

AGE EFFECTS ON SEED PRODUCTIVITY IN NORTHERN  
BLACK SPRUCE (*PICEA MARIANA*)

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By

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## ABSTRACT

Climate change is predicted to increase rates of fire activity in boreal forests. A shortened fire return interval may result in different outcomes of community structure in the northern boreal forest, since the age of a forest influences seed production and potential post-fire regeneration. With two closely timed fires, dominant boreal conifers such as black spruce (*Picea mariana*) may be vulnerable to regeneration failures after fire because of the long time required to reach reproductive maturity. I report on the relationship between stand age and seed productivity of black spruce in northern Yukon Territory and central Alaska. I used fire history maps to select sites of various stand ages, including stand ages that would occur in a short fire return interval (less than 80 years) versus longer fire intervals (up to 200 years). At each site, I measured stand density and basal area using the point-center-quarter method. Ten black spruce trees were randomly selected for cone surveys and age analysis. I also selected a subset of five trees for detailed analyses of cone and seed production within yearly cohorts. The results of this study illustrate the strong relationships between stand age and stand basal area with cone and seed production of northern black spruce. The resulting equations can be used to predict the seed capacity and regeneration potential of black spruce stands with known stand basal area or stand age. I estimate, along with the number of seeds required to produce a two year old black spruce seedling on high quality seedbeds, stands burned at an age less than 50 years will likely have reduced black spruce post-fire density. On low quality seedbeds, black spruce forests are more vulnerable to regeneration failures and fire cycles less than 150 years are likely to result in reduced recruitment. Under a shortened fire return interval these northern black spruce forests are likely to have reduced post-fire density.

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## 1.0 INTRODUCTION

### 1.1 Climate change and fire frequency in the northern boreal forest

Fire is the most common natural disturbance in the boreal forest of North America (Stocks et al. 2002). This disturbance is regulated by both biotic and abiotic factors (Paine and Levin 1981, Pickett and White 1985), including weather conditions, ignition agents, and fuel variability (Schoennagel et al. 2004). Of these contributing variables, weather conditions most strongly influence forest fires (Flannigan and Wotton 2001). Fuel moisture, lightning ignition, and wind action all influence the severity, intensity, and frequency of forest fires (Flannigan and Wotton 2001). Because fire activity reacts immediately to environmental conditions (Overpeck et al. 1990), we expect there to be shifts in the natural fire regime as a direct result of altered weather patterns associated with global climate change (Flannigan et al. 2005).

Fire weather conditions are evaluated using the Fire Weather Index (FWI), which integrates daily precipitation, humidity, temperature, and wind speed (Van Wagner 1987). Future weather conditions predicted under climate change are expected to increase the FWI for the western boreal forests of Canada (Flannigan et al. 1998, Parisien et al. 2005). Increases in extreme fire weather are predicted to cause increases in fire initiation (Price and Rind 1994, Krawchuk et al. 2008), intensity and spread of fires (Fried et al. 2004), length of the fire season (Wotton and Flannigan 1993), and annual area burned (Flannigan et al. 2005, Tymstra et al. 2007, Krawchuk et al. 2008, Balshi et al. 2009). These changes will likely lead to a shortened fire return interval for most of the North American boreal forest.

Boreal forests in northwestern North America are disturbed by fire cycles that typically occur about once every one hundred years (Yarie 1981, Viereck 1983). Patterns of post-fire regeneration often lead to the same species composition and distribution as the pre-fire stand

(Johnson 1992). These stable patterns of forest composition have been typical of the northern boreal forest for many centuries (Lynch et al. 2002, Tinner et al. 2008). However, paleoecological records indicate that stable species configurations were disrupted by rapid changes in the fire cycle leading to new stable configurations (Lynch et al. 2002, Tinner et al. 2008). Currently, the fire cycle of the northern boreal forest is changing to a disturbance regime with higher a frequency and longer season of disturbance, and more annual area burned (Flannigan et al. 2005, Tymstra et al. 2007, Krawchuk et al. 2008, Balshi et al. 2009). These changes may disrupt the current stable-species configuration, resulting in different community structure in northern boreal forests (Paine et al. 1998, Johnstone and Chapin 2006b). Therefore, in order to predict changes to species composition it is essential to understand the processes that maintain these stable cycles in the northern boreal forest.

## **1.2 Black spruce biology**

Black spruce (*Picea mariana* (Mill.) B.S.P.) forests are the dominant cover type in the north-western boreal forest, extending over 40% of the forest in interior Alaska and northern Yukon Territory (Van Cleve et al. 1983). Cone serotiny and aerial seedbanks are the main regulators of post-fire regeneration in these black spruce forests (Zasada et al. 1992). Cone production, or yearly cone cohorts, accumulate in the canopy allowing for many years of cone production to be present at one time (Zasada et al. 1992, Greene and Johnson 1999). In addition, black spruce cones are semi-serotinous, which means that resin seals the cone scales closed, keeping seed locked inside (Zasada et al. 1992). This is an adaptation to fire because the heat melts the resin, which allows for large quantities of seed to be released immediately after fire (Cameron 1953, Zasada et al. 1992). In the absence of fire, the resin slowly breaks down and the cone scales open, releasing small amounts of seed over time (Zasada et al. 1992, Atkinson and

Haavisto 1996, Greene and Johnson 1999). The amount of seed released immediately after fire is 1.5 times greater than the amount of seed released in a nearby unburned stand (Viereck 1979). Half of the available seed in a stand is released in the first 60 days after a fire (Wilton 1963). Within one to two years after a fire, the seed rain is equivalent to the seed rain in unburned stands (Zasada and Norum 1983). Serotiny and aerial seedbanks allow for a large amount of seed to be dispersed immediately after fire, an adaptation that is an important driver for the success of black spruce in areas of high fire frequency (Johnson 1992, Zasada et al. 1992).

In addition to cone serotiny and aerial seedbanks, environmental conditions are important drivers of stable successional cycles (Johnstone et al. 2010a). Black spruce stands have thick organic layers, ranging from ~7 to 40 cm deep in upland forests (Hollingsworth et al. 2006) to meters deep in bogs and fens (Vitt et al. 2000). Soil organic layers are strongly linked to higher levels of moisture (Van Cleve and Viereck 1981) because of the hydraulic properties of the moss layer and the slow decomposition rates (Fenton et al. 2005). These properties create cool, moist, and organic-dominated soils characteristic of black spruce forests (Fenton et al. 2005). Following fire, these forest floors are usually partially combusted, leaving a poor seedbed of high porosity and dark color that puts small seedlings at a high risk of desiccation (Johnstone and Chapin 2006a). The large amount of seed released by black spruce after fire ensures that some seeds will find favorable microsites for regeneration and survival (Viereck 1983). Additionally, black spruce seeds are larger and provide a greater carbohydrate reserve when compared to small seeded species, such as broadleaf trees (Viereck 1983). Even though black spruce seed size is comparable to other conifers, such as white spruce (Leadem et al. 1997), the abundant seed rain after fire ensures black spruce will have high rates of seedling germination and establishment. Consequently, the production of aerial seedbanks is critical to ensuring that black spruce is able

to regenerate under a range of fire severities and rapidly recolonize a stand during the initial phases of post-fire regeneration (Greene and Johnson 1999, Johnstone and Chapin 2006a).

### **1.3 Factors influencing cone and seed production**

Natural seed production is influenced by many factors, but particularly by those related to tree and stand attributes (Leadem et al. 1997). Stand and tree characteristics such as density, spatial arrangement of trees, tree age, tree height, diameter at breast height (dbh), basal area, animal herbivory, and health of tree crowns, can directly influence the natural seed production at both the individual and stand level (Leadem et al. 1997). Relationships between basal area and seed productivity have been established for black spruce in central Saskatchewan and Quebec (Greene and Johnson 1999). Seed productivity of black spruce has also been linked to canopy position and stand density (Atkinson and Haavisto 1996, Greene and Johnson 1999).

Additionally, cool temperatures may limit the production of mature seeds in conifer forests and this becomes more acute with increasing latitude and elevation (Zasada and Grigal 1978, Henttonen et al. 1986, Zasada 1988, Sirois 2000).

Seed production and the age that black spruce trees become reproductively mature, varies across latitudinal gradients. In the southern boreal forest, black spruce starts producing cones at 15 years old (Fowells 1965, Schopmeyer 1974). In Finland, black spruce produces consistent cone crops between the ages of 25 and 50 (Koski and Tallquist 1978). Black and Bliss (1980) found that black spruce near its northern Canadian limit were reproductively mature between the ages of 25 and 30 years, and were reliably producing cone crops at approximately 85 years old. Johnson and Greene (1999) found that 50 – 100 year old black spruce stands in central Saskatchewan and Quebec hold about 4.5 million viable seeds per hectare at one time. Black and Bliss (1980) estimated that northern black spruce stands peak in seed production between the

ages of 100 – 200 years old producing 132,000 seeds per hectare. Their estimates decreased for younger and older stands producing 69,000 and 60,000 seeds per hectare, respectively (Black and Bliss 1980). The age at which black spruce of central Alaska and Yukon Territory are sexually mature is uncertain. Additionally, the age where the aerial seedbank has become depleted due to lower productivity levels in older stands is suggested to decline around 200 years old (Black and Bliss 1980).

Although black spruce forests maintain a stable regeneration cycle with a fire return interval of about 100 years, compound disturbances, such as a two closely timed fires, could interrupt the equilibrium of these northern forests (Johnstone et al. 2010). With repeat disturbances, black spruce stands may be burned at an age where they are not reproductively mature. Johnstone and Chapin (2006) have shown that a shortened burn interval (less than 30 years) results in a low level of post-fire conifer recruitment, even though the pre-fire stands were dominated by conifers. Furthermore, other compound disturbances, such as budworm outbreaks followed by fire, have similar results of reduced conifer recruitment (Payette et al. 2000). The decline in black spruce recruitment after a short fire interval is associated with a low seed production in the recently disturbed black spruce stands (Payette et al. 2000, Johnstone and Chapin 2006b). This suggests that the potential regeneration of black spruce after disturbance strongly depends on the amount of seed stored in the aerial seedbank (Payette et al. 2000, Johnstone and Chapin 2006b). Low amounts of seed produced by a stand prior to burning could lead to shifts in successional trajectories from self-replacing black spruce stands to small seeded and wind dispersed species after burning (Johnstone and Chapin 2006b). Therefore, a shortened fire return interval could interrupt black spruce forests that have evolved with historical fire intervals of 100 years and have maintained self-replacement equilibrium for many generations.

Understanding the properties that influence cone and seed production will help to predict the changes in post-fire regeneration of northern black spruce forests likely to occur under an altered fire regime.

#### **1.4 Project objectives**

The main objective of this project is to assess how the size of the seed bank and thus available post-fire seed may change with stand age. I tested the hypothesis that seed production, and therefore regeneration potential, was not independent of tree or stand age. Data from this study will help to fill the knowledge gaps surrounding the reproductive cycle of northern black spruce, which include: (1) age of sexual maturity, (2) age of consistent cone production, (3) age of seed production peak, and (4) age of seed production decline. I investigated the best predictor of cone/seed production at the stand level using three different stand traits: tree basal area per hectare, mean tree age, and oldest tree age. I also assessed the relationship between cone production and site characteristics to identify additional drivers of cone production. Seed quality and quantity were compared among cohorts (2008, 2007, and 2006+ cone cohorts), to test the relative importance of each yearly cohort to the overall seed capacity of the stand. Furthermore, by using existing literature on seedling survival (Johnstone and Chapin 2006a), I estimated a minimum density of seeds required to achieve a target (self-replacement) seedling density. In addition, I was able to estimate the range of fire return intervals where post-fire recruitment may be limited by seed availability.

## 2.0 METHODS

### 2.1 Study area description

I sampled study sites in black spruce forests of northern Yukon Territory, Canada and interior Alaska, United States (Figure 1). These areas are part of the Taiga Cordillera ecozone, which is the northern part of the boreal forest (Yukon Ecoregions Working Group (YEWG) 2004). The region has short, cool summers and long, cold winters. The mean annual temperature ranges from  $-10^{\circ}\text{C}$  at the northern limit ( $\sim 68^{\circ}\text{N}$ ) to  $-4.5^{\circ}\text{C}$  at the southern limit ( $\sim 61^{\circ}\text{N}$ ). Snow and ice cover the region for up to eight months of the year (YEWG 2004). Mean annual precipitation is low, ranging from 250 – 500 mm/year. The zone is dominated by low density, slow growing, black spruce forest. The region has widespread permafrost and a shallow drainage system, which has Cryosolic, Gleysolic, and Organic soils (YEWG 2004).

### 2.2 Field sampling

Sampling took place from June 17 – July 11, 2009. This was at the beginning of the growing season, which allowed measurements to be taken on the previous three years of cone production, as well as the current year's immature cohort. June sampling is practical for measuring the previous year's cone crop, since the previous year's seeds have had enough time to mature, but are still maintained in the cones (C. Brown, unpublished data). Annual cohorts of cones were differentiated on the basis of cone color and canopy placement (Eremko et al. 1989). A short time period for sampling was desirable to avoid or minimize biases associated with cones aging over the growing season.

I used fire history maps of Yukon Territory and Alaska to locate fire perimeters dating back to the 1940s with road access into the fire perimeters. I sampled a total of 30 sites, 20 in central Alaska and 10 in northern Yukon Territory. Each site was a distinct fire scar or



population. I selected sites based on the following criteria: at least 80% black spruce stem density, *Sphagnum* and/or feathermoss (*Hylocomium* and/or *Pleurozium*) dominated understory, and mesic moisture conditions. Sixteen sites were selected based on the fire history maps and eight sites were chosen based on known estimates of the stand ages (Hollingsworth et al. 2006, C. Brown, unpublished data). The remaining six sites were selected to maximize geographic and stand age dispersion.

A buffer zone of at least 100 m was left between the road and the study sites. To ensure random selection of a start point in all sites a random distance between 1 and 100 m was added to the 100 m buffer zone. This was the sampling start point, from which a random bearing (oriented away from the road) was used as the direction of the sampling transect.

I used the point centre quarter method (PCQ) (Mueller-Dombois 1985) to measure tree density (stems per hectare) and total basal area per hectare. I established a 100 m transect at each site, with five points at 25 m intervals used as sampling centers (Figure 2). At each of the five points, I measured the distance to the nearest tree in each of the four cardinal azimuths (N, S, E, and W). When black spruce was not the nearest tree, measurements were taken on the closest tree specimen and on the nearest black spruce tree. This allowed for both total stand density and also black spruce density to be calculated. Ten black spruce trees (two trees per point) were randomly selected to be sectioned at the ground level for stem disk collection and exact cone counts (Figure 2). Of those ten trees, five (one per point) were randomly selected for cone collection (Figure 2).

A general site classification and description was done for each site. The classification of community type was based on the dominance of indicator plants in the forest understory and on mineral soil pH (Hollingsworth et al. 2006). In addition to the community classification, soil

organic layer depth, mineral soil texture, thaw layer depth, slope, aspect, and latitude and longitude coordinates were measured at each of the sites. Soil pH and organic layer depth were measured at three of the PCQ points (end and center points). Organic layer depth was measured by excavating a small plug of soil from the ground with a serrated knife and recording the distance from the top of the mineral horizon to the top of the moss layer. A small amount of mineral soil collected from the first 2 cm of the mineral horizon was saturated in distilled water to measure pH. A pH meter was used for these measurements and pH indicator strips (VWR International, West Chester, PA) were used to verify the meter readings at a minimum of one site per day. Mineral soil texture was determined in the field by hand texturing the uppermost mineral horizon and followed the Canadian System of Soil Classification (Canada Soil Survey Committee 1978). At each of the five PCQ points, thaw layer depth was measured. A metal probe with 5 cm increments was inserted into the soil layer to measure the distance from the top of the permafrost to the top of the moss layer. I measured slope with an inclinometer and aspect with a compass, while elevation and geographic coordinates were measured at the center point of the sampling transect with a hand held GPS (Garmin).

### *2.2.1 Cone and tree sampling*

Cones were sampled separately in four cohorts, representing different years of production. As cones mature, they lose moisture and change color from a purplish-green to brown to grey (Eremko et al. 1989). Therefore, I used color as an indicator to distinguish the cohorts, with bright purple = 2009 cohort, brownish-purple = 2008 cohort, brown = 2007 cohort, and brownish grey or grey = 2006 or older. Where there was difficulty in distinguishing cone cohorts based on color, I used canopy placement to establish the relative order of production.

Due to practical considerations, cone counts were obtained using slightly different methods for large and small trees. For large trees, cones in each cohort were counted using binoculars from the ground on one side of the tree. These estimates were then multiplied by two to account for both sides of the tree. The 2008 and 2007 cohorts were not clearly distinguished while using the binoculars, and therefore were grouped together. Also for large trees, a quick total estimate of the entire cone crop was recorded. These estimates were compared to the exact cone counts from felled trees to assess the error associated with visually estimating the number of cones present on standing black spruce trees. For small trees, we were able to count all of the cones by bending the top of the tree down and counting cones from all sides of the tree.

Exact cone counts and estimates of tree age were obtained from the ten trees felled for stem disk collection. Of these, five trees were randomly selected for collection of a sub-sample of 20 cones from each cohort on each tree. If there were fewer than 20 available cones in a cohort then all of the cones in that cohort were collected. For some of the older cohorts there were both open and closed cones, and samples were inclusive of both types. Since the current year's cones (2009) were not mature, the 2009 cones were counted, but not collected. Stem disks for determining tree age were collected from just above the moss layer or as close to the top of the soil as possible and the entire stem disk was collected. The distance from the ground level, or where the stem disk was collected, to the root collar was measured. The root collar was determined by removing the moss layer until the bottom of the main stem was found, which was considered to be the general region of the root collar.

## **2.3 Lab analysis**

### *2.3.1 Cones*

Black spruce cones are semi-serotinous in nature and require heat for seed release. To simulate fire conditions, we used the following protocol to remove the seeds from the cones under lab conditions (Leadem et al. 1997, Green, S., personal communication). First, the cones were soaked in hot tap water for 24 hours, then they were air dried for 24 hours, and finally heated in an oven at 60°C for 16 hours. The cones started to open up after the first repetition of the protocol. The cones were then agitated in a container to release the seeds. This seed extraction procedure was repeated for each group of 20 cones per cohort until most of the seeds had fallen out. Cones were examined at the end of each cycle to see how many seeds were left in the cones. If there was a large proportion (more than 10) of scales unopened and seeds still remaining in the cones, cycles of the seed extraction procedure was continued until there was a small number or no seeds left in the cones. I assumed that all of the seeds that would have been released in a natural fire would have been released after each sample had undergone its required number of seed extraction cycles (repeated until there were few seeds left in the cones). I can make this assumption, since black spruce cones usually have a small number of seeds remaining in the cones even up to 20 years after a fire (Wein 1975).

### *2.3.2 Seed viability and germination trials*

Seeds from each tree and cohort sample were counted by hand. Additionally, a germination test was performed on a random sub-sample of 0.100 g of seed (~100 seeds) for every seed sample. Germination of seeds can be up to 10 – 20% lower than the proportion of filled seeds determined by a cutting test or alcohol floatation test (Safford 1974). Furthermore, seed viability tests including hydrogen peroxide tests and cutting tests are very laborious and often underestimate the true viability or germination potential of seed samples (Leadem et al.

1997). By performing germination trials the actual germination potential of the different seed cohorts was captured and the test was simple enough to test all of the seed samples in a timely manner. Seeds were placed on filter paper in petri dishes and kept moist with deionized water for one month. All samples were placed in a lab at a room temperature setting ( $\sim 20^{\circ}$  C) with 20 hours of growing light provided by artificial and natural lighting. A seed was considered germinated once the hypocotyl was twice the length of the seed (Leadem et al. 1997).

### *2.3.3 Tree age determination*

Tree disks were air dried and processed through a band saw to create a level working plane. All stem disks were sanded using 50 grit paper on a stationary belt sander followed by 80, 120, 220, 320 and 400 grit paper, where the last two were sanded by hand. Sections with very faint growth rings were also sanded with 600 grit paper. By sanding the stem disks with progressively finer paper I was able to obtain a smooth finish with visible growth rings (Stokes 1968, Schweingruber 1988). Once prepared, stem disks were scanned using the WinDENDRO software program (WinDENDRO, Regent Instruments Inc. 2008). I determined tree age by counting the number of all visible growth rings. Each disk was aged twice with two radii that extended from the pith to the bark. Radii were oriented at least  $90^{\circ}$  apart in order to try and capture all of the rings present.

In order to analyze the sites at a stand level, an age estimate for each stand is required. Often the oldest tree of a stand is taken as the stand age (or number of years since fire). Cross-dating of belowground stems to aboveground stems are methods used to find missing rings and to achieve a precise age estimate (Cook and Kairiukstis 1990). However, there can be up to 20 missing rings in ground age estimates in northern black spruce (DesRochers and Gagnon 1997). Discontinuous rings, narrow rings, missing rings, adventitious roots, and a taper of growth rings

from the ground level down to the root collar region, all contribute to the age underestimation of black spruce (DesRochers and Gagnon 1997). Therefore, cross-dating of black spruce stems can be tedious and complex, and may be inconclusive of the actual age. For trees that are older than 100 years, the number of very tight rings, partially formed rings, and reaction wood increases, making cross-dating even more difficult. Furthermore, to maximize the effectiveness of cross-dating, ground level stem disks should be cross-dated against underground stem disks, which were not collected for this study. Because of these difficulties, I did not attempt to perform cross-dating of black spruce stems and assumed that annual ring counts provided a minimum age estimate for the tree.

## **2.4 Data analysis**

### *2.4.1 Seed and viable seed calculations*

Derived cone, seed, and viable seed calculations on the individual level and the stand level were calculated by using the cone and seed information from all the sampled cone cohorts. For every cohort sample the total number of seeds was divided by the number of cones in the sample to get the number of seeds per cone:

$$A_{ij} = B_{ij}/c_{ij} \quad [1]$$

where  $A_{ij}$  is the number of seeds per cone for the  $j^{\text{th}}$  cohort of the  $i^{\text{th}}$  tree,  $B_{ij}$  is the number of seeds per cohort of the collected sample, and  $c_{ij}$  is the number of cones of the collected sample. The number of seeds per cone was then multiplied by the number of cones for that cohort resulting in a number of seeds per cohort:

$$S_{ij} = A_{ij}(C_{ij}) \quad [2]$$

where  $S_{ij}$  is the number of seeds per cohort  $j$  on the  $i^{\text{th}}$  tree and  $C_{ij}$  is the number of cones in the  $j^{\text{th}}$  cohort of the  $i^{\text{th}}$  tree. The number of seeds per cohort was then totalled within an individual tree to give the number of seeds per tree:

$$S_T = \sum S_{ij} \quad [3]$$

where  $S_T$  is the number of seeds per tree and  $S_{ij}$  is the number of seeds for the  $j^{\text{th}}$  cohort of the  $i^{\text{th}}$  tree. To calculate the number of viable seeds per tree, the proportion of viable seeds was multiplied by the number of seeds per cohort, for each cohort, and then was totalled across cohorts for each individual tree:

$$V_{ij} = S_{ij}(G_{ij}) \quad [4]$$

$$V_T = \sum V_{ij} \quad [5]$$

where  $V_{ij}$  is the number of viable seeds for the  $j^{\text{th}}$  cohort of the  $i^{\text{th}}$  tree,  $S_{ij}$  is the number of seeds for the  $j^{\text{th}}$  cohort of the  $i^{\text{th}}$  tree,  $G_{ij}$  is the proportion of viable seeds for the  $j^{\text{th}}$  cohort of the  $i^{\text{th}}$  tree, and  $V_T$  is the total number of viable seeds per tree. To arrive at the number of seeds or viable seeds per hectare, the number of cones per cohort was averaged across sampled trees within a site:

$$\overline{C}_{jl} = C_{ij}/k_l \quad [6]$$

where  $\overline{C}_{jl}$  is the average number of cones for the  $j^{\text{th}}$  cohort in the  $l^{\text{th}}$  stand and  $k$  is the number of samples in the  $l^{\text{th}}$  site. Then the average number of seeds per cone was multiplied by the average number of cones per cohort, for each cohort. This was then summed across all three cohorts to get the average number of seeds per tree:

$$\overline{S}_{jl} = (\sum A_{ij})/k_l \quad [7]$$

$$\overline{S}_l = \overline{S}_{1l}(\overline{C}_{1l}) + \overline{S}_{2l}(\overline{C}_{2l}) + \overline{S}_{3l}(\overline{C}_{3l}) \quad [8]$$

where  $\bar{S}_{jl}$  is the average number of seeds per cone for the  $j^{\text{th}}$  cohort in the  $l^{\text{th}}$  site,  $A_{ij}$  is the number of seeds per cone for the  $j^{\text{th}}$  cohort of the  $i^{\text{th}}$  tree,  $k$  is the number of samples in the  $l^{\text{th}}$  site, and  $\bar{S}_{1l}(C_{1l})$  is the multiplication of the number of seeds per cone and the number of cones per cohort, which was summed across all three cohorts to give an average number of seeds per tree,  $\bar{S}_l$ . The average number of seeds per tree was then multiplied by the stand density (stems/ha) to arrive at the number of seeds per hectare, which was divided by 10,000  $\text{m}^2$  to get the number of seeds/ $\text{m}^2$ :

$$S_l = \bar{S}_l(D_l). \quad [9]$$

The number of viable seeds was calculated a similar way, but with an extra step of multiplying the average proportion of viable seeds per cohort by the average number of seeds per cohort:

$$\bar{V}_l = \bar{G}_{1l}(\bar{S}_{1l}) + \bar{G}_{2l}(\bar{S}_{2l}) + \bar{G}_{3l}(\bar{S}_{3l}) \quad [10]$$

where  $\bar{V}_l$  is the average number of viable seeds per tree in the  $l^{\text{th}}$  site and  $\bar{G}_{1l}(\bar{S}_{1l})$  is the multiplication of the average proportion of viable seeds and the average number of seeds per cohort and is then totaled across all three cohorts. This was then multiplied by the stand density (stem/ha) to get the number of viable seeds per hectare, which was then divided by 10,000  $\text{m}^2$  to get the number of viable seeds per  $\text{m}^2$ :

$$V_l = \bar{V}_l(D_l). \quad [11]$$

#### 2.4.2 Bivariate relationships of cone and seed production

The data set presented here consisted of counts with a large proportion of zeros, which exhibited both non-normality of error terms, as well as heteroscedasticity (variance increases linearly with mean; Figures 3 and 4). Classical linear regression models have limited use for modelling count data. These approaches assume that the data being analyzed have constant variance (homoscedastic) and that the error terms are normally distributed. With count,



proportion, and binary response variables these assumptions are rarely satisfied (Crawley 2007). Ecologists have dealt with these issues by transforming the response variable or by using a non-parametric method. Once the data are transformed, then the linear model assumptions are often satisfied and a linear model can be used (Crawley 2007).

In order to include all of the data in the analysis, I performed a two-stage analysis, first modelling zeros and ones, then modelling values greater than zero. The data inclusive of both zeros and ones were based on presence or absence of cones and seeds. A generalized linear model fitted with a binomial error distribution and a logit link was used to assess this relationship. This model takes into account that the data are strictly bounded (0 – 1), the variance is not constant, and the error terms are non-normal (Crawley 2007). To assess the relationship between stand mean age and the proportion of trees with cones, I also used a binomial error distribution and a logit link function. However, the data was not separated into zeros and ones, but had the proportion of trees with cones for each site as the response variable. I could then determine the expected proportion of trees producing cones in a stand for a given stand mean age.

I  $\log_{10}$ -transformed the remaining non-zero values for individual trees. Once the data were transformed and assessed for normality and homoscedasticity (Figure 5), then a linear model was used to model the bivariate relationships for the tree-level data. The stand level data were not zero inflated, as there were only four zero values for viable seeds and three for cone and seed densities. Therefore, zeros were included in the linear regression models of stand-level data. I added a constant value (the minimum value from the response variable data set) to all of the response values prior to the  $\log_{10}$ -transformation. Given that a value of one would have been very large in the data sets, the minimum value was used to avoid changing the underlying

relationships. For the remaining bivariate relationships zeros were included and the smallest values of the data set were added to all values prior to transformation and regression.

#### *2.4.3 Reproductive output across cone cohorts*

The data set for this analysis consisted of count data and proportion data. In order to assess these data, contingency tables were used. A Pearson's  $\chi^2$  test was used to investigate if there were significant differences between the three separate cohorts in the number of cones, number of seeds per cone, and the proportion of viable seeds. Pearson's Chi-squared test uses contingency tables to compare the observed frequencies to expected frequencies and is an appropriate test for count and proportion data (Crawley 2007). A  $\chi^2$  distribution is used for the test statistic (Crawley 2007). The test was used to detect a difference among all three cohorts for each variable under investigation, as well as for pairwise comparisons between the different cohorts.

#### *2.4.4 Multiple regression using site characteristics as predictors of cone production*

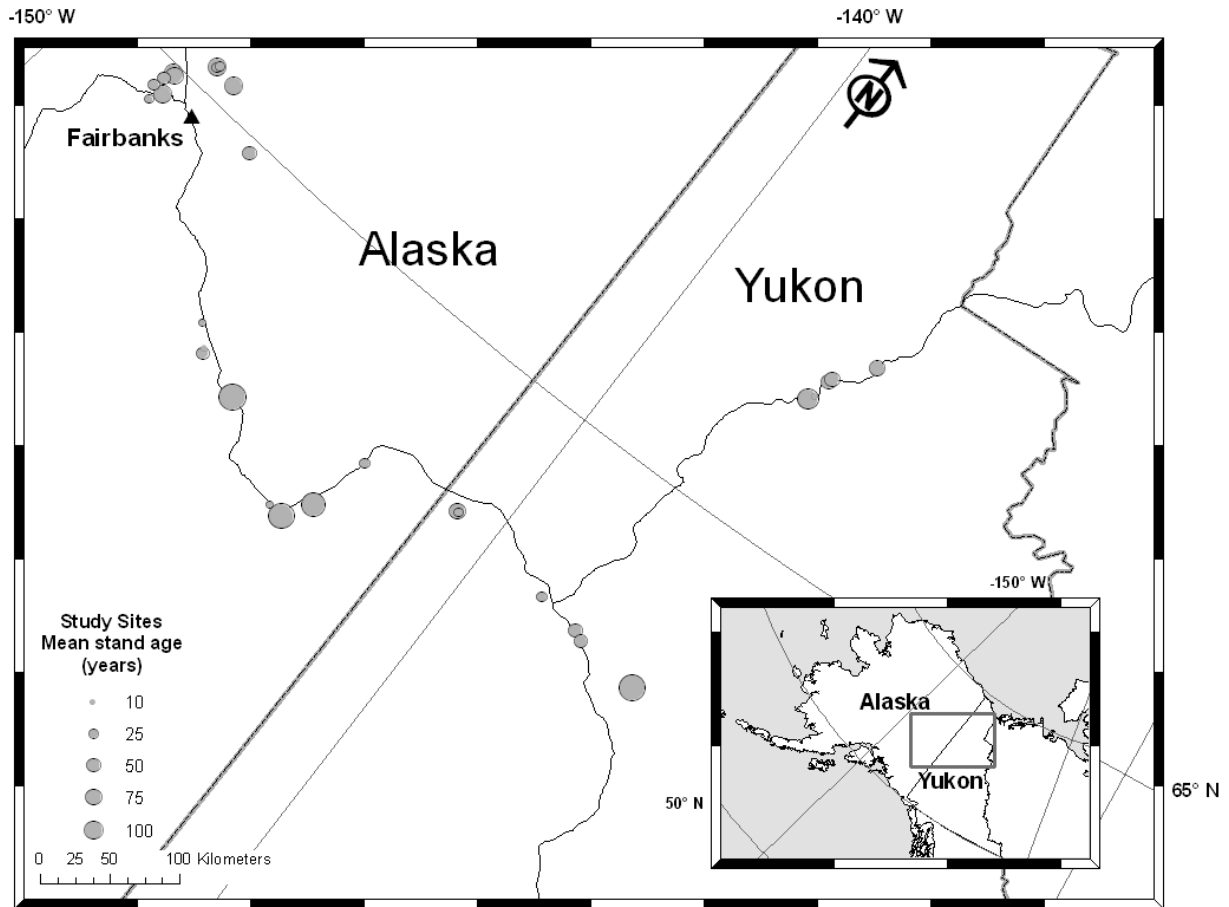
I used a multiple linear regression model to analyze the effect that the site environmental characteristics had on cone production. Because stand mean age and basal area per hectare were highly correlated, two separate multiple regression analyses were performed which each included one of these variables. Soil organic layer depth was also highly correlated with basal area per hectare and stand mean age. In order to test whether organic layer depth modifies the basal area-cone production and stand mean age-cone production relationships I used age-corrected variations in soil organic layer. To get age-corrected soil organic layer depth, I used the residuals from the stand age-soil organic layer depth regression. Some of the environmental variables that were collected in the field are largely driven by stand age. For example, I expect that increases in stand mean age would result in increases in soil organic layer, and decreases in soil pH and

active layer depth. Therefore, I examined if there was collinearity among the environmental variables prior to the multiple regression analyses. As expected there was collinearity between active layer depth and soil organic layer. I chose to use the age-corrected soil organic layer instead of active layer depth in both of the multiple regressions. There was no correlation among the remaining predictor variables, which included soil pH, stand density, elevation, and slope.

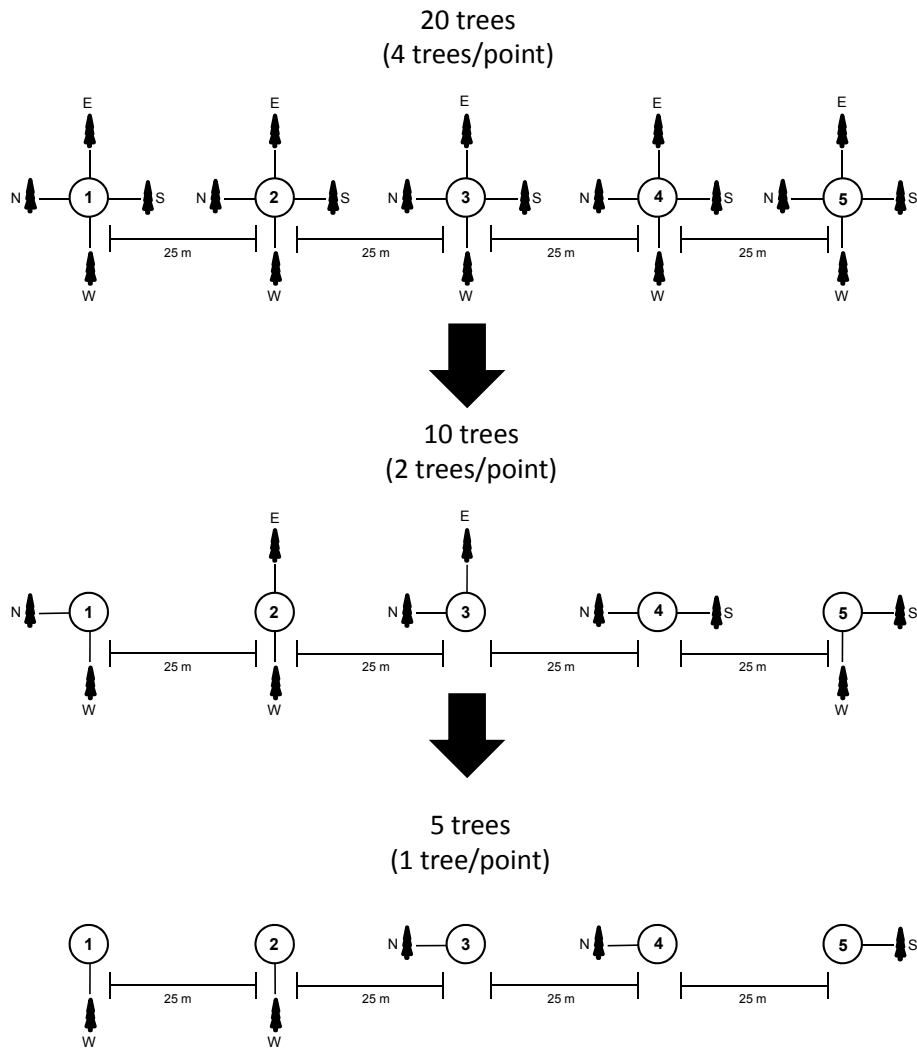
I used the multiple regression analysis as an analytical approach to find the best predictor variables of cone production. I followed the Principle of Parsimony, which means that the model should be in its simplest form (Crawley 2007). The simplest models are those that have the fewest parameters and account for the most variance. To avoid overparameterization, I had less than  $n/3$  parameters in each model (Crawley 2007). All six explanatory variables were included in the linear model and I randomly selected four two-way interaction terms to be added until I had gone through all the interaction terms. All significant interaction terms were then put back into the model with the main effect variables and then removed if they were no longer significant. The non-significant explanatory variables were then removed. I used stepwise regression where each variable was analyzed in each step of the models and were removed or added back depending on significance. In order to determine the best model I used Akaike's Information Criteria (AIC), which measures the goodness of fit and model complexity (Zuur et al. 2009). The lower the AIC value the better the model fits the data (Zuur et al. 2009). Non-significant explanatory variables were kept in the models to have the smallest AIC values.

#### *2.4.5 Comparison of generated equations across studies and regions*

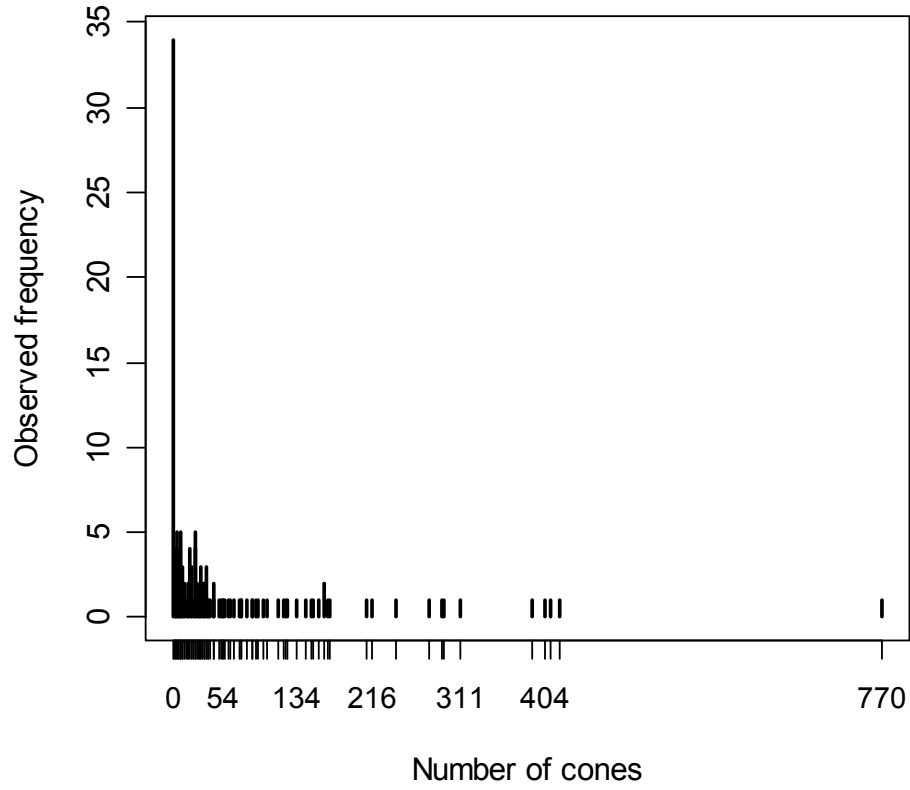
Greene and Johnson (1999) developed an equation that predicts seeds (seeds/m<sup>2</sup>) based on dimensionless basal area (area/area). This equation is directly comparable to the basal area-viable seed relationship from this study. Given that both of these equations predict values without error, small differences in coefficients between equations would likely lead to significantly different predictions. I used my model coefficients and the associated standard errors to examine if Greene and Johnson's (1999) equation would predict similar seed production values with given basal areas. If the coefficients from Greene and Johnson's (1999) equation fell within the standard error limits from my generated equation then they were considered to not be significantly different. However, if the values were outside the standard error limits then the equations were considered to be significantly different.

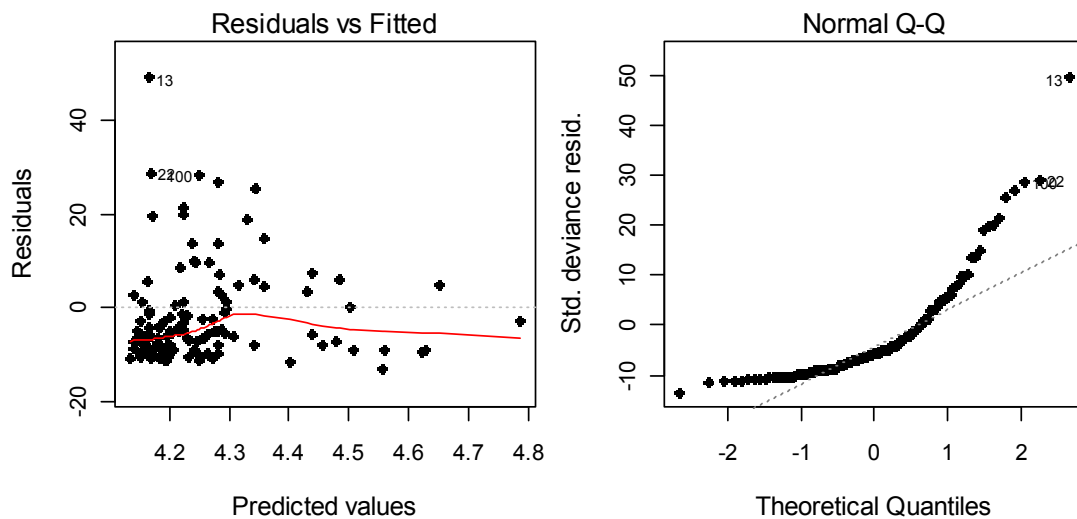


**Figure 1:** Map of the study sites located in Yukon Territory, Canada and Alaska, USA. Insert shows the larger region of the study area. Grey circles represent study sites, where the size of the circle corresponds to the stand mean age illustrated in the legend. The solid black lines represent highways and the dotted grey lines represent the border between Yukon Territory and Alaska.



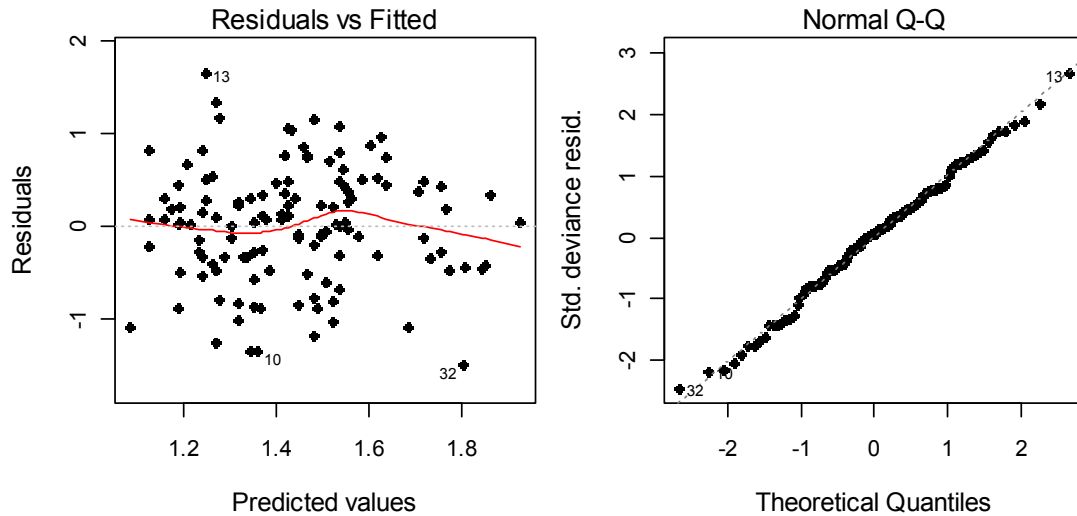
**Figure 2:** Diagram of sampling scheme used to select trees at each site. Tree sub-samples are indicated for example only, as the exact tree locations varied by site according to the random selection procedure. The first sampling scheme was used for stand density, cone estimates, and basal area measurements (top,  $n = 20$ ). The second sampling scheme was used for tree disk collection and exact cone counts separated into cohorts (middle;  $n = 10$ ). The last sampling scheme of five trees was used for cone collection (bottom;  $n = 5$ ).





**Figure 4:** Diagnostic plots for examining model residuals and estimating model fit of the tree age-cone production relationship. The left panel shows a plot of standardized residuals and fitted values of the raw data from the analysis of the effects of tree age on number of cones per tree. The expected distribution when the model meets its underlying assumptions is to have even scatter of points, with no apparent pattern. The plot indicates that there is heteroscedasticity of the data. The right panel shows a Q-Q (quantile-quantile) plot where the sample values were ranked and plotted as dots and numbers generated from a normal distribution are plotted as the line. Because the sample points are skewing from the line it shows that the data are non-normal.





**Figure 5:** Diagnostic plots for examining model residuals and estimating model fit of the  $\log_{10}$ -transformed tree age-cone production relationship. The left panel shows a plot of standardized residuals and fitted values of the  $\log_{10}$ -transformed data from the analysis of the effects of tree age on number of cones per tree. The expected distribution when the model meets its underlying assumptions is to have even scatter of points, with no apparent pattern. The plot indicates that the data have improved homoscedasticity relative to the raw, untransformed data residuals. The right panel shows a Q-Q (quantile-quantile) plot where the sample values were ranked and plotted as dots and numbers generated from a normal distribution are plotted as the line. Because the sample points are close to the line it shows that the data are approximately  $\log_{10}$ -normal.

## 3.0 RESULTS

### 3.1 Site characteristics

All sites in this study were classified as mesic black spruce forest (Hollingsworth et al. 2006). As would be expected, there was some variation of site characteristics within this general classification (Table 1). Sites ranged in elevation from 224 – 797 m and had slope angles ranging from flat to 15°. Soil organic layer (SOL) depth ranged from 2.1 – 31.0 cm. Sites that were older typically had a thicker soil organic layer. Mineral soil pH ranged from 3.5 – 6.3 and averaged 5.0 across study sites. Thaw depth ranged from 27 – 66 cm and the five sites with the deepest active layer were 40 years old or younger. Mineral soil textures consisted of mixtures of silt, clay, and gravel (Table 1). A large proportion of study sites were surface cover dominated by the moss *Hylacomium splendens*, or *Cladonia* sp. and *Cladina* sp. lichens. The vascular plant understory was usually dominated by ericaceous species, such as *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, *Ledum decumbens*, and *Ledum groenlandicum*.

### 3.2 Age distribution

Sampled trees ranged in age from 6 to 338 years old (Figure 6). Nineteen sites had a mean age of 80 years old or less, five sites had a mean age between the ages of 81 and 150, and six sites had a mean age older than 150 years. Mean age was 54 for the sites located in the Yukon and 73 for Alaskan study sites. The median was similar for both study areas, but more of the older study sites were located in Alaska, resulting in a wider age distribution for this part of the study area (Figure 6).

Tree age varied within sites and the variation increased as stands became older. In stands with mean ages over 100 years, there was an average difference between maximum and minimum tree ages of 132.4 years ( $n = 5$ ). This is almost six times the average difference of stands with a mean age less than 100 years (23.6 years;  $n = 25$ ) (Figure 6). Within stands, there

were three types of age distributions: (1) distinct pulse or single cohort was when stands had a single pulse of recruitment occurring within ten years, (2) pulse with long tail occurred when the majority of stems recruited within a ten year pulse, but had a tail of younger trees with delayed recruitment occurring over more than ten years, and (3) continuous recruitment was when age distributions showed recruitment occurring over many years. Generally, stands with distinct pulses of recruitment had mean ages of 50 years or younger (Figure 7), while stands with a distinct pulse and tail of delayed recruitment had stand mean ages between 50 and 100 (Figure 7). Some stands with mean ages between 50 and 100 also showed continuous recruitment, however all stands with a mean age of 100 or greater showed age distributions consistent with continuous recruitment (Figure 7). For sites up to 100 years old, the relation between oldest tree and mean age closely followed a 1:1 ratio, where mean age closely predicted age of the oldest tree (Figure 8). For stands that had a mean age older than 100 years, the mean age substantially underestimated the age of the oldest tree (Figure 8). As tree age increased, the distance from the ground level to the root collar of the tree also increased due to an associated increasing moss layer (Figure 9). This accumulating organic layer depth will contribute to the age underestimation when ground level samples are far from the root collar. Young stands indicate black spruce stands have a single pulse of recruitment, occurring in the first ten years after fire, while older stands suggest that recruitment occurs continuously or over many decades. Because the accumulating organic layer is likely to increase the aging errors of older trees, the ability to clearly decipher the stand age distribution declines in older stands. Continuous recruitment does occur in black spruce stands, however, aging errors increase the difficulty associated with determining the frequency with which this happens.

Bivariate relationships between mean stand age, oldest tree age, and basal area per hectare, were all positive (Figure 10). Basal area per hectare was more strongly related to mean age than the age of the oldest tree (Figure 10). As would be expected, mean age was highly correlated to oldest tree age (Figure 8). However, this correlation was weaker for older stands because the age variance increased with age (Figure 8).

### **3.3 Individual data**

Cone production ranged from 0 – 1138 cones per tree. Of the trees selected for cone collection, the youngest tree with cones was 20 years old. By the time an individual black spruce was 50 years old there was a 0.50 probability that it had produced cones (Figure 11). Once a tree had reached 100 years old or older, individuals had a 0.90 probability of having cones (Figure 11). When comparing the number of cones estimated by visual counts and actual cone counts, I underestimated cone production by about seven cones per tree. However, the error had a large range from underestimating by 938 cones to overestimating by 435 cones. As the trees became larger it was harder to see the number of cones from the ground, since black spruce cones are grown close to the main stem of the tree. Even though my average estimate was only seven cones under the actual counts, there was a lot of variation in over- and under- estimating the number of cones present on an individual tree.

Tree age was positively correlated with the number of cones per tree and the number of seeds per tree (Table 3, Figure 12). The number of viable seeds per tree was marginally significantly correlated to tree age at the 0.10 probability level ( $P = 0.051$ ). Tree basal area ( $m^2$ ) was positively related to all three response variables: number of cones per tree, number of seeds per tree, and the number of viable seeds per tree. Tree basal area was generally a better predictor than tree age for all cone, seed, and viable seed relationships (Table 3, Figure 12). As an

individual tree ages or increases in basal area, the number of cones, seeds, and viable seeds produced increases. Because these data were  $\log_{10}$ -transformed the relationship has a steep slope, meaning that once an individual black spruce becomes reproductively mature, cone and seed production increases rapidly with tree age. All models were only based on data that included exact cone counts.

One individual tree was considerably larger than any other sampled individual (Figure 12, basal area column). It had a basal diameter of 24.6 cm and an age of 150 years. The tree was growing in a stand that was very mature and had begun thinning due to older trees dying. This particular tree had dead branches in the top one-half of its stem. However, it was still alive, since there were green needles on some of the lower branches. This individual had a total of four cones, which was considerably lower than other individuals in the same stand that had a larger number of cones, especially older cones (2006+). Perhaps, this individual was dying and was putting energy into surviving rather than into reproductive structures.

Although tree age was positively correlated with the number of cones per tree and the number of seeds per tree, tree age was not correlated with average proportion of viable seeds (Figure 13). Tree age was positively related to the number of seeds per cone, where increases in stand age had increases in the number of seeds per cone. With an increase in the number of cones produced as a stand ages and increases in the number of seeds per cone, seed production increases more than would be expected with increases in cone production alone.

### **3.4 Population data**

Cone production ranged from 0 – 78.86 total cones per  $m^2$  (Table 2). The amount of seeds in the aerial seed bank ranged from 0 – 2044 seeds per  $m^2$ , while the estimated number of viable seeds ranged from 0 – 273 viable seeds per  $m^2$  (Table 2). The proportion of trees in a

stand that had cones increased with mean stand age (Figure 14). Approximately fifty percent of sampled trees had cones when the mean stand age was 40 years and between 65% and 100% of trees had cones when the mean stand age was 80 years or older (Figure 14).

Based on the  $\log_{10}$ -transformed data of both the predictor and response variables, there was a positive relationship between the number of cones, seeds, and viable seeds per hectare and all three predictor variables: mean age, oldest age, and basal area per  $\text{m}^2$  (Table 4, Figure 16). Mean age showed the best fit (smallest AIC values) and was the better predictor of cone and seed production (Table 4, Figure 15). The strength of the relationships with stand mean age as the predictor variable was generally stronger than the same relationships shown at the individual level. This probably resulted from losing some of the individual variability associated with the tree level data when the values were averaged at the stand level data.

### **3.5 Comparison of reproductive output between cone cohorts**

Cone and seed production varied within the different years of cone cohorts or years of production: 2008, 2007, and 2006 (cone cohort analysis also included 2009). The number of cones per cohort was not significantly different between the four cohorts: 2009, 2008, 2007, and 2006 (Table 5; Figure 16). The number of seeds per cone differed significantly between all three cohorts. The highest number of seeds per cone was in the 2008 cohort and as the cones aged the number of seeds per cone decreased. Although cones from the 2006 cohort were frequently encountered (in 51% of trees with cones), they typically held few seeds. The proportion of viable seeds was significantly different across the three cohorts (Table 5; Figure 16), with the highest percent of viable seeds in the youngest cohort and decreased with increasing cone age. The percent of viable seeds for the 2008 and 2007 cohorts was marginally different at the 0.10 probability level. All other pairwise comparisons of the percent of viable seeds were significantly

different (Table 5; Figure 16). The 2008 and 2007 cone cohorts were significantly different from the 2006 cohort in the number of viable seeds per cone, however there was not a significant difference between the 2008 and 2007 cone cohort (Table 5).

### **3.6 Cone production predicted by site characteristics**

Stepwise multiple linear regression relating cone production ( $\log_{10}$ -transformed) to site characteristics was carried out to assess the explanatory power of site characteristics in comparison to age and basal area. Both models started with five additional explanatory terms, these included elevation, slope, stand density, age corrected-soil organic layer (SOL) depth, and soil pH. The multiple regression model that included basal area per hectare had a higher  $R^2$  value (0.8236) and lower AIC value (14.608) when compared to the model that included stand mean age ( $R^2 = 0.7359$ , AIC = 24.2459) (Table 6). The interaction between slope and elevation was the only significant term in the model with stand mean age and was also significant in the model with stand basal area. A significant interaction term means that the effects of these two variables are modified by the presence of the other. The main effects of these terms, one of which is significant in the stand basal area model, have little meaning given that the main effects become less significant in the context of interaction. Stand density was also a significant term in the stand basal area model (Table 6). Due to collinearity among the predictor variables the significance in predicting cone production is hard to determine and may be misleading. Models with non-collinear terms would be better for predicting cone production on a stand level.

### **3.7 Effects of stand age on regeneration potential**

By using the estimated equations from the age-viable seeds/m<sup>2</sup> relationship and the number of viable seeds required to produce a two year old seedling (Johnstone and Chapin 2006a), I was able to predict an estimated post-fire seedling density based on stand mean age (Figure 17). The predicted estimates are separated based on burn severity, where moderately

burned soils require 383 viable seeds per two year old seedling, which is much higher than the 61 viable seeds required on severely burned soils (Johnstone and Chapin 2006a) (Figure 17). Based on this study's model predictions and Johnstone and Chapin's (2006b) viable seed:seedling data, moderately burned soils require the pre-fire stand to be well stocked with viable seed and this generally occurs when a stand has matured and is about 150 years old in stand mean age (Figure 17). For stands that are severely burned there is a smaller requirement of viable seed, where stands that are roughly 50 years in stand mean age should provide enough viable seed to replace the average stem density of 4000 stems per hectare (Figure 17).

### **3.8 Comparing estimated parameters and predictions**

Greene and Johnson (1999) presented seed production as a function of dimensionless basal area, arriving at the generated equation:  $Q_d = 163400B_D^{0.95}$  (Table 7). The estimated model coefficients are directly comparable to those presented in this study. The results from this study gave the following equation:  $Q_d = 1738B_D^{0.50}$ . Both equations fit the form:  $Q_D = b(B_D)^a$ , where  $Q_D$  is the number of seeds per  $m^2$ ,  $B_D$  is a dimensionless measure of basal area (area/area), with  $a$  and  $b$  representing the y-intercept and slope, respectively. This study predicted a y-intercept of  $1738 \pm 3.02$  ( $\pm$  SE) (Table 7; values are back transformed from table values). The predicted slope value was  $0.50 \pm 0.13$  ( $\pm$  SE) (Table 7). The coefficients presented by Greene and Johnson (1999) do not fall within the standard error range for the coefficients presented from this study. This means that the equations are considerably different and would predict different values for seed production with the same basal area values.



**Table 1:** Summary of stand environmental characteristics.

Site ID	Mean age	Root collar depth (cm)	Elevation (m)	Slope (°)	Aspect (°)	SOL depth (cm)	Soil pH	Thaw depth (cm)	Soil texture	Moisture classification	Latitude	Longitude
21	11.8	4.7	460	0	-	12.8	5.53	46	n/a	mesic	63.8019	-145.1085
26	13.0	3.4	652	0	-	10.8	4.87	59	silt	mesic	65.9935	-137.2866
6	14.6	2.6	506	0	-	3.8	5.73	66	silt	sub-mesic	63.3276	-142.8950
8	16.3	4.2	408	0	-	7.8	4.93	65	gravelly silt	mesic	63.9172	-145.4039
9	21.5	7.0	134	0	-	8.6	5.73	35	silt loam	mesic	64.7145	-148.2959
24	24.0	6.2	668	3.5	175	15.6	5.95	32	silt loam	mesic	64.0412	-140.6436
12	26.0	6.8	558	4	85	4.2	5.50	63	gravelly silt	subxeric	65.1827	-147.8734
13	29.6	8.6	460	5	324	6.2	4.50	58	gravelly silty clay	subxeric to mesic	65.1704	-147.8922
4	30.6	n/a	616	2	140	11.2	6.23	27	silt	sub-mesic	63.9172	-142.2050
3	32.9	n/a	587	14	290	7.2	5.57	46	silt loam	mesic	63.9445	-138.8964
10	38.0	12.2	165	4	350	14.8	5.20	28	silt	mesic	64.8009	-148.3916
16	40.1	7.2	224	15	230	2.1	5.17	59	silt loam	sub-xeric to mesic	64.8836	-148.3574
22	42.2	14.4	528	5	20	27.0	5.80	38	gravelly silt loam	mesic	63.7749	-145.0805
2	48.4	n/a	623	5.5	110	4.6	5.60	52	silt loam	mesic	63.8536	-138.0346
1	51.2	n/a	639	0	-	6.2	5.37	41	silt loam	mesic	63.8903	-138.1985
15	55.3	15.0	242	2	310	24.2	4.70	32	n/a	sub-xeric to mesic	64.9118	-146.6174
29	60.2	14.0	630	6	292	12.0	4.90	33	silt	mesic	66.1472	-137.2182
27	63.0	18.2	622	0	-	18.8	4.80	34	silty clay	mesic	66.1240	-137.2430
28	67.3	17.7	721	9	254	12.4	4.05	45	silt loam	mesic	66.3695	-136.7246
25	70.7	13.3	695	7	111	14.4	5.25	28	silt loam	mesic	64.0424	-140.6652
18	79.8	19.8	594	6	134	24.0	3.87	34	gravelly silt loam	mesic	64.9443	-148.2681
19	86.5	20.1	244	5	185	15.6	4.43	39	gravelly silt loam	mesic	65.1569	-147.4894
17	87.4	18.3	677	8	330	17.0	4.30	38	gravelly silt	mesic	64.9474	-148.3038
14	88.3	22.7	465	1	20	12.8	3.97	38	silt	mesic	65.1698	-147.8908
11	88.8	28.8	500	9	20	27.0	3.90	37	silt	subxeric to mesic	64.8002	-148.1925
30	113.7	19.4	618	3	75	10.6	4.05	34	silt	mesic	65.9569	-137.3612
5	154.1	16.6	797	2	26	15.6	6.27	27	n/a	mesic	63.5019	-142.4071
23	182.9	19.6	496	0	-	24.4	5.90	36	silt	mesic	63.3150	-142.6531
20	184.5	28.6	449	0	-	31.0	4.80	32	silt loam	sub-mesic	63.8085	-144.9771
7	196.6	21.9	446	3	3	23.6	3.47	29	n/a	sub-mesic	63.6962	-144.3301

**Note:** Site, number given to site location; mean age, mean of tree ages within site; root collar depth, distance between ground level and tree root collar measured in centimeters (average of ten measurements); elevation, site elevation in meters above sea level; slope, slope of site in degrees; aspect, orientation of slope in degrees; SOL, soil organic layer measured in centimeters (average of five measurements); soil pH, pH of the top of the mineral horizon (average of three measurements); thaw depth, active layer depth measured from ground level to start of permafrost in centimeters (average of five measurements); soil texture, composition of mineral soil, where n/a indicates not available data; moisture classification, amount of moisture at site based on Johnstone et al. 2008; latitude and longitude; the coordinates for site locations.

**Table 2:** Summary of age, density, cone production, seed production, and viable seed production in each of the study sites ( $n = 30$ ).

Site ID	Mean age	Oldest age	BA per hectare	Black spruce density (stems/ha)	Stand density (stems/ha)	Cones per m <sup>2</sup>	Seeds per m <sup>2</sup>	Viable seeds per m <sup>2</sup>
21	11.8	13	0.84	6824	-	0.00	0.00	0.00
26	13.0	17	0.26	10370	-	0.00	0.00	0.00
6	14.6	18	0.18	5120	9707	0.00	0.00	0.00
8	16.3	20	0.21	3111	-	0.28	0.00	0.00
9	21.5	24	2.52	7305	8661	5.15	7.02	2.63
24	24.0	35	0.14	2944	-	0.60	2.43	0.48
12	26.0	29	0.04	517	519	0.56	1.67	0.46
13	29.6	35	0.06	636	762	1.90	2.64	0.89
4	30.6	37	0.13	969	-	4.14	17.40	4.50
3	32.9	38	0.53	1624	1775	10.90	41.45	10.47
10	38.0	41	1.46	3966	-	3.67	3.57	0.18
16	40.1	45	4.23	3412	5117	1.79	1.80	0.17
22	42.2	48	6.24	5986	6956	4.91	7.34	1.53
2	48.4	50	9.74	6830	9371	5.77	11.24	1.04
1	51.2	55	7.38	8784	-	4.35	22.17	4.28
15	55.3	79	0.82	1435	-	4.61	8.44	1.50
29	60.2	69	3.42	3422	3464	21.79	61.42	4.64
27	63.0	72	5.89	3899	-	15.48	47.45	7.40
28	67.3	99	0.59	975	-	17.36	43.04	1.37
25	70.7	79	14.57	7708	-	52.62	193.51	19.56
18	79.8	169	4.65	2946	-	12.65	31.92	3.78
19	86.5	94	13.71	6730	-	7.99	12.75	2.50
17	87.4	157	0.37	712	-	7.57	21.70	2.38
14	88.3	97	9.80	5670	-	15.57	35.17	3.52
11	88.8	98	14.11	4885	-	14.22	48.48	15.60
30	113.7	129	9.41	4195	-	78.86	204.42	27.26
5	154.1	232	7.62	3297	-	16.38	63.69	11.18
23	182.9	205	15.40	4938	-	10.09	26.89	5.22
20	184.5	338	6.65	3901	-	24.21	100.34	23.37
7	196.6	261	10.49	6452	-	11.39	43.74	8.96

*Note:* Mean stand age; mean age of study site; oldest age, oldest tree age within site; BA per hectare, basal area per hectare (m<sup>2</sup>/ha); black spruce density, density of black spruce stems only (stems/ha); stand density, density of all stems in study site (stems/ha; where different from black spruce density); cones per m<sup>2</sup>, the estimated number of cones produced by the site on a per m<sup>2</sup> basis (cones/m<sup>2</sup>); number of seeds per m<sup>2</sup>, the estimated number of seeds produced by the site on a per m<sup>2</sup> basis (seeds/m<sup>2</sup>); viable seeds per m<sup>2</sup>, the estimated number of viable seeds produced by the site on a per m<sup>2</sup> basis (viable seeds/m<sup>2</sup>).

**Table 3:** Summary of bivariate relationships between reproductive output variables and individual tree characteristics, based on the models presented in Figure 12. The data of the relationships were  $\log_{10}$ -transformed and the resulting line equation fits the form:  $Q_D = b(B_x)^a$ , where  $Q_D$  is the number of cones per tree, seeds per tree, or viable seeds per tree,  $B_x$  is the predictor variable of the model (tree age or tree basal area), with  $a$  and  $b$  representing equation coefficients.

Model		AIC	a	SE <sub>a</sub>	b	SE <sub>b</sub>	r	P	n
Response Variable	Predictor Variable								
Cones/tree	Tree Age	238.92	0.69	0.21	0.19	0.21	0.27	0.001	124
	Tree Basal Area	209.94	0.91	0.13	3.8	0.35	0.52	<0.001	124
Seeds/tree	Tree Age	261.53	0.78	0.26	1.49	0.47	0.26	0.003	116
	Tree Basal Area	232.5	1.07	0.16	5.67	0.42	0.52	<0.001	116
Viable Seeds/tree	Tree Age	243.73	0.51	0.26	0.92	0.47	0.16	0.051	110
	Tree Basal Area	231.41	0.71	0.17	3.68	0.45	0.36	<0.001	110

*Note:* All data were  $\log_{10}$  transformed prior to analysis. The value of  $n$  decreases, since the number of sites with zero values for the response variable increased. AIC, Akaike's information criterion,  $a$ , intercept;  $SE_a$ , standard error associated with  $a$ ;  $b$ , slope;  $SE_b$ , standard error associated with  $b$ ;  $r$ , correlation coefficient;  $P$ ,  $P$ -value for the bivariate relationship;  $n$ , sample size. The sample size varies because the number of samples with zero values increased from cones/tree to viable seeds/tree.

**Table 4:** Summary of bivariate relationships between reproductive output variables and stand characteristics, based on the models presented in Figure 15. The data of the relationships were  $\log_{10}$  transformed and the resulting line equation fits the form:  $Q_D = b(Bx)^a$ , where  $Q_D$  is the number of cones per  $m^2$ , seeds per  $m^2$ , or viable seeds per  $m^2$ ,  $Bx$  is the predictor variable of the model (stand mean age, stand oldest age, or basal area (area/area)), with  $a$  and  $b$  representing equation coefficients. Models included all of the study sites ( $n = 30$ ).

Model		AIC	a	SE <sub>a</sub>	b	SE <sub>b</sub>	r	p
Response Variable	Predictor Variable							
Cones/ $m^2$	Mean Age	29.04	1.57	0.20	-1.94	0.34	0.83	<0.001
	Oldest Age	35.22	1.37	0.20	-1.73	0.37	0.78	<0.001
	Basal Area	45.78	0.55	0.11	2.79	0.43	0.66	<0.001
Seeds/ $m^2$	Mean Age	28.03	1.47	0.19	-0.29	0.34	0.81	<0.001
	Oldest Age	32.10	1.30	0.19	-0.13	0.35	0.78	<0.001
	Basal Area	45.63	0.49	0.11	4.04	0.43	0.62	<0.001
Viable Seeds/ $m^2$	Mean Age	36.94	1.54	0.23	-1.26	0.39	0.78	<0.001
	Oldest Age	41.10	1.35	0.22	-1.07	0.41	0.74	<0.001
	Basal Area	52.75	0.50	0.13	3.24	0.48	0.58	<0.001

**Note:** All data were  $\log_{10}$  transformed prior to analysis. Coefficients of the line equation represent:  $y$ , the predicted  $y$  value for a given  $x$  value;  $Bx$  is the value for the predictor variable;  $b$ , slope;  $a$ , intercept. Table values represent: AIC, Akaike's information criterion,  $SE_a$ , standard error associated with  $a$ ;  $SE_b$ , standard error associated with  $b$ ;  $r$ , correlation coefficient;  $P$ ,  $P$ -value for the bivariate relationship;  $n$ , sample size.

**Table 5:** Pearson's  $\chi^2$  test results from the comparison of cones per cohort, seeds per cone, viable seeds per cone, and proportion of viable seeds per cohort across cone cohorts (2009, 2008, 2007, 2006). Models comparing all three cohorts are summarized and when significant, the results from pairwise comparisons are included.

<b>Variable</b>	<b>Cohorts</b>	<b>df</b>	<b><math>\chi^2</math></b>	<b>P</b>
Cones per cohort	2009, 2008, 2007, 2006	3	5.61	0.132
Seeds per cone	2008, 2007, 2006	2	27.11	<0.001
	2008 – 2007	1	4.86	0.027
	2008 – 2006	1	27.17	<0.001
	2007 – 2006	1	10.88	<0.001
Percent of viable seeds	2008, 2007, 2006	2	18.25	<0.001
	2008 – 2007	1	3.16	0.075
	2008 – 2006	1	18.24	<0.001
	2007 – 2006	1	8.24	0.004
Viable seeds per cone	2008, 2007, 2006	2	8.06	0.018
	2008 – 2007	1	1.21	0.271
	2008 – 2006	1	8.21	0.004
	2007 – 2006	1	3.86	0.049

*Note:* 2009 data were only included for cone counts, as seeds were not sampled.

**Table 6:** Results from a multiple regression model with cone production per m<sup>2</sup> (log<sub>10</sub>-transformed) as a response variable and site characteristics as predictor variables. Models were separated to include either stand basal area or stand mean age.

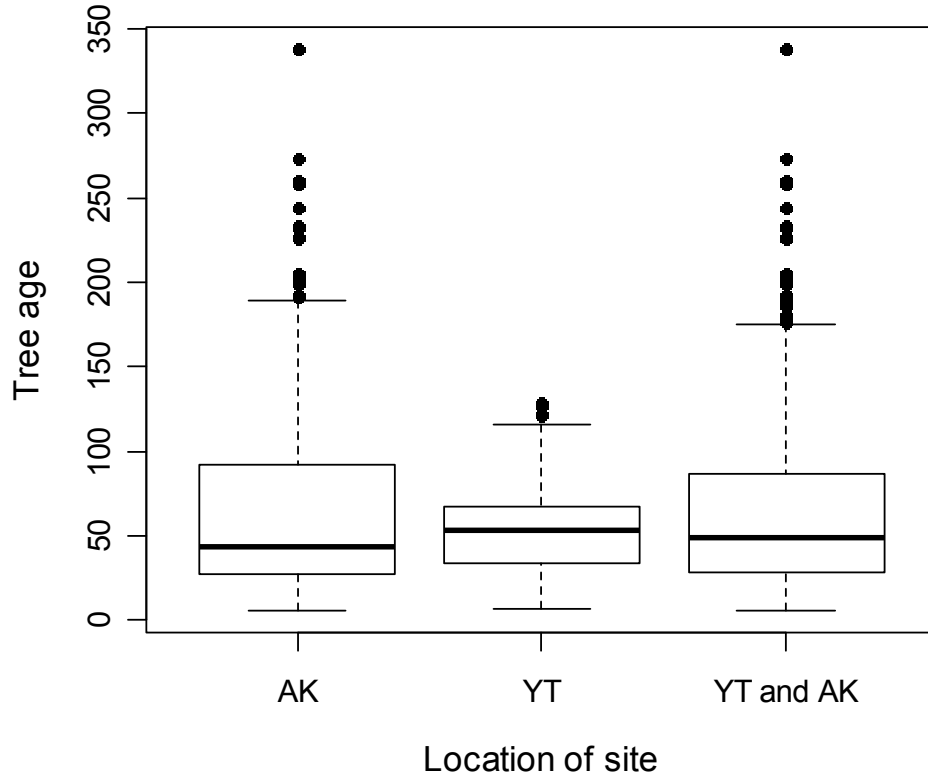
<b>Predictor Variable</b>	<b>Standardized Coefficient</b>	<b>SE</b>	<b>P</b>	<b>AIC</b>	<b>R<sup>2</sup></b>	<b>P</b>
Intercept	1.0450	0.1384	<0.001	14.608	0.8236	<0.001
Stand basal area	0.7680	0.0717	<0.001			
SOL (age-corrected)	-0.1629	0.1042	0.1312			
Slope	-0.1165	0.0030	<0.001			
Elevation*Slope	0.0002	0.00005	<0.001			
Stand density	-0.0001	0.00002	<0.001			
Intercept	-1.9790	0.3129	<0.001	24.2459	0.7359	<0.001
Stand mean age	1.5000	0.1818	<0.001			
Slope*Elevation	-0.00007	0.00003	0.014			

*Note:* Basal area per hectare, total basal area of site per area (hectare; was log<sub>10</sub>-transformed prior to analysis); SOL, soil organic layer measured in centimeters (average of five measurements) was age-corrected to avoid collinearity; ALD, active layer depth; stand density, the number of trees in a site per area (hectare); elevation, site elevation in meters above sea level.

**Table 7:** A comparison of equations and seed estimates from predictive equations relating stand basal area to seed production of black spruce, as developed in this study and presented in Greene and Johnson (1999). The equation is represented by  $Q_D = b(B_x)^a$ , where  $Q_D$  is the number of viable seeds per  $m^2$ ,  $B_x$  is the predictor variable basal area (area/area), with  $a$  and  $b$  representing equation coefficients. The range of the number of seeds produced by each equation and the associated parameter values are also summarized.

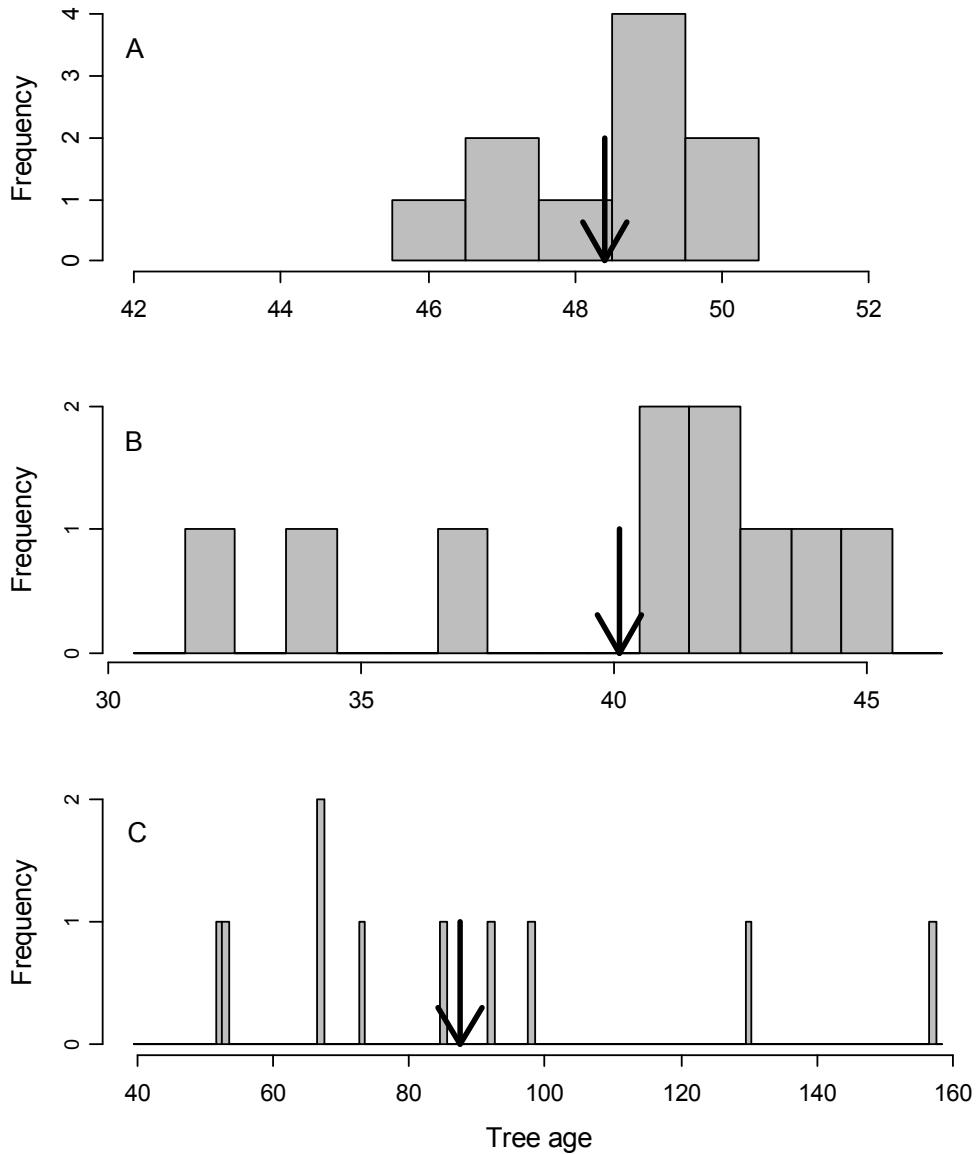
Study Area	Estimated Parameters				No. of seeds per $m^2$ based on basal area (area/area):	
	a	SE <sub>a</sub>	b	SE <sub>b</sub>	$0.04 \times 10^4$	$15.4 \times 10^4$
Yukon and Alaska	0.50	0.13	1 738	3.02	3.48	68.20
Sask. and Quebec	0.95	-	163 400	-	1.22	347.85

*Note:* Study area: equation from this study (Yukon and Alaska) or from Greene and Johnson (1999; Saskatchewan and Quebec); estimated parameters from the generated equations where  $a$  is the intercept and  $b$  is the slope; SE, are the associated standard errors; range of the number of seeds per  $m^2$  predicted by equations using the range of basal area (area/area) values from this study (0.04-15.4  $m^2/ha$ ).

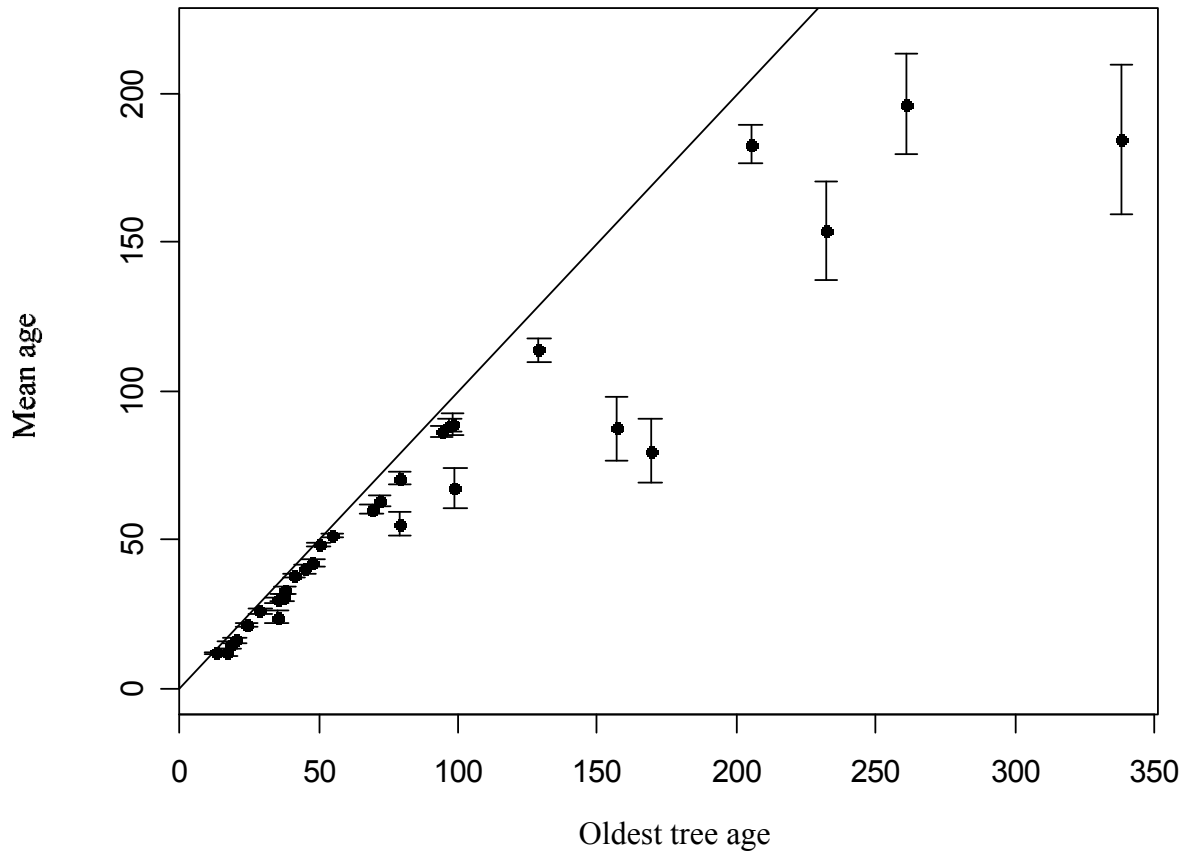


**Figure 6:** A boxplot summarizing the age distribution of all sites (YT and AK) and separated into the two study areas: Alaska (AK) and Yukon Territory (YT). Ages are the raw tree age estimates of individuals within sites. The line in the center of the boxes represents the median of the data, with the boxes encompassing the 25% – 75% quartiles of the data. The whiskers extending beyond the boxes represent the 95% quartiles, and extreme values beyond the whiskers shown as filled circles.

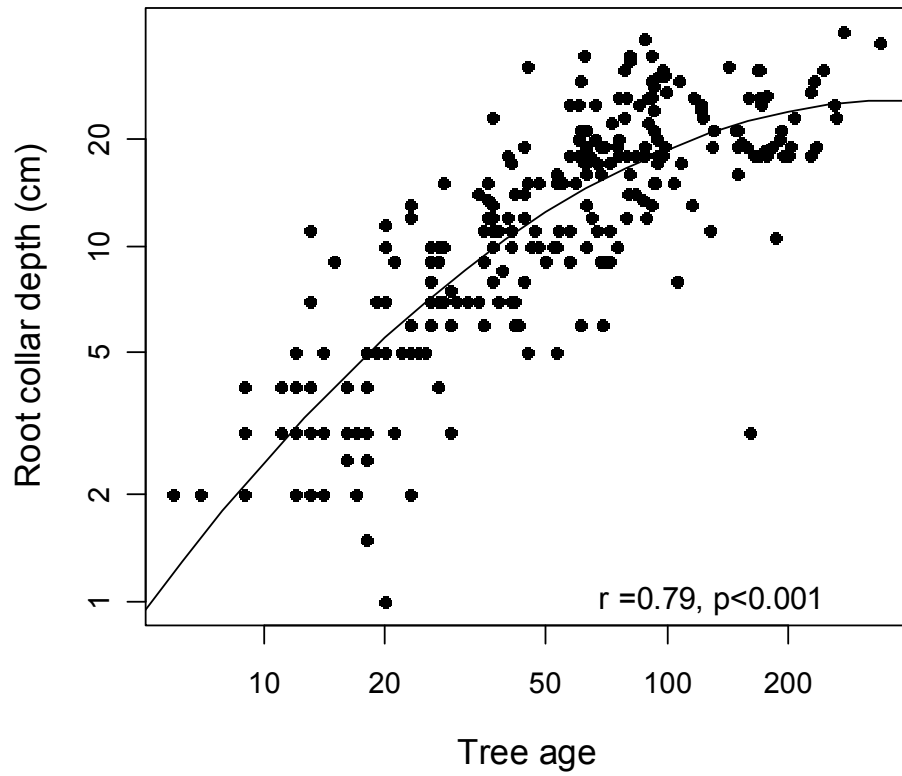




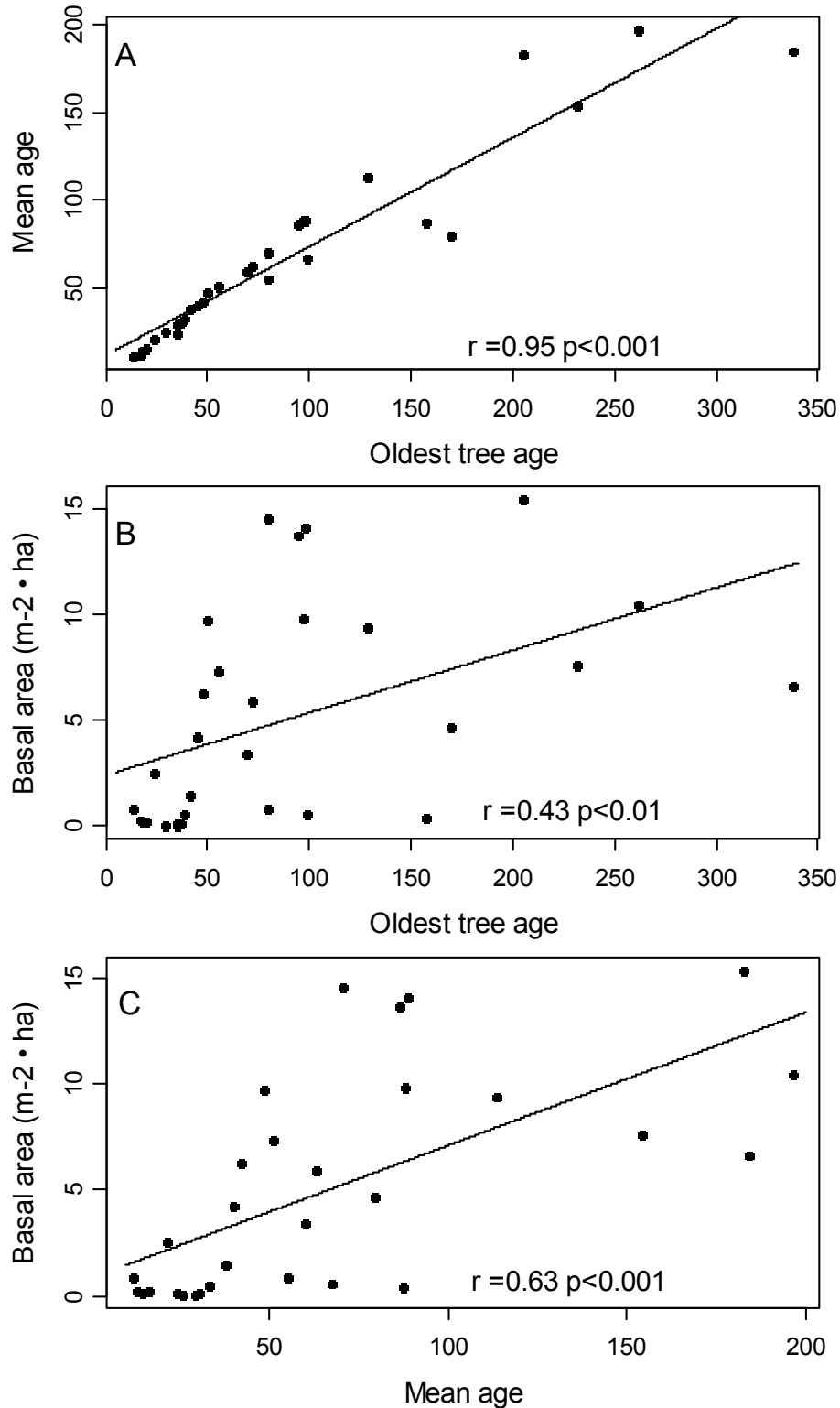
**Figure 7:** Three examples of age-frequency distributions from the 30 study sites, where each panel (A, B, and C) shows an example of the three different age distribution types. A) shows a distinct pulse of recruitment occurring in less than ten years, B) illustrates a distinct pulse and some delayed recruitment occurring over more than ten years, but less than 20 years, and C) shows a stand with no distinct pulse, but rather continuous recruitment occurring over many years, 105 years in this case. The arrow indicates the mean stand age and each site has a sample size of  $n = 10$ .



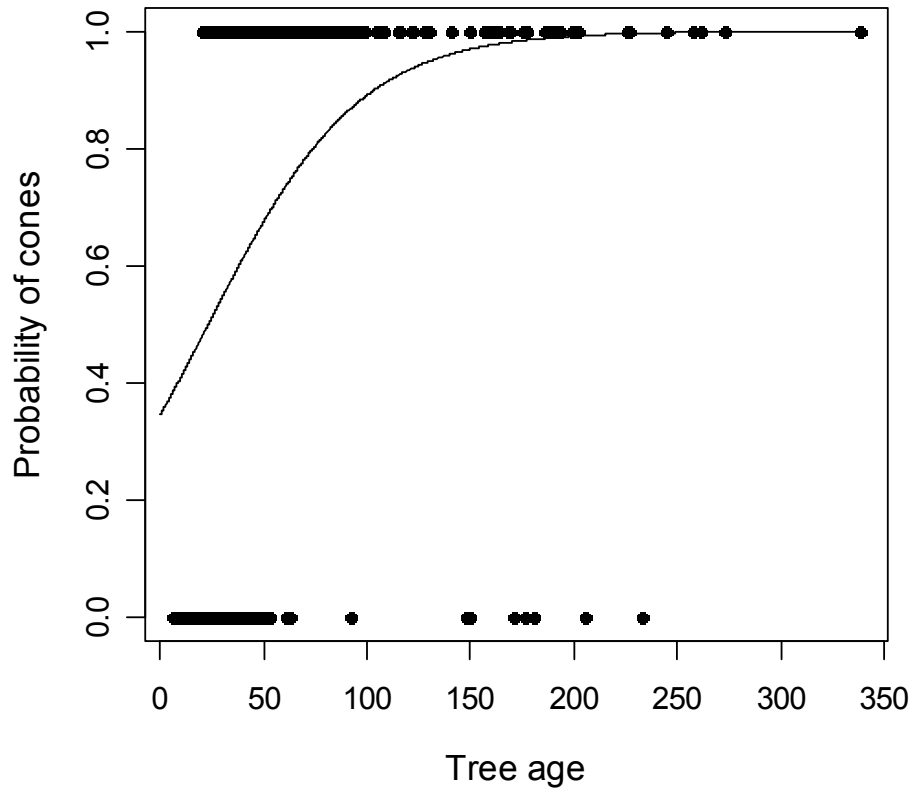
**Figure 8:** A scatterplot of oldest tree age within a site and the mean stand age, where each circle represents one site ( $n = 30$ ). Error bars are the standard errors of the mean age within each site, based on ten trees per site. The plotted line shows a 1:1 regression line for reference.



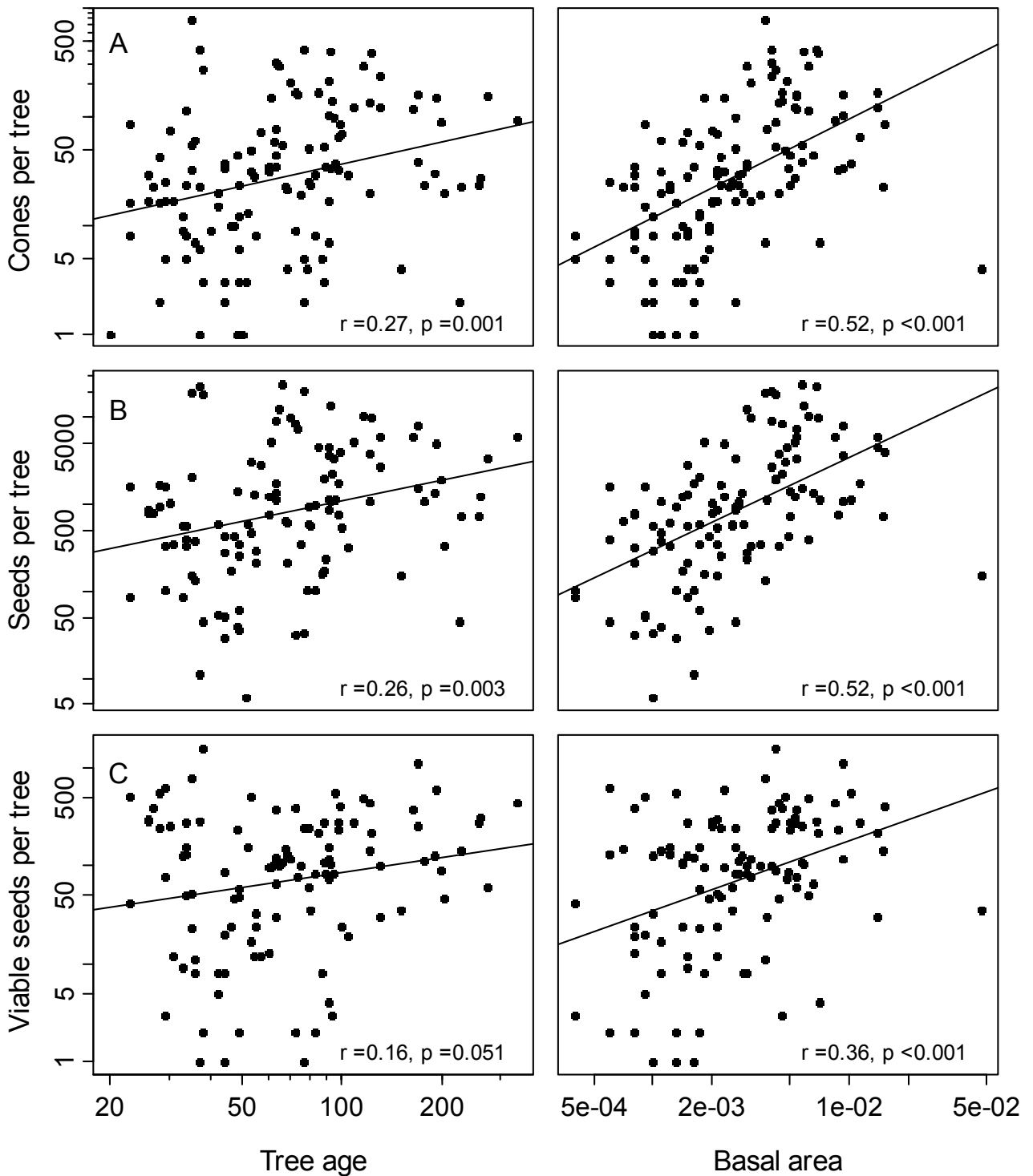
**Figure 9:** Non-linear relationship between tree age and root collar depth (cm). Each point represents an individual tree ( $n = 252$ ) and each axis is plotted on a  $\log_{10}$  scale.



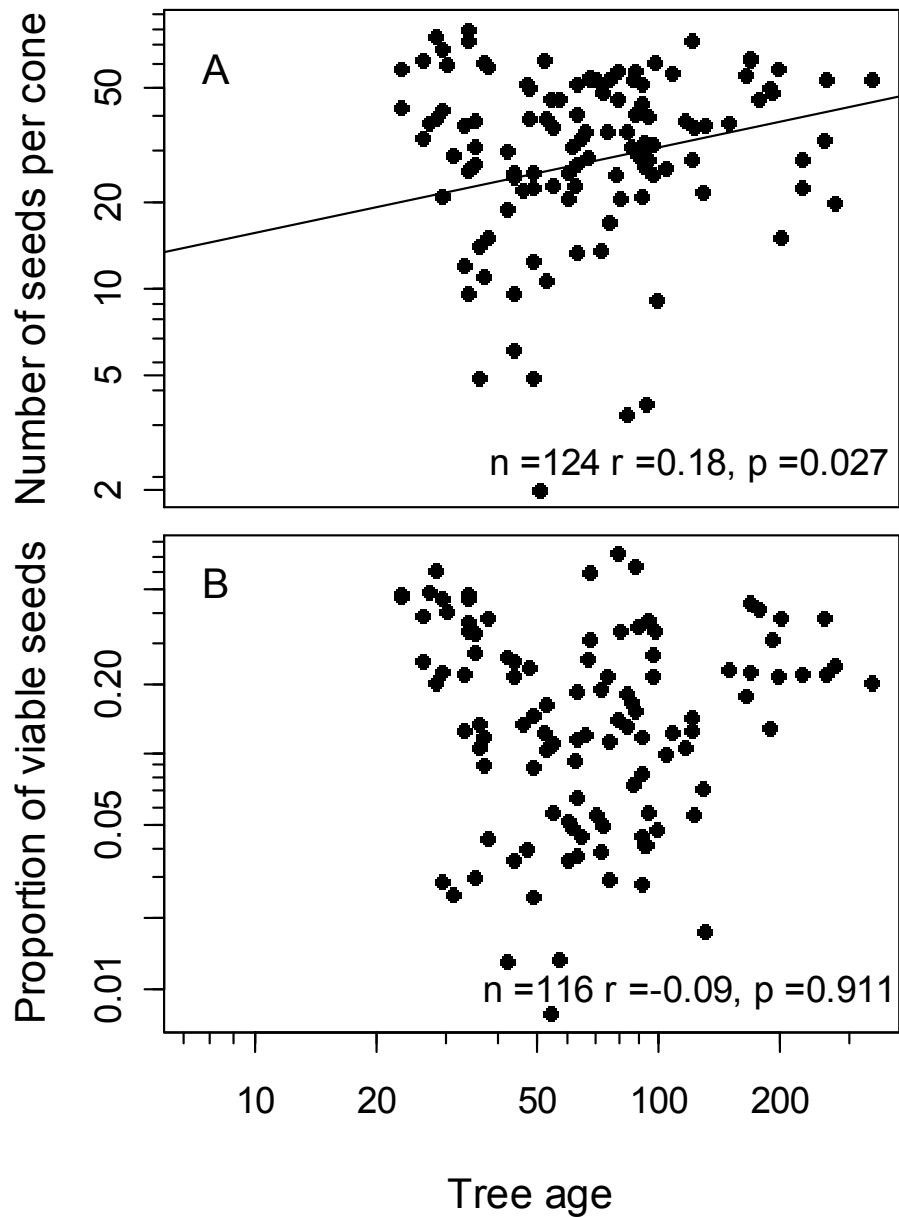
**Figure 10:** Bivariate relationships between predictor variables: mean age, oldest tree age, and basal area ( $\text{m}^2/\text{ha}$ ), where each closed circle represents one site ( $n = 30$ ). Each panel shows the pairwise relationship between two predictor variables: A) oldest tree age and mean stand age, B) oldest tree age and site basal area ( $\text{m}^2/\text{ha}$ ), and C) mean stand age and site basal area ( $\text{m}^2/\text{ha}$ ).



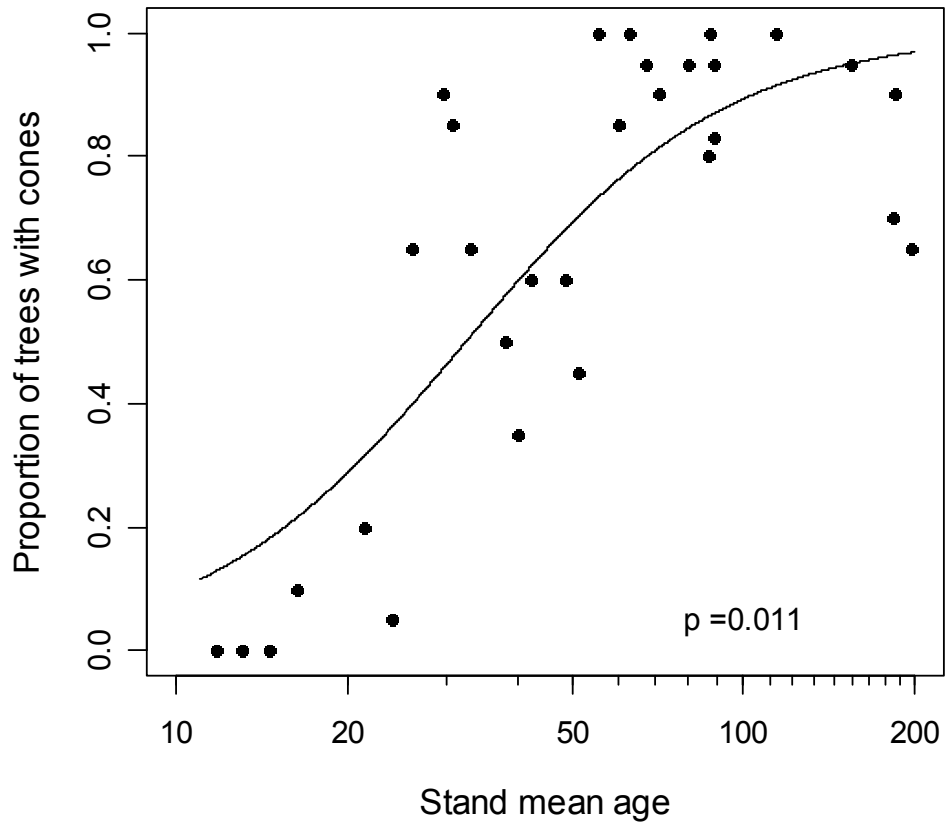
**Figure 11:** Logistic regression between tree age and the probability of a tree having cones ( $P < 0.001$ ). Each point represents an individual tree ( $n = 288$ ).



**Figure 12:** All bivariate relationships between the two predictor variables: tree age and tree basal area ( $\text{m}^2/\text{m}^2$ ) and the three response variables: number of cones per tree (Row A;  $n = 124$ ), the number of seeds per tree (Row B;  $n = 116$ ), and the number of viable seeds per tree (Row C;  $n = 110$ ). Points represent individual trees and all axes are plotted on a  $\log_{10}$  scale.

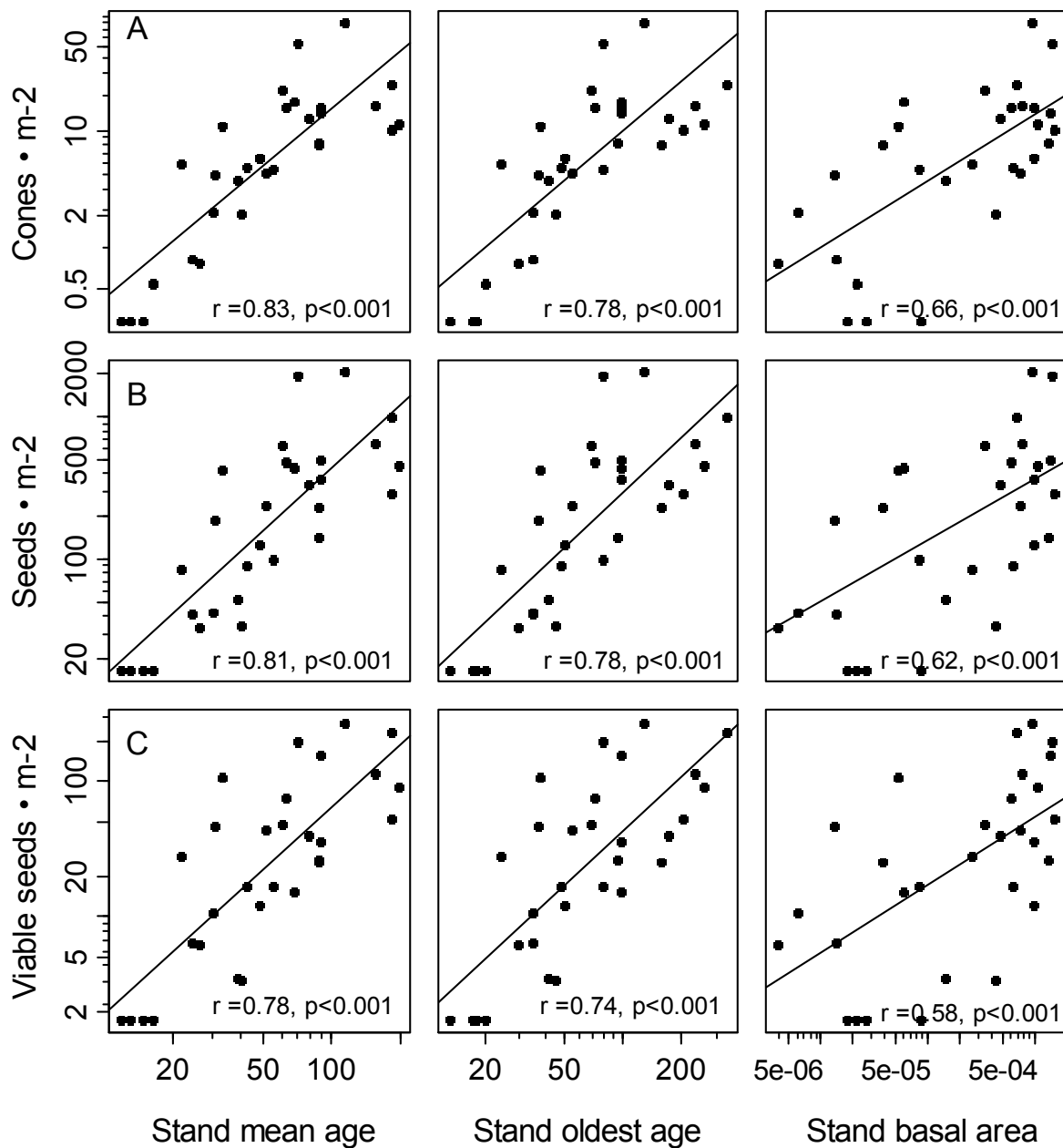


**Figure 13:** Bivariate relationships between tree age and two response variables: A) the number of seeds per cone and B) the proportion of viable seeds. Each point represents a tree and the axes are plotted on a log<sub>10</sub> scale. The sample size,  $n$ , decreases from number of seeds per cone to the proportion of viable seeds because there were trees with cones, but no seeds.

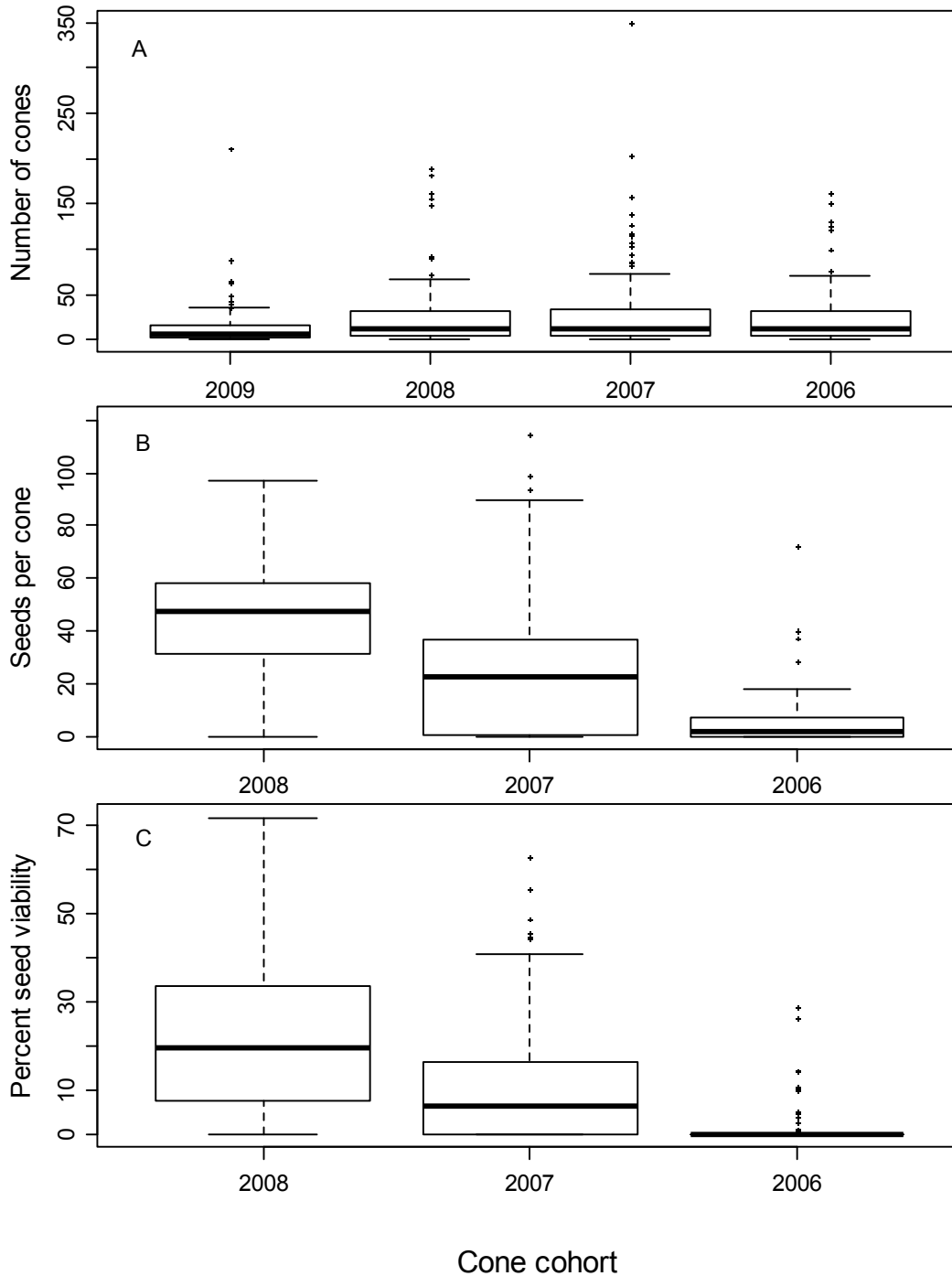


**Figure 14:** Logistic regression between stand mean age and the proportion of trees with cones ( $P = 0.011$ ). Each dot represents a site ( $n = 30$ ) and stand mean age is on a  $\log_{10}$  scale.

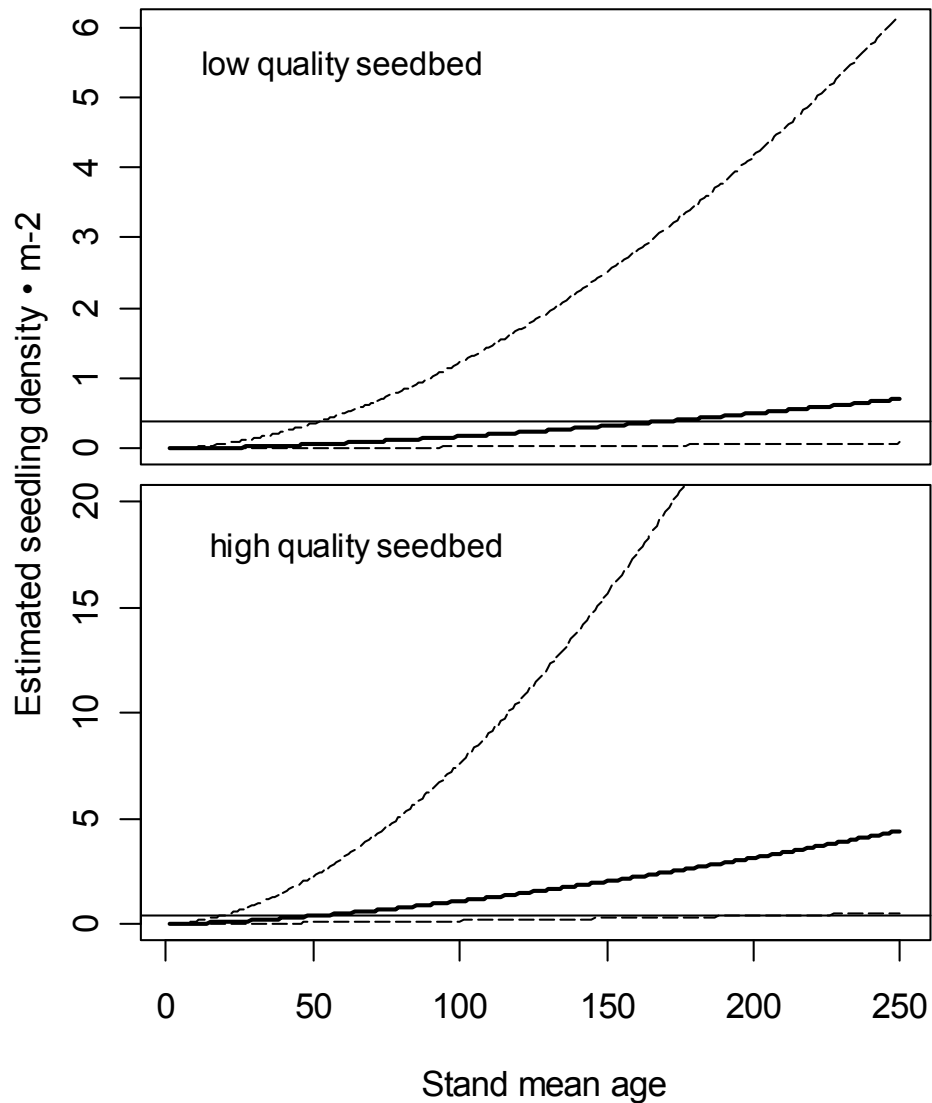




**Figure 15:** All bivariate relationships between the three predictor variables: stand mean age, site oldest age, and site basal area (area/area) and the three response variables: viable seeds per m<sup>2</sup> (Row A), seeds per m<sup>2</sup> (Row B), and cones per m<sup>2</sup> (Row C). Points represent individual sites ( $n = 30$ ) and all axes are plotted on a log<sub>10</sub> scale.



**Figure 16:** Three boxplots summarizing the reproductive output between cone cohorts: A) the number of cones per cohort, which there were only significant differences between the 2009 cohort and the remaining cohorts, B) the number of seeds per cone, where all pair-wise comparisons were significantly different, and C) the percent seed viability per cohort, where there was a significant difference between 2008 – 2006 cohorts and 2007 – 2006 cohorts (Table 5). The line in the center of the boxes represents the median of the data, with the boxes encompassing the 25% – 75% quartiles of the data. The whiskers extending beyond the boxes represent the 95% quartiles, and extreme values are beyond the whiskers shown as filled circles.



**Figure 17:** Estimated seedling density predicted by mean stand age. Lines are estimated based on the generated equation from the mean stand age-viable seeds per  $m^2$  relationship and the number of viable seed required to produce a two year old seedling on moderately burned soils (low quality seedbeds, top figure) and severely burned soils (high quality seedbeds, bottom figure; Johnstone and Chapin 2006b). The solid lines are based on the parameter estimates from the age-viable seed relationship, while the long-dashed lines represent the upper and lower boundaries of the parameters based on the associated standard errors. The short-dashed line represents a target density of  $0.40$  stems per  $m^2$ , the average stem density across the sampled study sites.

## 4.0 DISCUSSION

### 4.1 Age effects on cone and seed production

The main objective of this study was to assess how seed production varies with stand age and to fill some of the knowledge gaps surrounding the life history of northern black spruce. I found evidence of a positive relationship between stand age and seed production of black spruce. I also found evidence, which confirms existing literature, that seed production is positively related to basal area per hectare (Greene and Johnson 1999). Sexual maturity, estimated as the initiation of cone production, occurred at a mean stand age of 16 years, while seed and viable seed production started at a mean stand age of 21 years. Once cone and seed production were initiated, there was a steep increase in the number of cones and seeds produced as the stand age increased. There was no evidence of a peak or decline in cone or seed production up to the mean stand age of 197 years. Although there was no peak there was slight evidence of a plateau in cone and seed production; however this pattern is inconclusive given a the small sample size of stands over the age of 200 years. Furthermore, with the addition of more data points and a non-linear statistical analysis there may be a plateau in cone and seed production for older black spruce stands.

The results of this study are consistent with the literature on seed production in northern black spruce forests. I estimated that stands between the ages of 50 and 100, which are ages used in previous studies of black spruce seed estimates, produced  $2.27 \times 10^5 - 5.75 \times 10^5$  viable seeds per hectare. These values are an order of magnitude lower than what has been measured in northern Ontario, as well as a study conducted in central Saskatchewan and Quebec ( $2.90 - 8.10 \times 10^6$  seeds per hectare and  $\sim 4.5 \times 10^6$  filled seeds per hectare, respectively; Skeates and Haavisto 1987, Greene and Johnson 1999). On the other hand, these values are comparable to northern Northwest Territories ( $6.28 \times 10^5$  seeds per hectare; Black and Bliss 1980). Greene and

Johnson (1999) estimated the number of filled seeds per hectare, which may overestimate viability because a small proportion (10 – 20%) of filled seeds are often not mature enough for germination (Safford 1974, Sirois 2000). Black and Bliss (1980) and Haavisto and Skeates (1987) estimated the total number of seeds per hectare, which would be greater than values estimating the number of viable seeds, since black spruce tends to have a large proportion of empty or non-viable seeds (O'Reilly et al. 1982). The large proportion of empty seeds in black spruce is a result of aborted gametophytes, which occurs when a seed is self-pollinated or there are pollination failures (O'Reilly et al. 1982). By using the average germination percent from this study (12.9%), Black and Bliss (1980) fall within the same range of viable seed production observed in this study. However, Greene and Johnson (1999) and Haavisto and Skeates (1987) still have much higher values of seed production, over a factor of 10 in both cases, which may be linked to latitudinal differences in temperature.

Climate limitations on the production of mature seeds in conifer forests can be a significant problem for viable seed production and decreases in viable seed production become more acute with increasing latitude and elevation (Zasada and Grigal 1978, Henttonen et al. 1986, Zasada 1988, Sirois 2000). In Finland, a strong north-south gradient in seed maturity has been measured for Scots pine (*Picea sylvestris*; Henttonen et al. 1986). For example, there was an increase in the probability of seeds reaching 50% anatomical maturity (embryo fills at least one third of the embryo cavity) from 0.02 at 68 – 69°N latitude to 0.50 at 65 – 67°N latitude (Henttonen et al. 1986). Zasada and Grigal (1978) found that white spruce (*Picea glauca*) had a larger number of immature seeds north of the Arctic Circle in Alaska compared to those located south of the Arctic Circle. Based on this information and long-term weather records Zasada and Grigal (1978) concluded the decrease in seed maturity with increasing latitude was a reflection

on the critical role that temperature has in the process of seed maturation. Sirois (2000) also found a decline in filled seed production with increases in latitude for black spruce in eastern Canada. The number of filled and mature seeds in northern sites was positively related to the sum of growing degree-days (sum of days with mean daily temperature  $>5^{\circ}\text{C}$ ; Sirois 2000). For northern climates, the number of growing degree-days is limited and this affects the maturation of developing seeds (Henttonen et al. 1986, Sirois 2000). Furthermore, there is a low proportion of viable pollen in northern regions, which would increase the number of immature or unfilled seeds in black spruce forests of northern latitudes (Elliott 1979, Sirois 2000). The decrease in the number of viable seeds as trees are located further north may explain the higher values of seed production from Greene and Johnson (1999) and Haavisto and Skeates (1987), which had study sites located in more southern locations of Canada.

#### **4.2 Linking age and basal area effects to a shortened fire return interval**

There are few publications that provide allometric equations from the relationships between reproductive output to stand or tree characteristics, such as basal area or age (Haavisto and Skeates 1995, Greene and Johnson 1999). Stand and tree characteristics, such as density, spatial arrangement of trees, tree age, tree size (height or basal area), animal herbivory, and tree health, can directly influence the natural cone and seed production at both the individual and stand level (Leadem et al. 1997). Correlating reproductive production to stand and tree attributes is important for understanding what factors promote seed crops and how resilient black spruce forests are to disturbances (Leadem et al. 1997, Johnstone et al. 2009). With increases in fire activity across most of the North American boreal forest likely with climate change (Kasischke and Turetsky 2006), understanding the regeneration capacity in relation to fire return interval (or stand age) is essential to predicting outcomes of succession in these forests (Yarrington and

Yarrangton 1975, Johnson et al. 1994, Lavoie and Sirois 1998, Gutsell and Johnson 2002, Johnstone and Chapin 2006b).

In mature boreal forests, regeneration after fire is highly correlated to the pre-fire composition. When forests are burned with an average fire cycle between 50 and 150 years, stand self-replacement usually occurs (Viereck 1983, Greene and Johnson 1999, Johnstone and Chapin 2006b). However, reductions to the average fire return interval result in departures from the normal post-fire species composition (Johnstone and Chapin 2006b). Fire return intervals less than 30 years have low levels of conifer recruitment, even when the pre-fire stand was dominated by conifers (Johnstone and Chapin 2006b, Brown and Johnstone, unpublished). Low densities of post-fire conifer seedlings may be caused by low levels of viable seed in the aerial seed banks (Jasinski and Payette 2005, Johnstone and Chapin 2006b). On average, 61 and 383 viable seeds are required to produce a live, 2-year old black spruce seedling on severely to moderately burned soils, respectively (Johnstone and Chapin 2006a). Moderately burned soils are poor quality substrates for seedling establishment because of the unstable moisture supply associated with the large proportion of organic layer left after fire (Zasada and Norum 1983, Charron and Greene 2002, Johnstone and Chapin 2006a).

Variations in fire severity create landscapes with different seedbed qualities, which require varying amounts of viable seed for stand self-replacement (Johnstone and Chapin 2006a). Predicted by the models presented in this study, a 4000 stems per hectare black spruce forest (average density across study sites) would have reduced black spruce density if severely burned at an age of  $\leq 50$  years. This is consistent with empirical observations of conifer regeneration failures when stands burned at ages less than 30 years old (Johnstone and Chapin 2006b). For less severe fires that consume little of the soil organic layer, stands with ample viable seed are

required. Based on the models from this study, stands less than 150 years old could have reduced post-fire black spruce densities. However, consumption of organic layers during fire will vary across micro-environments of these northern forests. Given that fires often burn with intermediate severities, regeneration after these fires will require an age between the above estimated ages. With the variation in viable seed production and the loss of viable seed during fire (Zasada et al. 1979), 50 years is the minimum age where self-replacement after fire is likely to be achieved. Fire return intervals longer than the minimum 50 years may have reduced post-fire seedling densities as well as seedbed quality is poor.

#### **4.3 Predictors of seed production**

Basal area is a quick measurement that provides information on aboveground biomass accumulation, whereas determining age is often more laborious, but provides knowledge on forest succession and stand dynamics. Both age and basal area were correlated with cone and seed production in this study. At the tree level, basal area was a better predictor of cone and seed production than age. However, mean stand age was a better predictor than stand basal area of cone and seed production at the stand level. Mean stand age was calculated from the ten trees sampled for cones, whereas stand basal area was calculated from the 20 trees used for density measurements. A comparison of the coefficient of variations for stand mean age and stand basal area showed that basal area was more variable than stand mean age (0.99 compared to 0.78 for stand mean age). Both predictor variables, age and basal area, were strong indicators of cone and seed production. Therefore, basal area could be used as a proxy for age to estimate cone and seed production of individual black spruce trees, given the ease of field measurements, as well as the strong relationship between basal area and seed production. However, depending on the purpose



of the data collection, stand age is useful for modeling given that it is the base mechanism that affects stand basal area and many environmental characteristics.

Individual basal area is affected by small scale variations in environmental conditions, including canopy position and light availability (Atkinson and Haavisto 1996, Greene et al. 1999, Greene et al. 2002). Atkinson and Haavisto (1996) found that dominant black spruce trees, or those that receive light from all sides and are above the average crown level of a stand, produce more cones than codominant trees or those in intermediate size classes. Greene and others (2002) found that white spruce and balsam fir growing in forest edges, exposed to high amounts of sun, had higher cone production when compared to trees growing within the stand that receive smaller amounts of sunlight. However, Atkinson and Haavisto (1996) also found that the average number of seeds per cone was much higher for trees with an intermediate crown class (individuals with crowns located at the general crown height of the stand that receive light primarily from above). Intermediate crown classes have greater protection from the elements given that they are surrounded by taller and bigger individuals (Atkinson and Haavisto 1996). The cones on intermediate individuals will have slower rates of cone opening and therefore, retain a higher proportion of seeds when compared to individuals of dominant crown classes that are more exposed (Atkinson and Haavisto 1996). Both crown class and light interception have a large influence on cone and seed production of individual trees. This individual variation needs to be taken into consideration when interpreting and predicting cone and seed production in black spruce forests. Sampling designs that include a large sample of different individuals will help to capture all of the variability associated with cone and seed production.

#### **4.4 Site characteristics as predictors of cone production**

In addition to age and basal area, the most influential variables to cone production were the age-corrected soil organic layer depth, the interaction between slope and elevation, and stand density. A thick organic layer is characteristic of northern black spruce forests (Bonan 1990, Johnstone et al. 2010). These thick layers have cool, moist mineral soils with slow organic layer decomposition, and low levels of available nutrients (Jorgenson 1984, Bonan 1990, Hollingsworth et al. 2006). These properties restrict tree growth and further promote the accumulation of thick organic layers, which further reduces soil temperature and the amount of available nutrients (Bonan 1990). This is consistent with the findings from this study that increases in soil organic layer depth negatively affect cone production. Where there were thick layers of soil organic matter, cone production was less than in stands that have thinner organic layers. In comparison, stands with thinner soil organic layers would have warmer soils, which enhance productivity and nutrient cycling through faster rates of decomposition and nutrient mineralization (Van Cleve and Viereck 1981, Van Cleve et al. 1983, Bonan 1990). Increases in stand density resulted in decreases of cone production. This may be attributed to competition between individual trees, where limited resources may be an issue (Canham et al. 2004). The interaction of elevation and slope decreased cone production with increases in both elevation and slope. It has been found that increases in elevation have effects on the post-fire seedling densities of black spruce, which may be linked to cone and seed production of these stands (Johnstone et al. 2010).

#### **4.5 Reproductive output of cone cohorts**

Black spruce typically have three to four cone cohorts present on an individual tree in northern latitudes (Zasada et al. 1992), and sometimes up to six cohorts in more southern

locations (Greene and Johnson 1999). Even though yearly cone production is held in the canopy of black spruce forests, the regeneration potential is highest in the youngest cone cohorts (Chai and Henry 1952, Atkinson and Haavisto 1996). Based on the proportion of viable seeds in each cohort, the results of this study showed that the two youngest cone cohorts provide approximately 94% of the available viable seed of an individual tree. These results are similar to other studies. For example, Atkinson and Haavisto (1995) found seven different cone cohorts on black spruce in northern Ontario, where cones three to seven years old had similar low numbers of seeds per cone, when compared to cones one and two years old (Atkinson and Haavisto 1996). Chai and Hansen (1952) found 19 different cone cohorts on black spruce trees in Minnesota. They found that there were still viable seeds in the oldest cones sampled, and that viability was highest in the youngest cohorts, which gradually diminished as the cones aged (Chai and Henry 1952). This study also found low numbers of viable seed in cones older than two years, which made up a small fraction of the entire viable seed bank of an individual or stand.

The decrease in the proportion of viable seeds associated with cone age is a result of several factors, including the dispersal of viable seeds as the semi-serotinous cones open (Atkinson and Haavisto 1996). In soil, black spruce seeds lose viability between 10 and 16 months after being released from the cones (Fraser 1975). However, seeds that are retained inside the cones of the aerial seedbank can maintain longevity for many years, for up to 19 years in some cases (Chai and Henry 1952, Black and Bliss 1980, Atkinson and Haavisto 1996, Greene and Johnson 1999). Serotiny is considered to be an adaptation to fire, where dry and hot conditions can induce cone opening (Nathan et al. 1999). The heaviest (viable) seeds are lost first as black spruce cones open, leaving the lighter, empty, non-viable seeds in the cones (Atkinson and Haavisto 1996). In addition, viability is often reduced as seeds age (Atkinson and Haavisto

1996). Many environmental factors contribute to the seed longevity and germination, such as temperature and moisture (Black and Bliss 1980). Moisture reduces seed viability and therefore, the drier the tissue is kept the longer it will maintain viability (Ellis and Roberts 1980, Ellis et al. 1986). Pathogen growth, depletion of food reserves, and metabolism can be inhibited in the dry and cold state, reducing the chance of losing viability (Vertucci and Roos 1990). The results of this study did not find a significant difference in proportion of viable seeds across the three sampled cone cohorts. This suggests that because of the dry and cold environmental conditions in these northern forests and cone serotiny, black spruce are able to retain seed viability for many years. It has been found that seed viability is retained in the older cones, but because the seed number is low in the opened older cones, the total number of viable seeds is minimal (Chai and Henry 1952, Atkinson and Haavisto 1996).

Although the advantage of serotiny is clear, it remains unknown why some species have a higher degree of serotiny than others. For example, black spruce is only semi-serotinous when compared to other serotinous species (Midgley 2000). *Banksia* species are strongly serotinous, retaining seeds inside the cones for up to 10 years (Midgley 2000). On the other hand, *Leucadendron* and *Protea* are weakly serotinous retaining seeds for only a few years (1 – 4) (Midgley 2000). There is a large cost with maintaining an increased degree of serotiny. The plant has to provide a continual supply of mechanical support to the cones as well as a vascular supply in order to keep the cones alive, which prevents opening (Midgley 2000). It has been shown that extreme serotiny produces greater population growth, in forests with fire being a common disturbance (Enright et al. 1998). Then why do some species only have weakly serotinous cones? The answer must lie in the cost:benefit analysis where the costs of an increased degree of serotiny outweigh the benefits (Midgley 2000). Black spruce is less serotinous than other

northern tree species (e.g., *Pinus banksiana*). For these northern black spruce forests, where plant resources can be limited, perhaps it requires less energy to produce large cone crops that retain seeds for 1-2 years than it is to maintain serotiny in cones for many years. For large seeded species that require more energy to produce a single cone or seed, it may be advantageous to invest in an increased degree of serotiny. Whereas the smaller seeded species, such as black spruce it is probably less expensive to produce cones and seeds than it is to maintain an increased degree of serotiny. Furthermore, if trees live in an environment where they can reliably produce cones every year then it becomes less important to maintain the seeds from a good year of cone production over long periods of time.

#### **4.6 Aging errors**

There are many difficulties associated with aging black spruce, especially those grown under harsh environmental conditions (Black and Bliss 1980). Black spruce develop adventitious roots along the basal part of the stem in order to stabilize the stem and provide better aeration of the roots in the rapidly growing moss layer of the forest floor (LeBarron 1945). This means that the true root collar of black spruce trees is underneath the adventitious roots (Telewski and Lynch 1991), and there can be up to 20 additional growth rings in underground stem sections when compared to the age at ground level (DesRochers and Gagnon 1997). Therefore, studies using ground level stem disks or cores like this one will typically underestimate the true age of black spruce trees (LeBarron 1945, Gagnon and Morin 1992, Gagnon et al. 1992). In addition, black spruce often have a reverse taper, where the ring formation starting at the crown of the tree does not always reach the base of the stem (Esau 1960). Missing or incomplete rings are common in black spruce trees where the growing season is short and trees do not have enough time to complete an entire growth ring (Black and Bliss 1980). It is apparent that achieving an

accurate age is very difficult, since nowhere along the stem is there an entire series of growth rings (DesRochers and Gagnon 1997). Furthermore, black spruce reproduce asexually by layering (Laberge et al. 2000), which could mean that some of the age variation in older sites is due to growth of younger clones of the parent trees.

The tree ages determined in this study are likely biased by aging errors associated with the growth patterns of black spruce, in addition to natural variation in tree ages. It is also evident that as the stands increase in age, the distance between the ground level and the root collar increases, so that ground level samples further underestimate the true age. Given the nearly 1:1 relationship between oldest tree age and mean stand age for stands up to 100 years old, age estimates in this study are likely to be more accurate for young stands than old stands. The small age variation in young stands is consistent with observations of recruitment after fire typically occurring in a single pulse, usually in less than 10 years after fire (Johnson and Fryer 1989, DesRochers and Gagnon 1997, Gutsell and Johnson 2002, Johnstone et al. 2004). However, the wider age distribution in older stands suggests that some recruitment occurs continuously across many decades. These aging discrepancies between young and old stands have implications for interpreting forest age structures and patterns of recruitment after fire (Johnson and Fryer 1989, Johnson et al. 1994, Peters et al. 2002). For older stands, procedures such as cross-dating using below ground sections or numerous sections along the stem will help to determine a more accurate age of black spruce trees and stands (Norton and Ogden 1990). Such analyses go beyond the scope of this project as precise age estimates are not essential to understanding the general patterns between stand age and seed production. For the purposes of this study tree ages were considered to be minimum tree ages. Therefore, it can be assumed that all of the tree ages would be older if accurate aging techniques, such as cross-dating with belowground stem disks,

were used. It is important for studies investigating forest dynamics that rely on accurate ring estimates, to use precise aging techniques for determining tree ages and establishment periods.

#### **4.7 Conclusions**

This results of this study illustrate the strong relationships between stand age and stand basal area with cone and seed production of northern black spruce. The equations presented here can be used to predict the seed capacity and regeneration potential of black spruce stands with known stand basal area or stand age. These can be a key component to improving our ability to predict regeneration and succession patterns after disturbance, especially under the current conditions of global climate change and increases in extreme fire weather for most of the North American boreal forest (Flannigan et al. 2005, Parisien et al. 2005, Balshi et al. 2009).

The results suggest that fire cycles less than 50 years could result in reduced black spruce densities on severely burned soils because of the low number of viable seed in these young forests. For recruitment on organic seedbeds, forests need to be reproductively mature with large quantities of viable seed to maintain self-replacement after fire. The results of this study suggest that post-fire sites with organic seedbeds are more vulnerable to alternate successional pathways under a shortened fire return interval and fire cycles less than 150 years may result in decreased post-fire black spruce density. This knowledge is important for predicting regeneration patterns after fire and for understanding the life history of these dominant black spruce forests of interior Alaska and northern Yukon (Van Cleve and Dyrness 1983).

An unusual fire event or compound disturbances may weaken the stable successional cycles of these northern black spruce forests (Payette et al. 2000, Johnstone and Chapin 2006b). These events could potentially permit abrupt changes in species configurations. Under a shortened fire cycle, black spruce stands may burn at an age where they are not reproductively

mature or have enough viable seed to self-replace after fire. These disturbance events may shift the post-fire communities to alternate species configurations, which may include higher components of small seeded and wind dispersed species such as deciduous species. These alternate pathways of secondary succession will alter many of the landscape level properties that contribute to the ecosystem function. Evapotranspiration, albedo, and surface roughness all affect land-atmosphere energy exchange, which is largely controlled by finer scale characteristics, including leaf area, biomass, and canopy architecture of the dominant species (Chapin et al. 1996). Therefore, an alternate landscape makeup will result in different ecosystem function, which could include changes in atmosphere energy exchange (Chapin et al. 2000), and carbon turnover (Hobbie et al. 2000). Thus, a shortened fire return interval could affect species regeneration potential, shifting species configurations, which can have impacts on the long-term response of this ecosystem to global climate change.



## 5.0 LITERATURE CITED

- Atkinson, G. T. and V. F. Haavisto. 1996. Intermediate crown class black spruce cones have more seeds. Page 4 in Great Lakes Forest Research Centre, Minister of Supply and Services Canada, Ottawa, ON.
- Balshi, M. S., A. D. McGuire, P. Duffy, M. Flannigan, J. Walsh, and J. Melillo. 2009. Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. *Global Change Biology* **15**:578-600.
- Black, R. A. and L. C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. *Ecological Monographs* **50**:331-354.
- Bonan, G. B. 1990. Carbon and nitrogen cycling in North American boreal forests. I. Litter quality and soil thermal effects in interior Alaska. *Biogeochemistry* **10**:1-28.
- Brown, C. Unpublished data. Vegetation shifts in latitudinal treeline: The effects of an alternate fire return interval. Ph. D. Thesis. University of Saskatchewan, Saskatoon, SK.
- Brown, C. and J. Johnstone. - Unpublished.
- Cameron, H. 1953. Melting point of the bonding material in lodgepole pine and jack pine cones. Canada Department for Silviculture, Leaflet No. 86:3.
- Canada Soil Survey Committee. 1978. The Canadian system of soil classification. Research Branch, Canada Department of Agriculture, Ottawa, ON.
- Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. *Canadian Journal of Forest Research* **34**:778-787.
- Chai, T. S. and L. H. Henry. 1952. Characteristics of black spruce seed from cones of different ages. *Minnesota Forestry Notes* **2**.
- Chapin, F. S. III, A. D. McGuire, J. T. Randerson, R. Pielke Sr., D. Baldocchi, S. E. Hobbie, N. Roulet, W. Eugster, E. Kasischke, E. B. Rastetter, E. B. Zimov, and S. A. Running. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology* **6 (Suppl. 1)**:211-223.
- Chapin, F. S. III, H. L. Reynolds, C. D'Antonio, and V. Eckhart. 1996. The functional role of species in terrestrial ecosystems. Pages 403-428 in B. Walker, editor. *Global Change in Terrestrial Ecosystems*. Cambridge University Press, Cambridge.
- Charron, I. and D. F. Greene. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. *Canadian Journal of Forest Research* **32**:1607-1615.
- Cook, E. and L. A. Kairiukstis, editors. 1990. *Methods of dendrochronology: Applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, Netherlands, Boston.
- Crawley, M. J. 2007. *The R book*. John Wiley & Sons Ltd., Chichester, England.
- DesRochers, A. and R. Gagnon. 1997. Is ring count at ground level a good estimation of black spruce age? *Canadian Journal of Forest Research* **27**:1263-1267.
- Elliott, D. L. 1979. The current regenerative capacity of the northern Canadian trees, Keewatin, N. W. T., Canada: Some preliminary observations. *Arctic and Alpine Research* **11**:243-251.
- Ellis, R. H., T. D. Hong, and E. H. Roberts. 1986. Logarithmic relationship between moisture content and longevity in sesame seeds. *Annals of Botany* **57**:499-503.
- Ellis, R. H. and E. H. Roberts. 1980. Improved equations for the prediction of seed longevity. *Annals of Botany* **45**:13-30.

- Enright, N. J., R. Marsula, B. B. Lamont, and C. Wissel. 1998. The ecological significance of canopy seed storage in fire-prone environments: A model for non-sprouting shrubs. *Journal of Ecology* **86**:946-959.
- Eremko, R. D., D. G. W. Edwards, and D. Wallinger. 1989. A guide to collecting cones of British Columbia conifers. Page 114 p *in* Canadian Forest Service, Ministry of Forests, British Columbia.
- Esau, K. 1960. Anatomy of seed plants. John Wiley & Sons, Ltd., New York, NY.
- Fenton, N., N. Lecomte, S. Légaré, and Y. Bergeron. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications. *Forest Ecology and Management* **213**:151-159.
- Flannigan, M. and B. M. Wotton. 2001. Climate, weather and area burned. Page 335-357 *in* Forest fires: Behavior and ecological effects. Johnson, E. A and Miyanishi, K. editors. Academic Press.
- Flannigan, M. D., Y. Bergeron, O. Engelmark, and B. M. Wotton. 1998. Future wildfire in circumboreal forests in relation to global warming. *Journal of Vegetation Science* **9**:469-476.
- Flannigan, M. D., K. A. Logan, B. D. Amiro, W. R. Skinner, and B. J. Stocks. 2005. Future Area Burned in Canada. *Climatic Change* **72**:1-16.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. Government Printing Office, Washington, D.C.
- Fraser, J. W. 1975. A technique for tagging tree seed to facilitate identification or recovery in nursery and field experiments. *Canadian Journal of Forest Research* **5**:492-495.
- Fried, J., M. Torn, and E. Mills. 2004. The impact of climate change on wildfire severity: A regional forecast for northern California. *Climatic Change* **64**:169-191.
- Gagnon, J. D. and H. Morin. 1992. Establishment period of black spruce (*Picea mariana*) after fire. Pages 112-114 *in* LUNDQUA Report 34, T. S. Bartholin, B. E. Berglund, D. Eckstein, and F. H. Schweingruber, editors. Lund University, Lund.
- Gagnon, R., G. Villeneuve, H. Morin, and H. St-Pierre. 1992. Dating mistakes of mature black spruce (*Picea mariana*) after fire and their impact on population dynamics studies *in* Proceedings of Disturbance Dynamics in Boreal Forest Workshop, University of Umea, Sweden.
- Greene, D. F. and E. A. Johnson. 1999. Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. *Canadian Journal of Forest Research* **29**:462-473.
- Greene, D. F., C. Messier, H. Asselin, and M. J. Fortin. 2002. The effect of light availability and basal area on cone production in *Abies balsamea* and *Picea glauca*. *Canadian Journal of Botany* **80**:370-377.
- Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M. J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* **29**:824-839.
- Green, S. - Personal Communication.
- Gutsell, S. L. and E. A. Johnson. 2002. Accurately ageing trees and examining their height-growth rates: Implications for interpreting forest dynamics. *Journal of Ecology* **90**:153-166.

- Haavisto, V. F. and D. A. Skeates. 1995. Variability in black spruce cone and seed production. Page 4 p *in* Great Lakes Forest Research Centre. Minister of Supply and Services, Ottawa, ON.
- Henttonen, H., M. Kanninen, M. Nygren, and R. Ojansuu. 1986. The maturation of *Pinus sylvestris* seeds in relation to temperature climate in northern Finland. *Scandinavian Journal of Forest Research* **1**:243-249.
- Hobbie, S. E., J. P. Schimel, S. E. Trumbore, and J. R. Randerson. 2000. Controls over carbon storage and turnover in high-latitude soils. *Global Change Biology* **6**:196-210.
- Hollingsworth, T. N., M. D. Walker, F. S. III Chapin, and A. L. Parsons. 2006. Scale-dependent environmental controls over species composition in Alaskan black spruce communities. *Canadian Journal of Forest Research* **36**:1781-1796.
- Jasinski, J. and S. Payette. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. *Ecological Monographs* **75**:561-583.
- Johnson, E. A. 1992. *Fire and vegetation dynamics: Studies from the North American boreal forest*. Cambridge University Press.
- Johnson, E. A. and G. I. Fryer. 1989. Population dynamics in lodgepole pine-engelmann spruce forests. *Ecology* **70**:1335-1345.
- Johnson, E. A., K. Miyanishi, and H. Kleb. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta-Picea engelmannii* forest. *Journal of Ecology* **82**:923-931.
- Johnstone, J., L. Boby, E. Tissier, M. Mack, D. Verbyla, and X. Walker. 2009. Postfire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. *Canadian Journal of Forest Research* **39**:1575-1588.
- Johnstone, J., F. S. III Chapin, T. N. Hollingsworth, M. Mack, V. E. Romanovsky, and M. Turetsky. 2010a. Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research* **40**:1302-1312.
- Johnstone, J. F. and F. S. III Chapin. 2006a. Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems* **9**:14-31.
- Johnstone, J. F. and F. S. III Chapin. 2006b. Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems* **9**:268-277.
- Johnstone, J. F., F. S. III Chapin, J. Foote, S. Kemmett, K. Price, and L. Viereck. 2004. Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research* **34**:267-273.
- Johnstone, J. F., T. N. Hollingsworth, F. S. III Chapin, and M. C. Mack. 2010b. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* **16**:1281-1295.
- Jorgenson, T. 1984. The response of vegetation to landscape evolution on glacial till near Toolik Lake, Alaska. Pages 134-141 *in* Proceedings of the International Symposium, Society of American Foresters Regional Technical Conference. Society of American Foresters, Fairbanks, Alaska.
- Kasischke, E. S. and M. R. Turetsky. 2006. Recent changes in the fire regime across the North American boreal region-Spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters* **33**:L09703.
- Koski, V. and R. Tallquist. 1978. Results of long-time measurements of the quality of flowering seed crop trees. *Folia Forestali* **364**:1-60.

- Krawchuk, M. A., S. G. Cumming, and M. D. Flannigan. 2008. Predicted changes in fire weather suggest increases in lightning fire initiation and future area burned in the mixedwood boreal forest. *Climatic Change* **92**:83-97.
- Laberge, M. J., S. Payette, and J. Bousquet. 2000. Life span and biomass allocation of stunted black spruce clones in the subarctic environment. *Journal of Ecology* **88**:584-593.
- Lavoie, L. and L. Sirois. 1998. Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. *Journal of Vegetation Science* **9**:483-492.
- Leadem, C. L., S. L. Gillies, H. K. Yearsley, V. Sit, D. L. Spittlehouse, and P. J. Burton. 1997. Field studies in seed biology. British Columbia Ministry of Forests, Victoria, BC.
- LeBarron, R. K. 1945. Adjustment of black spruce root systems to increasing depth of peat. *Ecology* **26**:309-311.
- Lynch, J. A., J. S. Clark, N. H. Bigelow, M. E. Edwards, and B. P. Finney. 2002. Geographic and temporal variations in fire history in boreal ecosystems of Alaska. *Journal of Geophysical Research* **107**:8152.
- Midgley, J. 2000. What are the relative costs, limits and correlates of increased degree of serotiny? *Australia Ecology* **25**:65-68.
- Mueller-Dombois, D. 1985. The ecology of natural disturbance and patch dynamics: Aims and methods of vegetation ecology. Academic Press, Orlando, New York.
- Nathan, R., U. N. Safriel, I. Noy-Meir, and G. Schiller. 1999. Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree. *Journal of Ecology* **87**:659-669.
- Norton, D. A. and J. Ogden. 1990. Problems with the use of tree rings in the study of forest population dynamics. Pages 284-288 in L. Kairikükštis and E. Cook, editors. *Methods of dendrochronology: Applications in the environmental sciences*. Kluwer Academic Publishers, Norwell, Mass.
- O'Reilly, C., W. H. Parker, and J. E. Barker. 1982. Effect of pollination period and strobili number on random mating in a clonal seed orchard of *Picea mariana*. *Silvae Genetica* **31**:90-94.
- Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* **343**:51-53.
- Paine, R. T. and S. A. Levin. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145-178.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535-545.
- Parisien, M. A., K. G. Hirsch, V. Kafka, J. B. Todd, N. Flynn, and M. Flannigan. 2005. Fire behavior potential in central Saskatchewan under predicted climate change. Prairie Adaptation Research Collaborative. Canadian Forest Service, British Columbia.
- Payette, S., N. Bhiry, A. Delwaide, and M. J. Simard. 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: The catastrophic impact of insect defoliators and fire on the spruce-moss forest. *Canadian Journal of Forest Research* **30**:288-305.
- Peters, V. S., S. E. Macdonald, and M. R. T. Dale. 2002. Aging discrepancies of white spruce affect the interpretation of static age structure in boreal mixedwoods. *Canadian Journal of Forest Research* **32**:1496-1501.
- Pickett, S. T. A. and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic, Sand Diego, CA.

- Price, C. and D. Rind. 1994. The impact of a 2 X CO<sub>2</sub> climate on lightning-caused fires. *Journal of Climate* **7**:1484-1494.
- Safford, L. E. 1974. *Picea* in Forest Service, USDA. Seeds of woody plants in the United States, Washington, D.C.
- Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* **54**:661-676.
- Schweingruber, F. H. 1988. *Tree rings: Basics and applications of dendrochronology*. Kluwer Academic, Boston.
- Sirois, L. 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest-tree line transect. *Canadian Journal of Forest Research* **30**:900.
- Skeates, D. A. and V. F. Haavisto. 1987. Black spruce cone and seed production: Yield from Ontario collections. Ontario Ministries of Natural Resources, Ottawa, ON.
- Stocks, B. J., J. A. Mason, J. B. Todd, E. M. Bosch, B. M. Wotton, B. D. Amiro, M. D. Flannigan, K. G. Hirsch, K. A. Logan, D. L. Martell, and W. R. Skinner. 2002. Large forest fires in Canada, 1959–1997. *Journal of Geophysical Research* **108**.
- Stokes, M. A. 1968. *An introduction to tree-ring dating*. University of Chicago Press, Chicago.
- Telewski, F. W. and A. M. Lynch. 1991. Measuring growth and development of stems. Pages 503-555 in J. P. Lassoie and T. M. Hinckley, editors. *Techniques and approaches in forest tree ecophysiology*. CRC Press Inc., Boston, Mass.
- Tinner, W., C. Bigler, S. Gedye, I. Gregory-Eaves, R. T. Jones, P. Kaltenrieder, U. Krähenbühl, and F. S. Hu. 2008. A 700-year paleoecological record of boreal ecosystem responses to climatic variation from Alaska. *Ecology* **89**:729-743.
- Tymstra, C., M. Flannigan, O. B. Armitage, and K. A. Logan. 2007. Impact of climate change on area burned in Alberta's boreal forest. *International Journal of Wildland Fire* **16**:153-160.
- Van Cleve, K. and C. T. Dyrness. 1983. Introduction and overview of a multidisciplinary research project: The structure and function of a black spruce (*Picea mariana*) forest in relation to other fire-affected taiga ecosystems. *Canadian Journal of Forest Research* **13**:695-702.
- Van Cleve, K., C. T. Dyrness, L. A. Viereck, J. Fox, F. S. III Chapin, and W. Oechel. 1983. Taiga ecosystems in interior Alaska. *BioScience* **33**:39-44.
- Van Cleve, K. and L. Viereck. 1981. Forest succession in relation to nutrient cycling in the boreal forests of Alaska. Pages 184-211 in D. C. West, H. Shugart, and D. B. Botkin, editors. *Forest Succession: Concepts and applications*. Springer-Verlag, Berlin.
- Van Wagner, C. E. 1987. *Development and structure of the Canadian forest fire weather index system*. Canadian Forest Service, Ottawa, ON.
- Vertucci, C. W. and E. E. Roos. 1990. Theoretical basis of protocols for seed storage. *Plant Physiology* **94**:1019-1023.
- Viereck, L., editor. 1983. *The effects of fire in black spruce ecosystems of Alaska and northern Canada*. Wiley.
- Viereck, L. A. 1979. Characteristics of treeline plant communities in Alaska. *Holarctic Ecology* **2**:228-238.
- Vitt, D. H., L. A. Halsey, I. E. Bauer, and C. Campbell. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences* **37**:683.
- Wein, R. W. 1975. *Vegetation recovery in arctic tundra and forest-tundra after fire*. Canadian Department of Indian and Northern Affairs, Ottawa, ON.

- Wilton, W. C. 1963. Black spruce seedfall immediately following a fire. *The Forestry Chronicle* **39**:477-478.
- Wotton, B. M. and M. Flannigan. 1993. Length of the fire season in a changing climate. *The Forestry Chronicle* **69**:477-478.
- Yarie, J. 1981. Forest fire cycles and life tables: A case study from interior Alaska. *Canadian Journal of Forest Research* **11**:554-562.
- Yarrangton, M. and G. A. Yarrangton. 1975. Demographay of a jack pine stand. *Canadian Journal of Botany* **53**.
- Yukon Ecoregions Working Group (YEWG). 2004. Yukon boreal cordillera and taiga cordillera. *in* C. A. C. Smith, J. C. Meikle, and C. F. Roots, editors. *Ecoregions of the Yukon Territory: Biophysical properties of Yukon landscapes*, Summerland, British Columbia.
- Zasada, J. C. 1988. Embryo growth in Alaskan white spruce seeds. *Canadian Journal of Forest Research* **18**:64-67.
- Zasada, J. C. and D. F. Grigal. 1978. The effects of silvicultural system and seed bed preparation on natural regeneration of white spruce and associated species in interior Alaska. Pages 213-220 *in* Fifth North American Forest Biology Workshop, Gainesville, FL.
- Zasada, J. C. and R. A. Norum. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. *Canadian Journal of Forest Research* **13**:903-913.
- Zasada, J. C., T. L. Sharik, and M. Nygren, editors. 1992. The reproductive process in boreal forest trees *in* Shugart, H., Leemans, R., and Bonan, G. B., editors. *A systems analysis of the global boreal forest*. Cambridge University Press.
- Zasada, J. C., L. Viereck, and J. Foote. 1979. Black spruce seed fall and seedling establishment. *in* L. Viereck and C. T. Dyrness, editors. *Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska*. Forest Service, Portland, OR.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.