following model was used $Y_{ijkl} = \mu + \tau_i + \mathrm{T}_{j(i)} + P_{k(ij)} + \varepsilon_{ijkl}$, where Y_{ijkl} is the seedling growth, τ_i is the vegetation variable (fixed effect), T is the nested block effect (transect within treatment, random effect), P is the nested plot effect (plot within transect-treatment combination, random effect) and ε_{ijkl} is the residual error (seedlings). Model residuals were tested and square root transformations were applied only to Drayton Valley to obtain normalized residuals. Correlation was tested between all vegetation variables in each region. Uncorrelated (< 0.20) vegetation variables that were found to be significant or almost significant in ANOVA tests were then used to build regression models for seedling growth in each region. Mixed models were constructed using lme as follows y = intercept **+** $ß_1X_1$ + $ß_2X_2$ etc. where y is growth of a seedling $ß_1$ is the influence of vegetation variable 1, $ß_2$ is the influence of vegetation variable 2, etc for all significant uncorrelated vegetation variables. Again, each seedling was a sampling unit and plot was treated as a random factor nested within transect. These models were run in the "dredge" function ("MuMIn" package) to select variables and calculate coefficients used in the final model, which was chosen based on AIC. Residuals for final models were checked and it was confirmed that no further transformations were required.

Herbicide effectiveness and impact on seedling growth for the first year following treatment were analysed using R 2.15.1. Data from the paired transects in the Grande Prairie region were used for to test for significant differences in measured vegetation response (seedling growth and cover of competing vegetation) between transects with and without herbicide. The vegetation variables tested in the following analyses were seedling growth as well as competing vegetation variables (Table 2- 4). The following model was used, $Y_{ijkl} = \mu + \tau_i + T_{j(i)} + P_{k(ij)} + \varepsilon_{ijkl}$, where Y_{ijkl} is the vegetation response, τ_i is the herbicide treatment (fixed effect), T is the nested block effect (transect within treatment, random effect), P is the nested plot effect (plot within transect-treatment combination, random effect) and ε_{ijkl} is the residual error (seedlings or vegetation).

RESULTS

ARTIFICIAL SEEDING AND FIRST YEAR SUCCESS

On coniferous-dominated sites, substrate had a significant effect ($p < 0.0001$) on germination of white spruce following seeding onto a variety of natural and prepared substrate types. Substrates resulting from site preparation were better for seed germination than untreated coarse organics (Figure 2- 4 A). Shelf sites composed of loosened mineral soil on the side of the scarified trench and scraped rotten wood supported better ($p \leq 0.0750$) germination of white spruce than any other substrate (Figure 2- 4 A). Undisturbed litter and feather moss substrates as well as loose piles mineral soil cast off from scarification had negligible germination success compared to other microsites (Figure 2- 4 A). Other substrates created by site preparation – scalped mineral soil, exposed organic layer (FH), and lower trench positions – were moderately successful (Figure 2- 4 A).

The first summer success following sowing of white spruce seed onto unprepared microsites in deciduous-dominated sites showed that substrates also had a significant effect ($p < 0.0001$) on germination of white spruce. Rotten wood was a significantly better ($p < 0.0001$) germination substrate than any other substrate examined (Figure 2- 4 B); success was negligible on thin and thick litter, moss, and exposed mineral soil.

SEEDLING ESTABLISHMENT ON ASPEN-DOMINATED MIXEDWOODS FROM NATURAL SEEDING FOLLOWING A MAST SEED CROP

The most widely available substrate was surface organic material >5cm deep (Figure 2- 5 A); it comprised the greatest proportion of area occupied by each substrate type in all regions. Each of solid wood, rotten wood, and thin organics were found to cover less than 20% of the sites in all regions, while the least available substrates in these broadleaf stands were post-disturbance mosses and mineral soil (Figure 2- 5 A).

The analyses of substrates occupied by white spruce natural regeneration (Figure 2- 5 B) showed a similar pattern to the substrate availability (Figure 2- 5 A), with the exception of solid wood. Across all regions, white spruce seedlings rarely occupied solid wood (Figure 2- 5 B) despite its relative availability. Although there were some slight regional differences, most seedlings were found on thick organics – also the most available substrate – while post-disturbance mosses and mineral soil tended to be occupied slightly more often than they were available (Figure 2- 5 A & B). Rotten wood was not widely available and was not preferred, except for the Grande Prairie site; here rotten logs were more abundant than in other regions, and were frequently occupied (Figure 2- 5 A & B).

Post-disturbance moss was the most strongly preferred substrate with a strong positive effect on white spruce seedling establishment in all regions except Peace River (Figure 2- 5 C). The substrate with the strongest negative effect on first-year success was solid wood in all regions (Figure 2- 5 C). All other substrates were neither uniformly negative nor positive across all regions (Figure 2- 5 C).

In Peace River, mineral soil was more strongly preferred than other substrates (Figure 2- 5 C). Edson was the only region where mineral soil was not a preferred substrate for seedling establishment, although only slightly (Figure 2- 5 C). The thin organic substrate had a positive effect on seedling survival in all regions except Drayton Valley where it was slightly negative (Figure 2- 5 C). Effects of thick organics and rotten wood on the establishment of white spruce seedlings were variable by region and no clear pattern can be seen for preference of these substrates (Figure 2- 5 C).

Mortality and growth: the effects of substrate and vegetation

Mortality

In all regions, at least one vegetation variable showed a significant difference between plots in which naturally regenerated white spruce seedlings between the ages of one and three live *versus* died (Table 2- 5). Although no clear patterns were evident across all regions, grass cover tended to be higher in plots where seedlings died and this was significant in some regions. This was most evident in Drayton Valley where all variables measuring competing grasses – cover of live grass, live grass in cone, cover of all live and dead grass, and all dead and live grass in cone – were had a significantly negative impact on seedling survival (Table 2- 5). Additionally, the cover of all live and dead vegetation, all live and dead vegetation in the cone, and live vegetation in the cone were significantly negatively associated with seedling survival in Drayton Valley (Table 2- 5).

In Grande Prairie, forbs in cone as well as cover of short forbs were significantly higher in plots where seedlings survived, whereas seedling survival was lower with greater live grass cover (Table 2- 5). Similarly, in Edson, the cover of short forbs was significantly higher in plots with surviving white spruce seedlings.

A different pattern was found in Peace River where second summer survival of white spruce seedling survival was positively associated with competing saplings; number of saplings, saplings in the cone, cover of tall saplings, and the cover of short saplings were greater in plots with surviving white spruce seedlings (Table 2- 5A). Also at the Peace River site, both temporary spring flooding and especially cover by aspen leaf litter in spring reduced seedling survival to the fall (Table 2- 5B, Figure 2- 6).

Growth

In all regions except Edson, at least one vegetation variable had a significant effect on seedling growth (Table 2- 6). Square root transformations were required for Drayton Valley data to obtain normal model residuals, but no other data were transformed for these analyses.

Peace River had the greatest number – nine significant vegetation variables ($p \leq 0.05$) for predicting growth (Table 2- 6), of which three were chosen for inclusion in a model: number of saplings, forbs in the cone, and total grass in cone (Table 2- 7). All three vegetation variables were positively related to seedling growth, i.e. seedling growth was measured to be greater where number of saplings, forbs in the cone, and total grass in cone were also found to be greater.

Grande Prairie had only one significant variable, saplings in cone were negatively related to growth; cover of live grass was also tested for inclusion in the model, as it was almost significant (Table 2- 6). The best-fit model only included saplings in cone (Table 2- 7). Unlike Peace River, the saplings had a negative effect on seedling growth in Grande Prairie

Drayton Valley was found to have one significant variable – cover of tall saplings was negatively related to growth – when tested separately; however, total vegetation in cone was also included as it was almost significant (Table 2- 6). The best-fit model only included an intercept, so the second best model

– based on AIC – was used (Table 2- 7). Here, saplings also had a negative effect on the growth of white spruce seedlings.

Herbicide

Herbicide treatments completed in Grande Prairie were not found to have a significant impact on growth of seedlings ($p = 0.195$) in the first summer after treatment. However, herbicide treatment did have a significant negative affect on most vegetation variables (Table 2- 8). Competing saplings tended to be the most affected, while forbs and grasses were less so (Table 2-8).

FIGURES

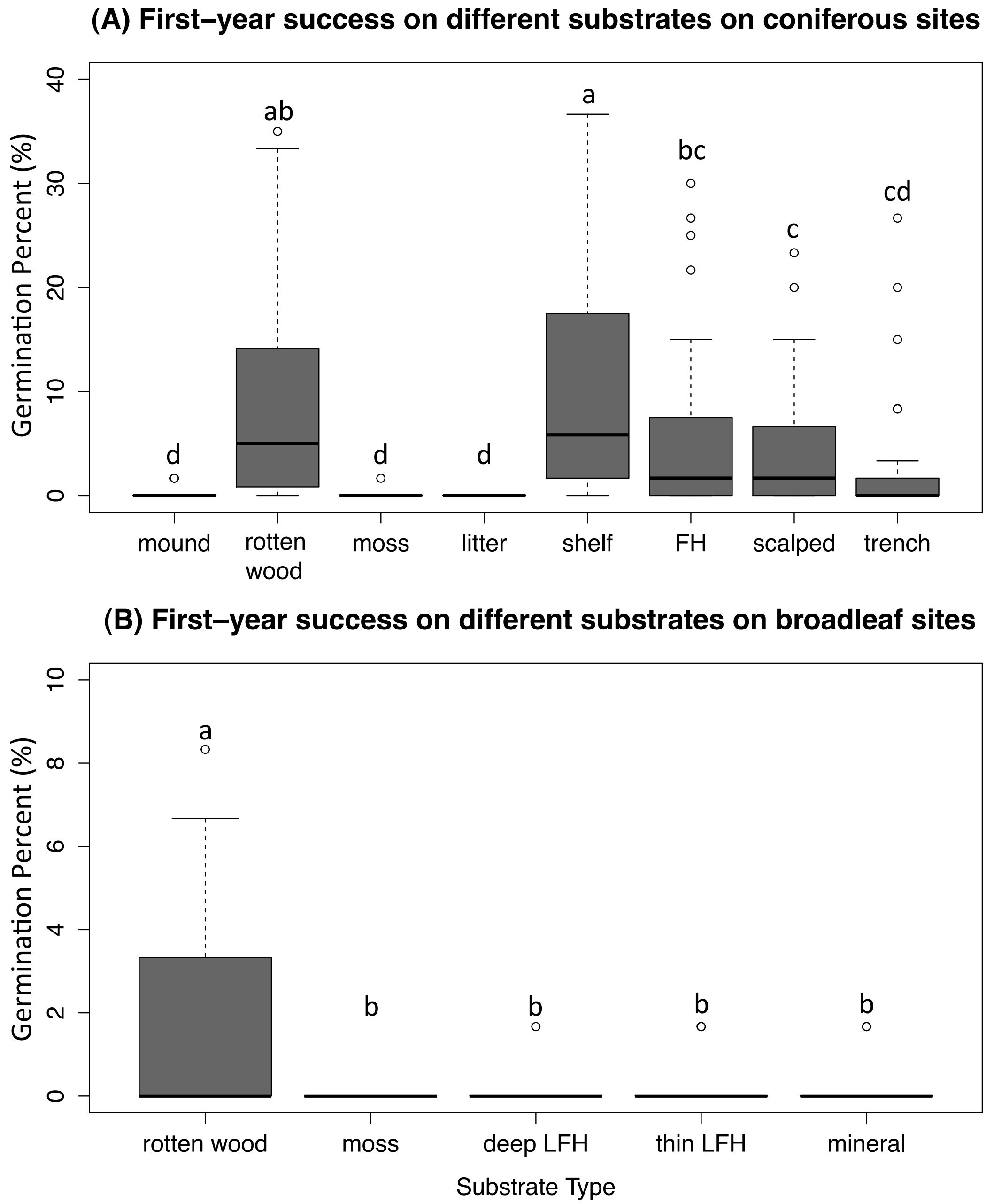

Figure 2- 4: Germination of seeded white spruce seedlings surviving after one growing season as a percentage of seeds sown of seeded white spruce on substrates in (A) harvested conifer-dominated mixedwood forest with site preparation (scarification) and (B) deciduous-dominated mixedwood forest without site preparation. Letters a-d denote significant differences ($p \leq 0.05$) between substrates. On coniferous sites (A) litter and moss (feather moss) were present without scarification; all others were impacted by – or the result of – scarification. Descriptions of substrates can be found in Table 2- 1

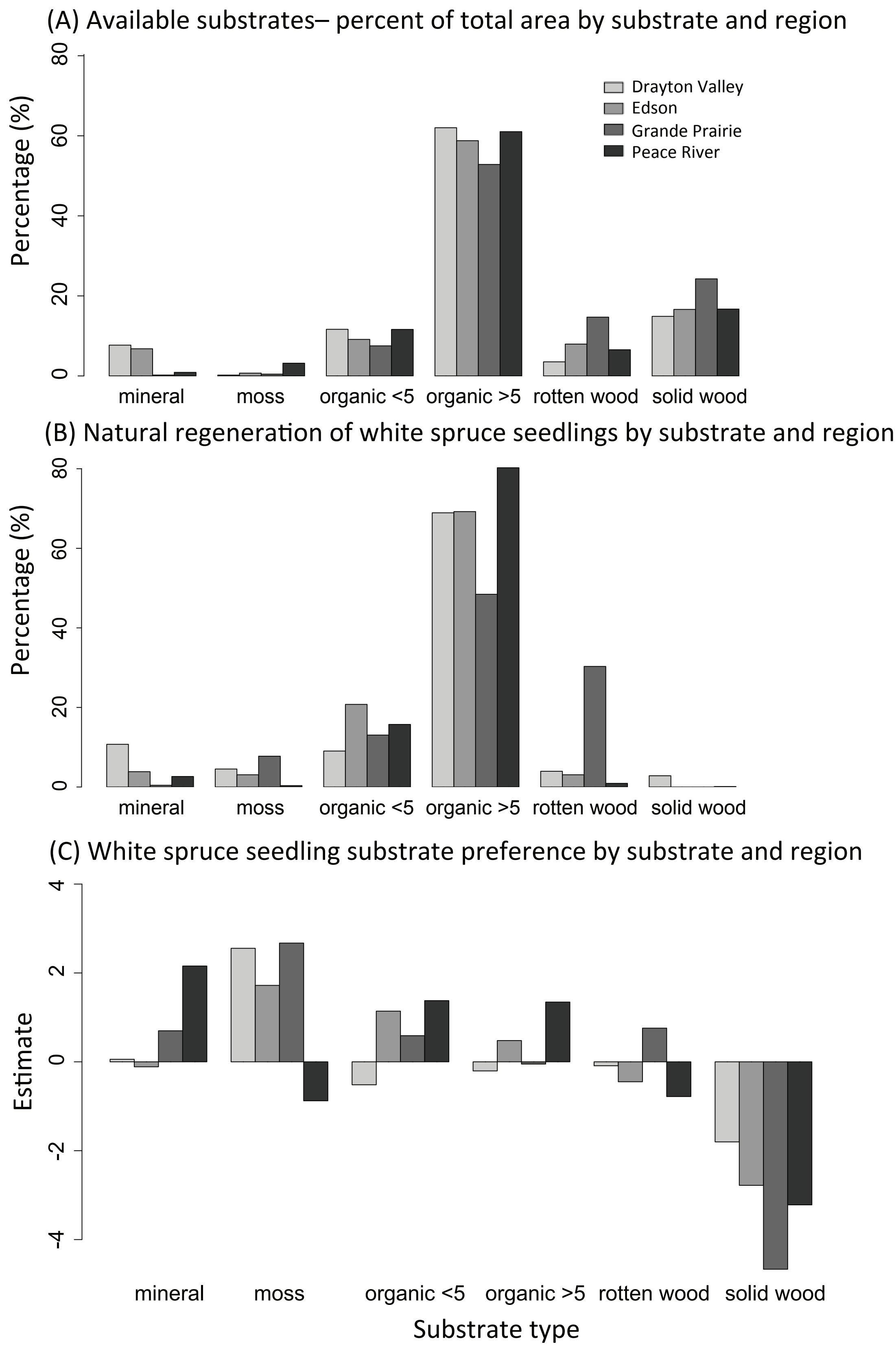
(A) Available substrates– percent of total area by substrate and region
Percentage (%)
0
20
40
60
80
Drayton Valley
Edson
Grande Prairie
Peace River
mineral
moss
organic <5
organic >5
rotten wood
solid wood
(B) Natural regeneration of white spruce seedlings by substrate and region
Percentage (%)
0
20
40
60
80
mineral
moss
organic <5
organic >5
rotten wood
solid wood
(C) White spruce seedling substrate preference by substrate and region
Estimate
-4
-2
0
2
4
mineral
moss
organic <5
organic >5
rotten wood
solid wood
Substrate type

Figure 2- 5: Results of substrate availability and seedling preference analyses for natural regeneration of white spruce in unprepared deciduous dominated mixedwood two years after logging. (A) Availability of different substrate types as a percentage of substrates encountered in random locations, categorized into each of six microsite categories, separately for each region. (B) Microsites supporting a naturally regenerated white spruce seedling in relation to all six substrate types, separately for each region. (C) Substrate preference for white spruce seedlings as indicated by the estimate for the influence of substrate on the probability of encountering a naturally established seedling. Estimates are from categorical models (proc CATMOD in SAS v 9.2); analyses were run for each region separately. Positive values indicate preferred substrates while negative values indicate non-preferred substrates. Exact descriptions of substrates can be found in Table 2- 3.

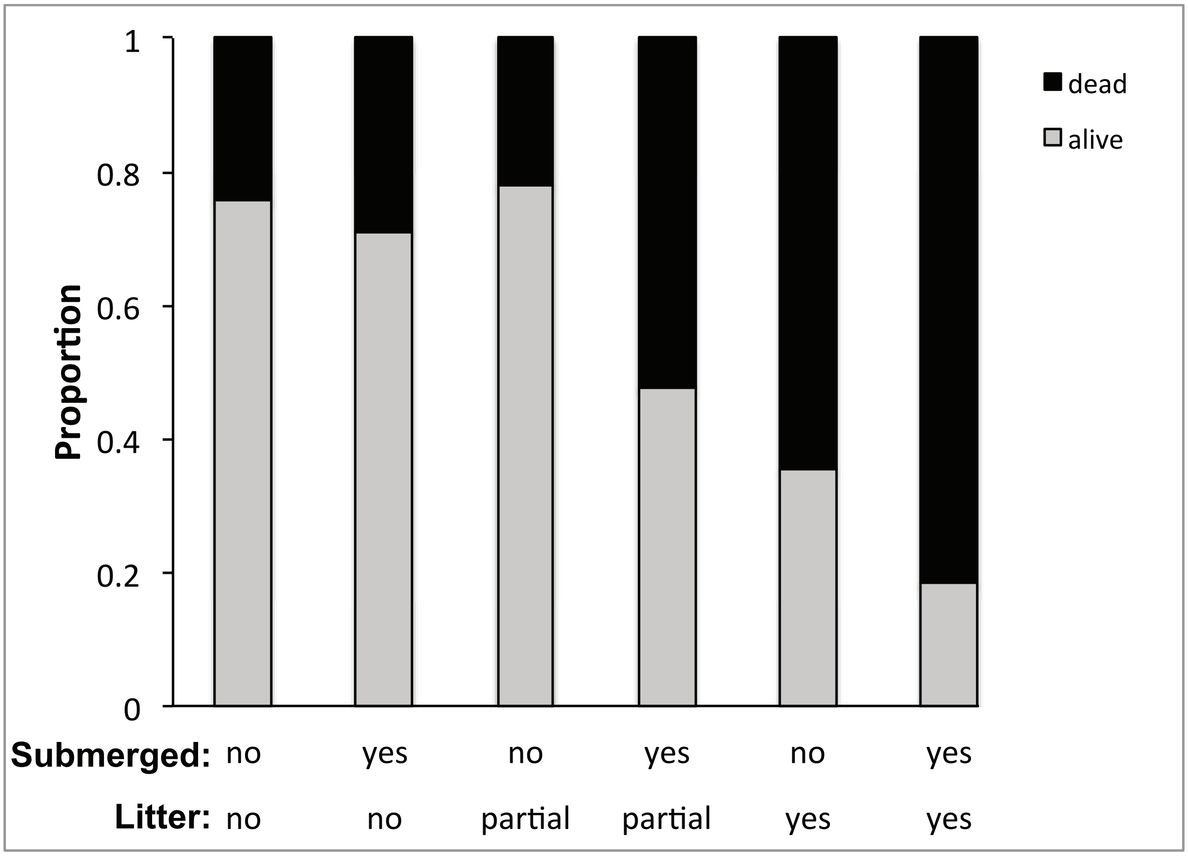

Figure 2- 6: Proportion of seedlings that lived and died by the end of their second growing season (Fall 2007) at the Peace River site as a function of whether they were covered by leaf litter (no, partially, yes) and whether they were temporarily submerged by water (no, yes) in the Spring of 2007. Each bar represents a possible combination of conditions (submergence and litter cover) and the proportion of seedlings that lived (grey) or died (black) in those conditions.

TABLES

Table 2- 5: Seedling mortality. (A) Comparison (significant difference) of vegetation variables between plots in which naturally regenerated white spruce seedlings lived *versus* died in four forest regions and between 2006 and 2007. P-values (p) are indicated for each measure vegetation variable in each region. Significant ($p \leq 0.05$) variables in each region are marked in bold. If vegetation variables were positively associated with seedling survival (i.e. lower mortality) the effect column is noted as POS, positive. Conversely, if vegetation variables were negatively associated with seedling survival (i.e. higher mortality) the effect column is noted as NEG, negative. Degrees of freedom are as follows Peace River 863, Grande Prairie 105, Drayton Valley 449, Edson 130. (B) Results of categorical models examining the influence of cover by leaf litter and submergence in water on the probability of seedling survival at the Peace River site. Range of cover values for each site can be found in Appendix 2-1.

(A)

	Peace River		Grande Prairie		Drayton Valley		Edson	
Age	1		3		3		3	
	p	effect	p	effect	p	effect	p	effect
No. of saplings	**<0.0001**	**POS**	0.2287		0.5490		0.1819	
tall sapling cover	**0.0010**	**POS**	0.0777		0.9998		0.1982	
saplings in cone	**0.0028**	**POS**	0.4250		0.6525		0.4071	
short sapling cover	**0.0147**	**POS**	0.6361		0.2505		0.5741	
tall forb cover	0.0656		0.0770		0.5128		0.6452	
forbs in cone	0.4756		**0.0170**	**POS**	0.5525		0.3124	
short forb cover	0.2641		**0.0027**	**POS**	0.8960		**0.0262**	**POS**
cover of live grass	0.2004		**0.0431**	**NEG**	**0.0001**	**NEG**	0.3257	
live grass in cone	0.3907		0.1774		**<0.0001**	**NEG**	0.3631	
cover of all grass	0.0968		0.0918		**0.0004**	**NEG**	0.1569	
all grass in cone	0.3100		0.0541		**<0.0001**	**NEG**	0.2608	
all live veg. cover	0.7958		0.1133		0.3798		0.5475	
all live in cone	0.5463		0.0841		**0.0437**	**NEG**	0.2414	
total of all cover	0.9456		0.5799		**0.0225**	**NEG**	0.5091	
total of all in cone	0.7910		0.0841		**0.0016**	**NEG**	0.8614	

(B)

Source	d.f.	Chi-square	p
Intercept	1	4.90	0.0268
Covered	2	125.86	<0.0001
Submergence	1	13.91	0.0002

Table 2- 6: Seedling growth. Significance of the influence of vegetation variables on white spruce seedling growth between 2006 and 2007, exact age in each region is noted below. P-values (p) are indicated for each measure vegetation variable in each region and significant (p ≤ 0.05) variables in each region are marked in bold. If vegetation variables were positively associated with seedling growth the effect column is noted as POS, positive. Conversely, if vegetation variables were negatively associated with seedling growth the effect column is noted as NEG, negative. Untransformed data were used for Peace River, Grande Prairie, and Edson; Drayton Valley growth measurements were square root transformed prior to tests. Degrees of freedom are as follows Peace River 466, Grande Prairie 53, Drayton Valley 237, Edson 54. Range of cover values for each site can be found in Appendix 2-1.

	Peace River		Grande Prairie		Drayton Valley		Edson	
Between ages	0 -1		3 - 4		3 - 4		3 - 4	
	p	effect	p	effect	p	effect	p	effect
No. of saplings	**0.0020**	**POS**	0.0671		0.0682		0.1650	
tall sapling cover	0.0542		**0.0332**	**NEG**	0.0861		0.2641	
saplings in cone	0.4884		0.0713		**0.0033**	**NEG**	0.5228	
short sapling cover	0.7729		0.7211		0.0798		0.4691	
tall forb cover	0.1415		0.1601		0.4942		0.6714	
forbs in cone	**0.0145**	**POS**	0.5458		0.5301		0.8954	
short forb cover	**0.0229**	**POS**	0.7458		0.8627		0.9239	
cover of live grass	**0.0466**	**POS**	0.2531		0.0577		0.8688	
live grass in cone	**0.0009**	**POS**	0.4084		0.2286		0.4595	
cover of all grass	**0.0009**	**POS**	0.1394		0.4907		0.4647	
all grass in cone	**0.0001**	**POS**	0.1415		0.5112		0.5049	
all live veg. cover	**0.0242**	**POS**	0.9584		0.5510		0.4150	
all live in cone	**0.0192**	**POS**	0.7688		0.9498		0.6277	
total of all cover	0.0529		0.8462		0.6843		0.6179	
total of all in cone	0.4329		0.0886		0.5790		0.5568	

Table 2- 7: Final models for seedling growth (G) in relation to measured vegetation variables. The final model and R^2 of this model are listed. The standard error for the estimate (SE) as well as significance (p) is shown for each variable in the model.

Region	Sample Size	Model		SE	p	r^2
Peace River	562	G = 0.211Sn + 0.130Fc + 0.169Gc + 7.306				0.2672
			Sn: number of saplings	0.0719	0.0036	
			Fc: forbs in cone	0.0417	0.0020	
			Gc: all grass in cone	0.0404	0.0000	
			intercept	1.9456	0.0002	
Grande Prairie	98	G = -0.854Sc + 49.900				0.3898
			Sc: saplings in cone	0.2781	0.0033	
			intercept	5.9574	0.0000	
Drayton Valley	331	G = -0.01788St + 4.88				0.4724
			St: cover of tall saplings	0.0083	0.0332	
			intercept	0.2693	0.0000	

Table 2- 8: Significance of herbicide treatment in Grande Prairie on vegetation in the end of the first summer after treatment measured only from paired transects (treated and control). 254 plots were surveyed on 10 pairs of transects, 100 degrees of freedom for all tests. Significant ($p \leq 0.05$) negative affects are marked in bold

	Control		Herbicide		
	Mean	95% CI	Mean	95% CI	p
No. of saplings	8.45	(-4.92, 21.82)	0.41	(-2.39, 3.22)	**<0.0001**
tall sapling cover	12.68	(-10.36, 35.7)	0.82	(-3.18, 4.83)	**<0.0001**
saplings in cone	14.96	(-8.09, 38.00)	2.11	(-5.05, 9.26)	**<0.0001**
short sapling cover	7.19	(-8.24, 22.62)	1.96	(-4.76, 8.69)	**<0.0001**
tall forb cover	21.01	(-7.89, 49.90)	17.86	(-3.89, 39.60)	**0.0067**
forbs in cone	30.00	(-3.90, 63.90)	26.54	(-6.31, 59.38)	0.0672
short forb cover	27.54	(-0.88, 55.97)	30.36	(-9.36, 70.08)	0.7933
cover of live grass	13.16	(-10.71, 37.03)	6.82	(-8.01, 21.65)	0.2154
live grass in cone	11.32	(-11.90, 34.53)	5.89	(-9.89, 21.68)	0.4641
cover of all grass	25.35	(-26.96, 77.66)	9.07	(-13.74, 31.88)	**0.0184**
all grass in cone	20.18	(-29.31, 69.67)	6.57	(-12.35, 25.49)	0.0733
all live veg. cover	46.10	(18.97, 73.22)	38.18	(6.59, 69.77)	**0.0006**
all live in cone	41.67	(11.24, 72.09)	30.04	(-1.95, 62.02)	**<0.0001**
total of all cover	56.27	(22.88, 89.66)	41.54	(8.98, 74.09)	**<0.0001**
total of all in cone	50.57	(14.40, 86.74)	31.10	(-2.75, 64.95)	**<0.0001**

Discussion

What substrates are best supporting the regeneration of white spruce in the boreal mixedwood? Substrate suitability and availability

Substrates present after forest harvesting were evaluated for natural regeneration potential during the first four years following logging. Overall, organic substrates that were thick and coarse were unsuitable seedbeds in both coniferous and deciduous forests, while rotten wood was significantly better and the most suitable naturally occurring substrate for both forest types. Results demonstrated that post-disturbance mosses and thin organic substrates can support white spruce natural regeneration much better than originally thought, while mineral substrates did not always support successful germination and establishment. We must consider the quality and availability of these unexpectedly beneficial substrates further in order to better understand the role they play.

Our results showed two distinctly different moss qualities for the establishment of white spruce seedlings: as a poor substrate (germination success of seeds, Figure 2- 4) and as a preferred substrate (establishment of natural seedlings, Figure 2- 5 C). The type of mosses present in each case likely explains this difference. Where mosses acted as a poor substrate– particularly on coniferous sites (Startsev et al. 2008) –, feather mosses were present; these mosses provide an unsuitable substrate due to unsuitable moisture conditions, its thickness acting as a physical barrier to the mineral soil (Nienstadt & Zasada 1990, Nilsson et al. 1996, Gärtner et al. 2011), and chemical interference (Nilsson et al. 1996). Feather mosses die out in the years following disturbance (Nilsson et al. 1996, Wurtz & Zasada 2001) and are replaced by thinner weedy mosses such as *Polytrichum* sp. This likely significantly affected our results as measurements were taken in the fourth growing season following disturbance except in Peace River where measurements were taken recently following disturbance and here mosses were not abundant, nor preferred. Similar mosses are likely not present in aspen-dominated stands where feather mosses do not thrive (Startsev et al. 2008). These weedy post-disturbance mosses are thinner and finer allowing the seedling to be in closer contact with the stable moisture source in the mineral soil while accessing sufficient light (DeLong et al. 1997, Greene et al. 1999, Wang & Kemball 2005, Greene et al. 2007, Gärtner et al. 2011). Similarly, thin organics were more preferred than thick organics, which further demonstrates the overall benefit to the seedling of easy access to mineral soil layers.

If access to mineral soil were so important, our results that exposed mineral soil is not the most preferred substrate for natural regeneration would seem contradictory. However, mineral soil substrates are also prone to frost heaving, even for naturally established seedlings. While these substrates may be able to support the germination of white spruce, subsequent establishment may be reduced due to winter mortality. Additionally, the substrates resulting from site preparation show that not all mineral soil sites are able to support seedling establishment when seeded. While shelf sites excelled, loose cast-off mineral mounds and trench substrates were very poor; exposed mineral soil where no site preparation was done must share characteristics with these two substrates. Logging tends to expose mineral soil along skid trails (Solarik et al. 2010) where heavy machinery and tree removal scrape the forest floor, churn up duff layers, and compact soils (Wurtz & Zasada 2001, Martin-DeMoor et al. 2010, Gärtner et al. 2011). While scraped soils may be a suitable mineral substrate, churned layers are likely to have similar characteristics to cast-off soil from site preparation which is loose and prone to desiccation, washing-out and sometimes frost-heaving. On the other hand, compacted soils would have poor root penetration in addition to sharing characteristics with prepared trenches, which are prone to cold-air pooling and flooding.

In the Peace River site we were able to examine the sites in early spring, in a year with spring flooding at the beginning of their second growing season; this site also had significant numbers of aspen suckers. Flooding combined with burial in aspen leaf litter from new suckers was lethal to many of these small seedlings and their combination caused over 80% seedling mortality. Flooding and saturated soils prevent seedling roots from accessing oxygen causing seedling mortality. Dense aspen suckers can shed thick layers of large leaves that may cover small spruce seedlings blocking sunlight, smothering them and increasing mortality from snow press below leaf litter. (DeLong et al. 1997). Litterfall is likely a reason for the limited period of recruitment of spruce seedlings immediately after disturbance in some stands (Peters et al. 2006); there is a small window of opportunity for these very small seedlings to establish before aspen suckers have grown and built up capacity to shed thick layers of leaf litter.

As expected, rotten wood was found to be one of the best substrates for first year success of seeded white spruce, however it was not preferred for natural seedling establishment on harvested broadleaf-dominated sites. Logging traffic tends to break up and scatter rotten wood pieces (Wang & Kemball 2005, Johnstone & Chapin 2006) making it an unsuitable substrate as smaller pieces may become exposed and are more susceptible to desiccation than intact rotten logs. Rotten wood capable that is of supporting seedling establishment may therefore be a small percentage of all rotten wood and it therefore plays a very minor role in harvested areas compared to what would be expected on undisturbed sites.

How does competing vegetation affect the growth and mortality of natural white spruce regeneration?

Neighbouring vegetation was not overall negatively associated with seedling mortality and growth for these very young seedlings, a result supported by some studies (e.g. Heineman et al. 2005, Man et al. 2008), but not all. Heineman et al. (2005) found a similar result where planted interior spruce (*Picea glacua* x *englemanii*) on mesic sites did not grow better with vegetation control during the five years studied. For the very youngest seedlings both saplings and forbs were positively associated with seedling survival depending on the region; similarly, seedling growth in Peace River was positively associated with associated vegetation. Neighbouring vegetation, however, is not universally beneficial for seedling survival and growth (Man et al. 2008) and there was a tendency for associated vegetation to have a negative influence in Drayton Valley where the vegetation cover was greatest. Within the median range of growing conditions, good sites would have higher cover of neighbouring vegetation as well as higher rates of growth. Similarly, poor sites would support neither seedlings nor associated vegetation and lower seedling growth would be observed together with lower vegetation cover.

Despite this, increased grass cover was negatively related to seedling survival in Grande Prairie and Drayton Valley– a result found in other studies as well (Carter & Chapin 2000, Man et al. 2008) – suggesting a mechanism other than growing site may be influencing mortality. While small seedlings may be able to survive quite well under grass, the influence of snowfall may have a significant effect in this situation. Snow press - heavy snow loading causing the grass to collapse - can crush the seedling below causing growth deformities and mortality (Eis 1981). Thick grass layers can prevent the ground from warming quickly in the spring, reducing the growing season of small seedlings (Carter & Chapin 2000, Man et al. 2008, Pitt et al. 2010). Alternately, dense grass cover can harbour large rodent populations (Carter & Chapin 2000) including voles, which are known to increase seedling mortality by consuming bark and girdling seedlings. Higher cover of broadleaf saplings may reduce this grass cover and exposure, thereby benefitting spruce seedling survival (Man et al. 2008, Pitt et al. 2010).

However, this is for seedlings that are tall enough to withstand the smothering effect of leaf litter.

Herbicide

Herbicide treatments had no significant effect on leader length or mortality of white spruce seedlings, although there was an overall significant reduction of neighbouring vegetation. This is most likely due to the fact that measurements took place one year post-treatment and the benefit of reduced competing vegetation – and therefore increased available resources (Man et al. 2008) – could not yet be seen (Heineman et al. 2005). Pitt et al. (2010) found only very small differences growth immediately after treatment and in young seedlings the benefits of shelter may outweigh the benefits of more light. It is also possible that after vegetation control, seedling growth occurs by increased diameter, not leader length, of seedlings (Carter & Chapin 2000, Pitt et al. 2010).

Conclusions

High quality substrates that are able to provide the correct moisture conditions are important for seedling germination and establishment; substrates in close contact with mineral horizons, with thin or no organic layers, are best. With this in mind, scarification creates excellent conditions for white spruce seedling establishment, but it may not always be necessary as other intact substrates found after forest harvesting can perform well. Thin organic soils as well as thin and dying mosses should be considered valuable substrates for natural regeneration of white spruce in broadleaf-dominated boreal mixedwood forests. When these are found in abundance, site preparation may be unnecessary to aid in reforestation if an adequate seed source is present. Sites with thick organic layers and feather mosses should be considered for site preparation treatments to increase the quantity of preferred substrates if natural regeneration of white spruce is desired.

Rotten wood was not a consistently preferred substrate and it is likely negatively impacted by logging operations, so it should not be relied on post-harvesting to support large numbers of seedlings. However, it can act as an excellent substrate to support the establishment of future regeneration so leaving snags and other standing trees for recruitment of future deadwood would be an advisable practice.

Associated vegetation was linked to high cover and volumes of spruce seedlings, especially on the youngest sites, suggesting that in the early phases, spruce seedlings benefit from shelter, suggesting that moderate levels of associated vegetation are good for establishment. On older sites or where competition is severe, however, there is evidence in the literature that vegetation control might benefit growth. Although we were unable to see the benefits of herbicide treatment on seedling growth and survival within the time frame studied, it is likely that a future improvement would be seen where competing vegetation is reduced.

It is now clear that natural spruce regeneration can successfully establish following disturbance other than fire provided that there is a seed source and good microsites present. This allows us to further our understanding of the regeneration dynamics of white spruce in the boreal mixedwood forest; white spruce is able to successfully regenerate naturally in a range of conditions beyond those created by fire or under an existing canopy as a part of secondary succession. With greater insight, naturally regenerating white spruce as a component of a boreal mixedwood forest following harvesting is a potentially successful management strategy.

III. How do prescribed burning and variable retention impact natural regeneration in the European boreal?

INTRODUCTION

BACKGROUND

Current forest management practices in Fennoscandia have been employed across the landscape for several decades with the primary objectives being to maximize fibre production and economic returns leading to the problem of an over-simplified forest (Gustafsson et al. 2010), while the issue of conservation has been prioritized in protected areas. More recently, there has been a recognition of the importance the "forest matrix" – managed forests surrounding islands of protected areas – and the role it plays in overall conservation and biodiversity of forest species (Gustafsson et al. 2010, Gustafsson et al. 2012). Globally, this role has been recognized; extensive interest and research have been invested into finding a potential solution that can balance fulfilling the demand for timber as well as the need to conserve and restore the other many functions of the forest matrix (Gustafsson et al. 2012, Lindenmayer et al. 2012). Retention forestry modeled on natural processes – where features are permanently retained at the time of harvesting, often in the form of scattered or aggregated trees (Lindenmayer et al. 2012) – is a possible answer to achieve this balance (Gustafsson et al. 2010, Gustafsson et al. 2012).

One key issue with current forest management practices is that there is insufficient deadwood left in the forest matrix; dead wood is an essential habitat for thousands of species of arthropods and fungi in the

Fennoscandian boreal forests, many of which are red-listed species (Ehnström 2001). Deadwood also plays an essential role in nutrient cycling, carbon storage and natural regeneration (Brassard & Chen 2006). Managed forests only contain approximately 12% of the dead wood that natural forests in the European Boreal do (Ehnström 2001) and current requirements are that five trees per hectare be retained (Gustafsson et al. 2010) to recruit dead wood, a number insufficient to support a healthy diversity of saproxylic beetle species (Hyvärinen et al. 2006) and polypores (Junninen et al. 2008). New management techniques could help to reduce the impact of the extinction debt – future species being lost due to current or past practices - of saproxylic organisms that the European boreal forest is currently facing by making forest management practices more sustainable in terms of ecological function and saproxylic species diversity (Hyvärinen et al. 2006).

Novel forest management practices following a "natural disturbance" model include green-tree retention levels above current requirements – a minimum of five trees per hectare (Gustafsson et al. 2010) – and prescribed burning; these could help to reduce the negative impacts of logging particularly on deadwood and the species that rely on it (Junninen et al. 2008). Current practices leave relatively small-sized logging residuals in clearings and these break down relatively quickly; thus, there is a need for longer-term deadwood recruitment that may be fulfilled by increasing green-tree retention in forest practices. In addition to the recruitment of future deadwood, green-tree retention could also increase forest-like habitat features in the midterm while the surrounding forest is regenerating (Martikainen et al. 2006). Hyvärinen et al. (2006) recommends increasing the retention of green-trees above current levels and applying prescribed burn treatments to benefit saproxylic species. Increased retention combined with prescribed burning can increase the mid-term and long-term supply of deadwood due to the mortality of reserve trees following fire – as opposed to remaining live – and the large piece size of the deadwood that will remain on the landscape for some time (Hyvärinen et al. 2006). Additional benefits of prescribed burning on coleopteran and fungal communities have been reported in other studies (e.g. Muona & Rutanen 1994, Martikainen et al. 2006, Junninen et al. 2008) due to these species' adaptation to a natural disturbance regime based upon regular fires; re-introduction of this disturbance could benefit these communities.

Incorporation of retention harvesting and prescribed burning into forest management could increase deadwood availability on the landscape as well as other habitat features important to threatened saproxylic species; however it is also important that these practices are able to support the regeneration of healthy forests in order to be a sustainable and economically viable management option in the long-term. Other studies have found that green-tree retention – especially at 50 m^3/ha – decreases mortality of planted seedlings by decreasing early herbivory of deciduous seedlings (den Herder et al. 2009) and damage from pine weevils (*Hylobius abietis and H. pinastri*) to conifers (Pitkänen et al. 2005). However, while there have been studies of the success of planted trees following cutting with high levels of green-tree retention and prescribed burning in the European boreal forest (e.g. Pitkänen et al. 2005, den Herder et al. 2009), there has been little work on the impacts of these techniques for natural regeneration. Some work has focussed on this in similar studies in North America (e.g. Man et al. 2009), but it is important to also understand the responses of European boreal species to these treatments. In recent years, between 15% and 20% of Finnish forests are naturally regenerated after harvesting (Finnish Forest Research Institute 2012), so it is important to evaluate the impacts of these techniques on natural regeneration and to investigate if natural regeneration is in fact a viable management option following the implementation of these novel practices.

In order to understand the implications of these management practices for natural regeneration, it is important to understand the ecology of the species of interest for forest management: birch (*Betula pendula* Roth and *B. Pubescens* Ehrh.), Scots pine (*Pinus sylvestris* L.), European trembling aspen (*Populus tremula* L.) and Norway spruce (*Picea abies* (L.) Karst.). By developing a firm understanding of their ecology, we can better predict and therefore manage the natural regeneration of these species in response to partial cutting with increased retention and prescribed burning. To provide a background on the natural regeneration of the four above-mentioned species, the following section is a review of their ecology in regards to their habitat, seed production and dispersal, germination, establishment and primary causes of early mortality.

LITERATURE REVIEW: SILVICS OF FOUR EUROPEAN BOREAL TREE SPECIES

Birch

Two birch species inhabit the boreal and temperate forests of northern and central Europe: silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.). Although these species differ slightly in their habitat and morphology, they share many characteristics. The birches (*Betula* L.) are ecologically and economically important components of the landscape and economies from Siberia to the Atlantic and from the Arctic tree line to the Mediterranean (Atkinson 1992, Yrjölä 2002, Hynynen et al. 2010). They are extensively managed, particularly in the Nordic (Norway, Sweden and Finland) and Baltic (Estonia, Latvia and Lithuania) countries (Hynynen et al. 2010, Yrjölä 2002). Birch is considered a pioneer tree species and possesses reproductive and ecological characteristics that support this. It is able to reproduce sexually as well as vegetatively. However, it is vulnerable to many sources of mortality and damage throughout its lifecycle.

Birch occurs across northern and central Europe as pure stands, mixed forests or scattered individuals (Atkinson 1992, Hynynen et al. 2010). It is the most common and productive native broadleaved tree in northern Europe and is very important across the conifer-dominated boreal landscape; many ecological communities depend exclusively on birch (Atkinson 1992, Hynynen et al. 2010). Although it is considered to be a pioneer, birch is able to form a climax forest in some conditions (Atkinson 1992). On good site conditions, birch grows rapidly for about 60 years at which point growth slows and the trees start to decline by age 100 (Hynynen et al. 2010, Yrjölä 2002). It is an excellent colonizer of disturbed ground and bare soil, particularly following disturbance events such as clear-cutting or fire (Atkinson 1992, Hynynen et al. 2010). Birches are prolific seed producers, grow very rapidly at juvenile stages, and tolerate poor soils, but are shade intolerant (Atkinson 1992, Nilsson et al. 2002, Hynynen et al. 2010).

Birch is a widely managed tree across Nordic and Baltic countries and is valued as a deciduous tree with good stem form and fibre quality to produce a range of forest products including energy, pulp, dimensional lumber and veneer (Hynynen et al. 2010, Yrjölä 2002). It is regenerated in pure or mixed stands through natural regeneration as well as artificially through seeding and planting (Yrjölä 2002, Hynynen et al. 2010). Following regeneration, stand tending and thinnings are applied to reach optimal production and quality in a managed stand (Yrjölä 2002, Hynynen et al. 2010). Birch is often found in plantations that are being managed for Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.), which often results in mixed-species managed stands (Nilsson et al. 2002, Hynynen et al. 2010, Lehtosalo et al. 2010). Although the cost of establishment is low, naturally regenerated birch stands often require more intensive stand management to achieve optimal productivity and may have a lower final stem quality than artificially regenerated stands (Hynynen et al. 2010).

Birch does best on sites with good soil nutrients such as fertile forest sites or agricultural fields (Hynynen et al. 2010). Soils should be well drained such as fine sand or silty sand; if the texture is too fine aeration is insufficient for birch roots (Hynynen et al. 2010). Downy birch is more tolerant of saturated or poorly aerated conditions than silver birch (Atkinson 1992). Downy birch is particularly sensitive to drought and dry conditions; the southern limits of its range are correlated with summer rainfall (Atkinson 1992, Hynynen et al. 2010). The presence of birch also has an effect on the site due to its litter characteristics. Compared to a coniferous litter, birch has a higher pH, faster decomposition and nutrient cycling (Hynynen et al. 2010). There also tends to be more understory vegetation in birch forests than under conifers because of higher light conditions under the canopy and the enriching effect of birch litter (Hynynen et al. 2010).

Birch is well known for its ability to produce massive quantities of seed; the youngest trees flower for the first time at five to 10 years old (Atkinson 1992, Hynynen et al. 2010). Below a birch canopy, over 2000 seeds m^{-1} may reach the forest floor; however, depending on the season, a low percentage (usually < 20%) of these are viable (Atkinson 1992). In northern climates, seed production is not always regular and large crops may be produced every two to three years (Hynynen et al. 2010).

Birch is monoecious, with both male and female flowers (catkins) emerging with the leaves in the spring (Atkinson 1992, Hynynen et al. 2010). Pollen is wind-dispersed and can travel long distances, which contributes to the genetic variation of birch populations (Hynynen et al. 2010). Self-pollination is prevented through a biochemical mechanism in birch (Atkinson 1992). Hybridization between the two species is known to occur (Hynynen et al. 2010). Female catkins - even unpollinated ones, although they produce no seed - will persist and ripen over the summer (Atkinson 1992, Hynynen et al. 2010). Seeds mature in late summer and female catkins begin to disintegrate in the autumn to release very small (silver birch 3-5 mm, downy birch 2-4 mm) winged fruits (Atkinson 1992, Hynynen et al. 2010). Female catkins may remain on the tree and continue to release seed over the winter months (Hynynen et al. 2010). During the time mature seeds are on the tree, up to 10% may be lost due to gall midges (*Semudobia* sp.) (Atkinson 1992).

The small winged seeds are dispersed primarily by wind and most are found within 40 m to 50 m of the source tree (Atkinson 1992, Hynynen et al. 2010). There are some cases of exceptional seed dispersal over the surface of snow and even further in meltwaters, though these mechanisms are not considered major components of the overall spread (Atkinson 1992). Good dispersal mechanisms are important for birch to colonize newly disturbed areas because birch seeds are very short-lived and are unable to remain viable as part of the seedbank (Atkinson 1992). As little as 6% of all seed released could be viable by the end of the first winter (Atkinson 1992). After dispersal, birch seeds are subject to predation by insects, small mammals and birds (Nilsson et al. 2002).

Birch seeds are dormant when they are first shed in the autumn and require a combination of moist chilling and exposure to light for germination to occur (Atkinson 1992, Hynynen et al. 2010). It was found that at least 48 hours of exposure to light with a high red to far-red ratio combined with stratification broke the dormancy of most seeds (Atkinson 1992). The only wavelengths that had a negative effect on germination were far-red; this light quality is present in shaded conditions below a canopy (Atkinson 1992). Providing optimal chilling conditions is able to remove light exposure requirements; conversely, optimal light exposure removes chilling requirements in several situations (Atkinson 1992). Increasing the temperature of germination conditions from 15 °C to 20 °C causes an increase of germination rates without additional stratification or light exposure (Atkinson 1992).

Bare soil with no other competitive ground vegetation provides excellent conditions for germination and the success of young seedlings (Atkinson 1992, Nilsson et al. 2002, Hynynen et al. 2010). These conditions can be the result of any disturbance; fire and scarification are the two most widely described disturbances in forest management, while smaller scale events such as uprooting, exposed roadsides or erosion also create suitable surfaces (Atkinson 1992, Hynynen et al. 2010). In addition to less competition for light and nutrients, bare soil can provide a consistent moisture supply for germinating seeds (Kinnard 1974, Nilsson et al. 2002, de Chantal et al. 2003*a*)

Exposed conditions are essential as germinants are only able to grow to a height of about 2 cm before energy from the seed has been depleted and good light conditions are required for survival and further growth; vegetation as minor as dense moss can prevent this (Atkinson 1992). In ideal conditions, birch is a very strong competitor and can outgrow other ground vegetation (Atkinson 1992, Nilsson et al. 2002). Competition is a major cause of germinant and seedling mortality (Atkinson 1992, Hynynen et al. 2010). Other sources of mortality at this stage include herbivory (vertebrate and invertebrate), trampling by game or livestock and environmental factors such as drought, frost or flooding, and bacterial and fungal pathogens (Kinnard 1974, Atkinson 1992, Nilsson et al. 2002, Hynynen et al. 2010).

Birch, particularly downy birch, is capable of vegetative reproduction by producing stump sprouts (Atkinson 1992, Hynynen et al. 2010). Basal buds form both above and below the soil line near the root collar and grow annually, creating clusters of buds (Atkinson 1992, Hynynen et al. 2010). These buds are triggered to release and sprout following a reduction or loss of apical dominance due to events such as a fire or broken top (Atkinson 1992, Hynynen et al. 2010). However, basal buds are sensitive to extreme temperatures and must be protected by soil or litter layers in order to sprout following a fire (Atkinson 1992).

After a release is triggered, the quantity of the sprouts and survival is highly variable and depends on many factors including the individual tree, climate and season (Hynynen 2010). Shading and competition for light causes shoot mortality and in these conditions most sprouts die before a height of 5 cm is reached (Atkinson 1992). If they survive the initial establishment phase, sprouts can have incredibly fast initial growth, but this is short-lived and after four or five years they are outcompeted (Atkinson 1992, Hynynen et al. 2010). These stump sprouts have different morphological characteristics than seedlings in similar conditions: greater leaf area, greater crown density and higher chlorophyll content (Hynynen et al. 2010).

Once established from seed or stump sprouts, birch saplings continue to be exposed to damage and mortality: herbivory from large and small mammals, invertebrates, pathogens and environmental events. One of the largest and most widespread damaging agents for birch trees is moose (*Alces alces*) that browse leaves and young twigs causing a reduction in growth (Hynynen et al. 2010). However, the greatest damage from moose is broken main stems and leaders, which occurs during the browsing and can cause stem deformities (Hynynen et al. 2010). Moose damage is very difficult to prevent; fencing, which is costly, is one of the few options and not practical on a large scale

(Hynynen et al. 2010). Other large mammals that browse birch trees include white-tailed deer (*Odocoileus virginianus*), roe deer (*Capreolus capreolus*) and reindeer (*Rangifer tarandus*).

Small mammals, particularly voles and hares, are also significant damage agents for birch trees. Voles are especially problematic as they eat the cambium of young trees and are capable of girdling the lower stem resulting in tree death, disfiguration or scarring (Hynynen et al. 2010). Voles are capable of destroying entire plantations if not effectively managed; their numbers can be controlled through reducing the surrounding ground vegetation that provides nutrition and shelter for a vole population (Hynynen et al. 2010). Hares are less problematic, but still cause damage by removing seedling branches or the leader (Hynynen et al. 2010).

Scots pine

Scots pine (*Pinus sylvestris* L.) is a widely distributed species with a natural range covering most of north and central Europe and reaching across Russia to Asia (Sullivan 1993). Its natural range extends from the north Atlantic coast of Norway to southern Spain and across Russia into China (Carlisle & Brown 1968). It has also been introduced to the north-eastern United States and adjacent Canada for forest management and as an ornamental (Sullivan 1993). In northern Europe, particularly Sweden and Finland, it is one of the primary species for forest management (Yrjölä 2002, Nilsson et al. 2002) and is a major part of the European boreal forest (Sullivan 1993).

Scots pine is a shade intolerant pioneer species that relies on openings and stand initiating disturbances such as fire to regenerate on most sites (Sullivan 1993, Mielikäinen & Hynynen 2003). Without disturbance, most boreal sites in Finland with sufficient water and nutrients will progress over time to a Norway spruce (*Picea abies* (L.) Karst.) forest. Managed forests are mostly even-aged, though multi-layer stands can be successfully created with another species (Sullivan 1993, Mielikäinen & Hynynen 2003). Scots pine is often regenerated in managed forests by means of either planting or natural regeneration (Mielikäinen & Hynynen 2003). Intensive thinning treatments and other intensive management are often done in Scots pine stands to maximize productivity (Yrjölä 2002).

Scots pine is managed for both timber and non-timber resources across its natural and introduced range. Energy, pulp, lumber, and veneer are all produced from Scots pine (Sullivan 1993, Yrjölä 2002); it is also valued for some lesser-known products. For example, in Finland, it was the primary species used in the production of tar, a significant industry for many decades (Mielikäinen & Hynynen 2003). In North America it is extensively managed for Christmas trees and used as an ornamental in landscaping (Sullivan 1993).

In managed forests, Scots pine is regenerated primarily through planting, but natural regeneration and seeding are also practised (Mielikäinen & Hynynen 2003). During a rotation, stand improvement (brushing, pruning and fertilization) as well as thinning from below are common practices to improve stand productivity and tree quality (Mielikäinen & Hynynen 2003). An entire rotation may last anywhere from 80 to 160 years depending on the site and latitude (Yrjölä 2002, Mielikäinen & Hynynen 2003). At the end of a rotation, clearcut harvesting is common (Yrjölä 2002), but leaving retention trees is a growing practice for the many purposes: seed trees, creating a shelterwood or biodiversity values (Mielikäinen & Hynynen 2003).

Natural regeneration of Scots pine in managed stands is encouraged through site preparation to expose mineral soil and by leaving residual seed trees (Karlsson 2000, Nilsson et al. 2006). The best sites for encouraging natural regeneration are relatively dry and have poor to medium fertility (Mielikäinen & Hynynen 2003, Nilsson et al. 2006). Natural regeneration of Scots pine may fail due to competition from ground vegetation, insufficient seeds or inadequate site preparation (Nilsson et al. 2006). However, broadleaf regeneration in limited quantities is accepted with planted trees and is viewed to promote biodiversity in addition to benefitting the overall productivity of the stand (Mielikäinen & Hynynen 2003)

Historically, forest fires have allowed Scots pine to regenerate as relatively even-aged stands across the landscape (Sullivan 1993). Despite its adaptation for fire-dominated ecosystems, the bark of Scots pine is relatively thin and cannot survive high-intensity fires (Sullivan 1993, Kuuluvainen & Rouvinen 2000). Following a disturbance, large numbers of pine seedlings become established before major vegetative competition begins on the site (Kuuluvainen & Rouvinen 2000). However, Scots pine does not always require a large disturbance to regenerate and it may successfully regenerate in smaller openings and gap-disturbances within a canopy (Kuuluvainen & Rouvinen 2000). On very poor or dry sites where the litter layer is very thin, Scots pine may regenerate under its own canopy without a disturbance (Sullivan 1993).

Scots pine is capable of flourishing on relatively dry sites with poor to medium nutrients and is usually the best option for forest management in these conditions (Sullivan 1993, Nilsson et al. 2012). Medium fertility sites with moist soils are also good for pine, but it may be challenging for seedlings to establish due to vegetative competition (Nilsson et al. 2002). Extreme sites such as dry rocky outcrops and extremely wet peat soils are also capable of supporting Scots pine (Sullivan 1993), although growth is not sufficient for timber production in these situations.

Scots pine is only capable of reproducing sexually and usually produces cones for the first time at a fairly young age (Carlisle & Brown 1968, Sullivan 1993); a typical age for cone production to start is 10 or 15 years old (Sullivan 1993). Cone production is variable (Nilsson et al. 2006), but large cone crops have been found to occur roughly every four to seven years (Hagner 1965, Carlisle & Brown 1968, Sullivan 1993). An individual tree's seed production depends on several factors: genetics, site characteristics and tree size (Karlsson 2000). Scots pine responds to a stand-opening disturbance, such as a partial harvest, with a large cone crop due to increased light in the canopy and resource availability for the trees (Karlsson 2000). However, due to the seed production cycle of Scots pine, the resulting crop of trees is not seen for four or five years after the disturbance takes place (Karlsson 2000, Nilsson et al. 2006).

A four year reproduction cycle means that weather can impact the success of the regeneration over four seasons: development of reproductive buds, flowering and pollination, seed maturation and dispersal (Carlisle & Brown 1968, Karlsson 2000). Initiation of reproductive buds is best in warm summers (Karlsson 2000), then flowering and pollination occurs in late spring (May to June) of the following year; however, fertilization does not occur until 12 months after pollination (Carlisle & Brown 1968, Sullivan 1993). During the second summer following flowering, seeds mature then overwinter in cones (Sullivan 1993). Each cone contains between five and 40 seeds (Carlisle & Brown 1968). Self-pollination does occur, but results in reduced viability of seeds (Carlisle & Brown 1968).

Two years after flowering, seeds are dispersed in May or June in the wind; dispersal is improved by dry and windy weather (Sullivan 1993, Ahola & Leinonen 1999, Karlsson 2000, Nilsson et al. 2006). Cones open following alternating dry and wet weather (Sullivan 1993). Scots pine seeds are about

3.5 mm to 5.5 mm long and have a single wing to aid with aerial dispersal (Carlisle & Brown 1968). Seeds are dispersed relatively short distances, typically no more than 100 m (Carlisle & Brown 1968, Sullivan 1993, Nilsson et al. 2006). Greater distances can be achieved in high wind events, across frozen surfaces or in water bodies, though these modes account for a small proportion of seed dispersal (Carlisle & Brown 1968).

In order for germination to occur in the spring, seeds should be exposed to sufficient moisture and light with a high red to far-red ratio (Carlisle & Brown 1968, Ahola & Leinonen 1999, de Chantal et al. 2003*a*), however shaded light (low red to far-red ratio) has not been found to inhibit germination if temperatures are favourable (Ahola & Leinonen 1999). Warmer temperatures (in the range of 10 ˚C to 20 ˚C) increase germination rates (Ahola & Leinonen 1999), but sufficient moisture is still required as germinating seeds are vulnerable to desiccation (Sullivan 1993). Moist chilling is used to pre-treat seeds before sowing to increase germination rates (de Chantal et al. 2003*a*). Early germination gives seedling roots a better chance to establish reducing the risk of desiccation during the growing season and frost heaving during the winter (de Chantal et al. 2003*a*). Scots pine seeds do not remain viable for very long after dispersal; if germination does not take place the first year seeds become unviable (Karlsson 2000).

It is often found that exposed mineral soil, particularly A- and B-horizons (de Chantal et al. 2003*a*), is the most beneficial for the regeneration of Scots pine (Sullivan 1993, Kuuluvainen & Rouvinen 2000, Nilsson et al. 2006). Scarification has been studied extensively and has been found to increase seedling densities, increase germination, benefit the survival of young seedlings and increase height growth over the first years (Nilsson et al. 2006). Mounding also exposes a good seedbed, but drought can be an issue on the elevated microsite that is created (de Chantal et al. 2003*a*). Seed trees increase the amount of seed available on a site, which can lead to increased seedling densities; however, regeneration directly adjacent to residual trees is poor due to competition for light, water and nutrient resources (Kuuluvainen & Rouvinen 2000). Removal of this overstorey increases the resources available to regenerating seedlings, but has been found to cause mortality for other reasons including mechanical damage and exposure (Sullivan 1993, Nilsson et al. 2002).

Regeneration of Scots pine in unmanaged areas has historically occurred after a disturbance, primarily a fire cycle of either low or moderate severity fires in the European boreal (Kuuluvainen & Rouvinen 2000). Mature trees usually are able to survive these fires and provide a seed source while the understory is removed, creating a seedbed with low competition (Kuuluvainen & Rouvinen 2000). However, if a fire is too severe, seeds may not be able to germinate due to exposure and desiccation (Kuuluvainen & Rouvinen 2000). Since Scots pine seeds do not remain viable for many years after dispersal, some trees must survive to provide a seed source to support on-going regeneration (Kuuluvainen & Rouvinen 2000). Without fire or other large-scale disturbances, availability of suitable microsites is poor. Kuuluvainen & Rouvinen (2000) found that decayed wood sites and any exposed mineral soil supported the greatest density of successful Scots pine seedlings in a forest without recent fire disturbance. A majority of these understory seedlings will not survive, but some will persist as suppressed individuals in lower forest layers (Kuuluvainen & Rouvinen 2000).

One of the most important factors for the successful establishment of Scots pine is high light conditions (Sullivan 1993). Seedlings are capable of developing different morphological traits in conditions with high light, including greater needle length, projected leaf area, height growth, above ground biomass and thicker stems (de Chantal et al. 2003*b*). This adaptive ability gives pines a competitive advantage in open conditions and resulting in relatively high growth rates (de Chantal et al. 2003*b*). Despite the need for good light, Scots pine seedlings are found to have higher rates of survival under a light shelterwood, but their long-term growth is lower in such conditions (Nilsson et al. 2006). If Norway spruce is planted on the same site under a shelterwood, the planted seedlings will outcompete the natural Scots pine regeneration (Nilsson et al. 2006). Unfortunately, as previously mentioned, the removal of the canopy layer increases the mortality of understory seedlings (Sullivan 1993, Nilsson et al. 2002)

Scots pine is subject to damage and mortality from several abiotic and biotic factors throughout its lifecycle. Seeds and cones are subject to predation from birds and small mammal species (Sullivan 1993) as well as insects (Carlisle & Brown 1968). One of the largest threats to young seedlings is the pine weevil (*Hylobius abietis*), which is capable of consuming needles, twigs, and cambium as an adult (Nilsson et al. 2006). Larvae live and grow in the stumps of harvested conifers; once matured, adults cause mortality of nearby seedling by consuming the thin cambium (Pitkänen et al. 2008). Pine weevil damage can be reduced by leaving residual trees that may provide an alternate food source for the weevils or by scarifying the site as it has been suggested that the weevils avoid crossing a scarified substrate to access the seedlings (Nilsson et al. 2006). Seedlings are also sensitive to desiccation (de Chantal et al. 2003*b*), overheating (Kuuluvainen & Rouvinen 2000, de Chantal et al. 2003*a*) and frost heaving (de Chantal et al. 2003*a*, Nilsson et al. 2006).

Saplings of Scots pine are frequently browsed by ungulates including moose (*Alces alces*), roe-deer (*Capreolus capreolus*) and other species throughout its native and introduced range (Sullivan 1993, Nilsson et al. 2006). Although Scots pine is not as highly preferred by moose as deciduous species (Andrén & Angelstam 1993), heavy browse still occurs – particularly in winter – and can decrease the height growth and vigour of saplings (Persson et al. 2005). Insects that can damage saplings or mature trees include defoliators, budworms, bark beetles, wood borers and weevils (Carlisle & Brown 1968, Sullivan 1993). Fungi such as needle casts, cankers, and gall rusts can also affect saplings (Carlisle & Brown 1968, Sullivan 1993, Nilsson et al. 2006).

European trembling aspen

European trembling aspen (*Populus tremula* L.) is a very widely distributed species across Eurasia (Bärring 1988) with very little commercial value (Worrell 1995, Myking et al. 2011) other than some specialty pulp products (e.g. Sappi 2011). It is capable of surviving in a large range of ecosystems and sites because it easily adapts to local conditions (Worrell 1995, Myking et al. 2011). These traits allowed trembling aspen to be one of the first colonizing tree species in Europe following the ice age (Worrell 1995, Myking et al. 2011). It is also classified as a pioneer species: it grows quickly and can establish on disturbed sites, requires high light conditions and is relatively short-lived (Worrell 1995, Myking et al. 2011). Trembling aspen is quite resilient and does not require high summer temperatures for growth; further, it can survive some drought conditions and severe frosts (Worrell 1995, Myking et al. 2011).

The adaptability and genetic variation of aspen allows it to exist on many different site types. Topographically it can be found from upper slope positions (such as cliffs) down to gullies and lower slope positions (Worrell 1995). Although aspen does best on rich mineral soils with good drainage, it can also be found on scree slopes, sandy soils, heavy clays and peat soils (Worrell 1995). Poor site conditions cause high mortality rates and low productivity of the stand (Worrell 1995). Aspen litter decomposes rapidly, increasing the nutrient cycling on a site (Worrell 1995).

Individuals can live well over 100 years in Scandinavia (Myking et al. 2011, Lankia et al. 2012), but Worrell (1995) reported the maximum age to be less in the UK. Clones can exist via root networks and continue to reproduce individual stems vegetatively for thousands of years (Myking et al. 2011). The short-lived nature of individual trees means that in order for aspen to continue to exist on the landscape, relatively frequent disturbances and regeneration opportunities are required (Myking et al. 2011). The exclusion of frequent fires from the European boreal may reduce the ability of aspen to maintain its populations (Myking et al. 2011)

Historically, operational management of aspen has been with the extensive use of herbicides to reduce its growth and mechanical brushing (Bärring 1988, Myking et al. 2011). Aspen has very little value as a commercial species; it is used for some specialty pulp production (Myking et al. 2011, Sappi 2011) and has limited use in specialty applications such as sauna benches. However, it is most often considered a nuisance species because it hinders the growth of more valuable tree species through vegetative competition (Bärring 1988, Myking et al. 2011). More recently, its value for biodiversity has been realized (Kouki et al. 2004) and it is gradually being accepted as part of mixed stands; an aspen overstorey sheltering Norway spruce regeneration (*Picea abies* (L.) Karst.) is a possible multi-layered system (Worrell 1995, Myking et al. 2011). In a forestry context, aspen is not typically purposefully regenerated. Hybrid aspen (*Populus tremula* x *tremuloides*) could be intensively managed (Worrell 1995, Myking et al. 2011) for energy wood production.

Throughout the range of aspen, it plays a very important role in the biodiversity of ecosystems because it supports a wide diversity of other species. Many endangered saproxylic fungi and invertebrates depend upon decaying aspen wood (Worrell 1995, Myking et al. 2011). It provides habitat and forage for a wide diversity of other mammals, invertebrates, fungi and birds, particularly cavity nesters (Worrell 1995, Myking et al. 2011). Aspen is the main winter forage for many large ungulates in Fennoscandia and this is impacting the dynamics of aspen regeneration (Ericsson et al. 2001). Although aspen produces huge quantities of seed, most successfully regenerated aspen stems have originated from vegetative reproduction (Worrell 1995, Myking et al. 2011)

It was previously thought that regeneration of aspen by seed was extremely limited, but seedling establishment has recently found to play a greater role than originally assumed in landscape colonization (Myking et al. 2011). Proof of this is the rapid migration that aspen made following glacial recession (Myking et al. 2011). Seed production varies from year to year (Bärring 1988), though very little is understood about the environmental influences on this; warm weather in the summer before blooming may increase the formation of reproductive buds (Worrell 1995). Trees independent of clones may begin flowering after only 10 or 15 years, clonal individuals will usually not flower until they are 20 to 30 years of age (Myking et al. 2011). Trees are dioecious and there are typically twice as many male individuals as female individuals across a landscape, though this varies slightly by region (Bärring 1988, Worrell 1995, Myking et al. 2011).

Male and female flowers emerge in the spring prior to leaves; male flowers disperse pollen by wind and it can travel great distances (Myking et al. 2011). After fertilization, seeds mature quite quickly in about four or five weeks (Worrell 1995, Myking et al. 2011). Huge quantities of viable seed are produced; there can be more than 50 million per tree (Bärring 1988). Germination rates of seeds have been found to be as high as 90%; despite this, there are very few aspen individuals established from seed (Bärring 1988, Worrell 1995, Myking et al. 2011). Aspen seems to reproduce poorly by seed because of low germination rates and high mortality of germinants due to environmental conditions (Worrell 1995). The seeds of trembling aspen are very small (0.06 g to 0.14 g per 1000) and are very short lived, remaining viable for less than one year following dispersal (Worrell 1995, Myking et al. 2011). Seeds have long hairs that aid in wind dispersal (Worrell 1995, Myking et al. 2011) allowing them to travel up to 500 m (Bärring 1988).

Following dispersal, environmental conditions have a major influence on germination and establishment because seeds do not have endosperm to support their initial growth (Bärring 1998). Trembling aspen does not have a requirement for a moist chilling period prior to germination (Myking et al. 2011) and can germinate very quickly after dispersal when moisture conditions are good (Worrell 1995). However, because the germinants are so small and receive no support from the seed, there is a very high rate of mortality due to drought or being washed away (Worrell 1995). After six days, sufficient roots have developed to greatly reduce these risks (Worrell 1995). Aspen is not particular about the seedbed it will germinate on as long as there is sufficient moisture and heat (Worrell 1995). Exposed mineral soil or burnt organic matter is best able to provide these conditions and support the establishment of young germinants (Worrell 1995, Myking et al. 2011). The establishment of aspen seedlings requires good light conditions and sufficient water availability. Juvenile aspen are able to grow as much as 1 m per year on sites with moist soils and good nutrient availability (Myking et al. 2011). Windthrow is able to provide a good seedbed of mineral soil and protect saplings from ungulate herbivory (de Chantal & Granström 2007, Myking et al. 2011), although they are still susceptible to small mammals and insects.

Fire not only provides good conditions for seedling establishment, but also has been found to promote conditions favourable for the vegetative reproduction of aspen (Bärring 1988, Myking et al. 2011). Suckering from an extensive root system is the most common means of reproduction for trembling aspen, although individuals less than five or six years old are also able to produce stump sprouts (Worrell 1995, Myking et al. 2011). The extensive root system of aspen is able to survive in the forest floor and can re-sprout in the event of a disturbance - even if no aspen trees are present in the overstorey for long periods of time (Worrell 1995, Ericsson et al. 2001). Ramets are primarily produced from relatively shallow (about 4 cm deep) roots that spread up to 35 m or 40 m from the parent tree (Bärring 1988, Worrell 1995, Myking et al. 2011). These roots can grow laterally at a rate of about one meter per season (Myking et al. 2011), which allows expansion into adjacent areas (Worrell 1995).

Massive production of ramets is triggered by a loss of apical dominance and decreased auxin levels from the parent tree, although this is not essential for ramet production (Bärring 1988). Disturbances such as forest fire and stand harvesting increase the suckering response from the root system (Bärring 1988, Worrell 1995, Myking et al. 2011). Each parent tree may produce hundreds of sprouts, though few of these survive to maturity (Worrell 1995, Myking et al. 2011). Initial suckering response to a disturbance may produce ramet densities of up to 200,000 stems per hectare, but more commonly half this number or less are produced (Bärring 1988, Worrell 1995). Most of these survive less than five years and will die out due to competition (Worrell 1995, Myking et al. 2011) and herbivory (Ericsson et al. 2001). Successful ramets will remain dependent upon the parent root system for up to 25 years and will usually die if the connection is severed too early as they do not form their own root system very quickly (Bärring 1988, Worrell 1995).

The production of dense stands of ramets has been studied in the context of ecological value and significance for ungulate populations. There is concern that increased browsing pressure over the long term will lead to a decline in recruitment and eventually the loss of aspen throughout the landscape (Ericsson et al. 2001, Kouki et al. 2004, Myking et al. 2011). Young aspen are highly preferred by browsers (de Chantal & Granström 2007, Myking et al. 2011) and will be selected out of a mixed stand (Edenius et al. 2002*a*). Browsing can cause extensive damage to trembling aspen; the important browsing species include moose (*Alces alces*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) (Myking et al. 2011). Aspen is the primary winter food source for moose in particular (Andrén & Angelstam 1993, Ericsson et al. 2001); this can lead to heavy damage and mortality of regeneration (de Chantal & Granström 2007). Ramets are damaged by the consumption of bark, branches and leaders which can lead to poor form, reduced growth, delayed maturation and mortality (Ericsson et al. 2001, Myking et al. 2011). The majority of this damage is found on trees below 3 m to 4 m in height (Ericsson et al. 2001) making it possible for aspen to outgrow this vulnerable stage if browsing pressure can be controlled (de Chantal & Granström 2007, Myking et al. 2011).

<u>Norway spruce</u>

Norway spruce (*Picea abies* (L.) Karst.) is long-lived conifer (Fraver et al. 2008) native to north and central Europe and is important to the economies and natural landscapes of many countries (Sullivan 1994, Ahola & Leinonen 1999). It is shade tolerant and is capable of forming climax forests (Mielikäinen & Hynynen 2003, Nilsson et al. 2006, Fraver et al. 2008). Although it is an extensively managed species, natural regeneration is a very rare management strategy for a variety of reasons and most Norway spruce stands have been established as a result of artificial planting or seeding

(Mielikäinen & Hynynen 2003). Vegetative reproduction is also possible in the form of branch layering (Vacek et al. 2012). Norway spruce occurs as either pure stands or mixed with other conifers or broadleaved tree species (Sullivan 1994).

Norway spruce occurs from the west coast of Norway extending eastward across Russia, where it gradually hybridizes with and transitions to Siberian spruce (*Picea obovata* Ledeb.) (Sullivan 1994). It is common across the landscape of northern Europe as far south as Poland (Sullivan 1994). Further south in Austria, Germany and even Greece, it occupies upper elevation areas where precipitation is high (Sullivan 1994). It is one of the characteristic species of the European boreal forest where it flourishes in sites with good moisture and nutrient availability (Sullivan 1994, Ahola & Leinonen 1999, Nilsson et al. 2012). Norway spruce does not require large or severe disturbances to regenerate and does well establishing under a partial or complete canopy (de Chantal et al. 2003*b*, Nilsson et al. 2006, Fraver et al. 2008). This allows Norway spruce to dominate as a late successional species and eventually form a climax forest in the boreal region (Fraver et al. 2008, Nilsson et al. 2012).

Norway spruce is an intensively managed species across its natural and introduced range and is one of the most important commercial species in northern Europe (Sullivan 1994, Ahola & Leinonen 1999). It is used for the production of wood products including energy, pulp, dimensional lumber and veneer (Yrjölä 2002), but is also favoured by Europeans as Christmas trees (Sullivan 1994). Pure plantations that have been tended (brushed, pruned or fertilized) and thinned before harvest are common in the north European landscape (Nilsson & Örlander 1995, Nilsson et al. 2012). However, in central Europe and increasingly in the north as well, Norway spruce is being managed as a component of a mixed forest to increase timber yields and biodiversity (Sullivan 1994, Mielikäinen & Hynynen 2003). In Scandinavia, a few managers are using Norway spruce as an understory crop below a birch overstorey; the two species require similar sites and birch provides a shelter for spruce saplings that are able to tolerate the shaded conditions (Mielikäinen & Hynynen 2003). After initial establishment of a mixed stand, optimal growth is achieved through overstorey cuttings to release the spruce regeneration (Mielikäinen & Hynynen 2003).

Almost all regeneration of Norway spruce in managed stands is done using planted seedlings; some artificial seeding is practised but natural regeneration is not common. Natural regeneration is very unreliable due to a highly variable seed crop, a lack of suitable microsites in managed forests and poor seedling establishment (Hagner 1965, Kuuluvainen & Kalmari 2003, Mielikäinen & Hynynen 2003). Site preparation, such as mounding or scarification, is done for both planting and seeding to help improve germination, survival and establishment (Nilsson & Örlander 1995, Kuuluvainen & Kalmari 2003, Nilsson et al. 2006). This reduces ground vegetation, increases water availability and increases soil temperatures (Nilsson & Örlander 1995, de Chantal et al. 2003*a*). However, despite breeding for superior seedlings and site improvements, the initial growth of Norway spruce is slow when compared to Scots pine (*Pinus sylvestris* L.) and other pioneer species (Sullivan 1994, Nilsson et al. 2012)

Norway spruce is most productive on moist and rich forest sites and does not grow as well on sites with medium fertility (Sullivan 1994, Nilsson et al. 2012). Fine textured soils, such as sandy loams or silts, are the preferred substrate because coarse and rapidly draining soils do not provide suitable moisture (Ahola & Leinonen 1999). The roots of Norway spruce may tolerate saturated conditions and soils with poor drainage; however permanently waterlogged sites are uninhabitable (Sullivan 1994). Ideal sites may have a ground cover of nutrient-loving herbaceous or shrubby vegetation, however spruce canopies are often so dense that light is blocked and understory vegetation is quite sparse (Sullivan 1994, Ahola & Leinonen 1999, Kuuluvainen & Kalmari 2003, Nilsson et al. 2012). Norway spruce litter affects the forest soil characteristics by decreasing soil pH and increasing Manganese concentrations (Sullivan 1994).

Norway spruce trees produce their first cone crop at about 30 or 40 years old (Sullivan 1994). Among trees of the same age, dominant individuals produce greater cone crops and quantities of seed than co-dominant or suppressed trees within the stand (Sullivan 1994). Flowering occurs in spring: May or June in cool regions, earlier in warmer areas (Andersson 1965). Norway spruce is monoecious and male and female flowers occur on the previous years' growth. Norway spruce is wind pollinated and self-pollination usually results in empty seeds. Andersson (1965) measured 20% to 25% of seeds in Norway spruce populations in Sweden to be empty. Following pollination, seed development occurs over the summer months until maturation is reached in the late autumn (Andersson 1965, Sullivan 1994). Each seed has a mass of about 4 mg and has a single wing attached to aid with dispersal (Ahola & Leinonen 1999). Seeds are dispersed primarily by wind in the spring following maturation (Leinonen et al. 1993) and some are carried great distances over the snow surface, but most land within one tree length (Andersson 1965, Sullivan 1994). Germination occurs in the early summer months after dormancy is broken (Sullivan 1994, Ahola & Leinonen 1999).

Norway spruce has very variable seed production and is known as a masting species (Hagner 1965, Sullivan 1994, Kuuluvainen & Kalmari 2003). Large cone crops are produced at intervals that vary by region and latitude; in northern climates good seed crops may occur every 12 to 13 years while southern climates may see large numbers of seed produced every three to four years (Sullivan 1994). Hagner (1965) reported good cone crops in the north of Sweden every seven to 11 years and every four or five years, or more frequently, in the south. It has been found that exceptional flowering years occur the spring after a hot summer with low precipitation (Andersson 1965). Seed orchards are commonly used and carefully managed to increase reliable seed production for artificial regeneration (Sullivan 1994, Owens et al. 2001).

Seed dormancy is broken through pre-treating of the seeds or by exposure to the correct cool and moist environmental conditions (Leinonen et al. 1993, de Chantal et al. 2003*a*). Norway spruce has developed mechanisms that allow it to germinate in very low light conditions – like those found below a dense canopy - if temperatures are greater than 10 ˚C (Ahola & Leinonen 1999). The moist chilling requirement for germination is eliminated after exposure to light (Sullivan 1994). Additionally, in the presence of light, germination can take place over a wider range of temperatures, though it has been suggested that temperatures over 25 ˚C have an inhibitory effect (Ahola & Leinonen 1999, de Chantal et al. 2003*a*). Even in the most favourable light and temperature conditions, Norway spruce is unable to germinate without adequate moisture and is extremely sensitive to drought during this period (de Chantal et al. 2003*a*). If conditions are dry and warm, germination and establishment are significantly reduced (de Chantal et al. 2003*a*).

There have been many studies investigating which seedbeds and microsites are optimal for the germination and survival of both naturally and artificially regenerated Norway spruce. In managed areas, site preparation such as light scarification to expose the A- and B-horizons is recommended; layers below the B-horizon can be too coarse and the free draining material results in desiccation of seeds and seedlings (de Chantal et al. 2003*a*). Nilsson et al. (2006) found that scarification can increase the survival and initial growth of

Norway spruce seedlings. Mounding creates exposed mineral soil and a raised microsite allowing the seedling to be in a competitive position relative to surrounding ground vegetation, although the risk of frost heaving is increased (de Chantal et al. 2003*a*, Kuuluvainen & Kalmari 2003). Exposed mineral soil reduces competition by removing surrounding ground vegetation, and also increases soil temperatures and provides greater moisture to germinants and seedlings (Nilsson & Örlander 1995, de Chantal et al. 2003*a*, Kuuluvainen & Kalmari 2003).

In unmanaged forests, exposed mineral soil is still the best substrate for Norway spruce establishment, although this microsite may be rare in late successional forests (Kuuluvainen & Kalmari 2003). Tip up mounds are able to create this microsite; however, these are limited in the managed forests of the European boreal region (Kuuluvainen & Kalmari 2003). Decayed wood microsites - such as logs in advanced stages of decay - were beneficial because they retain moisture well, contain nitrogen from microbial decay and are elevated above competing ground vegetation, which is particularly important on moist fertile sites (Kuuluvainen & Kalmari 2003). Favourable microsites often have an exceptionally high regeneration density resulting in mortality from competition within seedlings on the same site (Kuuluvainen & Kalmari 2003).

One of the most important factors for the survival and establishment of Norway spruce is water availability (de Chantal et al. 2003*a*, Kuuluvainen & Kalmari 2003). Warm and dry growing seasons can create drought stress and increase mortality due to insufficient soil moisture or respiration demand that roots are unable to keep up with (Nilsson & Örlander 1995, de Chantal et al. 2003*a*). Roots of germinants as well as of planted seedlings must be well enough established in the soil prior to the start of the main growing season to prevent desiccation (de Chantal et al. 2003*a*). Seedlings planted earlier in the spring have a greater chance of doing this and therefore have decreased risk of desiccation (de Chantal et al. 2003*a*). However, root competition for water resources with adjacent ground vegetation is another factor that may result in drought stress of the seedlings (Nilsson & Örlander 1995, de Chantal et al. 2003*a*).

Ground vegetation also competes for light and can shade the seedlings causing slow growth, but Norway spruce is usually able to survive this and is a good competitor in partially shaded or shaded conditions (de Chantal et al. 2003*b*). It does not have a significant morphological response (such as increased projected leaf area or biomass) to high light conditions, making it a poor competitor in open areas where pioneer species have an advantage (de Chantal et al. 2003*b*). Gap partitioning in small openings allows spruce to establish in the presence of pioneer species (de Chantal et al. 2003*b*). However, shelterwoods or management with some retention also creates good conditions for seedling establishment (Nilsson & Örlander 1995, de Chantal et al. 2003*b*). These partial cover conditions, especially when combined with site preparation, reduce competition from pioneer species, exposure to frost or drought and predation by pine weevil (*Hylobius abietis*) - a major pest in Northern Europe (Nilsson et al. 2006).

One of the biggest threats to Norway spruce in almost all life stages is drought. Other environmental damage includes growing season frost, though Norway spruce has been found to be relatively frost hardy, tolerating midsummer temperatures of -4 ˚C (Sullivan 1994). Norway spruce seedlings are prone to mechanical damage due to a relatively high height to diameter ratio (de Chantal et al. 2003*b*).

Norway spruce is relatively resistant to mammalian herbivory and is playing an increased role in managed forests partially because of this (Nilsson et al.

2012, Sullivan 1994). Some bark stripping from moose (*Alces alces*) and red deer (*Cervus elaphus*) is reported and leads to scarring or mortality in extreme cases (Sullivan 1994, Randveer & Heikkilä 1996). Roe deer (*Capreolus capreolus*) are known for minor browsing damage in Sweden (Nilsson et al. 2006). Grouse and other forest chicken birds as well as hares are reported to browse branchlets and needles but do not cause any significant damage (Sullivan 1994).

Perhaps one of the greatest threats to Norway spruce, particularly the establishment of seedlings, is the pine weevil (Nilsson & Örlander 1995, Nilsson et al. 2006). This insect is often attracted to freshly damaged or cut trees, such as when a shelterwood overstorey is removed (Nilsson & Örlander 1995, Nilsson et al. 2006). Although the entire life cycle of pine weevils takes place in harvested areas as previously described – see the Scots pine section – it is the adults that cause the most damage by consuming the twigs and cambium of young seedlings (Pitkänen et al. 2008). Leaving some retention trees after final harvest and practising scarification have been found to reduce the impact this insect has on regeneration (Nilsson et al. 2006). Another option is to use the insecticide permethrin to treat seedlings before or during planting, which effectively reduces damage from pine weevil (Nilsson & Örlander 1995, Nilsson et al. 2006).

Outcomes and expectations

Based on the different ecology of the species of interest, it is expected that there will be significant differences in the regeneration response of each species following disturbance. The treatments applied in the study described herein include prescribed burning and green-tree retention that created different understory conditions in terms of microsite conditions, seed availability and overstorey influences; this was, therefore, expected to impact the natural regeneration following treatments. This experiment was designed to test if novel forest management practices including prescribed burning and four levels of green-tree retention significantly impact the subsequent natural regeneration of each species 11 years after treatments were applied with regard to the: density of all regenerated stems, species composition as a proportion of regeneration of all species, average diameter of regeneration larger than 10 cm tall and average height of regeneration larger than 10 cm tall. We were also interested to see if the density of selected top quality' stems based on health and vigour was sufficient to meet government-recommended regeneration densities.

It was expected that pioneer species including birch, Scots pine and trembling aspen benefit from the treatments with increased levels disturbance; prescribed burning and a lower overstorey canopy affected the regeneration of pioneer species by increasing regeneration densities, the proportion of the stand that they occupy, mean height and diameter. 11 years following treatments, it was expected that birch densities will exceed those recommended by the government, but the result for Scots pine was expected to be less predictable. Since Norway spruce is a late-successional species, slow regeneration following treatments low densities and small seedlings compared to pioneer species was expected. Despite this, Norway spruce will likely occupy a greater proportion of the regeneration in treatments with substantial retention as it has a competitive advantage in shaded conditions relative to pioneer species. Each species will likely respond in a manner dictated by its ecological characteristics and will therefore result in different regeneration characteristics following treatments.

MATERIALS AND METHODS

EXPERIMENTAL SITE

Location

This experiment was located in Eastern Finland in the regions of Lieksa and Ilomantsi (approximately 63° 10' N, 30° 40' E, Figure 3- 1). The experimental units were distributed across a landscape area 20 km by 30 km in size. Surrounding landforms are low hills primarily covered by semi-natural boreal forests with some harvested areas and agricultural fields. Low-lying areas contain lakes, bogs and other wetland types. Vegetation types in this area transition from the South to the Middle Boreal vegetation zones. All experimental sites were established on state-owned (Metsähallitus) lands. One of the features of this forest area compared to the rest of the Finland is that it is located relatively close to natural forests that exist to the East in Russia.

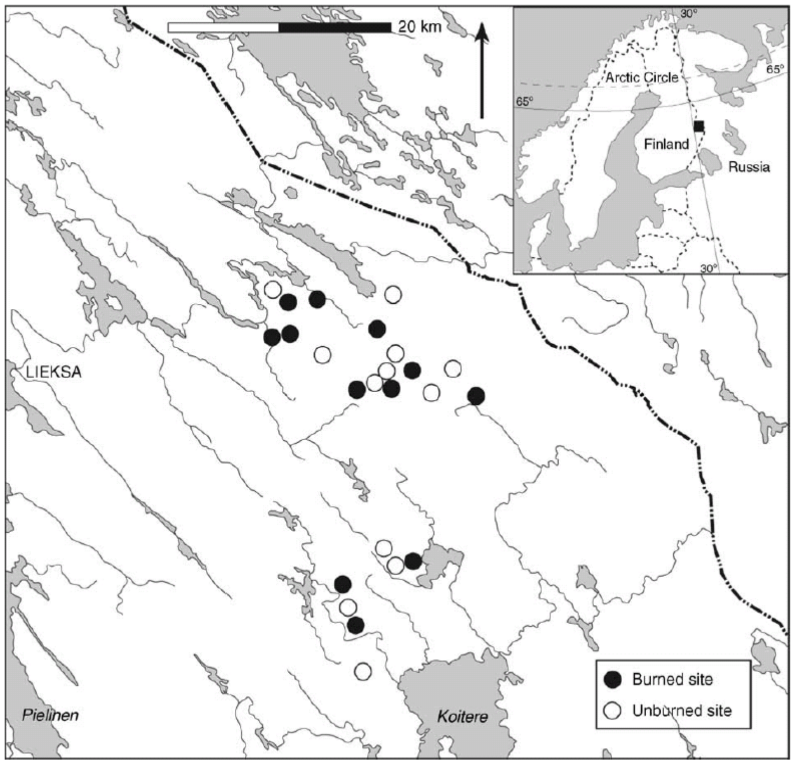

Figure 3- 1: Layout of experimental units in Eastern Finland. Six of the 24 treatments areas were located within Patvinsuo National Park (not indicated) and no harvesting treatments were applied to these areas although three of the areas were burned. The remaining 18 treatment areas were harvested to one of three levels of retention (0 m^3/ha, 10 m^3/ha, or 50 m^3/ha, six at each retention level) and half the areas were burned (three at each retention level). Map from Hyvärinen et al. 2005

Environmental characteristics

The climate in this region is continental with relatively cool and moist conditions. The growing season lasts approximately 150 days (Pitkänen et al. 2008), with between 190 to 270 days achieving temperatures above 0 °C (Pirinen et al. 2012). The mean daily temperature of the coldest month (January) temperature is -10.5 °C, while the mean daily temperature of the warmest month (July) is 16.5°C (Pirinen et al. 2012). On average, precipitation falls about 200 days per year (Pirinen et al. 2012). Mean annual precipitation is 620 mm with half of this being snowfall (Pirinen et al. 2012); the annual period of snow cover lasts from late November to late April.

Prior to treatments, all sites selected for this experiment had very similar characteristics in terms of forest stand structure, site type and management history. Stands were approximately 150 years old and the overstorey was dominated by mature Scots pine (*Pinus sylvestris,* 72% by volume) (Hyvärinen et al. 2005). Other overstorey trees included Norway spruce (*Picea abies*, 22%), birch (*Betula pendula* and *B. pubescens*, 5%), trembling aspen (*Populus tremula*, <1%) and grey alder (*Alnus incana*, <1%) (Hyvärinen et al. 2005). The average total live volume before treatments were applied was 287.9 m^3/ha ± 71.1 m^3/ha (Hyvärinen et al. 2005). All sites had similar volumes of live, dead and downed wood that were not statistically significantly different (Hyvärinen et al. 2005). The stand understory was classified as *Myrtillus*-type vegetation, primarily being comprised of dwarf shrubs and feather mosses. Soils were sandy and well-draining with a moraine parent material (den Herder et al. 2009).

Management history

The selected stands were considered to be semi-natural forests as they had not undergone any clearcutting or other intensive forestry practices. Evidence of this was the presence and distribution of dead and downed wood in the stand (Hyvärinen et al. 2005). There was some evidence that selective harvesting had taken place from the early 1900s to 1950s, but no management activities had occurred for the past 60 years (Hyvärinen et al. 2005). Charring and other signs of previous fires were found on the sites, most likely from forest fires and slash-and-burn agricultural practices that were common in this region prior to the 20th century (Hyvärinen 2006). Fire history in the study stands was explored by dendrochronological analyses before the treatments were applied (Kaipainen 2001); the last fires were dated almost exclusively to the late 1800s (one area was, however, burned in 1905). Despite these old disturbances over the years, these stands are considered to have a short management history compared to other forests in the area and have many characteristics similar to that of a natural forest. For a comparison between three typical classes in the study region – natural, semi-natural and intensively managed – see Junninen et al. (2006).

Treatments

The design of this experiment was a two-way factorial design where forest harvesting (four levels) and prescribed burning (two levels) were applied to the units resulting in a total of eight different treatment combinations. Each treatment combination was replicated three times resulting in a total of 24 treatment areas (units). Each experimental unit was 2.5 ha to 4.7 ha in size, similar to a standard cutting area in operational Scandinavian forestry. Although the overall site characteristics were the same for each unit, there was a lot of microsite variation contained within a unit. Soils ranged from rocky or sandy to organics and peat. Topography varied from level to convex or concave with variable moisture along slopes. With the exception of the six stands located within Patvinsuo National Park (Patvinsuo), all treatments were applied randomly across the landscape.

Trees were harvested from the treatment areas in the winter of 2000-2001 and four levels of residual trees were left on each unit: 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and 100% (approximately 288 m^3/ha). Each retention level was applied to six units. Clearcutting (0 m^3/ha) was selected to represent forest practices in Finland up to the 1990s (Hyvärinen et al. 2005). In the 1990s, government recommendations and forest operations changed; the new practice was to leave 5 m^3/ha to 10 m^3/ha following the final harvest. Therefore 10 m^3/ha was selected as the second level of retention (Hyvärinen et al. 2005). 50 m^3/ha was selected as the third retention level because it has been suggested that this is the quantity of retention required on the landscape for future deadwood recruitment to best promote saproxylic communities in mature forests (Hyvärinen et al. 2005). Uncut forests were the final retention level selected to represent natural forests (Hyvärinen et al. 2005). Residual trees in the harvested areas were left primarily in groups of about 30 stems representing a range of age classes, although a few trees were left as individuals (den Herder et al. 2009). Up to 13 of these groups were left scattered throughout the treatment area (den Herder et al. 2009).

Following harvesting, prescribed burning was applied to half of the units of each retention level (three per level, 12 total burned units) and the other half were left unburned. Prior to burning, fire guards 1 m to 3 m wide were created by removing flammable surface material around the perimeter of the unit (Hyvärinen et al. 2005). Areas adjacent to the treatment area were wetted to prevent fire escapes (Hyvärinen et al. 2005). Prescribed burning was carried out June 27-28, 2001 (Hyvärinen et al. 2005). Ignition was done around the perimeter of the unit allowing fires to build as they naturally grew towards the centre of the unit, resulting in generally greater fire intensity and severity in the centre of the unit (Hyvärinen et al. 2005). Prescribed burning was carried out in a short time period with relatively similar weather conditions; despite this, there was still a great amount of variation in burn severity and intensity within and between units (Hyvärinen et al. 2005). The burning procedure is described in further detail in Hyvärinen et al. (2005).

Four weeks following treatments, mortality of retained green trees was observed on burned units, while mortality in unburned units was negligible (Hyvärinen et al. 2005). Units where 10 m^3/ha was retained experienced the highest mortality rate with Norway spruce, Scots pine and birch dying at 94%, 73% and 93% respectively (Hyvärinen et al. 2005). 50 m^3/ha retention areas experienced slightly less mortality with rates of 77%, 22% and 72% for Norway spruce, Scots pine and birch respectively (Hyvärinen et al. 2005).

Four weeks after treatments, lowest mortality was observed in the unharvested stands where rates were 27%, 6% and 3% for Norway spruce, Scots pine and birch respectively (Hyvärinen et al. 2005). Duff layer thickness was reduced in burnt stands: 4% in unharvested units and 27% in harvested units (Hyvärinen et al. 2005). In the years shortly following prescribed burning, forbs, shrubs and trees began to re-grow in the understory. Fireweed (*Epilobium angustifolium*) and grasses dominated the forb re-growth, while the dominant dwarf shrubs were crowberry (*Empetrum nigrum*), blueberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*) (den Herder et al. 2009). Most early regeneration on the units was composed of deciduous trees, particularly birch seedlings and aspen suckers (den Herder et al. 2009). There were also scattered Scots pine and Norway spruce regeneration in the treatment areas (den Herder et al. 2009).

Regeneration sampling

Sampling design

Sampling the natural regeneration on the treatment areas was done in 2012, 11 years after the harvesting and burning treatments were applied. To ensure comprehensive sampling within experimental units - including edges - sampling points were established in a 50 m x 50 m grid pattern in each unit. Due to the variable unit sizes, a different number of sampling points were established in each unit; the mean number of plots was approximately 14. Points that fell in groups of reserve trees were still measured, but the location was noted. Circular fixed-area plots were established with the centre point at the grid's vertexes. The first sampling point was located at a point 25 m East/West and 25 m North/South of a random corner of the unit. All subsequent plots were located systematically in the 50 m x 50 m grid across the unit. The grid was marked in the field using a compass, 25 m fibreglass tape and Garmin 12 handheld GPS unit to mark locations as accurately as possible. Sampling points were established using a 40 cm section of PVC pipe that was labelled with the plot identifier and inserted into the ground to a depth of 20 cm to 30 cm. These points were recorded with the GPS unit to accuracy of 10 m or better.

The area of the plots ranged from 3.1 m^2 to 53.8 m^2 depending on the density of trees; high density areas had smaller plots, while low density areas had larger plots; 10 trees per plot was the targeted minimum. In this way, sample plots containing no trees or hundreds of trees were limited. The appropriate plot size according to local tree density was selected prior to individual tree sampling and measurements. The plot perimeter was located by rotating a measured cord of the selected radius 360° around the centre.

Plots at the border of the treatment area presented challenges. A plot was determined to be "out" of the unit area if the centre point fell beyond the border of the treatment area. Plots where some portion was beyond the treatment boundary were measured using the "mirage method," which is commonly applied in forest mensuration. The area of the plot that fell beyond the boundary was reflected over the boundary and all trees falling within the reflected area were counted twice. This was not common and had to be done less than 5 times in all 295 plots. A few plots contained planted trees from a different experiment were sampled but the data from the entire plot were removed prior to analysis. Plots in areas of extremely low or high regeneration densities - apparently due to soil or other environmental conditions - were retained for analysis, even when they appeared to be outliers.

Measurement procedure

Natural regeneration was quantified within the plots as follows. Regeneration was not considered if it was greater than 7.5 cm diameter at "breast height" (1.3 m, DBH); in forest mensuration this size is considered to be a dividing point between the "pole" forest layer and regeneration. All trees meeting this criterion were recorded by species and marked with a wax crayon to avoid duplicated measurements. Borderline seedlings were determined to be in or out of the plot based on the centre point of the stem at root collar. This way, decisions could easily be made for leaning or crooked trees. The total count of all species was later used to calculate the stems per hectare (density) of the regeneration based on the plot area. These were the only data collected for regeneration less than 10 cm in height, as these trees were very numerous and often face very high mortality rates during early growth.

In the case of vegetative reproduction from a buried root system, it was impossible to differentiate unique individuals based on mother tree and unrealistic to record each vertical growth from the root system. Instead, the most dominant sucker in a group was measured for all attributes described below. The group of suckers was delineated by proximity to each other as well as how significantly the roots were interconnected. Interconnected roots were discovered by applying an upward force to the dominant stem and visually watching for movement from neighbouring suckers. This was mainly applied to dense groups of aspen trees (*Populus tremula*) and rowan (*Sorbus* sp).

For trees greater than 10 cm in height, additional information was recorded for each specimen: height, diameter, health and presence of mammal browse. Height was measured at the maximum of the previous seasons' growth to the nearest cm using a 4 m wooden height measuring pole. The regeneration was measured to the height of the previous seasons' growth because work took place over the growing season resulting in increased leader heights later in the field season. If a tree was not growing vertically, the measurement was still taken vertically from the root collar to the top of the previous growth, not along the length of the stem. If a terminal leader was dead or broken, the height of the tallest lateral branch was measured. Tree heights greater than 4 m could not be accurately measured with the equipment available so they were noted as greater than 400 cm; this occurred in less than 1% of all measurements.

Although it is common practice to measure tree DBH, this was not possible as many trees were not yet tall enough. Diameter was measured at the root collar of the seedling to the nearest millimetre using 15 cm callipers. All diameter measurements were made perpendicular to the main stem direction at the base. If there was a stem deformity or irregular growth at the root collar, stem diameter was measured above the deformity, but as low as possible. Diameter changes over the growing season could not be compensated for in the measurements.

Health was measured subjectively to incorporate growth, form, insect and disease damage. Mammal browse was noted as either "hare" or "moose" wherever it was identifiable. Both types of browse were combined for future analyses as the incidence of hare browse recorded was overall very low (approximately 8% of all browse) and the damage caused by hares was twig clipping very similar to a majority of moose browse and will therefore likely impact the tree health in a similar way. Further comments on the severity of the browse were included especially in cases of major damage. Tree health was evaluated and given a score from 0 to 3 as follows:

- 0: Excellent vigour, good form and no visible insect or disease damage

- 1: Good growth, minor form abnormalities, slight foliar or lateral branch damage
- 2: Poor growth, moderate main stem deformation or vigour-impacting health issues
- 3: Very poor growth, severe main stem deformation or immanent-death

Analyses

Analyses were done using R 2.15.3 and SAS 9.2 on the following regeneration data:

- density of all stems,
- species proportion of total stem density
- height of stems greater than 10 cm tall,
- diameter of stems greater than 10 cm tall, and
- browse on stems greater than 10 cm tall.

An experiment-wide level of significance of $\alpha = 0.05$ was selected and used for all tests. This was adjusted for some sets of pair-wise comparisons to achieve an overall significance level of 0.05.

Tree density was analysed for all stems combined as well as separated by species. Scots pine, Norway spruce, birches and aspen were included for these analyses. R was used for initial analyses including calculating stems per hectare, sampling plot summaries and treatment summaries. Exploratory graphics (boxplots) were done using R. Normality and homogeneity of variance of the residuals was tested using SAS prior to ANOVA analyses. The density data were found to be non-normal and had heterogeneous variance of the residuals, so transformations were completed by species. Scots pine density data were square-root transformed, Norway spruce and birch densities were log-normal (ln) transformed and trembling aspen could not be successfully transformed at the sampling plot level. Instead, trembling aspen densities were averaged to the experimental unit level and there was no nested term included in the ANVOA of these data. The transformed data of Scots pine, Norway spruce and birch met all assumptions and was used for all testing of regeneration density, but boxplots for visual analyses were created using untransformed data. ANOVA analyses for Scots pine, Norway spruce and birch were run in SAS using mixed model analyses with two fixed effects (retention level and burn/unburned) and their interaction; the sampling plots were treated as random term nested within the treatment combinations (i.e. sampling plots were treated as subsamples). If either of the main effects or interaction term were significant in the ANOVA, further pair-wise comparisons of least-square means were completed between treatment combinations of particular interest: burned versus unburned data within each retention level and pairwise comparisons between retention levels (a total of six comparisons) within burned or unburned treatments separately. Comparisons of burned versus unburned within each retention level were tested with no adjustment of alpha because the contrasts were orthogonal. Pairwise comparisons among retention levels within burning treatments were tested with an adjusted alpha of 0.05/6 because each set of 6 contrasts was non-orthogonal.

In each plot, the top-quality regeneration trees for Scots pine, Norway spruce, birches and aspen were identified based on a health score of 0 or 1 to incorporate seedling health and vigour, but not size, as described in the measurement procedures. These selected top quality' needed to have densities greater than the government recommendations in order for natural regeneration to be considered a viable regeneration method. These select densities were summarised to experimental unit level, descriptive statistics (median, 5th and 95th percentiles) and graphical analyses by species using boxplots were completed using R. A one-sided, one-sample t-test was completed in SAS to compare the species sample mean of each treatment to the government standards for Scots pine, Norway spruce and birch, which were 2000, 1800 and 1600 stems per hectare respectively (Metsätalouden Kehittämiskeskus Tapio 2006). Prior to completion of the t-tests, these density data were log-normal transformed to correct non-normality.

Percent regeneration composition by species was calculated as follows: the total stems per hectare of a species (sum of all sample plots) in an experimental unit was divided by the total of stems per hectare of all species measured in that unit to give a percent composition of the species by unit. These data were then visually inspected with boxplots generated in R and descriptive statistics (mean and standard deviations) were calculated. Residuals of the percent composition data met the assumptions of ANOVA (normality and homogeneity of variance). ANOVA was used at the experimental unit level to test for effects of retention level, burn treatment and their interaction on percent composition for each species separately. Following significant results in ANOVA tests, selected pair-wise comparisons were completed as described above for stem density.

Percent composition of the entire community of regenerating species was analyzed using PerMANOVA to test for significant differences due to retention level, burn treatment or their interaction. If any were differences were found, further pair-wise comparisons were made as described above for density of individual species.

The mean height and diameter of seedlings greater than 10 cm in height by species were calculated in each plot. Graphs were created to show mean height and diameter of a species by treatment and descriptive statistics (mean and standard deviations) were calculated. These height and diameter data were found to be not significantly different than normal and have homogeneous variances so no transformations were completed. ANOVA tests and pair-wise comparisons were completed for mean heights and diameters of each sampling plot as previously described for density analyses using experimental unit nested within treatment. Additionally, diameter and height distributions were created by species and treatment to create a visual representation of the distribution of tree sizes. For diameter, regeneration density per hectare in 10 mm diameter classes (16 total classes) was calculated. Similarly, 25 cm (16 total classes) height classes were used for and density for each height class calculated.

Proportional browse was calculated as the stems that were browsed as a proportion of all stems that could have been browsed. Browse was analysed by treatment for all species combined as well as species separately; browsed seedling were calculated as a proportion of all seedling that potentially could be browsed. Due to its ecological importance for browsers, rowan (*Sorbus* sp) was included as one of the species included in this analysis. Some sampling plots were removed from this analysis because they were located within fenced game exclosures (see den Herder et al. 2009). ANOVA was used at the experimental unit level without a nested term to test for the effect of retention level, burn treatment and their interaction on browsed stems as a proportion of all stems. No transformations were completed as these data were not significantly different from normal and had homogeneous variances. Following significant effects in the ANOVA, pair-wise comparisons were completed as described above. Calculations, descriptive statistics and plots were constructed using R 2.15.3 and post-hoc tests were completed using SAS 9.2.

RESULTS

Summary of the data

After removal of four sub-plots due to planted trees, sampling resulted in a total of 299 fixed-radius sub-plots for all treatment areas with an unbalanced number of sub-plots for each treatment combination. In total, there were seven tree species recorded: silver birch (*Betula pendula*), downy birch (*Betula pubescens*) (together regarded as "birch"), Scots pine (*Pinus sylvestris*), European trembling aspen (*Populus tremula*), Norway spruce (*Picea abies*), rowan (*Sorbus aucuparia*) and grey alder (*Alnus incana*) (a minor species not included in analyses). 6966 naturally regenerated trees were sampled for density and the size of these trees ranged from less than 10 cm to over 400 cm in height and 2 mm to 154 mm in diameter at root collar. Of the sampled trees, 4444 were greater than 10 cm and only these were measured for health, height, diameter and incidence of browse.

Density

There were significant effects of burn and retention treatments on regeneration density but no significant interactions between the two (Table 3- 1). Except for Norway spruce, all species had greater regeneration density in the burned treatment than in unburned at a given retention level (Figure 3- 2). This resulted in greater total density of all species combined in burned treatments (Figure 3- 2). The difference in total regeneration density between burned and unburned was only significant at 10 m^3/ha retention (pairwise test, $p = 0.0425$) where there was a median of 15518 stems/ha in burned areas and only 7032 stems/ha in unburned areas (Figure 3- 2A). The effect of retention treatment on density was significant for all species combined and each species by itself except Norway spruce (Table 3- 1). Treatments with partial cutting tended to have greater densities than uncut treatments with the same burning treatment, once again with the exception of Norway spruce (Figure 3- 2). All treatments with cutting had greater regeneration density than the uncut treatment; the greatest difference existing between burned treatments with 10 m^3/ha retention and uncut areas ($p = 0.0035$). Green-tree retention at 10 m^3/ha combined with burning resulted in the highest total regeneration densities, although regeneration with 50 m^3/ha green-tree retention was not significantly less.

Birch and Scots pine showed similar responses to the treatments. The level of green-tree retention significantly impacted both species while prescribed burning significantly affected the density of Scots pine and was almost significant ($p = 0.0507$, Table 3- 1) for birch. For both species, the median regeneration density was highest in the burned treatments with 10 m^3/ha retention (Figure 3- 2). For both burned and unburned treatments, regeneration densities of birch and Scots pine were greater in treatments with harvesting than those that were uncut (Figure 3- 2B, C). At the same retention level, burning treatments had greater median densities for birch. Scots pine had significantly greater densities in burned treatments at 0 m^3/ha retention ($p = 0.0093$), 10 m^3/ha retention ($p = 0.0003$) and uncut ($p = 0.0030$), but not at 50 m^3/ha retention ($p = 0.2653$).

Trembling aspen and Norway spruce showed different regeneration density patterns than birch and Scots pine; regeneration of trembling aspen was not significantly affected by burning whereas Norway spruce regeneration did not respond to the retention treatments (Table 3- 1). Regeneration density of trembling aspen (Table 3- 1) was higher in harvested areas than uncut treatments, particularly in burned areas (Figure 3- 2D). Although the effect of burning was not significant, in treatments with cutting applied burned areas had greater densities than unburned ones at the same retention level (Figure 3- 2D). There was a high degree of variability in regeneration of trembling aspen density among treatments (Figure 3- 2D); all treatments had some areas with 0 stems/ha of trembling aspen, but only the uncut burned treatment areas had 0 stems/ha in all areas. Maximum densities exceeded 40,000 stems/ha within a sub-sample area. Contrary to all other species, Norway spruce regeneration density tended to be lower in the burned treatment (Figure 3- 2E), although no significant pair-wise differences were found.

Composition

Retention had an overall effect on the composition of the regeneration community ($p = 0.005$) while we were unable to show a statistically significant difference for burning (Table 3- 2). In burned or unburned harvested stands, the regeneration community tended to be dominated by birch and Scots pine, with a lesser component of trembling aspen; Norway spruce and rowan were a lower proportion of the regeneration where harvesting had occurred (Figure 3- 3). Burning increased the dominance of birch and Scots pine in harvested areas, but had a mixed effect on trembling aspen and decreased the Norway spruce and rowan components (Figure 3- 3).

Retention level had an overall significant effect on the proportion of birch, trembling aspen and rowan with no interaction effects (Table 3- 3). However, the result of pairwise comparisons showed that retention treatments did not significantly affect regeneration composition except for trembling aspen in unburned treatment areas (Figure 3- 3C). Unburned areas with 0 m^3/ha retention had a significantly higher proportion of trembling aspen than any of the other retention treatments ($p \leq 0.0025$). Although retention was found to have a significant effect on the proportion of birch and rowan (Table 3- 3), no statistically significant differences were shown in pair-wise comparisons between the treatment combinations. The proportion of birch regeneration tended to be greatest in harvested stands, particularly with 10 m^3/ha retention (Figure 3- 3A). Conversely, the proportion of rowan regeneration was greatest in unharvested stands (Figure 3- 3E). Norway spruce tended to benefit from increased retention particularly in burned areas, however effect of retention was not significant (Table 3- 3).

Prescribed burning did not have a significant impact on any species except Norway spruce (Table 3- 3). Burning decreased the proportion of Norway spruce regeneration (Figure 3- 3D), which was the opposite trend seen for other species (Figure 3- 3). In Figure 3- 3A and B, it can be seen that the proportion of birch as well as pine tended to greater on sites with higher disturbance (burning and harvesting). Rowan dominated the regeneration community in unharvested stands – which did have very low overall density, but was a minor component of harvested stands (Figure 3- 3E).

<u>Height</u>

The effect of retention level was significant for birch and almost significant for Scots pine, while prescribed burning was significant for both species (Table 3- 4) although both species had similar overall trends (Figure 3- 4). The result of pairwise comparisons showed that burning did not impact the average height of either species in harvested areas, but in uncut treatments burning significantly reduced regeneration height for birch and Scots pine (Figure 3- 4). In burned treatments, the average regeneration heights decreased with increasing retention for birch (Figure 3- 4A) and for Scots pine (Figure 3- 4B). However, within unburned areas uncut treatments had greater average heights than harvested areas for birch (Figure 3- 4A) and significantly greater average heights than harvested areas for Scots pine (Figure 3- 4B, $p \leq 0.0003$). There was a significant interaction between retention and burning treatments in terms of the mean height of birch and

Scots pine (Table 3- 4). Within disturbed areas (harvested or burned), increased retention level decreased the height of birch and Scots pine

Trembling aspen height was not significantly affected by retention or burning (Table 3- 4); there was no trembling aspen regeneration greater than 10 cm in height in the burned uncut treatment areas (Figure 3- 4C). Further pairwise comparisons found that the difference between burned and unburned sites was almost significant ($p = 0.0515$), although no other major differences in the mean height of trembling aspen existed between treatments.

Burning and retention treatments, but not their interaction, had a significant effect on the height of Norway spruce regeneration (Table 3- 4). Generally, spruce regeneration was shorter in burned treatments at the same retention level, but this difference was only significant in uncut treatments ($p = 0.0287$, Figure 3- 4D). Uncut unburned treatment areas had the greatest average height of Norway spruce regeneration (228 cm), which was greater than for any harvested treatment (Figure 3- 4D).

<u>Diameter</u>

Regeneration diameter and height had very similar treatment responses for each species, which was expected as they are highly correlated. Mean diameters for all species, except trembling aspen, were significantly affected by the retention harvesting and/or the burning treatments. Birch and Norway spruce were significantly affected by both retention and burning treatments without an interaction effect, while Scots pine had a significant interaction as well (Table 3- 5). The mean regeneration diameter of trembling aspen was not significantly affected by retention level, prescribed burning or their interaction (Table 3- 5).

Retention treatments had a significant effect on the mean diameters of birch and Norway spruce (Table 3- 5). However, further pairwise comparisons resulted in no significant differences of interest for birch although mean diameters tended to decrease with increased retention in disturbed (harvested or burned) areas (Figure 3- 5 A). Within unburned areas, the mean diameter of Norway spruce is greater in uncut stands than in those that were harvested (Figure 3- 5 D), although the effects of advanced regeneration must be considered when interpreting this. When considering the influence of retention level within the significant interaction effect for Scots pine, it can be seen that mean diameters within burned treatments are significantly less in unharvested areas than in harvested areas ($p \leq 0.0022$); the reverse is true for unburned areas where the unharvested treatments tended have greater diameters (Figure 3- 5 B). Overall, the impact of retention level on Scots pine was similar to that for birch where mean diameters tended to decrease with increased retention in disturbed areas (Figure 3- 5 B).

Prescribed burning had a significant effect on the mean diameters of birch and Norway spruce, although the effect was almost significant for Scots pine as well (Table 3- 5). The result of pairwise comparisons found that the mean diameter of birch in unharvested stands was significantly less in burned than unburned treatment areas ($p = 0.0194$, Figure 3- 5 A). Pairwise comparisons found no significant differences of interest between burned and unburned treatments for Norway spruce. Similar to birch, the mean diameter of Scots pine was significantly less in unharvested treatments that were burned than unburned ($p = 0.0003$, Figure 3- 5 B). Overall, within harvested treatments, burned and unburned sites tended to have fairly similar mean diameters, while these differed greatly in unharvested treatments and advanced regeneration must be considered when interpreting these results.

Browse

Proportion of browse was not significantly impacted by the treatments for any individual species; however, when all species were combined, retention had a significant effect ($p = 0.0448$) on the proportion of browse (Table 3- 6). For all species combined, unburned 0 m^3/ha retention areas had greater proportion of browse than other unburned treatments (Figure 3- 6A). By individual species, rowan was the most heavily browsed; the maximum proportion of rowan browse for a treatment was at least 42% greater than for any other species. Norway spruce was the least browsed species, with zero incidence of browse recorded for any treatment.

Density of selected top quality' stems

When only the healthiest and most vigorous stems (quality score of zero or one) were selected, the density of regeneration decreased (Figure 3- 7) compared to overall densities, but overall patterns of density by treatments were similar to those seen for total density of each species. These new densities, separated by species, tended to be greater for birch and Scots pine and government recommendations were often met (Table 3- 7; Figure 3- 7 A, B). Trembling aspen (Figure 3- 7 C, no recommended density) had lower densities while Norway spruce had the lowest densities; the median density of spruce was always less than that recommended although this was often not found to be statistically significant (Table 3- 7; Figure 3- 7 D).

The median density of top quality' stems was often at or below government recommendations for birch and Scots pine for all harvested treatments, while unharvested treatments tended to have means below those recommended. Birch density was significantly lower than recommended in uncut treatments (Table 3- 7) and clearly benefitted from harvesting (Figure 3- 7 A). We were unable to detect that the density of top quality' Scots pine in any treatment was significantly less than those recommended by the government (Table 3- 7; Figure 3- 7 B), although uncut treatments had densities much lower than those recommended. Burning clearly increased the densities of selected birch and Scots pine while harvesting tended to have a similar effect (Figure 3- 7 A, B).

Although there is no recommendation for the density of trembling aspen, we are still able to see which treatments resulted in higher densities of top quality' regeneration (Figure 3- 7 C). The median density of selected aspen stems did not exceed 1000 stems/ha in any treatment, but burned areas with any harvesting treatment applied and unburned areas with no retention had the greatest densities.

TABLES

Table 3- 1: ANOVA results for treatment effects on the density of regeneration. Numerator (num df) as well as denominator degrees of freedom (denom df) are reported; also included are p-values for each treatment and their interaction. Retention level includes all four retention treatments of 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and uncut; prescribed burning levels included burned or unburned. Signficance α = 0.05.

species	effect	num df	denom df	p-value
all	retention level	3	16	0.0029
	prescribed burning	1	16	0.0163
	retention-burn interaction	3	16	0.7914
birch	retention level	3	16	0.0001
	prescribed burning	1	16	0.0507
	retention-burn interaction	3	16	0.4221
Scots pine	retention level	3	16	0.0004
	prescribed burning	1	16	<.0001
	retention-burn interaction	3	16	0.1513
trembling aspen	retention level	3	16	0.0307
	prescribed burning	1	16	0.8335
	retention-burn interaction	3	16	0.1770
Norway spruce	retention level	3	16	0.3499
	prescribed burning	1	16	0.0259
	retention-burn interaction	3	16	0.8211

Table 3- 2: perMANOVA results for comparing the composition of regeneration communities between treatments as well as their interaction. Numerator (num df) as well as denominator degrees of freedom (denom df) are reported; also included are p-values. Retention level includes all four retention treatments of 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and uncut; prescribed burning levels included burned or unburned. Signficance α = 0.05.

effect	num df	denom df	p-value
retention level	3	16	0.005
prescribed burning	1	16	0.068
retention-burn interaction	3	16	0.397

Table 3- 3: ANOVA results for treatment effects on the percent composition of a species as part of the total regeneration community. Numerator (num df) as well as denominator degrees of freedom (denom df) are reported; also included are p-values for each treatment and their interaction. Retention level includes all four retention treatments of 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and uncut; prescribed burning levels included burned or unburned. Signficance α = 0.05.

species	effect	num df	denom df	p-value
birch	retention level	3	16	0.0399
	prescribed burning	1	16	0.4913
	retention-burn interaction	3	16	0.9878
Scots pine	retention level	3	16	0.3986
	prescribed burning	1	16	0.0959
	retention-burn interaction	3	16	0.1619
trembling aspen	retention level	3	16	0.0052
	prescribed burning	1	16	0.8757
	retention-burn interaction	3	16	0.0828
Norway spruce	retention level	3	16	0.0738
	prescribed burning	1	16	0.0153
	retention-burn interaction	3	16	0.4952
rowan	retention level	3	16	0.0351
	prescribed burning	1	16	0.2817

retention-burn interaction	3	16	0.7644

Table 3- 4: ANOVA results for mean regeneration height by species. Numerator (num df) as well as denominator degrees of freedom (denom df) are reported; also included are p-values for each treatment and their interaction. Retention level includes all four retention treatments of 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and uncut; prescribed burning levels included burned or unburned. Signficance α = 0.05. For analyses, trembling aspen and Norway spruce did not have sufficient individuals greater than 10 cm in all treatment areas resulting in a lower sample size (lower denom df).

species	effect	num df	denom df	p-value
birch	retention level	3	16	0.0055
	prescribed burning	1	16	0.0032
	retention-burn interaction	3	16	0.0129
Scots pine	retention level	3	16	0.0686
	prescribed burning	1	16	0.0008
	retention-burn interaction	3	16	<.0001
trembling aspen	retention level	3	9	0.0684
	prescribed burning	1	9	0.1039
	retention-burn interaction	2	9	0.1991
Norway spruce	retention level	3	12	0.0168
	prescribed burning	1	12	0.0194
	retention-burn interaction	2	12	0.6644

Table 3- 5: ANOVA results for mean regeneration diameter by species. Numerator (num df) as well as denominator degrees of freedom (denom df) are reported; also included are p-values for each treatment and their interaction. Retention level includes all four retention treatments of 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and uncut; prescribed burning levels included burned or unburned. Signficance α = 0.05. For analyses, trembling aspen and Norway spruce did not have sufficient individuals greater than 10 cm in all treatment areas resulting in a lower sample size (lower denom df).

species	effect	num df	denom df	p-value
birch	retention level	3	16	0.0248
	prescribed burning	1	16	0.0241
	retention-burn interaction	3	16	0.1383
Scots pine	retention level	3	16	0.8159
	prescribed burning	1	16	0.0563
	retention-burn interaction	3	16	0.0015
trembling aspen	retention level	3	9	0.0941
	prescribed burning	1	9	0.5004
	retention-burn interaction	2	9	0.2665
Norway spruce	retention level	3	12	0.0321
	prescribed burning	1	12	0.0102
	retention-burn interaction	2	12	0.9538

Table 3- 6: ANOVA results for browse proportion for all species as well as species separately. Spruce is not included as 0% browse was recorded for all treatments. Numerator (num df) as well as denominator degrees of freedom (denom df) are reported; also included are p-values for each treatment and their interaction. Retention level includes all four retention treatments of 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and uncut; prescribed burning levels included burned or unburned. Signficance α = 0.05.

species	effect	num df	denom df	p-value
all	retention level	3	16	0.0448
	prescribed burning	1	16	0.2149
	retention-burn interaction	3	16	0.1662
birch	retention level	3	16	0.6056
	prescribed burning	1	16	0.2581
	retention-burn interaction	3	16	0.9054
Scots pine	retention level	3	16	0.2569
	prescribed burning	1	16	0.7605
	retention-burn interaction	3	16	0.8090
trembling aspen	retention level	3	9	0.8089
	prescribed burning	1	9	0.4987
	retention-burn interaction	2	9	0.9702
rowan	retention level	3	13	0.0920
	prescribed burning	1	13	0.5464
	retention-burn interaction	3	13	0.4624

Table 3- 7: T-test results for density of "top quality" stems – those selected for having superior health, vigour and stem form – by species and treatment compared to the government-recommended density for forest regeneration in managed forests. Degrees of freedom (df) are reported; also included are p-values for each treatment and their interaction. Retention level includes all four retention treatments of 0 m^3/ha, 10 m^3/ha, 50 m^3/ha and uncut; prescribed burning levels included burned or unburned. P-values have been adjusted (p/2) for a 1-tailed test of whether regeneration densities were significantly less (α = 0.05) than those recommended by the government. The mean density of birch in the 50 m^3/ha burned treatments was found to be significantly greater than the recommended density and is indicated by $\bar{x} > H_0$.

species	treatment combination	df	p-value
birch	0 m^3/ha burned	2	0.2226
	0 m^3/ha unburned	2	0.0704
	10 m^3/ha burned	2	0.0572
	10 m^3/ha unburned	2	0.4423
	50 m^3/ha burned	2	$\bar{x} > H_0$
	50 m^3/ha unburned	2	0.4911
	uncut burned	2	0.0492
	uncut unburned	2	0.0492
pine	0 m^3/ha burned	2	0.0627
	0 m^3/ha unburned	2	0.0541
	10 m^3/ha burned	2	0.0580
	10 m^3/ha unburned	2	0.0709
	50 m^3/ha burned	2	0.0944
	50 m^3/ha unburned	2	0.0874
	uncut burned	2	0.1176
	uncut unburned	2	0.1176
spruce	0 m^3/ha burned	2	0.0684
	0 m^3/ha unburned	2	0.1887
	10 m^3/ha burned	2	<.0001
	10 m^3/ha unburned	2	0.0772
	50 m^3/ha burned	2	0.0369
	50 m^3/ha unburned	2	0.0916
	uncut burned	2	0.0234
	uncut unburned	2	0.0234

FIGURES

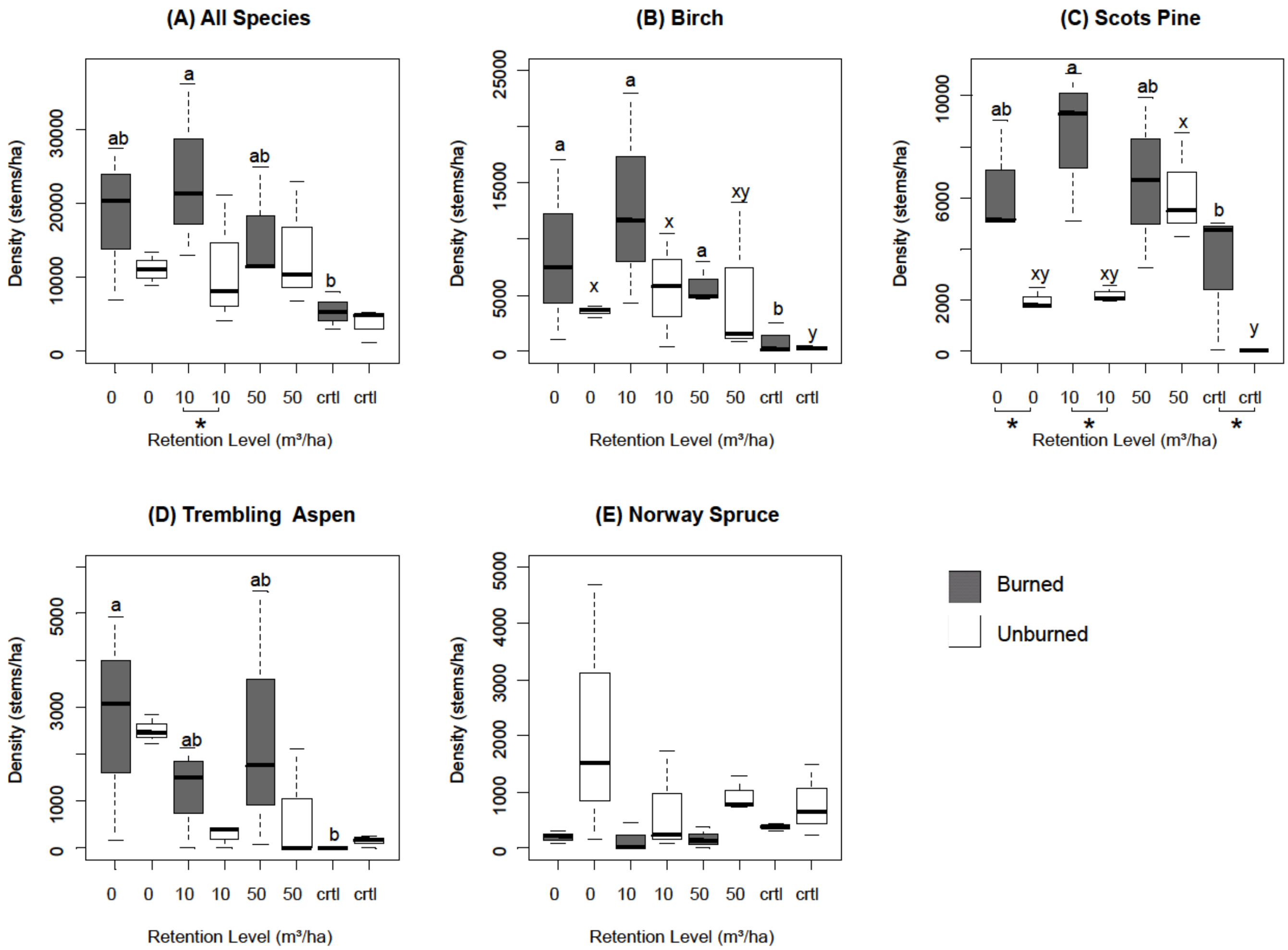

Figure 3- 2: Regeneration density of all stems by treatment combinations for all species combined and by individual species. The middle bar of each box indicates the median; the lower and upper ends of the box indicate the 25th and 75th percentiles, respectively. The 5th and 95th percentiles are shown by the whiskers. The y-axis is the density of regeneration in stems per hectare for each sub-plot averaged to the unit level; note the different y-axis scales. The letters above the boxes indicate significant differences between retention levels (α = 0.05) of burned (ab) and unburned (xy) treatments. Significant differences between burned and unburned treatments of the same retention level are indicated by * by the labels on the x-axis. All statistical tests were performed on transformed data, but original units are shown above.

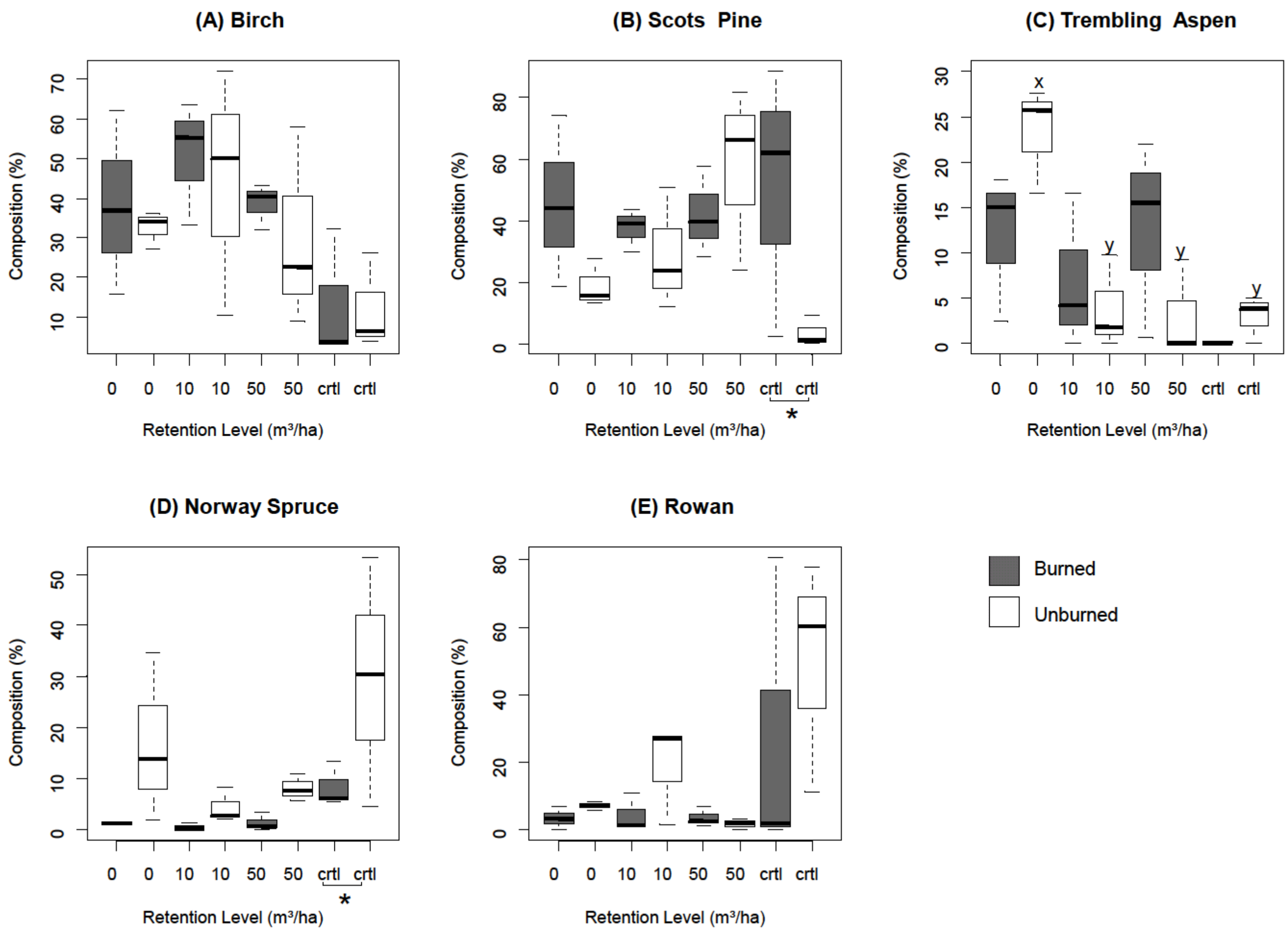

Figure 3- 3: Percent composition of a species as part of all sampled regeneration per unit for all treatments by species. The middle bar of each box indicates the median; the lower and upper ends of the box indicate the 25th and 75th percentiles, respectively. The 5th and 95th percentiles are shown by the whiskers. The letters above the boxes indicate significant differences between retention levels (α=0.05). Significant differences between burned and unburned treatments of the same retention level are indicated by * by the labels on the x-axis. Within a given treatment, the composition for all species sums to approximately 100, alder was excluded from these analyses as it is a minor species. Note the different y-axis scales.

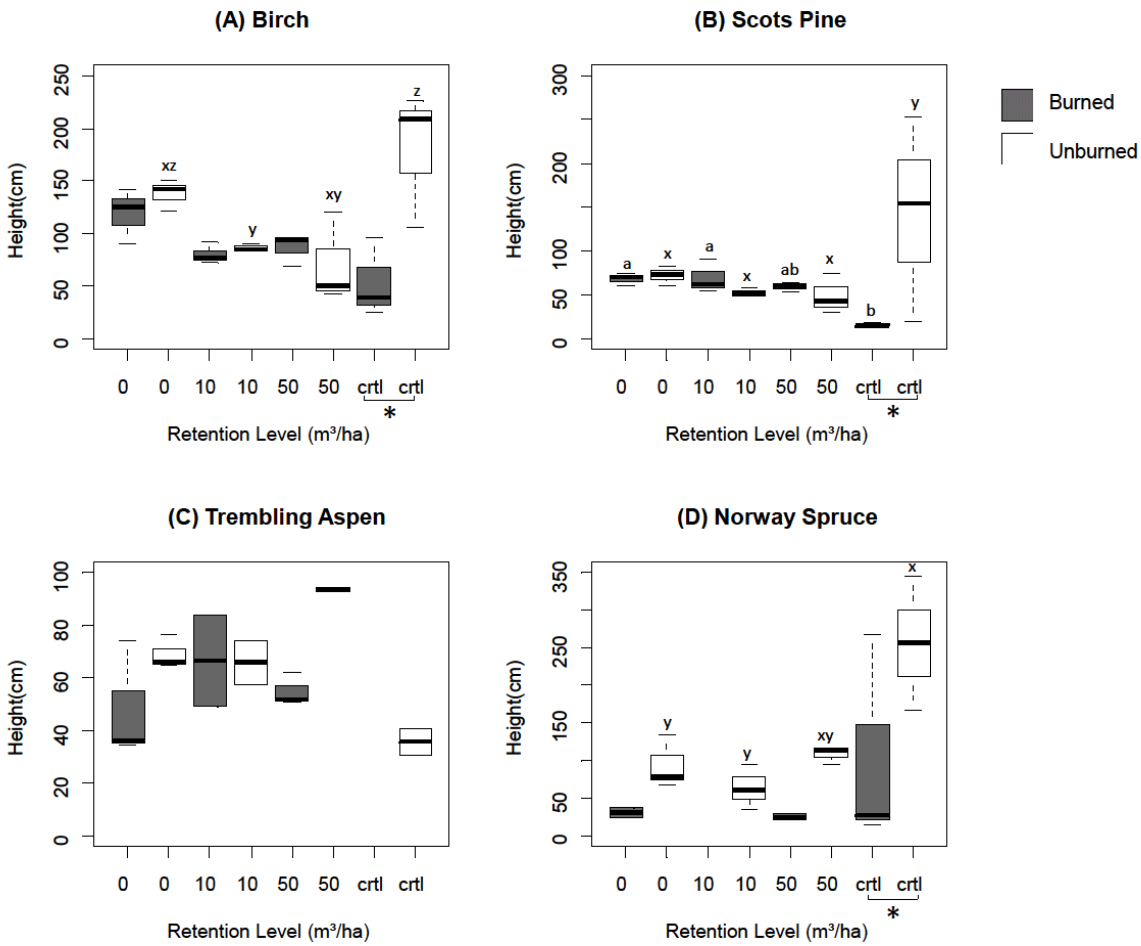

Figure 3- 4: Regeneration height for all treatment combinations by species. The middle bar of each box indicates the median; the lower and upper ends of the box indicate the 25th and 75th percentiles, respectively. The 5th and 95th percentiles are shown by the whiskers. The letters above the boxes indicate significant differences between retention levels (α=0.05) of burned (a, b) and unburned (x, y, z) treatments. Significant differences between burned and unburned treatments of the same retention level are indicated by * by the labels on the x-axis. Y-axis shows regeneration height by species for stems >10 cm in height as a sub-plot average; note the different y-axis scales.

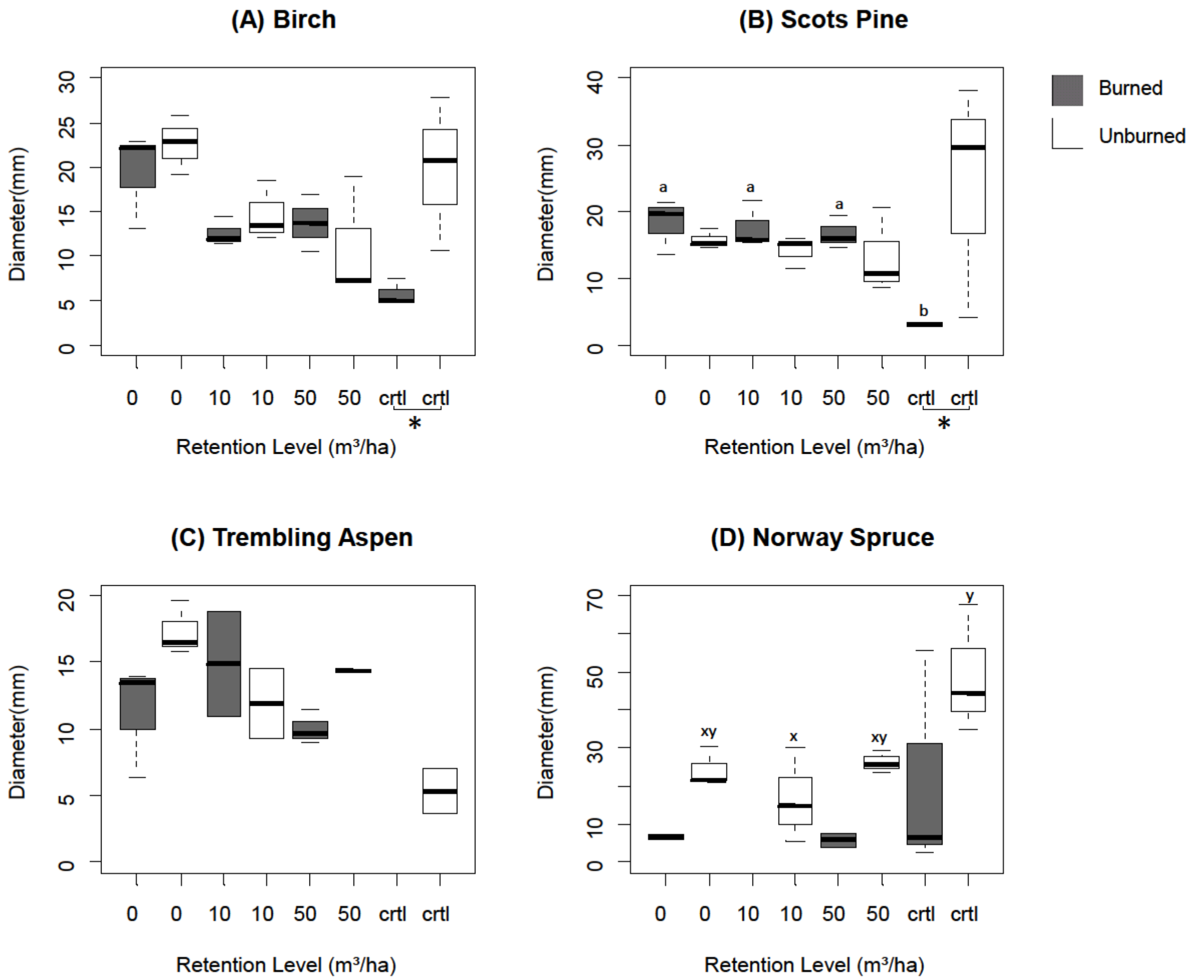

Figure 3- 5: Root collar diameter for all treatment combinations by species. The middle bar of each box indicates the median; the lower and upper ends of the box indicate the 25th and 75th percentiles, respectively. The 5th and 95th percentiles are shown by the whiskers. The letters above the boxes indicate significant differences between retention levels (α=0.05) of burned (a, b) and unburned (x, y) treatments. Significant differences between burned and unburned treatments of the same retention level are indicated by * by the labels on the x-axis. Y-axis shows regeneration diameter by species for stems >10 cm in height as a sub-plot average; note the different y-axis scales.

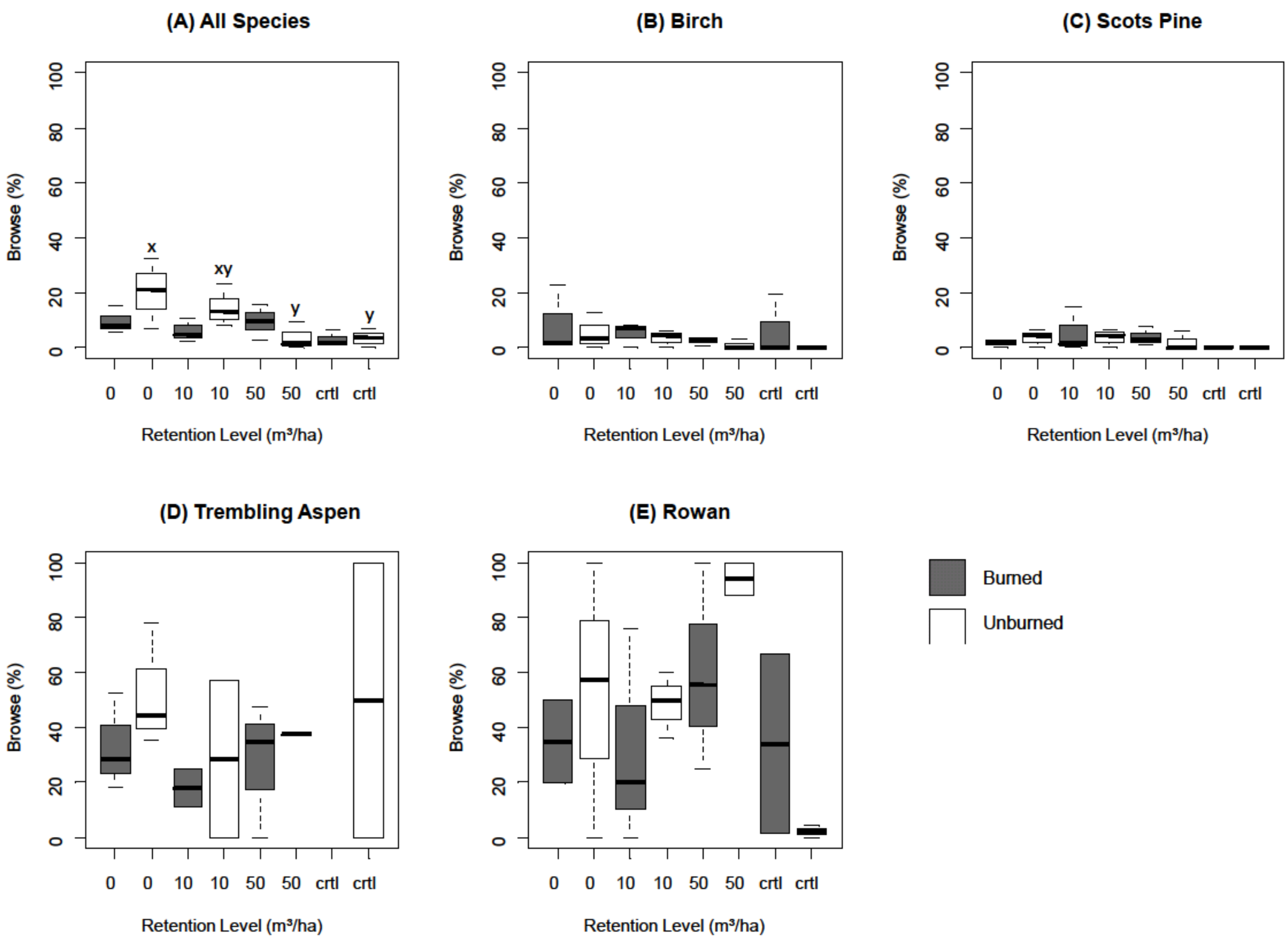

Figure 3- 6: Overall browse as a proportion of stems present for all treatment combinations by species combined and by species. The letters above the boxes indicate significant differences between retention levels (α=0.05). Y-axis shows the average proportion of browsed stems in a unit as a proportion of all stems in the unit.

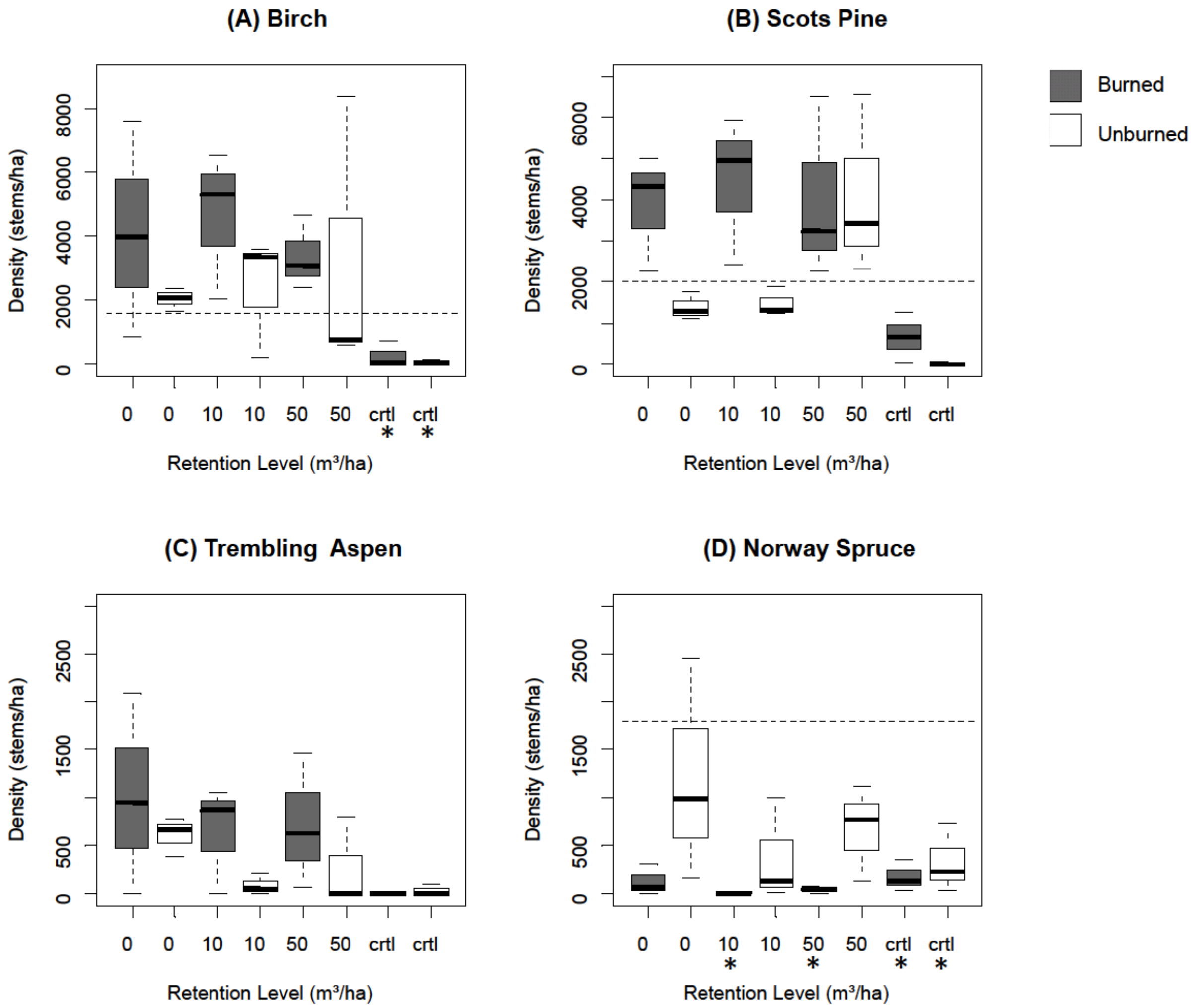

Figure 3- 7: Density of selected 'top quality' stems based regeneration health and vigour for each species. The middle bar of each box indicates the median; the lower and upper ends of the box indicate the 25th and 75th percentiles, respectively. The 5th and 95th percentiles are shown by the whiskers. The y-axis is the density of regeneration in stems per hectare for each sub-plot averaged to the unit level; note the different y-axis scales. The horizontal dashed line indicates the government-recommended densities of 1600 stems/hectare, 2000 stems/hectare and 1800 stems/hectare for birch, Scots pine and Norway spruce, respectively. * on the x-axis indicates where regeneration density is significantly less than the government-recommended density. All statistical tests were performed on transformed data, but original units are shown above.

Discussion

Overview

Prescribed burning and partial cutting with different levels of green-tree retention greatly influenced forest regeneration in terms of density, composition, size and incidence of browse damage. Overall, the results showed that these practices can result in healthy natural regeneration and that partial retention at levels tested may actually benefit natural regeneration. The response of individual species typically reflected their known ecological properties regarding disturbance and subsequent regeneration. Prescribed burning resulted in the mortality of retained trees at a different rate for each retention level, an interaction of treatments that may have resulted in some confounding effects.

Prescribed burning benefitted both birch and Scots pine in terms of density, but did not have a significant effect on the size of post-treatment regeneration; this was probably due to effects on the mortality of advanced regeneration, which then influenced average regeneration size. The greatest difference in partial cutting treatments existed between harvested and unharvested treatments; when harvested there were very few significant differences among the different retention levels. Increased retention tended to decrease the size of regenerating pioneer species, which was likely a result of shading rather than competition for other resources. Browsing impacted different species according to previously documented moose preferences, but was affected little by the treatments. Densities of selected top quality' stems followed trends that mirrored overall stem densities for each species. Although there were very few treatment combinations that resulted in densities significantly lower than those recommended for each species, this was likely only due to low power in statistical testing; often median densities were clearly lower than those recommended even if not statistically significant.

EFFECTS OF PRESCRIBED BURN

Density

Prescribed burning had a significant effect on the density of all species combined as well as birch, Scots pine and Norway spruce, but not trembling aspen. Birch and Scots pine are pioneer species and demonstrated a strong increase in regeneration density in burned conditions, a response supported by previous literature (Atkinson 1992, Holm 1994, Kuuluvainen & Rouvinen 2000). Fire is a disturbance agent that historically allowed the regeneration of these species (Sullivan 1993, Kuuluvainen & Rouvinen 2000, Mielikäinen & Hynynen 2003) and their regeneration ecology has adapted to this. Trembling aspen displayed a more variable response to prescribed burning, while Norway spruce had a decrease in regeneration density in burned areas probably as a result of the mortality of advanced regeneration due to burning.

Prescribed burning had a positive effect on the regeneration densities of birch and Scots pine. Forest fire causes soil disturbance and may occasionally expose mineral soil resulting in reduced vegetative competition and ground cover in addition to adding charcoal to the soil (Nilsson & Wardle 2005) that evidently benefitted the germination, establishment and survival of these seedlings. Mortality of competing vegetation increases the sunlight that reaches the seeds helping to break dormancy for both birch and Scots pine (Atkinson 1992, Ahola & Leinonen 1999, de Chantal et al. 2003*a*, Hynynen et al. 2010) and improving the growing conditions for established seedlings (Sullivan 1993, de Chantal et al. 2003*b*). Soil temperatures are higher in these conditions, which may aid in seed germination, but also increases the risk of drought (Sullivan 1993, Ahola & Leinonen 1999). Following initial establishment, den Herder et al. (2009) found that lower mortality of birch in burned treatments was a result of decreased damage from small mammals; however, Pitkänen et al. (2005) found that prescribed burning increased mortality of Scots pine seedlings due to pine weevil, but this could be mitigated by green-tree retention.

The regeneration density of aspen tended to increase with prescribed burning, but the effect of this was not significant. This was likely due to the clonal growth of aspen that results in spatial clumping of the regeneration and makes it difficult to detect true differences between the treatments. Although disturbances such as burning should increase the vegetative reproduction of trembling aspen (Bärring 1988, Worrell 1995, Myking et al. 2011), regeneration density in this situation was probably highly dependent on the location of "parent" trees in the pre-disturbance conditions. Ramet production is triggered by a loss of apical dominance (Bärring 1988, Myking et al. 2011) so the damage or mortality of "parent" trees is also required.

Norway spruce regeneration had very low densities that were further negatively affected by prescribed burning due to the mortality of existing pre-treatment regeneration. Norway spruce is extremely sensitive to desiccation and overheating during germination (Nilsson & Örlander 1995, de Chantal et al. 2003*a*, Kuuluvainen & Kalmari 2003), which likely caused high mortality of the few seed that were available on the exposed burned substrate. Thus, unburned treatments had greater spruce seedling densities due to the survival of advanced regeneration and more favourable germination conditions.

Composition

Burning had no overall significant effect on the composition of the regeneration community, although there were some clear effects on certain species. Generally, the pioneer species that reproduce primarily by seed (birch and Scots pine) became more dominant in burned conditions. The exception to this was in the 50 m^3/ha retention treatments where unburned areas clearly had a more dominant Scots pine component than burned areas, probably as result of the strong response of trembling aspen in burned conditions. Additionally, the many Scots pine retention trees (~50 m^3/ha) in this treatment likely provided a seed source to the openings where conditions were still sufficiently exposed for germination of Scots pine seeds, but ground cover competition was too great on the unburned soil for the widespread establishment of tiny birch seeds that require high light and an open seedbed for successful germination (Atkinson 1992, Hynynen et al. 2010).

Previous literature has suggested that burnt seedbeds may be ideal for trembling aspen seed germination and ramet densities also increase with burning (Bärring 1988, Worrell 1995, Myking et al. 2011). Despite this, burning was not found to have a significant effect on the proportion of trembling aspen regeneration, although in harvested areas with some level of retention the proportion of aspen increased with burning relative to unburned areas. Trembling aspen regeneration density is likely more dependent on the presence of "parent" trees, which were < 1% of the pre-treatment forests (Hyvärinen et al. 2005), than prescribed burning.

Norway spruce occupied a very low proportion of the stand overall, but was further negatively impacted by burning. Previous literature suggests that Norway spruce regeneration may benefit from ground disturbance (Nilsson & Örlander 1995, de Chantal et al. 2003*a*, Kuuluvainen & Kalmari 2003);

however, birch and Scots pine likely had a greater seed source and these species are much better competitors under exposed burned conditions (de Chantal et al. 2003*b*); this likely explains their dominance of the site.

Rowan was included in these analyses even though it is not a commercially managed species because it occupied a significant proportion of regeneration in some treatments and is considered in browse damage analyses. Burning did not have a significant effect on the proportion of rowan in the regeneration despite reported high mortality due to burning and a very high capacity to produce stump sprouts (Zerbe 2001). Conditions may not have been favourable in disturbed areas to support strong regeneration of rowan by either sprouting or seedlings, perhaps due to low moisture conditions or high herbivory.

<u>Size</u>

Prescribed burning had a significant impact on the height and diameter of regeneration, particularly in uncut treatments where this disturbance removed advanced regeneration. In uncut treatments, burned areas have significantly lower mean heights (Scots pine, birch and Norway spruce) and diameters (Scots pine and birch) than in unburned areas. Burning may create better growth conditions for newly established seedlings either through modifying the soil or canopy conditions in these treatments, but these effects could not be seen due to the influence advanced regeneration had in unburned conditions. Burning caused the mortality of a majority of advanced regeneration, and effect particularly noticed in uncut stands, thereby resulting in significantly younger and smaller regeneration in burned areas. Norway spruce advanced regeneration is particularly affected by this as it is very sensitive to fire (Sullivan 1994) and subsequent regeneration is slow-growing relative to other species with pioneer growth traits (Nilsson et al. 2012, de Chantal et al. 2003*b*). As a result, Norway spruce has greater height and diameter in unburned stands than in burned ones at any retention level where more advanced regeneration survived from pre-treatment forests. The height and diameter of trembling aspen varied, but burning had no significant effect on the size of the regeneration; instead severe browsing likely had a significant impact on especially the height, but also the diameter, of trembling aspen regeneration (Ericsson et al. 2001, de Chantal & Granström 2007, Myking et al. 2011).

Browse

Burning had no effect on browse either overall or by species. Instead, proportion of stems browsed depended more on the species measured. Trembling aspen and rowan are considered highly preferred species that are important for moose's winter diet; birch and Scots pine are moderately preferred (Andrén & Angelstam 1993, Shipley et al. 1998, Edenius et al. 2002*b*, de Chantal & Granström 2007), whereas Norway spruce is avoided (Sullivan 1994). 11 years following treatment, regeneration is generally sapling-sized and moose are the primary browsers (den Herder et al. 2009); they may not be able to detect a difference between burned and unburned sites resulting in little treatment effect on browsing at this stage. Since browse was measured as a proportion of stems available, higher densities of trees available for browse tends to reduce the overall proportion of browsing (Andrén & Angelstam 1993, Edenius et al. 2002*b*).

Selected stems

Prescribed burning increased the density of selected top quality' stems for all pioneer species – birch, Scots pine and trembling aspen – and decreased the density of selected Norway spruce regeneration. The density of selected stems for each species follows a similar pattern to the one found for all species combined and is likely governed by the same ecological principles.

Prescribed burning has similar effects as site preparation in terms of reducing organic material covering the mineral soil (den Herder et al. 2009) and reducing competing ground vegetation (Nilsson & Wardle 2005) and has similar benefits for pioneer species regeneration as a result. Although some of the treatments resulted in average densities less than those recommended, these were not found to be significantly below – likely due to few degrees of freedom resulting in a low power to detect significance through t-testing.

The density of Scots pine was not significantly lower than the government recommendation in any treatment, but was higher than the recommended density in all burned treatments with some level of harvesting. As previously discussed, Scots pine clearly benefits from burning due to its ecological properties. Natural regeneration is a practical management option to meet recommended Scots pine densities (2000 stems/ha); without burning treatments, 50 m^3/ha retention would result in the best densities. Birch benefitted from prescribed burning, although burning did not create such strong differences as it did for Scots pine; birch met the recommended densities (1600 stems/ha) in both burned and unburned treatments and can be successfully regenerated naturally following harvesting. Norway spruce, however, was negatively influenced by burning resulting in densities significantly lower than those recommended (1800 stems/ha) and would require artificial regeneration to meet these densities in both burned and unburned conditions.

There is no recommended density for trembling aspen although there are generally more selected top quality' stems in burned areas that had been harvested. Moose browse had a large impact on the quality of aspen trees; median browse proportions were over 20%. Browse proportions tended to be lower in burned treatments and overall densities higher resulting in more top quality' stems that are capable of maturing into trees with good form in future stands.

EFFECTS OF GREEN-TREE RETENTION

Density

Harvesting had a significant effect on the regeneration density, while there were no significant differences between different retention levels within harvested treatments. Within burned or unburned treatments, any level of harvesting resulted in greater overall regeneration than uncut treatments; the removal of overstorey competition and increased resource availability clearly benefitted the regeneration densities of all species except Norway spruce. Retention trees can reduce the amount of water, light and nutrients available to seedlings (de Chantal et al. 2003*b*); however there was no significant reduction in density or size of any species in areas with partial harvesting compared to clearcut treatments. The benefits of retention for regeneration – such as shelter from environmental extremes or reduced predation – and other values must also be considered.

Harvesting increased the regeneration densities of both birch and Scots pine – likely by creating conditions with increased light availability and decreased competition. In order to germinate and establish birch and Scots pine both need exposure to sunlight (Carlisle & Brown 1968, Atkinson 1992, Ahola & Leinonen 1999, de Chantal et al. 2003*a*, Hynynen et al. 2010) and availability of microsites with relatively low vegetative competition (Sullivan 1993, Nilsson et al. 2002). Undisturbed sites, such as those in the uncut treatments, do not provide good conditions for pioneer species regeneration. Nilsson et al. (2002) found similar results where the survival of birch seedlings increased with decreasing retention although the survival of Scots pine was not significantly affected. Despite this, regeneration densities for these species in treatments with partial retention were not significantly less than those in clearcut areas suggesting that retained trees did not have a profoundly negative influence on regeneration. Green-tree retention may increase seedling densities by providing a seed source (Kuuluvainen & Rouvinen 2000, Nilsson et al. 2006) then benefit the survival of these seedlings by providing shelter from environmental extremes (Nilsson & Örlander 1995, Nilsson et al. 2002, de Chantal et al. 2003*b,* den Herder et al. 2009) and reducing predation mortality and damage to the seedlings (Pitkänen et al. 2005, de Chantal & Granström 2007, den Herder et al. 2009).

Trembling aspen benefitted from low levels of green-tree retention, especially in unburned areas where clearcutting produced the highest densities of regeneration. Trembling aspen is considered a pioneer species that regenerates best in open disturbed conditions (Worrell 1995, Myking et al. 2011), which supports our result that higher densities of trembling aspen regeneration were found in the most disturbed sites - those that were harvested and burned. In unburned sites, complete overstorey removal was required for high ramet densities, whereas in burned sites any level of harvesting resulted in high densities of trembling aspen. However, this response is dependent on the existence of "parent trees" in the pre-treatment stand to support clonal sprouting. Uncut areas did not provide suitable conditions and resulting regeneration was very low. Den Herder et al. (2009) found that early mortality of trembling aspen regeneration from small mammal browse was reduced by increasing retention, which may have benefitted the survival of ramets in treatments with partial cutting although there was no clear evidence of this.

Norway spruce regeneration was not affected by green-tree retention; within burned or unburned treatments, similar regeneration densities were found at all levels of retention. Although Norway spruce seedlings should be more successful with some overstorey retention to limit the competition from early pioneer species (de Chantal et al. 2003*b*, Nilsson et al. 2006, Farver et al. 2008), it is probable that spruce seedfall was too low on all sites to be able to detect any differences. Pre-treatments forests on this site, and therefore retention patches as well, were only comprised of 22% Norway spruce that were mostly quite small and young trees (Hyvärinen et al. 2005), which appears to have provided insufficient seed to have impact regeneration densities.

Composition

Retention level did have a significant effect on the overall species composition of the regeneration with the greatest differences existing between uncut and cut or partially cut treatments. Birch existed in relatively low proportions in uncut treatments – even where burning scorched the canopy and left the main stems still standing – suggesting that the lower light conditions below even a thin overstorey may limit the success of birch seedlings even when a favourable seedbed is present. Birch and pine both occupied a greater proportion of the regeneration in harvested stands - likely due to increased germination in unshaded conditions (Carlisle & Brown 1968, Ahola & Leinonen 1999, de Chantal et al. 2003*a*, Hynynen et al. 2010), increased belowground resources supporting the seedlings' rapid juvenile growth (Atkinson 1992, Sullivan 1993, Nilsson et al. 2002, Hynynen et al. 2010) and relatively low mortality. De Chantal et al. (2003b) found that Scots pine seedlings are able to adapt their morphology to increase their competitive advantage in high light conditions which may have increased the dominance of Scots pine on harvested sites. Scots pine also dominated regeneration in burned unharvested stands, conditions which are considered very similar to past fire disturbance regimes that Scots pine has adapted to (Sullivan 1993, Mielikäinen & Hynynen 2003).

Trembling aspen occupied a greater proportion of the stand at all levels of cutting where a burning treatment was applied, whereas in unburned areas clearcut treatments were the only areas where aspen occupied greater than 10% of the regeneration. This is likely an effect of the mortality of pre-treatment "parent" trees causing a strong suckering response from the root system (Bärring 1988, Worrell 1995, Myking et al. 2011) and favourably exposed conditions for those sprouts to survive. Retention level did have a significant effect on the proportion of rowan in the regeneration community and it tended to be more dominant in uncut areas. Zerbe (2001) found similar results to these and credited this to rowan's ability to tolerate vegetative competition and shaded conditions, capacity to regenerate from its root system and its reliance on animals to spread seed; the residual forest provides good habitat and cover for the foraging animals, which would increase seed dispersal on unharvested sites.

Norway spruce was the most dominant in undisturbed treatment areas (unburned uncut), which is well supported by literature and current practices; Norway spruce is a late successional species that naturally regenerates under a forest canopy (de Chantal et al. 2003*b*, Nilsson et al. 2006, Fraver et al. 2008). Assisted regeneration is required to re-establish the species in disturbed areas; otherwise, pioneer species dominate the site (Hagner 1965, Kuuluvainen & Kalmari 2003, Mielikäinen & Hynynen 2003).

Size

Both height and diameter of birch, Scots pine and Norway spruce regeneration were significantly affected by level of partial cutting, particularly between cut and uncut stands. The much greater average height and diameter in unburned uncut stands can be attributed to the presence of advanced regeneration. With the uncut unburned treatment not included, we can look at the growth responses in the remaining treatments to primarily be measures of regeneration originating post-treatment, with a more minor component of advanced regeneration. Once this has been done, birch in particular and also Scots pine, have decreased height and diameter with increased retention; the minimum regeneration size occurred in burned uncut stands where advanced regeneration suffered mortality from the burning treatment and the existing regeneration is young and receives less direct sunlight because the stems of the dead burned trees have remained standing. In uncut treatments, by comparing the post-treatment regeneration in burned stands to the much larger surviving advanced regeneration in unburned stands, the significant interaction effect on height (birch and Scots pine) and diameter (Scots pine) can be explained.

Retained trees influenced the size of the regeneration in the treatment areas; as the amount of retention decreased from 100% to 0 m^3/ha in harvested treatments, the height and diameter of birch and Scots pine regeneration tended to increase, although this trend was not significant. This may have been a result of greater growth in more open conditions or earlier establishment - which was not quantified in this study - of the regeneration following disturbance. Both Scots pine and birch are capable of achieving high rates of juvenile growth, but require high light conditions to achieve optimal growth (Kuuluvainen & Rouvinen 2000, de Chantal et al. 2003*a*, Hynynen et al. 2010) as seen in harvested treatments, but this decreased due to retained trees. This was especially seen in uncut stands where regeneration is smallest. Although live retention trees can reduce available water and nutrients (Kuuluvainen & Rouvinen 2000, Hynynen et al. 2010), standing dead trees no longer compete for underground resources suggesting that shading may be the primary cause of reduced growth where retained trees were killed by fire. Standing retained trees that have died as a result of prescribed burn treatments will fall over the coming years allowing more sunlight to reach the ground thereby increasing the growth rates and recruitment of Scots pine and birch.

Norway spruce height and diameter were significantly affected by harvesting particularly in unburned treatments. Uncut treatments have greater mean regeneration diameter and height than those treatments with partial cutting, a result that can be attributed to the presence of large advanced regeneration in uncut stands. These stems were most likely harvested or damaged during harvesting treatments and would therefore not be present except in small retention patches.

Although trembling aspen ramets are capable of very high initial growth rates of over 1 m per year (Myking et al. 2011), nothing even close to this was observed. Additionally, partial harvesting had no effect on height or diameter of the regeneration; it would appear that severe browsing, primarily by moose, had a great impact on regeneration height and diameter as many other studies have documented (e.g. Ericsson et al. 2001, de Chantal & Granström 2007, Myking et al. 2011).

Browse

Although harvesting treatments did not have a significant effect on the proportion of browse for individual species, they did have a significant overall effect on all species combined when harvested and unharvested treatments were compared. Proportion of browse decreased in unburned areas with 100% retention compared to areas that were harvested. This is supported by den Herder et al. (2009) who reported increased moose browsing in clearcut areas where preferred deciduous pioneer species are abundant, visual monitoring for predators is unimpaired and access is easier due to fewer obstacles (retained trees and subsequent windthrow). However, Edenius et al. (2002*b*) suggested that retention trees might increase the attractiveness of a forage site for browsers due to increased cover. It was also stated that this effect might not influence browsing relatively small openings with surrounding cover (Edenius et al. 2002*b*), which may have also played a role in our treatment areas. It is also important to keep in mind that proportion of browse is a function of stems available and is heavily influenced by species preference.

Aspen is one species that is particularly affected by browse to the point where moderate and severe levels of browse (greater than 20%; Zakrisson 2007) can cause poor growth form that prevents saplings from developing into trees or even results in mortality (Ericsson et al. 2001, Myking et al. 2011). Increased levels of retention and subsequent windthrow can provide barriers against large browsers and mechanical protection to small trees for several years giving young aspen trees a chance to successfully re-establish (de Chantal & Granström 2007, Myking et al. 2011) although windthrow was not yet widespread in the treatment areas sampled. Green-tree retention could therefore help to re-establish aspen trees on the landscape by protecting them from severe browse.

Selected stems

As previously mentioned, the densities of selected top quality' stems for each species reflected the total stem density for each species in terms of relative response to each treatment as dictated by their known ecological properties. With the exception of Norway spruce, harvesting treatments at any level increased regeneration densities compared to uncut stands; birch and Scots pine met or exceeded government recommendations (1600 and 2000 stems/ha, respectively) in all harvested treatments. These species are able to meet government recommendations separately and will exceed recommendations when the selected top quality' stems for all species are combined. As before, the power to detect significant differences was relatively low due to few degrees of freedom for each treatment (two).

Following treatment with partial or complete harvesting, whether burned or unburned, natural regeneration of birch and Scots pine was sufficient to meet government recommendations and natural regeneration of these species should be considered a viable alternative after harvesting. Birch clearly requires harvesting to have sufficient regeneration as the two uncut treatments had densities significantly lower than those recommended - likely as a result the for high light conditions required for successful germination and establishment of birch (Atkinson 1992, Nilsson et al. 2002, Hynynen et al. 2010). Scots pine had exceptionally high densities of top quality regeneration in 50 m^3/ha retention treatments on both burned and unburned areas, possibly as be a result of previously mentioned effects of retention trees on increasing overall density combined with decreased levels of moose damage in these areas. Retaining green-trees - to increase other values in forest management - at a volume that is higher than what is currently recommended did not significantly negatively impact the natural regeneration of both of these species.

Norway spruce was not able to successfully regenerate following treatments and would require artificial regeneration in order to successfully establish following any of the treatments studied. All treatment combinations had medians below the recommended density (1800 stems/ha), which was further reduced by prescribed burning. The amount of green-tree retention had no impact on the density of selected top quality' Norway spruce regeneration and even unharvested treatments had poor regeneration.

Trembling aspen tended to have higher densities of top quality' regeneration in harvested areas, particularly those that are also burned. High levels of retention result in future downed woody debris as the retained trees face mortality or become windfall; this in turn can increase the density of high quality aspen trees by providing mechanical protection from moose browse (de Chantal & Granström 2007), a major damaging agent for trembling aspen.

MANAGEMENT RECOMMENDATIONS

Natural regeneration is a viable management option for pioneer species following partial cutting - whether it is combined with prescribed burning or not - and retention did not have a negative impact on the natural regeneration even at 50 m^3/ha. Recommendations as a result of this study can be considered in commercially managed forests or protected areas where the objectives are to have healthy regeneration following disturbance as well as to increase biodiversity relative to what is achieved with status quo forest practices. Managed forests would benefit in terms of habitat (Ehnström 2001, Hyvärinen et al. 2006) and support of threatened saproxylic species (Muona & Rutanen 1994, Martikainen et al. 2006, Junninen et al. 2008) in both the long term and short term from increased retention to 10 m^3/ha or 50 m^3/ha while still allowing for sufficient natural regeneration. Although there are clear benefits of prescribed burning for natural regeneration, the widespread practice is debatable due to high costs and generally poor public perception. Prescribed burning in unharvested protected areas could help to restore the natural patterns and processes of historic disturbance regimes resulting in the regeneration of healthy pioneer forests while also increasing habitat diversity and availability, especially regarding pyrophilic and saproxylic organisms.

Commercial forests would benefit from having retention increased in partial harvesting systems from the current minimum (Hyvärinen et al. 2006, Junninen et al. 2008) of five trees per hectare (Gustafsson et al. 2010) –

approximately 2 m^3/ha to 4 m^3/ha –up to 10 m^3/ha or 50 m^3/ha. These levels of retention result in sufficient densities of Scots pine and birch natural regeneration to meet government recommendations, although these were measured 11 years following treatments. An additional benefit of retention at volumes higher than those currently used in practice was reduced incidence of browse damage in the regeneration – also found in young seedlings (Pitkänen et al. 2006, den Herder et al. 2009) – while the height and diameter growth of regeneration was not significantly impacted. Benefits of retention at the levels studied include improved long-term conservation of saproxylic and other beetle communities (Muona & Rutanen 1994, Hyvärinen et al. 2006, Martikainen et al. 2006) and polypore assemblages (Junninen et al. 2008) by increasing long-term availability of decaying wood (Ehnström 2001, Hyvärinen et al. 2006, Junninen et al. 2008). As with other natural regeneration systems, future stand tending and thinning may be required to achieve optimal densities.

Prescribed burning not only created a suitable substrate that increased the regeneration densities of birch and Scots pine, but it also benefits coleopterans (Muona & Rutanen 1994, Martikainen et al. 2006) including saproxylic beetles (Hyvärinen et al. 2006). Prescribed burning in forests is not currently practised in Fennoscandia, but is a management alternative that should be strongly considered because it has many potential benefits for both regeneration and conservation of threatened species, especially when combined with green-tree retention.

Trembling aspen tended to have increased regeneration density and decreased browse damage in harvested areas including those with partial retention. Additionally, partial retention may help reduce predation on young aspens (de Chantal & Granström 2007, den Herder et al. 2009), which could help to increase the likelihood of re-establishing healthy trembling aspen populations on the landscape. Although trembling aspen is not commercially valued and is often removed from managed forests to reduce competition (Myking et al. 2011), it is an ecologically important species that is not widespread in Fennoscandian forest (Worrell 1995, Martikainen 2001, Kouki et al. 2004, Myking et al. 2011). For these reasons, it is recommended to adopt forest practices that include prescribed burning and green-tree retention that help to increase the regeneration of trembling aspen on the landscape (Martikainen 2001, Kouki et al. 2004) and protect it from severe browsing (de Chantal & Granström 2007).

Norway spruce natural regeneration was not widespread in any treatment combination studied; the uncut unburned stands had the best regeneration of Norway spruce as it is a late successional species that does not benefit from disturbance for regeneration. Current artificial regeneration practices are essential in a managed forest through planting seedlings or seeding to obtain adequate regeneration densities (Mielikäinen & Hynynen 2003). Advanced regeneration, particularly of Norway spruce, suffers mortality as a result of prescribed burning. Norway spruce will not naturally be a major component of regeneration in a disturbed area, but it is shade-tolerate and may regenerate under a deciduous canopy (Mielikäinen & Hynynen 2003).

While anthropogenic disturbances are not traditionally considered part of protected area management, prescribed burnings to mimic natural disturbances have been suggested in order to represent more early successional communities, particularly those featuring trembling aspen, in protected areas (e.g. Kouki et al. 2001, Kouki et al. 2004). Prescribed burning without partial cutting allows for the successful regeneration of pioneer species, namely birch and Scots pine, albeit in lower densities and sizes than in harvested treatments. However, this disturbance was found to have a profoundly negative influence on trembling aspen regeneration compared to treatments in which harvesting was combined with prescribed burning. Some level of partial cutting should be applied in combination with burning to specifically benefit trembling aspen regeneration as well as other tree species in pioneer communities in protected areas.

CONCLUSIONS

This study found that natural regeneration following harvesting with retention (0 m^3/ha, 10 m^3/ha or 50 m^3/ha) resulted in sufficient natural regeneration to meet recommendations in Finland, which was further increased for some pioneer species by prescribed burning. Partial retention was beneficial for the establishment of natural regeneration and often resulted in higher regeneration densities. Leaving more retention than what is currently required would increase habitat for other biota such as saproxylic fungi and animals while also benefitting natural tree regeneration. The retained trees in partial harvest treatments likely influenced the regeneration in multiple ways: by providing seed (Kuuluvainen & Rouvinen 2000, Nilsson et al. 2006), sheltering seedlings (Nilsson & Örlander 1995, Nilsson et al. 2002, de Chantal et al. 2003*b,* den Herder et al. 2009) and reducing predation damage to the seedlings (Pitkänen et al. 2006, de Chantal & Granström 2007, den Herder et al. 2009). The size of new regeneration tended to decrease, although not significantly, with increasing green-tree retention; pioneer species in particular were likely negatively affected by shading from retained overstorey trees.

Using prescribed burning in combination with this green-tree retention created good conditions for the regeneration of a stand with mixed pioneer species. Historically, fire has been a major disturbance factor in the study region and pioneer species (birch, Scots pine and trembling aspen) seem to have adapted to this; the regeneration density and dominance of these species was increased by burn treatments. Despite the cost of prescribed burning, it can provide key processes and habitats that threatened pyrophilic species depend on and should be considered a good forest management alternative resulting in healthy natural regeneration. In uncut stands, prescribed burning allows for the regeneration of pioneer species, albeit with slightly suppressed growth, and could be used as a management tool to increase pioneer communities in protected areas.

IV. Conclusions and Future Research

These studies demonstrated that substrate and surrounding vegetation play a key role in determining the success of naturally regenerated seedlings. Thick organic and litter layers are detrimental to seedling establishment; however seedling establishment following harvesting can be successful on thin organic material and mineral soil. These results suggest that forest managers could manipulate conditions to create better opportunities for natural regeneration through site preparation, prescribed burning, and vegetation control. Even with these techniques in place, natural regeneration is seldom relied on in practice, but there is great opportunity to utilize this as our understanding of natural regeneration grows.

Substrate was found to play an important role on seedling regeneration; this result was found to be true in both studies despite the fact that each was focussed at a different location, scale and timeline. In the boreal mixedwood of Alberta, substrates immediately surrounding seedlings were examined in the first four growing seasons after harvesting; substrates with thin or no organic layer were preferred for seedling establishment. Consequently, site preparation created excellent substrates for seedling germination and establishment. Similarly in Eastern Finland, the prescribed burning – which reduces surface organics and competing vegetation –benefitted the natural regeneration of many pioneer species; an effect that was still seen 10 years following treatments. However, prescribed burning or site preparation is not always required to create suitable microsites; natural regeneration was able to establish on existing post-harvest substrates in both regions.

Competing vegetation is a potential problem for conifer regeneration on intact substrates where there is no disturbance that may remove other propagules from the seedbed. Prescribed burning impacts this to varying degrees across the harvested area, while site preparation tends to create smaller disturbed areas leaving surrounding vegetation. Herbicide was found to be effective at reducing vegetation, although the long-term effects of this were not studied. Neighbouring vegetation was rarely negatively associated with white spruce growth and survival in Alberta, but this effect may be more pronounced for pioneer tree species or on sites very rich conditions and subsequently higher levels of cover. In addition to the potential competitive impact of neighbouring vegetation, deciduous litter from trembling aspen lead to increased mortality in very small seedlings. Especially when combined with spring flooding, heavy litter fall prevents the seedling from reaching oxygen and light, which is intolerable for very small seedlings. This may result in delayed or "failed" white spruce regeneration simply because very small seedlings are unable to survive the heavy litterfall of the deciduous overstorey.

Although all of the management options studied – site preparation and scarification, herbicide use, and prescribed burning – have potential benefits for natural regeneration, it is important to remember that they are often not necessary to successfully establish natural regeneration. These can be part of the strategy used to manage conditions after harvesting to facilitate natural regeneration. The results of these studies should be used to give forest managers a better understanding of the importance of substrate so that natural regeneration can be successfully used as a silvicultural strategy on a larger scale. In order to better facilitate natural regeneration, regeneration strategies can be adapted to focus on substrate management along with ensuring good seed sources. Managing local seed sources by leaving retention and reacting to mast years is critical for successful natural regeneration. Future research may even allow us to predict mast years, which will further strengthen our ability to predictably use natural regeneration in forest management.

In Finland, prescribed burning had the greatest benefit for the regeneration of pioneer species, particularly Scots pine, which regenerated with a mix of broadleaf trees. At the same time, retention patches increased regeneration density by providing a seed source and did not negatively affect the size of regeneration. Thus, these innovative forest practices including retention patches have the potential to benefit forest regeneration in addition to threatened species in the European boreal. These practices have great potential benefits for the intensively managed landscape of the European boreal, but the potential challenges of delayed stand establishment and managing mixed stands are often met with resistance. A paradigm shift to place more value on natural ecological patterns and processes must occur within the community of forest owners and managers to accept and overcome these challenges.

Managers must accept that even in ideal conditions, natural regeneration will establish more slowly and contain a wider mix of species when compared to plantations. The focus of forest management must shift to a strategy that balances economy and ecology instead of solely production; government standards may need adjustment to support this. Legislation and standards regarding forest regeneration should be adjusted to be accepting of more natural regeneration; increase the time allowed for the establishment of natural regeneration and modify stocking standards to include diverse species. It is likely that natural regeneration will result in a stand that is partially stocked with conifers and has broadleaf species as the remaining components. Managing and accepting a mixed forest may be one of the greatest challenges in the future of naturally regenerated stands, particularly when the species have contrasting life histories as broadleaves and conifers often do.

Future research is required to overcome the challenge and better understand the management of mixed forests with extended rotation periods as a result of natural regeneration. How will the long-term productivity and fibre output from these stands be impacted and does that change current cutting allowances? How and when will the future stand be tended and harvested? Both long-term field studies of intimate species mixtures in the boreal forest and modeling techniques will be required better understand how to manage two or more species together that have different life histories. In turn, this data will help to predict the wider economic and environmental impact of managing mixtures with extended rotations. Additionally, understanding the costs and required inputs of these techniques over a full rotation will help to make them more accessible to forest managers.

As we gain a better understanding of the ecosystems we are working in, it has become clear that current intensive management regimes and silvicultural strategies may not be in our best interests economically, or in the best interest of diversity within ecosystems. Natural regeneration can be more economical and can increase diversity in the forest. Biodiversity is increased not only by a greater mix of tree species, particularly broadleaf trees, but also by an increase in habitat provided by these trees. Many threatened species of fungi and animals in the European boreal rely on both dead and live broadleaf trees; previous intensive management reduced this habitat. In order to remedy this situation in the European boreal and prevent it from occurring in the boreal mixedwoods of North America, regimes incorporating natural patterns and processes including partial cutting, prescribed burning and natural regeneration should be used in forest management. Both studies have demonstrated that natural regeneration has great potential as a management strategy in both European and North American boreal forests. Despite their different histories and different locations, many similarities exist between these boreal forests that can be used as an opportunity to learn from each other and progress towards improved forest management.

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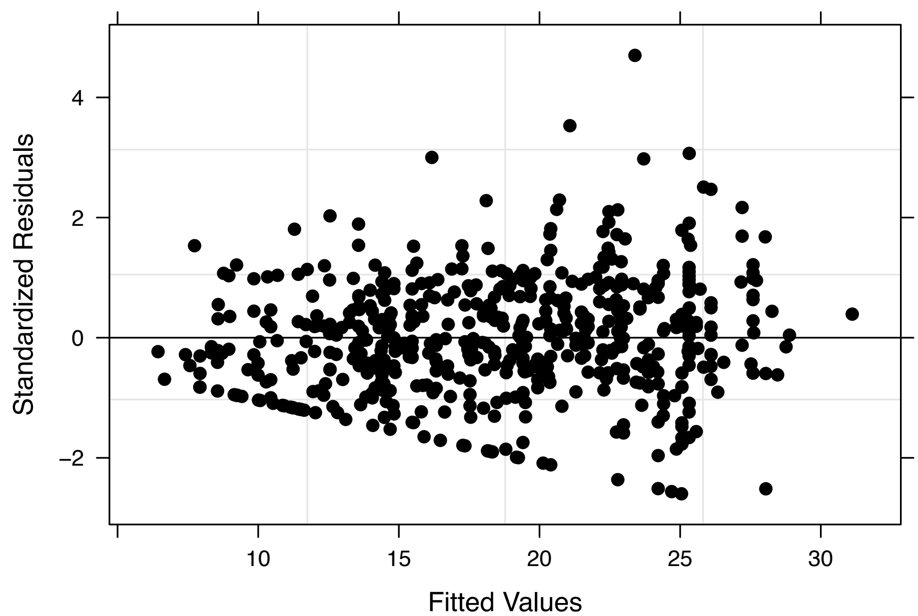
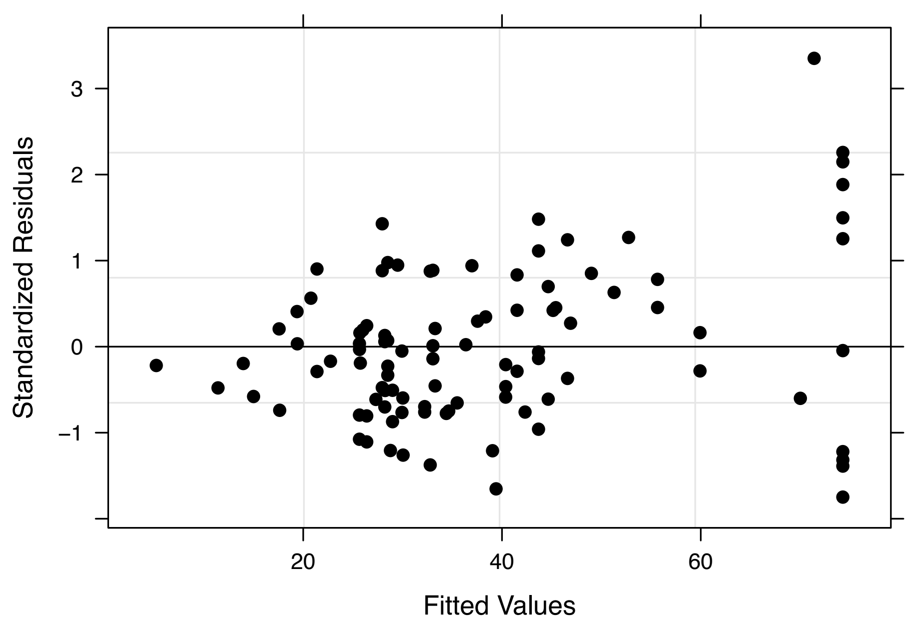
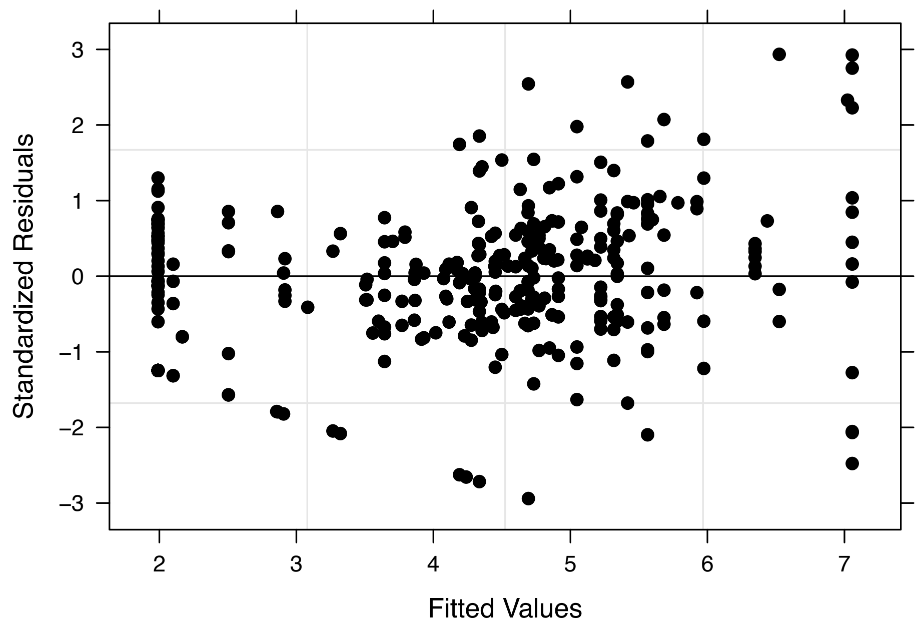
APPENDIX I: RESIDUAL PLOTS FOR GROWTH MODELS



Appendix 1-1: Peace River residuals for final models of seedling growth in relation to measured vegetation variables.



Appendix 1-2: Grande Prairie residuals for final models of seedling growth in relation to measured vegetation variables.

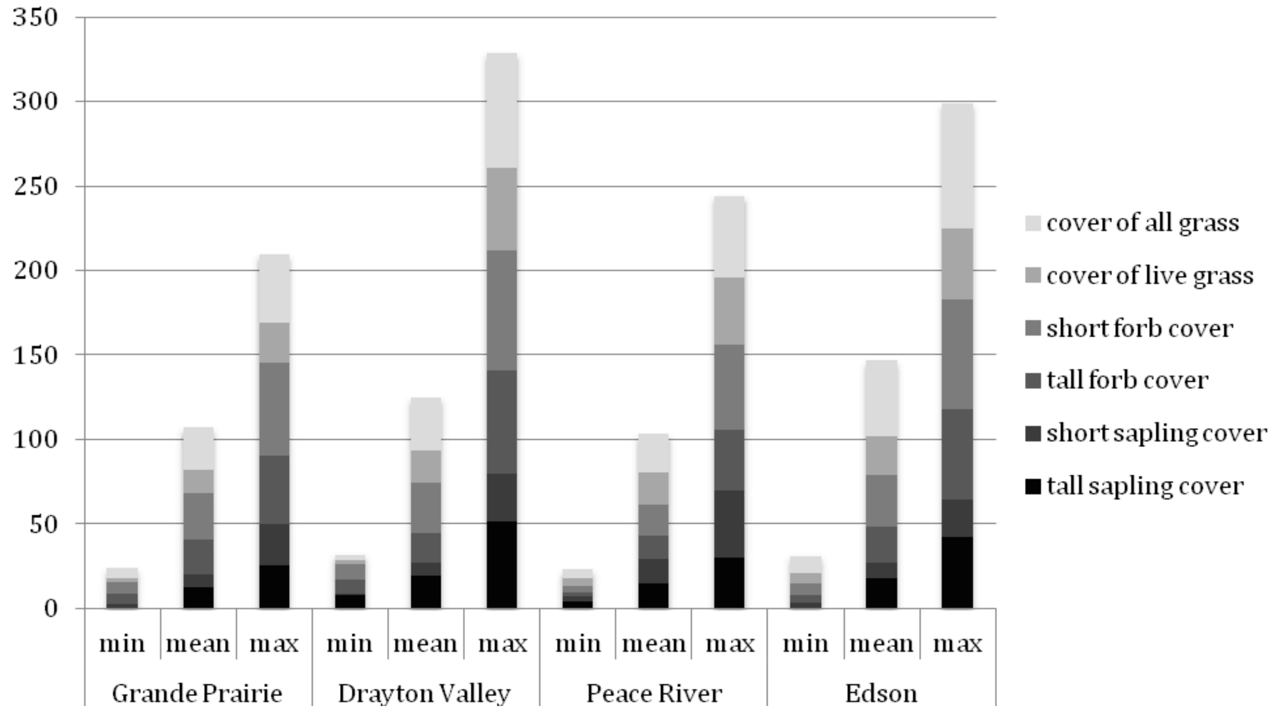


Appendix 1-3: Drayton Valley residuals for final models of seedling growth in relation to measured vegetation variable

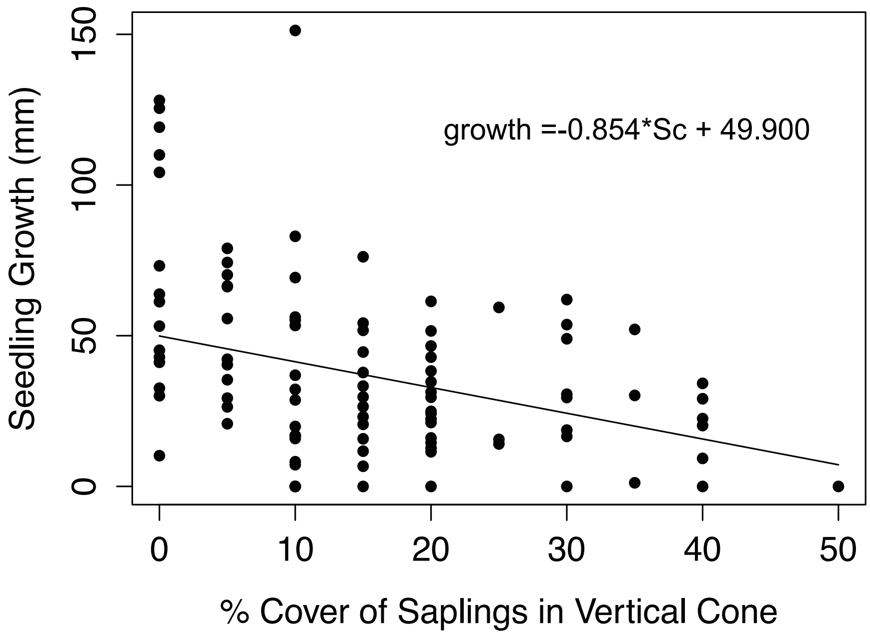
Appendix II: Vegetation cover values

	Grande Prairie			Drayton Valley			Peace River			Edson		
	min	mean	max	min	mean	max	min	mean	max	min	mean	max
No. of saplings	2	8	16	4	11	31	5	15	27	2	12	25
tall sapling cover	2	13	26	8	19	51	4	15	30	2	18	42
saplings in cone	3	15	34	9	20	58	6	20	46	2	20	44
short sapling cover	1	7	24	1	7	29	3	15	40	1	9	22
tall forb cover	6	21	41	8	17	61	3	14	36	5	22	54
forbs in cone	6	30	59	17	32	80	5	22	53	11	36	75
short forb cover	7	28	54	9	30	71	4	18	50	7	31	65
cover of live grass	3	13	24	3	20	49	5	19	39	6	23	42
live grass in cone	2	11	22	1	16	47	5	19	39	4	20	43
cover of all grass	6	25	41	3	31	68	5	23	49	10	45	74
all grass in cone	3	20	38	1	22	63	4	22	50	7	37	68
all live veg. cover	26	46	68	38	58	82	26	55	80	35	60	78
all live in cone	18	42	67	31	52	86	19	53	81	35	60	78
total of all cover	33	56	76	43	67	88	26	57	82	44	75	90
total of all in cone	19	51	74	33	56	89	19	56	83	40	69	86

Appendix 2-1: Cover values for all vegetation measures in all regions. "Min" shows the minimum recorded value averaged for all transects, "mean" shows the mean recorded value averaged for all transects, and "max" shows the maximum recorded value averaged for all transects.



Appendix 2-2: Cover values of vegetation measured in fixed-area plots around seedlings. . "Min" shows the minimum value averaged for all transects, "mean" shows the mean value averaged for all transects, and "max" shows the maximum value averaged for all transects. Here, it can be seen that Drayton Valley sites tended to have the highest cover of vegetation, while Grande Prairie was the lowest.



Appendix 2-3: Scatter plot and regression equation for Grande Prairie: growth as related to percent cover of saplings in the vertical cone. In the regression equation "Sc" is percent cover of saplings in the vertical cone.