Resiliency of boreal forest tree species on a reclaimed oil sands mine and natural forest stands in northeastern Alberta

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Conservation Biology

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University of Alberta

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Abstract

Disturbances in the boreal forest are common, so the species that comprise these forests must be resilient to them. This research examines the resiliency, here defined as the regeneration of boreal tree species following disturbance on both reclaimed and natural sites. The suckering response of seedling origin trembling aspen (*Populus tremuloides*) to cutting was first studied on an oil sands mine reclamation site. Aspen sucker regeneration varied from 0 to 47 suckers per cut tree. Soil, height, and competition all affected suckering. Sucker initiation was 7.8 times more likely on peat soil, 10% more likely per 10 cm increase in tree height, and 10% less likely per 10% increase in total competition. Competition hampered root suckering the most when cover of competing species was greater than 52.5%. Overall, trembling aspen responded vigorously to disturbances on mine reclamation sites which is a promising sign of resilience for these novel and young ecosystems. In natural forests, the regeneration of black spruce (*Picea mariana*) and trembling aspen in the first growing season after wildfire was examined. Regeneration of black spruce did not differ between bog and semi-upland habitats ($\bar{x} = 11{,}979$ stems ha^{-1}). However, a high amount ($\bar{x} = 10{,}916$ stems ha^{-1}) of aspen regeneration was observed in semi-upland habitats previously dominated by black spruce indicating a potential shift in successional trajectory. Black spruce regeneration densities were positively related with forb cover after wildfire, suggesting better available seedbeds. Aspen regeneration did not vary by fire severity ($\bar{x}_{low} = 93{,}384$, $\bar{x}_{mod} = 122{,}909$, $\bar{x}_{high} = 104{,}000$ stems ha^{-1}), but aspen regeneration was reduced by competing vegetation. Overall, both tree species showed resiliency to wildfire. However, pure semi-upland black spruce stands may be at risk of changing successional trajectories, challenging the direct regeneration hypothesis as our current view of successional trajectory after wildfire.

Preface

Chapter 2 of this thesis has been published as:

Jean SA, Pinno BD, Nielsen SE (2019) Trembling aspen root suckering and stump sprouting response to above ground disturbance on a reclaimed boreal oil sands site in Alberta, Canada. New Forests. I was responsible for data collection, analysis, and manuscript composition. B.D. Pinno and S.E. Nielsen were involved with research design and contributed to analyses and manuscript edits.

Chapter 3 of this thesis has been submitted for publication as:

Jean SA, Pinno BD, Nielsen SE (2019) Early regeneration dynamics of pure black spruce and aspen stands following wildfire in boreal Alberta. Forest Ecosystems. I was responsible for data collection, analysis, and manuscript composition. B.D. Pinno and S.E. Nielsen were involved with research design and contributed to analyses and manuscript edits.

Acknowledgments

First and foremost, I'd like thank Brad Pinno. Thank you for taking me on as an undergraduate intern nearly five years ago and giving me many opportunities since then to gain valuable work experience. Thank you for taking me on as a graduate student and supporting and guiding me through my entire M.Sc. degree. Over all these years, as both an undergrad and graduate student, you have been constantly engaged, thoughtful, and constructive towards my work and I am very grateful for that.

To Scott Nielsen I am grateful for your time and improvements you have made to my work. Thank you for letting me be part of your lab group and giving me a home while Brad established his lab at the university. My sincere thanks for the time and effort of my external examiner Justine Karst.

For assistance with field and lab work my gratitude to Ryan Lalonde, Chris Wohl, Jim Weber, Edith Li, and Ruth Errington. Many thanks to Ryan Lalonde who was there through it all, you made my two summers of field work very enjoyable and I am extremely grateful for all your help dealing with the hundreds of soil samples in the lab.

I am grateful for sharing experiences with my lab mates Ryan Lalonde, Jenn Buss, and Kaitlyn Trepanier. Thank you for your support, laughs, adventures, and friendship through it all, I am very fortunate to have such a close-knit lab group. To my lab mates at the Northern Forestry Center Sanatan Das Gupta and Kwadwo Omari thank you for your support and feedback on my analyses and manuscripts. To my lab mates in the ACE lab thank you for taking me in when I did not have a lab at the university and continuing to include me once I had a lab of my own. Thank

you Emily Cicon and Rob Belanger for keeping me company in the office and giving me a helping hand when I needed it.

Thank you to friends and family for their continuous love and support through the ups and downs over these last couple years. Your advice and encouragement has contributed immensely to my success. A very special thanks to my loving parents who were always willing to be my audience while I practiced presentations to help calm my nerves.

Finally, my gratitude toward the funders who supported this research: Canadian Natural Resources Limited and Natural Resources Canada's Energy Innovation Program.

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Chapter 1 – General Introduction

Alberta's Boreal Forest

The boreal region covers 381,046 km^2 in Alberta, occupying 58% of the province (Downing and Pettapiece, 2006). It is characterized by a mosaic of vast deciduous, mixedwood, and coniferous forests interspersed with extensive wetlands (Downing and Pettapiece, 2006). This diverse landscape provides critical habitat to a rich abundance of plant and wildlife species (Brandt et al., 2013; Downing and Pettapiece, 2006). Not only is the boreal important wildlife habitat, it also provides numerous goods and services to Albertans such as: timber, fresh water, climate regulation, water purification, recreation, primary production, and nutrient cycling (Hassan et al., 2005). These goods and services make the boreal zone important for Albertans and the province's resource-based economy (Brandt et al., 2013).

Disturbances in Alberta's Boreal Forest

Due to the abundance of resources in the boreal region, industrial activities (i.e. forestry and oil and gas production) are expanding in the area (Brandt et al., 2013). Consequently, infrastructure related to these industrial activities is also being built. Linear disturbances such as roads, railways, pipelines, seismic lines, and utility corridors fragment Alberta's boreal landscape (Brandt et al., 2013). As industries expand, they disturb larger areas of land, which eventually need to be reclaimed.

The oil and gas industry is seen to have a much larger impact on the boreal compared to other industries, including forestry. Surface mines disturb the landscape to a much greater extent compared to harvesting, and infrastructure related to the oil sector also has a greater presence on the landscape. Open-pit oil sands mining involves removing overburden material in order to access the oil-bearing sand (Errington and Pinno, 2016). Prior to mining, the surface soil layers are salvaged and either placed in a stockpile for future land reclamation, or directly placed onto a new reclamation site (Errington and Pinno, 2016). Overburden materials, which consist of lean oil sands (<10% oil), Pleistocene glacial deposits, and Cretaceous silts, shales, and sandstones are used to construct new landforms such as dykes or overburden dumps (MacDonald et al., 2012; Errington and Pinno, 2016). Oil sands underlie about 14.2 million hectares in north and eastern Alberta (Brandt et al. 2013). Of this area, 480,000 ha are available for surface mining; 76,000 ha have been cleared and disturbed by oil sands mining so far (Government of Alberta, 2012). After oil sands mining takes place, the Alberta government requires that the land be reclaimed and native plant communities, characteristic of natural forests in the region, are re-established (Alberta Environment, 2010). As land managers, we must determine ways to effectively reclaim these disturbed lands once mining has commenced. Fortunately, we can use natural disturbances as a learning tool to help us understand processes that will better facilitate reclamation.

Boreal ecosystem dynamics are driven by natural disturbances (Brandt et al., 2013). There are several natural disturbances that occur on large and small scales in the boreal, including: fire, windthrow, insect and disease outbreaks. Fire is the most important disturbance in the boreal region (Brandt et al., 2013). It is a major stand-renewing agent and plays an essential role in regulating the effects of insects and diseases (Weber and Flannigan, 1997). Fire also shapes boreal ecosystems by influencing species composition, age structure, productivity, and biodiversity (Weber and Flannigan, 1997). Forests in the boreal are resilient to fire, and almost all dominant tree species in the region are adapted to respond to fire.

Resiliency of the Boreal Forest

Ecosystem resilience is defined as the capacity of an ecosystem to return to the pre-condition state following a disturbance, including maintaining its essential characteristic taxonomic composition, structures, ecosystem functions, and process rates (Holling, 1973). Species' reproductive potential and environmental factors both play a major role in determining ecosystem resilience (Yan et al., 2011). Only resiliency of tree species was studied in this research project, and will be the focus herein.

Many tree species in the boreal mixedwood are adapted to stand renewing fires that commonly take place in the region. The dominant tree species are trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), black spruce [*Picea mariana* (Mill)], and white spruce [*Picea glauca* (Moensch) Voss] (Downing and Pettapiece, 2006). Aspen are well adapted to disturbance because they have a high capacity for vegetative reproduction (Greene et al., 1999). Root suckers are the main form of regeneration after disturbance; however stump sprouts can also be produced (Greene et al., 1999). Other, less common, broadleaf species found in the boreal mixedwood include balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.) having strong vegetative reproduction like aspen (Greene et al., 1999). Jack pine and black spruce both hold aerial seed banks in the form of serotinous and semi-serotinous cones, respectively (Greene et al., 1999). White spruce is the only dominant species in the boreal mixedwood that is not adapted well to fire (Greene et al., 1999). Instead, they rely on seed dispersal from surviving individuals after a disturbance (Greene et al., 1999). Balsam fir [*Abies balsamea* (L.) Mill.] is another conifer found in the region that is similar to white spruce in that it is not adapted well to disturbance (Greene et al., 1999). Balsam fir is also considered a late successional species and has a high shade tolerance (Greene et al., 1999). Overall, tree species in the boreal mixedwood are able to cope well with natural disturbances, whether it is an immediate or delayed response.

Environmental factors, such as disturbance severity, stand characteristics, competition, and seedbed quality, can also affect the resiliency of an ecosystem. High severity disturbances can consume biological legacies (e.g., seed banks, sprout producing roots, and surviving seed sources) inhibiting any local regeneration. High severity disturbances can also reduce the soil quality by accelerating nutrient losses through volatilization and leaching (Maynard et al., 2014). Stand characteristics, such as basal area and age, can also determine stand resiliency. Regeneration densities of early successional species (i.e., trembling aspen, paper birch, jack pine, and black spruce) tend to be positively related to their respective pre-disturbance basal area (Ilisson and Chen, 2009b; Greene and Johnson, 1999). Younger stands may be less resilient to disturbance because their reproductive abilities may not be fully developed (Pinno et al., 2013). Competition from early successional forb and grass species may affect the resilience of tree species in the boreal. Forbs and grasses can block sunlight from shade-intolerant early successional tree species, causing mortality. Increased competition for other resources (e.g., water and nutrients) can weaken tree seedlings, potentially inhibiting them from reaching maturity. These fast growing forbs and grasses also can occupy good quality seedbeds before tree seeds have a chance to germinate. High quality seedbeds are important for tree species that regenerate via seed (e.g., black and white spruce, jack pine). Most seeds require either exposed mineral soil or a thin layer of organic material to germinate successfully. Germination substrates also need to be moist for seeds to germinate and seedlings to survive. A lack of high quality seedbeds could therefore significantly hamper tree resiliency after disturbance. Overall, many environmental factors are important in determining the resiliency of tree species.

Research Objectives

Establishing trees on a reclamation site is important for boreal ecosystem structure and function (Pinno and Errington, 2015). Typically, late successional conifers (e.g. white spruce) are planted on a site, while early successional species (e.g. trembling aspen) are left to seed-in naturally. Initial tree growth on reclaimed land has been shown to be similar to that of natural forests (Huang et al., 2014). However, it is unknown if the trees established on reclaimed land will be resilient to disturbance, thereby making them sustainable forests in the long term. Testing the resilience of a reclaimed system could be a valuable tool for assessing the success of reclaimed land (Welham, 2013). Chapter two of this thesis will look at the sprouting response of trembling aspen to cutting on a reclamation site, thereby gaining a base understanding of the resiliency of an important boreal tree species growing on reclaimed land and subjected to disturbance. These trees are different from most natural stands because they are seedling-origin, meaning each tree has its own root system, where natural aspen stands usually have a shared, clonal, root system. Seedling-origin aspen have been understudied and, to our knowledge, the sprouting response of naturally established seedling-origin aspen has not been studied.

It is well known that boreal forests respond well to disturbances, especially fire. However, a changing climate is expected to drive fires towards being more sever and frequent (de Groot et al., 2012). Understanding the early regeneration dynamics of boreal tree species may help us understand how climate change will affect these species in the long term. Chapter three of this thesis will examine the resiliency of natural black spruce and trembling aspen stands after wildfire. Black spruce forests are understudied in Alberta because they are less merchantable. However, they comprise a large area of the boreal landscape and regeneration dynamics should be known for future forest management. Aspen is well studied, but how fire severity affects early regeneration has been understudied. Most research on aspen regeneration has occurred after prescribed burns or many years post-fire. This research provides results of early aspen regeneration dynamics after a major wildfire event.

We can use the rates and patterns of post-disturbance development from natural forested ecosystems as a benchmark for reclaimed areas (Welham, 2013). Therefore, the overarching idea of this research is to compare resiliency on reclaimed land versus natural forests. This, however, is not a direct comparison study because tree age, stand structure, and disturbance extents differ between sites.

Excluding University of Alberta guidelines, the format of this thesis follows the submission guidelines for Spinger Scientific Journals (*New Forests* and *Forest Ecosystems*).

Chapter 2 – Trembling aspen root suckering and stump sprouting response to above ground disturbance on a reclaimed boreal oil sands site

Abstract

Trembling aspen is an important early successional species in the boreal region that commonly regenerates via root suckering and, to a lesser extent, stump sprouting after aboveground disturbance such as harvesting or wildfire. However, the response of aspen to disturbance on reclaimed oil sands sites is not known. To determine the suckering and sprouting response of 6-year-old seedling origin aspen growing on a reclamation site, we destructively sampled 87 individual trees in May 2017. Trees were selected across two soil types, forest floor-mineral mix and peat-mineral mix, and three height classes, 100-199 cm, 200-299 cm, and >300 cm. In August 2017, we returned to each cut tree to assess the type (sucker vs. stump sprout) and abundance of regeneration. Aspen readily responded to disturbance; however, responses were highly variable between trees, ranging from zero to 47 suckers and zero to 42 sprouts. Trees growing on peat-mineral mix were 7.8 times more likely to produce at least one sucker and generally had a higher abundance of suckers. Tree height was also positively correlated with suckering probability and abundance, while competition from surrounding vegetation decreased the probability and abundance of suckering, especially when cover of competing species was greater than 52.5%. The probability of stump sprouting was not affected by soil type or tree size, but did decrease with increases in tree competition. Overall, trembling aspen respond vigorously to disturbances on mine reclamation sites which is a promising sign of resilience for these novel and young ecosystems.

Introduction

Trembling aspen is a widespread, early successional species in Alberta's boreal forests (DeByle and Winokur, 1985; Downing and Pettapiece, 2006; Peterson and Peterson 1992). As an early successional species, it is able to respond quickly to disturbances through its ability to reproduce vegetatively through root suckers (Schier and Smith, 1979; Bartos and Meuggler, 1981; Peterson and Peterson, 1992). The quick development of aspen root suckers after disturbance provides many benefits useful for forest regeneration, which can also be applied to land reclamation. Root suckers develop leaves quickly which mitigate water stress by reducing solar radiation to the forest floor and early litter production from aspen suckers aids in the development of a surface organic layer of soil that is commonly lost after disturbance (Rowland et al., 2009). These two factors are also important on reclaimed areas, as they encourage the development of a natural understory and soil-plant nutrient cycle (Pinno and Errington, 2015).

Root suckers are generally produced when a disturbance removes or kills the above ground portions of the tree (Frey et al., 2003). The mortality or removal of the aboveground portions of the tree causes an imbalance between two hormones, auxin and cytokinin, within the tree, initiating sucker growth (Farmer, 1962; Eliasson, 1971; Schier, 1972; Steneker, 1974). Auxin is produced in the twigs and buds of the trees and is transported to the roots where it promotes root growth and inhibits sucker growth (Eliasson, 1971; Hicks, 1972; Schier, 1972). Cytokinins, on the other hand, are produced at the root tips and are transported towards the stem, and are known to initiate root suckering on many plants by counteracting the activity of auxin (Peterson, 1975; Hicks, 1972; Thimann, 1977). Therefore, mortality or removal of the above ground portion of a tree will stop auxin production, causing an increase in the cytokinin:auxin ratio, initiating root sucker growth (Winton, 1986; Wolter, 1968). In stands less than 25 years old, removal of stems can also produce stump sprouts; however, this is not seen as a primary source of reproduction in aspen (Heeney et al., 1980). Younger trees are able to produce stump sprouts because they possess dormant buds around the stump collar, but as a tree matures these buds are lost (Tredici, 2001). Dormant collar buds allow young trees to sprout to survive under a variety of stressful conditions (e.g. herbivory, site exposure, pathogens, and desiccation) (Tredici, 2001). Generally, species that produce stump sprouts only have a single stump sprout survive to maturity (Keim et al., 2006; Lockhart and Chambers, 2007).

The response of aspen root suckering to disturbances in natural stands is substantial, with regeneration one year post fire reaching as high as 240,000 stems ha^{-1} (Wang, 2003) and over 69,000 stems ha^{-1} being regenerated one year after harvest (Mundell et al., 2008). Suckers also undergo self-thinning almost immediately after establishment with high mortality of root suckers. Several long-term studies have shown that regardless of initial sucker abundance, after about 5 years of self-thinning stands generally have similar long-term average densities of around 20,000 stems ha^{-1} (Steneker, 1974; Bella, 1986; Perala, 1984).

The role of tree height in relation to the number of root suckers produced after disturbance has not been directly studied. However, we can assume that taller trees have more extensive root systems that would allow them to produce more root suckers and stump sprouts. King and Landhäusser (2018) found that large diameter (DBH = 6.4 cm) aspen trees had significantly larger root systems compared to small diameter (DBH = 4.4 cm) aspen trees, and as a result produced more root suckers. Larger root segments can also store greater amounts of carbohydrates, which is a limiting factor for suckering (Waschowski et al., 2014). Root carbohydrate reserves are relied upon for maintenance (respiration) of surviving root tissue and the regeneration of new stem, leaf, and root tissue until the suckers are able to produce enough energy for these processes on their own (Lambers et al., 2002).

In terms of tree and stand age, suckering has been observed in stands of varying ages (20-150 years); with older trees (≥80 years) often producing fewer suckers than younger trees because their root systems are typically beginning to decay (Maini, 1968; Peterson and Peterson, 1992); although some young stands have also been found to have high amounts of root decay (DesRochers and Lieffers, 2001). There has been some evidence of trees less than 20 years old producing root suckers. Horton and Maini (1964) observed root suckering in a 5 year old clonal aspen stand that had been slashed; while King and Landhäusser (2018) observed root suckering in planted aspen seedlings that were 8 and 12 years old. However, root suckering potential of young aspen seedlings that established naturally has not been studied.

Since aspen more commonly reproduce vegetatively via root suckers, they are considered a clonal species, and are studied as such. However, some research has shown that aspen are more frequently revegetating disturbed areas sexually via seed than previously thought (Stefani et al., 2018; Krasnow and Stephens, 2015). Disturbed areas, such as mine land reclamation sites, provide ideal conditions for aspen seeds to germinate, having exposed soil and less competition for resources such as water, nutrients, and light. These conditions are not often found in natural forests, even after disturbance, which is why seedling-origin aspen have been understudied (Jelinski and Cheliak, 1992). Disturbance could affect seedling-origin aspen differently than clonal aspen. Removing the stem of a seedling could cause a greater response from the root system because it is dependent on the apical dominance of a single stem; whereas cutting a single stem that belongs to a clonal root system would have much smaller effects on apical dominance. On the other hand, seedlings also have much smaller root systems, and could suffer after a disturbance because of smaller carbohydrate reserves. King and Landhäusser (2018) studied sprouting response to disturbance in planted seedlings and suggested that the response of these seedling-origin stands over a wider range of site conditions represents a critical knowledge gap.

Soil properties, including temperature, moisture, pH and nutrients, can also effect root suckering in aspen (Frey et al., 2003). Warmer soil temperatures (12 °C and above) have been considered to be the most important factor for sucker initiation (Fraser et al., 2002) as higher soil temperatures degrades auxin and promotes cytokinin synthesis, stimulating sucker initiation (Schier et al., 1985; Hungerford, 1988). The effects of soil nutrients, pH, and moisture on sucker initiation have not received as much attention (Frey et al., 2003) but it can be hypothesized that increases of nutrient availability and/or pH that is commonly seen after wildfires stimulates the initiation of root suckering (Frey et al., 2003). Both very dry and water-saturated growing conditions have been found to reduce sucker initiation (Horton and Maini, 1964; Schier et al., 1985). Sucker initiation on water-saturated sites is limited due to a lack of oxygen, and excess water promotes early root mortality and decay (Frey et al., 2003). Vegetative competition, especially from grasses, can also significantly reduce suckering in aspen (Landhäusser and Lieffers, 1998). Not only is there competition for resources, but a thick litter layer of grass can insulate the ground, reducing soil temperatures (Hogg and Lieffers, 1991; Landhäusser and Lieffers, 1998).

The two most commonly used soils in oil sands mine reclamation are forest floor mineral mix (FFMM) and peat mineral mix (PMM). These soils have very different properties that could influence aspen suckering and sprouting (Howell et al., 2016; Tremblay, 2017). It has been shown that natural aspen seedlings establish and grow faster on PMM than on FFMM because of its high water holding capacity (Pinno and Errington, 2015; Tremblay, 2017). Therefore, the trees on PMM should be more robust and should be capable of producing greater amounts of suckers and stump sprouts. Trees growing on PMM should also have an advantage because there is generally less understory competition, particularly from grass and forb species, found on these sites. PMM also warms faster in the spring compared to FFMM (Tremblay, 2017), likely due to less vegetation, which should allow greater sucker initiation on PMM. Nutrient availability and water holding capacity are also greater on PMM (Howell et al., 2016), creating more ideal conditions for sprout initiation. Overall, PMM seems to be better suited for sucker and sprout initiation compared to FFMM.

In Alberta, reclamation of an oil sands mine requires the re-establishment of a self-sustaining ecosystem, consisting of native species (Alberta Environment and Sustainable Resource Development, 2013). In order to meet this goal, various criterion need to be met including that reclaimed ecosystems display characteristics of resilience to disturbances. However, there are many questions surrounding the ability of young, seedling-origin aspen stands to regenerate after disturbance, and whether stem densities at the stand level will be sufficient to recover the forest (Macdonald et al., 2012). To the best of our knowledge, suckering of seedling origin aspen in young stands has not previously been studied. Determining the sprouting response of aspen after a disturbance on a reclamation site is a good first step when determining the resilience of a constructed ecosystem. Therefore, the overarching objective of this study is to determine if young aspen, which established on a reclamation site via seed, are capable of showing resiliency. Specifically, the two research questions asked in this study include:

1. Does tree size or environmental conditions (soil type and competition) have an effect on whether or not root suckers and stump sprouts are initiated?

2. If root suckers are initiated, what factors affect abundance of root suckers?

Methods

Study Area

This study took place on an oil sands mine located approximately 75 km northwest of Fort McMurray, Alberta, Canada (57° 20′ N, 111° 49′ W) in the Central Mixedwood Natural Subregion (Downing and Pettapiece, 2006). The natural forest in the area is characterized by trembling aspen dominated stands mixed with balsam poplar, white birch, white spruce, and balsam fir. Black spruce bogs and fens are also prevalent on the landscape. Upland soils are predominantly Gray Luvisols, while lowland soils are Organic (Soil Classification Working Group, 1998); both of these soils are commonly used in land reclamation as the basis of common reclamation soils (see below). The average temperature of the warmest month is 17.1 °C and the average temperature of the coldest month is -17.4 °C, mean annual precipitation is 419 mm (Fort McMurray 1981-2010 Environment Canada climate normal).

The reclamation area used in this study is an 88.6 ha overburden dump, constructed in 2011, and capped with two different reclamation cover soils, forest floor mineral mix (FFMM) and peat mineral mix (PMM). Soil types were placed in four blocks (2 blocks of each soil type) of approximately 22 ha each. FFMM is derived from upland forest soils, mainly Gray Luvisols mentioned above, and consists of the surface organic layers (LFH) and the underlying mineral soil (A and B horizons) salvaged to a maximum total depth of 30 cm. PMM is derived from Organic soils and consists of peat and underlying mineral soil salvaged at an approximate 60:40 ratio of peat:mineral (Errington and Pinno, 2016). Many soil properties differ between these two soil types (Table 1). Both FFMM and PMM soils used on the reclamation area were salvaged in the winter of 2010-2011 and directly placed to a depth of 0.5 m over 1.5 m of suitable (non-saline) subsoil. In the first growing season a cover crop of annual barley (*Hordeum vulgare*) and white spruce seedlings were planted at a density of 1,500 seedlings per hectare. Deciduous trees, such as trembling aspen and balsam poplar established naturally via seed from surrounding forests, the closest of which is located 300 m northeast of the reclamation area (Pinno and Errington, 2015). Aspen has established on site at an density of 3,455 stems ha^{-1} on FFMM and 9,485 stems ha^{-1} on PMM (Tremblay, 2017) by age 5 with 96% of the aspen originating from sexual reproduction (seedling origin), not from vegetative reproduction (Stefani et al., 2018).

Vegetation cover was different between soil types (Table 1) with average total vegetation cover on FFMM of 72% compared to 59% on PMM ($p = 0.02$). There was also significantly higher tree ($p < 0.01$) and invasive forb ($p = 0.02$) cover on PMM, while FFMM had significantly higher shrub ($p < 0.01$), native forb ($p = 0.02$), grass ($p < 0.01$), herbaceous (grass, native forb, and invasive forb cover combined; $p < 0.01$), and total ($p = 0.02$) cover. For more information about this study site please see: Pinno and Errington 2015, Tremblay 2017, and Stefani et al. 2018. These studies looked at aspen seedling establishment, aspen growth across soil types, and the effects of soil type on aspen and their associated below ground microbiome on this same study site.

Field Methods

To examine aspen regeneration via root suckers in different reclamation soils and competition levels, 87 tree centered plots were established across the site in the summer of 2017, using a stratified random sampling design. Forty-four plots were established in the PMM soil treatments, and 43 plots were established in the FFMM soil treatments. Plots represented a gradient of aspen tree sizes and competing vegetation across the treatment types. Twenty-nine of the selected trees were between 100 and 199 cm tall, 30 between 200 and 299 cm tall, and 28 >300 cm tall. Each selected tree was cut down in May of 2017 at 2.5 cm above the ground. Trees were cut in May to mimic spring wildfires that are common in the region due to readily available dry fuel (Kochtubajda et al., 2017). A tree cookie was also taken from each cut aspen to confirm tree age; all cut trees were six years old. In August of 2017, a 3.99 m radius (50 m^2) plot was established around each cut aspen in order to count the number of root suckers and stump sprouts produced by each tree. Root suckers were defined as sprouts originating from roots and stump sprouts were defined as sprouts originating from the stump collar of the tree. Excavated 8 m tall planted aspen had root systems with a radius of 5 m (King and Landhäusser, 2018); therefore our natural seed origin aspen with a maximum height of 4.6 m would have comparable root systems. Root suckers were easily identifiable, as they had larger leaves and greener stems compared to seed-origin aspen of similar size. Overall plant composition was determined within each 3.99 m radius plot. Percent of each functional group present was evaluated: trees, shrubs, invasive forbs, native forbs, grass, and bryophytes. At each plot, one sucker was randomly excavated to confirm origin and the root depth and diameter on the proximal side of origin was measured.

Data Analysis

All data was analyzed using R software (R Core Team 2018, Boston, MA). Since the response variables of number of root suckers produced and number of stump sprouts produced were over-dispersed count data and could not be transformed, negative binomial models were used. Data analyses for root suckers and stump sprouts were performed separately; however both response variables underwent the same statistical testing. First, to determine the effects of the site selector variables, soil type (FFMM and PMM) and tree height classes, a negative binomial model was used (*glm.nb* command in R 3.1.4; R 2018) with soil and height classes as the only two explanatory variables and the number of root suckers produced as the response variable. We then ran an analysis of deviance (*anova* command in R 3.1.4; R 2018). Height was chosen over stump diameter to represent tree size classes because it created stronger models and was consistently the more significant variable.

Secondly, logistic models (*glm* command in R 3.1.4; R 2018) were used to determine what explanatory variables (soil type, tree height, and vegetation cover) had an effect on the probability of a cut stem producing at least one sucker. To do this, count data was transformed into binary presence/absence data. Models were selected based on the lowest AIC score. Odds ratios for each significant variable were calculated by transforming the beta value; e^{β}. Pseudo R^2 values were calculated using the *rms* package (Version 5.1-1; Harrell, 2017).

Thirdly, zero-truncated negative binomial models were used to determine what explanatory variables had an effect on the abundance of root suckers produced by trees that showed sucker initiation. Beta values were transformed to integer values, 10^{β}, to more easily understand the magnitude of effects. These zero-truncated models were not carried out on the stump sprout data because only one stump sprout is expected to survive. To determine threshold values for the significant variables found in our models regression tree analyses were performed using the *mvpart* package (Version 1.1-1; Therneau and Atkinson, 2004).

Lastly, to understand the differences in ground cover between the two different soil types a MANOVA was performed on the vegetation cover data, by functional group (trees, shrubs, invasive forbs, native forbs, grasses). Tree and shrub cover were added up to calculate woody cover; invasive forbs, native forbs, and grasses were added up to calculate herbaceous cover. All functional groups were added together to calculate total cover at a plot. Here vegetation data were log transformed in order to meet the assumption of data normality.

Results

Responses in aspen root suckering was highly variable, ranging from 0 to 47 stems produced in PMM and 0 to 7 stems produced in FFMM for each cut tree. Of the 87 trees cut, 63% produced at least a single root sucker, 86% on PMM, and 40% on FFMM. Sucker producing roots were found at depths ranging from 0.5 to 6 cm below the soil surface, the mean depth was 1.6 cm with no difference between soil types ($p = 0.95$). On both soil types large trees had larger sucker producing roots (0.95 cm in diameter). However, medium and small trees on PMM had larger roots compared to the medium and small trees on FFMM. On PMM, average root size was 0.60 cm for medium trees and 0.71 cm for small trees, while on FFMM medium trees had a root size of 0.45 cm and 0.48 cm for small trees.

There was a significant difference in the number of root suckers produced on each soil type ($p < 0.01$), with more suckers being produced on peat, compared to forest floor ($p < 0.01$) (Fig. 1). On PMM, large trees (> 3 m tall) produced significantly more suckers than small trees (1 – 1.99 m tall; $p < 0.01$), while there was no significant difference in the amount of suckers produced between large trees and medium trees (2 – 2.99 m tall; $p = 0.06$) or medium and small trees ($p = 0.27$). On FFMM, there were no significant differences found between tree height and the number of suckers produced ($p = 0.94$). Finally, we found no significant interaction between soil type and tree height.

The probability of a cut stem producing at least one root sucker was significantly influenced by soil type, tree height, and total competition. The probability of root sucker initiation was 7.8 times greater on PMM compared to FFMM (Odd ratio in Table 2). Taller trees also had a higher probability of producing root suckers; with each 10 cm increment increase in height the probability of a tree producing a sucker increases by 10%. Vegetation competition reduced suckering; with each 10% decrease in surrounding total cover increasing odds of suckering by 10%. Total cover was used instead of each vegetation functional group to simplify models because all functional groups were found to have significant negative effects on sucker production. Models made with total cover also had a better fit compared to models using all the functional groups. Since total vegetation cover was used some sites have >100% cover, this is due to overlap of the different functional groups. There were no significant interactions found between variables in this model.

When suckers were present, the same three factors of soil type, tree height, and total competition had an effect on sucker abundance (Table 3). On average, trees growing on PMM produced 27 more root suckers than a similar sized tree cut on FFMM. Regardless of soil type, larger trees also tended to produce more suckers, with each increment increase of 10 cm in tree height producing 10 more suckers (Fig. 2). Competition decreased sucker abundance with each increment increase of 10% in total cover there are 10 fewer suckers produced (Fig. 2).

There are many thresholds that create more (far right side) or less (far left side) optimal aspen root suckering conditions (Fig. 3). Soil type creates the first threshold, with mean suckers produced on FFMM being only 1.31, providing the least optimal conditions. On PMM soil, tree height was the most important factor for abundant root suckering. Trees 285 cm tall or greater produced the most root suckers. Total understory vegetation cover also affects the abundance of suckers, with trees having less than 52.5% surrounding competition producing the most root suckers. The most optimal conditions for producing root suckers, of a tree growing on PMM being more than 285 cm tall and having less than 52.5% of total competition, was rare in our sampling design with only 9 trees meeting these conditions.

Stump sprouting also varied greatly, ranging from 0 to 11 produced on FFMM and 0 to 42 produced on PMM per cut stem. 89% of the trees cut on PMM, and 72% of trees cut on FFMM produced stump sprouts. However, neither soil type ($p = 0.66$) nor tree height ($p = 0.37$) had a significant effect on whether or not stump sprouts were produced. Competing vegetation, however, did reduce sprouting with the probability of a cut aspen to produce a stump sprout dropping by 5% per each 10% increment increase in tree cover ($p = 0.01$; Table 4). Any cut tree with ≥40% surrounding tree cover did not produce any stump sprouts. Tree cover, in this case, was the only vegetation cover type to have an effect on stump sprout initiation, therefore total vegetation cover was not used. Consequently, the best fit model only used tree percent cover. The model also showed a significant interaction between soil type and tree cover, showing that on PMM soil suckers were 1.7 times more affected by tree cover ($p = 0.04$).

Discussion and Conclusions

Aspen that have established on a reclamation area via seed responded readily to an above ground disturbance, through both root suckering and stump sprouting. Soil type, total plant cover, and tree height all had significant effects when it came to both root sucker initiation and abundance. Soil type had one of the largest effects on root suckering with greater sucker initiation and abundance on PMM. However, soil type also directly affects competition and tree size, which may magnify its significance (Mackenzie and Naeth, 2010; Pinno and Errington, 2015; Tremblay, 2017). It is known that understory vegetation establishes much more readily on FFMM compared to PMM (Mackenzie and Naeth, 2010; Naeth et al., 2013), and our results showed the same (72% total cover on FFMM and 59% total cover on PMM). Previous studies have shown that aspen establishment and growth is significantly greater on PMM compared to FFMM (Pinno and Errington, 2015; Tremblay, 2017) with less competition from other vegetation thought to be one of the main reasons for this. Higher amounts of competition from surrounding vegetation also had a large negative effect on root sucker initiation and abundance, with trees growing on PMM being 7.8 times more likely to initiate suckers and producing approximately 27 more suckers on average compared to trees growing on FFMM. Landhäusser et al. (2007) saw similar results with a 30% decrease in aspen root sucker emergence with the presence of *Calamagrostis canadensis* ([Michx.] Beauv.), likely due to the roots from the competing vegetation acting as a barrier to suckers as well as decreased soil temperatures from leaf litter insulating the soil. Pinno and Errington (2015) found that at vegetation covers greater than 51% aspen seedling establishment was reduced. This is similar to our results where competition levels greater than 52.5% reduced root sucker abundance. These results could indicate that a competition level of around 50% is the threshold for optimal aspen establishment either by seed or sucker.

Tree size was also very important for sucker initiation and abundance. We found that taller trees tended to produce more root suckers, especially on PMM. Larger trees should produce more root suckers, as they have larger root systems. King and Landhäusser (2018) observed that larger planted aspen seedlings (DBH of 6.4 ± 5.4 cm) had larger root systems and produced more root suckers compared to smaller planted seedlings (DBH of 4.4 ± 0.7 cm), matching our findings. Most aspen suckers originate from roots that are 0.5-2.5 cm in diameter, and are within the first 12 cm of the soil surface (Horton and Maini, 1964; DesRochers and Lieffers, 2001; Wachowski et al., 2014). All our sucker producing trees had roots producing suckers within the top 6 cm of soil across both soil types; smaller trees did have smaller diameter roots, which could explain why overall small trees produced fewer root suckers. On FFMM, we found that the sucker producing roots of small and medium trees were smaller than 0.5 cm on average. As suckers grow, they deposit wood onto the parent root meaning these roots were likely even smaller at the time of disturbance (DesRochers and Lieffers, 2001). Therefore, small and medium sized trees on FFMM likely produce fewer sprouts because the average sucker producing root size is outside of the optimum range.

Soil properties such as temperature, moisture, and nutrients could have also played a small role in root sucker initiation and abundance. PMM soil on our site does warm up as fast in the spring compared to FFMM (Table 1), likely due to less leaf litter insulating the soil. Warmer soil temperatures have been considered the most important environmental factor for controlling sucker initiation, as high temperatures facilitate auxin degradation and promote cytokinin synthesis (Schier et al., 1985; Hungerford, 1988). PMM on our site also has a greater water holding capacity compared to FFMM. Poor soil water holding capacity has been linked to an increase in aspen sucker mortality, as it reduces the trees capacity to withstand dry spells (Jacobi et al., 1998). Greater amounts of nutrients are also found in PMM due to its high organic matter content (Howell et al., 2016). The effects of soil nutrients on root sucker initiation have been understudied (Frey et al., 2003); however nutrient rich PMM does promote more robust trees compared to FFMM (Tremblay, 2017). More robust trees have larger root systems and greater carbohydrate stores, which would allow them to produce more suckers (King and Landhäusser, 2018; Wachowski et al., 2014). Further research should be conducted to determine the full effects of soil properties on root suckering of aspen growing on reclamation soils.

Stump sprouting was common among all soil and tree size classes (84% of all trees) but was reduced by surrounding tree cover, particularly on PMM. It is unclear why only competition from surrounding trees, and no other vegetation, had an effect on sprout initiation. However, Tredici (2001) suggests that stump sprouts require very high amounts of light in order to develop into effective replacement stems. Therefore, it could be possible that the shading impacts caused by high levels of tree cover had an effect on sprout initiation. Shading from smaller understory vegetation may not have had as great as an effect on sprout initiation because the sprouts originate slightly above ground level, keeping them above small plants. Since the disturbance took place during the spring, many understory species would not have been well enough established to be significant light competitors. Given the size of the trees that underwent disturbance (bole diameters ranging from 1 – 6 cm), it was expected that they would produce stump sprouts. Previous research has found that all temperate angiosperm trees will sprout in high percentages from stumps between 5 and 15 cm in diameter (Tredici, 2001).

Overall, the aspen seedlings growing on this reclamation area were resilient to disturbance with 89% of the trees cut responding by either producing root suckers, stump sprouts, or both. Our disturbance treatment, however, was very different from fire, the most likely and most destructive disturbance to affect a reclamation area. It is difficult to say how these trees would respond if the reclamation area were to burn. Fire would destroy the competing understory vegetation that interferes with root sucker initiation and could add beneficial nutrients to the soil, promoting root suckering (Frey et al., 2003). On the other hand, fire could consume the sucker producing roots found within the first 6 cm of the soil, severely hampering root sucker production. Although our disturbance treatment was different from common disturbances found in the boreal, this study still identified important drivers that can affect root sucker regeneration in seedling origin aspen growing on reclamation areas. As this study focused on regeneration potential of aspen seedlings immediately following disturbance, further studies are needed to identify the vigor and survival rates of aspen suckers on reclaimed areas over multiple years. This is an important next step in understanding the resiliency of aspen growing on a reclaimed boreal oil sands site.

Tables

Table 1. Basic soil characteristics of reclamation soils, including total carbon (TC), total nitrogen (TN), pH, bulk density (Db) at 5-10 cm, volumetric water content (VWC) at 12 cm, and temperature; reporting means with standard error in brackets (n = 6). Soil data is taken from previous studies performed on the same reclamation site (Howell et al. 2016; Tremblay 2017). Average percent cover of vegetation functional groups from data collected in this study (n = 87).

	TC (%)	TN (%)	pH	D_b (g cm^{-3})	VWC (%)	June temperature (°C)	Grass (%)	Invasive forb (%)	Native forb (%)	Shrub (%)	Tree (%)	Bryophyte (%)
FFMM	2.61 (0.29)	0.12 (0.01)	7.59 (0.12)	1.18 (0.03)	19.70 (1.95)	13.1	34	8	16	9	5	0
PMM	8.07 (1.98)	0.25 (0.07)	6.01 (0.52)	0.94 (0.20)	35.87 (2.40)	15.2	10	19	10	3	13	2

Table 2. Logistic regression model parameters of soil, height with increments of 1 cm, and total cover with increments of 1% relating to the presence/absence of suckers produced by aspen trees. Odds ratio pertains to how much more likely a tree is to produce at least one root sucker with each increment increase of a parameter, there were no significant interactions.

Variable	Odds Ratio	β	S.E.	*p*
Soil - PMM	7.75	2.047	0.608	<0.001
Height	1.01	0.008	0.004	0.035
Total Cover	0.96	-0.041	0.014	0.004

Pseudo $R^2 = 0.402$

Table 3. Zero-truncated negative binomial model parameters of soil, height with increments of 1 cm, and total cover with increments of 1% relating to the abundance of suckers produced by aspen trees, there were no significant interactions.

Variable	B	S.E.	*p*
Soil - PMM	1.433	0.221	<0.001
Height	0.005	0.001	<0.001
Total Cover	-0.014	0.004	<0.001

Pseudo $R^2 = 0.583$

Table 4. Logistic regression model parameters of soil, height with increments of 1 cm, and total cover with increments of 1% relating to the presence/absence of stump sprouts produced by aspen trees, likelihood ratio pertains to how much more likely a tree is to produce at least one stump sprout with each increment increase of a parameter.

Variable	Odds Ratio	β	S.E.	*p*
Tree Cover	0.54	-0.623	0.254	0.014
Soil – PMM: Tree Cover	1.69	0.525	0.251	0.036

Pseudo $R^2 = 0.444$

Figures

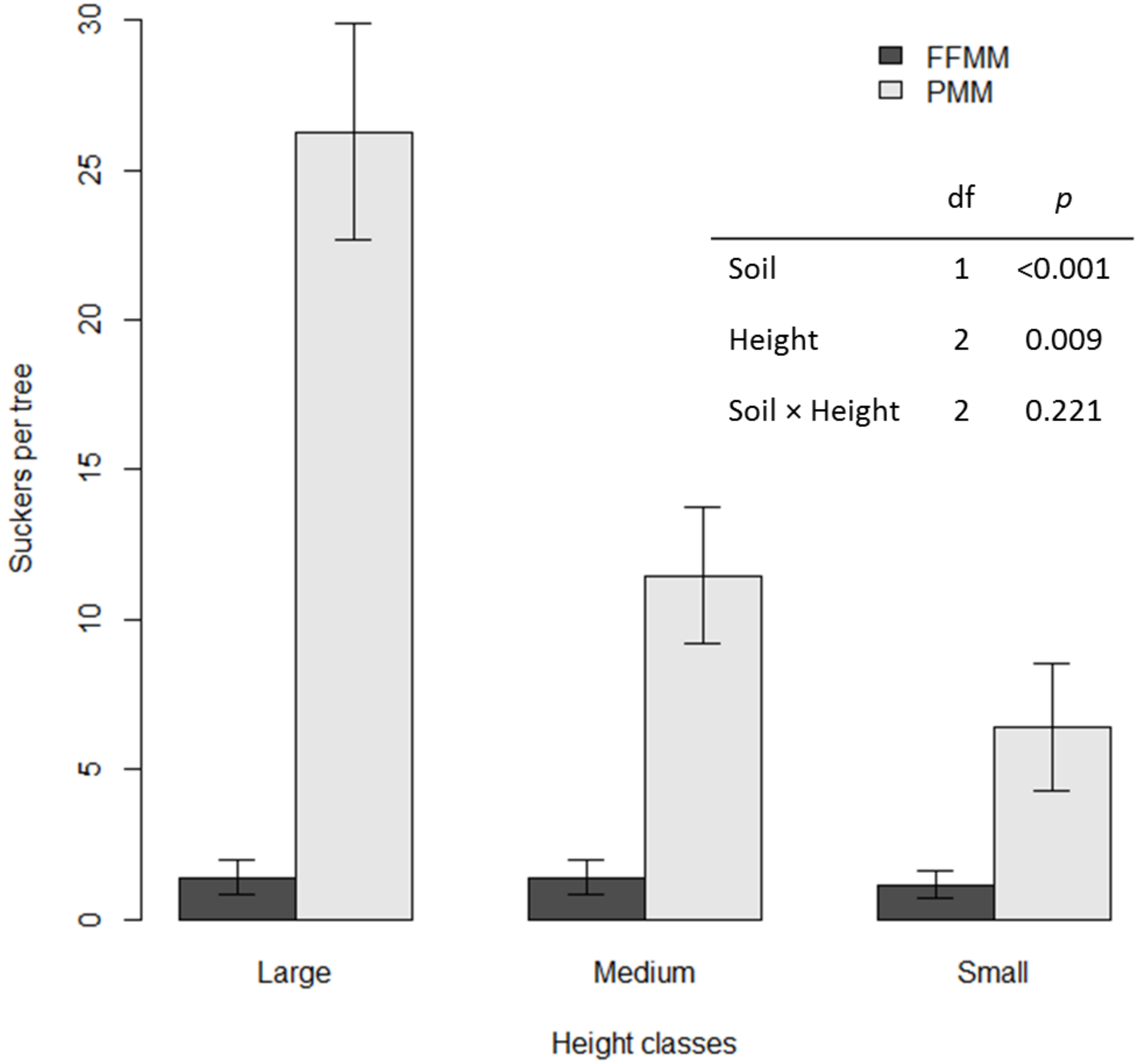

Figure 1. The average number of suckers produced (stems/ha) by large (>300 cm), medium (200 - 299 cm), and small (100 - 199 cm) trees on the different soil types.

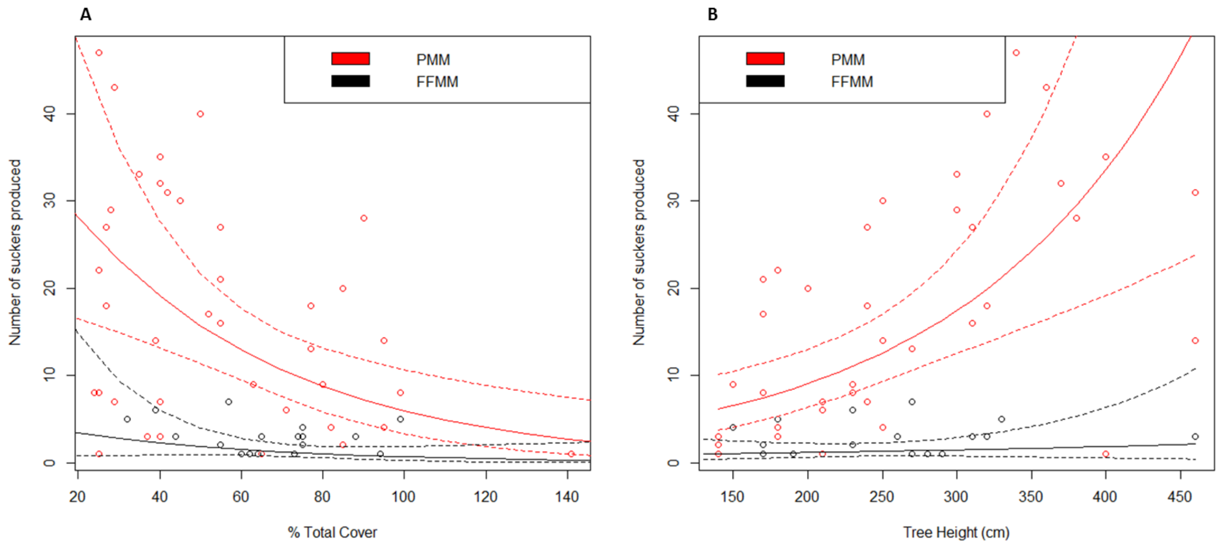

Figure 2. (A) Observed number of suckers produced over a range of total ground cover (%) on both soil types with a fitted zero-truncated negative binomial GLM curve (solid line) and 95% confidence bands (dotted lines). (B) Observed number of suckers produced over a range of tree heights (cm) on both soil types with a fitted zero-truncated negative binomial GLM curve (solid line) and 95% confidence bands (dotted lines).

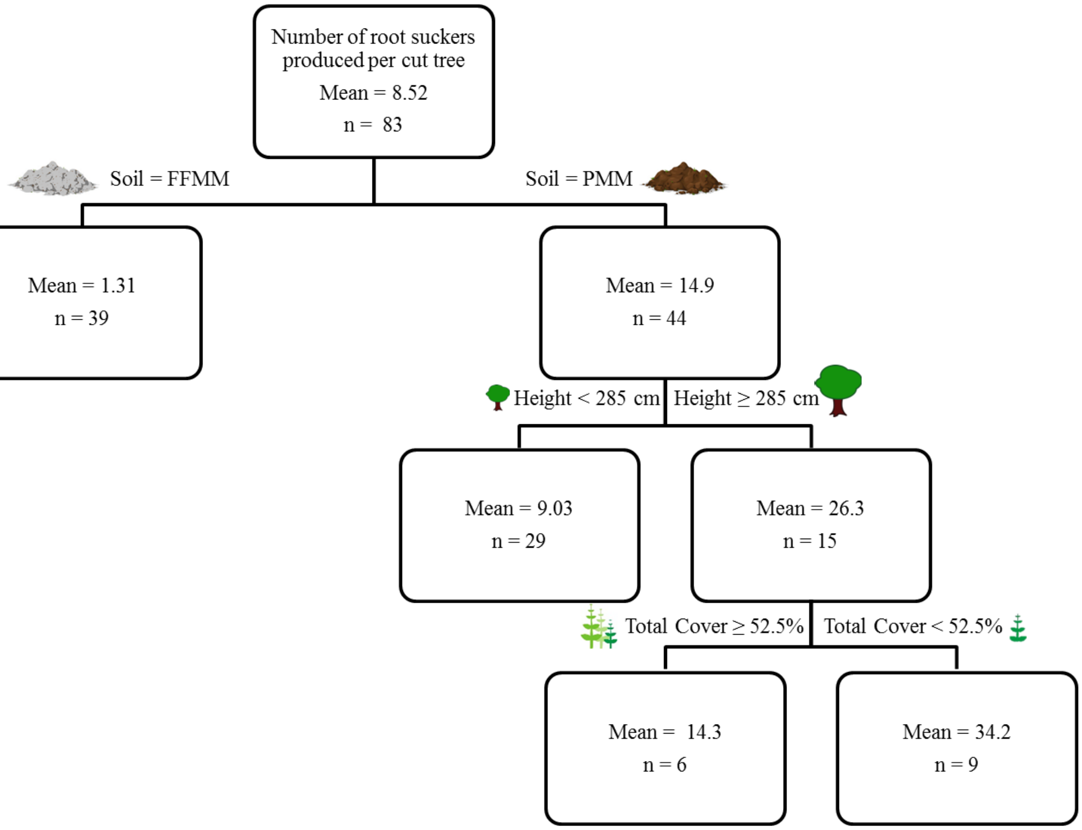

Figure 3. Regression tree analysis showing the conditions needed for different levels of root suckering pet tree, the most favorable conditions are on the far right and the least favorable are on the far left. Variance explained by the first split is 33%, second split is 25%, and third split is 12%.

Chapter 3 – Early regeneration dynamics of pure black spruce and aspen forests after wildfire in boreal Alberta, Canada

Abstract

Black spruce and trembling aspen are both common species found across the boreal forest. Black spruce forests dominate lowlands, while aspen dominate the uplands. Both species are well adapted to wildfire. Black spruce hold an aerial seedbank in the form of semi-serotinous cones, while aspen are able to reproduce rapidly via root suckering. In the summer of 2016, the Horse River wildfire burned 589,617 hectares of northern Alberta's boreal forest. To understand early regeneration dynamics of both pure aspen and pure black spruce forests, 65 different forest stands were measured. To determine how different habitat types affect black spruce regeneration, 12 plots were established in both bog and semi-upland habitats. To determine how fire severity affects aspen regeneration, 12 plots were established in each of low, moderate, and high burn severities, as well as 5 unburned plots to act as a control. Within all plots pre-fire and post-fire stand characteristics were determined along with regeneration densities. Seedbed availability was also determined in the black spruce stands, as they rely solely on recovery via seed. Black spruce regeneration did not differ between bog and semi-upland habitats, while aspen regeneration was significantly higher in semi-upland habitats. This could be an early indication of a shift in successional trajectory from a once pure black spruce forest to an aspen dominant forest in early successional stages. Black spruce regeneration densities were positively correlated with forb cover after wildfire, indicating better available seedbeds. Across both black spruce habitat types, charred organic matter was a preferred seedbed. In bogs, wet unburned organic matter was also highly preferred and more available. In semi-uplands, deadwood was a preferred seedbed, with much more of it being available compared to bogs. Fire severity did not have a significant effect

on aspen regeneration in pure aspen stands; regeneration density in all severity types was >90,000 stems ha^{-1}. We found that aspen regeneration densities were hindered by both an increase in post-fire forb and shrub cover, likely due to competition and cooler soil temperature. Overall, both tree species showed resiliency after wildfire. However, pure semi-upland black spruce stands are at risk of changing successional trajectories with a changing climate and fire regimes.

Introduction

Boreal forest ecosystem dynamics are driven by natural disturbances such as fire, windthrow, insect and disease outbreaks (Brandt et al., 2013). Fire is a major stand-renewing agent and plays an essential role in shaping boreal ecosystems by influencing species composition, age structure, productivity, and biodiversity (Weber and Flannigan, 1997). Approximately 0.7% of the forested land in the boreal region burns annually (Stocks et al., 2002) and this is expected to rise as fires become more frequent and harder to control due to a changing climate (de Groot et al., 2012).

Black spruce hold aerial seed banks in the form of semi-serotinous cones, enabling them to respond quickly to disturbances. Mature trees can hold up to 6 years of closed cones allowing for a large potential seed source (Greene et al., 1999). Although the majority of seed fall occurs in the first year post-fire, small amounts of seed rain can continue several years post fire, helping to ensure establishment during favorable years (Thomas and Wein, 1985). In the first 1 - 5 years post fire, black spruce seedlings can be found in densities up to 80,000 stems ha^{-1} (Foote, 1983; Johnstone and Chapin, 2006). This rate of regeneration, however, requires seedbeds that will allow for successful germination.

Although black spruce is capable of producing thousands of seeds post-fire, ideal seedbeds are needed for successful germination. Previous studies have found that the best establishment usually occurs on mineral soil, thin organic soil, or sphagnum because they are continually moist (Horton and Lees, 1961; Lloyd et al., 2007). Fire often creates these favorable seedbeds by removing soil organic horizons, lichen and moss mats, other competing vegetation, and by blackening and warming the soil (Black and Bliss, 1980; Auclair, 1983). Higher intensity fires produce more of these favorable seedbeds and result in good black spruce establishment; however, heavy ash layers on the soil can inhibit germination immediately after fire because of decreased water permeability (Kemball et al., 2006). To our knowledge, most research on seedbed preference has taken place in northern circumpolar regions (Lloyd et al., 2007; Johnstone et al., 2008; Mallik and Kayes, 2018); it would be beneficial to also understand preferences in more southerly portions of the boreal, as well to better understand regeneration dynamics in different black spruce habitats.

In Alberta, there are two main types of black spruce forests, upland and lowland. In upland sites mineral soil is typically found within 30 cm of the soil's surface and is imperfectly drained (Beckingham and Archibald, 1996). Lowland sites are classified as treed bogs and have organic soils that are ≥80 cm thick, the soils are hydric and can have standing water. Semi-upland sites tend to be more productive in terms of tree growth because the soils have better drainage and thinner organic layers. These two habitat types could provide different seedbeds for black spruce. Lowland sites will provide organic matter seedbeds, while uplands should provide more mineral soil seedbeds. Previous studies in other areas have shown both of these seedbed types to have greater amounts of black spruce regeneration; however, it is not yet known which of these two habitat types will promote more black spruce regeneration in Alberta.

Trembling aspen is well adapted to disturbances because they have a high capacity for vegetative reproduction (Greene et al., 1999). Sprouts from lateral roots (root suckers) are the main form of regeneration after disturbance; however stump sprouts can also be produced if the stem is removed (Greene et al., 1999). Root suckers are produced immediately after fire in numbers as high as 240,000 stems ha^{-1} (Wang, 2003). However, there is evidence of lower root suckering rates of aspen after high severity fires and under certain pre-fire stand conditions, such as unhealthy trees and low stand basal areas. Aspen can also colonize a site via windblown seeds capable of travelling long distances (Johnstone and Chapin, 2006). If preferable microsites, such as mineral soil, shallow organic matter, and mineral-organic matter mix, are present, aspen will regenerate successfully by seed, potentially occupying other habitat types (Landhäusser et al., 2010; Landhäusser et al., 2019).

Generally, it is thought that forests within the boreal will regenerate to similar species composition and stem densities as before fire, known as the direct regeneration hypothesis (Yih et al., 1991). However, deciduous trees may dominate a regenerating forest because of rapid asexual reproduction and long-distance transport of small wind-blown seeds (Johnstone and Chapin, 2006; Bergeron et al., 2014). These alternative successional trajectories can be driven by fire severity, pre-fire vegetation composition, site conditions, and fire effects on the reproductive potential of alternate dominant species (Peters et al., 2005; Johnstone et al., 2008). Species interactions, such as herbivory and plant competition can also alter the direction and timing of successional trajectories (Johnstone et al., 2008). For example, in black spruce dominated stands, adjacent deciduous trees (e.g. trembling aspen) can populate an area via lateral root suckering (Johnstone and Chapin, 2006; Johnstone et al., 2009). High severity fires also consume organic material and expose mineral soil leaving ideal seed beds for deciduous tree species, as well as other conifers, while scorching the aerial seed bank held by black spruce thereby reducing their viability (Johnstone et al. 2008; Johnstone et al., 2009). In aspen-dominated stands, higher severity fires tend to cause more prolific asexual regeneration compared to low severity fires (Wan et al., 2014; Shinneman et al., 2015). However, severe burns (forest floor is completely removed) have also been found to reduce aspen reproduction by consuming lateral roots (Wang, 2003), allowing other species to germinate on a mineral soil seedbed.

The goal of this study was to determine the effects of fire severity, habitat type, and stand characteristics on the regeneration of pure black spruce and pure aspen stands immediately after wildfire. We examined black spruce and aspen stands separately, as the emphasis of research questions differed. For black spruce stands we sought to determine whether: (1) habitat type (i.e., bog or semi-upland) affected regeneration of black spruce stands; (2) stand characteristics (i.e. age, DBH, height, basal area, competition, soil properties) affected regeneration in black spruce stands; and (3) seedbeds were occupied by black spruce seedlings in different habitat types. For aspen forests we sought to determine whether: (1) fire severity affected the regeneration of aspen stands; and (2) stand characteristics (i.e. age, DBH, height, basal area, competition, soil properties) affected regeneration in aspen stands. Answering these questions allows for a better understanding of the regeneration dynamics and potential successional trajectories after wildfire in pure aspen and black spruce forests.

Methods

Study Area

This study took place after the Horse River fire, which burned an area of 589,617 hectares, Canada's fourth largest wildfire on record (Natural Resources Canada, 2017). The Horse River Fire started on May 1, 2016 and was not classified as under control until July 5, 2016 (Natural Resources Canada, 2017). Record high temperatures, low relative humidity, and strong winds caused the fire to undergo a dramatic increase in size shortly after ignition. At the time of the fire, the green-up of vegetation had not begun, resulting in dry fuel being available on the forest floor (Kochtubajda et al., 2017). These extreme weather and fuel conditions made the Horse River wildfire very difficult to manage.

The Horse River fire occurred in the Central Mixedwood Natural Subregion of Alberta, characterized by aspen and aspen-white spruce forests on upland sites (Downing and Pettapiece, 2006). Semi-upland sites have imperfectly drained soils and are occupied by black spruce-dominated forests. Lowland areas consist of wet, poorly drained black spruce fens and bogs, which compose almost half the area of the subregion. Black spruce growing in lowland habitats is typically much smaller compared to those in semi-uplands. Upland soils are predominantly Gray Luvisols, semi-uplands are Gleysols, and lowland soils are Organic (Soil Classification Working Group, 1998). The subregion is characterized by short warm summers and long cold winters, with average temperature of the warmest month being 15.9 °C and average temperature of the coldest month being -18.7 °C (based on the Fort McMurray climate normal from environment Canada). The mean annual precipitation is 469 mm.

Field Methods

After initial scouting, it was determined that while aspen stands burned across a gradient of different fire severities, black spruce stands only burned at high severities. This discrepancy in burn severities caused us to select sites differently for each stand type. Black spruce-dominant stands (≥80% black spruce) were chosen by two general habitat types of black spruce in the area: semi-upland and bog. Aspen-dominant (≥80% aspen) stands were chosen across a gradient of fire severities (low, moderate, high, and unburned), and were all approximately the same age (~ 80 yrs.). Trees in both black spruce habitat types and across all aspen fire severities were approximately the same age (~ 90 yrs.). Sites were located off of roads, cut blocks, and cut lines. Buffers between plots and forest edges were double the average tree height of a stand (60 m for aspen and 30 m for black spruce).

In the summer of 2017, one year after the fire, 71 measurement plots were randomly placed in appropriate stands. Twelve plots were placed in each black spruce habitat type, and each habitat type had three unburned control plots. Twelve plots were placed in each aspen fire severity level, and there were five unburned control plots. At each site, circular plots with a radius of 5.67 m were established. Within each circular plot, North-South and East-West transects were also established. At each plot, tree regeneration, fire severity, and stand characteristics were measured and a soil sample taken. The Composite Burn Index (CBI) (Key and Benson, 2006) was used to estimate burn severity. The CBI uses five strata levels in a community to determine the magnitude of fire effects. For this research only the substrate and dominant/co-dominant tree strata were used because pre-fire characteristics for other strata levels were unknown.

Tree and stand measurements included canopy height, stand age, and diameter at breast height (DBH) from all trees with a DBH >7 cm. Canopy height was determined by measuring the heights of three average overstory trees. Tree cores were taken at breast height from three average-sized overstory trees to estimate stand age. Age was determined in the lab using CooRecorder software (Cybis Dendrochronology, 2018) after core preparation.

Soil grab samples, including litter, humus, and mineral soil, were collected from the Northeast, Southeast, Southwest, and Southeast quadrants of each plot. If mineral soil was not present in the black spruce bog stands, two depths of organic soil were taken. These samples were then analyzed for pH, electrical conductivity, and texture with electrical conductivity and pH measured in a soil to water ratio of 1:2 for mineral soils and 1:10 for organic soils using a sympHony™ pH meter (Hendershot et al. 2007). Mineral soil texture was determined using a Beckman Coulter LS 13 320 laser particle size analyzer system (ISO method 13320). Texture for organic soils was done by hand using the von Post scale of decomposition (Soil Classification Working Group, 1998).

Tree regeneration, the response variable, was measured using 20 subplots evenly spaced along the North South and East West transects within each plot. Subplot size depended on the stand type. Subplot size in aspen stands was 50 cm x 50 cm, as regeneration was very high. Subplots in black spruce stands were 100 cm x 100 cm, as regeneration rates were lower. In each subplot, seedlings or suckers were tallied and then averaged for the stand on a per hectare basis. Percent cover of vegetation functional groups (shrub, forb, grass, and bryophyte) was also estimated within each subplot.

To determine preferred seedbeds for black spruce seedling establishment, we returned to 21 of the 24 black spruce sites in the summer of 2018. Three of the sites, all bog, were not revisited due to inaccessibility. Plot layout was similar to what was setup in 2017, with North to South and East to West transects inside of a 5.67 m plot. However, a smaller circular regeneration plot was also established at plot center with a radius of 3.99 m. This smaller regeneration plot was used to count the number of black spruce seedlings establishing and note the seedbed type they were growing on. Thirty seedbed plots (5.67 cm radius) were placed along each transect, with a total of 60 in each stand. Within each seedbed plot, the amount of each dominant seedbed type was determined along with total vegetation cover. Seedbed types were classified as: mineral soil (concave and convex), unburned organic matter/hummocks (wet and dry), dead wood (within 5 cm), charred organic matter, and other (rock, water, etc.). Concave mineral soil, charred organic matter, wet unburned organic matter, and deadwood seedbeds all had mesic conditions. Convex mineral soil and dry unburned organic matter had subxeric conditions. We did not examine seedbed preferences for aspen because regeneration took place via root suckers.

Statistical Analysis

All data were analyzed using R software (R Core Team, 2018, Boston, MA). Since aspen and black spruce regeneration variables were over-dispersed count data and could not be transformed, general linear models with a negative binomial distribution were used. First, to understand the differences between selected sites, within each stand type, several MANOVAs were performed (*manova* command in R 3.1.4; R, 2018). To determine the differences among pre-fire stand characteristics, basal area, height, and age were used as response variables and site selectors of fire severity and habitat type were used as explanatory variables. To determine the differences among post-fire stand characteristics, forb cover, grass cover, shrub cover, bryophyte cover, % sand, % silt, % clay, pH, and EC were all used as response variables and site selectors of fire severity and habitat type were used as explanatory variables.

Secondly, to determine the effects of the site selector variables of habitat type for black spruce stands and fire severity for aspen stands, general linear models with a negative binomial distribution were used (*glm.nb* command in R 3.1.4; R, 2018). For the black spruce stands, two models were created. Both used habitat type as the only explanatory variable with one using black spruce regeneration and the other using aspen regeneration as the response variable. In the aspen stand model fire severity was the only explanatory variable used and the amount of aspen regeneration as the response variable. We then ran an analysis of deviance on each of the models (*anova* command in R 3.1.4; R, 2018). Thirdly, negative binomial models were used to determine what stand characteristics had an effect on regeneration rates. Models were chosen based on the lowest AIC score. Beta values were transformed to integer values, e^{β}, to more easily understand the magnitude of effects. Pseudo R^2 values were calculated using the *rms* package (Version 5.1-1; Harrell, 2017).

Lastly, seedling preference values were derived for black spruce using the formula:

$$\text{Preference}_{\text{seedbed}} = \frac{(\text{No. seedlings on seedbed } x)/(\text{Total no. of seedlings})}{(\text{No. of seedbed } x)/(\text{Total no. of seedbeds})}$$

Where a preference value of 1 indicates no preference for a seedbed, while greater values indicate preference and lower values indicate avoidance (Landhäusser et al., 2010). An ANOVA (*anova* command in R 3.1.4; R, 2018) was used to compare seedbed preferences among the two habitat types. To meet the statistical assumptions of normality and homogeneity of variance, substrate preference for aspen seedlings was ln(x + 1) transformed.

Results

Regeneration in black spruce stands

Pre-fire stand characteristics of basal area ($p = 0.049$) and height ($p = 0.007$) were significantly different between bog and semi-upland black spruce habitats (Table 5). However, there was no difference in stand age ($p = 0.147$) between habitat types. Post-fire stand characteristics of forb cover ($p = 0.021$), shrub cover ($p = 0.010$), and EC ($p = 0.042$) were all found to be significantly higher in bog habitats. No other post-fire stand characteristics were significant ($p > 0.05$).

Across all black spruce stands we saw regeneration primarily of black spruce (60%) and aspen (32%); however balsam poplar (*Populus balsamifera* L.) and jack pine (*Pinus banksiana* Lamb.) were also present in small numbers (7% and 1%). Black spruce regeneration was highly variable ranging from 0 to 43,000 stems ha^{-1} in bogs and 0 to 39,500 stems ha^{-1} in semi-upland forests. Aspen regeneration was also highly variable ranging from 0 to 17,000 stems ha^{-1} in bogs and from 0 to 36,000 stems ha^{-1} in semi-uplands. There was no significant difference in black spruce regeneration across the two habitat types ($\bar{x}_{\text{bog}} = 13{,}375$; $\bar{x}_{\text{semi-upland}} = 10{,}583$ stems ha^{-1}; $p = 0.698$), however semi-upland habitats allowed for significantly greater aspen regeneration via root suckers ($\bar{x}_{\text{bog}} = 8{,}000$; $\bar{x}_{\text{semi-upland}} = 10{,}916$ stems ha^{-1}; $p = 0.011$; Fig. 4). Black spruce regeneration was found to be positively correlated with forb cover ($\beta = 1.448$, $p < 0.001$, pseudo $R^2 = 0.396$). For each 1% increase in forb cover there was approximately 8,509 more regenerating black spruce seedlings ha^{-1} (Fig. 5). Aspen regeneration was greater in semi-upland habitats, but was not affected by stand and site characteristics including basal area, tree height, tree age, competition levels, or soil properties.

Seedbed type had a significant effect on the establishment of black spruce seedlings, with habitat types having significantly different availabilities of seedbeds ($p = 0.009$). Semi-upland habitats had significantly more dead wood seedbeds ($p < 0.001$), while bog habitats had significantly more dry unburned organic matter ($p = 0.014$).

In terms of seedbed availability in bog habitats, dry unburned organic matter was the most common at 58%, followed by charred organic matter at 22% and dead wood at 11%, convex mineral soil, wet unburned organic matter, and other seedbeds comprised of <10% of the available seedbeds (Fig. 6a). Of the 552 seedlings observed in bog habitats, 40% were establishing on dry unburned organic matter, 29% on charred organic matter, 27% on wet unburned organic matter, 3% on dead wood, and <1% on convex mineral soil (Fig. 6a).

Charred organic was the most common seedbed available in semi-upland habitats at 44%, followed by dead wood at 30% and dry unburned organic matter at 23%. Convex mineral soil, concave mineral soil, wet unburned organic matter, and other seedbeds made up <5% of available seedbeds (Fig. 6b). Of the 1457 seedlings observed, 48% established on dead wood, 45% on charred organic matter, 4% on wet unburned organic matter, 2% on dry unburned organic matter, and <1% on convex and concave mineral soil combined (Fig. 6b).

Preference values indicated that there were differences in black spruce establishment between seedbed types ($p = 0.021$). In both habitat types black spruce seedlings tended to prefer charred organic matter as a seedbed. In bogs, wet unburned organic matter was also a preferred seedbed, while dry unburned organic matter was preferred slightly. In semi-uplands, dead wood and wet unburned organic matter were other preferred seedbeds. Preference values for all other substrates were low.

Regeneration in aspen stands

There were no significant differences in aspen pre-fire stand characteristics ($p = 0.671$; Table 5). There were also no significant differences found among fire severities on post-fire stand characteristics ($p = 0.179$).

In pure aspen stands we saw regeneration primarily of aspen (99.5%); however, balsam poplar (0.4%) and white spruce (0.1%) [*Picea glauca* (Moensch) Voss] were also present in small numbers. Aspen regeneration ranged from 14,000 to 294,000 stems ha^{-1}. In general, moderate severity fires had the greatest regeneration, followed by high and low severity ($\bar{x}_{\text{low}} = 93{,}384$, $\bar{x}_{\text{mod}} = 122{,}909$, $\bar{x}_{\text{high}} = 104{,}000$ stems ha^{-1}; Fig. 7) with differences being marginally significant ($p = 0.082$). Unburned stands had little aspen regeneration, with only 5 regenerating aspen stems found across all 5 unburned stands. For burned stands, forb and shrub cover negatively affected regeneration of aspen ($\beta_{\text{forb}} = -0.017$, $p_{\text{forb}} = 0.036$, $\beta_{\text{shrub}} = -0.076$, $p_{\text{shrub}} < 0.001$, pseudo $R^2 = 0.475$). Specifically, a 10% increase in either forb or shrub cover decreased aspen regeneration by approximately 5,000 stems/ha (Fig. 8).

Discussion and Conclusions

Black spruce regeneration rates in bogs were generally higher than in semi-upland sites, but not significantly so. Black spruce regeneration densities averaged 11,979 stems ha^{-1} and were slightly lower than expected. Past studies have found that black spruce typically regenerate in numbers of around 40,000 stems ha^{-1} and as high as 80,000 stems ha^{-1} (Chrosciewicz, 1976; Foote, 1983; Johnstone and Chapin, 2006). Other studies, however, took regeneration measurements at least 5 years post-fire. Black spruce has been found to take 5 to 10 years to reach maximum seedling establishment (Johnstone et al., 2004). In fact, it took three years for black spruce to reach 50% of the net spruce establishment after fire in Alaska (Johnstone et al., 2004); therefore black spruce establishment could further increase in our stands within the next few years. Although initial black spruce regeneration densities were lower than expected, these forests would still be considered adequately re-stocked (Greene et al., 2002). Factors such as stand productivity and seedbed availability could play a role in causing variability in black spruce regeneration rates.

Semi-uplands and bogs differ in site productivity in Alberta's boreal mixedwoods. Pre-fire stand basal area and height were both found to be significantly greater in semi-uplands even when stand age was the same between habitats (Table 5). This suggests that semi-uplands have greater tree productivity. The subhydric conditions found in semi-uplands likely explain the majority of the difference in tree productivity. Black spruce growing on wetter sites have reduced growth rates compared to trees growing in drier sites (Bubier, 1991; Lacey and Dech, 2012). Less oxygen availability to the tree roots in water-saturated sites is considered to be the main reason for the lack of tree growth in boreal peatlands (Crawford, 1983; Lieffers and Rothwell, 1987). Greater tree productivity is linked to greater seed production (Viglas et al., 2013). Therefore, semi-upland forests would likely have seen greater amounts of seed rain post-fire. However, semi-uplands did not see significantly greater amounts of black spruce regeneration, and in fact, on average they saw slightly lower amounts of regeneration. This discrepancy can likely be explained by seedbed availability.

Across both habitat types, black spruce regeneration increased with an increase in forb cover, suggesting preferable seedbed availability for both forbs and black spruce. Black spruce tends to establish on mineral soil, thin organic soil, or moss seedbeds (Horton and Lees, 1961; Lloyd et al., 2007; Mallik and Kayes, 2018). It has been thought that these seedbeds are preferred because of their ability to provide constant moisture. We found similar results, with charred organic matter, which would be comparable to a thin organic soil, as a preferred seedbed at both habitat types. Moss (wet unburned organic matter) was also a preferred seedbed. Our results, however, did not show a preference for mineral soil. This could be explained by a lack of mineral soil availability. Previous studies have made no mention of deadwood as a preferred seedbed; however, deadwood and the soil around it was also a preferred seedbed on semi-upland habitats in this study. Moss seedbeds are thought to be the most optimal seedbeds because of their high moisture retention and low temperature (Wheeler et al., 2011; Mallik and Kayes, 2018). Bog habitats saw more moss seedbeds available compared to uplands, which may explain why bogs saw more black spruce regeneration on average. Our results are an important first step in understanding seedbed preferences in Alberta's boreal forest, allowing for better forest management and aiding in black spruce reforestation.

The large amount of aspen regeneration in previously pure black spruce stands was surprising. Bogs saw lower rates of aspen regeneration, averaging at 2,000 stems ha^{-1}. In semi-uplands, however, aspen regeneration averaged 10,917 stems ha^{-1} nearly matching the regeneration of black spruce. All measured aspen were root suckers (>50 cm tall one year post-fire, green stem, large leaves); therefore proximity to aspen stands was likely the main factor determining aspen regeneration. Most semi-upland sites were closer to aspen stands compared to bogs due to their topographic position, explaining why they saw significantly more aspen regeneration. Aspen regeneration was not effected by any post-fire stand characteristics, likely because root suckers are sustained by parent tree root systems for some time after fire (Lambers et al., 2002) and the amount of regeneration would be directly related aspen root densities. Aspen would not have been affected much by competition in black spruce stands because there is very little revegetation of other species. Aspen was also the most vigorous species regenerating in most stands.

These high numbers of aspen regeneration could indicate a change in forest successional trajectory. Successional processes in black spruce have traditionally been viewed as a simple cycle of self-replacement after fire (e.g. Van Cleve et al., 1991). However, with a changing climate and fire regimes it has been found that black spruce forests may be more susceptible to change than we originally thought (Johnstone et al., 2008). A change in successional pathways has already been seen in Alaska’s boreal forests (e.g. Johnstone and Chapin, 2006), with sites previously dominated by black spruce now seeing domination by deciduous tree in early successional stages. This study seems to be showing evidence of this occurring in Alberta’s boreal forests as well, especially in semi-upland habitats.

Increases in deciduous tree species cover will also contribute to a changing fire regime in stands previously dominated by black spruce. Black spruce have a large amount of fine twigs and needles, high resin content, low moisture content, and large quantities of fine ground fuels that are connected to the canopy creating a highly flammable environment (Johnstone et al., 2008).

Deciduous tree species are much less flammable due to higher moisture contents and reduced amounts of fine fuels (Hély et al., 2000). Our findings correspond with this, as we found that pure aspen stands burned at differing severity levels, while black spruce stands burned only at high severities. For forest managers understanding how black spruce forests can shift in successional trajectories can help predict how changes in fire regimes may shape future forest cover. This could also be useful for fire management. A goal of fire management is to transition certain forests from conifer to deciduous dominated because deciduous forests act as a fire break (Johnstone et al., 2008).

Aspen regeneration across different burn severity levels was not significantly different. However, an average regeneration rate of 105,944 stems ha^{-1} demonstrates that they will easily be fully stocked aspen forests (Greene et al., 2002). This large amount of regenerating aspen is similar to results found in some studies in Western Canada (e.g. Wang, 2003), but much higher compared to other studies in the Western United States (e.g. Brown and Debyle, 1987). Wang (2003) found that different levels of fire severity did have a significant effect on aspen regeneration, with severe burns producing significantly less root suckers compared to light and moderate burns. This contradicts the results found in this study and in a study done by Brown and Debyle (1987), where burn severity did not affect aspen regeneration. This contradiction is likely explained by the differences in root depth of aspen growing in different climates or on different soil types. If roots capable of producing suckers are deep in the soil, they will be insulated from high severity fire and will maintain their capacity to produce root suckers. In this study, some charring of the roots in the stands that experienced high severity burns could explain why, on average, high severity stands saw slightly less aspen regeneration. Low severity burns saw the least amount of regeneration on average, likely because there was not complete overstory mortality and sucker production was not initiated in all trees. Since there was not complete overstory mortality and there were still many suckers produced, it is likely that these forests will become uneven-aged stands. This could change our perspective on forest management, as it is generally assumed in the area that stands are even-aged after fire.

Increasing amounts of forb and shrub cover were found to inhibit aspen sucker regeneration. These findings support other studies showing that vegetative competition can significantly reduce aspen suckering (Landhäusser and Lieffers 1998). Not only is there competition for resources, but soil is also cooled, inhibiting sucker initiation (Hogg and Lieffers 1991; Landhäusser and Lieffers 1998). Shrub cover had a greater effect on aspen suckering compared to forb cover, although forb cover was typically much greater than shrub cover (Table 5). Shrubs are larger and are more capable of competing for resources than forbs, they also would shade the soil much more than forbs, cooling the soil and blocking light from a shade-intolerant species. This information could be used by forest managers in areas where aspen regeneration is low. Understory vegetation removal may be necessary to facilitate more root suckering.

In summary, both aspen and black spruce were resilient to fire in Alberta's boreal forest. However, we observed a shift in successional trajectory for stands that were previously pure black spruce to aspen dominated stands, especially in semi-upland black spruce habitats. We also demonstrated that variables, such as competition and seedbed availability, can affect variability in regeneration. These results allow for a better understanding of the regeneration dynamics and potential successional trajectories after wildfire in pure aspen and black spruce forests, useful for forest management.

Tables

Table 5. Pre and post-fire stand characteristics for each stand type sampled. Values are average (standard error), n = 12 for each stand type. Pre-fire forests were all comprised of ≥80% either aspen or black spruce; other tree species were not included.

Stand Type	Basal Area (m^2)	Height (m)	Age (years)	Forb (%)	Grass (%)	Shrub (%)	Bryophyte (%)	Clay (%)	Silt (%)	Sand (%)	Vonpost scale	pH	EC (µS/cm)
Black Spruce - Bog	6.74 (1.23)	11.1 (0.87)	89 (9.09)	11 (2.08)	1 (0.51)	8 (1.78)	3 (0.97)	-	-	-	3 (0.32)	5.01 (0.26)	139.67 (30.48)
Black Spruce - Semi-upland	13.91 (1.30)	14.4 (0.67)	74 (7.40)	8 (1.92)	2 (0.43)	2 (0.91)	11 (4.74)	24.43 (1.85)	38.77 (2.42)	36.81 (3.95)	-	5.20 (0.14)	87.78 (11.85)
Black Spruce - Unburned Bog	5.33 (1.70)	7.74 (2.31)	77 (26.23)	14 (3.94)	7 (6.48)	20 (6.48)	86 (2.52)	-	-	-	1 (0.22)	5.19 (0.24)	184.98 (41.18)
Black Spruce - Unburned Semi-upland	25.10 (5.84)	15.8 (1.20)	79 (8.92)	3 (1.15)	0	10 (3.45)	85 (5.14)	14.09 (1.04)	32.63 (2.32)	53.28 (1.56)	-	4.35 (0.24)	165.83 (46.25)
Aspen - Low	32.72 (3.45)	22.7 (1.06)	73 (6.03)	24 (3.27)	2 (0.85)	9 (1.98)	2 (0.80)	31.50 (2.51)	52.48 (2.52)	16.03 (3.24)	-	5.96 (0.10)	123.76 (14.21)
Aspen - Moderate	40.25 (10.18)	21.8 (1.01)	87 (5.40)	20 (2.61)	2 (0.64)	5 (0.88)	0 (0.26)	27.30 (2.19)	53.50 (3.23)	19.20 (3.60)	-	5.85 (0.05)	84.23 (5.20)
Aspen - High	27.30 (2.68)	21.5 (0.97)	80 (5.70)	26 (3.35)	1 (0.64)	6 (0.88)	1 (0.26)	26.49 (2.19)	50.50 (3.23)	23.02 (3.60)	-	5.85 (0.05)	106.29 (5.20)
Aspen - Unburned	22.85 (4.46)	21.9 (1.08)	60 (2.30)	20 (2.53)	1 (0.65)	10 (4.23)	1 (1.31)	18.06 (6.13)	25.58 (4.81)	56.36 (10.83)	-	5.62 (0.31)	84.33 (9.68)

Figures

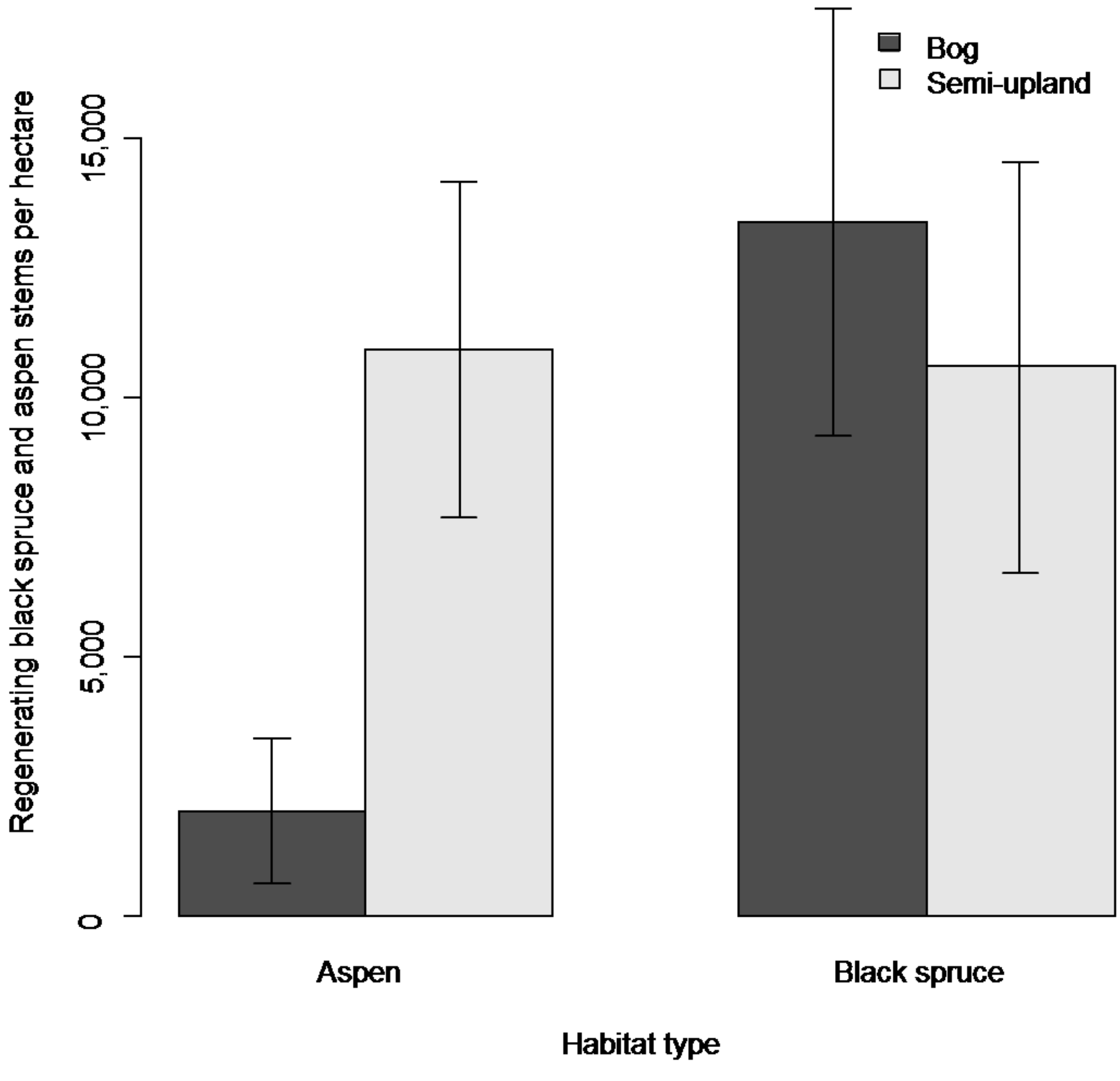

Figure 4. Black spruce and aspen regeneration on different black spruce habitat types.

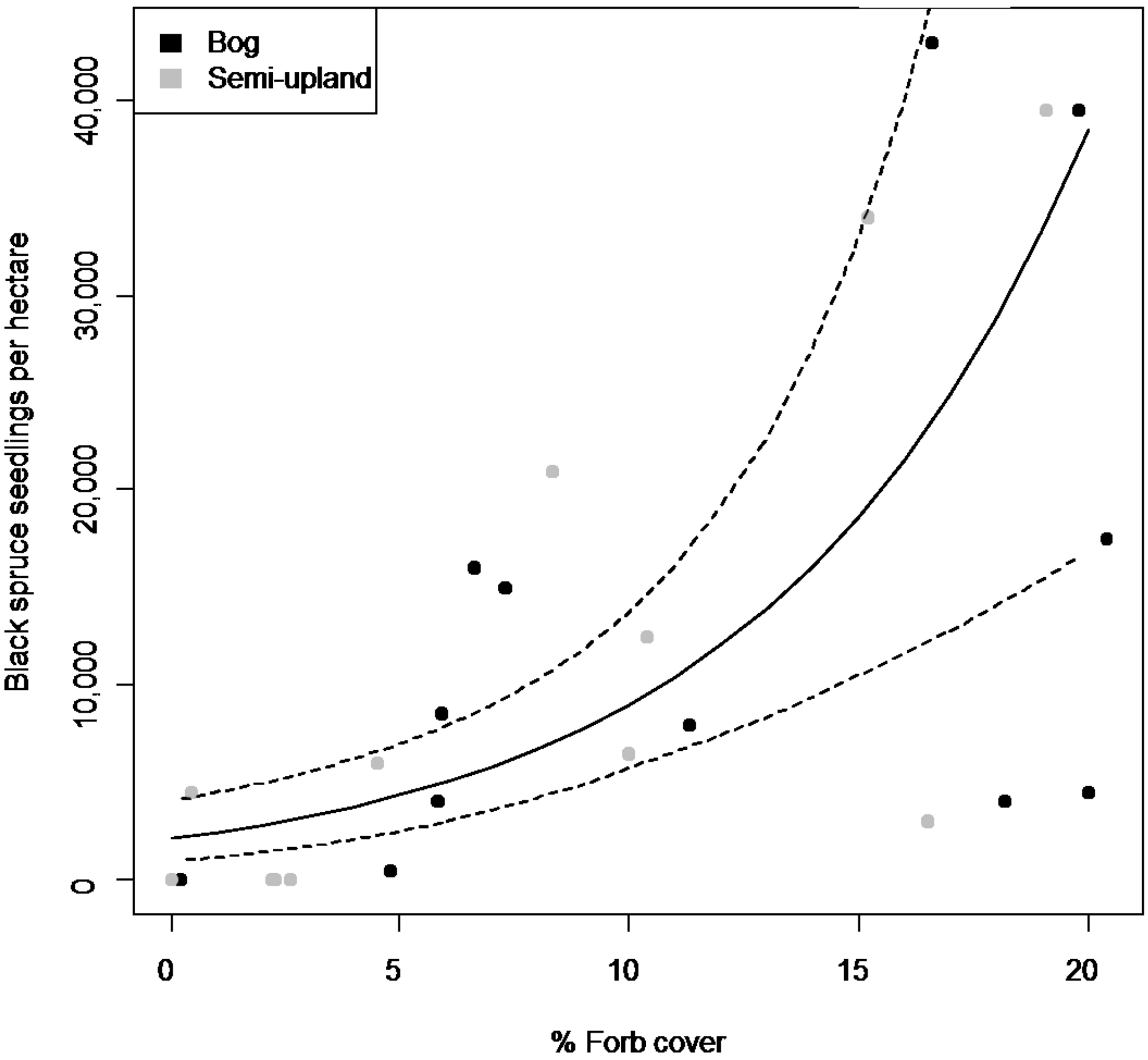

Figure 5. Observed number of black spruce regeneration over a range of forb cover (%) with a fitted negative binomial GLM curve (solid line) and 95% confidence bands (dotted lines).

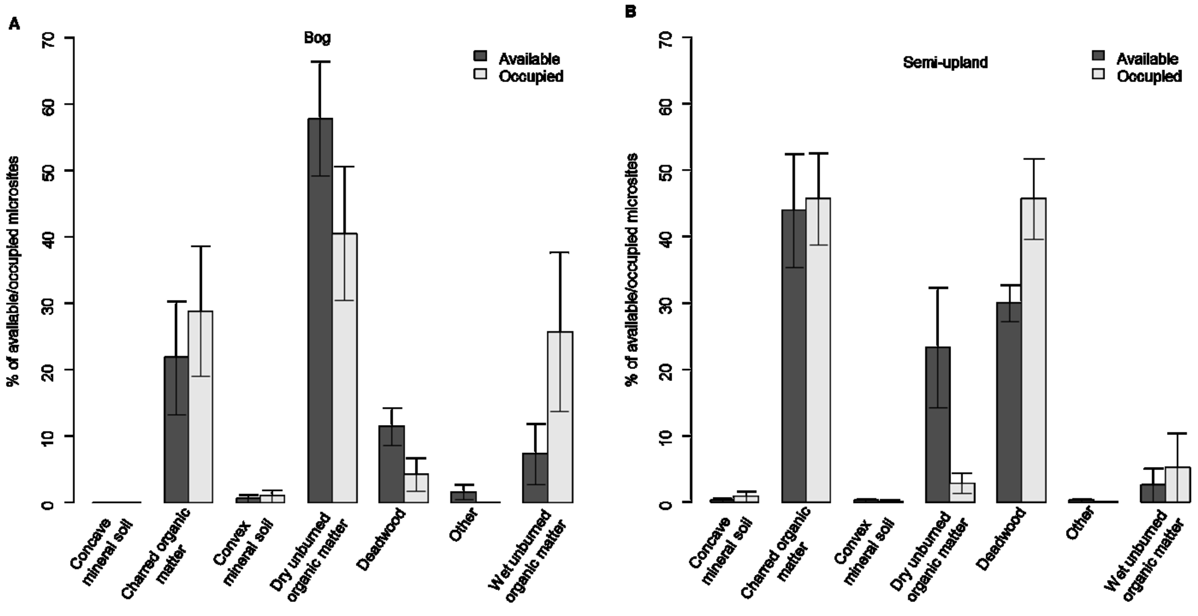

Figure 6. (A) Percent of black spruce seedlings occupying various seedbed types and the percent frequency of each substrate type in bog habitat types. (B) Percent of black spruce seedlings occupying various seedbed types and the percent frequency of each substrate type in semi-upland habitat types.

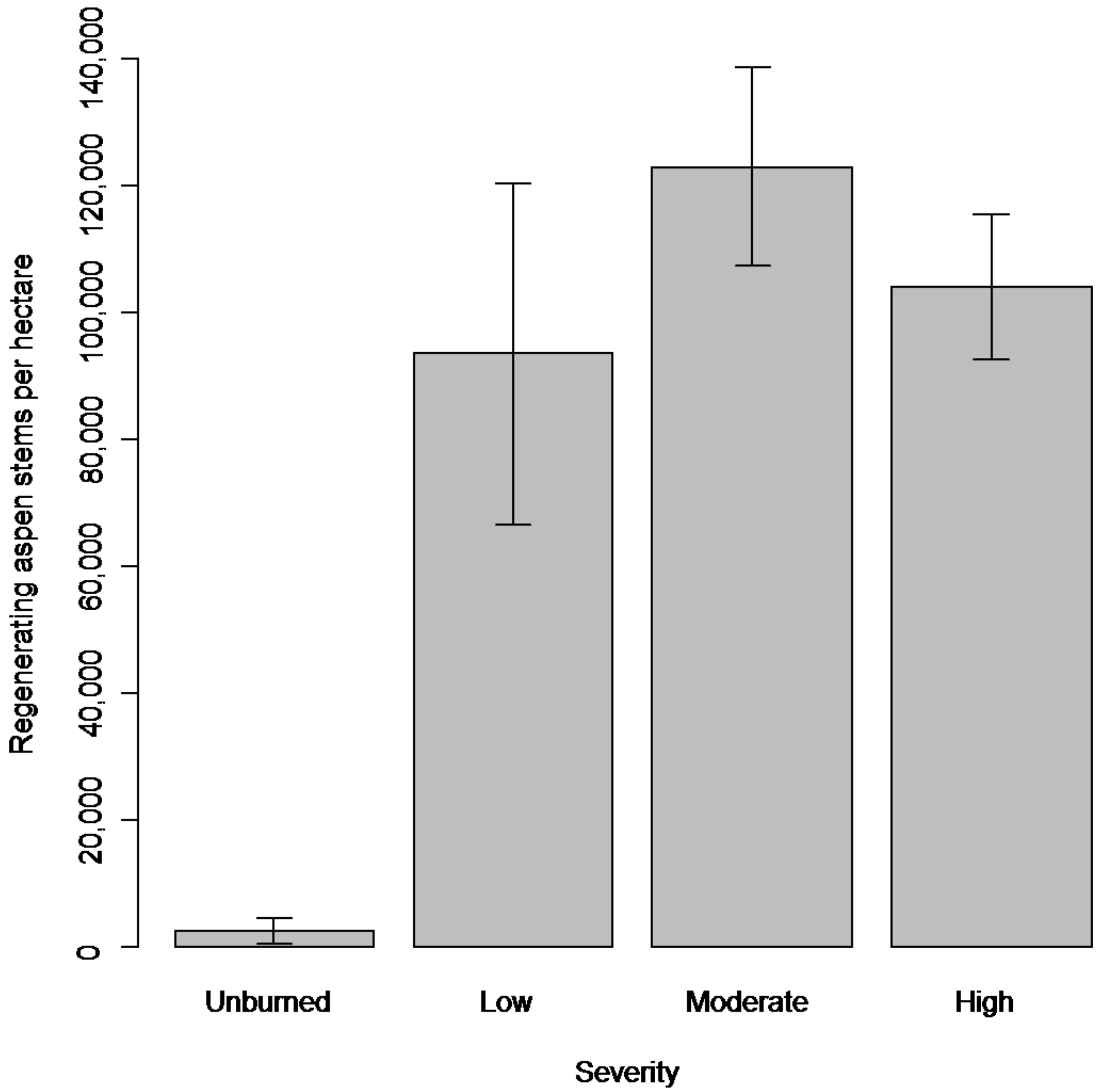

Figure 7. Aspen regeneration across the three fire severities (low, moderate, high) and in unburned stands.

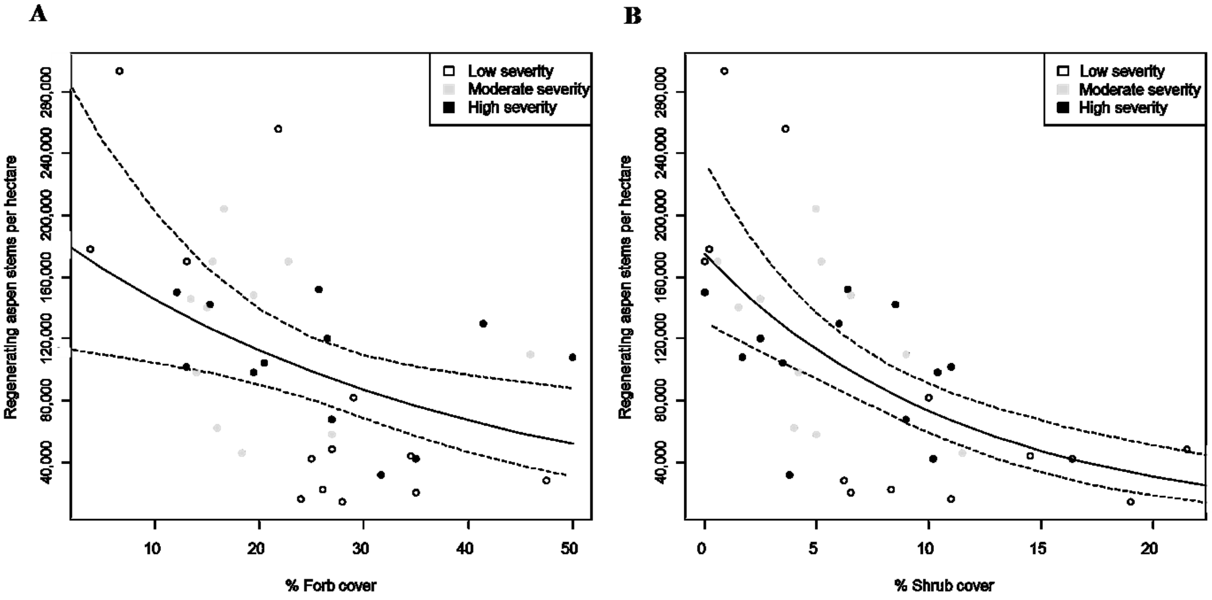

Figure 8. (A) Observed number of aspen regeneration over a range of forb cover (%) with a fitted negative binomial GLM curve (solid line) and 95% confidence bands (dotted lines). (B) Observed number of aspen regeneration over a range of shrub cover (%) with a fitted negative binomial GLM curve (solid line) and 95% confidence bands (dotted lines).

Chapter 4 – General Conclusion

The boreal forest is regularly subjected to different types of disturbances. Therefore, it is important that the land we reclaim in the boreal is resilient to these disturbances. Reclaimed land should be able to respond to natural and anthropogenic disturbances in a manner similar to how an analogous undisturbed landscape might respond to the same disturbance (Welham, 2013). In fact, this is a reclamation success criteria set by the government of Alberta, stating "Reclaimed ecosystems display characteristics of resilience to natural disturbances" (Alberta Environment and Sustainable Resource Development, 2013). In our research, we found that trembling aspen growing on a reclamation site are capable of responding to a disturbance. 89% of the trees growing on the reclamation area responded to uniform stem cutting by producing either root suckers, stump sprouts, or both, which is a good indication of resilience. Aspen sprouting response was affected by tree size, competition, and soil type. Trees growing on PMM were 7.8 times more likely to produce at least one root sucker and produced significantly more root suckers compared to trees growing on FFMM. Taller trees were more likely to produce at least one root sucker and also tended to produce more suckers on average. High amounts of competition inhibited root sucker initiation and reduced sucker abundance, with vegetation cover greater than 52.5% performing poorly. Overall, aspen growing on this reclamation area showed resilience to disturbance.

Natural black spruce and aspen forests both showed resilience to wildfire. At this point in time, both stand types would be considered adequately re-stocked (Greene et al., 2002). Black spruce regeneration did not differ between bogs and semi-uplands. However, a significant amount of aspen regeneration was found in semi-upland forest habitat. This could indicate a shift in successional trajectory to deciduous-dominated forests, perhaps suggesting that semi-upland forests are less resilient compared to bogs. Black spruce regeneration rates were positively correlated to forb cover, suggesting more suitable seedbeds. Across both forest types charred organic matter, wet unburned organic matter, and deadwood were the most preferred seedbeds by black spruce. In aspen stands, fire severity did not have a significant effect on root suckering, while high amounts of forb and shrub cover significantly decreased amount of suckering. These results are similar to the results from chapter two, where higher amounts of competition reduced the probability of sucker initiation and decreased sucker abundance. These results allow for a better understanding of the early regeneration dynamics and potential successional trajectories after wildfire, useful for land reclamation and forest managers such as foresters.

Limitations

The overarching aim of this study was to attempt to compare resiliency of trembling aspen on reclaimed land and in natural forests. It is difficult, however, to compare aspen sprouting densities between reclamation and natural sites because natural sites measured regeneration of entire stands, where reclamation sites measured regeneration of single trees. Trees present in the natural stands were also much older and much larger compared to the trees growing on the reclamation area. Therefore, direct comparisons cannot be made. We did find, however, that seedling-origin aspen growing on reclaimed land was capable of responding to disturbance even without a large clonal root system that would have been found in a natural stand. These results are still promising for aspen growing on reclamation areas.

To experimentally determine resiliency of aspen on reclaimed land we mimicked fire by manually cutting down trees. As mentioned in chapter two, fire could produce very different results. On the one hand, aspen could perform better because competition would be removed. On the other hand, PMM consists of dry organic material and may be easily consumed by wildfire resulting in all sucker producing roots being lost. It is difficult to say what the outcome would be, and the true outcome will not be seen until a reclamation area inevitably burns.

The true resiliency of a reclamation project cannot be determined by the study of a single species. Many other factors make up ecosystems, such as soil, mycorrhizae, understory vegetation, and other tree species. Many future projects could be done to determine the resilience of these ecosystem variables on reclaimed land. Eventually, the resiliency of reclaimed land could be determined to some extent; however, it will never truly be known as our understanding of resiliency is still developing itself.

Future Work

Many future studies could stem from this research. As mentioned above, many other parts of reclaimed ecosystems need to be studied before resiliency of reclaimed land can be determined as a whole. Other ecosystem aspects, such as other tree species, understory vegetation, and soil, should be studied across a variety of reclamation areas to ensure consistent responses across different reclamation techniques. Better responses could indicate better reclamation practices as well. This process will take years to complete, but determining true reclamation resiliency will be very difficult without it.

Future work directly related to chapter two would include monitoring root sucker survival and vigor for a few years after the parent tree was cut. We currently know that a parent tree will respond to disturbance, however, we do not know if the sprouts produced will survive to adulthood. This is imperative information to know when determining the success of aspen sprouting on reclaimed lands. More work could also be done on environmental factors that affect sprouting, especially in regards to soil properties such as nutrients and temperature. These seem to be important factors for root suckering, but they are also understudied.

Additional research related to chapter three would include continued monitoring of the semi-upland black spruce stands to observe and understand any changes in successional trajectory. With a warming climate, fires are expected to become more frequent in the boreal potentially causing these early successional deciduous stands to be more prevalent on the landscape and thus provoking changes in the ways we currently manage our forests. It would be interesting to continue to monitor the aspen stands burned by low severity fires. These stands did not see complete overstory mortality and, therefore, may become uneven-aged stands. This would change the way we view stand structure after wildfire, as we currently assume stands in the boreal to be even-aged. Monitoring these stands for additional mature tree mortality would be useful to determine if they will truly become uneven-aged stands.

Implications

Understanding the resiliency of trembling aspen is an important first step in determining the resiliency of reclaimed ecosystems. Aspen are an important early successional species in the boreal forest, and their successful regeneration after disturbances can help kick-start other ecological processes, such as soil-plant nutrient cycles. Therefore, their success after disturbance is imperative for a successful ecosystem response. Understanding the factors that affect aspen spouting response is also important. We found that PMM is important for successful root suckering; therefore, PMM should be incorporated when constructing upland reclamation sites. We also found that competition levels of 52.5% or higher were detrimental to root suckering, so maintaining low competition levels after a disturbance on a reclamation area would facilitate a higher abundance of root suckers.

These results could also be used be land managers to increase the amount of aspen growing on a reclaimed area. Managers could intentionally cut down aspen in order to facilitate the growth of suckers and ultimately increase the number of aspen trees growing on the reclamation site. This could help initiate the typical clonal aspen root system that's found in natural forests. Clonal aspen stands have the potential to be more resilient to disturbances and poor growing conditions because they have the ability to share resources. This could be a useful tool for land mangers interested in increasing the stocking rate of aspen.

Results from our study on black spruce regeneration could also prove to be useful in land reclamation. We found that forest type did not affect black spruce regeneration after fire, but it did affect the amount of aspen regenerating. High amounts of aspen regeneration in previously pure black spruce forests could indicate a shift in successional trajectory to deciduous-dominated forests. Therefore, if black spruce forests are a goal of land reclamation, bog forests will likely be more successful in maintaining these tree species. We also found that black spruce preferred charred organic matter, wet unburned organic matter, and deadwood as seedbeds. This will be useful information when constructing lowland black spruce forests, as it will help ensure black spruce establishment and suitable early growth.

Literature Cited

Alberta Environment and Sustainable Resource Development (2013) Criteria and indicators framework for oil sands mine reclamation certification. Fort McMurray, p 27

Alberta Environment (2010) Guidelines for reclamation to forest vegetation in the Athabasca Oil Sands Region (2nd ed.). Fort McMurray, Alberta: Terrestrial Subgroup of the Reclamation Working Group of the Cumulative Environmental Management Association

Auclair AND (1983) The role of fire in lichen-dominated tundra and forest-tundra. In: Wein RW, MacLean DA (eds) The role of fire in northern circumpolar ecosystems. Scope 18, John Wiley & Sons, New York, 235–256

Bartos DL, Mueggler WF, Campbell RB Jr (1991) Regeneration of aspen by suckering on burned sites in western Wyoming. US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, p 14

Bella IE (1986) Logging practices and subsequent development of aspen stands in east-central Saskatvhewan. For Chron 62:81–83

Bergeron Y, Chen HYH, Kenkel NC, Leduc AL, Macdonald SE (2014) Boreal mixedwood stand dynamics: Ecological processes underlying multiple pathways. For Chron 90: 202–213

Black RA, Bliss LC (1980) Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecological Monographs 50:331–354

Brandt J P, Flannigan MD, Maynard DG, Thompson ID, Volney WJ (2013) An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environmental Review 2:207-226

Brown JK, Bebyle NV (1987) Fire damage, mortality, and suckering in aspen. Can J For Res 17:1100–1109

Bubier JL (1991) Patterns of *Picea mariana* (black spruce) growth and raised bog development in Victory Basin, Vermont. Bulletin of the Torrey Botanical Club 118:399–411

Chrosciewicz Z (1976) Burning for black spruce regeneration on a lowland cutover site in southeastern Manitoba. Can J For Res 6:179–186

Crawford RMM (1983) Root survival in flooded soils. In: Gore AJP (ed) Mires: Swamp, bog, fen, and moor. Vol. 4A. General studies, Elsevier, Amsterdam

de Groot WJ, Flannigan MD, Cantin AS (2012) Climate change impacts on future boreal fire regimes. For Ecol Manage 294:35–44

DeByle NV, Winokur RP (1985) Aspen: ecology and management in the Western United States. US Department of Agriculture, Forest Service, Fort Collins, p 283

DesRochers A, Lieffers VJ (2001) Root biomass of regenerating aspen (Populus tremuloides) stands of different densities in Alberta. Can J For Res 31:1012–1018

Downing DJ, Pettapiece WW (2006) Natural regions and subregions of Alberta. Natural Regions Committee, Government of Alberta, Edmonton, p 122

Eliasson L (1971) Growth regulators in *Populus tremula* IV. Apical dominance and suckering in young plants. Physiol Plant 25:263–267

Errington RC, Pinno BD (2016) Early successional plant community dynamics on a reclaimed oil sands mine in comparison with natural boreal forest communities. Écoscience 22:133–144

Farmer RE (1962) Aspen root sucker formation and apical dominance. For Sci 8:403–410

Foote JM (1983) Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. Res. Pap. PNW-307, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon

Fraser EC, Lieffers VJ, Landhäusser SM, Frey BR (2002) Soil nutrition and temperature as drivers of root suckering in trembling aspen. Can J For Res 32:1685–1691

Frey BR, Lieffers VJ, Landhäusser SM, Comeau PG, Greenway KJ (2003) An analysis of sucker regeneration of trembling aspen. Can J For Res 33:1169–1179

Government of Alberta (2012) Oil sands environmental management quick facts. Retrieved December 12, 2017

Greene DF, Johnson EA (1999) Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. Can J For Res 29: 462-473

Greene DF, Zasada JC, Sirois L, Kneeshaw D, Morin H, Charron I, Simard MJ (1999) A review of the regeneration dynamics of North American boreal forest tree species. Can J For Res 29:824-839

Greene DF, Kneeshaw DD, Messier C, Lieffers V, Cormier D, Doucet R, Coats KD, Groot A, Grover G, Calogeropoulos C (2002) Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). The Forestry Chronical 78:281–295

Harrell FE (2017) Rms: Regression Modelling Strategies. R package version 5.1-1

Heeney CJ, Kemperman JA, Brown G (1980) A silvicultural guide to the aspen working group in Ontario. Ontario Ministry of Natural Resources, Forest Research Branch, Toronto, p 47

Hély C, Bergeron Y, Flannigan MD (2000) Effects of stand composition on fire hazard in mixed-wood Canadian boreal forest. Journal of Vegetation Science 11:813–824

Hendershot WH, Lalande H, Duquette M, (2007) Soil reaction and exchangeable acidity. In: Carter MR, Gregorich EG (eds) Soil sampling and methods of analysis. 2nd ed. Chapter 16. CRC Press, Florida

Hicks RR Jr. (1972) The aspen rooting test: a new bioassay. For Sci 18:21–22

Hogg EH, Lieffers VJ (1991) The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. Can J For Res 21:387–394

Horton KW, Maini JS (1964) Aspen reproduction: its characteristics and control. Can Dep For, For Res Branch, Ottawa

Horton KW, Lees JC (1961) Black spruce in the foothills of Alberta. Tech. Note 110, Canadian Department of Forestry, Forest Research Branch, Ottawa, Ontario

Howell DM, Das Gupta S, Pinno BD, MacKenzie MD (2016) Reclaimed soils, fertilizer, and bioavailable nutrients: determining similarity with natural benchmarks over time. Can J Soil Sci 00:1–10

Huang S, Pinno B, Vassov R, Tomm B, Yang Y (2014) Estimating and monitoring the long-term growth and productivity of boreal forests on reclaimed oil sands sites: Preliminary results and future outlook. JSM Proceedings, Advances in Ecological Modeling, Section on Statistics and the Environment, 3902-3916

Hungerford RD (1988) Soil temperatures and suckering in burned and unburned aspen stands in Idaho. USDA For Serv Res

Ilisson T, Chen HYH (2009) Response of six boreal tree species to stand replacing fire and clearcutting. Ecosystems 12: 820-829

Jacobi WR, Kelly EF, Troendle CA, Angwin PA, Wettstein CA (1998) Environmental conditions and aspen regeneration failure. USDA Forest Service, Golden CO

Jelinski DE, Cheliak WM (1992) Genetic diversity and spatial subdivision of *Populus tremuloides* (Salicaceae) in a heterogeneous landscape. Am J Bot 79:728

Johnstone JF, Chapin III FS (2006) Fire interval effects on successional trajectory in boreal forests of northwest Canada. Ecosystems 9:268–277

Johnstone JF, Chapin III FS, Foote J, Kemmett S, Price K, Viereck L (2004) Decadal observations of tree regeneration following fire in boreal forests. Can J For Res 34:267–273

Johnstone JF, Hollingsworth TN, Chapin III FS (2008) A key for predicting postfire successional trajectories in black spruce stands of interior Alaska. General technical report PNW-GTR-767, United States Department of Agriculture, Forest Service, Pacific Northwest Research Station

Johnstone JF, Hollingsworth TN, Chapin III FS, Mack MC (2009) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forests. Global Change Biology 1–15

Keim RF, Chambers JL, Hughes MS, Dimov LD, Conner WH, Shaffer GP, Gardiner ES, Day JW (2006) Long-term success of stump sprouts in high-graded baldcypress-water tupelo swamps in the Mississippi delta. For Ecol Manag 234:24–33

Kemball KJ, Wang GG, Westwood AR (2006) Are mineral soils exposed by severe wildfire better seedbeds for conifer regeneration? Can J For Res 36:1943–1950

Key CH, Benson NC (2006) Landscape assessment: ground measure of severity, the composite burn index; and remote sensing of severity, the Normalized Burn Ratio. In: Lutes DC, Keane RE, Caratti JF, Key CH, Benson NC, Sutherland S, Gangi LJ (eds) *FIREMON:* Fire Effects Monitoring and Inventory System. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT. Gen. Tech. Rep. RMRS-GTR-164-CD: LA, pp. 1–51

King CM, Landhäusser SM (2018) Regeneration dynamics of planted seedling-origin aspen (*Populus tremuloides* Michx.). New For 49:215–229

Kochtubajda B, Brimelow J, Flannigan M, Morrow B, Greenhough MD (2017) The extreme 2016 wildfire in Fort McMurray, Alberta, Canada. Bulletin of the American Meteorological Society 7:176–177

Krasnow KD, Stephens SL (2015) Evolving paradigms of aspen ecology and management: impacts of stand condition and fire severity on vegetation dynamics. Ecosphere 6:1–16

Lacey ME, Dech JP (2012) Comparison of black spruce (*Picea mariana*) radial growth reduction in different soil moisture regimes during a spruce budworm (*Choristoneura fumiferana*) outbreak. Can J For Res 42:1410–1419

Lambers H, Atkin OK, Millenar FF (2002) Respiratory patterns in roots in relation to their functioning. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots, the hidden half. New York, pp 521–522

Landhäusser SM, Lieffers VJ (1998) Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Can J For Res 28:396–401

Landhäusser SM, Mulak TL, Lieffers VJ (2007) The effect of roots and litter of *Calamagrostis canadensis* on root sucker regeneration of *Populus tremuloides*. Forestry 80:481–488

Landhäusser SM, Deshaies D, Lieffers VJ (2010) Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. J Biogeogr 37:68–76

Landhäusser SM, Pinno BD, Mock KE (2019) Tamm Review: Seedling-based ecology, management, and restoration in aspen (*Populus tremuloides*). For Ecol Manage 432:231–245

Lieffers VJ, Rothwell RL (1987) Rooting of peatland black spruce and tamarack in relation to depth of water table. Can J Bot 65:817–821

Lloyd AH, Fastie CL, Eisen H (2007) Fire and substrate interact to control the northern range limit of black spruce (*Picea mariana*) in Alaska. Can J For Res 37:2480–2493

Lockhart BR, Chambers JL (2007) Cherrybark oak stump sprout survival and development five years following plantation thinning in the lower Mississippi alluvial valley, USA. New For 33:183–192

Macdonald SE, Quideau SA, Landhäusser SM (2012) Rebuilding boreal forest ecosystems after industrial disturbance. In: Vitt D, Bhatti J (eds) Restoration and reclamation of boreal ecosystems, attaining sustainable development. Cambridge University Press, Cambridge, pp 123–161

Mackenzie DD, Naeth MA (2010) The role of the forest soil propagule bank in assisted natural recovery after oil sands mining. Restor Ecol 18:418–427

Maini JS (1968) Silvics and ecology of *Populus* in Canada. In: Maini JS, Cayford JH (eds) Growth and utilization of poplar in Canada. Can. Dep. For. Rural Devel., For. Branch, Ottawa. Dep. Publ. 1205, pp 20-69

Mallik A, Kayes I (2018) Lichen mated seedbeds inhibit while moss dominated seedbeds facilitate black spruce (*Picea mariana*) seedling regeneration in post-fire boreal forest. For Ecol Manage 427:260–274

Maynard DG, Paré D, Thiffault E, Lafleur B, Hogg KE, Kishchuk B (2014) How do natural disturbances and human activities affect soils and tree nutrition and growth in the Canadian boreal forest? Environmental Review 22: 161-178

Mundell TL, Landha¨usser SM, Lieffers VJ (2008) Root carbohydrates and aspen regeneration in relation to season of harvest and machine traffic. For Ecol Manag 255:68–74

Naeth MA, Wilkinson SR, Mackenzie DD, Archibald HA, Powter CB (2013) Potential of LFH mineral soil mixes for reclamation of forested lands in Alberta. Oil Sands Research and Information Network, University of Alberta, School of Energy and the Environment, Edmonton, pp 64

Natural Resources Canada (2017) The state of Canada's forests - annual report 2017. In Government of Canada. Retrieved October 6, 2017

Perala DA (1984) How endemic injuries affect early growth of aspen suckers. Can J For Res 14:755–762

Peters VS, MacDonald SE, Dale MR (2005) The interaction between masting and fire is key to white spruce regeneration. Ecology 86:1744-1750

Peterson EB, Peterson NM (1992) Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces, Canada. Forestry Canada, Northern Forestry Centre, Edmonton, p 252

Peterson RL (1975) The initiation and development of root buds. In: Torrey JG, Clarkson DT (eds) The development and function of roots. Academic Press, New York, pp 125–161

Pinno BD, Errington RC (2015) Aspen seedling establishment on a reclaimed boreal oil sands site. Ecol Rest 33:43–50

Pinno BD, Errington RC, Thompson DK (2013) Young jack pine and high severity fire combine to create potentially expansive areas of understocked forest. Forest Ecology and Management 310: 517-522

Pinno BD, Errington RC (2015) Maximizing natural trembling aspen seedling establishment on a reclaimed boreal oil sands site. Ecological Restoration 33:43-50

Rowland SM, Prescott CE, Grayston SJ, Quideau SA, Bradfield GE (2009) Recreating a functioning forest soil in reclaimed oil sands in northern Alberta: an approach for measuring success in ecological restoration. J Environ Qual 38:1580–1590

Schier GA (1972) Apical dominance in multishoot cultures from aspen roots. For Sci 18:147–149

Schier GA, Smith AD (1979) Sucker regeneration in a Utah aspen clone after clearcutting, partial cutting, scarification and girdling. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, p 6

Schier GA, Zasada JC (1973) Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. Can J For Res 3:243–250

Schier GA, Jones JR, Winokur RP (1985) Vegetative regeneration. In: DeByle NV, Winokur RP (eds) Aspen: ecology and management in the western United States. USDA For Serv Gen Tech Rep RM-119, p 29–33

Shinneman DJ, Krasnow KD, McIlroy SK (2015) The role of fire in aspen ecology and restoration. WAA Brief 3

Soil Classification Working Group (1998) The Canadian System of Soil Classification. Agric and Agri-Food Can. Publ.

Stefani F, Isabel N, Morency M, Lamothe M, Nadeau S, Lachance D, Li EHY, Greer C, Yergeau E, Pinno B, Seguin A (2018) The impact of reconstructed soils following oil sands exploration on aspen and its associated belowground microbiome. Scientific reports 8:1–13

Steneker GA (1974) Factors affecting the suckering of trembling aspen. For Chron 50:32–34

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L., Skinner, W.R., 2002. Large forest fires in Canada, 1959–1997. J. Geophys. Res. 107, 1–12.

Thimann KV (1977) Hormone action in the whole life of plants. University of Massachusetts Press, Amherst

Thomas PA, Wein RW (1985) Delayed emergence of four conifer species on postfire seedbeds in eastern Canada. Can J For Res 15:727–729

Tredici PD (2001) Sprouting in temperate trees: a morphological and ecological review. The Bot Rev 67:121–140

Tremblay PY (2017) Effects of land reclamation practices on the productivity of young trembling aspen and white spruce on a reclaimed oil sands mining site in northern Alberta. Dissertation, University of Laval

Viglas JN, Brown CD, Johnstone JF (2013) Age and size effects on seed productivity of northern black spruce. Can J For Res 43:534–543

Wachowski J, Landhäusser SM, Lieffers VJ (2014) Depth of root placement, root size and carbon reserves determine reproduction success of aspen root segments. For Ecol and Manag 313: 83–90

Wan HY, Olson AC, Muncey KD, St. Clair SB (2014) Legacy effects of fire size and severity on forest regeneration, recruitment, and wildlife activity in aspen forests. For Ecol Manage 329:59–68

Wang GG (2003) Early regeneration and growth dynamics of *Populus tremuloides* suckers in relation to fire severity. Can J For Res 33:1998–2006

Weber MG, Flannigan MD (1997) Canadian boreal forest ecosystem structure and function in a changing climate: impacts on fire regimes. Environ Rev 5:145–166

Welham, C (2013) Factors Affecting Ecological Resilience of Reclaimed Oil Sands Uplands. Oil Sands Research and Information Network. Edmonton, Alberta: University of Alberta

Wheeler JA, Hermanutz L, Arino PM (2011) Feathermoss seedbeds facilitate black spruce seedling recruitment in the forest-tundra ecotone (Labrador, Canada). Oikos 120:1236–1271

Winton LL (1968) Plantlets from aspen tissue cultures. Sci 160:1234–1235

Wolter KE (1968) Root and shoot initiation in aspen callus cultures. Nat 219:509–510

Yan H, Zhan J, Zhang T (2011) Resilience of forest ecosystems and its influencing factors. Procedia Environmental Sciences 10:2201–2206

Yih K, Boucher DH, Vandermeer JH, Zamora N, (1991) Recovery of the rain forest of Southeastern Nicaragua after destruction by Hurricane Joan. Biotropica 23:106–113