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GROWTH AND PHOTOSYNTHETIC RESPONSES OF WHITE SPRUCE SEEDLINGS TO LEVELS OF TREMBLING ASPEN AND RED RASPBERRY COVER

By

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ABSTRACT

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KEY WORDS: competition, ground line diameter, height, microclimate, NEBIE, photosynthetically active radiation, *Picea glauca* (Moench.) Voss, *Populus tremuloides* Michx., regeneration, *Rubus idaeus* L., stem volume index.

The effect of competitive species upon crop tree regeneration and growth continues to receive attention from researchers due to the importance of the outcomes. This study takes a new approach, by examining the combined effects of varied levels of trembling aspen (*Populus tremuloides* Michx.) and red raspberry (*Rubus idaeus* L.) upon microclimate and 68-83cm high white spruce *(Picea glauca* [Moench.] Voss*)* seedling growth and rates of photosynthesis. Regression, curve estimation and response surface methodology were used to examine the interactions between the two competitive species and the crop species, to ascertain the importance of each competitor and in what aspect it competes. Both species reduced the available photosynthetically active radiation and negatively affected white spruce stem volume index growth, ground line diameter growth, height growth, and height/GLD ratio. However evidence suggests that aspen was the more competitive species, with the effect of raspberry marginalized when the two species are growing in combination.

The study also attempted to define the most suitable approach for quantifying the competition the seedling is under and what species in what areas need to be targeted for removal or management. A quadrant approach and total plot approach to assessing percent cover values within circular plots were compared. The results suggest that for determining white spruce seedling growth under competition from aspen and raspberry, a quadrant approach is unnecessary with total percent cover values above seedling height being equally effective at much lower cost.

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INTRODUCTION

Surrounding competitive vegetation affects the environment of white spruce (*Picea glauca* [Moench.] Voss) seedlings, and these environmental conditions control their rates of growth and physiological processes (Margolis and Brand 1990). There has been research into a variety of herbaceous and woody plants that compete with white spruce for light, nutrients and water. Current studies have attempted to define the effect of environmental conditions upon crop tree growth (Margolis and Brand 1990), but there is a lack of literature looking at the combined, interactive effect of multiple competitors. Several authors have emphasized the need for silviculture that is based upon a better understanding of non-crop species interactions and crop tree responses (e.g. Bell 1991, Wagner and Zasada 1991, Mallik *et al.* 1997).

Ontario allocates considerable resources to monitoring and managing disturbances that affect the forest (OMNR 2001). Incidents of natural disasters including fire, disease, insects and severe weather are reported to be equal to or at lower levels than previously recorded (OMNR 2001). Disturbances occur naturally in forest systems, however harvesting of wood by humans is the largest scale disturbance occurring in most forested areas (Radosevich *et al.* 2007). Whilst logging is an important part of Ontario's economy, it is an anthropogenic disturbance which has different effects on the environment than natural disasters. With almost 2/3 of Ontario's land consisting of forest (OMNR 2011), logging and regeneration of these sites in a sustainable way is vital to the ecological, economic and social well-being of the people living there and future generations (OMNR 2001). The crown owns and manages 90% of this forest, and the focus on research and biodiversity has made Ontario a world leader in sustainable forest management (OMNR 2011). Management policies are being implemented to make logging mimic some of the traits of natural disturbances. For example Ontario's Forest Management Guide for Natural Disturbance Pattern Emulation requires retention of trees and recommends leaving some dead wood to maintain biodiversity, as well as designing the shape, size and distribution of clearcuts to emulate the local historical pattern of natural disturbances such as wildfires (OMNR 2001).

Research based on the ecology and interactions of species in response to logging is crucial for the formation of such policies to develop silviculture capable of lessening the impact of the disturbance and allowing for successful regeneration of the crop tree, as well as maintaining biodiversity. Following a disturbance such as logging, new areas of warm soils, with high light levels, increased soil moisture and nutrient availability (Lieffers *et al.* 1993) are available for colonization by fast-growing pioneer species, which can quickly become dominant (Radosevich *et al.* 2007). While this is common and usually a natural stage in the successional process, it can delay and reduce the regeneration of the higher value crop trees that are desired by the forest industry (Balandier *et al.* 2006), by creating competition for light, nutrients and water (Radosevich *et al.* 1990).

Regeneration of white spruce in logged sites is not always successful, with the crop trees often being suppressed by undesirable competitive species (Campbell 1990, Mallik *et al.* 1997). Margolis and Brand (1990) used a survey by the Ontario Ministry of Natural Resources (OMNR) in 1988 to demonstrate this situation: 40-

60% of the plantations in Northern Ontario had poor levels of reforestation with low crop tree survival or high competition levels. These figures may have improved, but it still demonstrates the need for research into regeneration and competition. Margolis and Brand (1990) suggested that research is needed to determine the effects of silvicultural treatments on the seedlings' environment, and relate these environmental conditions to seedling development, including growth, physiology and biochemistry.

The negative effects of competition between plant species in young forest stands have been well documented (Balandier *et al.* 2006, Radosevich *et al.* 2007). Relationships between plant species are very complex and present many difficulties when attempting to derive silvicultural strategies (Radosevich *et al.* 2007). These plant interactions are being examined and the findings integrated into new competition management plans (Radosevich *et al.* 2007).

Control of competitive species has become a major part of silvicultural management plans due to the negative effect of competition upon crop species development (Radosevich *et al.* 1990). Sutton (1985) described the widespread problems in Canada, and blamed them upon exploitative forestry practices and insufficient consideration of regeneration processes. However Sutton was writing more than 25 years ago. Exploitative forestry practices may still exist, but more effort and research is being dedicated to understanding the ecological processes of regeneration in order to ensure more sustainable plantations and higher value yields of crop trees (Arseneault *et al.* 2011, Fleming and Smith 2011).

The aim of this study is to contribute towards improving the establishment of white spruce forest stands by understanding the mechanisms by which other plant species interact and compete with newly planted white spruce. Growth of a plant is the result of interactions between its physiological processes and its environment (Brand 1991). Goldberg (1990) put forth a conceptual model which splits competition into two factors: the effect of the competitive species on available resources, and the physiological response of the crop tree to these effects. My study addresses both of these issues, by investigating the growth and photosynthetic responses of six-year-old white spruce seedlings under microclimatic conditions created by varied levels of competition from mixtures of trembling aspen (*Populus tremuloides* Michx.) and red raspberry (*Rubus idaeus* L.). These are two of the most dominant and extensive competitive species present in young white spruce and mixed stands which interact with the white spruce in different ways (Bell *et al.* 2011), and little is known about their combined effect.

In order to make any management decisions, quantitative methodologies must be developed for use in the field to determine levels and types of competition. This study uses and assesses the appropriateness of parts of two of these which are currently in use, the quadrant approach from the "Silvicultural Treatment Assessment and Reporting System (STARS)" (Pinto *et al.* 2009) and the "Well-spaced Free-growing Regeneration Assessment Procedure for Ontario" (White *et al.* 2005), both of which are described further in the methodology.

LITERATURE REVIEWS

WHITE SPRUCE ECOPHYSIOLOGICAL RESPONSES TO COMPETITION

The growth of white spruce seedlings depends upon their inherent growth potential and the degree to which their surrounding environment allows them to reach this potential (Grossnickle 2000). Competition has been reported to account for as much as 70% of reduction in spruce growth (Filipescu and Comeau 2007a), although the intensity of this impact varies according to many factors such as species, microclimate, and silvicultural treatments. Spruce seedling performance on northern latitude reforestation sites is often reduced by competing vegetation (Grossnickle 2000). White spruce is a slow growing species, and according to Lieffers and Beck (1994) takes 70 years to become dominant in the canopy in mixedwood stands in the western boreal forest. This means competition remains important in its development for a long time. However the early stages of crop tree development are crucial. Research suggests that control of competitive species is most important in the first 4 - 6 years of spruce growth after planting (Wagner and Robinson 2006, Comeau and Harper 2009). In the early stages the planted spruce seedlings are not well established, with limited root systems (Burdett *et al.* 1984, Margolis and Brand 1990) and hence have little resilience to stress. As the faster growing competitive vegetation overtakes the height of the seedlings in these first years they can out-compete them for light, water and nutrient resources, resulting in stress, reduced growth and possibly mortality. After this time period, if the spruce seedlings have survived and the environmental conditions have facilitated their growth, then they are better established and have an improved ability to survive stress and competition.

The initial shoot growth of white spruce seedlings occurs in spring but is the result of stem units developed in the previous year's growing season (Grossnickle 2000). The shoots grow longer according to the environmental conditions and resource availability at the site during the current growing season (Grossnickle 2000). O'Rielly and Parker (1982) reported the shoot growth period to be between 6 and 7 weeks at a site in north-western Ontario. The number of needle primordia that are formed in the buds is determined by the environmental conditions the seedling is exposed to during its shoot development phase, all of which are affected by competing vegetation (Grossnickle 2000). Temperature, soil water potential, light intensity and photoperiod length, and nutrients are all important factors, with lower levels of each resulting in buds with fewer primordia (Pollard and Logan 1977, 1979, Colombo 1997). The number of needle primordia influences the level of shoot growth in the next growing season (Grossnickle 2000).

Whereas shoot growth over a season is pre-determined by the previous year, the diameter growth of a white spruce seedling is determined largely by the environmental conditions of the current year (Grossnickle 2000). Due to this fact, diameter growth is more sensitive to growing season changes and competition than height growth (Zedaker *et al.* 1987, Lautenschlager 1999, Grossnickle 2000, Jobidon 2000). Research by Groot (1999) supports this, with increases in diameter growth of seedlings with vegetation control, whereas height growth response was inconsistent.

Microclimatic factors such as light availability, air temperature, soil temperature and soil moisture are all important factors for plant growth. Levels of competitive vegetation affect both above and below-ground microclimate (Reynolds *et al.* 1997). In forest management where the aim is to improve the productivity of the crop tree, factors which affect microclimate should be taken into consideration. White spruce seedlings planted in clear cut areas of boreal forest are sometimes unsuccessful (Stiell 1976). Microclimate of these areas may contribute to the white spruce failure, due to late spring frosts and large amounts of competing broadleaf and grassy vegetation resulting from high light levels (Carlson and Groot 1997). Pitt *et al.* (1989) suggested a moderate overstory including some shrubs can be better for white spruce development than no surrounding vegetation. These can create a suitable microclimate with increased humidity and soil moisture, despite reducing light levels somewhat (Arnup *et al.* 1988).

LIGHT

Effect of Competing Vegetation on Light

Both the amount of light and the quality of light (in terms of the ratios of different wave bands) available for the crop species are critical for their development (Mortensen and Sandvik 1988). The quality of light decreases as it passes through the canopy, and poor quality light can reduce needle, stem and root dry weight, shoot length, and stem diameter of conifers (Mortensen and Sandvik 1988). Most models are based on the availability of photosynthetically active radiation (% PAR) due to consistent research showing this to be one of the most important resource in tree growth due to its effect on rates of photosynthesis (Stadt *et al.* 2005). Several studies have linked available PAR to height and diameter growth of crop trees and found correlations suggesting that PAR is critical to crop tree development (Lieffers and Stadt 1994, Wright *et al.* 1998, Duchesneau *et al.* 2001, Claveau *et al.* 2002). It is also one of the more manageable aspects of vegetative competition, as we have the ability to reduce or remove the surrounding canopy, meaning controlling available PAR is a major component in forest management when controlling competition.

The amount of light that reaches white spruce seedlings is affected by the competing vegetation, and this influences their physiological and morphological responses (Grossnickle 2000). White spruce has poor initial height growth which means it is often overtopped by other vegetation during the initial stages of development (Rowe 1955, Chen and Popadiouk 2002). Competitive species such as aspen and raspberry can hinder white spruce seedling development by growing more quickly and out-competing the spruce for resources, especially light (Rowe 1955, Awada and Redmann 2000, Donoso and Nyland 2006).

On productive reforestation sites the amount of solar radiation reaching white spruce seedlings is reduced as competitive vegetation increases (Brand 1991, Groot 1999, Grossnickle 2000). Increases in aspen basal area and raspberry have been shown to correlate with a decrease in light conditions, and lower growth rates of white spruce (Comeau 2001, Pinno *et al* 2001, Donoso and Nyland 2006, Filipescu and Comeau 2007b, Bell *et al.* 2011). Whilst trembling aspen has small leaves that move and do not create a closed overstory, they can still have a fairly large total leaf area, reducing available PAR below the canopy. Pinno *et al.* (2001) examined 96 juvenile aspen stands in Alberta, Canada, and found the maximum leaf area index (LAI) to be around 4 $m^2 \cdot m^{-2}$. Thevathasen *et al.* (2000) however reported 4 year old aspen to have an effective LAI of up to 1 $m^2 \cdot m^{-2}$ compared to raspberry with an effective LAI of up to 4 $m^2 \cdot m^{-2}$. The main competitive element of red raspberry is its dense canopy that reduces the light available for the white spruce, with less than 10% PAR recorded as passing through in a study by Shropshire *et al.* (2001). Research by Reynolds *et al.* (2002) in Ontario reports that when grown as monospecific cultures with black spruce seedlings for 6 years, aspen cover reduced available PAR and spruce growth more than red raspberry, however the combined effects of both species are unknown.

Lambers *et al.* (2008) describe average irradiance as decreasing exponentially through the plant canopy. Stadt and Lieffers (2005) found Beers Law could be used to successfully predict the amount of PAR transmitted through a canopy using leaf area index. Beer's law predicts the transmission of PAR (T) and the ratio of below vegetation (Q) and above vegetation PAR (Q0) using the leaf area index of the vegetation (LAI) and is written as:

$$T = Q/Q_0 = \exp(-K_{LAI}LAI)$$

K_{LAI} is known as the bulk extinction coefficient and is estimated from LAI and PAR transmission measurements (Stadt and Lieffers 2005). The equation can be transformed using the natural logarithm into the following:

$$\ln(T) = -k\ LAI$$

or

$$\ln(Q) = \ln(Q0) - (k\ LAI)$$

Taking this into account, a logarithmic relationship between PAR available at seedling height and the LAI or percent cover of the canopy and overtopping vegetation may be expected. The small and trembling leaves of aspen can however allow more light through than a dense, fixed position canopy, providing more sunflecks which can provide short durations of high intensity light for seedlings, even if the general background is of low light levels (Lambers *et al.* 2008).

Effect of Light on Physiological Processes

On a clear-cut regenerating site such as the one used in this study, the photosynthetic performance of spruce seedlings is largely determined by the amount and structure of the canopy formed by competing vegetation (Grossnickle 2000). Light reaching the spruce needles is reflected (6-12%), transmitted (0-40%) or absorbed (48-94%) (Grossnickle 2000). The amount that is absorbed depends mainly upon whether it is a sun or shade needle, the epidermal and hypodermal layers, and the amount of cholorophyll (Grossnickle 2000). Most of the light that is absorbed is lost as heat, with up to 5% being used for photosynthesis (Grossnickle 2000).

Low light can cause stress and limit photosynthesis and net carbon gain (Lambers *et al.* 2008). Photosynthesis increases with the intensity of light available to the needle, until saturation point is reached at which point there is no further benefit to higher light levels, and under strong light photoinhibition and photoxidation of the photosynthetic systems may occur (Coates *et al.* 1994, Lambers *et al.* 2008). Lambers *et al.* (2008) describe the steady state rate of CO_2 assimilation as increasing asymptotically with increasing light. This produces the general photosynthesis light response curve, where the initial linear increase in photosynthesis is limited by light, and once it reaches saturation point it begins to level off and is limited by the carboxylation rate (Lambers *et al.* 2008). According to Coates *et al.* (1994) the saturation point for individual white spruce needles is reached at 25 to 50% full sunlight on a clear day, although this would also depend on whether it was a sun or shade needle, and whole tree saturation points may be different. Light levels in Timmins Ontario can reach over 3000 μmol m^{-2} s^{-1}, yet the saturation points for white spruce photosynthetic system is generally between 600-800 μmol m^{-2} s^{-1} (Man and Lieffers 1997, Man and Greenway 2011). Coates and Burton (1999) found that 40% to 60% sunlight is needed for maximum rates of photosynthesis of white spruce shoots.

At times of the year such as spring and autumn when the aspen has no foliage, white spruce seedlings are able to take advantage of the more open growing conditions, with understory seedlings having relatively high photosynthetic rates (Constabel and Lieffers 1996, Man and Lieffers 1997). White spruce seedlings have both sun and shade needles, but in low light can focus on developing shade needles which are thinner and concentrate the limited light available onto a small volume of tissue in order to increase efficiency and create a positive photosynthetic/respiration balance (Chen 1997, Messier *et al.* 1999, Awada and Redmann 2000, Duchesneau *et al.* 2001). Shade needles have lower respiration rates per unit leaf area than sun needles and also have a larger proportion of spongy mesophyll to enhance absorbance (Lambers *et al.* 2008).

Effect of Light on Seedling Growth

Research suggests that white spruce is a mid-shade tolerant species, doing best in terms of volume growth at light levels exceeding 40-60% light, although gains past these levels up to 100% full light conditions are small (Logan 1969, Coates *et al.* 1994, Lieffers and Stadt 1994, Wright *et al.* 2000). Maximum diameter and stem volume growth occurs at 100% sunlight (Comeau *et al.* 1993, Coates and Burton 1999), with dense or closed overstories resulting in poor white spruce growth due to reduced photosynthesis and net carbon gain under low light conditions (Stiell 1976, Lambers *et al.* 2008).

The effect of competition in terms of reduced light has more of an impact on diameter growth than height growth. White spruce finishes height growth while the competitive species are growing foliage, meaning more light resources are available for the spruce while the shoots are growing, compared to when the spruce is allocating resources to diameter growth (Brand and Janas 1988). Brix (1972) found that total biomass and stem diameter growth of white spruce seedlings were much higher at light intensities of 1000ft-c than at 400ft-c, but height growth was not affected. Man and Greenway (2011) found artificial shade did not affect height growth of white spruce seedlings, but seedlings grown under no cover had 5% larger root collar diameters than seedlings shaded in the summer, and 9% larger than seedlings shaded year round. Eis (1967) found 4 year old white spruce seedlings in the field were twice as high when grown under 60% light compared to those grown at 20% light, and that those at 100% light had increased diameter growth and total biomass, but little further increase in height growth. Lieffers and Stadt (1994) reported similar results with annual height increment increasing from 5cm at 10% light to 25cm at 40% light, which was equal to growth at 100% light. This study also found height/diameter ratio decreased linearly as light intensity increased, from approximately 90 at 8% light to 58 at 100% light.

In response to low light, white spruce seedlings are able to grow their shoots in such a way to develop tree crowns which spread over a wider horizontal area, to capture more light (Oliver and Larson 1996, Chen 1997, Grossnickle 2000). Lieffers and Stadt (1994) found leader length, caliper, and the number of lateral buds on the current growth of the terminal leader to reach a maximum at 40% light and decrease linearly with decreasing light. White spruce seedlings grown under high light intensities are reported to have a lower percentage of biomass in leaves and stem, and higher percentage of biomass in roots (Brix 1972). If light is readily available the seedlings do not have to allocate as much resources to building apparatus to capture it.

AIR TEMPERATURE

Effect of Competing Vegetation on Air Temperature

White spruce seedlings under very little competition are exposed to more extreme and fluctuating air temperatures during the growing season (Grossnickle 2000, Filipescu and Comeau 2011). Parker *et al.* (2009) found air temperature was increased by woody vegetation at the top of the competing understory canopy, as mentioned in Oke (1987). Filipescu and Comeau (2011) found that the number of growing degree hours (sum of hours with air temperature above 5° C) was inversely related to the density of aspen cover, although the differences were small. The shade produced by the canopy can reduce extremely high temperatures especially midday in the summer (Childs and Flint 1987). Canopy density may also prevent extremely low temperatures and frost, especially overnight in spring and fall, by trapping warm air so less longwave radiation is lost from the ground to the atmosphere (Childs and Flint 1987, Grossnickle 2000). Cover can also protect seedlings from further damage from high radiation on days after a frost has occurred by providing shade (Man and

Lieffers 1996, Filipescu and Comeau 2011). Filipescu and Comeau (2011) found that as aspen cover represented by overstory leaf area index reduced, the frequency of hours with temperatures below 0° C increased linearly for one site, although the relationship was not significant at the other site, which they attributed to topographical differences. Shorter more shrub like canopies such as that of red raspberry can reduce the risk of extremely low air temperatures by restricting radiation loss, but not as effectively as taller aspen canopies (Stathers 1989, Donoso and Nyland 2006).

Effect of Air Temperature on Physiological Processes

Temperature influences rates of photosynthesis and respiration through its effects on the enzymatically catalysed reactions and membrane processes (Lambers *et al.* 2008). Grant *et al.* (2008) reported hourly net CO_2 uptake of black spruce (Picea mariana [Mill.] B.S.P.) to increase with warming air temperatures up to 15° C, and decrease with temperatures above 20° C. Extremely high temperatures that occur under no cover can cause increased photorespiration, a decline in net photosynthesis, and also long lasting reductions in photosynthesis rates from damage caused by excess irradiance (Lambers *et al.* 2008). Extremely low temperatures that can occur under no cover can cause late spring and summer frost damage to the white spruce seedlings, resulting in damage to buds and emerging shoots, increased susceptibility to photoinhibition and reductions in photosynthetic capability (Stathers 1989, Bigras and Hébert 1996, Groot and Carlson 1996, Man and Lieffers 1996, Lambers *et al.* 2008). Man and Lieffers (1996) found the light saturated rate of net photosynthesis of two year old white spruce seedlings grown in the open to be similar to those of seedlings grown under aspen overall, but significantly lower in spring and autumn when frosts are common. Lower transpiration rates and stomatal conductances occurred in the autumn for open grown seedlings (Man and Lieffers 1996). The light saturated rate of net photosynthesis, the photochemical efficiency and mesophyll conductance of white spruce seedlings increased from spring to summer and then decreased, with water use efficiency decreasing in the summer as leaf temperature increased, with the changes greater for open grown seedlings (Man and Lieffers 1996). In the summer when the seedlings under the aspen canopy were light limited, they responded by decreasing their compensation and saturation points to increase their photochemical efficiency compared to in spring and autumn and be able to maintain a positive carbon balance (Man and Lieffers 1996).

Effect of Air Temperature on Seedling Growth

Air temperature, particularly low air temperature can be a seriously limiting factor during the growing season in northern climates (Grossnickle 2000). Diameter growth of white spruce seedlings in high latitude forest tends to slow down in the later summer and fall, in accordance with the drop in air temperatures (Grossnickle 2000). Brix (1972) found white spruce seedlings grown under 9 different temperature regimes increased total biomass growth as temperature increased from 8 and 18° C, but no changes in biomass occurred when the temperature was increased from 18 to 24°C. He found the optimum temperature for white spruce height growth was 24° C, and between 18 and 24° C for diameter growth, although higher temperatures of 28° C had equal rates of diameter growth when light intensity was low. However Brix (1972) noted that these seedlings were grown indoors and irrigated, and states that in the field, shade can reduce evapotranspiration and prevent extreme soil temperatures, and so growth responses will be different. He also notes that soil temperatures could not be controlled separately and hence were fairly similar to the set air temperatures and growth responses are likely to have been affected by this as well.

White spruce seedlings have been reported as one of the boreal mixedwood species most susceptible to frost damage, with severe frost able to cause a reduction in growth by 50%, and a late frost in spring can kill newly flushed shoots (Nienstaedt 1985, Cole *et al.* 1999). Protection from these frosts, along with the other possible benefits from vegetative cover can result in greater shoot and needle growth in seedlings grown under cover from species such as aspen, in comparison to seedlings grown in the open (Man and Lieffers 1996).

SOIL TEMPERATURE

Effect of Competing Vegetation on Soil Temperature

Parker *et al.* (2009) found soil temperature was lower in areas with herbaceous and woody vegetation than open areas, due to shading and to leaf litter, consistent with Oke (1987). Filipescu and Comeau (2011) reported a significant decrease in mean soil temperature and growing degree hours (sum of average temperatures above 5° C) at 5 and 20cm as aspen density increased, which is consistent to previous research (Parker *et al.* 2009, Ma *et al.* 2010). Brand (1991) found vegetation control warmed soils slightly over the growing season (May-September) but only by 0.5- 1° C and had less of an effect than soil disturbance during harvesting and site preparation.

Effect of Soil Temperature on Physiological Processes

Low spring soil temperatures, especially when combined with flooded soil conditions, reduce the photosynthetic capacity of white spruce and their ability to take up nutrients, which negatively affects their growth (Grossnickle 1987, 2000, Lahti *et al.* 2005). Low soil temperatures in the growing season increase the resistance of water flow within the spruce roots, and so restrict the water uptake of the seedlings (Grossnickle and Blake 1985, Grossnickle 1988, Mellander *et al.* 2006).

Effect of Soil Temperature on Seedling Growth

Low soil temperatures can have a serious effect on the growth of seedlings in boreal regions, as they affect root growth and biomass partitioning (Lahti *et al.* 2005, Vogel *et al.* 2008, Filipescu and Comeau 2011). Chalupa and Fraser (1968) found a significant effect of soil temperature on white spruce seedling growth when air temperature was kept constant at 21 ℃. Over 8 months white spruce seedlings grown at soil temperatures 18 ℃ were 13.5cm high with a total dry weight of 0.7g, with growth decreasing as soil temperatures increased, down to just 5cm and 0.1g at 32 ℃. Seedlings grown at 18 ℃ developed a small number of thick roots, compared to the larger fine root system developed at the higher temperatures. Those seedlings grown at the lower temperatures had higher levels of soluble sugars per unit dry weight of tissue and a shoot: root dry weight ratio of 6.4:1 compared to 2.3:1 at intermediate and higher temperatures, suggesting a larger amount of photosynthates were invested in the roots at higher soil temperatures (Chalupa and Fraser 1968). It was noted that the seedlings grown at the higher temperatures were unhealthy and some mortality occurred (Chalupa and Fraser 1968), although it must be taken into consideration that constant air temperatures of 21 ℃ and soil temperatures of 32 ℃ are very high. Brand (1991) found that growth of white spruce seedlings increased as soil temperature increased. However his study was conducted in the field with many other confounding factors, rather than in an artificial setting, and the temperatures experienced by the spruce seedlings ranged from 7 ℃ to 22 ℃, and so the higher range of their temperatures were close to the lower temperatures used by Chalupa and Fraser (1968).

SOIL MOISTURE

Effect of Competing Vegetation on Soil Moisture

Available moisture is also a major factor in the growth and survival of white spruce seedlings. Parker *et al.* (2009) reported soil moisture to be lower in areas with high cover of competitive species. Brand (1991) found removal of vegetation reduced the number of days where soil moisture tension above 0.04MPa occurred: there was greater soil moisture availability for seedlings in sites where competing vegetation was controlled. Different species have different effects on soil water. It has been suggested that partial cover from species such as aspen can help reduce the impact of other species such as grass which are stronger competitors for soil water (Voicu and Comeau 2006, Filipescu and Comeau 2011). Raspberry does not have root systems as dense as grass but they can be deep and take up significant amounts of water from the soil (Balandier *et al.* 2006). Bell *et al.* (2011) reported red raspberry to be a strong competitor for soil moisture in their overview of species which compete with conifers, but did not include aspen as a competitor for soil moisture. In contrast to this several studies state aspen to be a strong competitor for soil moisture in northern plantations (Munson *et al.* 1993, Boucher *et al.* 1998, Robinson *et al.* 2001).

Effect of Soil Moisture on Physiological Processes

Reductions in available soil moisture due to competitive vegetation can reduce white spruce seedling growth and result in seedling water stress, as they rely on moisture from the top portion of the soil profile (Grossnickle 2000). Both the supply and demand functions of photosynthesis are affected by water stress, with the main impact being on stomatal and mesophyll conductance (Lambers *et al* 2008). As soil moisture declines, white spruce seedlings close their stomata and reduce their photosynthetic capacity (Grossnickle 2000, Lambers *et al.* 2008). The reduction in photosynthetic rates with increased water stress is related to declines in the biochemical components of the photosynthetic process (Lambers *et al.* 2008).

Effect of Soil Moisture on Seedling Growth

Low soil moisture restricts the growth of seedlings and increases the likelihood of mortality (Peterson *et al.* 1988, Grossnickle 2000, Harper *et al.* 2005). Planted seedlings often have a limited and disconnected root system from being grown in confined conditions and hence can be vulnerable to water stress (Burdett *et* *al.* 1984, Margolis and Brand 1990). In order to survive and grow, seedlings need to invest in new roots to acquire soil water, for which they are dependent on carbohydrate reserves and current photosynthesis which in turn is partially dependent on available soil moisture (Van Den Driessche 1987).

NUTRIENTS

Effect of Competing Vegetation on Nutrient Availability

Light, temperature and soil moisture are all interrelated and all affect nutrient availability in forest soils by influencing microbial activity and nutrient dynamics (Nadelhoffer *et al.* 1991). Low levels of canopy density means larger amounts of sunlight reach the ground, warming the soil and increasing nutrient cycling up to an optimal point, after which too high soil temperatures can damage the proteins and enzymes needed for biological decomposition (Pritchett 1979). Spruce species in general may be susceptible to competition in terms of nutrient resources. Early, fast growing species such as aspen and raspberry have an initial advantage over white spruce seedlings as they are more able to exploit the peak nutrient availability in spring with their seasonal growth strategy than the white spruce (Grossnickle 2000). Raspberry is more efficient than white spruce at competing for soil nitrate, with a high uptake reducing the spruce foliar nitrogen content (Jobidon 2000, Donoso and Nyland 2006). Bell *et al.* (2011) included red raspberry as a strong competitor for nutrients in their overview of species which compete with conifers; however aspen was not reported to be a strong competitor in this aspect.

Competing vegetation can provide some nutrient benefits. Dominance of aspen in regenerating stands can improve nutrient availability for white spruce seedlings by facilitating carbon and nutrient cycling in the soil, due to their large amount of roots, and the speed at which their fine roots and leaf litter decomposes (Wang *et al.* 1995, Finer *et al.* 1997, Prescott *et al.* 2000) . White spruce needles contain higher lignin than aspen leaf litter, and so take longer to decompose (Melillo *et al.* 1982). Raspberry can slow organic matter decomposition by shading the ground and reducing surface temperatures (Federer 1984, Barnes *et al.* 1999, Donoso and Nyland 2006). By taking up large amounts of nitrogen and water and fixing them as biomass raspberry can also act as a nutrient sink, and add nitrogen stored in their biomass when the canopy closes and they decompose (Bormann and Likens 1979, Donoso and Nyland 2006). In areas with high soil water content, raspberry can reduce erosion and leaching of nutrients by increasing the evapotranspiration of a site (Vitousek and Reiners 1975, Donoso and Nyland 2006).

Effect of Nutrient Availability on Physiological Processes

Spruce seedlings accumulate nutrient reserves in the later part of the growing season, meaning their initial growth at the beginning of the season is based on internal reserves (Chapin 1983, Grossnickle 2000). Photosynthesis is strongly related to nitrogen availability, with the majority of nitrogen in a leaf in the photosynthetic machinery and its functions. If light saturated, the rate of photosynthesis increases linearly with leaf nitrogen per unit area (Lambers *et al.* 2008).

Effect of Nutrient Availability on Seedling Growth

The limited root system of planted seedlings makes them vulnerable to nutrient deficiency as they are at a disadvantage compared to competing vegetation to begin with (Burdett *et al.* 1984). Spruce are capable of producing long lived, thick needles with a high leaf mass density, a low specific leaf area and a low leaf nitrogen concentration in response to low soil nitrogen and low soil moisture (Lambers *et al* 2008). Conifer species retain their needles for a long time compared to other types of tree species, between 5 and 30 years depending on the environment (Chapin and Van Cleve 1981, Hom and Oechel 1983, Lamhamedi and Bernier 1994, Grossnickle 2000). Generally root growth is reduced as nutrient availability increases, as the seedling does not need to allocate as much resources to acquiring nutrients, however total growth of the seedling increases with higher nutrient availability (Brand 1991).

Küssner *et al.* (2000) found that competition from three species including red raspberry reduced black spruce (*Picea mariana* (Mill.) B.S.P.) diameter by over 40%. Thevathasan *et al.* (2000) analysed soil samples and black spruce and competitive species growth in small planted plots. They found that soil nitrate accumulation benefited competitive species such as red raspberry and aspen but did not improve spruce growth, concluding that the competitive species need to be controlled for the spruce to use the resources. This is consistent with research by Lautenschlager (1999) who found that when raspberry was grown in mixed plantations with white spruce, adding nitrogen granular supplement benefited raspberry at the expense of white spruce. Competition from raspberry did not affect white spruce height but did reduce spruce diameter and biomass. Eventually as regeneration continues, the relatively low nutrient requirements of white spruce allows it to gain a competitive advantage over early successional species which are vulnerable to the low levels of nutrients commonly found in northern latitude forests (Grossnickle 2000).

COMPETITIVE SPECIES CHARACTERISTICS

Trembling Aspen Characteristics

Boreal mixedwood forests in Northern Ontario are often composed of aspen and white spruce (Grossnickle 2000). After a disturbance, aspen often dominates at first (Maundrell and Hawkins 2004), although aspen stems can naturally self-thin after an initial spread by suckering (Crouch 1983, Perala 1984, Mallik *et al.* 1997). As aspen is a faster growing species, it quickly becomes taller than the white spruce seedlings, reducing light availability and gaining a competitive advantage (Comeau *et al.* 1993). Mallik *et al.* (1997) called this the vertical competition strategy. This initial growth advantage reduces the survival and growth rate of the white spruce, until the spruce reaches the same height as aspen height growth slows with age, or gaps in the canopy occur (Smith *et al.* 1997, Messier *et al.* 1999). Bell *et al.* (2011) report aspen as a competitive species for conifers in terms of light. Due to this effect, it may seem like a good idea to remove the aspen to aid spruce growth. However this removal of woody competition may open the canopy and trigger germination of seeds of species such as red raspberry which reside in the soil seed bank, and so any benefits may be offset by the subsequent increase in competition from understory species (Miller *et al.* 2003, Man *et al.* 2008).

Aspen can have other benefits for white spruce growth. Work by Côté and Fyles (1994) suggested that aspen can reduce soil acidification and can efficiently improve the quality of the soil. Aspen can also provide certain benefits for white spruce growth, such as adding organic matter to the soil through deciduous leaves, moderating the microclimate, protecting from frost (Groot and Carlson 1996, Bell *et al.* 2000, Voicu and Comeau 2006), and improving the biodiversity, overall health, productivity and long term sustainability for mixedwood stands (Man and Lieffers 1999, Comeau *et al.* 2005).

Red Raspberry Characteristics

Red raspberry is one of the main species that contributes to silvicultural failures (Whitney 1982, Mou *et al.* 1993, Pitt *et al.* 1989, Lautenschlager 1999). Red raspberry competes for light, soil moisture, and nutrients (Mou *et al.* 1993, Bell *et al.* 2011) and is found in greatest amounts in the most productive regenerating forest (Lautenschlager 1999) where dense cover forms and reduces the growth of white spruce seedlings (Pitt *et al.* 1989).

Researchers have found that red raspberry invades early on in the successional process after a severe disturbance removing over 40% of the forest canopy has occurred and can become the dominant species within 2-4 years (Whitney 1982, Roberts and Dong 1993, Mou *et al.* 1993, Nyland 2002, Donoso and Nyland 2006). One explanation for the fast dominance of red raspberry is its large seed bank that is viable for almost a century (Whitney 1982), and the ability to spread using suckers (Ricard and Messier 1996, Donoso and Nyland 2006). Raspberry has a short lifespan, rapid height growth, and a low root–shoot ratio

(Donoso and Nyland 2006). This means the species rapidly produces aboveground cover and seeds after a site is opened up by a disturbance (Grime 1979). There are different opinions on how long raspberry dominance continues after a disturbance, with estimates ranging from 3 years (Marks and Bormann 1972) to 25 years (Lautenschlager 1997).

According to the literature, light is the main factor in raspberry coverage. Raspberry is shade intolerant with a high light saturation point (Donoso and Nyland 2006). As taller woody vegetation, such as aspen, grows and reduces the available light, allocation of photosynthate in red raspberry is increasingly shifted from growth to seed production, for the next disturbance (Ricard and Messier 1996). Lautenschlager (1999) found above 78% shade was the threshold for significantly reducing raspberry biomass, and that production under 30% shade and full sunlight were similar. Ricard and Messier (1996) found that where light penetration to the forest floor was 25% or greater (photosynthetic photon flux density) there was always red raspberry present. In areas where light penetration was below 7%, however, there was no raspberry, suggesting that eventually as the canopy closes and available photosynthetically active radiation (PAR) decreases raspberry dies out (Ricard and Messier 1996, Donoso and Nyland 2006).

COMPETITION MANAGEMENT

The forest industry is extremely important in Canada. It is the largest exporter of forest products in the world, with the industry being valued at $78.3 billion in 2007 (Canadian Forest Service 2009). Within the forestry sector there is a constant drive for improved productivity, efficiency, and cost reduction. A major part of this is research into the development of methods to increase crop tree growth and yield. A great deal of research has recently been undertaken into the effects of site preparation and logging techniques on the regeneration of white spruce (Boateng *et al.* 2009, Fu *et al.* 2007). Some studies such as that by Wood and Von Althen (1993) suggest that these techniques are more effective than raw planting or control measures used post-planting. There has also long been debate about whether it is better to plant single species stands or mixed stands to enable spruce growth. Recent studies concur that at least for Northern Ontario, Canada, mixedwood spruce and aspen stands are often a natural occurrence and are healthier and more ecologically diverse than white spruce alone (Man *et al.* 2008). Decisions on logging methods and mechanical site preparation are important for forest management and should not be discounted, but the focus of this study is post-harvest vegetation control.

Management of competing vegetation is essential for the establishment and early growth of crop tree seedlings (Walstad and Kuch 1987, Mallik *et al.* 1997). When competition is controlled, crop tree use of light, nutrients and water increase (Brand 1991). Lanner (1985) stated that conifers under competitive vegetation are only operating at 40% stomatal conductance of that of conifers in clear areas. If competition is controlled, then the growth rate and foliage density of conifers increase (Brand 1991). White spruce can survive suppressed by competition for a long time (Nienstadt 1957). If released from heavy competition, survival can increase by 25% (Waldron 1961). Proper release from moderate and minimal competition around 20-40 years of age (Jarvis *et al.* 1966) can increase white spruce volume by over 35% (Johnston 1986).

Management of competition generally involves temporary removal of overstory and understory vegetation, to increase resource availability (Munson *et al.*

1994). This creates favourable conditions for crop tree survival and growth (Newton *et al.* 1992). Increased light availability combined with subsequent increased soil temperature (Wood and Von Althen 1993) and soil moisture (Kochenderfer and Wendel 1983), results in higher levels of nutrient turnover and uptake (Nambiar and Sands 1993) as well as higher rates of photosynthesis (Eastman and Camm 1995).

The question can be asked whether one competitor species is worse for spruce development than another. More recently some studies have attempted to address this question. For example, Bell *et al.* (2000) compared nine early-successional boreal forest species for their relative competitiveness with jack pine and black spruce using regression analysis. They found that red raspberry had a more detrimental effect than did aspen on basal area of black spruce, based on percentage cover; however white spruce may have different responses. Man *et al.* (2008) undertook research that supports the comparison by Bell *et al.* (2000), concluding that woody species initially have a more detrimental effect on white spruce growth per LAI unit than herbaceous species, but that herbaceous species are more competitive overall as they have a much higher LAI. These studies demonstrate the need for research to examine specific species and their interactions, and not just competition as a whole.

Forest management studies conclude that competitors such as red raspberry and trembling aspen need to be controlled in regenerating stands, though there is still debate as to which methods are best and how much control is necessary, and the most appropriate methods will vary from site to site. Although the success of competition control techniques in silviculture varies a great deal between vegetation types, control methods, and stand location, in general if the competitive species are suppressed then the productivity of the crop tree species is increased (Wagner *et al.*

1989). Pitt *et al.* (2010) found that white spruce grew to be 4-64% taller and 68-178% larger if surrounding woody and herbaceous competition was controlled. Stewart *et al.* (1984) also found stand volume increased 40-100% when competition was controlled, in their review of over 200 studies in the United States (in Radosevich *et al.* 1990).

Herbicides are often used to reduce competition and allow planted white spruce seedlings to grow (Reynolds *et al.* 1997). The forest industry in Ontario relies heavily on the use of herbicides to aid regeneration of conifer plantations (Homagain *et al.* 2011). There has been much investment and research into chemical herbicide methods which are being integrated into current forest management practices. These methods have been shown to be successful in reducing the leaf area index of both woody and herbaceous competition and increasing white spruce growth through higher availability of light and soil nitrogen (Man *et al.* 2008). Chemical herbicides can be successful in reducing aspen competition (Lindgren and Sullivan 2001), by significantly reducing the leaf area index and increasing available light for the white spruce, more so than brush saw techniques (Reynolds *et al.* 1997). Homagain *et al.* (2011) found plots treated with Vision herbicide (containing Glyphosate) produced 120% more volume and fibre which was 36% more valuable than plots without competition management. Vision treated plots also produced 3.84 m^3 ha^{-1} more than Brush saw plots 16 years post-treatment, with a projected value for 2059 at $2337.53 per ha higher for the herbicide treated plots (Homagain *et al.* 2011).

Glyphosate ($C_3H_6NO_5P$), often in the form of Vision, is the most widely used herbicide in Canadian forest management practices (CCFM 2008). This is a method of causing mortality in the competing vegetation such as aspen, rather than causing stem dieback (Pitt and Bell 2005, Man *et al.* 2011). Glyphosate is an organophosphate as it contains carbon and phosphorous but it does not affect the nervous system in the same way as organophosphate insecticides, and is not a cholinesterase inhibitor (Pesticide News 1996). It is ¼ as toxic as aspirin (Sutton 1978), limiting the health risks for those using it, and is immobilized by most soils and quickly biodegraded (Sprankle *et al.* 1975a and b). The half-life of Glyphosate is reported to be between 20 and 100 days depending on soil conditions (Willis and McDowell 1983, Tortensson 1985), and it is rated as a non-leacher by Agriculture Canada (1993).

Glyphosate is a broad spectrum, non-selective systemic herbicide which works by being absorbed into the plant mainly though leaves and soft stalk tissue where it is then transported throughout the plant, meaning no part survives (Pesticide News 1996). Glyphosate affects various enzyme systems inhibiting amino acid metabolism in the shikimic acid pathway, which exists in plants and microorganisms but not in animals (Pesticide News 1996). It is effective in killing all plant types including grasses, perennials and woody plants over a time period of days or weeks (Pesticide News 1996), but conifers such as white spruce are fairly resistant to low levels, depending on their stage of development (Comeau and Harper 2009). It can be a successful method of reducing aspen and other competition at logging sites and improving crop tree growth. Man *et al.* (2011) reported a preharvest spray of glyphosate decreased the density of aspen regeneration by 60% compared to the areas treated with no spray. They also found growth of surviving aspen was reduced, allowing better conditions for crop tree growth in a mixedwood regenerated forest. After 5 years only 40-60% of aspen was above 1.3m in the areas sprayed with glyphosate pre-harvest, compared to 95% above 1.3m in the areas which were not sprayed (Man *et al.* 2011).

Herbicide can be successful as a release or site preparation treatment (Lieffers *et al.* 1993) but may not completely solve the problems caused by the competitive species. It can also require large inputs of cost and effort (Radosevich *et al.* 2007). Some harvesting practices themselves create a cycle that requires chemical herbicides, by clearcutting and aiming for shortened rotation cycles (Radosevich *et al.* 2007). There is research suggesting that glyphosate may reduce the density of deciduous species and so not support mixedwood stands (Pitt and Bell 2005). Applications of herbicide can cause short term damage to spruce seedlings by altering their physiological processes and influencing future growth (Grossnickle 2000). In some occasions the performance of the spruce seedlings is reduced, however in other cases the stress caused to the plant by the herbicide is outweighed by the increased growth due to control of the competing vegetation (Sutton 1978, Grossnickle 2000). The timing of the herbicide is important, as herbicides applied in late summer or early fall have the lowest levels of impact upon spruce, as there is no shoot growth occurring, the needles have fairly well developed cuticles which prevents the herbicide from the outside of the needle into the tissue, and the seedlings have reached a level of stress resistance in preparation for going into dormancy (Grossnickle 2000).

Chemical control of competitive species using herbicides is likely to continue, but with increasing research into the ecological interactions of species the reliance upon it may be reduced (Radosevich *et al.* 2007). Finally, there is a large amount of social pressure and controversy about the use of herbicides in forests, with research into biological alternatives to reduce costs and minimize health and ecological issues being called for (Lieffers *et al.* 1993, Mallik *et al.* 1997, El-Sayed 2005).

Chemical herbicides are not the only way to control competition. Indirect, biological methods such as brushsaws, mowers, grazing and mulching are another possible approaches and are sometimes considered more desirable (Mallik *et al.* 1997, Radosevich *et al.* 2007). Both approaches have been shown to be successful, but the requirements for each site may be different, and the indirect methods may be more suitable for long term control (Radosevich *et al.* 2007). One train of thought is that the need for herbicide could be reduced if different harvesting methods are used that take into account the competitive species and prevent them from becoming dominant, by creating a mixedwood and uneven aged forest (Radosevich *et al.* 2007). Forests planted with just one crop species are unlikely to become monocultures as is commonly believed, but they will not use all the ecological niches available, presenting an opportunity for competitive species to fill the gaps and out compete the crop tree (Radosevich *et al.* 2007). Use of a mixedwood forest with species such as aspen and white spruce may reduce or prevent the establishment and dominance of competitive species such as raspberry.

Natural methods of controlling red raspberry and other herbaceous competition could provide more socially acceptable, and possibly more ecologically appropriate, alternatives. One possible way of doing so could be by leaving some aspen, planting or allowing it to naturally regenerate. Aspen can reduce the available light and prevent the herbaceous competition from dominating, and is capable of growing quickly and well without much intervention (Man *et al.* 2008).

Determining the optimum densities of aspen and white spruce will be an important factor however, as too little aspen may not prevent the competitive species from becoming dominant, and too much may severely reduce the basal area and quality of the white spruce (Bokalo *et al.* 2007). The relative densities of the competitive species and the aspen are also important factors to take into consideration when planning a management prescription. Indeed, Landhausser and Lieffers (1998) studied the negative effects that Canada blue-joint grass (*Calamagrostis canadensis* [Michx.] P. Beauv.) can have on aspen growth, and suggested it will reduce aspen productivity, until the canopy closes, after which the grass cover will be reduced. This simplified study was conducted with plants in pots, however, and it may be that if the aspen is well established before the grass has become dominant, or if fully grown aspen is left when harvesting, then the aspen may be able to suppress the blue-joint grass.

It is not always necessary to entirely eliminate competitive species; most crop tree species will have a threshold of competition density below which competitive species will not have a significant effect upon productivity and may eventually die out during succession (Radosevich *et al.* 2007). However the threshold amount of competition for seedling survival and growth will likely be different to that of adult trees and depend upon the types of competition. Using aspen may reduce competition enough to allow the white spruce to survive and grow to a moderate size, however the maximum growth would only be achieved if all competition was eliminated (Radosevich *et al.* 1990).

At sites where competition is a problem for white spruce regeneration, it may be a more suitable approach to leave some aspen and accept the lower light levels in order to suppress the understory vegetation until the spruce is able to establish itself (Maundrell and Hawkins 2004). Lieffers *et al.* (1993) suggested that reduced light conditions from a partial canopy could be enough to reduce blue-joint grass sufficiently for the spruce seedlings to establish, and Maundrell and Hawkins (2004), working in a white spruce and aspen mixedwood stand in British Columbia, found that aspen overstory could be used successfully to control the competition from blue-joint grass and fireweed (*Epilobium angustifolium* ssp. *angustifolium* L.). Although my study focuses on aspen and raspberry there are similar possibilities. Comeau *et al.* (2009) found that planting white spruce under 19 year old aspen stands suppressed the understory competition and allowed the seedlings to establish and grow. The results may be different for newly regenerated aspen and it may not be as effective, but past research has demonstrated that aspen grows quicker than spruce and may still provide some protection (Bell *et al.* 2000).

Filipescu and Comeau 2007b suggest that the basal area of white spruce may be reduced by the presence of aspen. However this reduction may be outweighed by the increased survival rate of white spruce under aspen compared to that under other competitive species such as red raspberry. Additionally, aspen can benefit soil quality and microclimate, and may provide opportunity for possible biomass harvesting.

OBJECTIVES AND HYPOTHESES

OBJECTIVES

- To assess the effect of varying combinations of trembling aspen and red raspberry upon small scale microclimatic conditions.
- To assess the effect of varying combinations of trembling aspen and red raspberry upon white spruce seedling growth and rates of photosynthesis.

HYPOTHESES

Aspen and raspberry do not have the same effect on photosynthetically active radiation, temperatures, soil moisture or nutrients; thus, different combinations of trembling aspen and red raspberry cover should create variation in small scale microclimatic conditions and the photosynthetic rates and growth of white spruce seedlings.

Specific hypotheses

Microclimatic Variables

1) Sample plots with high cover of trembling aspen and/or red raspberry will have low available PAR levels due to canopy density. Red raspberry will have more of an effect on PAR than aspen due to higher LAI.
2) Sample plots with high cover of trembling aspen will affect air temperatures and protect the spruce from frost.
3) Sample plots with high cover of trembling aspen and/or red raspberry will have lower soil temperatures due to reduced solar radiation reaching the soil.
4) Areas with high cover of aspen and/or raspberry will have lower soil moisture content due to competition for water resources.

Photosynthesis Rates

5) White spruce seedlings under high cover of aspen and/or red raspberry will have lower rates of photosynthesis. Seedlings under low-moderate cover of trembling aspen will have higher rates of photosynthesis than those under no canopy density in the hottest months (August). This is expected due to shading reducing any extremely high temperatures that can cause increased photorespiration and a decline in net photosynthesis, and also by preventing long lasting reductions in photosynthesis rates from damage caused by excess irradiance (Lambers *et al.* 2008).

White Spruce Seedling Growth

6) A larger effect is expected for GLD growth than for height growth, due to the difference in the phenology of the competitive species and the white spruce. Significant differences between heights are not expected, although seedlings under aspen cover may have increased height compared to under raspberry or no cover. Seedlings under high cover of trembling aspen and/or red raspberry will have less ground line diameter growth. Those with little to no cover of aspen or raspberry will have larger diameter growth. These effects will result in larger H/GLD ratios under higher amounts of competition.

MATERIALS AND METHODS

SITE DESCRIPTION

The site is located in North-eastern Ontario in the Lake Abitibi ecoregion, Foleyet ecodistrict (Bell 2010). It is 15km south of the city of Timmins (48°20'N, 81°18' W) (Figure 1). The site is mostly flat with silty to silty clay soil (Bell 2010). Weather conditions during the study period are described in detail in the results section using data collected by the microclimate stations in this study.

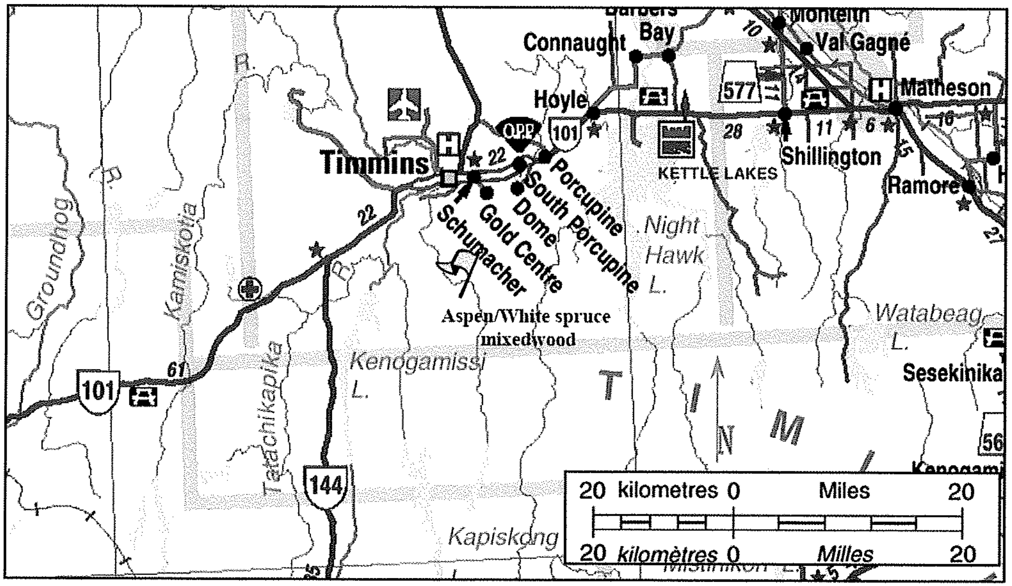

Figure 1. Map of the study site (marked with a flag) in relation to Timmins, Ontario (map source: http://www/mto.gov.on.ca).

The site is part of the Intensive Forest Management Science Partnership: NEBIE Plot Network research project. The aim of this project is to study the effects of a variety of silvicultural treatments upon fibre production, biodiversity, soil properties, and coarse wood components. NEBIE stands for N-natural disturbance, Ex-extensive, B-basic, I-intensive, and El-elite silviculture (Table 1, Bell 2011). The pre-harvest stand was dominated by 85-90 year old trembling aspen, white spruce and balsam fir with small numbers of black spruce and white birch. It was logged in fall 2002, site prepared with a power disc trencher in 2003 and planted with local white spruce stock in the spring of 2004. The white spruce seedlings were grown in 2003 with non-improved seed, and had an average height of 190mm. Glyphosate had been used to remove the majority of the competing aspen and allow the spruce to be free to grow. In the areas where this aspen was successfully reduced red raspberry became dominant, making the site a good representation of white spruce growing under a range from severe to very little competition from aspen and raspberry.

Table 1. Overall objectives and description of silvicultural activities in each intensity treatment level (Bell 2010).

	Extensive	**Basic**	**Intensive**	**Elite**
Objectives	stocking >40%, desired tree species free of major insect pests	stocking >60%, desired tree species free of interspecific competition and major insect pests	stocking >80%, desired tree species free of intra- and interspecific competition and major insect pests	stocking >80%, desired tree species free of nutrient deficiencies, intra- and interspecific competition and major insect pests
Harvest	Fall 2002: full tree logging to roadside (block 1), cut to length (blocks 2-4), leaving 25 residual trees per hectare			
Site preparation	none	Sept. 2003: power disc trencher	Sept. 2003: power disc trencher with second trench pass at 90° to the first pass	
Tree plant	none	Spring 2004: 1800 white spruce/ha	Spring 2004: 2200 white spruce/ha	
Vegetation management	none	Sept. 2005: back pack application of glyphosate to control all broad leaved trees and shrubs	Sept. 2005 and Aug. 2007: back pack application of glyphosate with 6 m wide no spray strips 27 m apart	Sept. 2005 and Aug. 2007: back pack application of glyphosate leaving a quality aspen every 5 m
Refill tree plant	none	May 2008: 583 white spruce/ha, only block 2	May 2008: 730 white spruce/ha	May 2008: 1020 white spruce/ha
Future	none	none	commercial thinning	pruning dead branches, commercial thinning

Sampling Designs

Selection of White Spruce Seedlings

White spruce seedlings were selected through a two-step process (1) an analysis of NEBIE Plot Network data and (2) randomly selecting a subsample of seedlings that were subject to a range of competitive conditions.

Fifth year post-harvest white spruce NEBIE stocking and species cover data was collected for the Timmins installation set for 2007. The data ranged across four blocks and five treatments with four plots randomly placed in each treatment with a 20 x 20m grid pattern laid out in each plot using posts. Ten quadrats were set up in each plot, systematically arranged running diagonally along a line from the NW corner to the SE corner of the plot, with the centre of each line in the centre of the 20 x 20m grid. . In total 200 2m X 2m quadrats were assessed. For my study, only blocks 1, 3 and 4 were used. Block 2 was lowland therefore moister than the other blocks, our intent was to reduce variation and confounding factors by not including it. The natural treatment was also not included in analysis as it was not logged and so contained mature white spruce instead of seedlings. Differences between blocks were not anticipated due to the same timing and type of treatment, and very similar soils (Bell 2010), however possible block effects were accounted for in the statistical analysis.

Quadrats which contained black spruce were excluded. All quadrats that contained white spruce were included (a total of 182 quadrats), with the percentage cover of red raspberry and aspen analyzed in a matrix in February 2010 to consider possible combinations of the two competitive species. Figure 2 shows the range of conditions found within quadrats containing white spruce seedlings in blocks 1, 3 and 4, across four different treatments, at the Timmins site from the 2007 stocking data. Interestingly, it did not seem that the two species coexisted at high percent covers (above 60% aspen and 40% red raspberry).

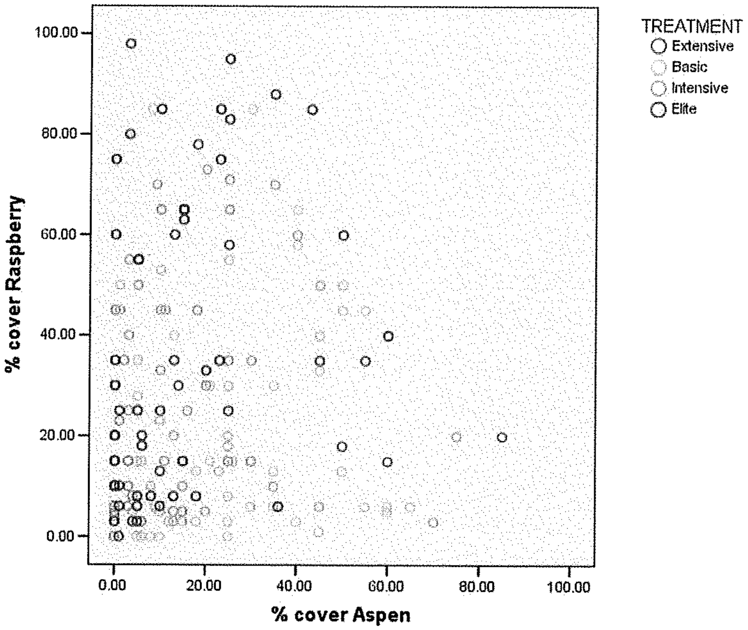

Figure 2. Combinations of percent cover of aspen and red raspberry within 2m quadrants also containing white spruce seedlings at the study site in 2007.

Step 2 involved randomly selecting a subsampling the population of white spruce 7-years post-harvest. The basic treatment provided a wide range of combinations of cover of the two competitive species, and represents the lowest-impact treatment (as extensive had very few combinations available) therefore sampling was focused here. It was necessary to include some samples from the intensive treatment to provide additional samples representing lower levels of aspen, and some samples from logged but untreated areas to provide the very high levels of aspen and red raspberry to provide adequate samples representing the existing spectrum. Applications of herbicide 3 to 5 years prior were not used as the focus of this study aside from creating the combinations of aspen and red raspberry under investigation; however attempts were made in the statistical analysis to account for possible cumulative effects it may have had on the white spruce seedlings.

Sample seedlings were selected for the amount of aspen in a 2m radius and the amount of raspberry stems in a 1.13m radius. These distances were assumed to be the area which would affect the seedling in terms of light, nutrient, and soil moisture competition, as they were roughly the same as the maximum height of these competitive species. There were several restrictions upon sample tree selection. The seedlings had to be at least 68cm high as this was the lowest height that the PAR sensors could be set at on the microclimate station tripods. They also had to be below the height of the red raspberry in order to assess the competitive effect of this species. Chosen seedlings were all between 68 and 83cm tall, to attempt to standardize and enable comparisons. A narrower range was not possible due to the limited number of seedlings within the size class. Seedlings were not included if they had an abnormal appearance, if they were located in areas of high or low relief, or had any other environmental abnormalities. Attempts were made to select seedlings with only aspen and red raspberry competition, but in most areas this was not possible to achieve and some small amounts of other competition were present. Seedlings with competitive species other than aspen or raspberry above white spruce seedling height were excluded, as were white spruce seedlings with more than 10% cover of other competitive species below seedling height.

Levels of competition from these two competitive species were estimated in May 2010 from the number of raspberry stems above and below 75cm within a 1.13m radius from the centre of the white spruce seedling, and basal area of aspen calculated from the diameter at breast height of all stems within a 2m radius. This method was used in absence of foliage to record the percent cover which was recorded in August and used for the statistical analysis. Crop tree centred plots used were similar to those used by Comeau *et al.* (1993) except the radius of plots in that study was 1.26m.

The height and ground level diameter of the white spruce seedlings were recorded using a metre stick and electronic callipers in May 2010. Sample seedlings were marked using flagging tape positioned 2m north of the seedling so as not to affect light. Locations of the seedlings were recorded both by GPS and by their direction and distance from the nearest NEBIE plot network grid post.

Basic and Intensive plots within each block were walked along the pre-existing 20m X 20m grid from the NEBIE research. As it is a young site it was possible to spot spruce seedlings fairly easily, and all seedlings that fit the criteria were examined. The buffer zones did not have a grid but were walked through thoroughly several times. All possible seedlings which fit the criteria in each block were plotted on scatter graphs according to the basal area of aspen and stem count of raspberries to ensure that a range of conditions were being covered. For blocks 1 and 3 25 seedlings were found which matched the criteria, and in Block 4 27 suitable seedlings were found, making for a total of 77 sample seedlings.

Microclimate Measurements

In May 2010, seventeen microclimate stations were installed at 17 of the 25 sample plots in Block 1. Block 1 was chosen due to greater accessibility for installation of equipment, battery changes, downloading data, and checks for bear damage. All the seedlings in the block were plotted on a scatter graph of aspen basal area and raspberry stem count and the sample seedlings were chosen to cover the spectrum of aspen and red raspberry cover as best as possible.

Microclimate stations were set up to the north of each seedling so as not to block the light. Levels of PAR for each of the seventeen seedlings were recorded and downloaded to assess relationships between aspen and raspberry cover and PAR levels. PAR was measured using PAR LITE Kip and Zonen Quantum sensors at a standardized 75cm high (roughly tree height in May) to the north of the white spruce seedling (Figure 3). Soil water content, soil temperature, and air temperature were recorded and downloaded to assess average conditions of the site, and to determine if there were any differences under the varying vegetative cover. Hourly, daily average, minimum and maximum values and the time at which they occurred were recorded using CR510 data loggers. Soil water content was measured using Campbell Scientific CS615 Water Content Reflectometer. Soil temperature was measured using Campbell Scientific 107B temperature probes at 10cm depth (roughly seedling root depth). Air temperature was measured using shielded Campbell Scientific CS500 Temperature and Relative Humidity Probes at 2m high (Figure 3).

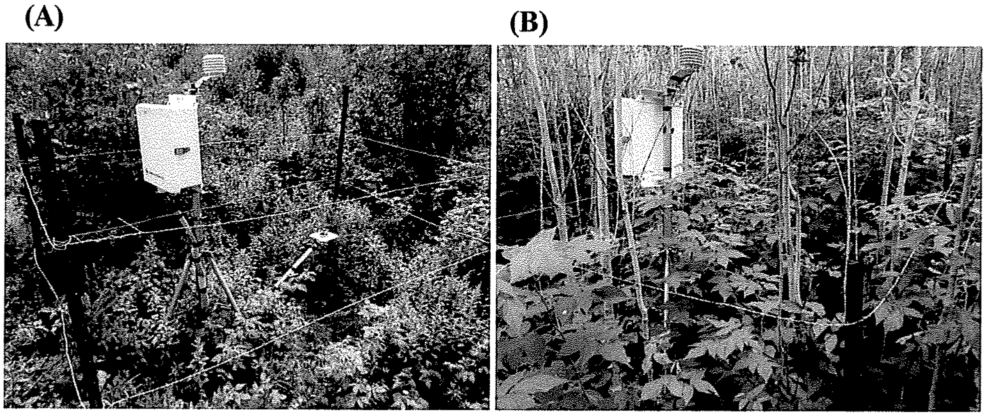

Figure 3. Photographs of microclimate stations under (A) low raspberry and low aspen cover and (B) high raspberry and high aspen cover.

Photosynthesis Measurements

A CIRAS-II machine (PP systems) was used to measure the photosynthesis rates of thirty-six white spruce seedlings randomly selected across the treatments and blocks. Seedlings were measured in a stratified random order using a random number generator (randomly selected within each treatment plot in each block for practical and time considerations moving the machine) between the 2nd and 17th of August 2010, under clear sunny conditions, within a three hour time slot (between 12 and 3pm), to attempt to standardize environmental conditions. Two branches at the top of each seedling were used for the photosynthesis measurements, one facing north and one facing south. Three readings were taken one after the other on each branch, resulting in six measurements per seedling. These were averaged to give a single reading of photosynthetic rate for each white spruce. The two branches were collected afterwards and taken back to the laboratory to be separated and scanned for leaf area determination, to adjust the photosynthesis rate values accordingly using the CIRAS II.

White Spruce and Vegetation Measurements

In August 2010 all seventy-five sample seedlings were revisited and re-measured to record their growth over the growing season. Height of the white spruce seedlings was measured using a metre stick marked with centimetres and millimetres. Ground line diameters (GLD) of the white spruce seedlings were measured using electronic callipers on the millimetre setting. Growth increments were calculated for height and diameter growth over the season by subtracting the

May values from the August values. Stem volume index was also calculated using the following equation for the volume of a cone in cubic centimetres:

$$\text{Volume} = \frac{\pi \times (\text{diameter})^2 \times \text{height}}{12}$$

This method was used by Brandeis *et al.* (2001) when looking at 4 year old Douglas-fir seedling growth, to take into account the taper of the stems. The stem volume index growth was calculated by subtracting the stem volume index in May from the stem volume index in August.

All species within 1.13m radius plots were recorded, and visual estimates of percent cover of aspen and raspberry were made in August 2010. This was undertaken by the same person to standardize measurements similar to the method used in Comeau *et al.* (1993). Aspen was recorded within a 2m radius as due to its height it would still affect the spruce seedlings from this distance. Vegetation was measured within quadrants of these circular plots, to record the direction of competition (Northwest, Northeast, Southeast, Southwest), as was the amount above and below the height of the white spruce seedlings (Figure 4). This assessment followed the Ontario Ministry of Natural Resources Silvicultural Treatment Assessment and Reporting System (STARS) (Pinto *et al.* 2009). The only difference was that instead of recording presence/absence of competition in each quadrant, percent cover of each species within each quadrant was recorded. Using a quadrant approach to assess the level of competition and free-to-grow status of seedlings is also recommended in the British Columbia Ministry of Forests Silviculture Survey Procedures Manual (BCMF 2010). Whilst some studies have used the quadrant approach to assess competition (Duchesneau *et al.* 2001), the majority of the research uses whole plot values (Comeau *et al.* 1993, Jobidon 2000, Maundrell and Hawkins 2004, Harper *et al.* 2005, Wagner and Robinson 2006, Mallik *et al.* 2007, Man *et al.*

2008, Parker *et al.* 2009). Both approaches have their merits and disadvantages, with a possible trade-off between detail and cost. For this study the quadrant approach, using percent cover above and below tree height was used to assess any added benefits of this more detailed method, where it was possible to add together values to form totals to use as whole plot approaches for comparison.

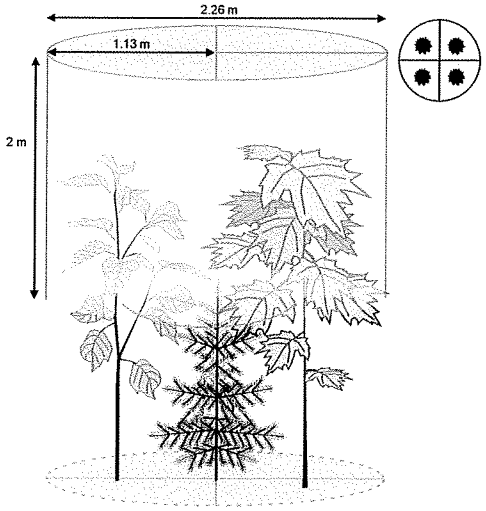

Figure 4. Diagram of STARS quadrant methodology to assess levels of competition for regenerating crop trees (Pinto et al. 2009).

A densitometer was used to calculate total canopy density at the height of each seedling in August. The instrument was held level at the top of each seedling, and the amount of clear sky in each square on the convex circular mirror was recorded (4 dots per square). Figure 5 shows a photograph of a densitometer and a diagram of the convex mirror with squares and dots within. The percent canopy density was calculated by multiplying the area of clear sky (number of dots) by 1.04 and then subtracting that number from 100. Readings were taken facing north, east, south and west and an average calculated for each white spruce seedling.

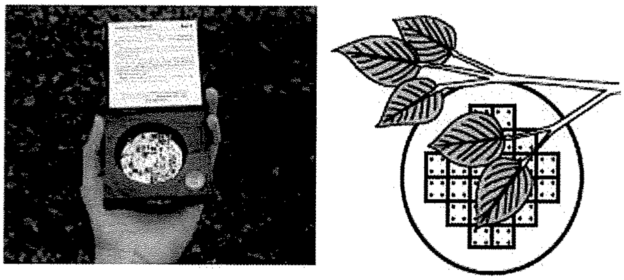

Figure 5. Image and diagram of a densitometer (Forest and Range 2004)

The seedlings were also classified using the well-spaced free-to-grow regeneration assessment procedure for Ontario (White *et al.* 2005, Appendix I). The aim of the criteria in this procedure is to assess the condition of the regenerating young stand.

Statistical Analysis

Microsoft Excel and SPSS version 13 are used for the scatter graphs and regressions, and Design Expert 7 was used to produce the response surfaces. All datasets were assessed for normality using skewness and kurtosis values, histograms with normality curves, P-P and Q-Q plots. Where necessary and possible data were transformed using the most suitable type of transformation. The dependent variables used to examine the effect of competition on white spruce seedling growth were height growth, ground line diameter (GLD) growth, stem volume index (SVI) growth, and height/GLD ratio in August. The growth variables were calculated by subtracting the values recorded in May (pre-season) from the values recorded in late August.

Effect of Competitive Species on Canopy Density.

Multiple regression in the form of a response surface was created to assess the relative importance of percent cover of aspen and raspberry on canopy density (%). In later analysis, both canopy density (as measured using the densitometer), and cover of aspen and raspberry are used as separate variables, to assess different approaches on explaining the effect of competition on microclimate and white spruce seedling growth. Canopy density data (as measured using the densitometer) is used to estimate the combined aboveground effects of both aspen and raspberry cover upon white spruce seedling growth and physiology. Percent cover of aspen and raspberry were used to examine the relative significance of the two competitive species and their interactive effects.

Microclimate Station Data.

Average, minimum and maximum values for air temperature, soil temperature and soil water content for each month are displayed and discussed. The main microclimatic factors that could affect white spruce seedling growth are listed along with mean values for the site (all microclimate stations combined) and summary statistics to assess the extent of variation in the values over the recorded time period (18th May to 22nd September). Cumulative PAR at each station was calculated by adding the hourly PAR measurements over the whole time period. Correlation coefficients were calculated to look for possible relationships between the microclimatic variables and canopy density and percent cover of aspen and raspberry. A matrix scatter plot was created to look for patterns that may have been missed by the correlations and further examine the possibility of a relationship between total aspen cover and average air temperature. Curve estimation was undertaken for explaining the variation in average air temperature and total aspen percent cover.

Levels of PAR from the main microclimate station at the site which was under no vegetative cover were used to compare to the amount reaching the white spruce seedlings at each of the sixteen microclimate stations used in this study. Although cloudy conditions are usually used for PAR analysis, no cloud cover information was available and so the variation could not be accounted for so a different approach had to be taken. Results from a clear sunny day with high PAR levels were used for the analysis to provide uniform conditions. The 8th of June 2010 was chosen due to stable levels of PAR and all sixteen stations having data for this day. The hourly PAR values from the 16 stations in this study and the NEBIE main microclimate station over 24 hour period on the 8th of June 2010 were plotted on a graph and colour coded according to levels of aspen and raspberry cover to enable comparisons to be made between the levels of competition from each species and the amount PAR available to the seedlings.

Full and reduced linear regressions to examine the effect of aspen and raspberry upon cumulative PAR over the growing season at the white spruce seedlings at the 12 microclimate stations were carried out using both the quadrant approach and total values of percent cover of each species above seedling height. Curve estimation was then run using total aspen above seedling height and canopy density to explain the variation in cumulative PAR and using cumulative PAR to explain variation in seedling growth. Scatterplots of the data with the various models shown in trendlines were then examined to check the fit, and the most suitable model was chosen from the combination of these methods.

Effect of Canopy Density and Percent Cover of Aspen and Raspberry on White Spruce Seedling Rate of Photosynthesis.

Curve estimation was run to examine the impact of canopy density on rates of photosynthesis of white spruce seedlings. To examine the relative impacts of aspen and raspberry above seedling height on white spruce rate of photosynthesis (Pn), a response surface was run using these two independent variables together. Finally, the impact of PAR on Pn was investigated using curve estimation

Effect of Canopy Density and Percent Cover of Aspen and Raspberry on White Spruce Seedling Growth

The possible effects of block and treatment on seedling growth were investigated using matrix scatterplots from SPSS, hierarchical cluster analysis and Canonical correspondence analysis using PC Ord version 6. This analysis shows the explanatory variables that have an effect upon the response variables. Each dependent variable was checked for normality using Q-Q plots and the Kolmogorov-Smirnov test (Lilliefors Significance Correction), with the significance at 0.05 (below this value represents data which is not normally distributed). Pre-season height, GLD, SVI^{sqrt} and H/GLD ratios were used to represent any treatment effect from the previous site preparation and herbicide treatments which could have an effect on further growth. These pre-season values were plotted on scattergraphs with the height growth, GLD growth, SVI^{sqrt} growth and H/GLD ratio in August to examine whether the pre-season size of the spruce would affect the growth/ post-season values.

Curve estimation was run to analyse the type of relationship between cumulative PAR and white spruce seedling height growth, GLD growth, SVI $growth^{sqrt}$ between May 18th and September 22nd and H/GLD ratio in August.

With possible treatment effect included by using original seedling size as a covariate, linear regressions were run on SPSS using linear and quadratic forms of the independent variables (canopy density and cover of aspen and raspberry) for each dependent variable (white spruce seedling height growth, GLD growth, SVI $growth^{sqrt}$, and H/GLD ratio in August). A full model regression using the most detailed set of variables was run first, and then reduced models were run in the following various stages: 1) percent cover of aspen and raspberry above and below seedling height in each of the quadrants (full model), 2) total percent cover of aspen and raspberry in each quadrant (quadrants), 3) total percent cover of aspen and raspberry above and below seedling height in the whole plot (above and below), and 4) total percent cover of aspen and raspberry in the whole plot (totals) and 5) canopy density (most reduced). This range of models from full to reduced was similar to that in Bell *et al.* (2000). For each model, all the independent variables in both quadratic and linear form were entered in a backward selection. This was to include both linear and curvilinear relationships, and to pick out the most significant independent variables from a large dataset. The regressions were re-run using those variables from the final model (using the 'Enter' method), and if the quadratic form was significant in the final model but the linear was not, then the linear was added in. Any variables in the final model which were not significant at the 10% level (<0.10) were removed one by one until only significant variables were included in the final models. If there were various ways to do this (e.g. the order variables were removed) then all possibilities were run, and the model with the highest adjusted R^2 was chosen for the final model.

Whilst using more detailed variables to predict white spruce seedling growth may be the most accurate, there are also reasons why it could be useful to use a reduced model. For measurements in the field, recording each competitive species in all 4 quadrants, above and below seedling height is time consuming and therefore costly. If the analysis demonstrated that only the above or only certain quadrants were significant, then the model could be reduced this way, however for each growth factor (height, GLD, SVI and ratio) different quadrants and vegetation height (above and below) appear to be significant (Table 2), meaning large numbers of variables need to be measured for this model to be reduced in this manner. Hence, other ways of reducing the model are looked at. The most reduced, simplest and therefore quickest and cheapest method for use in the field is to measure canopy density. Silviculturalists may require information that canopy density alone does not provide. For example they may wish to know which competitive species is having a greater effect on the white spruce seedling development, and hence be able to make decisions on the most suitable control methods, in which case aspen and raspberry above and below or totals could be the most appropriate. The other three models examined here, that are less expensive and time consuming than the full model using quadrants above and below, but more detailed than using just canopy density, are using quadrants, above and below in each plot, and totals in each plot. The quadrant approach could be used for targeted competition control, e.g. spot herbicide applications in quadrants that have the greatest effect on white spruce seedling growth, minimizing costs.

A two variable model using aspen and raspberry above seedling height to explain variation in white spruce seedling growth was examined further using response surfaces to visually examine the effects of aspen and raspberry above seedling height upon white spruce growth, and the interaction between the two. For each response surface, various non-linear forms as well as the linear model were analyzed, and the most appropriate model was selected. The output from the program suggesting which is the best model for each response surface is included in the appendix.

Where there was only one independent variable instead of large numbers curve estimation was used to assess whether non-linear regression would be a more appropriate approach. The various models used and their equations are included in Table 2. Whenever this method was used any models which did not make biological sense or fit the trend of the data were excluded. The various possible models are displayed as trendlines in the curve estimation graphs, with the most appropriate model represented by a red line. In cases where several models had similar explanatory power and fit, the significance of their coefficients were examined. The normality of the residuals from the final model chosen in each case were checked using Q-Q plots. The model chosen as the most appropriate is highlighted in the ANOVA and R^2 and coefficient tables in grey. The effect ofpercent canopy data and total aspen cover on white spruce seedling growth was examined in this way.

Table 2. List of models and formulas used in SPSS curve estimation procedures.

Model	Equation
Linear	$Y = b_0 + (b_1 \times x)$
Logarithmic	$Y = b_0 + (b_1 \times \ln x)$
Inverse	$Y = b_0 + (b_1 / x)$
Quadratic	$Y = b_0 + (b_1 \times x) + (b_2 \times x^2)$
Cubic	$Y = b_0 + (b_1 \times x) + (b_2 \times x^2) + (b_3 \times x^3)$
Power	$Y = (b_0 \times x^{b_1}) or \ln Y = \ln b_0 + (b_1 \times \ln x)$
Compound	$Y = b_0 \times b_1^x or \ln Y = \ln b_0 + (\ln b_1 \times x)$
S-curve	$Y = e^{(b_0 + b_1/x)} or \ln Y = b_0 + (b_1/x)$
Exponential (or Beer's Law)	$Y = b_0 \times \left(b^{(b_1 \times x)}\right) or \ln Y = \ln b_0 + (b_1 \times x)$

RESULTS AND DISCUSSION

COMPETITIVE SPECIES AND CANOPY DENSITY

White spruce seedlings that ranged between 68 and 83cm in height were strongly influenced by aspen and red raspberry competition in terms of the canopy they created. The effect of the two competitors was not equal, aspen tended to have a slightly stronger influence than red raspberry.

The most appropriate response surface model to explain canopy density using percent cover of aspen and raspberry was a linear model with the interaction term included (Figure 6). The model had a high adjusted R^2 value, explaining 81.1% of the variation in canopy density (Table 3).

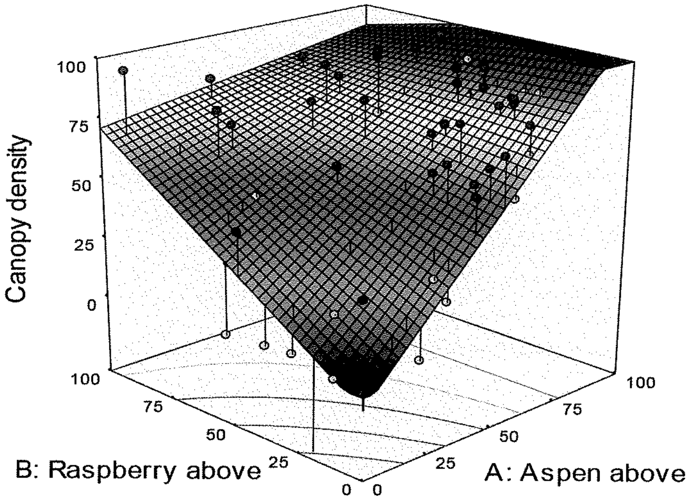

Figure 6. 3D response surface to explain variation in canopy density (%) using the total percent cover of aspen and raspberry above seedling height.

Table 3. Summary statistics for the response surface model to explain variation in canopy density using percent cover of aspen and raspberry above Sw seedling height.

Dependent variable	Variable	Coefficient	Std Error	t	p	Adj. R^2
Canopy density	Intercept	-4.284	4.677	-1.031		0.811
	Aspen above	1.208	0.102	11.859	**<0.0001**	
	Raspberry above	0.764	0.108	7.076	**0.0002**	
	Aspen above*Raspberry above	-0.010	0.002	-4.265	**<0.0001**	

Aspen cover had the largest correlation with canopy density, but raspberry cover and the combination of the two competitive species were also significant. As previous research by Thevathasan *et al.* (2000) found raspberry to have a much higher effective LAI than aspen, it is likely that the larger influence of aspen on percent canopy density is due to the positioning of the foliage and the equipment used. Aspen foliage overtops the spruce seedlings, whereas raspberry grows upwards more than over, and so may not contribute as much to percent canopy density measurements taken using a densitometer at the top of the seedling. The findings are consistent with research suggesting both species are important in the composition of the canopy (Pinno *et al.* 2001, Shropshire *et al.* 2001). The fact that raspberry is an important part of the canopy suggests that removing aspen as a management strategy to reduce canopy density to aid spruce seedling growth would not be sufficient at this site unless raspberry was targeted and controlled as well.

Clearly these species control the canopy density in this study and will therefore have the main effect on PAR This allows canopy density to be used as a variable to examine the overall (above seedling height) effect of both competitive species upon the white spruce seedling morphological and physiological responses. If light does affect the performance of white spruce seedlings, we can expect to see a response under this range of cover of the two competitive species.

MICROCLIMATE STATION DATA

Seasonal weather patterns were derived from a limited number of microclimate stations. The variables of greatest interest were air and soil temperatures and soil moisture. Table 4 provides a description of the general microclimate of the site, and the environmental conditions the white spruce seedlings are under, from the data recorded by the 16 microclimate stations in this study.

Table 4. Microclimatic conditions experienced by white spruce seedlings at the site between May 18th and September 22nd 2010.

	Air temperature (°C)			Soil temperature (°C)			Volumetric soil water content (%)		
	Avg	Min	Max	Avg	Min	Max	Avg	Min	Max
May	14.85	-7.29	36.88	12.27	1.35	22.81	38.20	23.10	51.60
June	13.75	-2.84	30.55	12.98	7.57	18.23	31.08	12.50	46.20
July	18.56	0.272	34.02	15.79	9.71	21.33	22.42	9.90	41.20
August	17.44	1.31	34.72	15.46	10.52	20.69	18.78	9.30	43.40
September	10.75	-3.64	26.29	12.06	6.47	20.28	24.72	10.50	46.90

Lowest air temperatures occurred mostly between 5and 6am in early May. Highest air temperatures occurred mostly between 1and 3pm in August (apart from two days in late May which recorded the maximum over the season between 2 and 4pm). Lowest soil temperatures occurred mostly between 8 and 10am in early May. Highest soil temperatures occurred between 5 and 7pm, mostly in late May and August. Lack of vegetative cover in May could have resulted in more cooling of the soil overnight due to lack of cover to trap the heat, as well as more heating of the soil during the day due to lack of cover to intercept the solar radiation (Childs and Flint 1987, Grossnickle 2000). Lowest soil water content occurred between 11am and 5pm in August. This was probably due to higher temperatures resulting in more evaporation, combined with more vegetation to intercept rain and use the water in the soil (Brand 1991, Munson *et al.* 1993, Parker *et al.* 2009). Highest soil water content occurred mostly between 4 and 6am in May. This was likely caused by lower temperatures and little or no solar radiation resulting in less evaporation, combined with less vegetation and foliage to intercept and use the water (Brand 1991, Parker *et al.* 2009).

The main microclimatic factors that could affect white spruce seedling growth are listed in Table 5. All factors have low ranges, standard deviations and variance except for cumulative PAR. This suggests that minimum and average air temperatures, average soil temperature, and minimum and average soil moisture were not critical factors in explaining the growth of the white spruce seedlings in this study. This does not support hypothesis 3 predicting variation in soil temperature, or hypothesis 4 which predicted lower levels of soil moisture in areas with high levels of aspen and raspberry, however Man *et al.* (2008) found similar results in terms of a lack of differences in soil moisture, and reasoned that competition only occurs for limited resources. Cumulative PAR could be the main microclimatic factor to affect growth, as this is the one factor where the recorded data varied a large amount between plots.

Table 5. Descriptive statistics for microclimatic conditions considered important to seedling growth. Data is from 16 microclimate stations installed at the site.

Factor	Mean	Range	Standard deviation	Coefficient of variation (%)
Minimum air temperature °C May 18th- June 30th	0.253	1.410	0.401	-
Average air temperature °C May 18th- Sept 22nd	15.889	1.220	0.309	-
Average soil temperature °C May 18th- Sept 22nd	14.377	1.480	0.411	-
Minimum soil moisture (%) May 18th – Sept 22nd	16.719	23.400	6.912	41.432
Average soil moisture (%) May 18th- Sept 22nd	26.379	25.190	6.589	24.978
Cumulative PAR (μmol m^{-2} s^{-1}) May 18th- Sept 22nd	433467.6	859541.84	267140.7	61.629

Data provided from the NEBIE main microclimate station (separate from this study) which is under no vegetative cover, showed that there were seventeen days where the temperature reached below freezing. Despite this, only four of the seventy-five white spruce seedlings showed frost damage (Figure 7), and these were under very low or no cover of aspen and raspberry, which supports hypothesis 2. This supports previous research suggesting possible benefits of some vegetative cover from these competitive species in terms of preventing very low air and soil temperatures and protecting seedlings from high irradiance the day after a frost (Childs and Flint 1987, Stathers 1989, Groot and Carlson 1996, Man and Lieffers 1996, Bell *et al.* 2000, Grossnickle 2000, Donoso and Nyland 2006, Voicu and Comeau 2006, Filipescu and Comeau 2011).

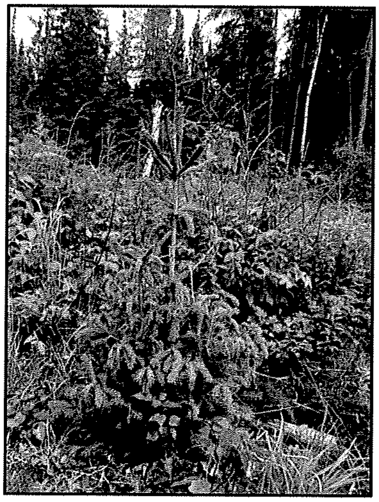

Figure 7. Photograph of a frost damaged white spruce seedling under no cover from aspen or raspberry.

Table 6 shows the results of a Pearson's correlation test between the microclimatic variables, canopy density and percent cover of aspen and raspberry. Strong correlations were found between canopy density and cumulative PAR and aspen and cumulative PAR, which supports hypothesis 1. Aspen had a significant but not strong correlation with average air temperature, yet not with the minimum air temperature in spring. This suggests that aspen may affect air temperature supporting hypothesis 2, but could have its main impact on white spruce growth in terms of being the strongest competitor for PAR.

Table 6. Pearson's correlation coefficient table for microclimate station data, canopy density and percent cover of aspen and raspberry.

Microclimatic factor	Statistic	Canopy density	Total aspen	Total raspberry
Minimum air temperature °C May 18th- June 30th	Pearson correlation	-0.242	0.033	-0.265
	Sig.	0.366	0.902	0.321
	N	16	16	16
Average air temperature °C May 18th- Sept 22nd	Pearson correlation	-0.272	**-0.537**	0.141
	Sig.	0.343	**0.048**	0.631
	N	14	14	14
Average soil temperature °C May 18th- Sept 22nd	Pearson correlation	-0.439	-0.238	-0.182
	Sig.	0.116	0.413	0.534
	N	14	14	14
Minimum soil moisture (%) May 18th – Sept 22nd	Pearson correlation	-0.174	-0.289	0.257
	Sig.	0.553	0.316	0.376
	N	14	14	14
Average soil moisture (%) May 18th- Sept 22nd	Pearson correlation	-0.102	-0.219	0.300
	Sig.	0.729	0.451	0.297
	N	14	14	14
Cumulative PAR (μmol m-^{2} s-^{1}) May 18th- Sept 22nd	Pearson correlation	**-0.891**	**-0.747**	0.408
	Sig.	**<0.0001**	**0.005**	0.188
	N	12	12	12

Canopy cover from aspen and raspberry, as well as other belowground interactions, could affect a variety of the microclimatic variables described above. Of all the possible relationships, only the effect of canopy cover and aspen on cumulative PAR, and the negative correlation between aspen and raspberry cover appear to be strong, with a weak negative relationship between aspen cover and air temperature.

The majority of the plots in Figure 8 display no apparent pattern. The percent cover of raspberry appears negatively correlated to the percent cover of aspen. This is to be expected from the phase one analysis of the NEBIE 2007 data (Figure 2), and the literature reporting the dependence of raspberry on light and its decline under denser canopies (Ricard and Messier 1996, Donoso and Nyland 2006), however the plots in these studies were purposefully selected for their combinations of aspen and raspberry coverage and so cannot be used to represent overall conditions.

As expected from the correlations and the literature, canopy density and total aspen have a negative effect on cumulative PAR (Rowe 1955, Brand 1991, Groot 1999, Awada and Redmann 2000, Grossnickle 2000, Donoso and Nyland 2006). Raspberry was expected to have a large negative effect on cumulative PAR at seedling height, however this was not the case in this dataset. This is in contrast to Shropshire *et al.* (2001) who reported raspberry cover as reducing PAR by 90%. Figure 8 also suggests that total aspen could also be displaying a negative effect on average air temperature, although it is difficult to draw conclusions from only 14 stations.

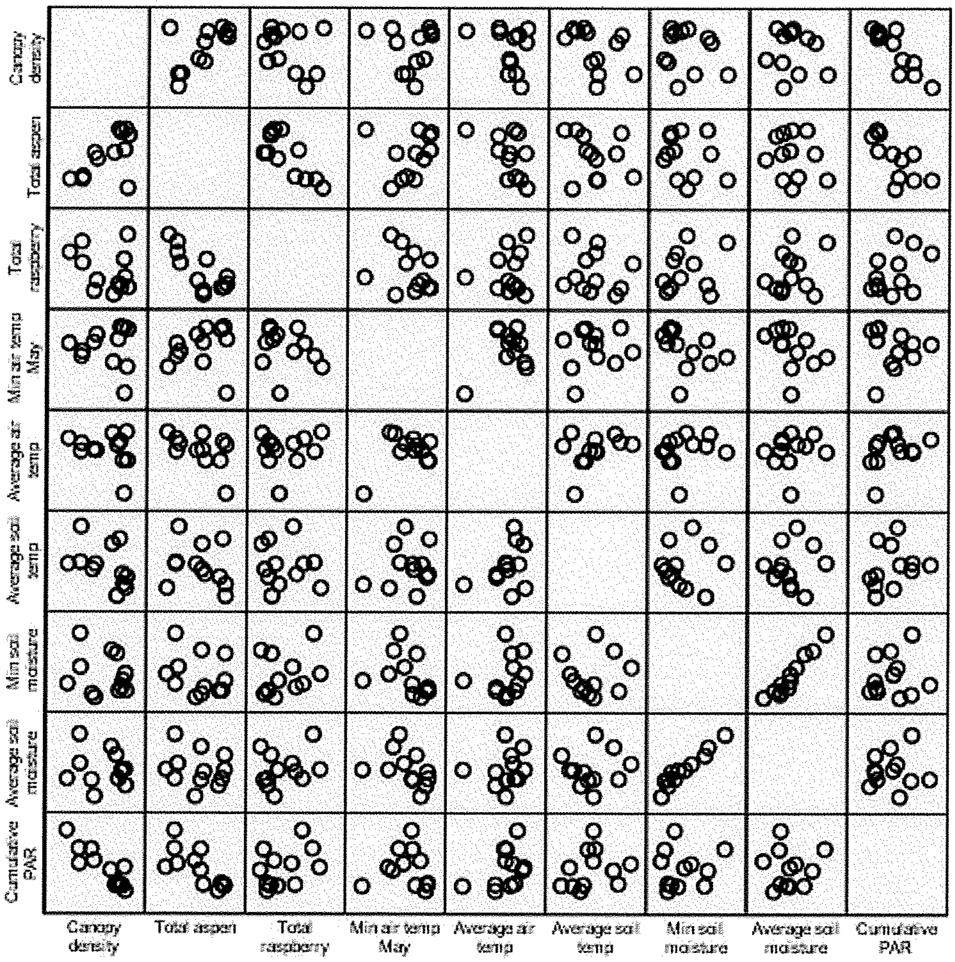

Figure 8. Matrix scatter plot to investigate possible relationships between canopy density, total percent cover of aspen and raspberry, and air and soil temperatures, soil moisture and cumulative PAR.

Air Temperature

Aspen cover can affect air temperatures throughout the season. The data shows a negative linear trend with average air temperature between May 18th and September 22nd. Figure 9 shows the curve estimation for explaining the variation in average air temperature using total percent aspen cover. The linear model was found to be the most suitable model as it fit the data, has the largest adjusted R^2 (Table 7) and significant coefficients (Table 8).

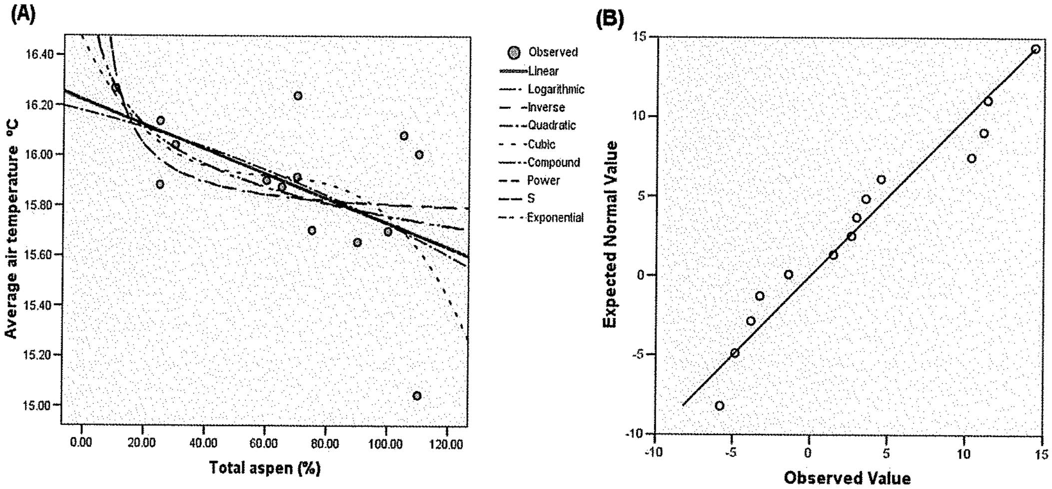

Figure 9. Curve estimation for explaining variation in average air temperature between May 18th and September 22nd using total percent cover of aspen (A) and Q-Q plot of the residuals from the linear model (B).

Table 7. ANOVA and adjusted R^2 values for regression models to explain variation in average air temperature between May 18th and September 22nd using total percent cover of aspen.

Model	F	Sig	Adj R^2
Linear	4.865	**0.048**	0.229
Logarithmic	4.457	**0.056**	0.210
Inverse	3.374	**0.091**	0.154
Quadratic	2.252	0.151	0.162
Cubic	1.509	0.272	0.105
Compound	4.827	**0.048**	0.227
Power	4.373	**0.058**	0.206
S	3.276	**0.095**	0.149
Exponential	4.827	**0.048**	0.227

Table 8. Coefficients for the models with the greatest explanatory power for explaining variation in average air temperature between May 18th and September 22nd using total percent cover of aspen.

Model	Variable	Coefficient	Std Error	Sig
Linear	Total aspen	-0.005	0.002	**0.048**
	Intercept	16.219	0.166	**<0.0001**
Compound	Total aspen	1.000	0.000	**<0.0001**
	Intercept	16.223	0.172	**<0.0001**
Exponential	Total aspen	0.000	0.000	**0.048**
	Intercept	16.223	0.172	**<0.0001**

The data does suggest a relationship between total percent cover of aspen and average air temperature between May 18th and September 22nd, with high percent cover of aspen resulting in lower air temperatures over the whole season. This suggests aspen is lowering the high summer temperatures by providing shade, and this is impacting the average air temperature, supporting hypothesis 2. This reduction of high temperatures is an effect reported by Childs and Flint (1987). It also supports Filipescu and Comeau's (2011) findings that growing degree hours (sum of hours with air temperature above 5° C) was inversely related to the density of aspen cover. It is in contrast to Parker *et al.* (2009) who found mean daily air temperature was increased by woody vegetation at the top of the competing understory canopy, as mentioned in Oke (1987). The explanatory power of the models in Figure 9 are very low at a maximum of 22.9% (Table 7), with only 14 datapoints available for analysis, hence it is difficult to draw conclusions and further research and analysis is needed.

One limitation of the equipment was that the height of the air temperature sensor was set at 2m, above the height of the seedling and sometimes the competitive canopy, especially that of raspberry. This may have weakened any effects at seedling height and so diluted the impact. For future research sensors which could be placed at lower heights could be used to improve below-canopy air temperature measurements at seedling height.

<u>PAR</u>

The canopy created by aspen and raspberry can limit the amount of light that reaches white spruce seedlings between 68 and 83cm tall. Canopy density has a strong negative relationship with cumulative PAR, although the data suggests aspen cover is more detrimental to PAR levels than raspberry cover. This supports the first part of hypothesis 1 on the effect of canopy density on PAR, but does not support the second part where raspberry was expected to have a larger impact on PAR than aspen due to higher LAI (Thevathasan *et al.* 2000).

The changes in PAR recorded over the 24 hours on the 8th of June, 2010 for the main station (used as a reference) and the sixteen stations used in this study (the 17th station malfunctioned and did not record data) are shown in Figure 10. The main station with no vegetative cover (represented by the black dashed line) shows a smooth curve while the stations under various degrees of cover from aspen and raspberry display lower values of PAR which fluctuate according to the time of day and the angle of the sun. For ease of understanding basic patterns, the graph is colour coded according to the percent cover of aspen and raspberry. Conditions ranged across a spectrum, however for this analysis, percent cover of the two species was split into low (0-50% cover) and high (51-100%).

The graph shows quite clearly that aspen cover was the main controlling factor of the amount of PAR reaching the white spruce seedlings. Low aspen cover, represented by red and yellow on the graph, resulted in consistently higher levels of PAR reaching the seedlings throughout the day when compared to those under high aspen cover, represented by grey and blue. The effect of aspen cover on available light is consistent with findings by Comeau *et al.* (2006), Mallik *et al.* (1997) and Filipescu and Comeau (2007b). Raspberry cover did not appear to affect the amount of PAR reaching the white spruce seedlings throughout the day. This was unexpected as it was predicted that raspberry would be a strong competitor for light due to its high leaf area index (Mou *et al.* 1993, Thevathasan *et al.* 2000, Shropshire *et al.* 2001). It is possible that the distribution of raspberry around the spruce as opposed to the overtopping canopy created by aspen is responsible for these results. High percent cover of raspberry with low percent cover of aspen for example, represented by yellow on the graph, had some of the highest PAR levels recorded. This suggests that when aspen and raspberry are growing in combination, aspen cover is the main factor affecting the levels of PAR available for the white spruce seedlings, with the effect of raspberry becoming negligible. One possible explanation for this is the positioning of the aspen foliage over the top of the spruce seedlings and the raspberry, with the raspberry growing mostly to the side, hence blocking less PAR.

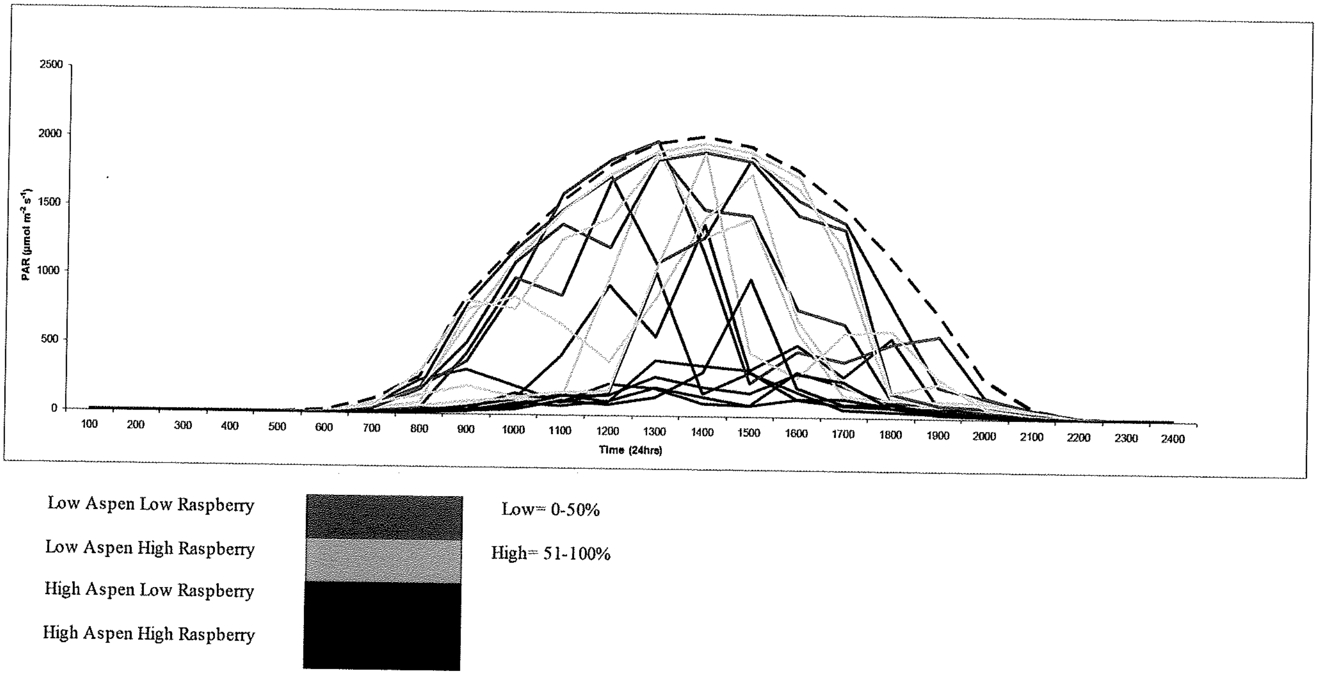

Figure 10. Hourly average PAR recorded during the 8th of June, 2010 at 16 microclimate stations and the NEBIE main microclimate station

The direction of the competitive species in relation to the seedling can affect the amount of PAR that is blocked by the canopy, depending on the time of day and angle of the sun. The majority of the direct PAR received by the seedlings comes from the South, and hence the aspen and raspberry cover in the SW quadrant being the most significant in terms of explaining variation in cumulative PAR at seedling height is not surprising, although the data suggests that the West is also significant. This could be due to diffused light which makes up a large part of the PAR available to seedlings under a canopy.

Linear regressions using the quadrant approach found aspen in the SW was the most significant variable to explain variation in cumulative PAR, with raspberry in the SW and NW also significant (Table 9). This produced a strong regression model, explaining 86.3% of the variation in cumulative PAR reaching the white spruce seedlings (Table 9). Total aspen and raspberry above seedling height was not as effective an approach, with raspberry insignificant and so excluded, and an adjusted R^2 of 0.522 (Table 9). Canopy density however also provided a fairly strong regression model explaining 77.4% of the variation in cumulative PAR over the growing season.

Table 9. Full and reduced linear regression model summary statistics to explain variation in cumulative PAR between May 18th and Sept 22nd using percent cover of aspen and raspberry above Sw seedling height.

Model	Variable	Estimate	Std Error	t	p	Adj. R^2
QUADRANTS	Intercept	707364.4	76573.482	9.238	**<0.0001**	0.863
	Rasp NE above	15313.547	5826.129	2.611	**0.031**	
	Rasp SW above	-15637.0	6370.163	-2.455	**0.040**	
	Aspen SW above	-30051.4	5153.680	-5.831	**<0.0001**	
TOTALS	Intercept	787984.0	111786.0	7.049	**<0.0001**	0.522
	Total aspen above	-7665.220	2124.445	-3.608	**0.005**	
CANOPY DENSITY	Intercept	1283407	141552.8	9.069	**<0.0001**	0.774
	Canopy density	-11442.1	1840.171	-6.218	**<0.0001**	

Canopy density and aspen cover above seedling height both have a negative effect on cumulative PAR at seedling height, which supports the first part of hypothesis 1 on the effect of canopy density on light. Table 10 shows the summary statistics for the models included in a curve estimation to examine the relationship between cumulative PAR, total aspen above seedling height, and canopy density, with the coefficients for the models with the greatest explanatory power shown in Table 11.

The most effective models for total aspen above seedling height were the compound, and exponential, with an adjusted R^2 of 0.595 (Table 10). However the linear model was almost as effective (Table 10). The coefficients for all of the aforementioned models were significant (Table 11) and all follow a similar pattern and fit the data (Figure 11). This made selecting the best model difficult. The cumulative PAR for the NEBIE microclimate station under no cover over the same time period was 1295281 μmol m-^{2} s-^{1}. The exponential model (Beers Law) was chosen on the basis that it intercepts the Y axis at around 100000, which is a likely figure compared to the NEBIE station data considering aspen makes up the majority of the canopy but not all. It also fits the exponential decrease of irradiance through the canopy and described by Lambers *et al.* (2008) and Stadt and Lieffers (2005) The most effective model with the highest adjusted R^2 for canopy density was a logarithmic model, although this only explained 0.9% more than the linear model (Table 10). It looks to intercept the Y axis at a point consistent with the NEBIE station value for cumulative PAR under 0% canopy density (Figure 11). A logarithmic relationship was expected from the literature (Stadt and Lieffers 2005), although the one used in this regression was not the same as Beers Law. Canopy density was a more effective independent variable to use than total aspen cover, possibly due to canopy density including the effect (even if minimal) of raspberry, or due to the larger margin for error in estimating percent cover of aspen compared to using a densitometer to measure canopy density.

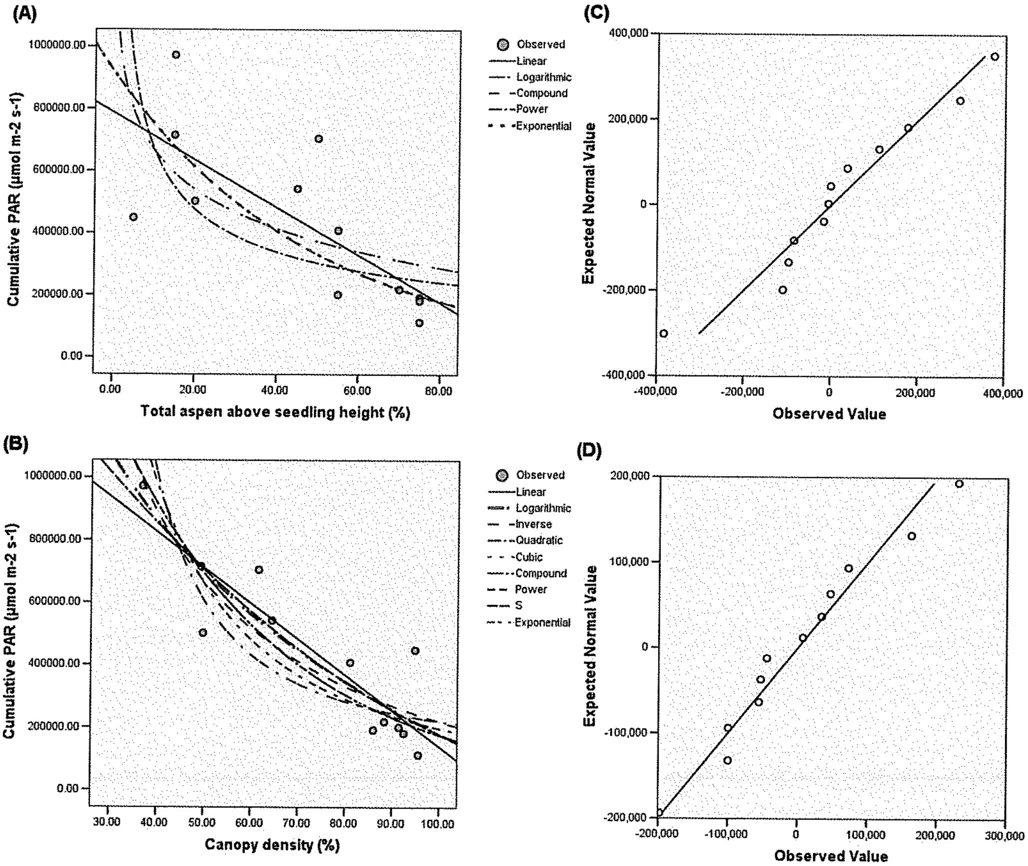

Figure 11. Curve estimation graphs for explaining variation in cumulative PAR between May 18th and Sept 22nd using total percent cover of aspen above Sw seedling height (A) and canopy density (B), and Q-Q plots of the residuals for the linear aspen above model (C) and logarithmic canopy density model (D).

Table 10. ANOVA and adjusted R^2 values for regression models to explain variation in cumulative PAR between May 18th and Sept 22nd at seedling height using total aspen above Sw seedling height and canopy density.

	Total aspen above			Canopy density		
Model	F	Sig	Adj R^2	F	Sig	Adj R^2
Linear	13.018	**0.005**	0.522	38.663	**<0.0001**	0.774
Logarithmic	5.487	**0.041**	0.290	40.747	**<0.0001**	0.783
Inverse				37.481	**<0.0001**	0.768
Quadratic				18.106	**0.001**	0.757
Cubic				18.106	**0.001**	0.757
Compound	17.155	**0.002**	0.595	25.260	**0.001**	0.688
Power	6.790	**0.026**	0.345	22.079	**0.001**	0.657
S				17.680	**0.002**	0.603
Exponential	17.155	**0.002**	0.595	25.260	**0.001**	0.688

Table 11. Coefficients for the models with the greatest explanatory power for explaining variation in cumulative PAR between May 18th and Sept 22nd at seedling height using total aspen above Sw seedling height and canopy density.

Independent variable	Model	Variable	Coefficient	Std Error	Sig
Total aspen above	Compound	Total aspen above	0.980	0.005	**<0.0001**
		Intercept	921803.8	240276.4	**0.003**
	Exponential	Total aspen above	-0.021	0.005	**0.002**
		Intercept	921803.8	240276.4	**0.003**
	Linear	Total aspen above	-7665.220	2124.445	**0.005**
		Intercept	787984.0	111786.0	**<0.0001**
Canopy density	Logarithmic	Ln(canopy density)	-747882	117162.2	**<0.0001**
		Intercept	3623176	500983.3	**<0.0001**
	Linear	Canopy density	-11442.1	1840.171	**<0.0001**
		Intercept	1283407	141522.8	**<0.0001**
	Inverse	1/Canopy density	4E+007	7313652	**<0.0001**
		Intercept	-228350	114296.2	0.074
	Quadratic	Canopy density	-21557.7	18855.922	0.282
		Canopy density *2	73.473	136.253	0.603
		Intercept	1600237	605617.3	**0.027**

RATES OF PHOTOSYNTHESIS

Competition from other species can reduce the PAR reaching white spruce seedlings by creating a dense canopy. This can result in lower rates of photosynthesis (Pn) and hence growth (Coates *et al.* 1994, Constabel and Lieffers 1996, Man and Lieffers 1996, Coates and Burton 1999, Grossnickle 2000, Stadt *et al.* 2005, Lambers *et al.* 2008). The results from this study show a negative relationship between canopy density and Pn, and support the predictions made in hypothesis 5.

The various possible models for the relationship between percent canopy density and the rate of photosynthesis of white spruce seedlings produced by curve estimation can be seen in Figure 12(A). The model with significant coefficients and the highest adjusted R^2 (Table 13 and 12) was a linear model, shown in red in Figure 12(A), with the Q-Q plot of the residuals shown in Figure 12(B). The decrease in rates of photosynthesis with an increase in canopy density is consistent with the existing literature, although previous data suggests that as PAR increases the photosynthesis should reach saturation point and so the measurements should level off rather than produce a linear model (Coates *et al.* 1994, Man and Lieffers 1997, Coates and Burton 1999, Grossnickle 2000, Lambers *et al.* 2008, Man and Greenway 2011). Whilst the linear model which best describes this dataset does not fit this trend, it should be noted that photosynthesis rates show a clear decline as canopy density increases past 80%, some white spruce seedlings between 0 and 80% canopy density had high rates of photosynthesis. This fits with reports of maximum rates of photosynthesis for white spruce needles being reached at 25 to 60% full sunlight if one makes the assumption that a seedling under 80% canopy density is receiving 20% sunlight (Coates *et al.* 1994, Coates and Burton 1999). It should also be noted that the logarithmic relationship reported between canopy density and PAR in this study (Figure 11) may be the reason for the linear relationship found between canopy density and Pn and the lack of any clear levelling off.

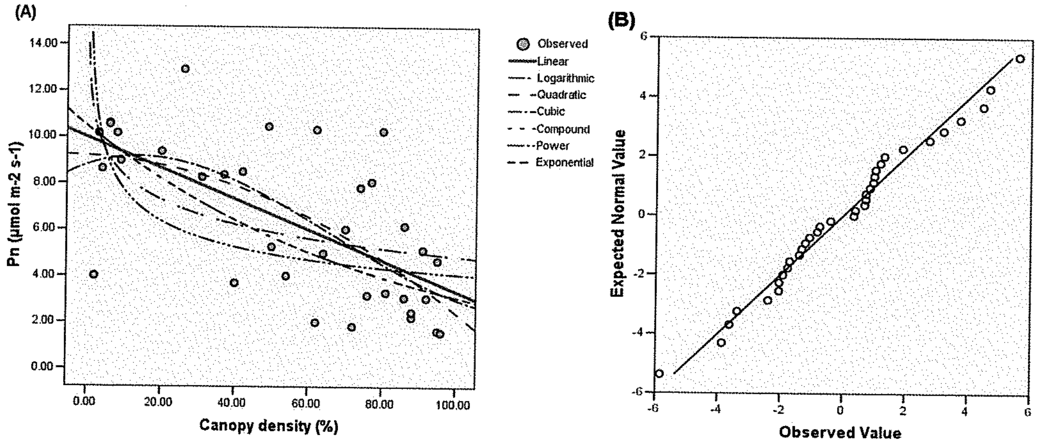

Figure 12. Curve estimation to explain variation in Pn using Canopy density (A) and Q-Q plot of the residuals from the linear model (B).

Table 12. ANOVA and adjusted R2 values for linear and non-linear regression models to explain variation in Pn using canopy density.

Model	F	Sig	Adj. R^2
Linear	23.149	**<0.0001**	0.394
Logarithmic	11.616	**0.002**	0.238
Quadratic	12.134	**<0.0001**	0.396
Cubic	7.953	**<0.0001**	0.380
Compound	21.357	**<0.0001**	0.375
Power	10.648	**0.003**	0.221
Exponential	21.357	**<0.0001**	0.357

Table 13. Coefficients of the models with the highest explanatory power for explaining variation in Pn using canopy density.

Model	Variable	Coefficient	Std Error	Sig
Quadratic	Canopy density	-0.009	0.057	0.874
	Canopy density *2	-0.001	0.001	0.309
	Intercept	9.208	1.146	**<0.0001**
Linear	Canopy density	-0.066	0.014	**<0.0001**
	Intercept	9.977	0.874	**<0.0001**

Aspen and raspberry do not have the same effect on canopy density and temperature and so do not have the same effect on white spruce seedling rate of photosynthesis. Aspen cover above seedling height has a stronger negative relationship on the rate of photosynthesis of white spruce seedlings than raspberry cover, which shows almost no relationship. As these measurements were taken in August, this data does not support the prediction in hypothesis 5 that the shade provided by aspen in the hot summer months would improve rates of photosynthesis by reducing respiration and photoinhibition. It is possible that the temperature and irradiance on the days data was collected was not high enough for these potentially damaging processes to occur.

Figure 13 shows the 3D response surface graph for the relationship between percent cover of aspen and raspberry above seedling height and the rate of photosynthesis. A linear response surface model was selected as most appropriate with the highest significance. The summary statistics of the model are in Table 14. It is possible aspen affects the rate of photosynthesis more than raspberry partly due to its larger negative effect on PAR than raspberry previously discussed.

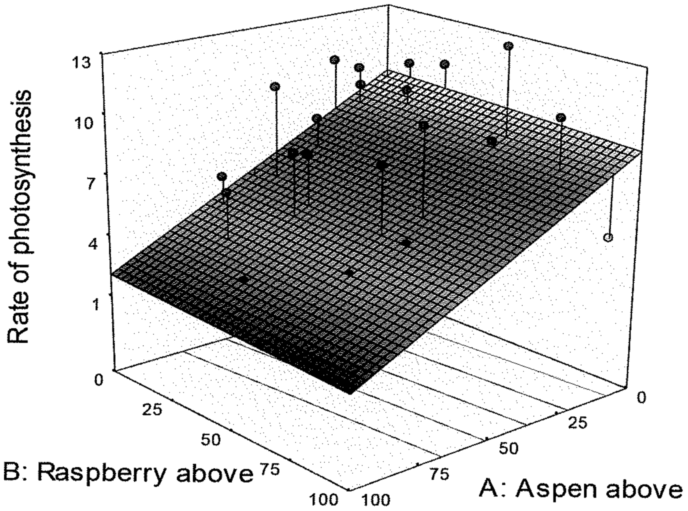

Figure 13. Response surface of linear model to explain variation in Sw seedling rate of photosynthesis (μmol m^{-2} s^{-1}) using percent cover of raspberry and aspen above Sw seedling height.

Table 14. Coefficient and ANOVA statistics for a linear model to explain variation in Sw seedling rate of photosynthesis (μmol m^{-2} s^{-1}) using percent cover of raspberry and aspen above seedling height.

Source	Coefficient	SE	Sig	F	Adj. R^2
Model		2.719	**0.001**	9.589	0.336
Aspen above	-0.074	0.017	**<0.0001**		
Raspberry above	-0.006	0.018	**<0.0001**		
Intercept	9.549	1.034	0.761		

The amount of light available to seedlings can limit the rate of photosynthesis that occurs. There is a positive logarithmic relationship between amount of PAR and Pn for the sample seedlings in this study.

Figure 14 shows the curve estimation to examine the relationship between PAR and Pn. The quadratic and cubic models were removed due to them showing photosynthesis at 0 PAR. The logarithmic and power models were very similar in explanatory power, with almost the same adjusted R^2 and significance of coefficients (Table 15), however the logarithmic was chosen as the most appropriate model as it fit the trend of the data slightly better (Figure 14). The data and models are close to the general asymptotic light response curve described by Lambers *et al.* 2008, with an initial almost linear increase in rate of photosynthesis as PAR increases, and levelling off when light levels reach the saturation point of the seedlings (Coates *et al.* 1994). Photosynthesis increases very quickly from 0 to around 400 μmol m^{-2} s^{-1}, and then the increase slows (Figure 14). This is close to the saturation levels of 600-800 μmol m^{-2} s^{-1} for white spruce reported by Man and Lieffers (1997) and Man and Greenway (2011). Although the data in Figure 14 does not level off completely, it might have done if there were more samples.

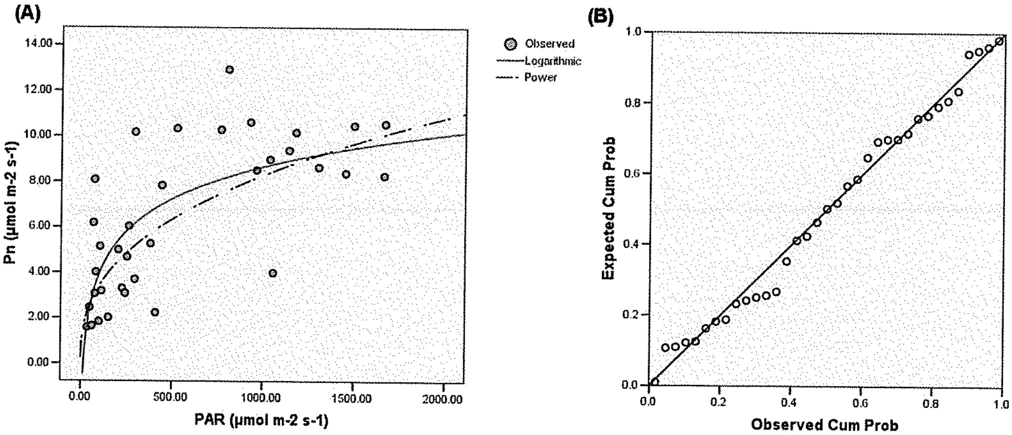

Figure 14. Curve estimation to explain variation in Pn using PAR (A) and Q-Q plot of the residuals from the logarithmic model (B).

Table 15. Coefficient and ANOVA statistics for models to predict white spruce seedling rate of photosynthesis (μmol m^{-2} s^{-1}) using PAR (μmol m^{-2} s^{-1}).

Model	Source	Coefficient	SE	Sig	F	Adj. R^2
Power	Model		0.043	**<0.0001**	36.9690	0.514
	Ln(PAR)	0.384	0.063	**<0.0001**		
	Intercept	0.582	0.217	**0.011**		
Logarithmic	Model		2.329	**<0.0001**	36.747	0.513
	Ln(PAR)	2.037	0.336	**<0.0001**		
	Intercept	-5.421	1.980	**0.010**		

SEEDLING GROWTH

Exploratory Analysis of Block and Treatment Effects on Seedling Growth

Since this study was established within a randomized complete block experiment an analysis was conducted to determine the relative effects of treatment, block and pre-season size of seedlings.

Figure 15 and Figure 16 provide evidence which suggests a lack of relationship between block and tree growth, and that a relationship exists between treatment and tree growth, with clear differences between treatments in the scatterplot matrix and differential distribution of the colours in Figure 16 (right hand diagram).

Figure 17 shows block not to be an important factor due to the block centroids all being in the middle of both axis and close together. Figure 17 also shows support for the hypothesis that aspen and raspberry may have differing effects upon white spruce seedling growth, as the arrows for raspberry all point in one direction, and those for aspen in another. Quadrants however, do not appear to be important as they are not separated and are mixed up together with similar length arrows. It also shows that treatment appears to be strongly related to aspen cover, and has an effect upon the white spruce growth responses; therefore it needs to be accounted for in further analysis.

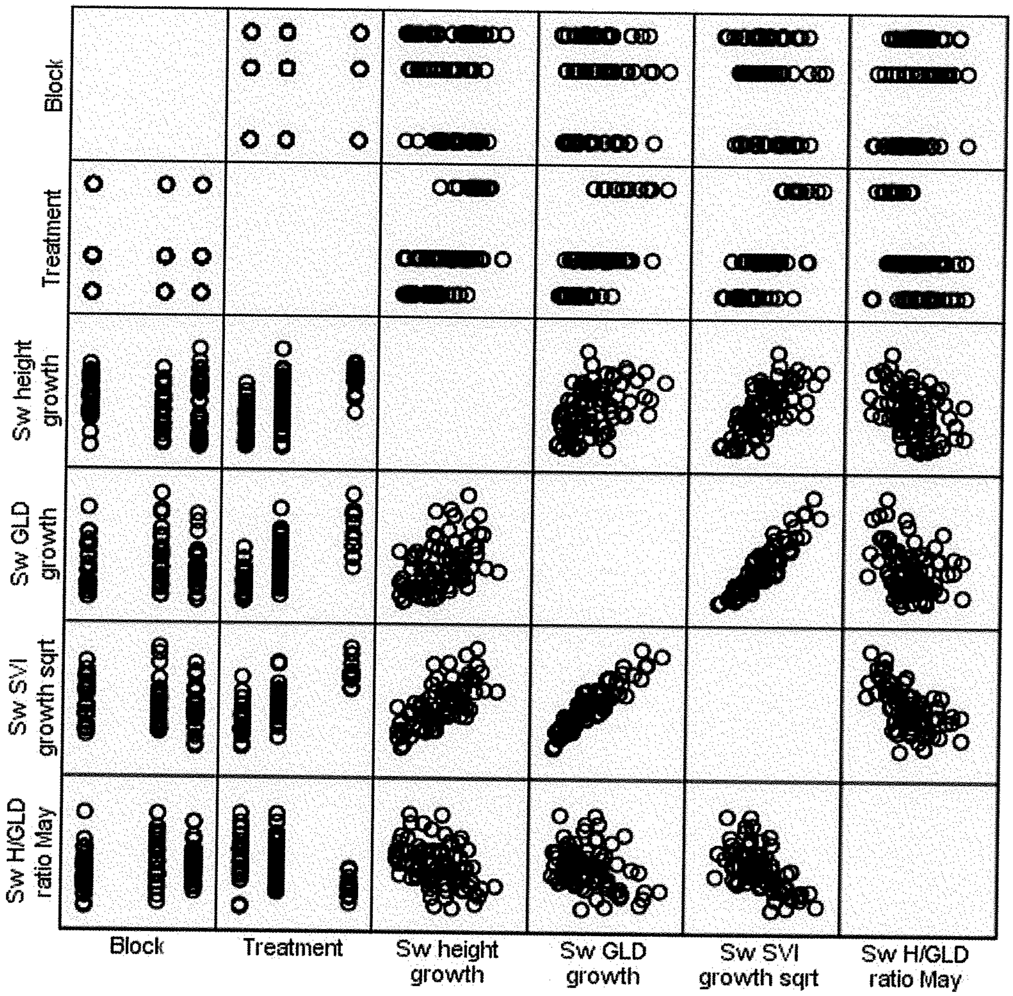

Figure 15. Matrix scatterplot to assess relationship between block and treatment on Sw seedling growth.

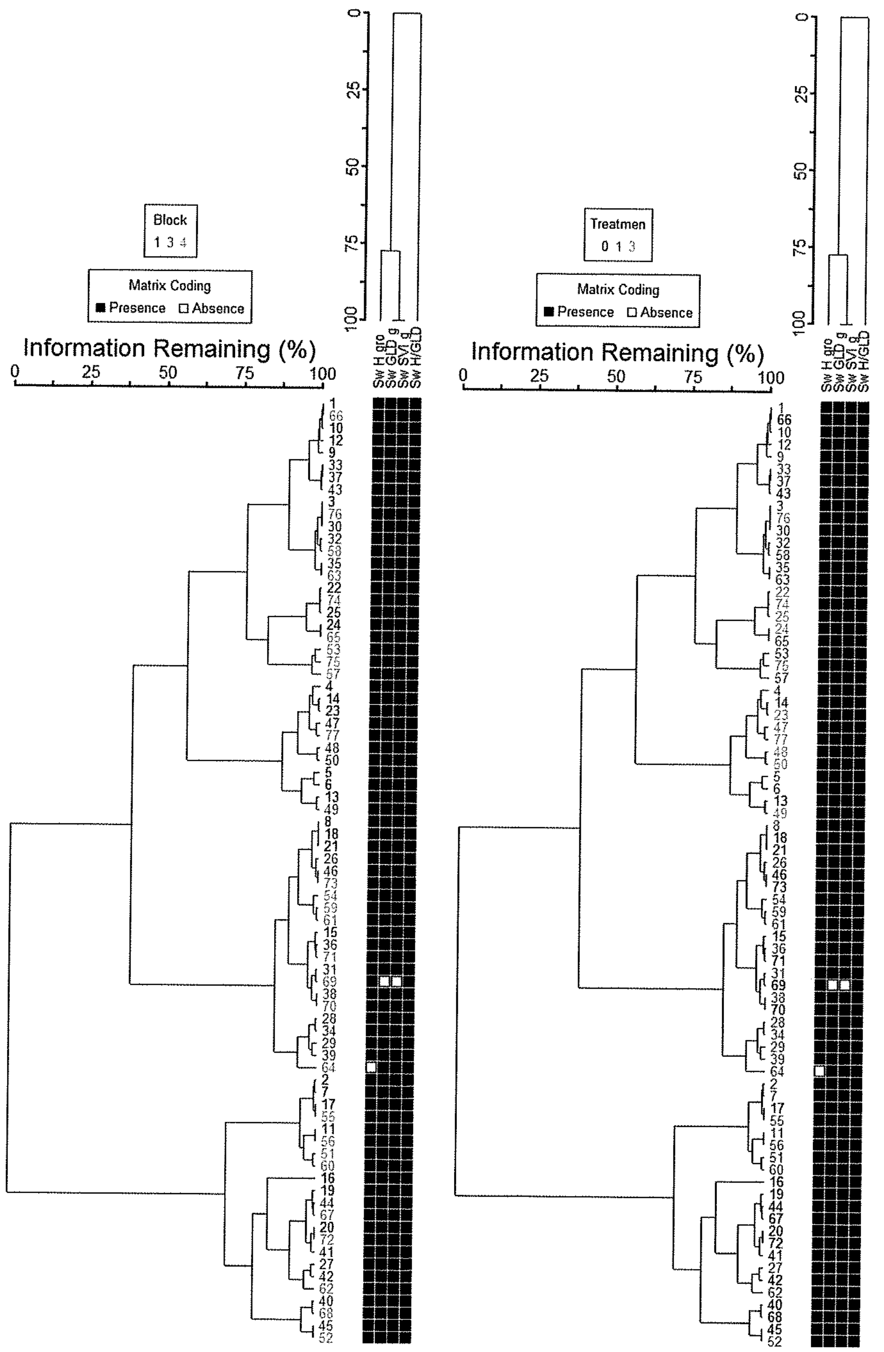

Figure 16. Two way cluster analysis of the data according to block (left) and treatment (right)

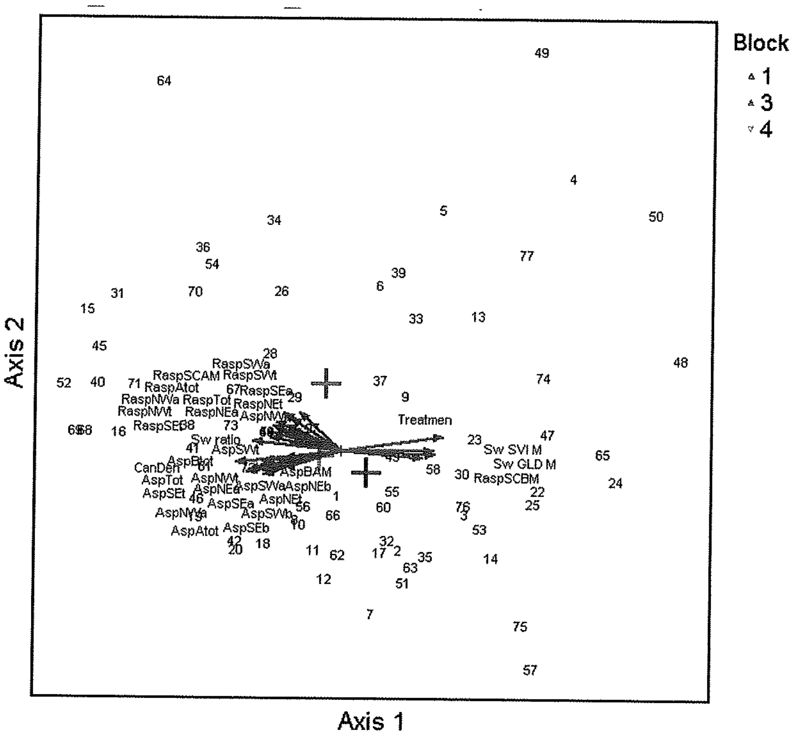

Figure 17. Hierarchical cluster analysis of the full dataset

Height growth, GLD growth and H/GLD ratio were normally distributed (Table 16). SVI growth was not normally distributed and a square root transformation was used to improve normality and allow the use of regression and response surface modelling (Table 16, Figure 18). Ln and Log10 were also applied as the other most frequently used transformations, however square root was the most effective at improving the distribution.

Table 16. Results of normality testing of Sw growth dependent variables using the Kolmogorov-Smirnov test.

Dependent variable	Kolmogorov-Smirnov		
	Statistic	df	Sig.
Sw height growth	0.061	77	0.200
Sw GLD growth	0.097	77	0.073
Sw SVI growth	0.145	77	**<0.0001**
Sw SVI growth^{sqrt}	0.080	77	0.200
Sw H/GLD ratio August	0.062	77	0.200

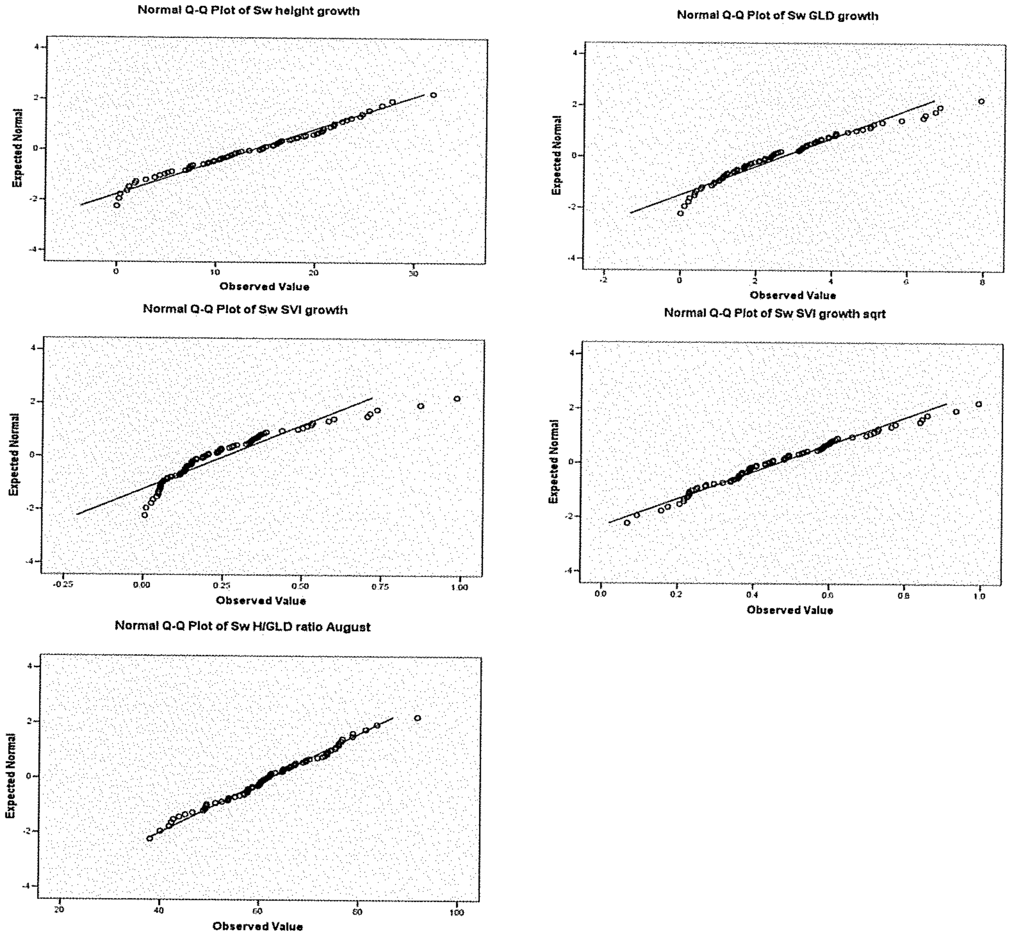

Figure 18. Q-Q plots of Sw growth dependent variables

Possible residual effects of treatment upon white spruce seedling growth were accounted for by analysing relationships between pre-season seedling measurements and growth over the season. If treatments resulting in freedom from competition have resulted in increased growth over the previous six years, whilst the herbicide itself is not active anymore, the larger seedlings will have a better root system and more photosynthetic apparatus and capability, resulting in larger growth over the season being measured. Whilst attempts have been made to minimize this possible confounding factor using a set height range of seedlings, pre-season size can also be used as covariates in regression analysis to account for the effect of treatment on current growth. Pre-season size was significantly related to SVI growth and H/GLD ratio, but not with height or GLD growth. Treatment may have residual effects on volume growth and H/GLD ratio of white spruce seedlings seven years post spray, hence the pre-season measurements need to be included as covariates to account for this effect, however it does not appear to be affecting the height or GLD growth of the seedlings in this study.

Pre-season height showed no relationship with height growth over the season, and so was not used as a covariate (Figure 19). Pre-season GLD showed a possible relationship (Figure 19) and so was included as a covariate in the regression modelling, however it was not significant and so was not selected in any of the final models. Pre-season SVI^{sqrt} showed a distinct relationship with SVI^{sqrt} growth (Figure 19) and so was included as a covariate in all regression models. Pre-season H/GLD ratio also demonstrated a very distinct linear trend with post-season H/GLD ratio (Figure 19) and so was included as a covariate in these regression models.

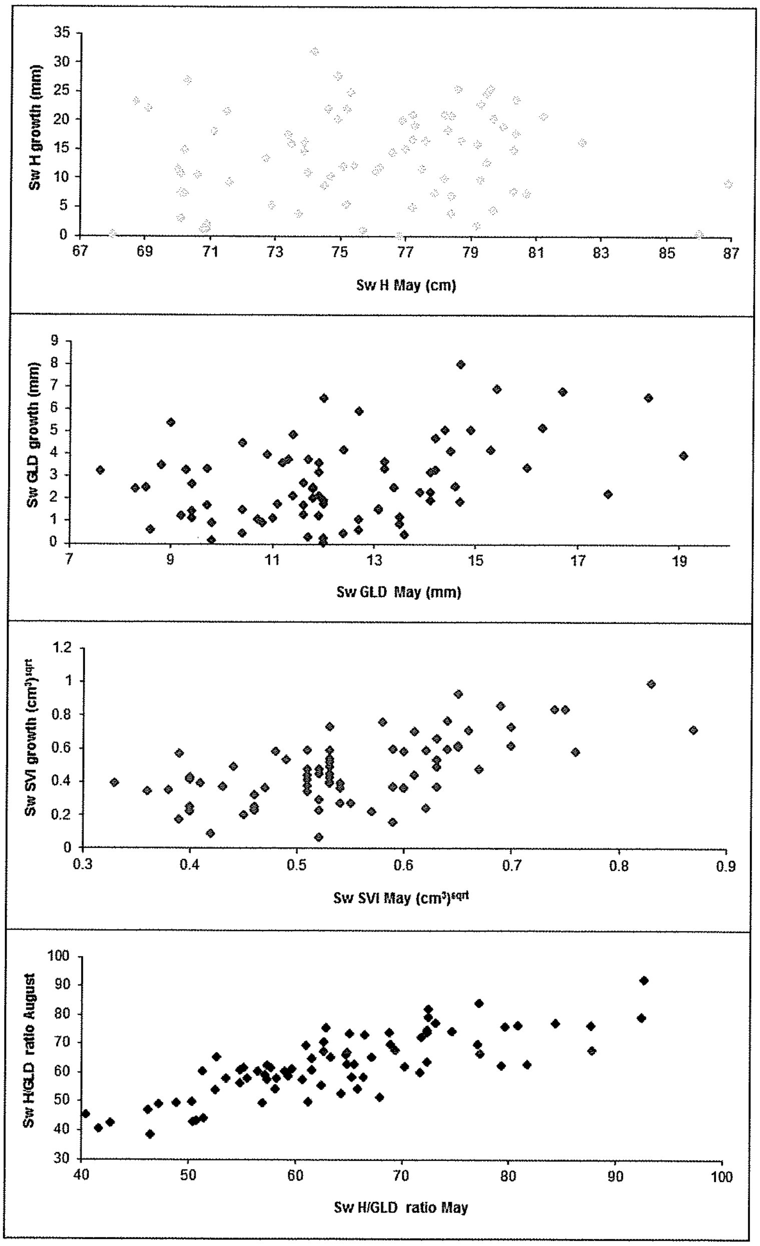

Figure 19. Effect of pre-season (May) Sw size on height growth, ground line diameter growth, stem volume index growthsqrt and H/GLD ratio in August.

Effect of PAR on White Spruce Seedling Growth

The amount of competition affects the growth of the white spruce seedlings partly through its effect on canopy density and therefore upon the amount and quality of available PAR (Mortensen and Sandvik 1988, Stadt *et al.* 2005). The effects of levels of PAR upon plant growth have been well documented (Lieffers and Stadt 1994, Wright *et al.* 1998, Duchesneau *et al.* 2001, Claveau *et al.* 2002). These studies have consistently demonstrated that lower PAR levels under large amounts of competition generally cause lower rates of photosynthesis and reduced growth rates of the seedlings, findings which are supported by this study.

Figure 20 shows curve estimation for the relationship between cumulative PAR and white spruce seedling growth, with the summary statistics for each model displayed in Table 17. The models with the highest adjusted R^2 have their coefficients displayed in Table 18. For height growth, the linear, quadratic, exponential, growth and compound models were excluded because they intercepted the Y axis above 0 suggesting growth at 0 PAR. The same applies for the exponential and compound GLD growth models, the quadratic, exponential, linear and compound SVI growth^{sqrt} models, and the quadratic height/GLD ratio August model. The residuals from the models found to be the most appropriate were checked for normality, and the Q-Q plots are displayed in Figure 21.

The linear model had the highest explanatory power for variation in SVI growth^{sqrt}. Linear and logarithmic models had very similar explanatory power in terms of adjusted R^2 but both the coefficients were significant in the linear model whereas the intercept was not in the logarithmic. Power appeared to be the most suitable model for the relationship between cumulative PAR over the season and GLD growth, with significantly higher R^2 than the linear model (Table 17). Compound had a slightly lower adjusted R^2 than the linear model for explaining variation in H/GLD ratio in August however only in the compound model were both the coefficients significant (Table 18), although the overall significance value for the model suggests none of the models were effective (Table 17). This suggests other interactions of the competition on the growing environment of the white spruce seedlings must be occurring.

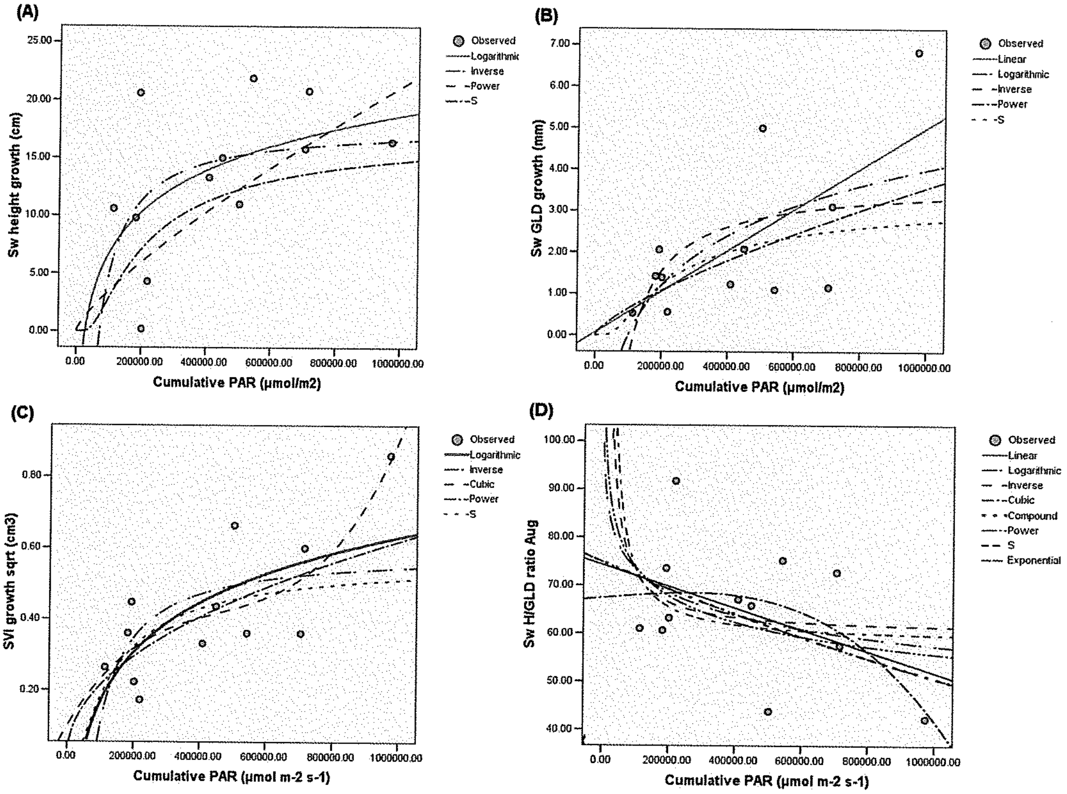

Figure 20. Curve estimation graphs for explaining variation in Sw seedling height growth (A), GLD growth (B), SVI growth^{sqrt} (C), and height/GLD ratio in August (D) using cumulative PAR from May 18th to September 22nd.

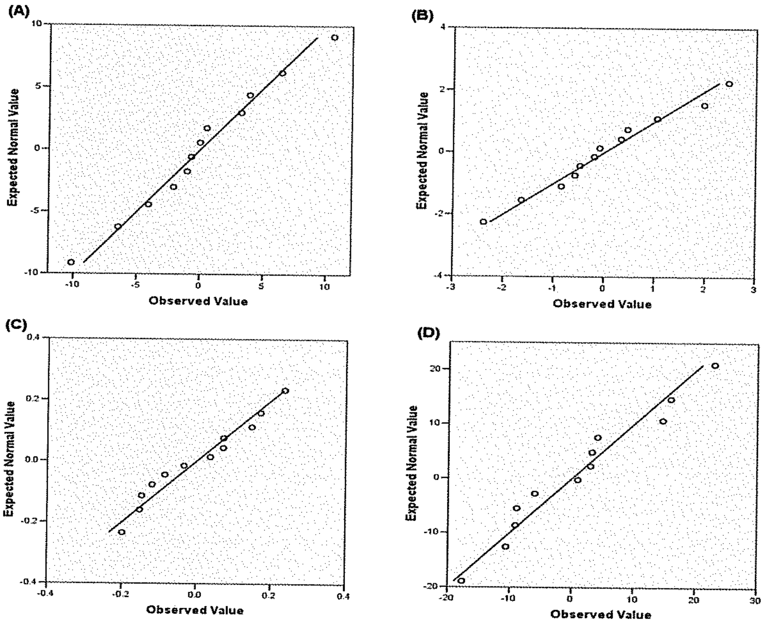

Figure 21. Q-Q plots of residuals from models using cumulative PAR at seedling height from May to September to predict Sw seedling height growth using a logarithmic model (A), GLD growth using a linear model (B), SVI growth^{sqrt} and H/GLD ratio in August (D) using a logarithmic model

Table 17. ANOVA and adjusted R^2 values for linear and non-linear regression models to explain variation in Sw seedling growth using cumulative PAR from May 18th to Sept 22nd .

	Height growth			GLD growth			SVI growth^{sqrt}			H/GLD ratio		
Model	F	Sig	Adj R^2	F	Sig	Adj R^2	F	Sig	Adj R^2	F	Sig	Adj R^2
Linear				9.086	**0.013**	0.424				2.453	0.148	0.177
Logarithmic	3.913	**0.076**	0.209	5.994	0.034	0.312	9.002	**0.013**	0.421	1.375	0.268	**0.033**
Inverse	2.731	0.129	0.136	3.824	0.079	0.204	5.176	0.046	0.275	0.517	0.489	-0.046
Cubic							4.844	0.033	0.512	0.985	0.447	-0.004
Compound										2.968	0.116	0.152
Power	2.041	0.184	0.086	7.216	0.023	0.361	8.768	0.014	0.414	1.673	0.225	0.058
S	1.242	0.291	0.022	6.226	0.032	0.322	5.447	0.042	0.288	0.685	0.427	-0.029
Exponential										2.968	0.116	0.152

Table 18. Coefficients for the non-linear models with the greatest explanatory power for explaining variation in Sw growth using cumulative PAR from May 18th to Sept 22nd.

	Model	Variable	Coefficient	Std Error	Sig
Height growth	Logarithmic	ln(Cumulative PAR)	5.176	2.617	**0.076**
		Intercept	-52.871	33.498	0.146
GLD growth	Linear	Cumulative PAR	4.94E-006	0.000	**0.013**
		Intercept	0.066	0.824	0.938
	Power	ln(Cumulative PAR)	0.743	0.277	**0.023**
		Intercept	0.000	0.000	0.784
SVI growth^{sqrt}	Logarithmic	ln(Cumulative PAR)	5.62E-007	0.000	**0.004**
		Intercept	0.180	0.076	**0.040**
H/GLD ratio August	Linear	Cumulative PAR	-2.2E-005	0.000	0.148
		Intercept	74.279	7.221	**<0.0001**
	Compound	Cumulative PAR	1.000	0.000	**<0.0001**
		Intercept	74.863	8.553	**<0.0001**
	Exponential	Cumulative PAR	-3.8E-007	0.000	0.116
		Intercept	74.863	8.553	**<0.0001**

Effect of Canopy Density and Percent Cover of Aspen and Raspberry on White Spruce Seedling Growth

Various models using competition from aspen and raspberry, from the most detailed full model quadrant approach, through various reduced models down to the simplest using just one variable (canopy density) can be used to explain variation in white spruce seedling growth. The effectiveness of each model depends on the desired growth variable. The full model approach is the most effective but requires the greatest input of time and funds. Cover of aspen and raspberry above seedling height is capable of producing very similar results at much lower input. The models demonstrate the negative effect of canopy density and percent cover of aspen on white spruce seedling growth, supporting hypothesis 6 in this regard. The effect of raspberry is uncertain in the full model and quadrant approach, but negative in the more reduced models, although the species is not as strong a competitor as aspen. In all models except the full model, GLD growth is explained better by canopy density and percent aspen and raspberry cover than height growth, supporting hypothesis 6 that competition affects diameter more than height, as shown by other studies (Zedaker *et al.* 1987, Lautenschlager 1999, Grossnickle 2000, Jobidon 2000). This is likely because the white spruce finishes height growth while the competitive species are still growing foliage, meaning more light resources are available for the spruce while the shoots are growing, compared to when the spruce is allocating resources to diameter growth (Brand and Janas 1988).

The final regression models for seedling height growth, GLD growth, SVI growth^{sqrt} and H/GLD ratio, from the full model (quadrants above and below) down to the most reduced (canopy density) are displayed in Table 19.

The full model is the best model for predicting white spruce growth and H/GLD ratio, with the highest adjusted R^2 in every case. This demonstrates the usefulness of measuring competitive vegetation in quadrants above and below seedling height if accuracy is the most important factor, especially for height growth where the full model explains 14% more of the variation than the next best model (total aspen and raspberry above and below) (Table 19).

The model using canopy density is not effective at estimating height growth, explaining just 29.1% of the variation, as opposed to 52.8% explained using the full model (Table 19). However it appears to have similar effectiveness as the full model at explaining SVI growth^{sqrt} (6.9% less variation explained than full model) and H/GLD ratio (7.9% less variation explained than full model).

The quadrant approach could be used, however as can be seen in Table 19, with the exception of H/GLD ratio, all the quadrants are significant for either aspen or raspberry, and so a minimum of 4 percent cover measurements have to be taken. For explaining variation in H/GLD ratio of white spruce seedlings using the quadrant approach is the most effective without using the full model, however it only explains 3.8% more of the variation than using just aspen and raspberry above seedling height. It should also be noted that the full model and quadrant approach both show a positive effect of raspberry in the north on white spruce seedling growth, which suggests a possible flaw in the statistics as this does not appear to make biological sense, and do not concur with the overall negative influence of raspberry in the more reduced models.

For explaining the variation in height growth, GLD growth and SVI growth^{sqrt} without using the full model, using aspen and raspberry cover above seedling height is the most effective model, explaining the most variation between the seedlings, and requiring just two variables to be measured. Therefore, the choice of model depends upon its purpose. If the focus is on height growth then the full model should be used. However with the focus on practicality and use for silviculturalists the most likely model to be used is one consisting of the total aspen and raspberry above seedling height. This model is most effective at predicting volume growth and ratio, explaining 62.2% of SVI growth^{sqrt} (when combined with SVI in May^{sqrt} as a covariate) and 68.4% of H/GLD ratio (Table 19). It explains only 41.5% of GLD growth, but this is only 8.3% less than using the full model, and requires only 2 variables to be measured as opposed to 6 using the full model. Regeneration surveys such as these are time consuming and create a huge amount of information, a large amount of which can go unused if forest managers do not have time to go through it all (Brand *et al.* 1991). If the information can be simplified at little or no cost to effectiveness it becomes a more useful decision making tool.

Table 19. Full and reduced regression model summary statistics for explaining variation in Sw seedling growth using canopy density and percent cover of aspen and raspberry competition.

		Sw height growth (cm)					Sw GLD growth (mm)					Sw SVI growth(cm^3)^{sqrt}					Sw H/GLD ratio				
Model	Variable	Estimate	Std Error	t	p	Adj. R^2	Estimate	Std Error	t	p	Adj R^2	Estimate	Std Error	t	p	Adj R^2	Estimate	Std Error	t	p	Adj R^2
FULL MODEL (% cover aspen and rasp in quadrants above and below seedling height)	Intercept	27.916	1.773	15.747	**<0.0001**	0.528	5.128	0.432	11.883	**<0.0001**	0.498	0.335	0.104	3.222	**0.002**	0.647	15.675	3.798	4.127	**<0.0001**	0.734
	Sw SVI May^{sqrt}											0.650	0.153	4.249	**<0.0001**						
	Sw H/GLD ratio May																0.695	0.066	10.522	**<0.0001**	
	Rasp NW above	-1.576	0.301	-5.235	**<0.0001**		-0.161	0.073	-2.204	**0.031**		-0.020	0.006	-3.198	**0.002**						
	Rasp NW above^2	0.058	0.014	4.279	**<0.0001**		0.007	0.003	2.083	**0.041**		0.001	0.000	2.444	**0.017**						
	Rasp NW below						0.098	0.044	2.234	**0.029**											
	Rasp NE below	0.986	0.440	2.240	**0.028**																
	Rasp NE below^2	-0.102	0.043	-2.387	**0.020**																
	Rasp SE above	-0.222	0.105	-2.112	**0.038**		-0.091	0.031	-2.988	**0.004**							0.244	0.134	1.816	**0.074**	
	Rasp SW above						0.070	0.031	2.272	**0.026**							-0.414	0.128	-3.241	**0.002**	
	Aspen NW above	0.311	0.139	2.238	**0.029**												0.349	0.146	2.385	**0.020**	
	Aspen NW below	-2.465	0.633	-3.893	**<0.0001**												-0.598	0.262	-2.284	**0.026**	
	Aspen NW below^2	0.137	0.045	3.043	**0.003**																
	Aspen NE above						-0.047	0.023	-2.083	**0.041**		-0.005	0.002	-2.268	**0.026**						
	Aspen SE above						-0.297	0.079	-3.758	**<0.0001**							0.989	0.413	2.394	**0.019**	
	Aspen SE above^2						0.010	0.003	2.841	**0.006**							-0.034	0.016	-2.155	**0.035**	
	Aspen SW above	-0.326	0.102	-3.199	**0.002**							-0.008	0.002	-3.899	**<0.0001**						
	Aspen SW below																-1.215	0.683	-1.779	**0.080**	
	Aspen SW below^2																0.102	0.061	1.678	**0.098**	
QUADRANTS (% cover aspen and rasp in quadrants)	Intercept	26.410	2.151	12.280	**<0.0001**	0.385	4.461	0.546	8.165	**<0.0001**	0.410	0.242	0.108	2.245	**0.028**	0.573	14.343	4.134	3.469	**0.001**	0.722
	Sw SVI May^{sqrt}											0.788	0.152	5.190	**<0.0001**						
	Sw H/GLD ratio May																0.754	0.069	10.903	**<0.0001**	
	Rasp NW total	-1.05	0.433	-2.423	**0.018**												-1.100	0.419	-2.625	**0.011**	
	Rasp NW total^2	0.033	0.015	2.198	**0.031**												0.034	0.014	2.403	**0.019**	
	Rasp NE total	0.595	0.353	1.685	**0.096**							-0.003	0.002	-1.696	**0.094**		1.299	0.345	3.77	**<0.0001**	
	Rasp NE total^2	-0.026	0.012	-2.163	**0.034**												-0.045	0.012	3.785	**<0.0001**	
	Rasp SW total						0.164	0.082	2.004	**0.049**							-0.223	0.113	-1.972	**0.053**	
	Rasp SW total^2						-0.006	0.003	-2.219	**0.03**											
	Aspen NE total	-0.14	0.079	-1.779	**0.080**		-0.05	0.019	-2.652	**0.01**							0.17	0.072	2.349	**0.022**	
	Aspen SE total						-0.156	0.06	-2.586	**0.012**		-0.013	0.005	-2.293	**0.025**						
	Aspen SE total^2						0.004	0.002	2.405	**0.019**		0.000	0.000	2.109	**0.038**						
	Aspen SW total	-0.172	0.083	-2.081	**0.041**		-0.043	0.024	-1.386	**0.071**		-0.006	0.002	-2.574	**0.012**						

		Height growth					Sw GLD growth					Sw SVI growth^{sqrt}					Sw H/GLD ratio				
Model	Variable	Estimate	Std Error	t	p	Adj. R^2	Estimate	Std Error	t	p	Adj R^2	Estimate	Std Error	t	p	Adj R^2	Estimate	Std Error	t	p	Adj R^2
ABOVE AND BELOW (% cover aspen and rasp above and below seedling height)	Intercept	23.750	1.609	14.757	**<0.0001**	0.388	4.973	0.365	13.623	**<0.0001**	0.415	0.360	0.110	3.272	**0.002**	0.622	19.405	4.346	4.465	**<0.0001**	0.684
	Sw SVI May^{sqrt}											0.601	0.155	3.880	**<0.0001**						
	Sw H/GLD ratio May																0.628	0.072	8.764	**<0.0001**	
	Rasp above total	-0.136	0.027	-4.953	**<0.0001**		-0.011	0.006	-1.701	**0.093**		-0.001	0.001	-2.466	**0.016**						
	Aspen above total	-0.114	0.025	-4.495	**<0.0001**		-0.041	0.006	-7.057	**<0.0001**		-0.004	0.001	-6.305	**<0.0001**		0.473	0.173	2.733	**0.008**	
	Aspen above total^2																-0.003	0.002	-1.822	**0.073**	
	Aspen below total																-0.989	0.428	-2.309	**0.024**	
	Aspen below total^2																0.017	0.009	1.903	**0.061**	
TOTALS (total % cover aspen and rasp)	Intercept	24.690	1.891	13.056	**<0.0001**	0.334	4.709	0.340	13.844	**<0.0001**	0.372	0.313	0.117	2.681	**0.009**	0.591	15.218	4.149	3.668	**<0.0001**	0.665
	Sw SVI May^{sqrt}											0.678	0.159	4.266	**<0.0001**						
	Sw H/GLD ratio May																0.661	0.071	9.311	**<0.0001**	
	Rasp total	-0.118	0.029	-4.130	**<0.0001**							-0.001	0.001	-1.671	**0.099**						
	Aspen total	-0.077	0.020	-3.779	**<0.0001**		-0.030	0.004	-6.781	**<0.0001**		-0.003	0.000	-5.605	**<0.0001**		0.070	0.023	3.069	**0.003**	
CANOPY DENSITY (densitometer)	Intercept	22.328	1.709	13.067	**<0.0001**	0.291	5.062	0.363	13.962	**<0.0001**	0.407	0.356	0.112	3.179	**0.002**	0.608	15.679	4.248	3.691	**<0.0001**	0.655
	Sw SVI May^{sqrt}											0.604	0.158	3.828	**<0.0001**						
	Sw H/GLD ratio May																0.650	0.076	8.540	**<0.0001**	
	Canopy density	-0.142	0.025	-5.669	**<0.0001**		-0.039	0.005	-7.291	**<0.0001**		-0.004	0.001	-6.223	**<0.0001**		0.078	0.030	2.654	**0.010**	

As percent cover of aspen and raspberry above seedling height can produce similar results to the full model at lower cost, this model is examined further. Analysis shows that both species are related to white spruce seedling growth and H/GLD ratio, however aspen has a larger effect on all growth variables except height growth.

The effects of aspen and raspberry above seedling height upon white spruce growth and the interaction between the two are shown in a response surface in Figure 22. The most appropriate model was linear for height, GLD and SVI growth^{sqrt}, with the interaction term included for height/GLD ratio in August (total output and model assessment in Appendix). The summary statistics and coefficients for the SVI growth^{sqrt} and height/GLD ratio in August response surfaces are displayed in Table 20; the statistics for the height and GLD models are already included in Table 19.

The model used to predict stem volume index growth^{sqrt} had the highest explanatory power with an adjusted R^2 of 0.549. This is lower than the linear regression model in Table 19 due to the SVI in May^{sqrt} not being included. The 2FI model for the height/GLD ratio included the interaction between aspen and raspberry, and had an adjusted R^2 of 0.344, which was much lower than the linear model with quadratic terms in Table19. There is a large amount of variability not accounted for by the models, and so their explanatory power is limited. That the stem volume index growth values had to be transformed must be taken into consideration. However the response surfaces do show the significance of these two competitive species upon white spruce seedling and provide a helpful visual of the effect of aspen and raspbery above seedling height upon white spruce height, GLD and SVI^{sqrt} growth. Different types of species have varying competitive effects due to differences in resource requirements and allocation of these resources, an effect demonstrated by several studies (Goldberg and Werner 1983, Balandier 2006, Man *et al.* 2008). The results from this study support previous research demonstrating the difference in the effect of different types of species on crop tree seedling growth (Man *et al.* 2008, Bell *et al.* 2011). For height growth, aspen and raspberry appear to have a similar significance (Figure 22, Table 19), but they do not explain most of the variation. Aspen has a much larger negative effect on seedling GLD, SVI^{sqrt} growth and height/diameter ratio than raspberry does (Figure 22, Table 19), suggesting that is the species that should be targeted for control. This is consistent with other research reporting the negative impacts of this species on white spruce seedling growth due to impacts on the microclimate (Rowe 1955, Awada and Redmann 2000, Comeau 2001, Pinno *et al* 2001, Chen and Popadiouk 2002, Donoso and Nyland 2006, Filipescu and Comeau 2007b), and the data on the greater effect of aspen on PAR reported in this study.

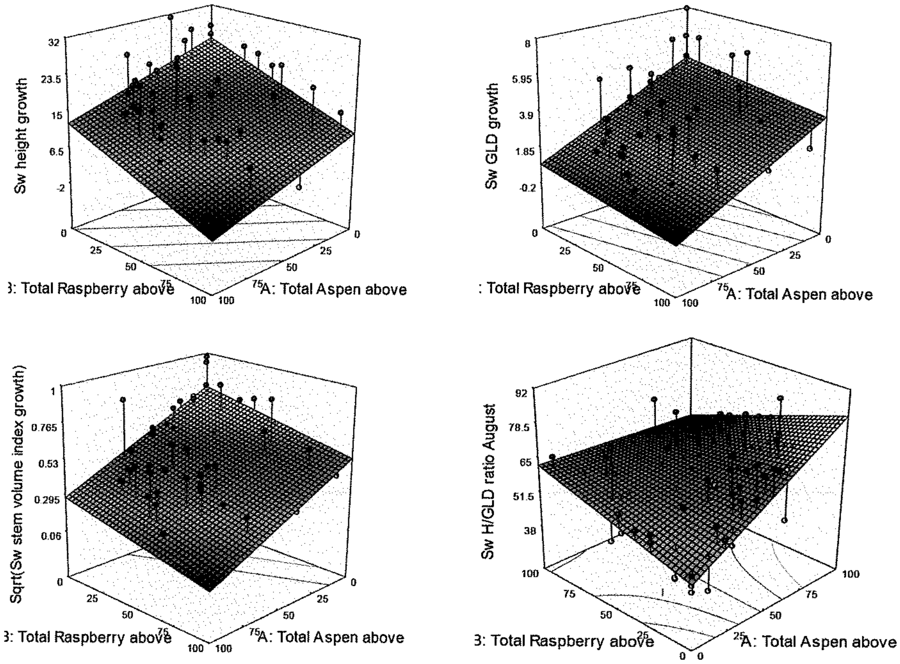

Figure 22. Response surfaces to explain variation in Sw seedling height growth(cm), GLD growth(mm), stem volume index growth^{sqrt}(cm^3) and H/GLD ratio in August (cm) using percent cover of aspen and raspberry above seedling height. Note the different orientation of the H/GLD ratio graph.

Table 20. Summary statistics for the response surface models to explain variation in Sw seedling SVI growth^{sqrt} and height/GLD ratio in August using percent cover of aspen and raspberry above seedling height.

Dependent variable	Variable	Coefficient	Std Error	t	p	Adj. R^2
SVI growth^{sqrt}	Intercept	0.768	0.036	21.630	**<0.0001**	0.550
	Aspen above	-0.005	0.001	-8.575	**<0.0001**	
	Raspberry above	-0.002	0.001	-3.655	**<0.0001**	
Height/GLD ratio	Intercept	45.577	3.162	14.412	**<0.0001**	0.344
	Aspen above	0.365	0.069	5.301	**<0.0001**	
	Raspberry above	0.172	0.073	2.357	0.581	
	Aspen above*Raspberry above	-0.004	0.002	-2.455	**0.017**	

Canopy density can be used as a simple and low input model to explain variation in white spruce seedling growth. This model shows the negative relationship between canopy density and white spruce seedling growth and H/GLD ratio, although it is not as effective as the more detailed approaches.

As it is a single variable model it is feasible to examine the nature of the relationship that exists. The relationship between canopy density and white spruce seedling growth is shown in a curve estimation graph in Figure 23. Table 21 shows the ANOVA summary statistics and adjusted R^2s of the various regression models. Models could not be calculated past the cubic level for height growth and GLD growth due to the presence of 0.00 values. The coefficients of the models with the highest explanatory power are displayed in Table 22. Linear models for the height and GLD growth are not included as these coefficients are already displayed in Table 19. The most appropriate models had their residuals checked for normality using Q-Q plots. These are displayed in Figure 24.

GLD growth and stem volume index growth all increase as canopy density decreases, which is consistent with the literature which reports maximum GLD and stem volume growth at 100% (Logan 1969, Coates *et al.* 1994, Lieffers and Stadt

1994, Wright *et al.* 2000). The data also shows increased height growth as canopy density decreases, which supports findings by Eis (1967) and Lieffers and Stadt (1994) although both these studies found increases in height growth to level off past 40 to 60% cover, rather than continue to increase linearly. This is in contrast to Brix (1972) and Man and Greenway (2011) which found shade did not affect height growth, although these were not using canopy density so that may explain the difference. For this dataset, height growth and SVI growth^{sqrt} are best described using a linear model. For GLD growth a cubic model is the most effective, with a quadratic model second best, but the cubic only explains 1.3% more of the variation and the quadratic only 0.6% more than the linear model (Table 21). As only the intercept is significant in both the cubic and quadratic (Table 22) the linear should be adopted as both the coefficients are significant.

For H/GLD ratio in August, the exponential and compound models are the most effective, with an adjusted R^2 of 0.348, with the linear model the next suitable with an adjusted R^2 of 0.32. All the coefficients in those models are significant (Table 22), yet the scatterplot in Figure 23 shows what appears to be a linear trend, suggesting the use of a linear model the most appropriate. Lieffers and Stadt (1994) reported a linear decrease in height/diameter ratio of white spruce seedlings as PAR increased, which is related to canopy density. The ratios found in this study and shown in Figure 23D are very similar to those recorded by Lieffers and Stadt (1994) who found ratios ranging from 90 at 8% light to 58 at 100% light, even though they used saplings between 1 and 3m tall, so many were larger than those in this study. As discussed, the phenology of white spruce allows for height growth before the foliage of the competition develops fully, however diameter growth occurs later when there are lower levels of PAR available (Brand and Janas 1988), which reflects in the larger H/GLD ratio of the seedlings under dense competition.

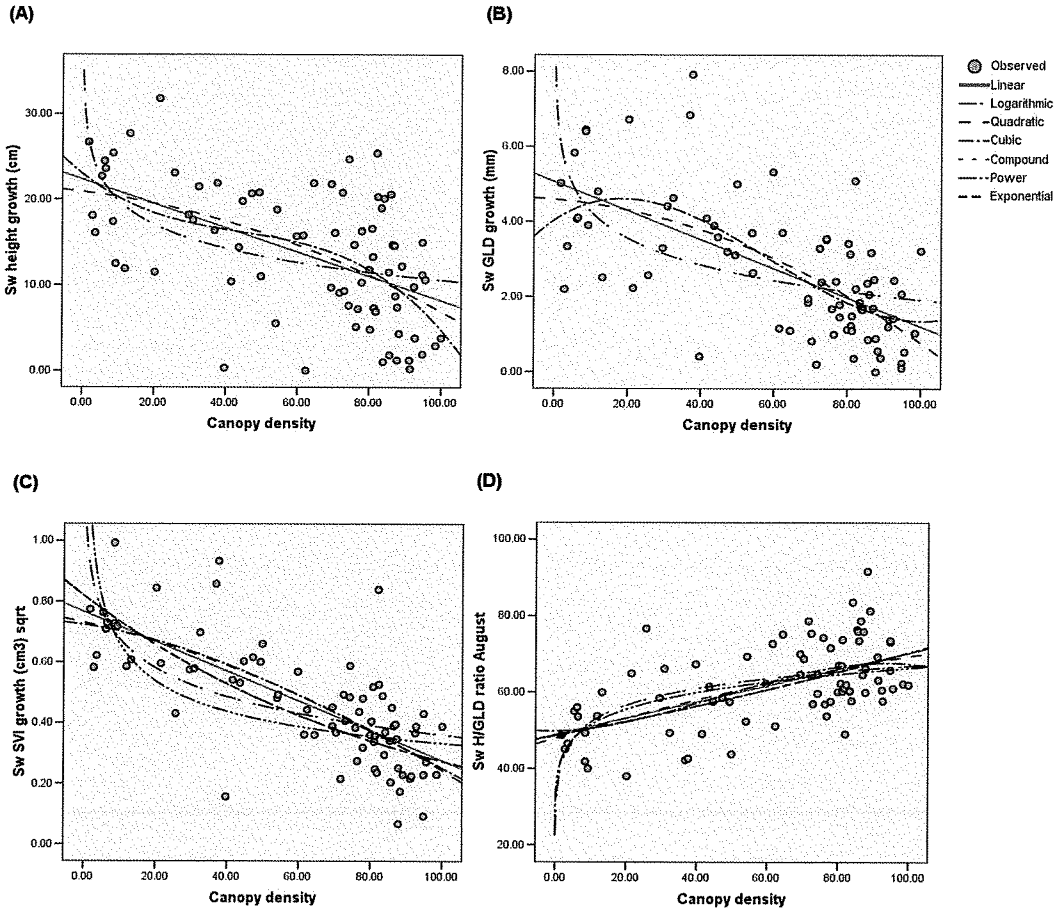

Figure 23. Curve estimation graphs for explaining variation in Sw seedling height growth (A), GLD growth (B), SVI growth^{sqrt} (C) and height/GLD ratio (D) using canopy density.

Table 21. ANOVA and adjusted R^2 values for linear and non-linear regression models to explain variation in Sw seedling growth using percent canopy density.

	Height growth			GLD growth			SVI growth^{sqrt}			H/GLD ratio		
Model	F	Sig	Adj R^2	F	Sig	Adj R^2	F	Sig	Adj R^2	F	Sig	Adj R^2
Linear	32.138	**<0.0001**	0.291	53.160	**<0.0001**	0.407	89.007	**<0.0001**	0.537	37.440	**<0.0001**	0.324
Logarithmic	24.088	**<0.0001**	0.233	30.730	**<0.0001**	0.281	55.365	**<0.0001**	0.417	31.994	**<0.0001**	0.290
Quadratic	16.366	**<0.0001**	0.288	27.760	**<0.0001**	0.413	45.023	**<0.0001**	0.537	18.595	**<0.0001**	0.316
Cubic	11.311	**<0.0001**	0.289	19.338	**<0.0001**	0.420	29.631	**<0.0001**	0.531	12.470	**<0.0001**	0.312
Compound							56.960	**<0.0001**	0.424	41.639	**<0.0001**	0.348
Power							35.223	**<0.0001**	0.310	35.463	**<0.0001**	0.153
Exponential							56.940	**<0.0001**	0.424	41.639	**<0.0001**	0.348

Table 22. Coefficients for the models with the greatest explanatory power for explaining variation in Sw seedling growth using canopy density.

	Model	Variable	Coefficient	Std Error	Sig
GLD growth	Cubic	Canopy density	0.066	0.059	0.269
		Canopy density *2	-0.002	0.001	0.122
		Canopy density *3	1.20E-005	0.000	0.178
		Intercept	4.038	0.645	**<0.0001**
	Quadratic	Canopy density	-0.008	0.023	0.724
		Canopy density*2	0.000	0.000	0.184
		Intercept	4.592	0.503	**<0.0001**
SVI growth^{sqrt}	Linear	Canopy density	-0.005	0.001	**<0.0001**
		Intercept	0.765	0.036	**<0.0001**
H/GLD ratio	Compound	Canopy density	1.004	0.001	**<0.0001**
		Intercept	48.636	1.903	**<0.0001**
	Exponential	Canopy density	0.004	0.001	**<0.0001**
		Intercept	48.636	1.903	**<0.0001**
	Linear	Canopy density	0.214	0.035	**<0.0001**
		Intercept	48.904	2.388	**<0.0001**

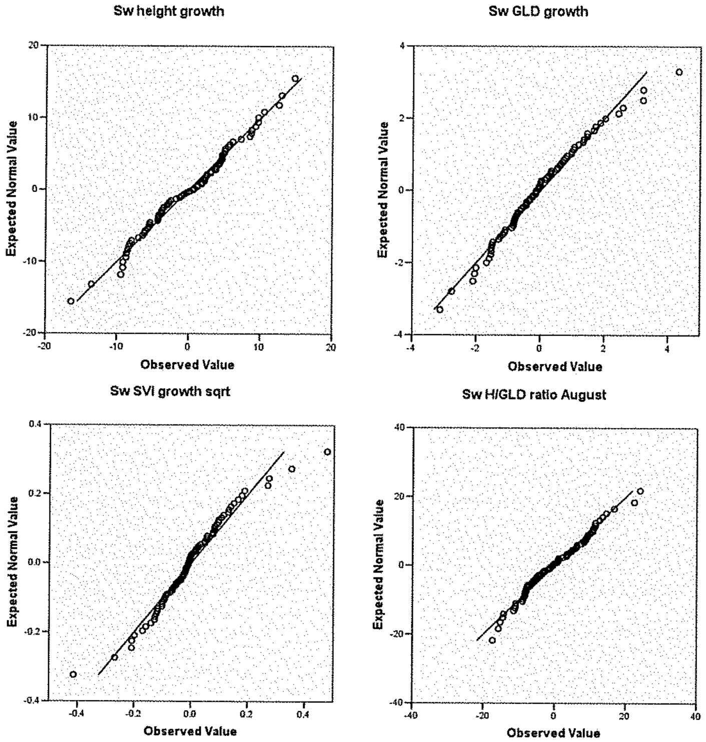

Figure 24. Q-Q plots of the residuals from the selected linear regression models to explain variation in Sw seedling height growth, GLD growth, SVI growth$^{\text{sqrt}}$ and height/GLD ratio using canopy density.

It is important to note that the H/GLD ratio in May was significant for the H/GLD ratios in August in the previously displayed linear regressions, and that including that as a covariate in a linear regression with canopy density resulted in a much higher R^2 than any of the non-linear regressions which use just one independent variable and so do not take this into account. The same applies to the SVI growth$^{\text{sqrt}}$ however the difference is much smaller and as the linear model is most the suitable regardless it is not an important factor as the covariate can just be included in the linear analysis as in Table 19.

Total percent cover of aspen is another possible single variable model to use to explain variation in white spruce seedling GLD growth, where it is possible to examine the nature of the relationship. The data demonstrates the linear negative correlation between aspen cover and seedling GLD growth.

As both the dependent variable and the independent variable had values of 0.00 a number of the non-linear regression models could not be run during the curve estimation for the relationship between percent cover of aspen and white spruce seedling GLD growth. The scatter graph and trendlines from the linear, quadratic and cubic models are displayed in Figure 25, with the ANOVAs and the adjusted R2 values displayed in Table 23, and coefficients in Table 24. The linear model has the highest explanatory power, fits the data, and is the only model where all coefficients are significant (Table 23 and 24). The data shows a clear trend of decreased GLD growth under increased aspen cover. This is unsurprising when one considers that aspen makes up the majority of the canopy for the sample seedlings, and decreased growth under aspen and increased canopy cover has been demonstrated in various studies in the literature (Comeau 2001, Pinno *et al* 2001, Donoso and Nyland 2006, Filipescu and Comeau 2007b, Bell *et al.* 2011).

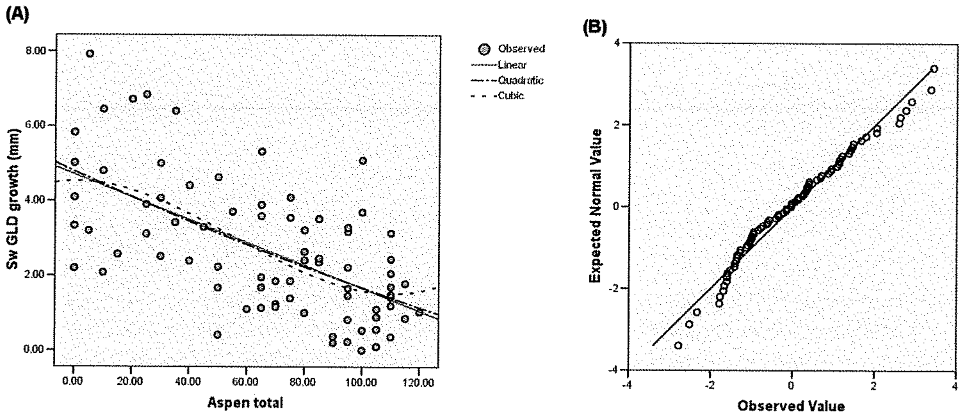

Figure 25. Curve estimation graph for explaining variation in Sw seedling GLD growth and Q-Q plot of the residuals from the linear model.

Table 23. ANOVA and adjusted R^2 values for linear and non-linear regression models to explain variation in Sw seedling GLD growth using total percent cover of aspen.

Model	F	Sig	Adj R^2
Linear	45.986	**<0.0001**	0.372
Quadratic	22.747	**<0.0001**	0.364
Cubic	15.448	**<0.0001**	0.363

Table 24. Coefficients for the models with the greatest explanatory power for explaining variation in white spruce seedling GLD growth. using total percent cover of aspen.

Model	Variable	Coefficient	Std Error	Sig
Linear	Aspen total	-0.030	0.004	**<0.0001**
	Intercept	4.709	0.340	**<0.0001**
Quadratic	Aspen total	-0.035	0.018	**0.049**
	Aspen total *2	3.95E-005	0.000	0.785
	Intercept	4.791	0.455	**<0.0001**
Cubic	Aspen total	0.001	0.042	0.976
	Aspen total *2	-0.001	0.001	0.375
	Aspen total *3	4.58E-006	0.000	0.344
	Intercept	4.453	0.529	**<0.0001**

WELL-SPACED AND FREE-TO-GROW ASSESSMENT

The well-spaced and free-to-grow assessment procedure is aimed at seven to eleven-year-old seedlings. The white spruce seedlings in this study were seven-years-old at the end of the 2010 growing season. Seventy-four of the seedlings met the well-spaced criteria (which reflects the distribution of crop trees) but only 7 seedlings could be defined as free-to-grow following the survey procedure in the manual, all of these in the intensive treatment (Appendix I). At a regeneration site such as this one, with high amounts of competition, and taking into account the selected height range of the sample seedlings, only 9% of the seedlings were 1.5 times taller than the other vegetation within a 1.2m radius. Hence it was determined that 91% of the seedlings that were between 68 and 83 cm at the beginning of the field season were not free-to-grow as they did not meet the criteria in the survey. Considering the large amounts of competition from aspen and very tall (up to over 2m) raspberry at the site, and the subsequent small size and growth rates of many of the seedlings, most of the sample seedlings will probably still be under 1.5m in their eighth year and would still have overtopping brush. It is important to note that these seedlings were chosen due to their being under competition, and it was uncertain whether they would become free to grow or not. The sample does not therefore reflect the status of all seedlings at the site; however it does provide evidence suggesting that this group of seedlings under competition from aspen and raspberry are unlikely to become free-to-grow within 8 years under the criteria in the free-to-grow regeneration assessment procedure for Ontario. This suggests that either further vegetation management treatments are required or that the regeneration survey needs to be deferred till age 10 or perhaps even 11 years-post-harvest. In the case of basic silviculture where limited funds are available it may be acceptable to defer assessment, whereas in the case of intensive silviculture further treatment would be recommended. To meet free-to-grow standards in these forests requires high costs in terms of treatments and simplification of the stand structure, as well as possible negative social reactions to the more intensive use of herbicides (Wagner *et al.* 1998), and some research challenges the effectiveness of such assessments at predicting white spruce seedling growth (Lieffers *et al.* 2007). It is possible that current free-to-grow assessments are simply not practical for application to boreal mixedwood sites such as these.

CONCLUSIONS AND RECOMMENDATIONS

Different combinations of aspen and raspberry cover created variation in small scale microclimatic conditions in terms of available PAR and average air temperatures and affected the growth and photosynthetic responses of white spruce, although not always in the manner expected. Competitive cover from both species reduced available PAR, white spruce seedling height growth, ground line diameter growth, stem volume index growth, and photosynthetic rates, and increased height/GLD ratio. This supports previous literature on the negative effects of competition on seedling growth. It was hypothesised that red raspberry would be more of a competitor than aspen due to larger LAI, and that if leaving some aspen could reduce raspberry it may be a better strategy for improving seedling performance. Contrary to this the results suggest that aspen is the most important competitor when growing in combination with red raspberry, when white spruce height is held constant.

Both species constitute a large proportion of the canopy surrounding white spruce seedlings at this site, suggesting if the goal of competition management is to simply reduce canopy density then a method needs to be used to target both species. Despite its large leaf area and abundance, red raspberry at this site is not as strong a competitor for white spruce seedlings in terms of available PAR and does not have a strong relationship with seedling growth. This could be of use to silviculturalists with a similar site or issue with these two species. Despite previous suggestions of maintaining aspen to reduce other competition, the results of this study suggest reducing aspen competition is unlikely to create a more detrimental scenario for white spruce seedlings in terms of competition from red raspberry.

This study also evaluated the appropriateness of several different methodologies. To explain variation in height growth and height/GLD ratio of six to seven year old white spruce seedlings under varied levels of competition from aspen and raspberry a full model approach using cover above and below seedling height in 4 quadrants is the most effective. When predicting the GLD and stem index volume growth of six to seven year old white spruce seedlings under varying levels of competition from aspen and raspberry, the percent cover of these two competitive species above the height of the seedling provide an almost equally effective alternative to using a complicated full model approach. This suggests that the effect of competition from aspen and raspberry upon white spruce seedling physiological and growth responses could be largely due to differences in PAR, as competitive species above seedling height were more significant than total values. This information could be of use to researchers in the field, by saving time and reducing costs through the ability to target the most important competition variables and hence be time and cost effective.

It is interesting to note however, that although changes in PAR may be the main influence of competition on seedling growth, other factors such as differences in air temperature related to levels of aspen and raspberry are affecting seedling growth. Whilst the results from the microclimate stations in this study did not pick up any significant patterns between soil moisture, soil temperature and aspen and raspberry cover, there may have been small differences that were not picked up by the methods used in this study. Analysis of foliar nutrients could be a useful additional piece of research in order to examine belowground interactions between aspen and raspberry and white spruce seedlings and explain some of the unaccounted for variation in seedling growth.

The results from this study indicate the importance of aspen competition, which could support the idea of the usefulness of free-to-grow criteria, and the use of continued and intensive management. However the findings that raspberry is not such an important competitor when growing with aspen suggests that assessing whether a seedling is free-to-grow should be based on more than the height of surrounding vegetation, and take into account the type and combination of species instead. For example crop trees under 1.5m, and under medium to high amounts of raspberry were still able to receive a medium amount of PAR. This suggests that different methodologies may be more suitable to assess competition at rich sites such as this.

FUTURE RESEARCH

There were many limitations encountered in this study which could be addressed with further research. The effect of competitive species such as aspen and raspberry upon microclimatic conditions such as air temperature, soil temperature and soil water content could be better understood by recording these variables over a year, and recording the percent cover or canopy density of each species seasonally or monthly. This study only estimated these variables in May and recorded percent cover and canopy density in August, meaning the effects of the competitive species in the transitional period between bare and full foliage upon the microclimate may have become lost in averages and the overall figures.

With time for further analysis growing degree hours (GDH) or days (GDD) for both air and soil temperature could be calculated, along with frost free periods (FFP) and hours with soil moisture below 25%, and possible relationships between these values and aspen and raspberry cover and seedling growth could be investigated. Seasonal patterns of PAR, air and soil temperature and soil moisture could also be plotted and examined for correlations with canopy density from these two competitive species.

The impact of combined competition from aspen and raspberry on nutrient availability would be a useful additional analysis. Foliar nutrients could be examined from each of the seedlings under the varied range of competition levels. This data might help explain some of the unaccounted for variation found in this study.

There are also many opportunities for additional research in this area. Competition studies are common, yet they often are conducted in artificial conditions and focus on the effect of one species at a time. Examining the combined and interactive effects of competitive species upon crop tree growth can provide a more realistic dataset and useful techniques for thresholds of crop tree response and competition management. The effect of competition will vary along the regeneration process as the seedlings age. Studies similar to this one could be undertaken on older seedlings, or on the same ones used in this study at a later date, for example 5, 10 or 20 years time. The effect of other crop trees and their major competitors should also be investigated. This study focused on the interaction effects of trembling aspen and red raspberry, but the combined effects of larger numbers of competitors could be examined, although care must be taken not to overcomplicate if the findings are to be useful for management.

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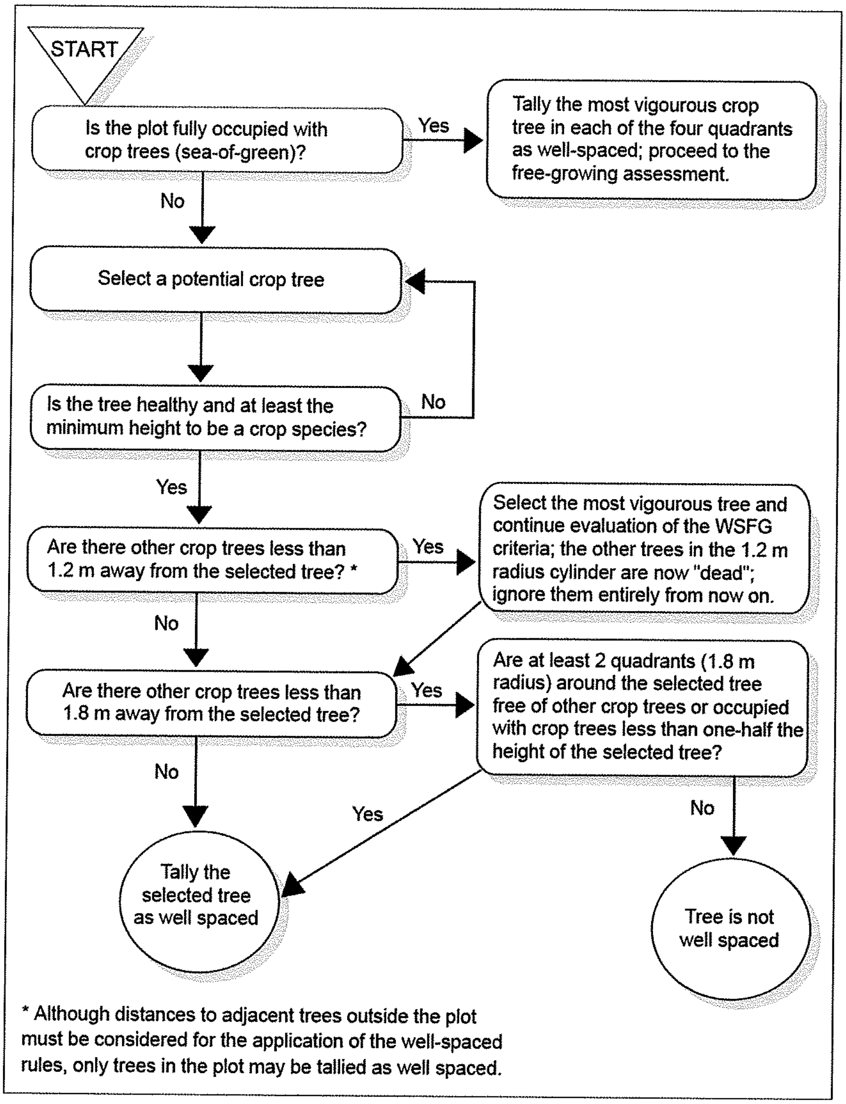
APPENDIX I: FIELD SURVEYS

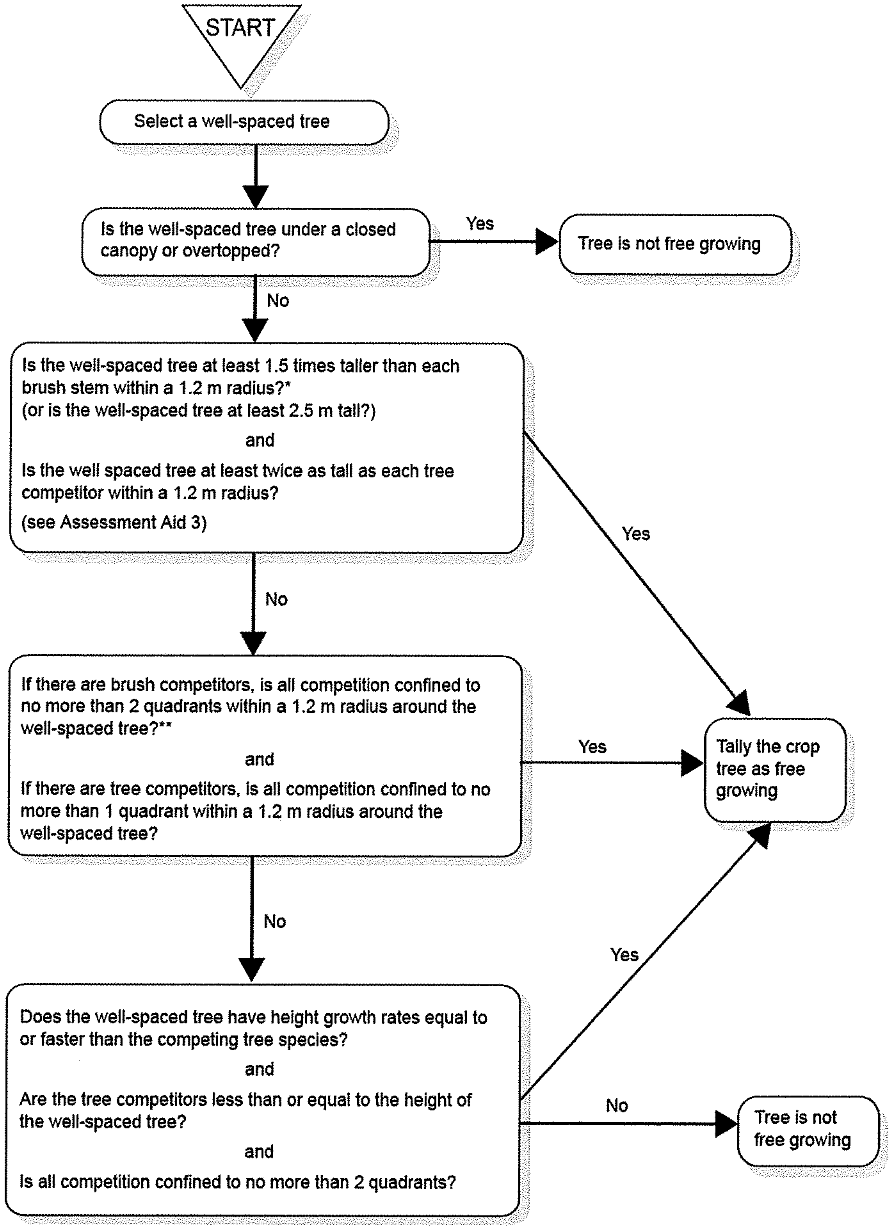
Surveys used for assessing well-spaced and free-to-grow status of crop trees



* Although distances to adjacent trees outside the plot must be considered for the application of the well-spaced rules, only trees in the plot may be tallied as well spaced.

Note:

- The *initial* quadrant (only) may be "rotated" (positioned) anywhere about the tree being assessed to maximize the number of unoccupied quadrants.
- Remember that a crop tree is defined as "a healthy, vigourous tree of either a target or acceptable species that meets a minimum height standard as defined in the silvicultural ground rule."
- All inter-tree distances are measured pith to pith (at tree base if in doubt).



* Raspberry rule: If the well-spaced tree is at least 1.5 m tall, ignore all tall woody shrubs of the genus *Rubus.*

** Only the initial quadrant may be "rotated" (positioned) around the tree being evaluated for free-growing.

APPENDIX II- RESPONSE SURFACE OUTPUT

Figure 6. Predicting canopy density (% measured by densitometer) using percent cover of aspen and raspberry above white spruce seedling height.

Sequential Model Sum of Squares

Source	Sum of Squares	df	Mean square	F	p
Mean vs Total	2.920E+005	1	2.920E+005		
Linear vs Mean	52059.63	2	26029.81	119.87	< 0.0001
2FI vs Linear	3204.92	1	3204.92	18.19	< 0.0001
Quadratic vs 2FI	1034.25	2	517.12	3.10	0.0510
Cubic vs Quadratic	1290.14	4	322.53	2.05	0.0972
Residual	10539.46	67	157.31		
Total	3.602E+005	77	4677.39		

Lack of Fit Tests

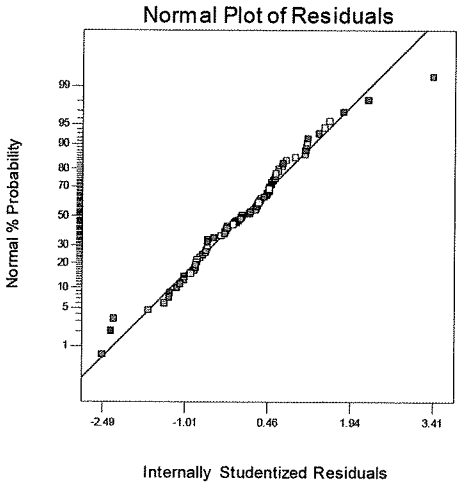
Source	Sum of Squares	df	Mean Square	F	p
Linear	14763.67	65	227.13	1.57	0.2399
2FI	11558.75	64	180.61	1.25	0.3850
Quadratic	10524.51	62	169.75	1.17	0.4299
Cubic	9234.37	58	159.21	1.10	0.4777
Pure Error	1305.09	9	145.01		

Model Summary Statistics

Source	Standard Deviation	R^2	Adjusted R^2	Predicted R^2
Linear	14.74	0.7641	0.7578	0.7367
2FI	13.27	0.8112	0.8034	0.7790
Quadratic	12.91	0.8264	0.8141	0.7829
Cubic	12.54	0.8453	0.8245	0.7667

ANOVA for Response Surface 2FI Model

Source	Sum of Squares	df	Mean Square	F	p
Model	55264.54	3	18421.51	104.54	< 0.0001
A-Aspen above	20702.56	1	20702.56	117.48	< 0.0001
B-Rasp above	2646.22	1	2646.22	15.02	0.0002
AB	3204.92	1	3204.92	18.19	< 0.0001
Residual	12863.84	73	176.22		
Lack of Fit	11558.75	64	180.61	1.25	0.3850
Pure Error	1305.09	9	145.01		
Corrected Total	68128.38	76			


Normal Plot of Residuals

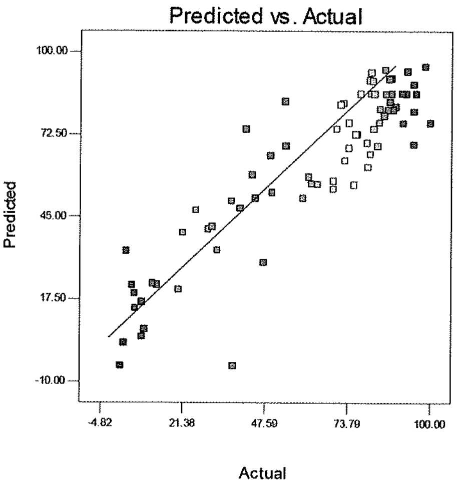

Predicted vs. Actual

Figure 13. Response surface of linear model to predict white spruce seedling rate of photosynthesis (μmol m^{-2} s^{-1}) using percent cover of raspberry and aspen above seedling height.

Sequential Model Sum of Squares

Source	Sum of Squares	df	Mean square	F	p
Mean vs Total	1407.04	1	1407.04		
Linear vs Mean	141.69	2	70.84	9.58	0.0005
2FI vs Linear	0.024	1	0.024	3.088E-003	0.9560
Quadratic vs 2FI	8.99	2	4.50	0.57	0.5700
Cubic vs Quadratic	17.83	4	4.46	0.53	0.7137
Residual	209.67	25	8.39		
Total	1785.25	35	51.01		

Lack of Fit Tests

Source	Sum of Squares	df	Mean Square	F	p
Linear	236.14	31	7.62	20.21	0.1746
2FI	236.12	30	7.87	20.88	0.1718
Quadratic	227.13	28	8.11	21.52	0.1691
Cubic	209.30	24	8.72	23.13	0.1630
Pure Error	0.38	1	0.38		

Model Summary Statistics

Source	Standard Deviation	R^2	Adjusted R^2	Predicted R^2
Linear	2.72	0.3746	0.3355	0.2363
2FI	2.76	0.3747	0.3142	0.1491
Quadratic	2.80	0.3985	0.2948	0.0028
Cubic	2.90	0.4456	0.2460	-0.2835

ANOVA for Response Surface Linear Model

Source	Sum of Squares	df	Mean Square	F	p
Model	141.69	2	70.84	9.58	0.0005
A-Aspen above	140.97	1	140.97	19.07	< 0.0001
B-Rasp above	0.69	1	0.69	0.093	0.7622
Residual	236.52	32	7.39		
Lack of Fit	236.14	31	7.62	20.21	0.1746
Pure Error	0.38	1	0.38		
Corrected Total	378.21	34			

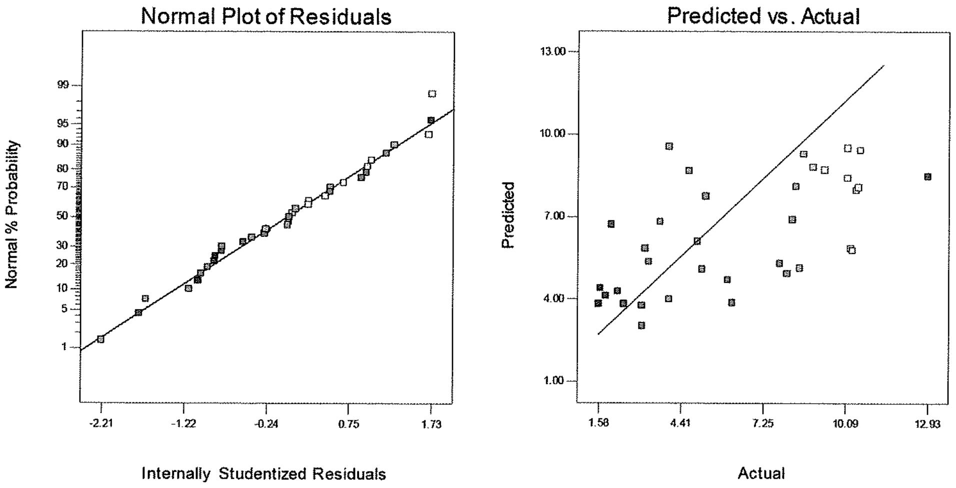


Figure 22. Response surfaces to predict white spruce seedling height growth (cm) using percent cover of aspen and raspberry above seedling height.

Sequential Model Sum of Squares

Source	Sum of Squares	df	Mean square	F	p
Mean vs Total	14252.80	1	14252.80		
Linear vs Mean	1839.04	2	919.52	25.04	< 0.0001
2FI vs Linear	60.17	1	60.17	1.65	0.2026
Quadratic vs 2FI	29.61	2	14.81	0.40	0.6718
Cubic vs Quadratic	167.81	4	41.95	1.14	0.3441
Residual	2459.74	67	36.71		
Total	18809.18	77	244.28		

Lack of Fit Tests

Source	Sum of Squares	df	Mean Square	F	p
Linear	2538.35	65	39.05	1.96	0.1373
2FI	2478.18	64	38.72	1.95	0.1405
Quadratic	2448.57	62	39.49	1.99	0.1336
Cubic	2280.76	58	39.32	1.98	0.1355
Pure Error	178.98	9	19.89		

Model Summary Statistics

Source	Standard Deviation	R^2	Adjusted R^2	Predicted R^2
Linear	6.06	0.4036	0.3875	0.3582
2FI	6.03	0.4168	0.3929	0.3602
Quadratic	6.08	0.4233	0.3827	0.3308
Cubic	6.06	0.4602	0.3876	0.2614

ANOVA for Response Surface Linear Model

Source	Sum of Squares	df	Mean Square	F	p
Model	1839.04	2	919.52	25.04	< 0.0001
A-Aspen above	742.10	1	742.10	20.21	< 0.0001
B-Rasp above	900.69	1	900.69	24.53	< 0.0001
Residual	2717.33	74	36.72		
Lack of Fit	2538.35	65	39.05	1.96	0.1373
Pure Error	178.98	9	19.89		
Corrected Total	4556.38	76			

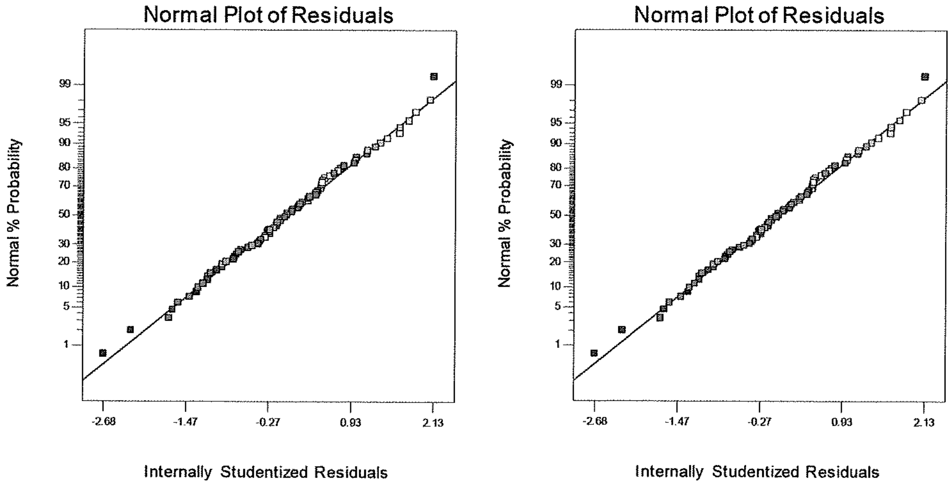


Figure 22. Response surfaces to predict white spruce seedling GLD growth (mm) using percent cover of aspen and raspberry above seedling height.

Sequential Model Sum of Squares

Source	Sum of Squares	df	Mean square	F	p
Mean vs Total	553.85	1	553.85		
Linear vs Mean	105.62	2	52.81	27.96	< 0.0001
2FI vs Linear	6.37	1	6.37	3.48	0.0660
Quadratic vs 2FI	0.042	2	0.021	0.011	0.9889
Cubic vs Quadratic	6.80	4	1.70	0.90	0.4691
Residual	126.56	67	1.89		
Total	799.24	77	10.38		

Lack of Fit Tests

Source	Sum of Squares	df	Mean Square	F	p
Linear	120.25	65	1.85	0.05	0.6726
2FI	113.88	64	1.78	0.82	0.7006
Quadratic	113.84	62	1.84	0.85	0.6773
Cubic	107.04	58	1.85	0.85	0.6722
Pure Error	19.52	9	2.17		

Model Summary Statistics

Source	Standard Deviation	R^2	Adjusted R^2	Predicted R^2
Linear	1.37	0.4304	0.4150	0.3806
2FI	1.35	0.4563	0.4340	0.3938
Quadratic	1.37	0.4565	0.4182	0.3629
Cubic	1.37	0.4842	0.4149	0.2997

ANOVA for Response Surface Linear Model

Source	Sum of Squares	df	Mean Square	F	p
Model	1839.04	2	919.52	25.04	< 0.0001
A-Aspen above	742.10	1	742.10	20.21	< 0.0001
B-Rasp above	900.69	1	900.69	24.53	< 0.0001
Residual	2717.33	74	36.72		
Lack of Fit	2538.35	65	39.05	1.96	0.1373
Pure Error	178.98	9	19.89		
Corrected Total	4556.38	76			

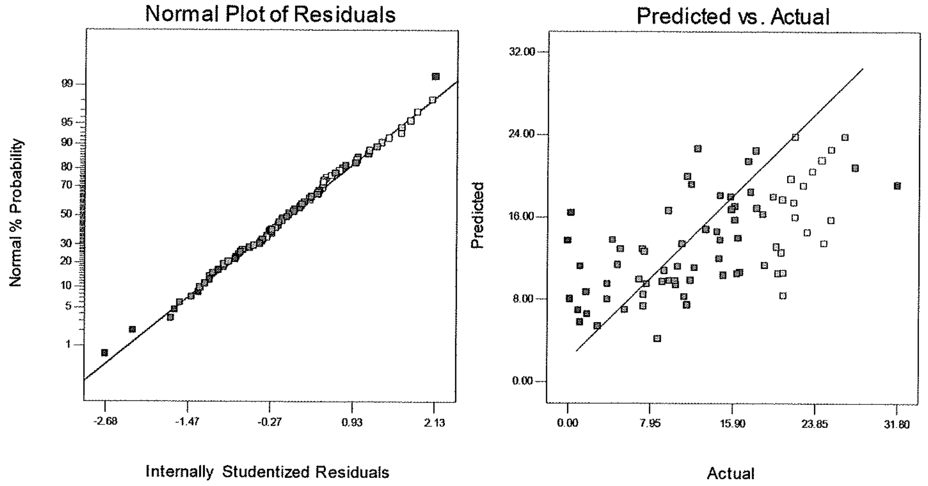


Figure 22. Response surfaces to predict white spruce seedling stem volume index growth$^{0.5}$(cm^3) using percent cover of aspen and raspberry above seedling height.

Sequential Model Sum of Squares

Source	Sum of Squares	df	Mean square	F	p
Mean vs Total	16.55	1	16.55		
Linear vs Mean	1.69	2	0.85	47.39	< 0.0001
2FI vs Linear	0.031	1	0.031	1.78	0.1866
Quadratic vs 2FI	0.013	2	6.549E-003	0.36	0.6964
Cubic vs Quadratic	0.052	4	0.013	0.71	0.5850
Residual	1.23	67	0.018		
Total	19.56	77	0.25		

Lack of Fit Tests

Source	Sum of Squares	df	Mean Square	F	p
Linear	1.13	65	0.017	0.83	0.6883
2FI	1.10	64	0.017	0.82	0.6971
Quadratic	1.09	62	0.018	0.84	0.6822
Cubic	1.04	58	0.018	0.86	0.6680
Pure Error	0.19	9	0.021		

Model Summary Statistics

Source	Standard Deviation	R^2	Adjusted R^2	Predicted R^2
Linear	0.13	0.5615	0.5497	0.5273
2FI	0.13	0.5720	0.5544	0.5264
Quadratic	0.13	0.5763	0.5465	0.5082
Cubic	0.14	0.5936	0.5390	0.4699

ANOVA for Response Surface Linear Model

Source	Sum of Squares	df	Mean Square	F	p
Model	1.69	2	0.85	47.39	< 0.0001
A-Aspen above	1.31	1	1.31	73.52	< 0.0001
B-Rasp above	0.24	1	0.24	13.43	0.0005
Residual	1.32	74	0.018		
Lack of Fit	1.13	65	0.017	0.83	0.6883
Pure Error	0.19	9	0.021		
Corrected Total	3.02	76			

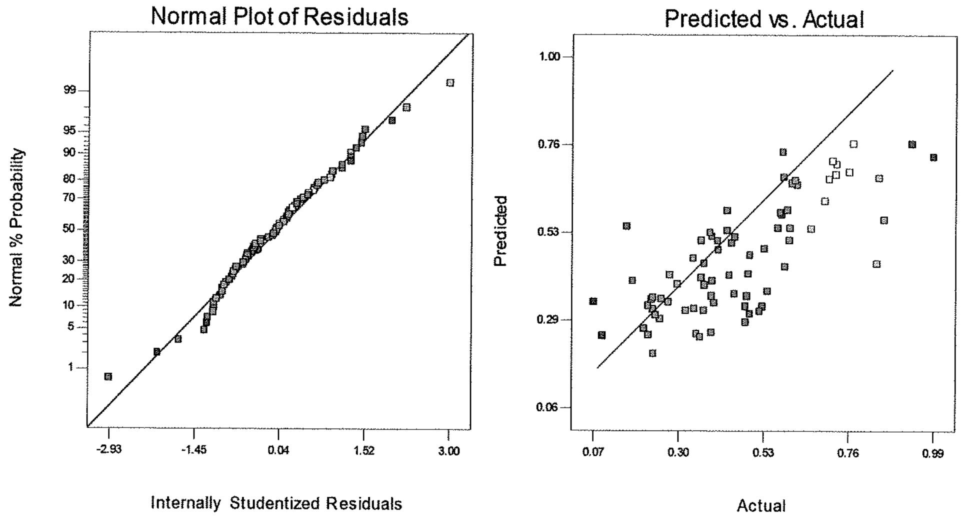


Figure 22. Response surfaces to predict white spruce seedling H/GLD ratio in August (cm) using percent cover of aspen and raspberry above seedling height.

Sequential Model Sum of Squares

Source	Sum of Squares	df	Mean square	F	p
Mean vs Total	2.965E+005	1	2.965E+005		
Linear vs Mean	2970.02	2	1485.01	17.26	< 0.0001
2FI vs Linear	485.39	1	485.39	6.03	0.0165
Quadratic vs 2FI	183.72	2	91.86	1.14	0.3240
Cubic vs Quadratic	610.30	4	152.58	2.01	0.1030
Residual	5086.19	67	75.91		
Total	3.059E+005	77	3972.51		

Lack of Fit Tests

Source	Sum of Squares	df	Mean Square	F	p
Linear	5979.90	65	92.00	2.15	0.1078
2FI	5494.51	64	85.85	2.00	0.1303
Quadratic	5310.78	62	85.66	2.00	0.1313
Cubic	4700.48	58	81.04	1.89	0.1523
Pure Error	385.71	9	42.86		

Model Summary Statistics

Source	Standard Deviation	R^2	Adjusted R^2	Predicted R^2
Linear	9.27	0.3181	0.2997	0.2611
2FI	8.98	0.3701	0.3442	0.3001
Quadratic	8.96	0.3898	0.3468	0.2899
Cubic	8.71	0.4552	0.3820	0.3003

ANOVA for Response Surface 2FI Model

Source	Sum of Squares	df	Mean Square	F	p
Model	3455.41	3	1151.80	14.30	< 0.0001
A-Aspen above	1187.80	1	1187.80	14.75	0.0003
B-Rasp above	24.73	1	24.73	0.31	0.5812
AB	485.39	1	485.39	6.03	0.0165
Residual	5880.22	73	80.55		
Lack of Fit	5494.51	64	85.85	2.00	0.1303
Pure Error	385.71	9	42.86		
Corrected Total	9335.63	76