University of Alberta

Characterization of leaf area index and understory vegetation development following pre-commercial thinning in boreal mixedwood forests

by

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Abstract

I examined the effect of pre-commercial thinning (PCT) on overstory leaf area (LAI) and understory vegetation in young boreal mixedwood stands ten years post-thinning. Results indicated that reducing aspen density to <1500 trees/ha (7m^2/ha) reduced overstory LAI and increased white spruce root collar diameter. Three methods for measuring LAI were compared. The direct method for measuring LAI using litter traps, was considered the reference, but provided the most variable estimates. Both hemispherical photography and LAI-2000 measurements underestimated LAI, likely due to the non-random distribution of leaves. The understory plant community responded to thinning with an increase in cover and a shift in abundance towards shade intolerant species. Understory species richness was not affected by thinning and introduced species abundance did not increase in response to thinning. Small shifts in understory cover and dominance observed are consistent with the fact that most understory boreal species are adapted to disturbance.

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Chapter 1. Introduction

1.1 The Boreal Forest

The boreal forest region comprises approximately half of the world's forested land, spanning the northern regions of North America and Eurasia with a mix of coniferous and deciduous trees (Bonan and Shugart 1989). In Canada, it rings the subartic from Newfoundland to the Northwest Territories, accounting for nearly two thirds of Canada's land and one third of the world's boreal zone (Baldwin 2004; Wilson 2003). It is a complex forest with intricately linked vegetation communities interacting with many environmental variables (Peinado et al. 1998). The most influential environmental factors in the boreal forest are climate, soils and disturbance regimes which have direct impacts on plant community development (Larsen 1980; Chen and Popadiouk 2002). These factors are interrelated such that climate affects soil moisture and temperature, nutrient cycling, and the occurrence of insect outbreaks and wildfire (Payette 1992).

Extreme variation in solar radiation, severe seasonal temperature changes (including long cold, dry winters and short mild, wet summers), short growing seasons, and soil moisture deficiencies limit the plant communities that can survive in, and which define, the boreal forest region (Bonan and Shugart 1989). Across the boreal region, the dominant tree genera are *Picea*, *Larix*, *Abies* and *Pinus* (Rowe 1972; Peinado et al. 1998). In the central and southern regions of the boreal, the broadleaved species such as *Populus* and *Betula* are more abundant and mixedwood stands in which conifers and broadleaf species are co-dominant are common (Larsen 1980).

Boreal forests are ecologically and economically valuable (Wilson 2003). The boreal forest plays a critical role in many of the earth's ecological processes, providing habitat to thousands of species of plants, animals and insects (Larsen 1980). The boreal forest is thought to have a significant influence on the global carbon cycle; as well, it filters millions of gallons of freshwater (Bonan and Shugart 1989; Kurz et al. 1992). Logging, mining, hydroelectric power, agricultural expansion and recreation are competing for use of the forest (Wilson 2003). Demand for lumber is exerting strong pressure on boreal forests globally, and in northern and western Canada, oil and gas exploration and extraction are also having a significant impact. The variety of demands on the boreal forest are having a major effect on the ecosystem, reducing the area, causing increased fragmentation, and degrading and altering the forest structure. There is an urgent need for an interdisciplinary and multifaceted understanding of the cumulative effects of all of these activities on boreal forest ecology.

The geographic focus of this review is the central and southern boreal forests of western Canada, with an emphasis on Alberta. Mixedwood forests, with a combination of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx.), are the dominant forest type on productive upland sites of this portion of the Canadian boreal forest (Lieffers et al. 1996).

Mixedwood Forests

In Alberta, boreal mixedwood forests cover approximately forty percent of the land, seventy percent of which is allocated to forestry companies for the logging of aspen into pulp and paper, and spruce into sawlogs (Alberta Environment Protection 1998). By definition, a boreal mixedwood stand has at least two or more hardwood or conifer species, where the dominant tree does not comprise more than eighty percent of the basal area (MacDonald 1996). Mixedwood forests occur at both the landscape and stand spatial scale. At the landscape scale, conifers and hardwoods develop as a result of environmental factors such as edaphic conditions, glaciation events and disturbance regimes (Haeussler et al. 2004). At the stand scale, the different species form discrete and continuous patches or a vertically stratified mixture (MacDonald 1996).

Mixedwood stands develop following disturbance as an early to mid successional stage on mesic sites (Chen and Popadiuk 2002). After a disturbance such as wildfire, a severe insect outbreak or forest harvesting, shade intolerant species such as trembling aspen establish along with pioneer shrubs species during the stand initiation stage (Moss 1953; MacDonald 1996) (Figure 1.1). White spruce often regenerates after fire on the exposed mineral soil, but depending on the availability of seed, the disturbance type and severity, as well as competition from surrounding vegetation, spruce regeneration may be delayed more than twenty years (Peters et al. 2005; Peters et al. 2006). Developing aspen rapidly outgrows the spruce forming a closed canopy over the slower growing species (Comeau et al. 2006). During this stand exclusion stage, the dense overstory aspen canopy restricts light to the understory, suppressing understory species growth. The aspen canopy will begin to thin, increasing light levels to the understory at a stand age of 25 years, but aspen will continue to dominate the canopy for approximately 40 years (Kabzems et al. 1986). Between a stand age of 60 or 80 years, the spruce will begin to overtake the canopy (Kabzems et al. 1986; Comeau et al. 2006). Understory shrub and forb layers develop and then decrease in abundance as the aspen canopy closes and light availability drops, and shift in composition with the transition from an aspen to spruce dominated stand (Towill 1996; Macdonald and Fenniak 2007). Spruce dominant stands rarely persist as a climax stage due to frequent disturbances (MacDonald 1996). In old growth forests, gaps in the canopy caused by tree falls create an uneven aged complex ecosystem (Chen and Popadiouk 2002). This is the general successional pathway followed by western Canadian boreal mixedwood forests, but regional differences occur due to variation in the effects of climate, soil, disturbance and settlement history, and plant and animal dispersal patterns (Weingartner 1996).

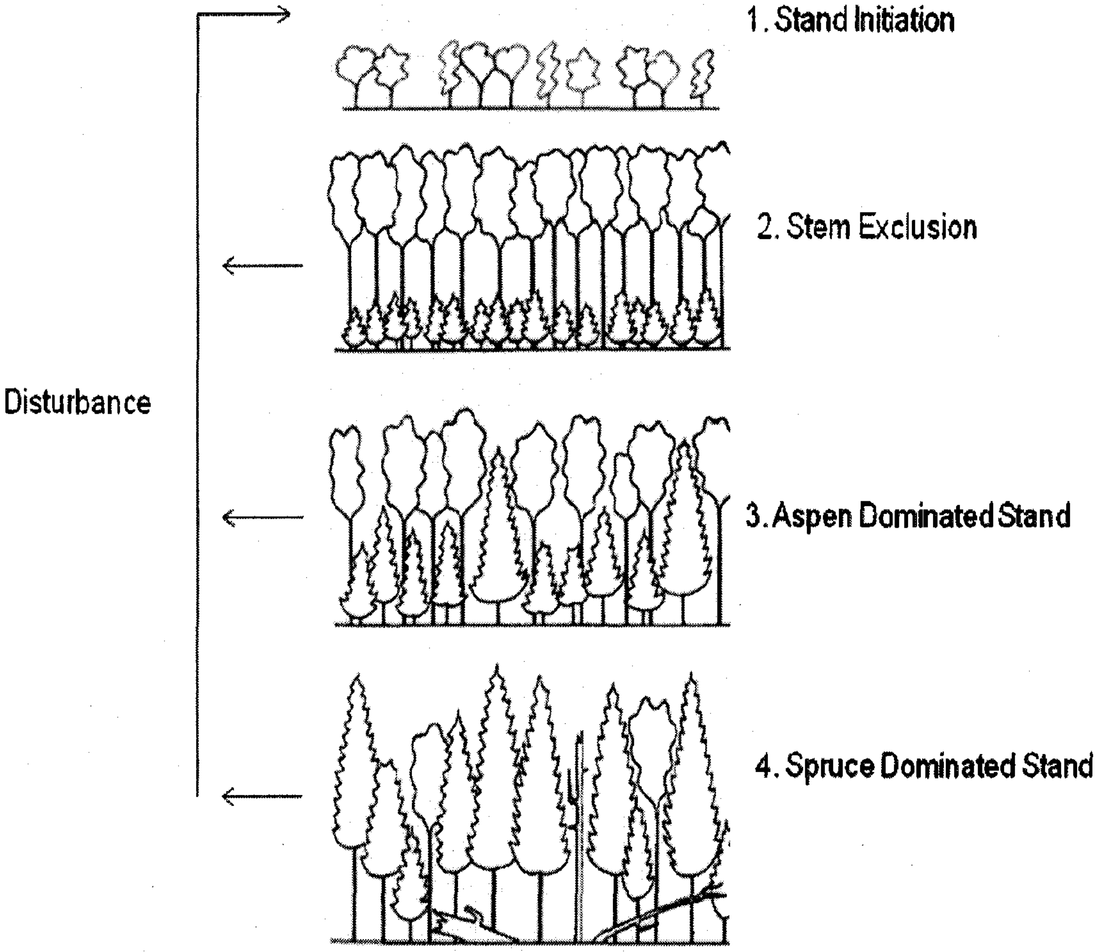


Figure 1.1. The successional pathway of boreal mixedwood forests following disturbance. (Modified from http://www.na.fs.fed.us/Spfo/Pubs/misc/ecoforest/fig1trees.gif)

Ecologically, mixedwood management is preferred to the segregation of forests into separate spruce and aspen plantations because it satisfies multiple ecosystem goals (Baker et al. 1996; Lieffers et al. 1996). Mixedwood forests are biologically and genetically more diverse, and this is thought to increase ecological resilience (MacDonald 1996; Cumming 2001; Chen and Popadiouk 2002). Increased diversity of ecological strategies of organisms in the community is thought to provide complexity that could enhance ecosystem stability (Weingartner 1996). In single species stands, the number of successional pathways is reduced decreasing the forest's resiliency to species loss.

According to Schieck et al. (1996), boreal mixedwoods are home to "one of the most diverse communities of breeding vertebrates on the continent." In order to maintain this community the boreal forest must retain a mix of early, mid and late successional stages, including mixedwood stands (Schieck et al. 1996; Baker et al. 1996) as well as pure stands of aspen and white spruce. Mixedwood forests are aesthetically more pleasing than monocultures and have higher recreational and tourism value (Comeau 1996; MacDonald 1996; Man and Lieffers 1999).

Forests that contain spruce and aspen may also be more productive than monocultures of spruce because aspen holds nutrients within the stand, enhances nutrient cycling due to its litter properties, and increases light availability to the forest floor (MacDonald 1996; MacPherson et al. 2001). Mixed stands are more resilient to pest, fire and disease outbreaks (Su et al. 1996; Gerlach et al. 1997; Cumming 2001; Comeau et al. 2005). An aspen overstory helps reduce damage to the spruce by wind, sun and temperature extremes, and competition with understory plants (MacDonald 1996; Comeau et al. 2005).

In the past two decades, logging in the Canadian boreal mixedwood forest has expanded due to new technology that allows for the utilization of broadleaf species and the exhaustion of lumber resources in other forest regions (Cormier 1996; Comeau et al. 2005). Softwood lumber is more valuable than hardwood and the division of forested land into coniferous and broadleaved tenures has lead to silvicultural practices that attempt to separate the species (Cumming and Armstrong 2001). This has raised concerns about the impacts of this type of logging on the structural and ecological diversity of the stand (Comeau et al. 2005). Mixedwood management retains landscape and stand diversity as well as crop production making it an improved method of management in the boreal forest (Wang et al. 1995; Lieffers et al. 1996; MacDonald 1996). Growing awareness of the economic and ecological advantages of mixtures compared to single species stands has lead to heightened interest in sustainable management of mixedwood forests.

Economically, mixedwoods are more valuable if a demand for aspen is maintained (Litchfield 1996). By supplying both aspen and spruce fiber, stands can fulfill different market demands and provide a greater number of products (Comeau et al. 2005). Mixedwood management has lower stand establishment costs because less energy is required to establish a mixedwood stand than a spruce stand, (Man and Liefers 1999). The aspen canopy reduces understory competition for the white spruce and protects it from environmental extremes, pests and disease. Stem quality of both spruce and aspen may improve with mixedwood management due to competition for light, and the overall yield of both species is potentially greater due to the stands greater ecological resilience to environmental factors (Simard et al. 2004).

When adopting a mixedwood management strategy, it is necessary to incorporate all of the ecological and economical factors at the stand and landscape scale (Comeau et al. 2005). Mixedwood management is a relatively new silvicultural approach that requires further investigation to support its successful implementation while sustainably managing for a broad range of goals. At the most basic level, creating mixtures of aspen and spruce at densities that will maximize the economic and ecological benefits while achieving yield targets for the component species, is of increasing interest to the forest industry (Comeau et al. 2006). Understanding the ecological, yield, and economic implications of different stand structures created by tending practices is of substantial interest.

Pre-commercial thinning

Pre-commercial thinning is a tending practice that has recently become popular for managing mixedwood and conifer stands across North America (Homyack et al. 2004). In boreal mixedwood stands, pre-commercial thinning is implemented to reduce the basal area of the overstory aspen to allow for improved growth of the understory spruce by increasing the amount of light reaching the understory, as well as improving water and nutrient availability (Simard et al. 2004; Comeau et al. 2005).

Pre-commercial thinning is implemented within 3 to 15 years of stand establishment, before, or as, aspen canopy closure begins. In a mixedwood stand it is used to avoid the 'competition bottleneck' described by Lieffers et al. (2002) that impedes spruce survival and growth. In order to retain the ecological and economic benefits associated with maintaining a mixedwood stand, aspen is not completely removed from the stand. The density of aspen must be manipulated based on the site specific objectives for each species (Comeau et al. 2005). Removing too much overstory aspen can lead to stem taper and larger branches that reduce stem quality in the aspen and spruce, and can cause top damage from snow bending and browsing in the spruce (Simard et al. 2004). In addition, increasing understory light levels above 40% can potentially result in competition from understory vegetation, in particular graminoids such as bluejoint reed grass (*Calamagrostis canadensis* (Michx.) Beauv.) (Lieffers and Stadt 1994; Comeau et al. 2005).

Pre-commercial thinning has been shown to promote growth of the understory conifers and browse species, reduce crop tree mortality, increase aspen and spruce stem diameter, basal area, growth rate and crown size, improve stem quality, shorten the saw log rotation, and increase the volume of harvested merchantable timber (Chen and Popadiouk 2002; Homyack et al. 2004; Simard et al. 2004; Lindh and Muir 2004; Macdonald and Mourelle 2004; Comeau et al. 2005).

In order to better understand the impacts of pre-commercial thinning on the boreal mixedwood forests, the ecological changes in the structure of the understory and overstory should be evaluated over the long term (Homyack et al. 2004). Only recently have the effects of this practice been studied, but the results are variable and unpredictable (Lindh and Muir 2004).

1.2 Light

Importance

The most limiting resource in the growth of young spruce in the boreal mixed wood forest is light (Stadt et al. 2001). Boreal forests are not exposed to large quantities of solar radiation because they are situated at high northern latitudes with short summers and long winters with low solar elevations (Lieffers et al. 1999). The amount of light available to these stands affects the abundance, growth and survival of understory and overstory vegetation (Messier 1996).

Photsynthetically active radiation (PAR) (380-710 nm) is used by the plants for photosynthesis and the radiation outside this range affects the thermal microsite environment (Larcher 1980). The overstory absorbs more light from the 400-700 nm range than from the far red range (725-735 nm) altering the ratio of red (655-665 nm) to far red radiation (R:FR), and thus the light quality available to the understory (Messier 1996).

Within forests, there is a heterogeneous mix of diffuse and direct light reaching the understory (Comeau et al. 1998). The position of the sun relative to the earth, the season and time of day combined with the sky conditions (cloud cover, pollution) determine the light conditions at the canopy of the forest (Lieffers et al. 1999). Light reaching the understory is further modified by size and location of canopy gaps, sun flecks, and the structure, composition and density of the canopy.

Canopy gaps allow for a varying amount of direct and diffuse radiation to reach understory vegetation below and around the gap center (Messier 1996). These gaps are often the result of tree falls, silvicultural treatments or the absence or poor regeneration of vegetation due to environmental conditions. Gaps can take a long time to close in the boreal because of the narrow shape of the crowns of northern tree species (Lieffers et al. 1999). The quality and quantity of the resultant light depends on the size of the opening, the height of the canopy, the angle of the sun and the season (Lieffers et al. 1999). The southern periphery of a gap will receive only diffuse light from the north and the northern edge will receive both direct and diffuse light (Canham et al. 1990). This variation in light will affect the growth and survival of the understory within and surrounding the gap, as well as micro-site temperature (Messier 1996). Light also penetrates into the edges of the stands surrounding gaps, with higher light levels in the stand on the north side of large gaps or openings, as compared to the south side or to levels in interior forest.

Sunflecks occur when an area of the forest floor receives a large increase in the amount of direct light relative to the surrounding area for as little as two seconds (Lieffers et al. 1999). The quantity of radiation supplied by sunflecks is extremely variable depending on the overall forest canopy transmission (Messier 1996). Sunflecks have been credited with contributing anywhere from 28-90% of the daily PAR available to the understory (Chazdon 1991). However, many boreal species cannot take advantage of these light bursts because they are unable to begin photosynthesizing in time (Lieffers et al. 1999). Numerous small gaps in the canopy can create homogenous diffuse light levels or high shade in the understory which have led to shorter and wider, shrub like understory trees (Oliver and Larson 1990).

The quality of light within the understory is the result of the composition, density and structure of the canopy. A greater proportion of hardwoods in a forest will result in a lower red to far red ratio because deciduous trees absorb less red light (Messier et al.

1998). The extent and density of the overstory will affect the amount of white light available in the understory (Comeau et al. 1998). Canopy clusters, gaps, different leaf angle orientations, leaf movements and seasonal leaf loss contribute to the variation in quality of light within a forest, in turn affecting plant diversity in the understory (Messier 1996).

Light and Management

In aspen spruce mixedwoods of the Alberta boreal forest, light quality and quantity change significantly with each successional stage. Pioneer species compete for space and resources after a stand-replacing disturbance such as a clearcut (Larsen 1980). Competition for light begins soon after establishment as fast growing shade intolerant species such as bluejoint (*Calamagrostis canadensis*), fireweed (*Epilobium angustifolium*) and aspen suppress slower growing and shade tolerant vegetation such as spruce (Lieffers and Stadt 1994; Chen and Popadiouk 2002).

The canopy closure stage decreases survival and growth of the understory shade intolerant shrubs and forbs (MacPherson et al. 2001). This allows for improved growth of white spruce, as they experience reduced levels of competition with the intolerant graminoids and forbs (Man and Lieffers 1999). White spruce will survive with a minimum of 8% full sunlight, reach maximum photosynthesis and height growth at 40-60%, and achieve greatest diameter and stem volume growth with full sunlight (Comeau 2001).

Vertical stratification of mixedwood forests is pronounced at the canopy closure successional stage. Lieffers et al. (2002) found that the leaf area index (LAI) in aspen spruce mixtures increased rapidly with stand age to maximum of around 6 m^2m^{-2} at 15 to 25 years after stand establishment. At this time, only 2% of full light reaches the understory and this is below the minimum light levels required for spruce survival.

Light transmission into the understory increases after approximately 25 years as the dense aspen canopy begins to thin. The intense competition between aspen stems causes a reduction in stem density and width and LAI, and light transmission increase (Chen and Popadiouk 2002). During the canopy closure stage, light levels at the ground drop to a minimum as spruce grows into the canopy. Depending on the ratio of aspen to spruce, low light levels may greatly reduce the abundance and richness of the understory shrub and forb layers (Lieffers et al. 1999). Forest management can be used to modify the light levels in the understory of forest stands at different successional stages to achieve economic and ecological goals. By manipulating the basal area of aspen and spruce, the rotation interval and yield can be improved and/or biological diversity of the understory vegetation can be maintained.

In the stand initiation and exclusion stage, forest managers can reduce the cover of potentially competitive understory vegetation such as bluejoint reed grass by leaving the dense aspen suckers and reducing light levels to the understory (Lieffers et al. 1999). Although white spruce can survive with low light transmission, these conditions can reduce volume and stem growth.

Pre-commercial thinning is used in the stem exclusion stage to increase light transmission to the understory spruce to encourage stem growth (Simard et al. 2004). It is commonly implemented once spruce has reached a height where competition with understory vegetation is no longer an immediate threat. The thinning intensity will depend on the forest manager's desired yield of aspen, the importance of competition suppression versus spruce growth, the time it will take for spruce to enter the aspen canopy before the canopy closes again, financial restrictions, and the ecological goals of the management plan.

Research on the relationship between light transmittance in the understory and basal area began in the last decade (e.g. Messier 1996; Comeau et al. 1998; Comeau 2001; Lieffers et al. 2002; Comeau and Heineman 2003; Macdonald and Mourelle 2004; Comeau et al. 2006). The Western Boreal Growth and Yield Association is performing a long term study in Western Canada to determine the intensity of pre-commercial thinning that will provide the greatest benefits economically and ecologically to the forest. In order to successfully manipulate light levels in a stand, we must understand the effects of stand structure, species composition, geographic location, and sky conditions on the quality and quantity of light in the understory; the response of understory vegetation such as spruce to abrupt changes in light conditions; and the relationship between overstory basal area and understory light conditions (Messier 1996; Comeau 2001).

In order to make optimal use of pre-commercial thinning, the forest manager must know the aspen basal area that will result in the required light levels. The relationship between aspen basal area and light has been quantified by several studies, but Comeau et al. (2006) found that the relationship was significantly different between biogeoclimatic zones and stands at different successional stages. Quantifying these relationships will allow for more efficient and successful management by foresters (Comeau et al. 2006).

In addition, the relationship between diversity of understory vegetation and light have received only limited attention in the boreal forests of western Canada.

1.3 Biodiversity

Importance

Forests are one of the most significant stores of biodiversity in the world (Kapos and Iremonger 1998). During the past twenty years, North American forest management practitioners have acknowledged the importance of biological diversity as an indicator of ecosystem health and sustainability and shifted to a more ecocentric approach (Sullivan et al. 1998). This has made it necessary to quantify diversity within forest stands that are being managed in order understand the impact of management practices.

Biodiversity includes the number of species found in the area of interest (species richness), as well as their abundance in relation to each other (species evenness) (Magurran 1988). Biodiversity can be an important indicator of ecosystem health, as ecosystem functioning is strongly correlated with biodiversity (Vanclay 1998; Schläpfer et al. 1999). However, the relationship between biodiversity and ecosystem health is not straightforward (Haeussler et al. 2004). The most common assumption is that greater biodiversity of a community is indicative of a forest that is more resilient to change and disturbance (Falencka-Jablonska 1998). In contrast, May (1973) states that stability can decrease with a rise in species diversity due to the nonrandom interactions between species.

The relationship between ecosystem productivity and diversity is also complex and is affected by the scale at which it is measured (Jennings et al. 2005). Jennings et al.

(2005) inferred that the relationship at a local scale is affected by different factors than at a regional scale. At low productivity, stressful sites had lower local scale diversity (alpha diversity) because fewer species are capable of surviving in these conditions. As the site became more productive and less stressful, alpha diversity followed a hump shaped curve, rising and then later falling when a few dominant species overtook the site. Regional diversity (gamma diversity) is thought to have a positive relationship with the productivity of the habitats within the region, but it is also a function of the range of habitats, the alpha diversity within each habitat and the change in diversity between them (beta diversity) (Whittaker 1972).

Although difficult to define and draw conclusions from, measurements of biodiversity serve as a valuable resource for assessing many different aspects of a community (Vanclay 1998). There are three main categories of techniques used to quantify biodiversity; species richness indices, species abundance models, and species proportional abundance indices (Magurran 1988). More complex methods are also available to analyze changes in biodiversity over time or in response to a disturbance. Diversity measures are valuable tools in the quantification of biodiversity but must be analyzed cautiously (Halpern and Spies 1995). Different indices and measures can provide different portrayals of the data and lead to incorrect conclusions (Gibson 2002). These indices and models do not take into account the ecological significance of each species and are best used in combination with each other and with species specific analysis for ecologically important species (Halpern and Spies 1995).

Ecological experiments on the effect of a treatment or disturbance on the diversity of a site, ecosystem or geographic region should incorporate the three scales of diversity (alpha, beta and gamma) into their measurements if possible. Using a combination of indices, and more complex methods such as ordination which provide insight into patterns of response in species composition, will provide the greatest understanding of the changes that occur due to the treatment or disturbance.

Diversity and Forest Management

Boreal forest management practices are now attempting to mimic the sporadic natural disturbance cycle that has defined the region (Deal 2001). However, there has been increasing concern regarding the impacts of management on the biodiversity of the ecosystem, as forest management still often results in conversion of diverse stands into stands with one or two tree species, where competing vegetation is controlled through herbicide treatments and brushing (Sullivan et al. 1996; Bell and Newmaster 2002).

Analysis of diversity of understory vegetation in these forests is of interest because the understory community is more diverse than the trees; thus analysis of responses in this community can provide an indication of the health of the stand (Haeussler et al. 2002). The diversity of this vegetation layer is a reflection of historical factors, environmental gradients such as light, canopy, soil and landforms, and the successional stage of the forest (Small and McCarthy 2005; Sullivan et al. 1996). Understory vegetation also plays a key role in nutrient cycling, influencing stand structure through competition, and providing habitat and forage for wildlife (Homyack 2004). Measuring biodiversity of understory vegetation can be difficult, as different indices can lead to different conclusions regarding the vegetation response to silvicultural practices (Lindh and Muir 2004). Species richness indices may provide a one dimensional measure of biodiversity as many species can survive but may not propagate in bad conditions. Treatments may also dramatically increase richness if they provide opportunities for invasive or weedy species to regenerate and grow. Abundance measures can provide a better, but not complete, indication of changing resource effects. The most in-depth approach to analyzing the effect of changing resources on the understory would be to incorporate analysis of changes in species composition as well as abundance. Species turnover indices and multivariate analysis such as ordination in combination will provide detailed insight regarding changes in community composition and the independent variables most closely correlated with this change.

There are three ways in which forest management can alter understory communities: complete removal, the large scale reduction of biodiversity, and alteration of the diversity and composition of the communities (Haeussler et al. 2004). The end results of these different responses of biodiversity are not easily predicted or well understood, especially over a longer time scale (Halpern and Spies 1995).

After a clearcut or stand replacing fire, the elimination of competition and opening of niches creates an environment that fosters high biodiversity (Haeussler et al. 2002). However, if a clearcut is followed by an extreme herbicide application or severe site disturbance, the bud bank, the seed bank, rhizomes and roots can be destroyed, delaying the natural regeneration of the forest understory (Sullivan et al. 1998). Moderate herbicide application and mechanical site preparation can reduce the dominance of the most abundant post-disturbance species, such as aspen or blue joint grass in the boreal, allowing for other species, such as spruce to survive, thus increasing or maintaining species diversity (Horsley 1994; Sullivan et al. 1998; Haeussler et al.

2002. Mechanical site preparation can provide a greater heterogeneity of microsites, in turn leading to increased species richness.

After an initial post-disturbance peak in diversity, competition for light and other resources with the rapidly growing overstory leads to a decline in species diversity (Haeussler et al. 2004). Management practices implemented after clearcut are thought to have a major impact on the long term understory diversity (Halpern and Spies 1995). Dense planting of spruce and dense natural regeneration of aspen suckers may limit the survival of shade intolerant species, favouring one or two species by reducing light availability, and altering the soil and microclimate (Haeussler et al. 2002).

Precommercial thinning of the overstory will increase light availability to the understory spruce trees and other vegetation (Thomas et al. 1999; Lind and Muir 2004). Thomas et al. (1999) and Lindh and Muir (2004) found that species richness increased with increasing intensity of thinning but did not find a statistically significant relationship between greater light levels and this rise in richness. The authors speculated that the understory lags in response to the light levels and damage during the application of the treatment, and that the increase in richness occurs as the canopy begins to close and new species are able to establish in the disturbed sites. Also, although it is assumed that the increase in richness is tied to an increase in early successional species, they were unable to prove this.

Macdonald and Mourelle (2004) studied the effects of partial harvesting later in rotation on the understory vegetation. They found similar results to Thomas et al. (1999), with delayed increase in species richness with an increase in thinning intensity. In addition, they found an increase in the number of early successional species, indicating a departure from the successional pathway towards old growth (Macdonald and Mourelle 2004). Lindh and Muir (2004) put forth a contrasting theory, stating that thinning may aid in the restoration of old growth forests by mimicking canopy openings and gaps and accelerating development of structural and environmental heterogeneity.

Old growth forests are considered to have specialized community composition (Halpern and Spies 1995). The cool, shaded and moist environment protects plants from severe temperature and light fluctuations creating an ideal environment for a large number of important species associated with old growth. There are three theories that can be used to describe the diversity of this forest stage: this stage provides for the physiological requirements of these specialist species: old growth species are better adapted to competition for these resources, and increased spatial complexity in the stand increases resource availability or niches. Although old growth forests are not common in the boreal due to frequent fire or insect outbreaks, they are an important component of the ecosystem. Rarely achieved through forest management practices, loss or extinction of the species adapted to these conditions is of growing concern (Lindh and Muir 2004).

Forest management should develop and apply silvicultural techniques which better mimic the natural successional pathway of forest stands (Haeussler et al. 2004). Precommercial thinning is one method that may accelerate how quickly stands return to mature or old growth forms, but more studies that are spread over a longer time frame will be needed to understand fully its effects (Lindh and Muir 2004). Many methods must be developed that can be applied at all stages of succession to all regions of the forest over a larger time scale to improve the sustainability in managing boreal forests.

1.4 Conclusions

The boreal forest of North America comprises a significant portion of the world's forested region. Home to a variety of habitats, environmental conditions and species, and the subject of intense anthropogenic use, the sustainable management of these forests to ensure their future is of great interest. Further research into the economic and ecological benefits of managing for mixedwood forests, using techniques such as pre-commercial thinning to control light and their effects on understory diversity, is needed.

1.5 Objectives

The objectives of my thesis research were to:

1. Evaluate the effect of pre-commercial thinning on leaf area index (LAI).
2. Compare four methods for measuring leaf area index: a) litter traps, b) hemispherical photographs, c) LAI-2000, and d) stand measurements (basal area) in the young mixedwood stands where pre-commercial thinning has been used to control aspen density.
3. Determine changes in the understory community after different levels of pre-commercial thinning.
4. Describe the relationship between the changing environmental variables (overstory basal area and leaf area) and the understory community

Chapter 2 presents results relating to objectives 1 and 2 and Chapter 3 presents results relating to objectives 3 and 4.

1.6 References

Adamowicz, W.L., and Burton, P.J. 2003. Sustainability and sustainable forest management. *In* Towards Sustainable Management of the Boreal Forest. 1st ed. NRC Research Press, Ottawa, Ontario pp. 41-64.

Baker, J.A., Clark, T., and Thompson, I.D. 1996. Boreal mixedwoods as wildlife habitat: observation, questions, and concerns. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 1995, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada and Ontario Ministry of Natural Resources, Sault Ste. Marie pp. 41.

Baldwin, A. 2004. An ethics of connection: social-nature in Canada's boreal forest. Ethics, Place & Environment **7:** 185-194.

Bell, F.W., and Newmaster, S.G. 2002. The effects of silvicultural disturbances on the diversity of seed-producing plants in the boreal mixedwood forest. Canadian Journal of Forest Research **32:** 1180-1191.

Bonan, G.B., and Shugart, H., H. 1989. Environmental Factors and Ecological Processes in Boreal Forests. Annu. Rev. Ecol. Syst. **20:** 1-28.

Boyd, R.S., Freeman, J.D., Miller, J.H., and Edwards, M.B. 1995. Forest herbicide influences on floristic diversity seven years after broadcast pine release treatments in central Georgia, USA. New Forests **10:** 17-37.

Burton, P.J., Messier, C., Weetman, G.F., Prepas, E.E., Adamowicz, W.L., and Tittler, R. 2003. The current state of boreal forestry and the drive for change. *In* Towards Sustainable Management of the Boreal Forest. NRC Research Press, Ottawa, Ontario, Canada pp. 1-40.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research **20**:101-107.

Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environmental Reviews **10**: 137-166.

Chazdon, R.L. and Pearcy, R.W. 1991. The importance of sunflecks for forest understory plants. BioScience **41**:760-766.

Comeau, P.G. 2001. Relationships between stand parameters and understorey light in boreal aspen stands. B.C. Journal of Ecosystems and Management **1**: 1-8.

Comeau, P.G. 2003. Estimating and managing understory light using aspen density and diameter in central and north-eastern B.C. University of Alberta, Centre for Enhanced Forest Management, EFM Research Note 02/2003.

Comeau, P.G., Filipescu, C.N., Kabzems, R., and Delong, C. 2004. Early growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern British Columbia. Canadian Journal of Forest Research **34**:2277-2283.

Comeau, P.G., Gendron, F., and Letchford, T. 1998. A comparison of several methods for estimating light under a paper birch mixedwood stand. Canadian Journal of Forest Research **28**: 1843-1850.

Comeau, P.G., and Heineman, J.L. 2003. Predicting understory light microclimate from stand parameters in young paper birch (*Betula papyrifera* Marsh.) stands. Forest Ecology and Management **180**:303-315.

Comeau, P.G., Heineman, J.L., and Newsome, T. 2006. Evaluation of relationships between understory light and aspen basal area in the B.C. central interior. Forest Ecology and Management **226**:80-87.

Comeau, P.G., Kabzems, R., McClarnon, J., and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. The Forestry Chronicle **81:** 559-574.

Comeau, P.G., Thompson, C.F., Harper, G.J., and Biring, B.S. 1996. Effectiveness of repeated manual cutting for release of Engelmann spruce from mixed-shrub communities in the Revelstoke District. EP 1135.01 Establishment and Progress Report.

Cormier, R.G. 1996. Utilization of boreal mixedwoods. Natural Resources Canada, Canadian Forest Service and Ontario Ministry of Natural Resources, Sault Ste. Marie, ON.

Cumming, S.G. 2001. Type and wildfire in the Alberta boreal mixedwood: what do fires burn? Ecological Applications **11**:97-110.

Cumming, S.G. and Armstrong, G.W. 2001. Divided land base and overlapping tenure in Alberta, Canada: a simulation study exploring costs of forest policy. The Forestry Chronicle 77:501-508.

Deal, R.L. 2001. The effects of partial cutting on forest plant communities of western hemlock- Sitka spruce stands in southeast Alaska. Canadian Journal of Forest Research **31:** 2067-2079.

Falencka-Jablonska, M. 1998. Biodiversity and forestry in Poland. *In* Assessment of biodiversity for improved forest planning. Kluwer Academic Publishers, Boston, USA pp. 83-89.

Franc, A. 1998. Some mathematical remarks on forest biodiversity. *In* Assessment of biodiversity for improved forest planning. Kluwer Academic Publishers, Boston, USA pp. 159-169.

Gerlach, J.P., Reich, P.B., Puettmann, K., and Baker, T. 1997. Species, diversity, and density affect tree seedling mortality from *Armillaria* root rot. Canadian Journal of Forest Research **27**:1509-1512.

Gibson, D.J. 2002. Methods in comparative plant population ecology. Oxford University Press, Toronto, Ontario.

Haeussler, S., Bartemucci, P., and Bedford, L. 2004. Succession and resilience in boreal mixedwood plant communities 15-16 years after silvicultural site preparation. Forest Ecology and Management **199:** 349-370.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., and Kranabetter, J.M. 2002. Silvicultural disturbance severity and plant communities of the Southern Canadian boreal forest. Silva Fennica **36:** 307-327.

Halpern, C.B., and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications **5**(4):913-934.

Hannon, S.J., Paszkowski, C.A., Boutin, S., Macdonald, S.E., Wheatley, M., and Eaton, B.R. 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. Canadian Journal of Forest Research **32:** 1784-1800.

Hellmann, J.J., and Fowler, G.W. 1999. Bias, precision, and accuracy of four measures of species richness. Ecological Applications **9:** 824-834.

Homyack, J.A., Harrison, D.J., and Krohn, W.B. 2004. Structural differences between precommercially thinned and unthinned conifer stands. Forest Ecology and Management **194**: 131-143.

Horsley, S.B. 1994. Regeneration success and plant species diversity of Allegheny hardwood stands after roundup application and shelterwood cutting. Northern Journal of Applied Forestry **11**(4):109-116.

Hunter, M. 2002. Fundamentals of Conservation Biology. 2nd Edition. Blackwell Science, Massachusetts, USA.

Jennings, M.D., Williams, J.W., and Stromberg, M.R. 2005. Diversity and productivity of plant communities across the Inland Northwest, USA. Oecologia **143**:607-618.

Kabzems, A., Kosowan, A.L., and Harris, W.C. 1976. Mixedwood section in an ecological perspective. Sask. Dep. Tour. Renew. Resour. Tech. Bull. 8.

Kapos, V., and Iremonger, S.F. 1998. Achieving Global and Regional Perspectives on forest biodiversity and conservation. *In* Assessment of Biodiversity for Improved Forest Planning. Kluwer Academic Publishers, Boston, USA pp. 15-29.

Krebs, C.J. 1994. Ecology. 4th ed. Addison-Wesley Educational Publishers, Inc., Don Mills, Ontario.

Kurz, W.A., Apps, M.J., Webb, T.M., and McNamee, P.J. 1992. The Carbon Budget of the Canadian Forest Sector: Phase I. Forestry Canada, Information Canada, Information Report NOR-X-326, Northwest Region, Northern Forestry Center, Edmonton, Canada. 93 pp.

Larcher, W. 1980. Physiological plant ecology. Springer-Verlag, New York.

Larsen, J.A. 1980. The Boreal Ecosystem. Academic Press, Inc., New York, New York.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research **29**: 796-811.

Lieffers, V.J., Pinno, B.D., Stadt, K.J. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. Canadian Journal of Forest Research **29**: 796-811.

Lieffers, V.J., and Stadt, K.J. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstorey light transmission. Canadian Journal of Forest Research **24**:1193-1198.

Lindh, B.C., and Muir, P.S. 2004. Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? Forest Ecology and Management **192**: 285-296.

Litchfield, M.S. 1996. Boreal mixedwoods – an industrial perspective. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 1995, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada, Canadian Forest Service, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 67-69.

MacDonald, G.B. 1996. The emergence of boreal mixedwood management in Ontario: background and prospects. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 1995, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada, Canadian Forest Service, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 11.

Macdonald, S.E., and Fenniak, T.E. 2007. Understory plant communities of boreal mixedwood forests in western Canada: Natural patterns and response to variable-retention harvesting. Forest Ecology and Management **242**:34-48.

Macdonald, S.E., and Mourelle, C. 2004. Effects of thinning and understory retention harvest on forest structure and understory plant communities. Sustainable Forest Management Network, Rep. 2003/2004.

MacPherson, D.M., Lieffers, V.J., and Blenis, P.V. 2001. Productivity of aspen stands with and without a spruce understory in Alberta's boreal mixedwood forests. The Forestry Chronicle 77: 351-356.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA.

Man, R., and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? The Forestry Chronicle **75**: 505-512.

May, R.M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, New York, USA.

Messier, C. 1996. Managing Light and Understory Vegetation in Boreal and Temperate Broadleaf conifer Forests. In Silviculture of Temperate and Boreal Broadleaf-conifer Mixtures. B.C. Ministry of Forests, British Columbia pp. 59-81.

Messier, C., Parent, S., and Bergeron, Y. 1998. Characterization of understory light environment in closed mixed boreal forests: effects of overstory and understory vegetation.Journal of Vegetation Science **9**:511-520.

Miller, K.V. and Miller, J.H. 2004. Forestry herbicide influences on biodiversity and wildlife habitat in southern forests. Wildlife Society Bulletin **32**(4):1049-1060.

Moss, E.H. 1953. Forest communities in northwestern Alberta. Can. J. Bot. **31**:212-252.

Oliver, C.D., and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill, Inc., New York.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. Pages 144-169 *in* H. H. Shugart, R. Leemans, and G. B. Bonan, editors. *A systems analysis of the global boreal forest.* Cambridge University Press.

Peinado, M., Aguirre, J.L., and de la Cruz, M. 1998. A phytosociological survey of the boreal forest (shape Vaccinio-Piceetea) in North America. Plant Ecology **137:** 151-202.

Peters, V.S., Macdonald, S.E., and Dale, M.R.T.2005. The interaction between masting and fire is key to white spruce regeneration. Ecology **86**(7):1744-1750.

Peters, V.S., Macdonald, S.E., and Dale, M.R.T. 2006. Patterns of initial versus delayed regeneration of white spruce in boreal mixedwood succession. Canadian Journal of Forest Research **36**:1597-1609.

Schieck, J., Roy, L.D., and Stelfox, J.B. 1996. Variation in vertebrate communities among three successional stages of aspen-dominated boreal mixedwood forests in Alberta. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 1995, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada, Canadian Forest Service and Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 86.

Schläpfer, F., Schmid, B., and Seidl, I. 1999. Expert estimates about effects of biodiversity on ecosystem processes and services. Oikos **84**(2): 346-352.

Simard, S.W., Blenner-Hassett, T., and Cameron, I.R. 2004. Pre-commercial thinning effects on growth, yield and mortality in even-aged paper birch stands in British Columbia. Forest Ecology and Management **190**: 163-178.

Small, C.J., and McCarthy, B.C. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management **217**:229-243.

Stadt, K.J., Lieffers, V.J., and Pinno, B.D. 2001. Modeling light dynamics in boreal mixedwood forests. Sustainable Forest Management Network.

Su, Q., MacLean, D.A., and Needham, T.D. 1996. The influence of hardwood content on balsam fir defoliation by spruce budword. Canadian Journal of Forest Research **26**:1620-1628.

Sullivan, T.P., Lautenschlager, R.A., and Wagner, R.G. 1996. Influence of glyphosate on vegetation dynamics in different successional stages of sub-boreal spruce forest. Wood Technology **10:** 439-446.

Sullivan, T.P., Wagner, R.G., Pitt, D.G., Lautenschlager, R.A., and Chen, D.G. 1998. Changes in diversity of plant and small mammal communities after herbicide application in sub-boreal spruce forest. Canadian Journal of Forest Research **28:** 168-177.

Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., and Austin, K.A. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. Ecological Applications **9:** 864-879.

Towill, W. 1996. Ontario's boreal mixedwood forest: distribution, extent, and importance. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 1995, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada, Canadian Forest Service and Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 21.

Uys, R.G., Bond, W.J., and Everson, T.M. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. Biological Conservation **118**:489-499.

Vanclay, J.K. 1998. Towards more rigorous assessment of biodiversity. *In* Assessment of Biodiversity for improved forest planning. Kluwer Academic publishers, Boston, USA pp. 211-232.

Wang, J.R., Comeau, P., and Kimmins, J.P. 1995. Simulation of mixedwood management of aspen and white spruce in northeastern British Columbia. Water, Air & Soil Pollution **82**(1-2):171-178.

Weingartner, D.H. 1996. Changing philosophies and management for boreal mixedwood. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 2005, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada, Canadian Forest Services and Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 55.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon **21**: 213-251.

Wilson, J. 2003. 'Internationalization' and the conservation of Canada's boreal ecosystems. Canadian - American Public Policy **56:** 1.

Chapter 2. Pre-commercial thinning effects on leaf area in young boreal mixedwood stands and a comparison of direct and indirect methods for measuring leaf area index

2.1 Introduction

Leaf area index (LAI) was defined by Watson (1947) as the ratio of leaf area to a given unit of land. Productivity of plant communities and stands of trees is closely related to LAI, as are water, nutrient and carbon cycling (Waring 1983; Landsberg and Waring 1997; Sampson et al. 1998; Mussche et al. 2001). LAI is often used in modeling canopy photosynthesis and evapotranspiration (Weiss et al. 2004).

LAI is influenced by stand composition, structure, age, site conditions and management practices (Jonckheere et al. 2004). LAI values in forests range between 0.4 (Le Dantec et al. 2000) and 41.8 m^2/m^2 (Ni *et al.* 2001). The highest values are associated with coniferous canopies, with broadleaf forests typically having values less than 8 m^2/m^2 (Beadle 1993). Canopy leaf area is inversely related to the amount of light reaching the forest floor, which can influence growth of understory vegetation including small trees (Comeau 1996; Chen and Klinka 1997).

In boreal mixedwoods, competition for light begins very early in post-disturbance colonization as shade intolerant species such as bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.), fireweed (*Epilobium angustifolium* L.) and aspen (*Populus tremuloides* Michx.) suppress slower growing trees such as white spruce (*Picea glauca* (Monech) Voss) (Chen and Popadiouk 2002). Within a few years, light often becomes the most limiting resource for understory spruce as aspen forms a dense overstory that reduces light to the understory (Man and Lieffers 1999; Stadt et al. 2001). Aspen leaf area reaches 6 m^2/m^2 at about age 15 (Lieffers et al. 2002). This high overstory leaf area results in suppression of understory spruce such that it often does not reach the overstory before the next disturbance (Chen and Popadiouk 2002).

Thinning can be used to manipulate overstory leaf area, thus modifying light levels in the understory of forest stands. Pre-commercial thinning is used in the stand initiation or stem exclusion stages to increase light transmission to understory spruce and thus encourage stem growth (Simard et al. 2004). However, altering the overstory leaf area will also alter the understory vegetation community (Lieffers and Stadt 1994; Constabel and Lieffers 1996). Removing too much aspen can encourage growth of shrubs and forbs that will in turn reduce the benefits of the thinning to white spruce due to increased competition. Alternatively, maintaining a high density of aspen will inhibit conifer survival and growth (Lieffers et al. 1999). In order to successfully manipulate light levels in a stand, we need an understanding of the effect of stand structure, species composition, geographic location and sky conditions on the quality and quantity of light in the understory, the response of understory vegetation to changes in light conditions, and the relationship between overstory basal area and understory light conditions (Messier 1996; Comeau 2001).

A variety of methods for measuring LAI are presented in the literature and these fall into two categories: direct and indirect (Mussche et al. 2001). Direct methods include destructive sampling and litter fall collection. Direct measures are considered the most accurate but are not often used because they are very time consuming and labour intensive (Jonckheere et al. 2004).

Litter fall collection is the most common of the direct measures and its precision is based on the size and number of traps used (McShane et al. 1983). LAI is determined by multiplying the weight of the leaf litter collected in the traps by the specific leaf area (SLA) (species-specific leaf area to dry weight ratio). The accuracy of this method relies on the assumption that the traps capture a representative sample of leaf area in the stand area to be measured (Jonckheere et al. 2004). However, due to the nature of leaf fall, it is difficult to know the actual area the litter trap is collecting from (Rhoads et al. 2004). Another source of error lies in the calculation of SLA, as it varies within and between species over the course of a growing season. Bouriaud et al. (2003) found that the specific leaf area varies with changes in soil chemistry, accounting for 8-24% of the error in LAI calculations.

Indirect methods for estimating LAI are usually preferred because they do not require as many man-hours and can be used to measure LAI over a growing season instead of providing a single final estimate (Mussche et al. 2001). In contrast to the direct method, indirect methods measure the total plant area index (PAI) because they are unable to differentiate between leaves, stems and branches. Nevertheless, LAI can be calculated by subtracting measures taken during leaf off (woody area index, WAI) from the leaf-on PAI measurements.

With indirect methods, LAI is calculated by inversion of gap fraction data (Nilson 1971; Welles 1990). Neumann et al. (1989) summarize various models that can be used to calculate leaf area index from indirect measurements. The Poisson model assumes random leaf spatial distribution, and tends to give consistent underestimates of LAI in forest canopies because leaves are aggregated on twigs, branches and trees (Neumann et al. 1989; Chanson et al. 1991). LAI-2000 Plant Canopy Analyzers (PCA, Li-COR, Lincoln, NE, USA) and hemispherical photographs are two of the most common instruments which rely on gap fraction inversion calculations for indirect estimation of LAI.

The LAI-2000 uses light transmittance measurements for five zenith angles to determine LAI (Li-COR Inc. 1992). Using a 150° field-of-view sensor, it measures the proportion of diffuse sky radiation reaching a point from five different angles. It compares the light level measurements taken in a clearing to those at the point of interest and calculates LAI using the inverse Poisson model (Welles and Norman 1991, Gower and Norman 1991, Jonckheere et al. 2004). The model relies on four assumptions about the foliage: it does not reflect light; the distance between leaf and lens is at least four times the leaf width; and the leaves are randomly oriented (Li-COR Inc. 1992).

Hemispherical (also called fisheye) photographs are taken at the point of interest and analyzed using computer software such as the Spot Light Interception Model (SLIM) to determine canopy openness (Comeau et al. 2006). SLIM was used to discriminate between sky and foliage in the digital images. SLIM estimates LAI using three models: the poisson, binomial and linear, allowing the user to take into consideration leaf angle and clumping, an option that is not available with the LAI-2000 output.

Stand density is another indirect method used to estimate leaf area or light and is considered one of the easiest measurements to take. The basal area (the total cross sectional area of all tree stems measured at breast height (1.3m above ground) expressed as square meters per hectare), age and average height of a stand play the key roles in determining leaf area and therefore light reaching the understory. Lieffers et al. (1999) found that light to the understory decreases with increasing leaf area and stand density until crown closure in boreal mixedwoods. Several studies have found a strong relationship between understory light and overstory basal area (Messier 1996; Man and Lieffers 1997; Comeau 2001). The relationship is dependent on stand composition, age, and edaphic conditions.

Hemispherical photographs and LAI-2000 estimates of PAI have been found to be highly correlated with each other and with litter fall estimates of LAI (Dufrêne and Breda 1995; Chason et al. 1991; Cutini et al. 1998; Mussche et al. 2001). However the indirect methods generally underestimate LAI by 30 to 70 percent compared with direct methods (Chason et al. 1991; Stenberg 1996; Cutini et al. 1998; Cutini 2002; Breda 2003). Chason et al. (1991) found that the assumption of random leaf distribution is violated in most forests and this can account for most of the underestimation generated by the indirect methods.

It is important to determine the accuracy of both indirect and direct methods to establish their capabilities over a range of conditions. Creating accurate models to estimate leaf area will provide a better understanding of forest canopy structure and the relationship between leaf area and forest productivity. In addition, if accurate correction factors can be developed for the indirect methods based on forest type, leaf area can be more easily estimated for a range of purposes.

The objective of the study presented in this chapter was to evaluate the effects of pre-commercial thinning of aspen on LAI and compare methods of LAI estimation:

1. In young mixedwood stands where pre-commercial thinning had been used to control aspen density, I compared four methods for measuring leaf area index: a) litter traps, b) hemispherical photographs, c) LAI-2000, and d) stand measurements (basal area);
2. In doing so, I was also able to determine the effect of varying levels of pre-commercial thinning on these measures of LAI.

2.2 Methods

Study Design

The study was performed in a young aspen white spruce mixture established near Grande Prairie, Alberta as part of the Western Boreal Growth and Yield Association (WESBOGY) long term sites (LTS). This study has 10 installations located across western Canada and is designed to examine the effect of density and mixtures on the productivity of white spruce and aspen at the individual and stand level (Bokalo et al. 2007).

The Grande Prairie WESBOGY LTS use a randomized complete block design with three replicate blocks containing one replicate of each of 15 treatments (Table 2.1).

The data for this study were collected in 2004 and 2006 at the installation south of Grande Prairie, Alberta (54°55′N, 118°55′W). The site is located in the Central Mixedwoods Ecological Subregion on a mesic low-bush cranberry (BM-d) ecosite

(Beckingham and Archibald 1996). The soil on this site is luvic gleysolic and has a mesic moisture regime. The slopes at these sites were less than 5% (Voicu and Comeau 2006). Top height (average of 50 tallest trees within each block) of the aspen in 2006 was 8.1 m.

These stands were harvested and planted with white spruce in 1991. Aspen regenerated naturally from root suckering following harvesting. Fifteen square plots were established in three sites and pre-commercial thinning treatments were assigned randomly to each plot in each block. Each plot is 0.04ha and is surrounded by 5m of treated buffer and 5m of untended buffer (Figure 2.1).

Table 2.1. Densities (trees/ha) for aspen (Aw) and white spruce (Sw) mixture treatments assigned to the plots in each replicate. Treatment was not applied to cells marked with an (x).

Aw Density Sw Density	0	200	500	1500	4000	Natural
1000	1	2	3	4	5	6
500	7	8	9	10	11	12
0	X	X	X	13	14	15

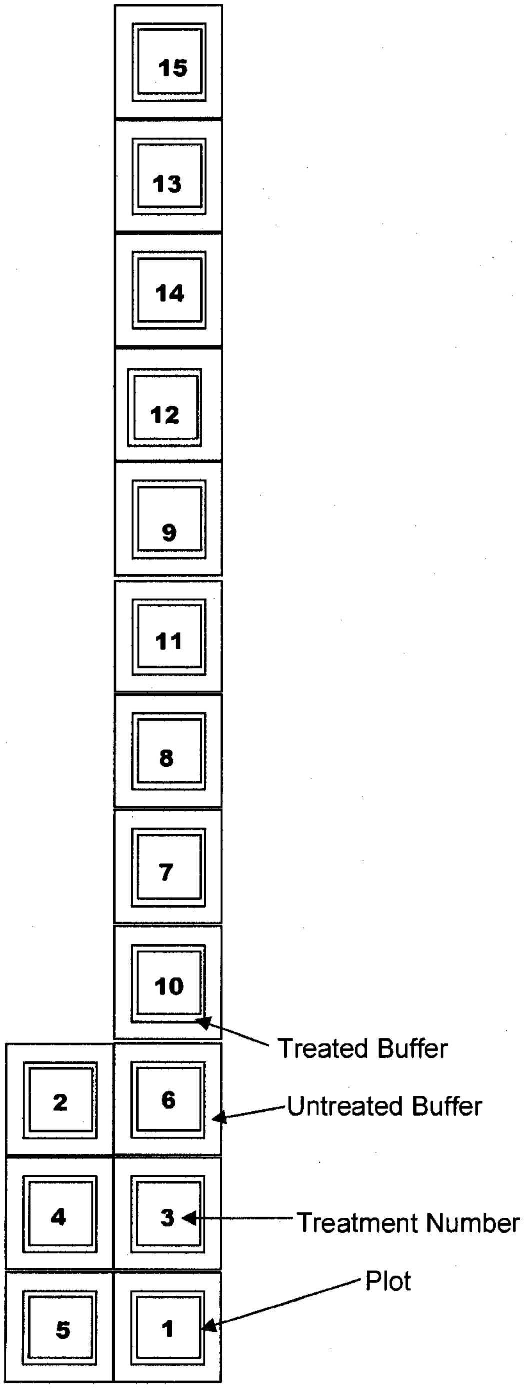


Figure 2.1. An illustration of the layout of the plots within one block (block 4003). Plots are 20x20m with a 5m treated buffer and at least a 5m untreated buffer (not to scale). Numbers indicate treatment numbers shown in Table 2.2.

After the white spruce were planted, competing woody vegetation was manually removed by cutting within a 0.5 m radius of each planted white spruce for 5 years while aspen was allowed to regenerate in the remaining space. In 1996 (age 5) aspen were thinned to the assigned treatment densities using brushsaws (0, 200, 500, 1500, 4000 trees per hectare or natural aspen density) (Table 2.1). In 1991 white spruce seedlings were planted at twice the prescribed density and were then thinned to appropriate densities (500 or 1000 white spruce per hectare) in 1996. The aspen treatment densities were maintained by brushing every year until 2006.

Tree measurements

Measurements of the aspen and white spruce were carried out by Weyerhaeuser in 2004 (3 years after final thinning) when the white spruce were 13 years old. In the plots where aspen had been thinned, the root collar diameter (RCD), diameter at breast height (DBH) and height were recorded for all trees in the plot. In the unthinned plots, measurements were recorded for all trees found in a 4x4m subplot within the plot. Basal area of the white spruce was estimated using RCD because many trees were not yet tall enough for DBH measurements.

LAI measurements

Three methods were used to measure LAI: LiCor LAI-2000 plant canopy analyzers, hemispherical photography and litter traps. The LAI-2000 and hemispherical photograph estimates of leaf area incorporate leaves, stems and branches. The LAI values arising from these indirect methods are estimates of plant area index (PAI). LAI-2000 plant canopy analyzers (Li-Cor Inc., Lincoln, NE) were used to measure PAI in August, 2006. For these measurements a 10x10m subplot was established in the center of each 20x20m plot and divided in four, 5x5m quadrats (Figure 2.2).

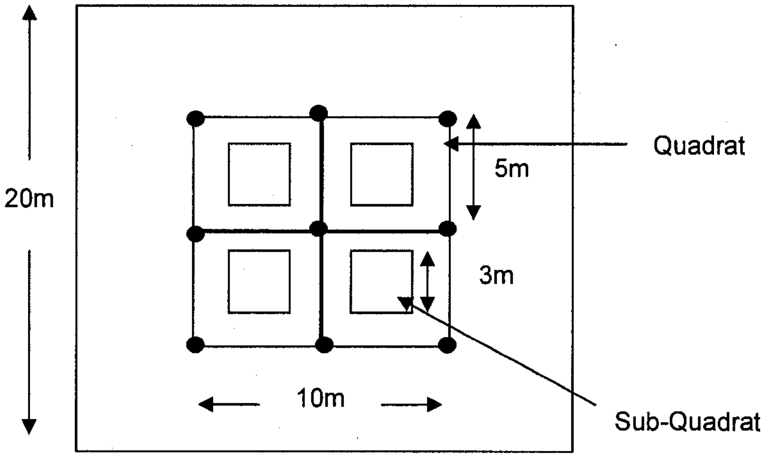


Figure 2.2. Layout of a plot within each block (not to scale). Within each 20x20m plot, four 5x5m quadrats and four 3x3m subquadrats were centered for LAI and understory measurements.

LAI-2000 measurements were taken at the nine corners of the quadrats with a 180° view restrictor installed on the sensor head. At each corner, a measurement was taken in the morning and afternoon with the sensor held at the top of the shrub layer (approximately 1m). In the morning (08h00-11h00), the sensor was oriented to the west and in the afternoon (13h00-19h00.), it was directed east. Simultaneous open sky readings were being taken every 15 seconds by another LAI-2000 unit which was mounted on a tripod in a large opening. To confirm cross calibration of the open sky and the roving sensors, an open sky reading was taken four times daily with the roving sensor located beside the open sky sensor.

LAI-2000 measurements were also made after leaf off in October 2006 to capture the area of the stems and branches (woody area index, WAI). For this, one measurement was taken at shrub height in both the morning and afternoon at the same nine corners of the quadrats.

LAI and PAI values were calculated using the program FV2000 (Li-Cor Inc., Lincoln, NB). The first four rings of the LAI-2000 sensor (equivalent to a sky view of 58.1° from vertical) were used to calculate the final values for leaf area index and light due to possible errors incurred when using the fifth ring (Comeau et al. 1998). Leaf-off measurements (WAI) were subtracted from leaf on (PAI) to provide a value of leaf area (LAI) versus leaf, branch and stem area.

Leaf area was also estimated using hemispherical photographs. A Nikon Coolpix 990 digital camera with a 185° field-of-view lens was used to take photographs at the four corners of the 10x10m sub-plot. The camera was mounted on a tripod one meter from the ground with the top of the image oriented northward. Photographs were taken in August 2006 in the early morning, late evening or during the day when uniform cloud cover was present to reduce glare from the sun. Using the Spot Light Interception Model (SLIM) software (Comeau et al. 2006), photographs were individually thresholded and analyzed to calculate the LAI with a field of view of 185 degrees.

Litter traps were used to collect litter from mid-August to the beginning of November 2006. Traps were placed in the three replicates of treatments 7-12 where aspen density varied from 0 to natural tree stems per hectare and white spruce density was 500 trees per hectare. In each plot, traps were placed in the four corners of the subplot where the hemispherical photographs were taken. The square traps (1x1m) were constructed with a frame made from PVC pipe and fiberglass screen. Trap sides were 50cm tall. Leaves were removed from the traps in September and again in November of 2006.

Of the 72 traps, 6 were destroyed by animals before the first collection and a total of 15 before the final collection. Following collection, leaves were dried at 70°C for two days, sorted to genus within each trap and weighed. A sub sample of thirty leaves of each genus from each plot was selected for measurement of genus-specific individual leaf area and weight for calculation of specific leaf area. Leaf area of the subsample was measured using WINFOLIA (Regent Instruments, Quebec, QC). Average specific leaf area for each genus was used to calculate total leaf area from the dry weights of leaves in each trap. All measurements of leaf area and mass included the petioles.

Statistical Analysis

Statistical analysis was completed using SAS software, version 9.1.3 (SAS Institute, Cary, NC). Graphs were prepared using SigmaPlot, Version 8.0 (SPSS Inc.). A mixed model ANOVA (PROC MIXED) with a randomized block experimental design was used to test whether the LAI estimates from each of the three methods were statistically different among the aspen thinning treatments (α=0.05). If it was significant, Tukey's adjustment was used for pair-wise testing among treatments. Spruce density was not included in this analysis because they had not penetrated the canopy. Prior to analysis, the residuals were tested for normality and homogeneity and the variables that did not meet the assumptions of ANOVA (aspen basal area and trees per hectare) were analyzed using the Friedman test. Transformations of these non-normal stand descriptors did not meet the assumptions required.

Linear and nonlinear models were tested to determine the best relationship between measures of leaf area based on the different methods using SAS (PROC MODEL, PROC NLIN and PROC REG) and Table curve 2D and 3D (AISN Software Inc. 2000). The best relationship was selected on the basis of the highest coefficient of determination (r^2 or adjusted r^2).

To determine the power of each method as well as the number of replicates needed for each treatment I used the paired t-test to estimate power, comparing each of the fifteen treatments. To determine the number of measurements to be recorded per plot, I followed the calculation procedures described by Stauffer (1982) and Bergerud (1988).

2.3 Results

The Grande Prairie WESBOGY plots ranged in aspen density from 0 to 70000 trees per hectare, stand basal area ranged from 0 to 46.1 m^2/ha and average aspen height ranged from 3.8 to 10.3 meters (Table 2.2, Figure 2.3).

Table 2.2.Mean values for selected stand characteristics for plots used in this study (as measured in 2004) (Aspen diameter at breast height (DBH) (95% confidence interval is given in parentheses).

Treatment Density	**Number of plots**	**Aspen density (n ha^{-1})**	**Aspen Basal Area (m^2 ha^{-1})**	**Aspen DBH (cm)**	**Aspen Height (m)**
0	6	0 (0)	0 (0)	N/A	N/A
200	6	200 (0)	0.90 (0.37)	7.45 (1.49)	7.44 (1.62)
500	6	483 (27)	2.25 (1.02)	7.52 (1.68)	8.06 (1.91)
1500	9	1436 (48)	3.53 (1.2)	5.45 (1.01)	6.73 (1.23)
4000	9	3906 (77)	8.08 (1.68)	5.09 (0.50)	7.34 (0.81)
Natural	9	48333 (14978)	31.04 (9.61)	2.87 (0.28)	4.83 (0.53)

a) b)

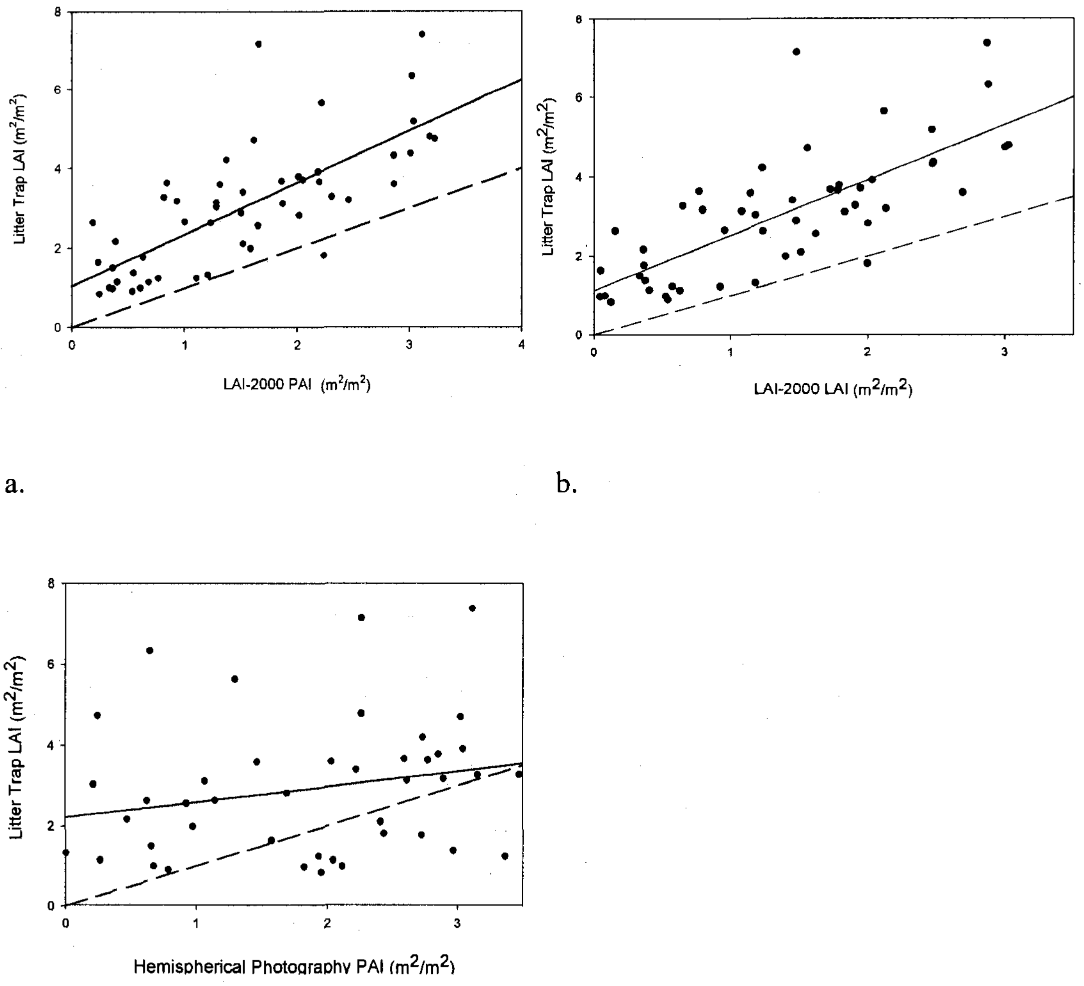
Figure 2.3. Photograph of a) Plot 7 with an aspen density of 0 trees/ha and a spruce density of 500 trees/ha. b) Plot 15 with a natural aspen density (70000 trees/ha) and a spruce density of 0.

Indirect Versus Direct Estimates of LAI

Figures 2.4 and 2.5 provide scatter plots showing the relationship between litter trap measurements of LAI and measurements provided by the different indirect methods. Results from simple linear regressions relating litter trap LAI or leaf weight to the estimates of PAI from hemispherical photographs and LAI-2000 are presented in Tables 2.3. Non-linear models did not provide improvements over linear models in terms of significance or distributions of residuals. There were no significant relationships between litter trap LAI or total leaf weight and hemispherical photograph estimates of PAI. However, a significant linear relationship was found between the litter trap LAI and LAI-2000 estimates of PAI ($p<0.001$, $r^2=0.55$).

By removing the influence of woody material (WAI), the relationship between LAI-2000 LAI and litter trap LAI improved marginally ($r^2=0.56$). The relationships between litter trap leaf weights and the indirect measures of LAI and PAI were stronger than those with litter trap LAI. The relationship between litter trap leaf weights and LAI-2000 PAI and LAI had r^2 values of 0.64 and 0.63, respectively (Figure 2.5, Table 2.3).

Results showed that indirect methods underestimated values of LAI compared to those based on the litter trap values. LAI-2000 PAI estimates were on average 50% lower than those of the total litter trap LAI values and hemispherical photograph PAI estimates were on average 87% lower.



a.

b.

c.

Figure 2.4. The relationship between direct estimates of LAI using litter traps and indirect estimates based on a) LAI-2000 PAI ($p<0.0001$, $r^2=0.55$) and b) LAI-2000 LAI ($p<0.0001$, $r^2=0.56$) and c) PAI from hemispherical photographs ($p=0.05$, $r^2=0.07$). The dashed line is a 1:1 line and the solid line is the regression described in Table 2.4.

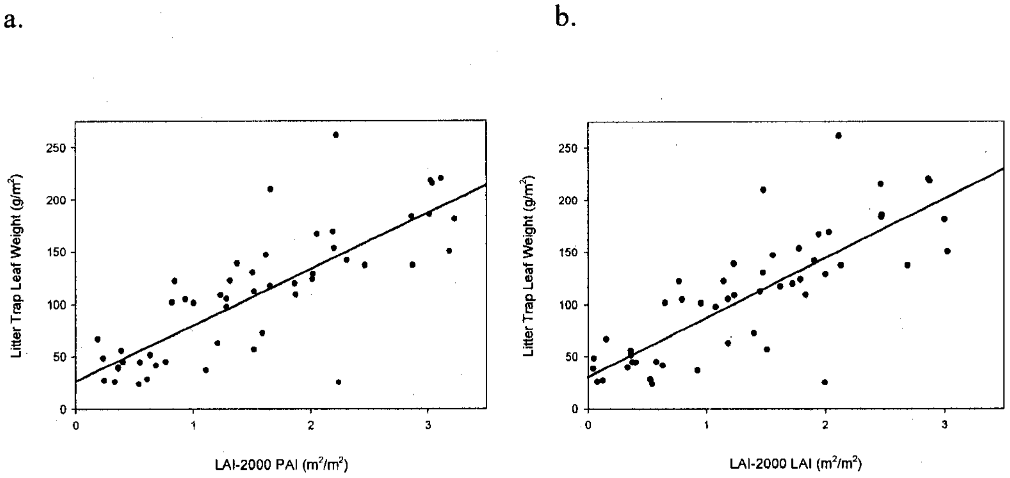


Figure 2.5. The relationship between total leaf weight from litter traps and optical estimates based on a) LAI-2000 PAI (p=<0.0001, r^2=0.64) and b) LAI-2000 LAI (p<0.0001, r^2=0.63). The solid line is the regression line described in Table 2.4.

Table 2.3. Results from simple linear regressions of leaf litter LAI and weight by the three different indirect methods for estimating LAI.

X	**Y**	**n**	**p>f**	**r^2**	**Regression**
Hemispherical PAI (m^2/m^2)	Litter Trap LAI (m^2/m^2)	51	0.05	0.07	Y = 2.21+0.38x
LAI-2000 PAI (m^2/m^2)		51	<0.0001	0.55	Y = 1.04+1.30x
LAI-2000 LAI (m^2/m^2)		51	<0.0001	0.56	Y = 1.13+1.39x
Hemispherical PAI (m^2/m^2)	Litter Trap Leaf Weight (g/m^2)	51	0.03	0.09	Y=73.49+16.16x
LAI-2000 PAI (m^2/m^2)		51	<0.0001	0.64	Y = 26.3+53.6x
LAI-2000 LAI (m^2/m^2)		51	<0.0001	0.63	Y = 30.5+56.9x

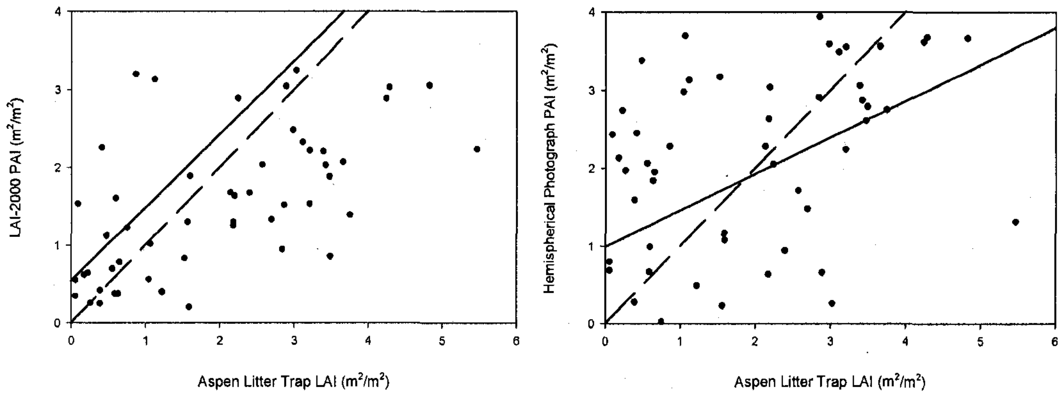
A significant relationship was found between all three indirect measures of PAI and LAI; and LAI for just aspen from the litter traps ($p<0.05$) (Table 2.4, Figure 2.6), but the regression lines did not fit the data well for the hemispherical photographs ($r^2=0.14$). The LAI-2000 measures of PAI and LAI had reasonable r^2 values, with the PAI value having a slightly better fit ($r^2=0.36$, 0.34). Values of litter trap birch and willow LAI were not related to the PAI and LAI estimates from the hemispherical photographs or LAI-2000 ($p>0.05$). The relationship between LAI-2000 and hemispherical photo estimates of LAI and PAI, and aspen and birch weight was not significantly different from the relationship with aspen or birch LAI (Table 2.5, Figure 2.7). The multiple regressions of LAI-2000 PAI and LAI on litter trap LAI for aspen, birch and willow were significant and strong ($p<0.0001$, $r^2=0.57$ for both), but the relationship with hemispherical PAI was not ($p=0.05$, adj. $r^2=0.15$) (Table 2.6).

Table 2.4. Results from simple linear regressions between direct measures of LAI separated by genus and the indirect estimates of LAI and PAI.

Y	**X**	**N**	**p>f**	**r^2**	**Regression**
Hemispherical Photograph PAI (m^2/m^2)	Aspen Litter Trap LAI (m^2/m^2)	51	0.007	0.14	Y = 0.98+0.47x
LAI-2000 PAI (m^2/m^2)		51	<0.0001	0.36	Y = 0.55+0.94x
LAI-2000 LAI (m^2/m^2)		51	<0.0001	0.34	Y = 0.66+0.97x
Hemispherical Photograph PAI (m^2/m^2)	Birch Litter Trap LAI (m^2/m^2)	51	0.42	0.01	Y = 0.07-0.01x
LAI-2000 PAI (m^2/m^2)		51	0.30	0.02	Y = 0.03+0.01x
LAI-2000 LAI (m^2/m^2)		51	0.23	0.03	Y = 0.03+0.02x
Hemispherical Photograph PAI (m^2/m^2)	Willow Litter Trap LAI (m^2/m^2)	51	0.62	0.005	Y = 1.16-0.08x
LAI-2000 PAI (m^2/m^2)		51	0.07	0.07	Y = 0.46+0.35x
LAI-2000 LAI (m^2/m^2)		51	0.05	0.08	Y = 0.44+0.40x

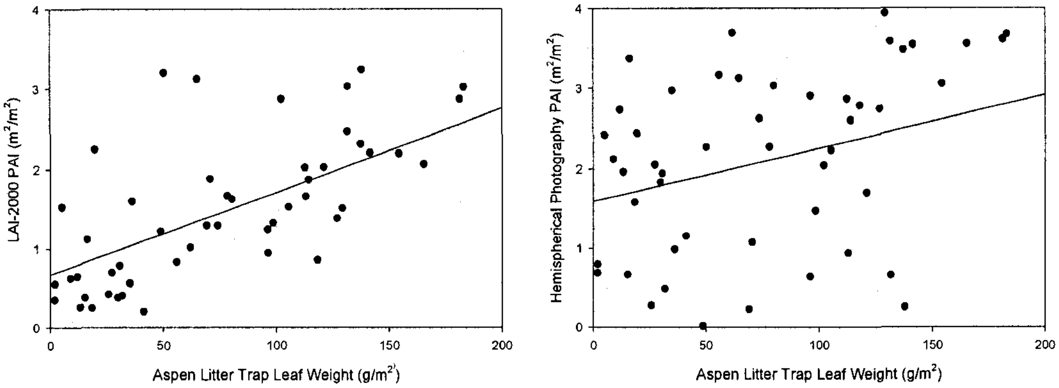
Table 2.5. Results from simple linear regressions of leaf litter weight for each genus versus the indirect estimates of LAI.

Y	X	n	p>f	r^2	Regression
Hemispherical Photograph PAI (m^2/m^2)	Aspen Litter Trap Wt (g/m^2)	51	0.01	0.12	Y = 43.0+18.3x
LAI-2000 PAI (m^2/m^2)		51	<0.0001	0.47	Y = 13.7+44.8x
LAI-2000 LAI (m^2/m^2)		51	<0.0001	0.45	Y = 18.5+46.7x
Hemispherical Photograph PAI (m^2/m^2)	Birch Litter Trap Wt (g/m^2)	51	0.44	0.01	Y = 2.27-0.27x
LAI-2000 PAI (m^2/m^2)		51	0.38	0.03	Y = 0.94+0.50x
LAI-2000 LAI (m^2/m^2)		51	0.17	0.04	Y = 0.85+0.62x
Hemispherical Photograph PAI (m^2/m^2)	Willow Litter Trap Wt (g/m^2)	51	0.66	0.004	Y = 28.5-1.74x
LAI-2000 PAI (m^2/m^2)		51	0.07	0.06	Y = 12.0+8.74x
LAI-2000 LAI (m^2/m^2)		51	0.05	0.08	Y = 11.0+10.1x



a) b)

Figure 2.6: The relationship of direct estimates of LAI for just aspen using litter traps and indirect estimates of PAI based on a) LAI-2000 ($p<0.0001$, $r^2=0.36$) and b) hemispherical photographs ($p=0.007$, $r^2=0.14$). The dashed line is a 1:1 line and the solid line is the regression line described in Table 2.5.



a) b)

Figure 2.7. The relationship of aspen leaf weight from litter traps and indirect estimates of PAI based on a) LAI-2000 ($p<0.0001$, $r^2=0.47$) and b) hemispherical photograph ($p=0.01$, $r^2=0.12$). The solid line is the regression line described in Table 2.6.

Table 2.6. Results of multiple linear regressions of indirect estimates of LAI and PAI on the direct measurements of LAI for the three main genera.

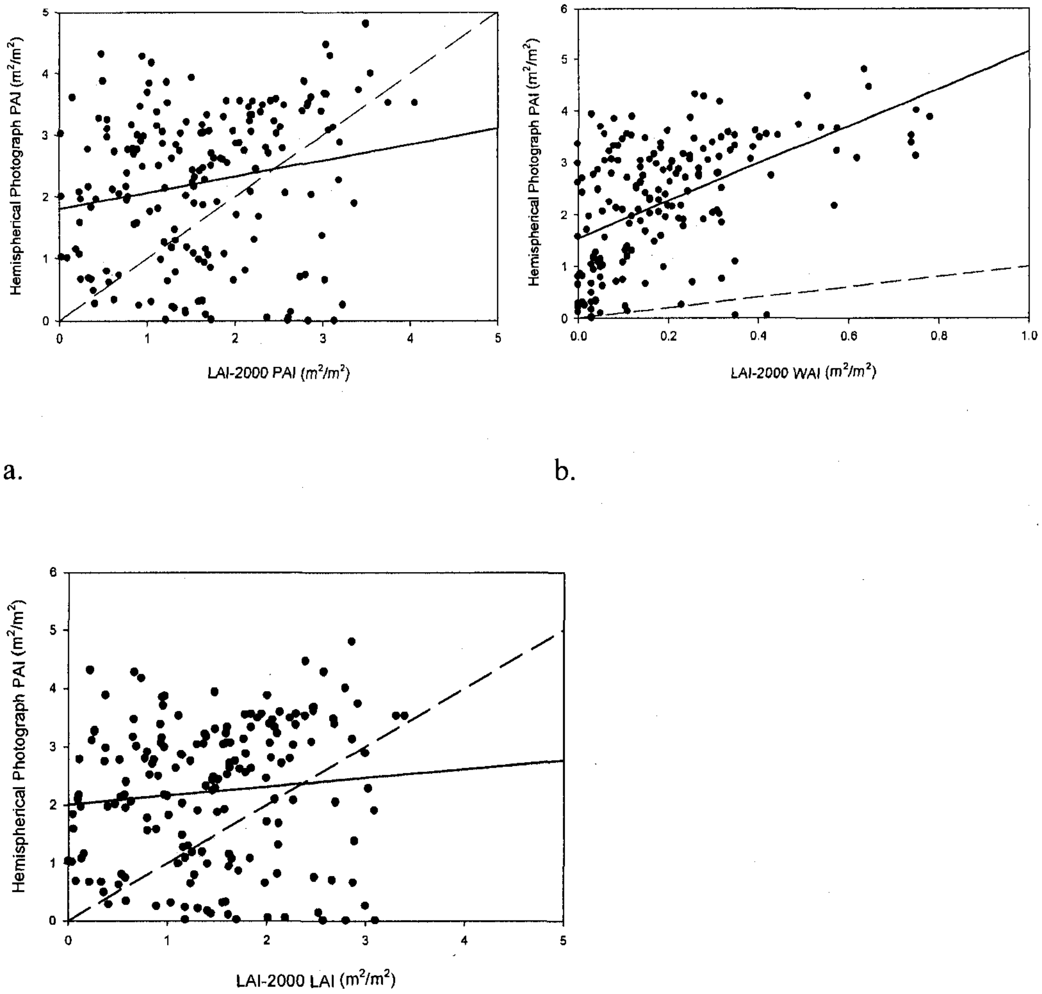
X	**Y**	**N**	**p>f**	**Adj. r^2**	**Regression**
Aspen (A), Birch (B) and Willow (W) Litter trap LAI (m^2/m^2)	Hemispherical Photograph PAI (m^2/m^2)	51	0.05	0.15	Y=1.58+0.31A-1.47B+0.03W
	LAI-2000 PAI (m^2/m^2)	51	<0.001	0.57	Y=0.15+0.47A+1.76B+0.34W
	LAI-2000 LAI (m^2/m^2)	51	<0.001	0.57	Y=0.057+0.44A+1.91B+0.34W

Relationships between indirect measures of LAI

There was a significant but weak relationship between estimates based on hemispherical photograph (PAI) ($p=0.009$, $r^2=0.04$) and the LAI-2000 (PAI and WAI) ($p=<0.0001$, $r^2=00.27$) (Table 2.7). The LAI-2000 measurements tended to underestimate PAI when hemispherical photographic PAI estimates were under $2m^2/m^2$ and increasingly overestimated PAI at higher hemispherical values (Figure 2.8a). The relationship between LAI-2000 LAI estimates and PAI estimates from hemispherical photographs was not significant ($p=0.16$, $r^2=0.01$).

Table 2.7. Results from linear regressions of hemispherical photography PAI and LAI-2000 PAI, WAI and LAI estimates (n=180).

Y	X	p>f	r^2	Regression Equation
Hemispherical Photograph PAI (m^2/m^2)	LAI-2000 PAI (m^2/m^2)	0.009	0.04	$Y = 1.81+0.26x$
	LAI-2000 WAI (m^2/m^2)	<0.0001	0.27	$Y = 1.54+3.61x$
	LAI-2000 LAI (m^2/m^2)	0.16	0.01	$Y = 2.01+0.15x$



a.

b.

c.

Figure 2.8. The relationship between estimates of a) PAI ($p=0.009$, $r^2=0.04$), b) WAI ($p<0.0001$, $r^2=0.27$), and c) LAI ($p=0.16$, $r^2=0.001$) based on LAI-2000 data, and estimates of PAI based on hemispherical photographs. The dashed line is a 1:1 line and the solid line is the regression line described in Table 2.8.

Modeling LAI from Stand Density

Linear and nonlinear regression models were used to examine relationships between stand basal area and LAI and PAI. Only hemispherical photograph PAI had a significant exponential relationship with aspen basal area, where leaf area tended to level out at approximately 7m^2/ha basal area (Figure 2.9). For all indirect estimates of leaf area (PAI and LAI), a multiple nonlinear regression including basal area of both aspen and spruce showed a significant improvement over nonlinear regression using only the aspen basal area. Hemispherical photograph estimates of PAI had the greatest variation explained (adj. r^2=0.61, n=45) by these models, and LAI-2000 LAI estimates had the least (adj. r^2=0.28, n=45) (Table 2.8). For litter trap total LAI, the multiple non-linear regression offered no improvement over non-linear regressions using only the aspen basal area.

Hemispherical photograph and LAI-2000 PAI had a significant nonlinear relationship with both aspen and white spruce basal area ($p<0.05$), but the most variation was explained by the multiple nonlinear regression. LAI-2000 and total litter trap LAI estimates had a significant linear and nonlinear relationship with white spruce basal area. In the multiple non-linear regressions both white spruce and aspen basal area were significant for all three methods.

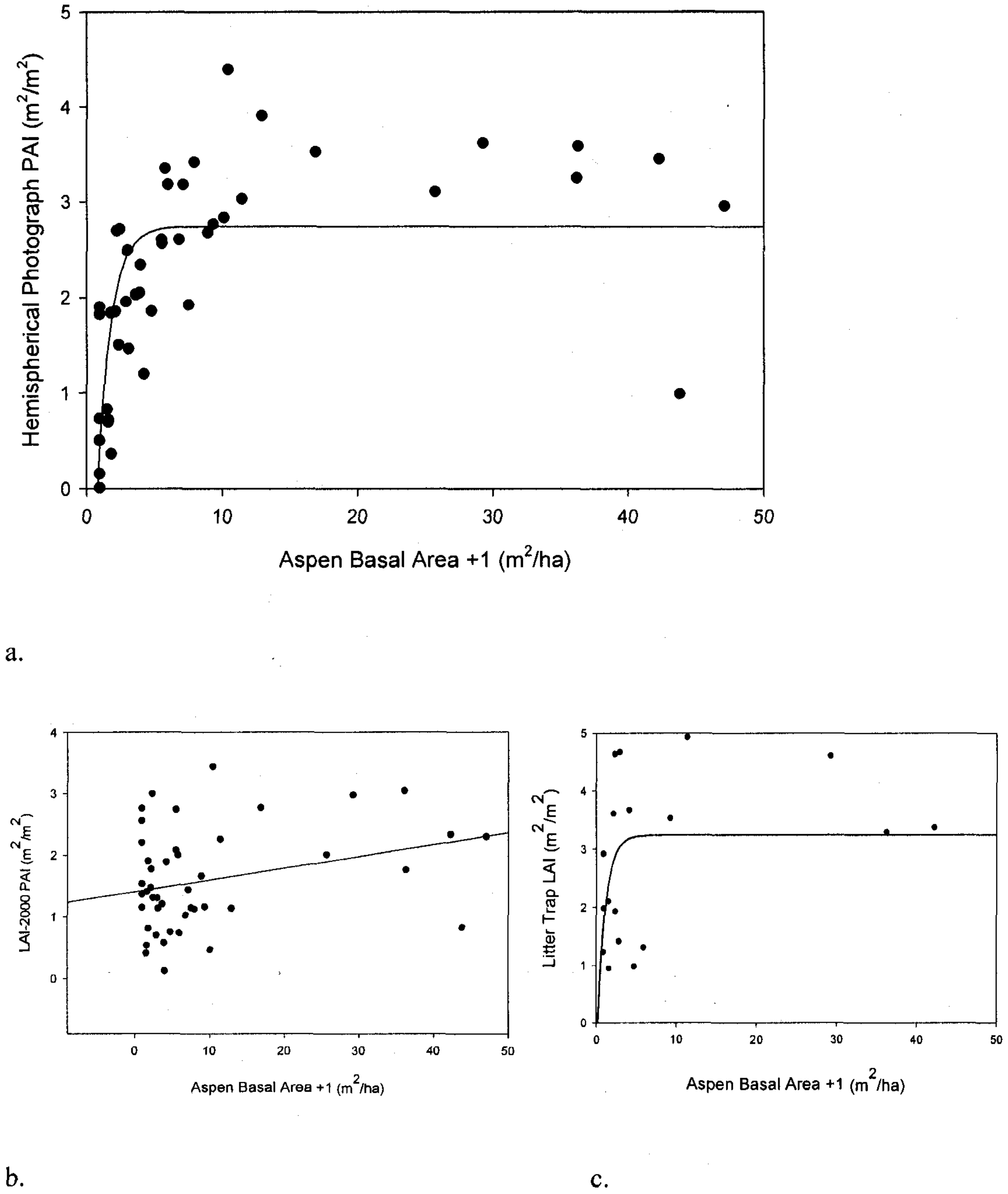


Figure 2.9. The relationship between aspen basal area and PAI and LAI as estimated from a) hemispherical photographs ($y=2.74-6.10e^{-x}$, $p<0.0001$, adj. $r^2=0.49$), b) LAI-2000 ($y=1.41+0.02x$, $p=0.05$, $r^2=0.09$) and c) litter traps ($y=3.24-3.87e^{-x}$, $p=0.12$, adj. $r^2=0.03$).

Table 2.8. Results from multiple non-linear regressions of indirect estimates of PAI and LAI versus aspen and white spruce basal area. Each of the included dependent variables were significant.

Y	**X**	**Z**	**p>f**	**Adj. r^2**	**Regression Equation**
Hemispherical Photograph PAI (m^2/m^2)	Aw BA (m^2/ha)	SW BA (m^2/ha)	<0.0001	0.61	$Y=1.723-1.53/x+1.09/z$
LAI-2000 PAI (m^2/m^2)			0.0002	0.32	$Y=2.79-2.39\ln x/x-3.04\ln z/z$
LAI-2000 LAI (m^2/m^2)			0.0004	0.28	$Y=2.45-2.27\ln x/x-2.41\ln z/z$

Effects of Thinning Treatments on LAI and PAI

Table 2.9 presents the average LAI estimates for each treatment density based on the three different methods of LAI estimation. Of the original 72 litter traps, 21 were destroyed by wildlife, leaving 51 traps. Litter trap LAI ranged from 0.9 to 4.9, hemispherical PAI ranged from 0.003 to 4.4 and LAI-2000 ranged from 0.1 to 3.4. Litter trap collection provided the highest estimates of LAI in each plot. The confidence intervals were large for all methods due to variation in gap frequencies and aspen density (Mussche et al. 2001).

Treatment effects on indirect measures of LAI and PAI were significant. Estimated PAI from hemispherical photography was significantly greater in the highest aspen density treatment ($3.64 m^2/m^2$) than in the three lowest aspen treatments (0, 200 and 500 trees/ha) (0.59, 1.36 and $2.16 m^2/m^2$). In addition, the complete aspen removal treatments had significantly lower PAI ($0.59 m^2/m^2$) than 1500 and 4000 trees/ha (1.79 and $2.99 m^2/m^2$). PAI estimates from the LAI-2000 for the complete removal were not significantly different from other treatment levels including natural aspen density. However, the natural aspen plots ($2.35 m^2/m^2$) were significantly different from the 500 and 4000 trees/ha plots (0.91 and $1.38 m^2/m^2$). The LAI-2000 WAI estimates of the natural treatment were greater than all other treatments, while the LAI-2000 LAI estimates of the natural treatment were only significantly different from the 4000 trees/ha treatment (Table 2.9).

Table 2.9. Effects of aspen thinning treatments on aspen basal area, density and various direct and indirect measures of leaf area. Means (confidence intervals) are given for the leaf area measures and median (distribution-free 95% confidence limits) are given for measures of aspen basal area and density (trees per hectare). Mixed ANOVA was used to determine p values for leaf area measures and Friedman's test was used for aspen basal area and density.

Aspen Trtmt TPH	**Aspen BA** (m^2/ha) **(n=45)**	**Aspen TPH (n=45)**	**Litter LAI Total** (m^2/m^2) **(n=18)**	**Litter LAI Aspen** (m^2/m^2) **(n=18)**	**Litter LAI Birch** (m^2/m^2) **(n=18)**	**Litter LAI Willow** (m^2/m^2) **(n=18)**	**PAI – Hemi** (m^2/m^2) **(n=45)**	**PAI - LAI-2000** (m^2/m^2) **(n=45)**	**WAI-LAI-2000** (m^2/m^2) **(n=45)**	**LAI – LAI-2000** (m^2/m^2) **(n=45)**
0	0 (0)	0(0)	2.03^{a} (2.10)	0.99^{abc} (1.71)	0.073^{a} (0.208)	0.97^{a} (0.98)	0.85^{a} (0.86)	1.92^{ab} (0.70)	0.068^{a} (0.058)	1.86^{ab} (0.68)
200	0.76 (0.53, 1.27)	200 (0)	1.65^{a} (1.55)	0.46^{a} (1.47)	0.048^{a} (0.206)	1.14^{a} (1.32)	1.44^{ab} (0.87)	1.17^{ab} (0.61)	0.062^{a} (0.058)	1.11^{ab} (0.59)
500	2.09 (1.23, 3.27)	500 (456-510)	2.34^{a} (5.01)	1.01^{ab} (2.46)	0.015^{a} (0.023)	1.32^{a} (2.57)	1.69^{ab} (0.77)	0.98^{a} (0.27)	0.13^{a} (0.074)	0.85^{ab} (0.29)
1500	3.27 (2.33, 4.73)	1425 (1388-1484)	3.96^{a} (1.43)	3.25^{bc} (0.78)	0.070^{a} (0.098)	0.64^{a} (2.23)	2.32^{bc} (0.51)	1.68^{ab} (0.73)	0.17^{a} (0.079)	1.51^{ab} (0.70)
4000	7.97 (6.40, 9.77)	3950 (3829-3982)	3.25^{a} (4.55)	1.63^{ac} (3.14)	0.052^{a} (0.151)	1.57^{a} (4.75)	2.99^{c} (0.43)	1.23^{a} (0.40)	0.19^{a} (0.080)	1.04^{a} (0.40)
Natural	35.21 (21.43, 40.66)	57500 (33355-63311)	3.75^{a} (1.84)	3.61^{c} (1.83)	0.046^{a} (0.178)	0.087^{a} (0.167)	3.21^{c} (0.71)	2.38^{b} (0.61)	0.37^{b} (0.13)	2.01^{b} (0.51)
p	<0.0001	<0.0001	0.15	0.0034	0.89	0.21	<0.001	0.0026	<0.0001	0.0062

Note: Values within columns followed by the same letter are not significantly different ($p<0.05$) using Tukey's test. No post-hoc comparisons were made among treatments for aspen basal area or density, as those data were analyzed by Friedman's test.

Definitions of Variables:
Aspen Trtmt TPH: target aspen treatment density (trees/ha); Aspen BA (m^2): aspen basal area; Aspen TPH: aspen trees/ha; Litter LAI Total: total litter trap LAI (m^2/m^2); Litter LAI Aspen: aspen litter trap LAI (m^2/m^2); Litter LAI Birch: birch litter trap LAI (m^2/m^2); Litter LAI Willow: willow litter trap LAI (m^2/m^2); PAI-Hemi: Hemispherical photograph PAI (m^2/m^2); PAI- LAI-2000: LAI-2000 PAI (m^2/m^2); WAI-LAI-2000: Log transformed LAI-2000 WAI (m^2/m^2); LAI-LAI-2000: LAI-2000 LAI (m^2/m^2).

Aspen treatment density did not have a significant effect on the total LAI based on the litter trap method. The high variability of the estimates at each density may have restricted the ability to differentiate between treatments. Analyzing the litter trap data by the three genera, aspen (*Populus tremuloides*), birch (*Betula papyrifera*) and willow (*Salix spp.*) provided greater insight (Table 2.9, Figure 2.10). The birch and willow LAI were not affected by treatment, but there were significant differences between aspen LAI at different treatment densities. In the natural aspen density plots litter trap aspen LAI (3.61 m^2/m^2) was significantly greater than in the 500 and 200 trees/ha treatments (1.01 and 0.46m^2/m^2). In the 4000 trees/ha treatments, the aspen litter trap LAI is low (1.63 m^2/m^2) and willow trap LAI is high (2.99 m^2/m^2) in comparison to the 1500 trees/ha or natural density plots (Table 2.9).

To compare effects of the treatments on estimates of LAI by the three methods, the means and 95% confidence intervals are depicted in Figure 2.11. The three methods were not significantly different from one another at each treatment density, due to high variability in the estimates. Litter trap LAI estimates and confidence intervals were consistently larger than those for the indirect methods of estimating PAI.

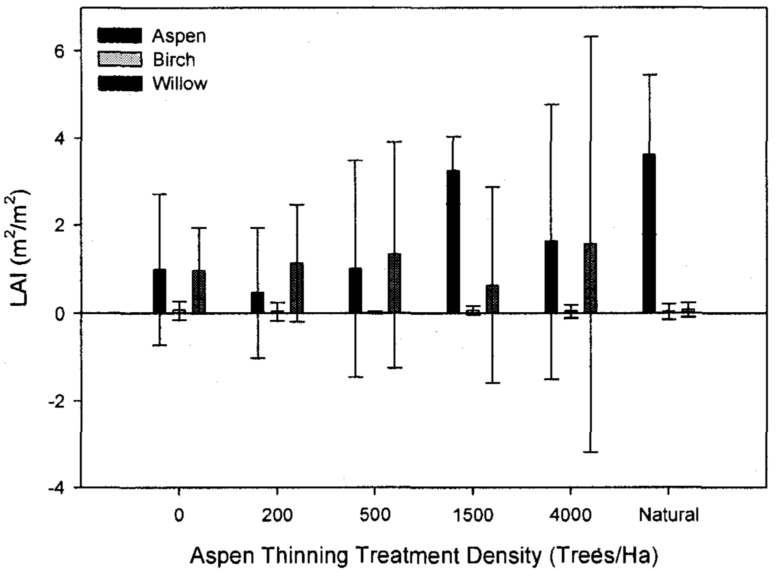


Figure 2.10. The mean litter trap LAI by genera for each thinning treatment. The error bars indicate the 95% confidence intervals.

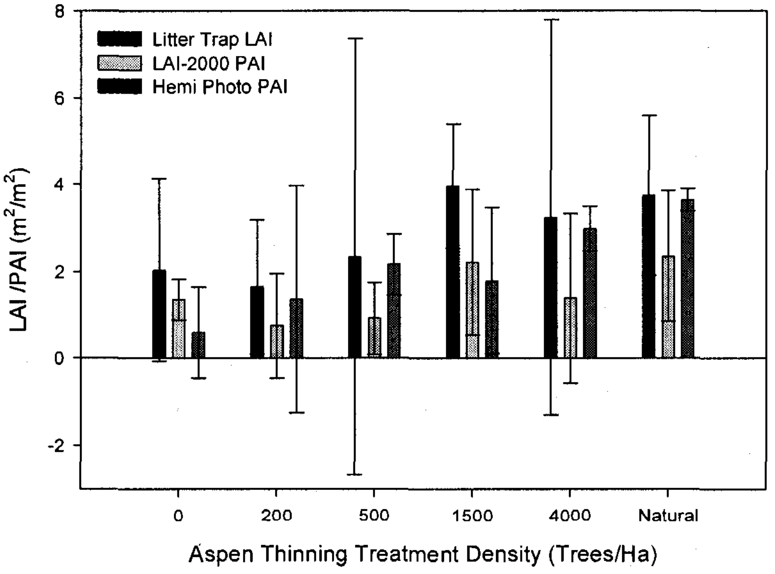


Figure 2.11. Effect of thinning treatments on LAI and PAI at 1m height determined using three different methods. Error bars indicate the 95% confidence intervals.

Table 2.10. Results from linear regressions of LAI estimates from litter traps comparing willow with aspen and birch leaf area.

X	Y	P	r^2	Regression Equation
Aspen Litter Trap LAI (m^2/m^2)	Willow Litter Trap LAI (m^2/m^2)	0.042	0.082	Y = 1.49-0.25x
Aspen and Birch Litter Trap LAI (m^2/m^2)		0.041	0.083	Y = 1.50-0.25x

A significant negative relationship existed between the litter trap LAI for willow and aspen as well as willow and the combination of aspen and birch (p=0.04) (Table 2.10).

Power and sample size

Based on standard deviations for each plot, sample size calculations for a 90% confidence interval with a 20% allowable error are shown in Table 2.11. These calculations follow procedures described by Stauffer (1982) and Bergerud (1988). Results from this analysis indicate that within each plot, an average of 11 litter traps, 15 LAI-2000 measurements, and 16 hemispherical photographs are needed to obtain an estimate of LAI or PAI with 90% confidence limits and 20% allowable error. For litter traps and LAI-2000, the average number of required measurements per plot peaks at the 1500 trees per hectare plots, and is lowest in the natural and 0 aspen density plots. Hemispherical photographs on the other hand, had the greatest range in the 0 aspen density plots and were lowest in the 4000 trees per hectare plots. In general, at the highest densities, fewer samples are required per plot due to lower levels of variation.

All three methods had low power (<0.50) to detect change in leaf area between the treatment densities. On average, LAI-2000 and hemispherical photographs had a power of 0.43, and litter traps 0.38. To achieve a power of 0.90, the number of replicates per treatment would have to increase on average from three to 101 for litter traps, 52 for LAI-2000s and 39 for hemispherical photographs. The power of the methods improved with an increase in the difference between the treatments. The confidence intervals for all three methods were very large indicating extensive variation among plots.

Table 2.11. Estimates of replicates required to obtain estimates of plot means of LAI with 90% confidence limits and 20% allowable error. Average sample size and range is in parenthesis.

Aspen Density (TPH)	Litter Traps	LAI-2000 PAI	Hemispherical photograph PAI
0	2 (2)	10 (1-38)	67 (17-210)
200	7 (1-16)	14 (2-26)	9 (1-25)
500	15 (5-30)	27 (5-69)	9 (2-23)
1500	19 (1-46)	26 (1-177)	9 (1-50)
4000	18 (1-49)	12 (1-29)	1 (1-5)
Natural (unthinned)	3 (1-7)	2 (1-5)	6 (1-57)

2.4 Discussion

This study showed that reducing aspen basal area had a significant negative exponential relationship on leaf area index in boreal mixedwood stands ten years after initial pre-commercial thinning treatments had been applied. The three measures used to quantify leaf area provided varying results with the indirect measures providing much lower estimates of leaf area than did litter traps. Hemispherical photograph estimates of PAI provided the best relationship with stand density and best distinguished among thinning treatments but did not have a strong relationship with LAI-2000 or litter trap estimates. LAI-2000 PAI and litter trap LAI estimates had a significant positive relationship.

Comparing measures of leaf area

The results show a good agreement between LAI-2000 LAI and PAI, and litter trap LAI estimates of leaf area. In contrast to previous findings in a variety of forest stands (Fassnacht et al. 1994; Cutini et al. 1998; Mussche et al. 2001), our direct leaf area estimates from litter traps were not related to PAI estimates from analysis of hemispherical photographs. Previous studies have found highly significant ($r^2>0.5$) linear relationships between LAI-2000, hemispherical photographs, and litter fall estimates of leaf area (Dufrêne and Breda 1995; Chason et al. 1991; Cutini et al. 1998; Mussche et al. 2001). Like us, they found that the indirect estimates were generally lower than the litter fall estimates (Chason et al. 1991; Cutini et al. 1998; Cutini 2002; Breda 2003).

A key reason for the underestimation of LAI by indirect methods could be the assumption of randomly distributed foliage used to calculate leaf area (Breda 2003). Gaps and clumping in the canopy will cause underestimations of the leaf area because the probability of light penetration is greater than if leaves were randomly distributed (Chason et al. 1991). Thinning affects the homogeneity of the canopy cover causing greater frequency of gaps than in control plots (Cutini et al. 1998). In the WESBOGY plots, the canopy in the thinned plots is far more heterogeneous than in the unthinned plots (Figure 2.11).

One source of differences between litter traps and indirect methods is that the former provide estimates of total leaf area, while the indirect methods estimate projected leaf area based on leaves hanging at an angle relative to the ground surface. Kucharik et al. (1998) reported that boreal aspen forests have a mean leaf inclination angle near 70° for a 70 year old aspen stand. If I had applied a 70° correction factor to LAI-2000 leaf area estimates to account for the leaf inclination angle, it would have decreased underestimation by the LAI-2000 by 30%. The use of models which account for non-random distribution of leaves (rather than uniform random distribution) might further improve agreement between the methods, however this would require additional measurements of parameters which were not collected in this study. Future studies should be conducted to address these issues in young aspen dominated stands.

As reported in other studies, the greatest underestimation occurred at the highest levels of litter trap LAI (Sampson and Allen 1995; Cutini et al. 1998). In un-thinned, dense canopies, it is common for the leaves to be concentrated in the upper canopy which is not fully captured by the indirect measures (Sampson and Allen 1995; Cutini et al.

1998; Mussche et al. 2001). Removing the leaf off measurements (WAI) from the LAI-2000 indirect estimates of PAI to obtain an estimate of LAI did not improve the relationship with litter trap estimates and in fact increased the underestimation of LAI. Kucharick et al. (1998) found that the relationship between leaf and woody area is not random, with foliage preferentially covering branches and stems. Branches account for less than 10% of plant area estimates by indirect methods in boreal forests, indicating that WAI estimates should be corrected for foliage overlap before being removed from PAI estimates.

Breaking down the litter trap leaf area by genus had little impact on the relationship between the direct and indirect LAI estimates. Aspen LAI and the indirect measures had a significant relationship although the variation explained for the LAI-2000 estimates was lower than that with total litter trap LAI and the variation was low (<0.30) for the hemispherical PAI estimates. Willow and birch LAI were not related to the indirect measures and were only a portion of total litterfall (averaging 38% of the total leaf weight in the traps). The confidence intervals were very large, especially for the birch and willow indicating that more samples per plot would have increased the accuracy and precision of the LAI estimates from the litter traps.

I found a significant relationship between hemispherical photographs PAI and LAI-2000 PAI and WAI estimates but insignificant relationships with LAI-2000 LAI estimates. Rhoads et al. (2004) found that hemispherical photographs had lower precision than the LAI-2000 because the LAI-2000s have high sensitivity to light fluctuations. Variation in hemispherical PAI estimates could also be attributed to discrepancies in manual thresholding.

In studies comparing indirect and direct measures of leaf area, the direct method is considered the reference point to determine the accuracy of the indirect methods. In this study, the accuracy of the litter trap method was limited because of a small number of samples and treatment replicates and high variability within and between plots. Without an accurate direct measure of LAI to compare to, the accuracy of the indirect methods could be assessed by examining the relationship between the measure of LAI and the aspen density. This would suggest that hemispherical photographs had a closer relationship to overstory canopy structure than did the LAI-2000 estimates, although the hemispherical photographs did not accurately estimate the actual broadleaf leaf area in these stands if litter traps are considered the reference point (i.e. they are representing other structural attributes of the stands).

Previous research shows that each method is capable of providing accurate and precise estimates of LAI provided that suitable sample sizes are used (Rhoads et al. 2004). The indirect methods are more efficient but should be calibrated against a direct measure. As seen here, the direct method can be difficult to use as it is the most time consuming and requires a large sample size which can be beyond the research budget. However, hemispherical photographs and LAI-2000 PCA rely on assumptions to calculate LAI that are generally violated in forests, especially young, thinned stands.

Effects of Pre-commercial Thinning on LAI

Aspen thinning had a significant effect on the indirect estimates of PAI but did not affect litter trap total LAI. Broken down by genus, pre-commercial thinning had a negative effect on aspen litter LAI but not on willow and birch litter LAI. The willow and birch litter LAI was less in the highest aspen density plots compared with the lowest aspen density plots. A negative relationship between willow and aspen LAI and visual inspection of the plots indicated that removing aspen from the overstory commonly lead to an increase in willow cover. This in-growth was not enough to maintain the same plant area index found in the natural aspen density plots

Hemispherical photograph estimates of PAI were most capable of differentiating between treatment densities and had the strongest relationship with aspen and white spruce basal area. Hemispherical photographs provide greater ability to distinguish between sky and plant area, and higher spatial resolution than the LAI-2000 (Chen et al. 1991). Our results suggest that in young boreal aspen stands, hemispherical photographs are the best descriptor of changes in leaf area with varying thinning intensities. However, without an accurate direct measure of leaf area to compare with, it is difficult to determine the accuracy of the indirect methods.

The thinning treatments resulted in a decrease in leaf area and an increase in light reaching the understory. The steep slope indicates that, ten years after the initial thinning, leaf area index of the overstory is equal for stands with a basal area greater than $7m^2$/ha (approximately 1500 tph).These stands have had time for their crowns to expand and close.

The power analysis and sample size calculations indicate that too few measurements were taken and there were not enough replicates to acquire a 90% confidence that the mean of LAI is within 20% of the measured LAI or PAI. Hemispherical photograph measures required the lowest number of replicates per treatment to achieve this level of precision at the plot level but a few more measurements per plot would have improved the measurement precision. This, coupled with large confidence intervals, indicates that a larger sample size, with more observations per plot was needed in order to expand the scope of statistical inference. On average, 11 litter traps, 15 LAI-2000 and 16 hemispherical measurements are needed per plot to achieve 90% confidence intervals with a 20% allowable error.

Gosz et al. (1972) found that precision of litter trap leaf area estimates was dependant on the size and number of traps used. Although commonly considered to be the most accurate method for measuring leaf area index (Fassnacht et al. 1994; Wilhelm et al. 2000; Mussche et al. 2001; Jonckheere et al. 2004), Morrison (1991) and McShane et al. (1983) found that depending on the size of the trap, litter traps can overestimate true values. Compared with harvesting, litter trap estimates of LAI are often higher (Jurik et al. 1985). A possible source of error for this method lies in the subsample of leaves used to estimate total leaf area. Specific leaf area can vary within a forest stand and collecting subsamples can introduce bias into the calculations (Bouriad et al. 2003). Further variation in leaf area is found with leaves at different heights in the canopy (Nippert and Marshall 2003; Eriksson et al. 2005).

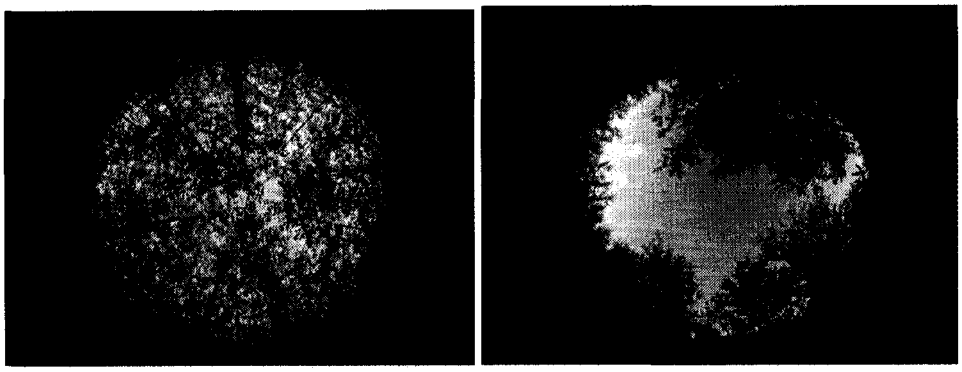


Figure 2.12. Hemispherical photographs of a thinned and unthinned plot.

2.5 Conclusions

Pre-commercial thinning in young boreal mixedwood forests had a considerable impact on overstory leaf area and aspen density (Figure 2.12). A significant exponential relationship between aspen basal area and overstory plant area index indicated that reducing the number of aspen trees below 1500 tph ($7m^2$/ha) resulted in a decline in the overstory plant area. Comeau (2001) also found a significant relationship between aspen basal area and understory light levels and recommended that the aspen basal area be maintained at less than $8m^2$/ha to provide adequate light for understory white spruce growth in young boreal mixedwood stands in northern British Columbia.

Results from this study indicate that the direct and indirect methods of estimating leaf area provide differing information about the forest canopy. Litter trap estimates were most closely related to LAI-2000 estimates, while hemispherical photograph estimates were related to stand measurements of density and basal area. The violation of assumptions used to calculate LAI by the indirect methods resulted in the underestimation of LAI as defined by the direct method. The relationship between the two indirect methods was significant but weak.

Hemispherical photographs had the closest relationship with stand measurements but both indirect measures had a significant multiple non-linear relationship with aspen and white spruce basal area. Hemispherical photograph estimates of PAI indicated that the leaf area increases with aspen basal area to $7m^2$ /ha (1500 tph) above which point crown closure results in a constant leaf area. Litter trap leaf area estimates did not have a significant relationship with aspen basal area but leaf area was significantly different among thinning treatment densities.

The choice of method for estimation of leaf area index will depend on the stand measurement one is trying to estimate, financial and time restraints. Litter traps are considered the most accurate measure of leaf area and provide the ability to separate leaf area by species, but require a large sample size and the greatest amount of time to implement to ensure accuracy. LAI-2000 plant canopy analyzers are the fastest method of estimating LAI but are not as sensitive to changes in canopy density. Hemispherical photographs are slightly more labour intensive in field set up and photo calibration, but provide more detailed light and leaf area data, as well as photos that can be kept on record for future reference.

Further research is required to develop more accurate models for the indirect methods that account for the non-random distribution of leaves, shoots and branches with varying stand composition, age and density. Without these adjustments to the indirect methods, it is necessary to calibrate the estimates based on direct methods. Additional studies with greater replication are needed to test the results found in this research.

Results from this study provide indications that pre-commercial thinning had a significant effect on the overstory canopy and that the density of the aspen has to be reduced below 1500 trees/ha in order to reduce the overstory plant area index for ten years after thinning. The monitoring of pre-commercially thinned stands over time could contribute to a better understanding how these stands and their leaf litter continues to grow and change over time. We recommend collection of data over a large spatial and temporal range in order to develop regressions that can be applied at a larger scale.

2.6 References

Baker, J.A., Clark, T., and Thompson, I.D. 1996. Boreal mixedwoods as wildlife habitat: observation, questions, and concerns. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 1995, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada and Ontario Ministry of Natural Resources, Sault Ste. Marie pp. 41.

Beadle, C.L. 1993. Growth analysis. In: D.O. Hall et al. (eds.), Photosynthesis and production in a changing environment: a field and laboratory manual. Chapman and Hall, London, p. 36-46.

Beckingham, J.D., and Archibald, J.H. 1996. Field guide to ecosites of northern Alberta. Can For. Ser. Special Report 5. 442 pp.

Bergerud, W. 1988. Sample sizes: for one mean. Biometrics Information Pamphlet No. 11. Research Branch, B.C. Ministry of Forests, P.O. Box 9519, Stn. Prov. Gov., Victoria, BC V8W 9C2. Unpublished notes.

Bokalo, M., Comeau, P.G., and Titus, S.J. 2007. Early development of tended mixtures of aspen and spruce in western Canadian boreal forests. Forest Ecology and Management. **242**:175-184.

Bouriaud, O., Soudani, K., and Breda, N. 2003. Leaf area index from litter collection: impact of specific leaf area variability within a beech stand. Canadian Journal of Remote Sensing **29**(3):371-380.

Breda, N.J.J. 2003. Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. Journal of Experimental Botany **54**(392):2403-2417.

Chason, J.W., Baldocchi, D.D., and Huston, M.A. 1991. A comparison of direct and indirect methods for estimating forest canopy leaf area. Agricultural and Forest Meteorology **57**:107-128.

Chen, J.M., Black, T.A., and Adams, R.S. 1991. Evaluation of hemispherical photography for determining plant area index and geometry of a forest stand. Agricultural and Forest Meteorology **56**:129-143.

Chen, H.Y.H., and Klinka, K. 1997. Survival, growth and allometry of planted *Larix occidentalis* seedlings in relation to light availability. Forest Ecology and Management **106**(2-3):169-179.

Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environmental Reviews **10**: 137-166.

Comeau, P.G. 2001. Relationships between stand parameters and understory light in boreal aspen stands. B.C. Journal of Ecosystems and Management **1**: 1-8.

Comeau, P.G., Gendron, F., and Letchford, T. 1998. A comparison of several methods for estimating light under a paper birch mixedwood stand. Canadian Journal of Forest Research **28**: 1843-1850.

Comeau, P.G., Macdonald, R., Bryce, R. 2006. SLIM Version 2.2e (Spot Light Interception Model). B.C. MOF.

Comeau, P.G., Kabzems, R., McClarnon, J., and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. The Forestry Chronicle **81:** 559-574.

Comeau, P.G., Thompson, C.F., Harper, G.J., and Biring, B.S. 1996. Effectiveness of repeated manual cutting for release of Engelmann spruce from mixed-shrub communities in the Revelstoke District. EP 1135.01 Establishment and Progress Report.

Constabel, A.J., and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Canadian Journal of Forest Research **26**:1008-1014.

Cutini, A. 2002. Litterfall and leaf area index in the CONECOFOR permanent monitoring plots. Journal of Limnology **61**(1):62-68.

Cutini, A., Matteucci, G., and Munoza, G.S. 1998. Estimation of leaf area index with the Li-Cor LAI 2000 in deciduous forests. Forest Ecology and Management **105**:55-65.

Dufrêne, E., and Breda, N. 1995. Estimation of deciduous forest leaf area index using direct and indirect measures. Oecologia **104**:156-162.

Eriksson, H., Eklundh, L., Hall, K., and Lindroth, A. 2005. Estimating LAI in deciduous forest stands. Agricultural and Forest Meteorology **129**:27-37.

Fassnacht, K.S., Gower, S.T., Norman, J.M., and McMurtrie, R.E. 1994. A comparison of optical and direct methods for estimating foliage surface area index in forests. Agricultrual and Forest Meteorology **71**:183-207.

Gosz, J.R., Likens, G.E., and Borman, F.H. 1972. Nutrient content of litter fall on the Hubbard Brook Experimental Forest, New Hampshire. Ecology **53**(5):769-784.

Gower, S.T., and Norman, J.M. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. Ecology 72:1896-1900.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B. and Coppin, P. 2004. Methods for leaf area index determination. Part I: Theories, Techniques and Instruments. Agricultural and Forest Meteorology **121**:19-35.

Jurik, T.W., Briggs, G.M., and Gates, D.M. 1985. A comparison of four methods for determining leaf area index in successional hardwood forests. Canadian Journal of Forest Research **15**:1154-1158.

Kucharik, C.J., Norma, J.M., Stith, T. Gower. 1998. Measurements of branch area and adjusting leaf area index indirect measurements. Agricultural and Forest Meteorology **91**:69-88.

Landsberg, J.J., and Waring, R.H. 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management **95**:209-228.

Le Dantec, V., Dufrêne, E. and Saugier, B. 2000. Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. Forest Ecology and Management **134**:71-81.

LI-COR, Inc. 1992. LAI-2000 Plant canopy analyzer operating manual. LI-COR Inc. Lincoln, Nebraska USA.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research **29**:796-811.

Lieffers, V.J., Pinno, B.D., Stadt, K.J. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. Canadian Journal of Forest Research **29**: 796-811.

Lieffers, V.J., and Stadt, K.J. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis,* and *Epilobium angustifolium* in relation to overstory light transmission. Canadian Journal of Forest Research **24**: 1193-1198.

Macdonald, G.B. 1996. The emergence of boreal mixedwood management in Ontario: background and prospects. *In* Advancing Boreal Mixedwood Management in Ontario, October 17-19, 1995, *Edited by* C. R. Smith, and G. W. Crook. Natural Resources Canada, Canadian Forest Service, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario pp. 11. 1991.

Man, R., and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? The Forestry Chronicle **75**: 505-512.

McShane, M.C., Carlile, D.W., and Hinds, W.T. 1983. The effect of collector size on forest litter-fall collection and analysis. Canadian Journal of Forest Research **13**:1037-1042.

Messier, C. 1996. Managing Light and Understory Vegetation in Boreal and Temperate Broadleaf conifer Forests. In Silviculture of Temperate and Boreal Broadleaf-conifer Mixtures. B.C. Ministry of Forests, British Columbia pp. 59-81.

Morrison, I.K. 1991. Effect of trap dimensions on mass of litterfall collected in an *Acer saccharum* stand in northern Ontario. Canadian Journal of Forest Research **21**:939-941.

Mussche, S., Samson, R., Nachtergale, L., DeSchrijver, A., Lemeur, R., and Lust, N.A. 2001. Comparison of optical and direct methods for monitoring the seasonal dynamics of leaf area index in deciduous forests. Silva Fennica **35**:373-384.

Neumann, H.H., den Hartog, G., and Shaw, R.H. 1989. Leaf area measurements based on hemispheric photographs and leaf litter collection in a deciduous forest during autumn leaf-fall. Agricultural and Forest Meteorology **45**:325-345.

Ni, J., Zhang, X-S., and Scurlock, J.M.O. 2991. Synthesis and analysis of biomass and net primary productivity in Chinese forests. Annals of Forest Science **58**:351-384.

Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. Agricultural and Forest Meteorology **8**:25-38.

Nippert, J.B., and Marshall, J.D. 2003. Sources of variation in ecophysiological parameters in Douglas-fir and grand fir canopies. Tree Physiology **53**:591-601.

Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., and Kobe, R. 2004. Comparing direct and indirect methods of assessing canopy structure in a northern hardwood forest. Canadian Journal of Forest Research **34**:584-591.

Sampson, D.A., Vose, J.M., and Allen, H.L. 1998. A conceptual approach to stand management using leaf area index as the integral of site structure, physiological function, and resource supply. In: Ninth Biennial Southern Silvicultural Res. Conf. USDA Forest Service, South. Res. Sta. Gen. Tech. Rep. SRS-20. p. 447-451.

Simard, S.W., Blenner-Hassett, T., and Cameron, I.R. 2004. Pre-commercial thinning effects on growth, yield and mortality in even-aged paper birch stands in British Columbia. Forest Ecology and Management **190**: 163-178.

Stadt, K.J., Lieffers, V.J., and Pinno, B.D. 2001. Modeling light dynamics in boreal mixedwood forests. Sustainable Forest Management Network.

Stauffer, Howard B. 1982. A sample size table for forest sampling. Forest Science **28**(4):777-784.

Stenberg, P. 1996. Correcting LAI-2000 estimates for the clumping of needles in shoots of conifers. Agricultural and Forest Meteorology **79**:1-8.

Voicu, M.F., and Comeau, P.G. 2006. Microclimatic and spruce growth gradients adjacent to young aspen stands. Forest Ecology and Management **221**:13-26.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Advances in Ecological Research **13**:327-354.

Watson, D.J. 1947. Comparative physiological studies in the growth of field crops. I: Variation in net assimilation rate and leaf area between species and varieties and within and between years. Annals of Botany **11**:41-76.

Weiss, M., Baret, F., Smith, G.J., Jonckheere, I., and Coppin, P. 2004. Review of methods for in situ leaf area index (LAI) determination. Part II. Estimation of LAI, errors and sampling. Agricultural and Forest Meteorology **121**:37-53.

Welles, J.M. 1990. Some indirect methods of estimation canopy structure. In: Goel, N.S., Norma, J.M. (eds.) Instrumentation for studying vegetation canopies for remote sensing in optical and thermal infrared regions. Harwood Academic, UK. p. 31-43.

Welles, J.M., and Norman, J.M. 1991. Instrument for indirect measurement of canopy architecture. Agronomy Journal. **83**: 818-825.

Wilhelm, W.W., Ruwe, K and Schlemmer, M.R. 2000. Comparison of three leaf area index meters in a corn canopy. Crop Sciences **40**:1179-1183.

Chapter 3. Understory vegetation response to pre-commercial thinning in young boreal mixedwood forests

3.1 Introduction

While some studies indicate that forest management practices are reducing the structural, biological, and genetic diversity of forest ecosystems (Hunter 1999), others indicate that several of the common forestry treatments have short-term or even negligible impacts (Boateng et al. 2000; Sullivan and Sullivan 2003; Haeussler et al. 2004). A better understanding of how management practices impact ecosystem health is needed (Hunter 1999). Ecosystem health is a complex concept that is difficult to quantify; however indicators of forest ecosystem vigour, stability, and resilience to disturbance or stress are often used to assess the impact of human activities (O'Neil 1986; Shaffer et al. 1988; Rapport et al. 1998).

In the boreal forest, nearly all of the plant species are found in the understory (Halpern and Spies 1995). Fewer than five overstory species comprise the canopy, but over 100 shrub, forb, graminoid and bryophyte species can be found in the understory of Alberta boreal mixedwoods. Measures of diversity are commonly used to quantify ecosystem health because changes in diversity are considered to be an indicator of possible changes in the ecosystem (Magurran 1988). However, indices of diversity have been found to be either insensitive to disturbance or too simplistic to describe the complex patterns of ecosystem response (Kevan et al. 1997).

The diversity of the understory vegetation layer is a reflection of historical factors, environmental factors such as light, canopy, soil and landforms, and the successional stage of the forest (Sullivan et al. 1996; Small and McCarthy 2005). In the boreal forest, overstory and understory composition is strongly influenced by disturbances such as fire and insect outbreaks. The frequency and severity of these disturbances plays a major role in the structural, biological and genetic diversity of the forest (Bergeron et al. 1998).

After a major disturbance such as a fire or clearcut, sites are quickly dominated by shade intolerant, pioneer species such as trembling aspen (*Populus tremuloides* (Michx.)), fireweed (*Epilobium angustifolium* L.) and bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.) (Bergeron 2000). Shade tolerant species like white spruce (*Picea glauca* (Monech) Voss) grow slowly under the rapidly developing aspen canopy. The aspen canopy eventually begins to thin and over the next forty years, white spruce gradually enters the overstory. Over a long period of time, the aspen will decline and in the absence of major disturbance, white spruce will eventually dominate the canopy.

In Alberta, major portions of the forest landscape are allocated to industry for harvesting (Alberta Environment Protection 1998). Vegetation management practices in these stands are implemented to improve the growing conditions for the slower growing coniferous crop trees by manipulating both understory and overstory broadleaf composition and density. These techniques can have direct and indirect impacts on the understory. Direct disturbance to the understory can occur during the application of these techniques and indirect impacts may occur through the alteration of light, temperature, and soil nutrient and moisture availability.

Pre-commercial thinning is a vegetation management practice that has become common over the last decade in Alberta (Canadian Council of Forest Ministers 2007). In mixedwoods, it is applied to reduce the overstory broadleaf density to allow for increased growth of the understory conifers by reducing competition for light, nutrients and water. Pre-commercial thinning has also been found to have positive effects on conifer and broadleaf stem diameter, crown size and overall yield (O'Hara 1989; Rice et al. 2001). In addition, it can decrease conifer mortality, and shorten the rotation age of the stand (O'Hara 1989; Rice et al. 2001; Sullivan et al. 2001). Several studies have found that thinning had negligible effects on the growth of remaining broadleaf trees 10 to 20 years post treatment (Penner et al. 2001; Bokalo et al. 2007).

The effect of this technique on growth and yield as well as diversity is dependent on the number of times it is applied and the intensity of each application. Determining the appropriate density of aspen to leave on site is key to the success of pre-commercial applications (Comeau et al. 2005). If the application does not remove enough of the overstory the canopy will continue to impede the understory crop tree growth. However, if the application is too severe, it could have a negative effect on aspen and spruce stem quality by increasing branch size and stem taper (Simard et al. 2004). Competition against the conifer from surrounding understory vegetation can become a problem when the light levels are increased above 40%, because this allows graminoids such as *Calamagrostis canadensis* to dominate (Comeau et al. 2005).

The diversity, abundance and composition of the forest understory community is affected by canopy disturbance through changes in below ground resources (nutrient and water availability), and overstory composition and density (Carleton and Maycock 1981; Gagnon and Bradfield 1986; Host and Pregitzer 1992; Gilliam et al. 1995). Light levels and moisture reaching the understory are controlled by canopy composition and canopy openings (Anderson et al. 1969; Paré et al. 1993; Brais et al. 1995; Messier et al. 1998).

Light transmittance through a white spruce canopy is a fraction of that of aspen due to a denser crown and opaque leaves (Lieffers and Stadt 1994; Constabel 1995; Messier et al. 1998). By reducing the number of aspen trees, and potentially eventually increasing spruce basal area, thinning will affect moisture availability as well as light. By determining the density of spruce and aspen remaining in the stand, thinning can thus influence future development of the understory community, with the potential for long-lasting effects.

Hannam et al. (2004) found that chemical and environmental properties of the forest floor differ between spruce and aspen stands. Aspen has high nitrogen requirements to maintain their rapid growth and leaf production, and several studies have shown that aspen stands have significantly greater nitrogen availability than do white spruce stands; this is due to the rapid decomposition of aspen's nitrogen-rich litter (Pastor and Bockheim1984; Bauhus et al. 1998; Ste-Marie and Paré 1999; Jerabkova et al. 2006). White spruce, conversely, has been shown to depress nitrogen availability as a result of its lower growth rates and slower turnover of nitrogen in its litter (Chapin et al. 1986). The needles are acidic and can increase soil acidity in spruce dominated stands (Chapin et al. 1986). However, Prescott et al. (2000) found no benefit of aspen on decomposition in mixedwood stands.

The response of the understory to pre-commercial thinning will vary with intensity of thinning. The intermediate disturbance hypothesis predicts that at moderate levels of disturbance, species diversity will be at a maximum (Connell 1978; Huston 1994). It is hypothesized that at low levels of disturbance, competition from existing plants prevent new species from establishing and at high levels of disturbance, only the most tolerant species can thrive.

Several studies have found that reducing canopy closure results in an increase in understory vegetation cover and richness for up to twenty years after the application (Doerr and Sandburg 1986; Klinka et al. 1996; Thomas et al. 1999; Lindh and Muir 2004; Lindgren et al. 2006). Thomas et al. (1999) and Lindgren et al. (2006) found that although species richness increased in thinning treatments, species evenness marginally decreased or was unaffected by the treatment.

Determining the effect that thinning will have on the abundance of early and late successional species as well as introduced species is also a concern. Introduced or exotic species are species that have been introduced to a new location by human activity. Introduced species can be invasive if they are able to out-compete native species for resources like light, nutrients or space. Invasive species are often fast growing, tolerant of a variety of environmental conditions, able to reproduce rapidly, and disperse widely. Although pre-commercial thinning is applied in order to more quickly achieve a stand with structural attributes associated with older coniferous stands, it is assumed that the thinning will also allow for early seral species and introduced species to establish as a result of increases in light availability (Collins et al. 1985; Thomas 1999; Lindgren 2006).

Results on the impacts of pre-commercial thinning on understory composition are inconsistent. Several studies have found that heavier thinnings reduce community diversity while light to moderate thinnings promote understory diversity through the provision of a heterogeneous stand where shade tolerant and intolerant species co-exist

(McConnell and Smith 1970; Alaback and Herman 1988). Both Lindh and Muir (2004) and Lindgren et al. (2006) found increases in old-growth related species in thinned versus unthinned stands but Thomas et al. (1999) did not find any significant difference in abundance of early and later successional species. Thomas et al. (1999) speculated that changes in understory composition are driven by more extreme changes than those induced through pre-commercial thinning.

By decreasing aspen density, pre-commercial thinning may accelerate stand succession from an aspen to a mixedwood stand. These stands are thought to have greater understory diversity than either pure aspen or spruce stands due to the increased structural heterogeneity which provides the opportunity for species associated with both stand types to establish (Grubb 1977). Macdonald and Fenniak (2007) found that aspen stands had greater shrub and forb richness at the plot scale but spatial heterogeneity in species composition (i.e., beta diversity) was greater in mixedwood and conifer dominated stands.

The objectives of this study were to:

1. Determine changes in the understory community after different levels of pre-commercial thinning
2. Describe the relationship between the changes in tree abundance (aspen and white spruce basal area and leaf area) and the understory community.

3.2 Methods

Study Design

The Grande Prairie WESBOGY PSP described in Chapter 2 was also used for this study.

Tree measurements

Tree measures were as described in Chapter 2.

LAI measurements

The methods used to measure litter trap LAI and hemispherical photograph and LAI-2000 PAI were described in Chapter 2. In addition, a third LAI-2000 measure was taken at ground level in August, 2006 to estimate total (overstory +understory) PAI. I calculated PAI using the program FV2000 (Li-Cor Inc., Lincoln, NB). Overstory PAI estimates (LAI-2000 measures taken at shrub height) were subtracted from the total PAI estimates to determine understory PAI estimates.

Understory measurements

Vegetation was sampled within the four, 3x3m sub-quadrats depicted in Figure 2.2 in July 2006. Vascular plants were identified to the species level and visual estimates of cover of each species were recorded to the nearest one percent. Cover estimates were also obtained for overall vegetation cover, shrubs, forbs, graminoids, mosses and bareground. Modal heights were recorded for the shrubs, forbs, graminoids and willows.

Results from the four sub-quadrats within each plot were averaged for subsequent analysis.

Statistical Analysis

Statistical analysis was completed using SAS software, version 9.1.3 (SAS Institute, Cary, NC). Graphs were prepared using SigmaPlot, Version 8.0 (SPSS Inc.). Prior to analysis, the residuals were tested for normality and homogeneity and the variables that did not meet the assumptions of ANOVA (bareground cover and willow height) were log transformed. Environmental variables that could not be transformed to meet the assumptions were analyzed using Friedman's test (aspen basal area, diameter at breast height, and spruce basal area, height, and root collar diameter).

Species richness and diversity measures were calculated using PC-ORD (McCune and Mefford 1999). These included species richness (S), Shannon's diversity index (H):

$$H=\sum p_i * \ln p_i$$

(Shannon and Weaver 1949), Simpson's diversity index (D)

$$D=\sum(p_i^2),$$

(Simpson 1949), Pielou's evenness index (E)

$$E=H/\ln \gamma$$

(Pielou 1975), and Whittaker's measure of β-diversity (β)

$$\beta=(\gamma/S_p)-1$$

(Whittaker 1972), where p_i is the proportional abundance of species *i* within the unit area, S_p is the mean species richness per plot for a given thinning treatment and γ is total species richness for that treatment. All diversity measures except β-diversity were calculated for all species as well as for the shrub, forb, graminoid and tree layers separately. An Indicator Species Analysis (ISA) was performed to determine which species are indicators of the treatment types.

To test whether understory cover, height and diversity estimates were statistically different among the thinning treatments ($\alpha=0.05$) a mixed model ANOVA (PROC MIXED) was used for this randomized block experimental design. The following models were used:

a. $Y_{ij}=\mu+ A_i + S_j + A_iS_j + B_k + \varepsilon_{ijkl}$ (aspen and spruce density)
b. $Y_{ij}=\mu+ A_i + B_k + \varepsilon_{ikl}$ (aspen density)
c. $Y_{ij}=\mu+ S_j + B_k +\varepsilon_{jl}$ (spruce density)

where A is the aspen density treatment (*i*=2,5; fixed), S is the spruce density treatment (*j*=1,2; fixed),B is the block (*k*=2; random), and ε is the random error. When the significance of the main fixed effect was $p<0.05$, I used the least square means comparison with Tukey's adjustment at $\alpha=0.05$ to further compare among treatment pairs. Because of missing treatment combinations (Table 2.2), two different versions of ANOVA model A were conducted to examine the impact of aspen treatment density, spruce treatment density and their interaction: model a-i: treatment combinations 1-12 (full range of aspen densities and a spruce density of 500 or 1000); and model a-ii. treatment combinations 4-6 and 10-15 (three highest aspen densities and all three spruce densities). For models B and C, all treatment combinations were analyzed together.

In order to examine the relationship between the measured overstory properties (aspen basal area, estimates of LAI and PAI) and the understory cover, height and diversity measures, linear and nonlinear models were tested using SAS (PROC MODEL, PROC NLIN, PROC STEPWISE and PROC REG) and Table curve 2D and 3D (AISN Software Inc. 2000). The best relationship was selected on the basis of increasing the coefficient of determination (r^2 or adjusted r^2). When using PROC STEPWISE, the maximum r^2 improvement (MAXR) was used to determine if including both aspen and spruce in the regression improved the strength of the relationship. Variables that did not meet the assumptions of normality and homogeneity were tested using Spearman's correlation (aspen basal area with willow, forb, and graminoid height; hemispherical photograph PAI with willow height).

A Redundancy Analysis (RDA; Rao 1964, ter Braak 1986, 1987a) was used to examine the influence of environmental variables (aspen basal area, aspen height, aspen DBH, spruce basal area, spruce height, spruce RCD and estimates of total, overstory and understory LAI and PAI) on understory species composition (Legendre and Anderson 1999). A detrended correspondence analysis (DCA) showed that the gradient length of the response variables was less than two standard deviations (1.208), indicating that RDA was appropriate for the data Legendre and Legendre 1998). RDA is a constrained ordination that assumes that species abundance values are linearly related to the explanatory variables. RDA was run using CANOCO for Windows 4.02 (Microcomputer Power, NY) after log transforming the species and environmental variables in order to improve the normality of the response variables. Aspen and white spruce were removed from the species matrix for this analysis. The environmental variables used were selected using forward stepwise selection with significance testing by Monte-Carlo permutation. Only significant environmental variables were included in the final RDAs. Species with an inter-set correlation value greater than 0.50 were included in the presentation of the results of the final RDA.

3.3 Results

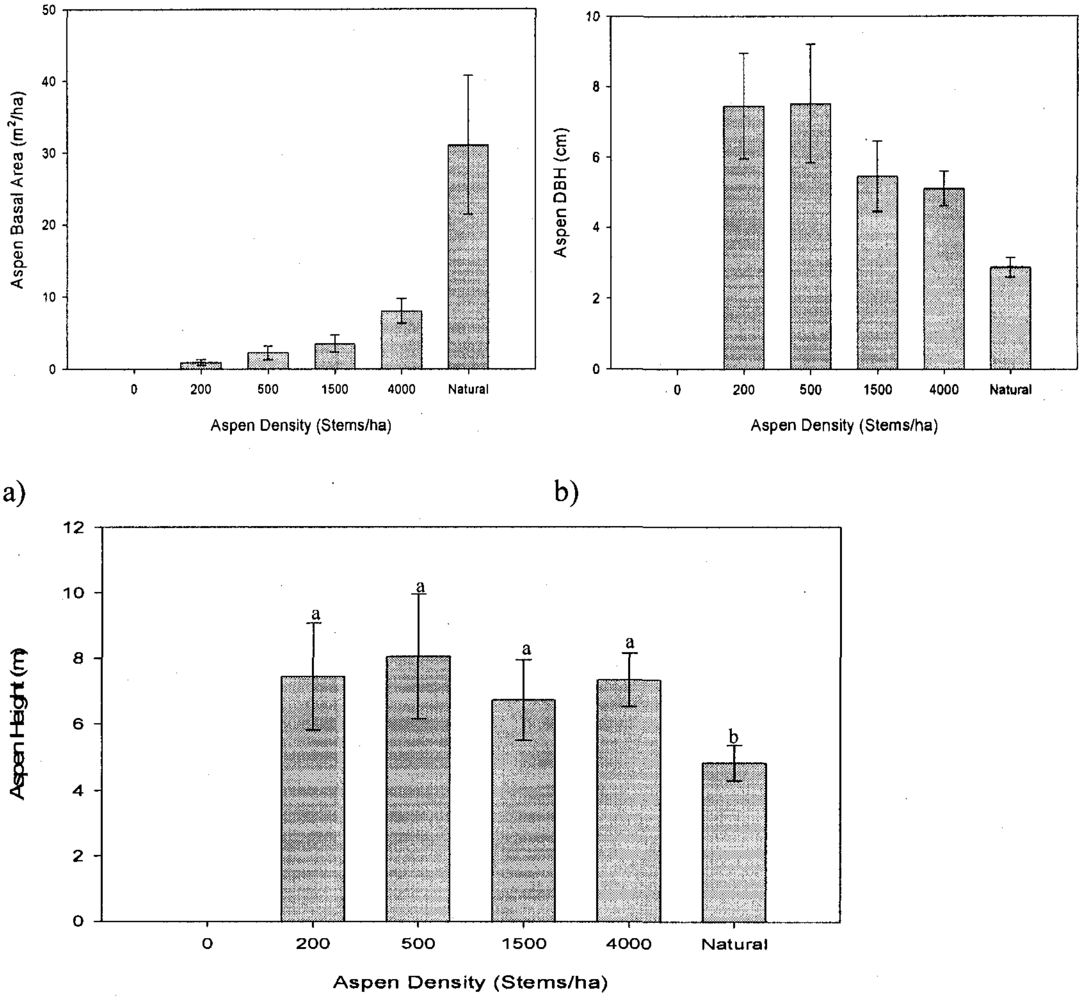
Forest Structure Changes with varying levels of PCT

Pre-commercial thinning had a pronounced effect on both the aspen and the white spruce (Figures 3.1 and 3.2). Aspen basal area ($p<0.0001$), diameter at breast height (DBH) ($p<0.0001$) and height ($p<0.0001$) were significantly different between aspen thinning treatments. Aspen basal area was the greatest in the natural sites (35.21m^2/ha), where it was also most variable among sites. Aspen DBH peaked in the lowest density sites (7.5cm) and decreased with increasing aspen basal area (2.9cm). Aspen average height was greatest in the 500 aspen stems/ha plots (8.06m) and lowest in the natural sites (4.8m).

The aspen thinning treatments did not have a significant effect on spruce root collar diameter (Friedman's test statistic=10.64, $p=0.06$) or spruce height (Friedman's test statistic=1.44, $p=0.92$) (Figure 3.2). Spruce root collar diameter (RCD) and height were greatest when the aspen treatment density was below 1500 trees/ha, which corresponds with the threshold for reducing overstory plant area. The interaction between aspen and spruce density treatments did not have a significant effect on any of the aspen or spruce size measures.

Spruce height ($p=0.21$) and RCD ($p=0.09$) were not significantly different between spruce density treatments (Figure 3.3). Spruce basal area was significantly different between spruce density treatments ($p=0.03$) and had a significant positive relationship with spruce height ($p<0.0001$). Spruce height, basal area and root collar diameter were not related to aspen height, basal area, diameter at breast height or trees per hectare ($p>0.05$).

Recall from Chapter 2 that indirect measures of overstory plant area index were significantly higher in higher density plots (Table 2.9) while total litter trap LAI was not significantly different between thinning treatments. The thinning treatment had a significant impact on aspen LAI with the greatest LAI in the natural density plots (Figure 2.10). A significant nonlinear relationship existed between LAI-2000 understory PAI estimates and aspen and spruce basal area (not shown; $p=0.0012$, adj. $r^2=0.24$).

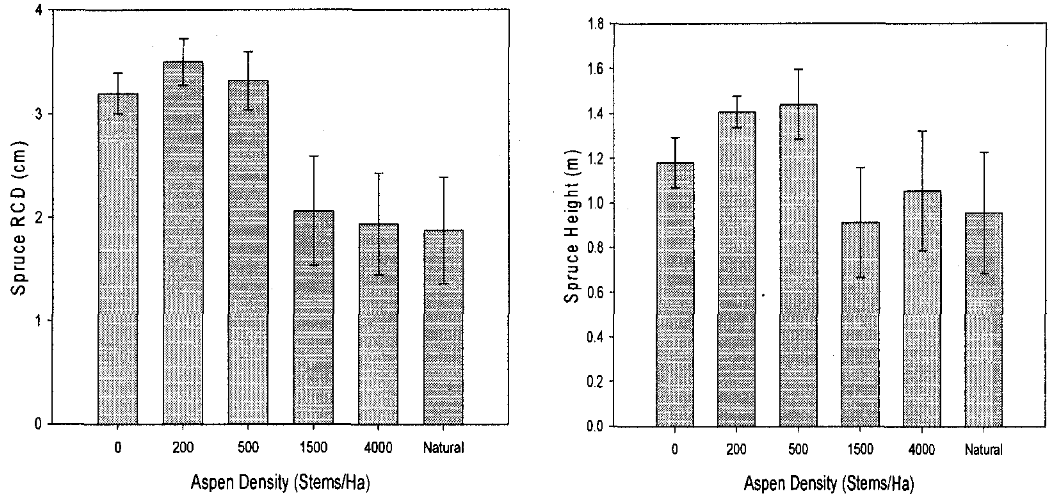


a)

b)

c)

Figure 3.1. Aspen treatment density had a significant effect on a) aspen basal area ($p<0.0001$) (using Friedman's test), b) aspen diameter at breast height (DBH: $p<0.0001$) (using Friedman's test), and c) aspen height ($p<0.0001$) (using mixed model ANOVA). Each bar represents the average for the aspen target density treatment. For the three lowest aspen densities (0, 200 and 500) there were two plots in each replicate (six in total) and the three highest aspen densities (1500, 4000 and natural) had three plots per replicate (nine in total). The error bars indicate the 95% confidence intervals. Different letters indicate a significant difference between treatments (Tukey's test).



a) b)

Figure 3.2. The effect of aspen target density on a) spruce root collar diameter (RCD: p=0.06) and b) spruce height (p=0.92) using Friedman's test. The interaction between aspen and spruce treatment density did not have a significant effect on spruce height or root collar diameter. The error bars indicate the 95% confidence intervals.

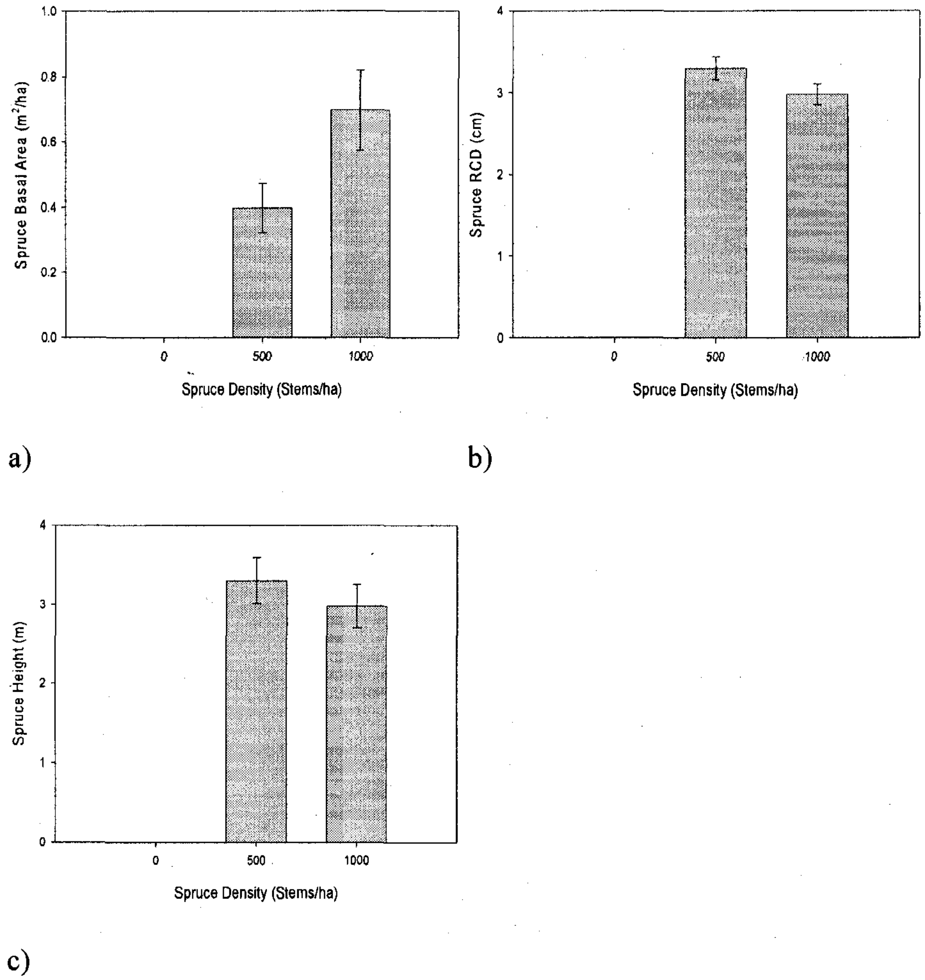


Figure 3.3.The effect of white spruce target density on a) white spruce basal area (p=0.03) (using Friedman's test), b) white spruce root collar diameter (RCD: p=0.09, AIC=67) (using mixed model ANOVA), and c) white spruce height (p=0.21, AIC=30) (using mixed model ANOVA). The error bars indicate the 95% confidence intervals.

Understory Cover

Pre-commercial thinning had a significant effect on cover of the understory (Figure 3.4) (Table 3.1). Based on the data from plots 4-6 and 10-15, aspen and spruce densities and their treatment interactions had a significant effect on cover; based on the data from plots 1-12 only the interaction term was significant. Understory cover was greatest in aspen-free plots (Figure 3.4). Grass cover was greatest in the 500 spruce trees/hectare treatment while bareground was greatest in the 0 spruce trees/hectare plots (Figure 3.5).

In addition to analyzing the impact of pre-commercial thinning on the understory community, I performed regression and correlation analysis in order to examine the relationship between the understory vegetation community and the overstory environmental variables, such as basal area and LAI. These overstory variables have been shown in the past to have a significant relationship with understory cover and diversity, and I am interested in determining how pre-commercial thinning may have affected these relationships (Thomas et al. 1999; Berger and Puettman 2000; Lemenih et al. 2004).

There was no significant relationship between aspen basal area and percent cover of mosses, shrubs or forbs ($p>0.05$) (Table 3.2). A weak non-linear relationship was found, however, between aspen basal area and total cover of all understory species ($p<0.0001$, adj. $r^2=0.17$), bareground ($p<0.0001$, adj. $r^2=0.05$) and graminoids ($p=0.03$, adj. $r^2=0.08$) (Figure 3.6). Percent cover of the understory varied substantially in the plots with low aspen density, with variation decreasing at higher aspen densities. Spruce basal area had a significant negative linear relationship with cover of bareground ($p=0.02$, $r^2=0.12$) and a positive relationship with graminoid percent cover ($p=0.001$, $r^2=0.22$) (Figure 3.7). However, these spruce basal area relationships are affected by the experimental design. The 0 spruce trees/ha plots have higher aspen densities, which may be playing a major role in the relationship.

Understory cover had significant relationships with measures of overstory and understory PAI. Total litter trap LAI had a significant non-linear relationship with graminoid cover ($p=0.01$, adj. $r^2=0.29$) but was not significantly related to other estimates of understory percent cover (Figure 3.8). Aspen, birch and willow litter trap LAI were not correlated with any estimates of understory percent cover.

Hemispherical photograph estimates of overstory PAI were linearly related to bareground ($p=0.002$, $r^2=0.23$) and graminoid cover ($p=0.001$, $r^2=0.23$) (Figure 3.9). Bareground cover increased with an increase in overstory PAI and graminoid percent cover decreased. LAI-2000 total PAI estimates had a significant positive linear relationship with bareground ($p=0.004$, $r^2=0.18$) and negative non-linear relationship with graminoid cover ($p=0.004$, adj. $r^2=0.21$) (Figure 3.9). LAI-2000 overstory PAI estimates had a significant non-linear relationship with bareground ($p<0.0001$, adj. $r^2=0.34$) and linear relationship with graminoid cover ($p=0.007$, $r^2=0.16$) (Figure 3.9). LAI-2000 understory estimates of PAI had a significant negative non-linear relationship with bareground ($p=0.02$, adj. $r^2=0.12$) and moss cover ($p=0.02$, adj. $r^2=0.11$), and a positive linear relationship with forb cover ($p=0.04$, $r^2=0.09$) (Table 3.3) (Fig. 3.9-3.10).

LAI-2000 estimates of understory PAI had a significant negative relationship with LAI-2000 estimates of overstory PAI ($p<0.0001$, $r^2=0.32$) (Figure 3.11) and no relationship with hemispherical estimates of overstory PAI ($p=0.51$, $r^2=0.01$).

Understory PAI was not altered by the aspen treatment densities ($p=0.29$).

Table 3.1. Results of mixed model ANOVAs examining the effect of aspen and spruce density on the cover, height, richness (S), evenness (E), Shannon's diversity index (H), Simpson's diversity index (D) and Whittaker's beta diversity (B) of the understory plant community (all species and for four vegetation categories). In order to examine the effect of the interaction between aspen and spruce, analysis was done on data from treatment combinations 1-12 (full range of aspen densities and a spruce density of 500 or 1000), and then on 4-6 and 10-15 (three highest aspen densities and all three spruce densities). To determine the effect of aspen or spruce density on the understory variables data from all 15 treatments were included in the analysis. Spruce density did not have a significant effect on any of the understory variables (not presented). Bolded p values were considered significant.

Response Variable		Effect of Aspen Density Treatment			Effect of Aspen and Spruce Density Treatments													
		Plots 1-15			Plots 1-12							Plots 4-6, 10-15						
						Aspen		Spruce		Aw+ Sw			Aspen		Spruce		Aw+Sw	
		df	AIC	p	AIC	df	p	df	p	df	p	AIC	df	p	df	p	df	P
Cover	Total	5	304.6	**0.03**	188.9	5	0.07	1	0.28	5	**0.02**	138.7	2	**0.02**	2	**0.01**	4	**0.02**
	Bareground	5	189.0	0.12	127.3	5	0.74	1	0.34	5	0.80	97.0	2	0.10	2	0.10	4	0.53
	Graminoid	5	330.4	0.31	215.4	5	0.61	1	0.64	5	0.92	160.9	2	0.99	2	0.27	4	0.82
	Forb	5	283.1	0.60	181.6	5	0.66	1	0.08	5	0.12	139.5	2	0.37	2	0.83	4	0.22
	Shrub	5	311.5	0.30	197.5	5	0.34	1	0.16	5	0.13	140.2	2	0.35	2	0.92	4	0.07
	Moss	5	207.5	0.76	138.3	5	0.72	1	0.99	5	0.59	95.5	2	0.71	2	0.59	4	0.42
Height	Graminoid	5	289.1	**0.01**	191.1	5	**0.01**	1	0.72	5	0.97	139.4	2	0.87	2	0.21	4	0.90
	Forb	5	279.9	0.80	181.0	5	0.56	1	0.12	5	0.86	140.8	2	0.56	2	0.15	4	0.60
	Shrub	5	317.7	0.50	206.4	5	0.69	1	0.8	5	0.85	155.4	2	0.57	2	0.79	4	0.71
	Willow (log)	5	-12.9	**0.02**	-3.3	5	0.06	1	0.51	5	0.06	-4.2	2	0.29	2	0.78	4	**0.03**
S	All species	5	242.3	0.12	156.7	5	0.16	1	0.55	5	0.60	110.0	2	0.08	2	0.85	4	0.29
	Graminoid	5	181.8	0.69	123.9	5	0.80	1	0.29	5	0.63	84.1	2	0.58	2	0.34	4	0.67
	Forb	5	187.5	0.13	122.1	5	0.08	1	0.83	5	0.24	90.1	2	**0.03**	2	0.66	4	0.11
	Shrub	5	180.0	0.20	122.5	5	0.40	1	0.47	5	0.75	91.4	2	0.38	2	0.75	4	0.63
	Tree	5	101.3	0.36	67.3	5	0.78	1	**0.04**	5	0.64	43.2	2	0.72	2	**0.01**	4	0.21
E	All species	5	-114.5	0.81	-60.1	5	0.80	1	0.63	5	0.48	-42.4	2	0.96	2	0.57	4	0.63
	Graminoid	5	-10.0	0.83	-3.9	5	0.33	1	0.73	5	0.15	0	2	0.38	2	0.12	4	0.27
	Forb	5	-182.2	0.69	-96.2	5	0.73	1	0.98	5	0.95	-74.9	2	0.45	2	0.76	4	0.96
	Shrub	5	-113.9	0.68	-65.9	5	0.88	1	0.96	5	0.60	-47.1	2	0.30	2	0.93	4	0.06
	Tree	5	43.9	0.28	24.3	5	0.67	1	**0.01**	5	0.83	24.3	2	0.32	2	**0.03**	4	0.43

H	All species	5	2.0	0.89	9.3	5	0.87	1	0.85	5	0.30	6.7	2	0.57	2	0.60	4	0.40
	Graminoid	5	44.5	0.88	32.5	5	0.68	1	0.97	5	0.12	21.5	2	0.32	2	0.19	4	0.33
	Forb	5	-51.3	0.19	-22.7	5	0.06	1	0.81	5	0.40	-12.0	2	0.09	2	0.73	4	0.23
	Shrub	5	-6.6	0.16	0.50	5	0.33	1	0.59	5	0.67	2.2	2	0.19	2	0.83	2	0.08
	Tree	5	40.5	0.20	27.8	5	0.65	1	**0.01**	5	0.80	17.7	2	0.41	2	**0.01**	4	0.58
D	All species	5	-150.9	0.85	-81.2	5	0.88	1	0.65	5	0.51	-64.6	2	0.77	2	0.44	4	0.79
	Graminoid	5	-15.7	0.79	-8.3	5	0.32	1	0.82	5	0.09	21.5	2	0.32	2	0.19	4	0.33
	Forb	5	-228.5	0.33	-129.0	5	0.25	1	0.81	5	0.68	-93.1	2	0.16	2	0.68	4	0.55
	Shrub	5	-127.1	0.23	-73.7	5	0.37	1	0.68	5	0.60	60.1	2	0.19	2	0.69	4	0.05
	Tree	5	6.2	0.20	4.2	5	0.61	1	**0.01**	5	0.83	3.0	2	0.39	2	**0.01**	4	0.67
B	All species	5	14.0	0.07	16.0	5	0.11	1	0.54	5	0.59	10.4	2	0.08	2	**0.90**	4	0.31

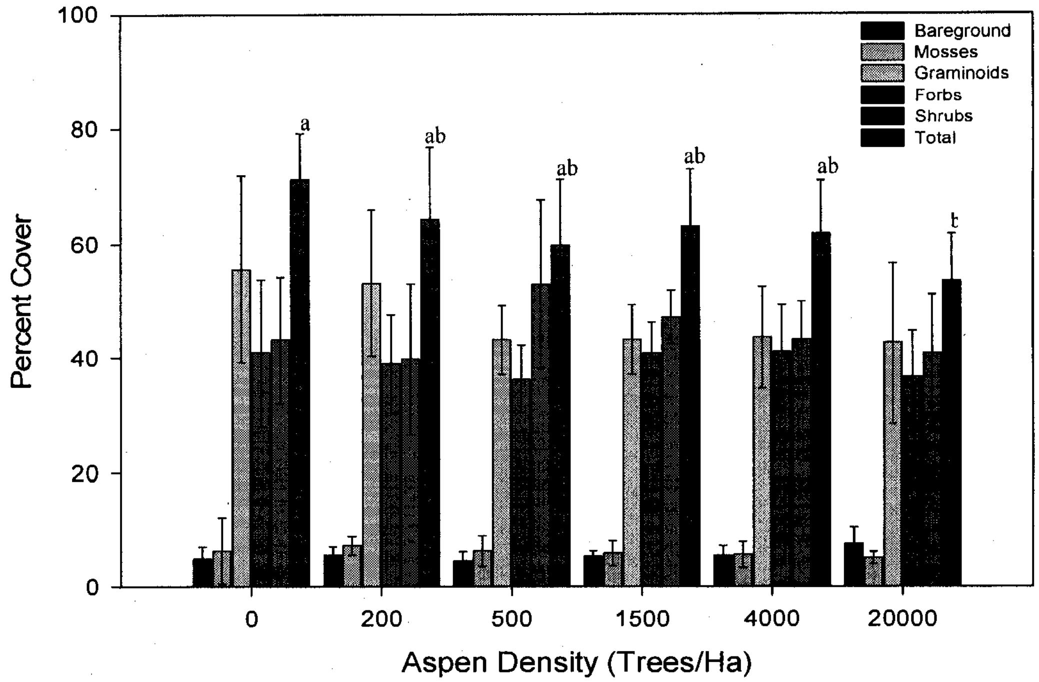


Figure 3.4. Percent cover of bareground, mosses, graminoids, forbs, shrubs and total understory species for each aspen thinning treatment. The error bars indicate the 95% confidence intervals. Different letters indicate a significant difference between treatments (Tukey's test, see also Table 3.1).

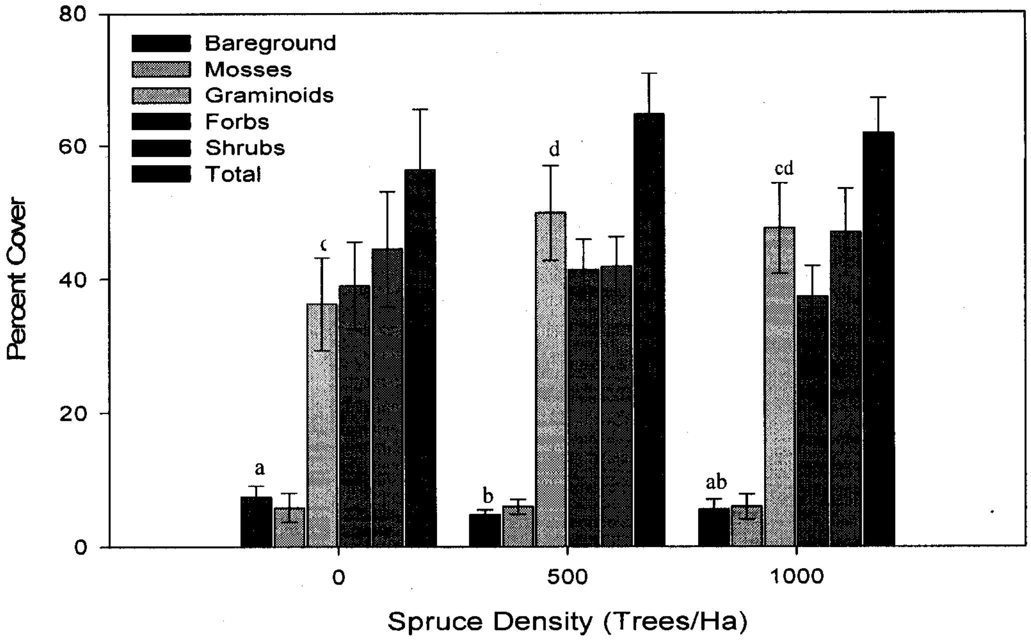


Figure 3.5. Percent cover of bareground, mosses, graminoids, forbs, shrubs and all understory species for each spruce thinning treatment. Error bars indicate 95% confidence intervals and different letters indicate a significant difference between treatments (Tukey's test, see also Table 3.1).

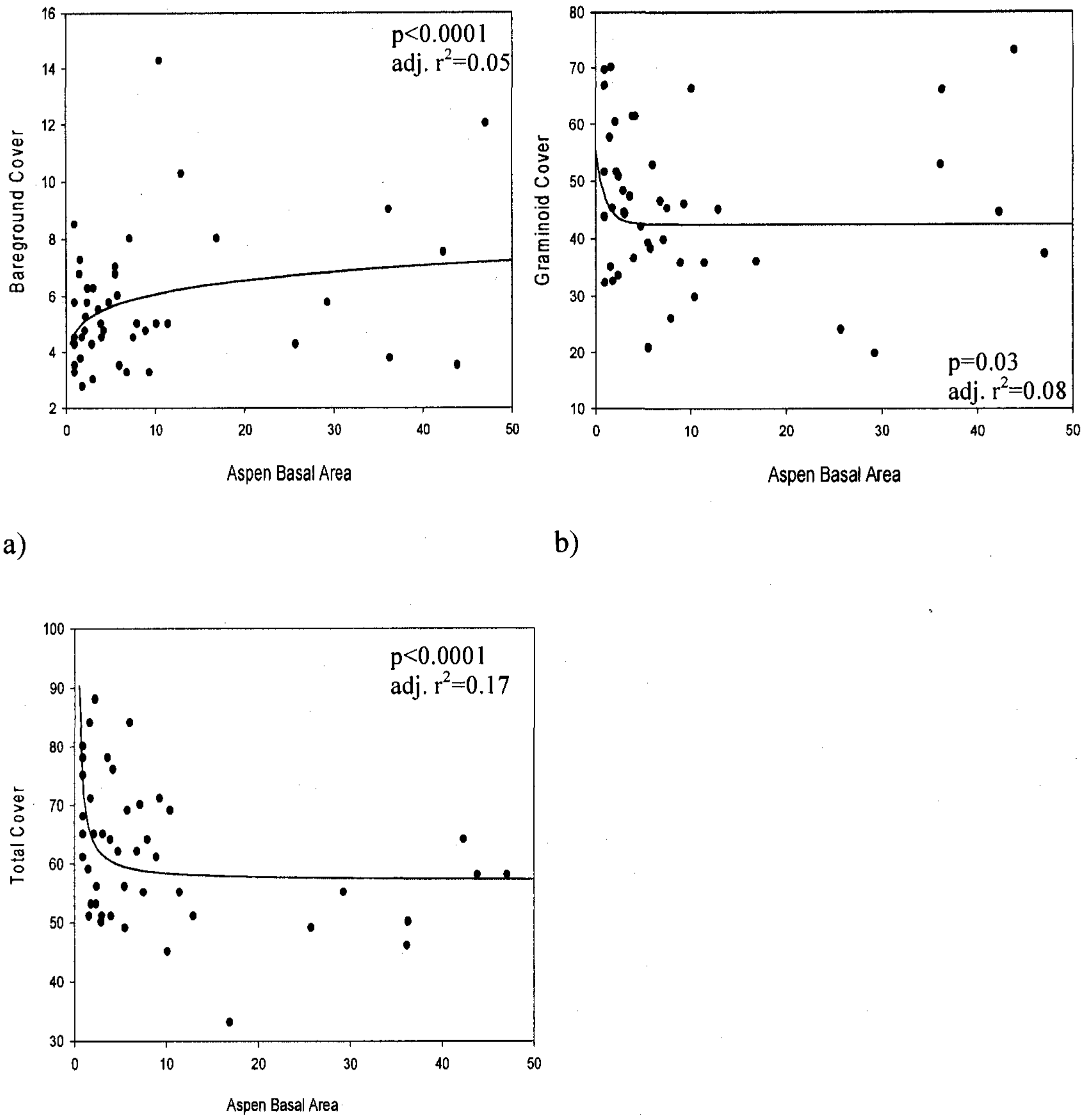
Table 3.2. Results from linear and non-linear regressions of a) aspen and b) white spruce basal area versus understory percent cover. See also Figures 3.7 and 3.8.

a)

Y	X	P	Adj. r^2	Equation
Bareground	Aspen Basal Area +1 (m^2)	<0.0001	0.05	$Y=4.71x^{0.11}$
Graminoid		0.03	0.08	$Y=43.21+34.89e^{-x}$
Forbs		0.14	0.05	$Y=40.79-0.16x$
Moss		0.27	0.03	$Y=6.66-0.05x$
Shrubs		0.28	0.03	$Y=45.76-0.15x$
Total		<0.0001	0.17	$Y=69.32x^{-0.073}$

b)

Y	X	P	Adj. r^2	Equation
Bareground	Spruce Basal Area +1 (m^2)	0.02	0.12	$Y=6.82-2.59x$
Graminoid		0.001	0.21	$Y=67.23-31.19e^{-x}$
Forbs		0.38	0.02	$Y=40.89-3.83x$
Moss		0.76	0.002	$Y=5.78+0.44x$
Shrubs		0.47	0.01	$Y=42.60+5.34x$
Total		0.23	0.03	$Y=58.76+6.78x$

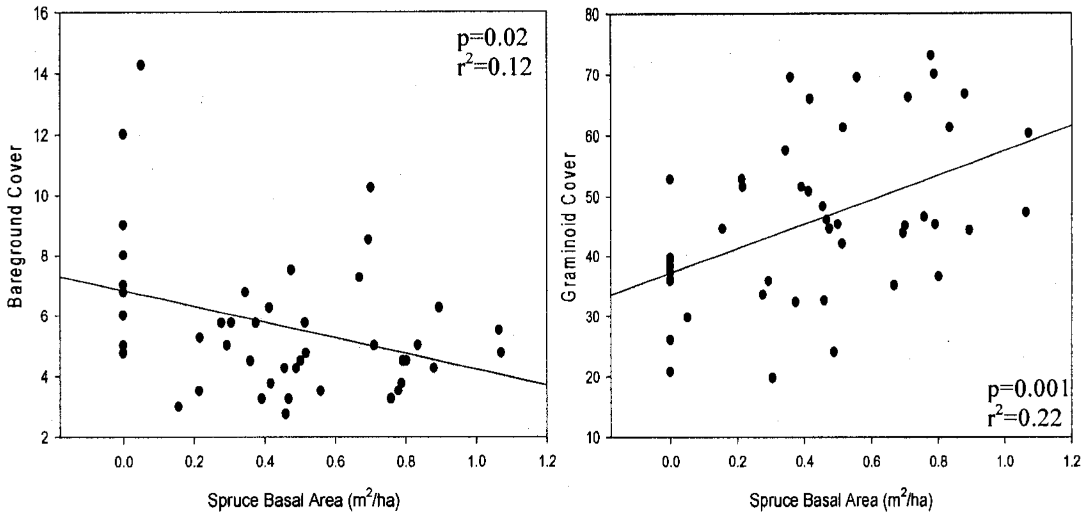


a)

b)

c)

Figure 3.6. The non-linear regression relationship between aspen basal area and: a) bareground cover; b) graminoid cover; and c) total understory percent cover. The solid line is the regression described in Table 3.2.



a)

b)

Figure 3.7. The linear regression relationship between spruce basal area and percent cover of a) bareground, and b) graminoids. The solid line is the regression described in Table 3.2

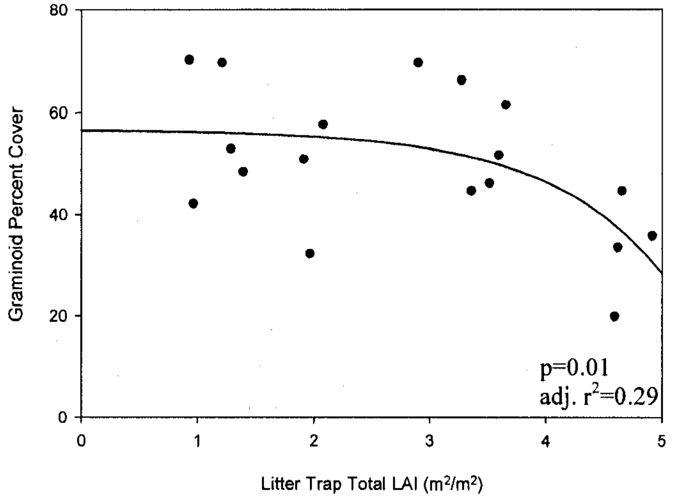


Figure 3.8. The non-linear regression relationship between total litter trap LAI and graminoid percent cover ($y=56.75-0.19e^x$).

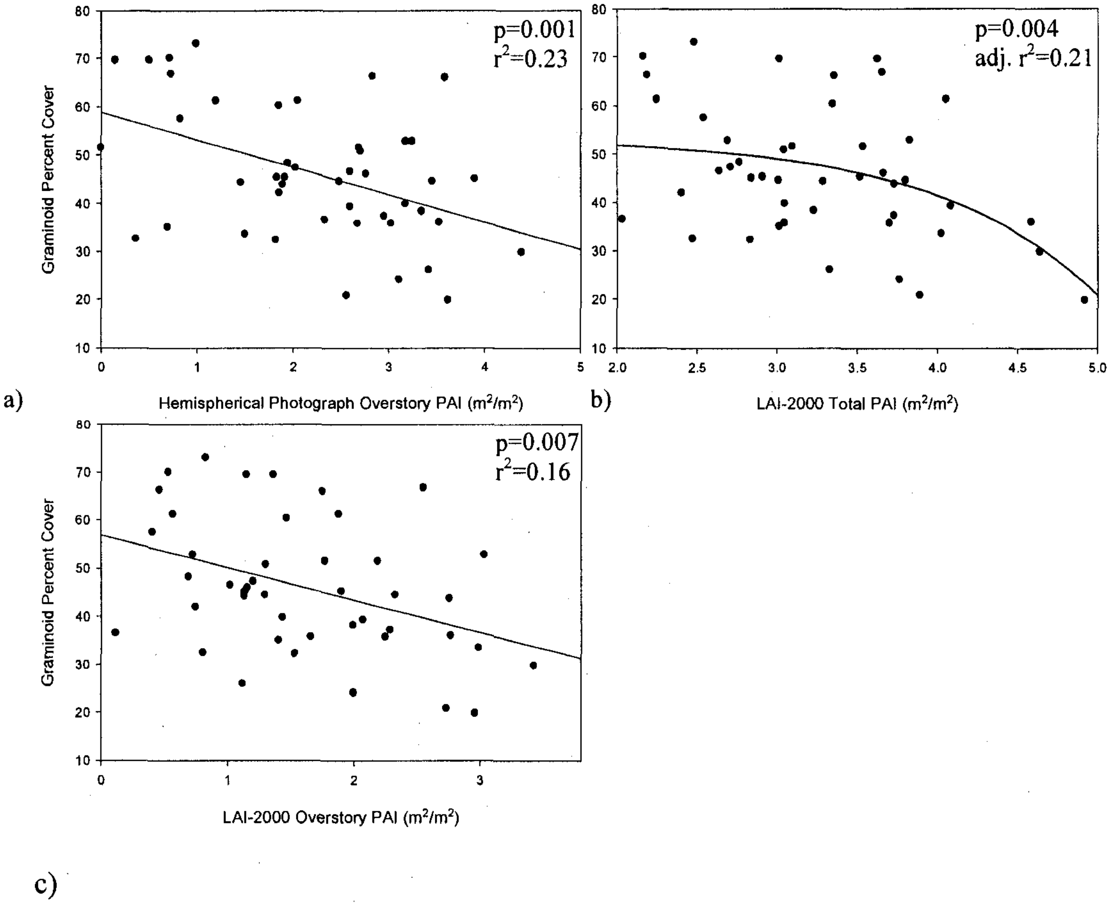
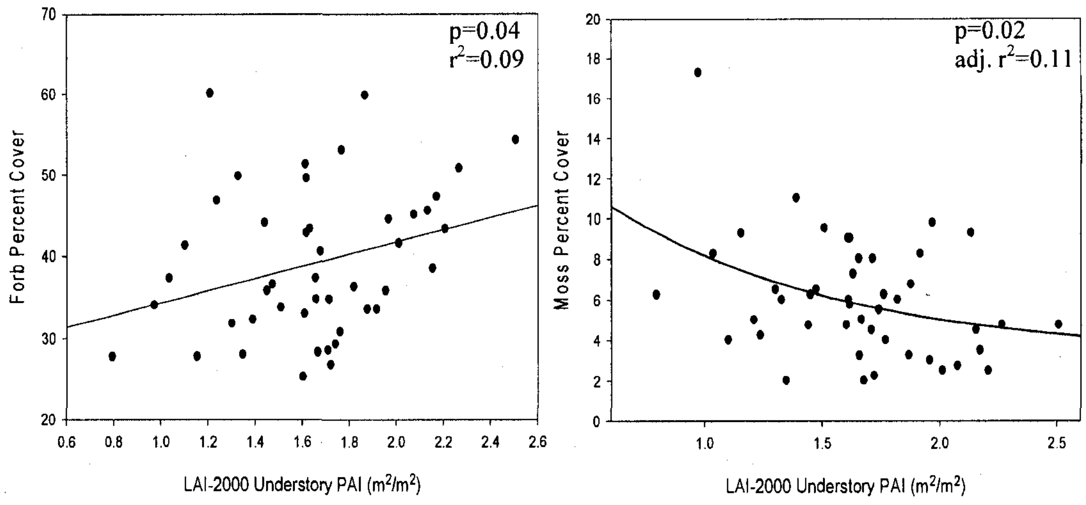


Figure 3.9. Linear and non-linear regression relationship of graminoid percent cover to PAI measured by a) overstory hemispherical photographs (y=58.85-5.71x), b) total LAI-2000 ($y=3.00-0.006e^x$) and c) overstory LAI-2000 (y=56.89-5.71x).



a) b)

Figure 3.10. Estimates of a) forb percent cover ($y=26.94+7.42x$) and b) moss percent cover ($y=3.22+13.45e^{-x}$) as a function of understory PAI measured by the LAI-2000 using a linear and non-linear relationship.

Table 3.3. Results from linear regressions of understory percent cover (all species and by category) on LAI-2000 estimates of PAI. See also Figures 3.9-3.11.

Y	X								
Percent Cover	LAI-2000 Overall PAI			LAI-2000 Overstory PAI			LAI-2000 Understory PAI		
	p	r^2	Equation	p	r^2	Equation	p	r^2	Equation
Bare ground	0.004	0.18	Y=0.93+1.46 x	0.004	0.25	Y=0.61+0.17x	0.02	0.12	Y=9.39-2.24x
Moss	0.43	0.01		0.98	0		0.12	0.05	
Gram inoid	0.007	0.16	Y=72.3-8.06x	0.007	0.16	Y=2.69-0.02x	0.31	0.02	
Forbs	0.43	0.01		0.81	0.001		0.04	0.09	Y=26.94+7.42x
Shrub	0.69	0.004		0.67	0.004		0.84	0.00 1	
Total	0.44	0.01		0.59	0.007		0.80	0.00 2	

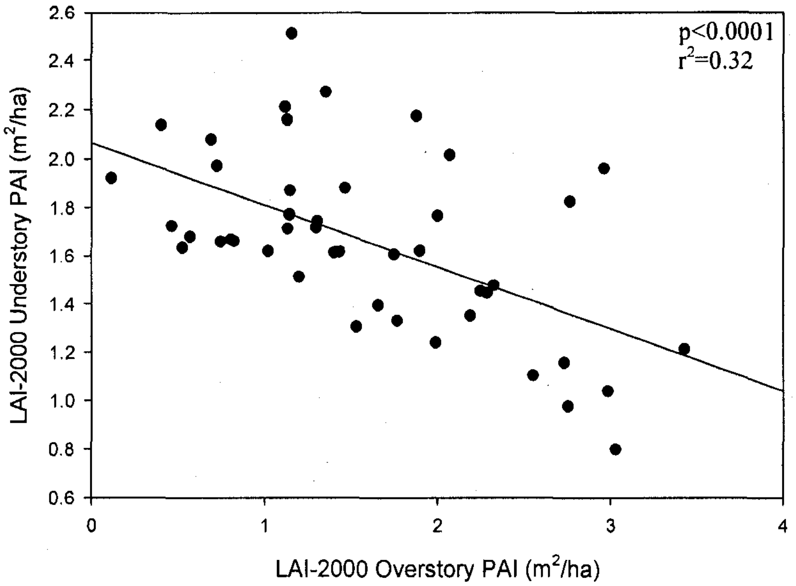
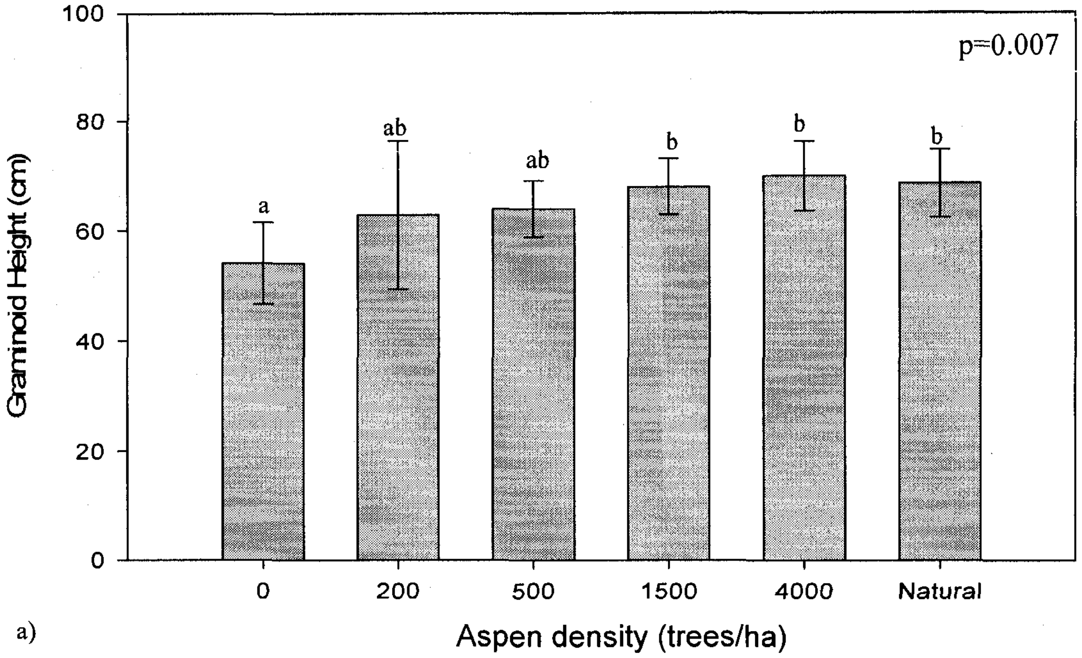


Figure 3.11. The relationship between LAI-2000 estimates of understory and overstory PAI. The linear regression equation is Y=2.05-0.26x (n=45).

Understory Height

Aspen thinning treatment density had a significant effect on the height of the graminoid and willow layers (Figure 3.12). Graminoid height generally increased with increasing aspen density and was significantly greater in the three highest aspen density treatments than in the aspen free sites (average height of 68.6cm in the natural aspen density plots versus 54.0cm in the aspen free plots). Willow height was also significantly greater in the two highest densities (4000 trees/ha and natural density) compared to the aspen free sites (average height of 300.4cm in the natural aspen density plots versus 151.2cm in the aspen free plots). Spruce density treatment and the interaction between spruce and aspen density did not have a significant impact on understory height (Table 3.1).

There was a significant positive correlation between aspen basal area and graminoid (p=0.0005, rho=0.50) and willow height (p=0.007, rho=0.40). (Figure 3.13) A significant positive linear relationship was also found between hemispherical photograph overstory PAI estimates and shrub ($p=0.007$ $r^2=0.16$), and graminoid height ($p=0.0004$, $r^2=0.26$) (Figure 3.14). Understory cover was not significantly related to LAI-2000 estimates of PAI or to spruce basal area.



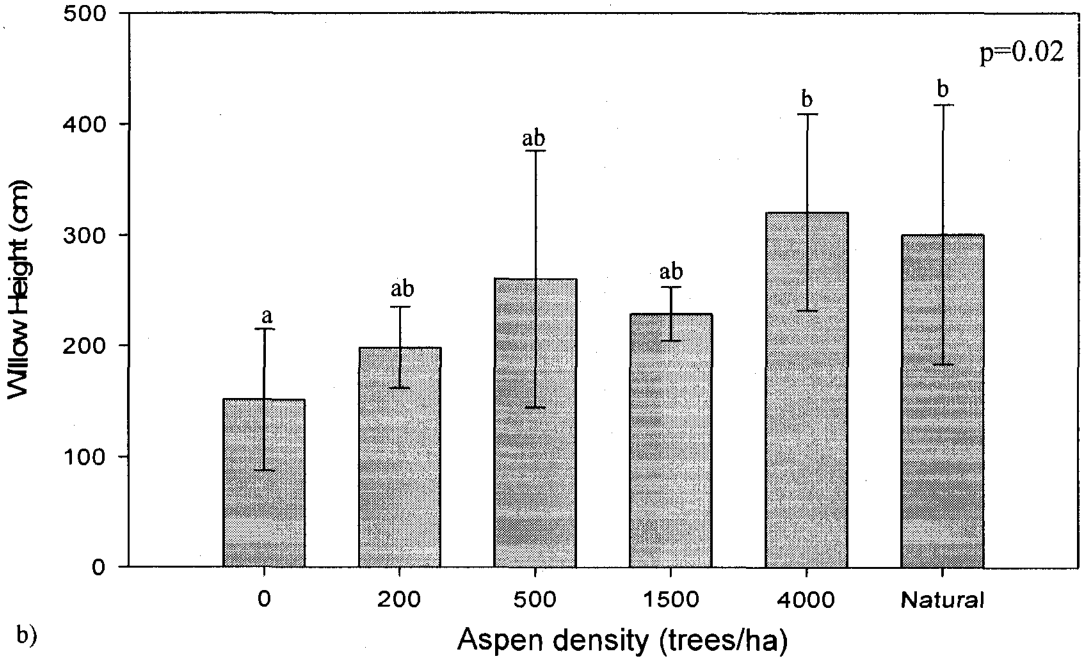
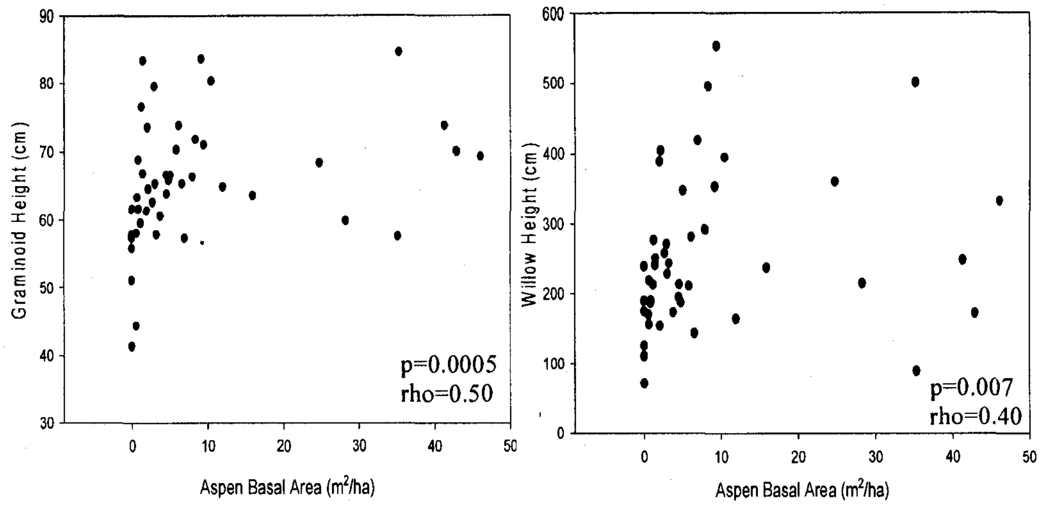
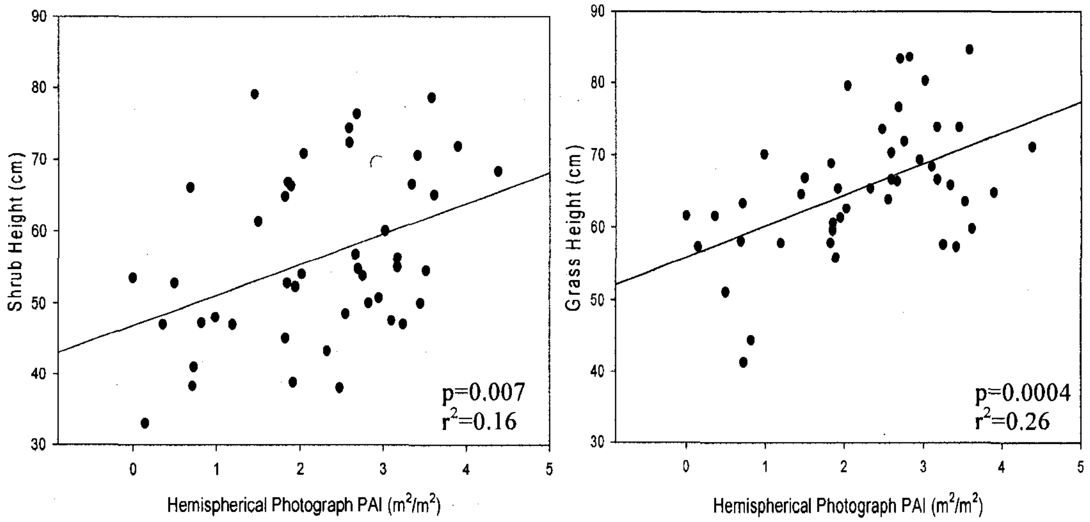


Figure 3.12. Mean values for a) graminoid height and b) willow height for each of the aspen thinning density treatments. The error bars indicate the 95% confidence intervals. Different letters indicate a significant difference between treatments (mixed model ANOVA followed by Tukey's test, see also Table 3.1).



a) b)

Figure 3.13. Scattergram of aspen basal area with a) graminoid height and b) willow height. In both cases, Spearman's rank correlation was significant and the relationship appears to be non-linear.



a) b)

Figure 3.14. The positive linear regression relationship between hemispherical photograph overstory PAI estimates and a) shrub (y=46.85+4.24x) and b) graminoid height (y=55.88+4.28x).

Understory Diversity

A total of 99 vascular plant species were found in the plots, including 20 graminoid, 50 forb, 26 shrub and 3 tree species (refer to Appendix A). Aspen treatment density did not have a significant effect on total species richness (S) (Figure 3.15), evenness (E), Shannon (H) or Simpson's (D) diversity index, or Beta diversity (Figure 3.16) (Table 3.2). The natural aspen plots had the lowest mean number of species per plot and the 200 stems/ha treatment had the highest. Broken down by category, aspen thinning treatment density had no effect on S, E, H or D for shrub, forb, graminoid or tree species (Fig. 3.17). Species richness was generally greatest in the 200 stems/ha plots (45 species/plot) and consistently lowest in the natural sites (40 species/plot).

Species richness, Shannon's index and Simpson's index were not significantly related to any of the measure of overall, understory or overstory PAI (Table 3.4). Species evenness had a significant positive relationship with LAI-2000 estimates of overall PAI (p=0.03) but the linear regression did not explain a large portion of the variation (r^2=0.10) (Fig. 3.18). None of the measures of understory diversity were related to aspen basal area (Table 3.5). Species richness, Shannon index and Simpson's index calculated for herbs, shrubs and grasses separately were also unrelated to aspen basal area and to estimates of overall, understory and overstory PAI. Forb species evenness was significantly related to overstory PAI as measured using LAI-2000 but the relationship was weak (p=0.03, r^2=0.10) (Fig. 3.19).

Indicator species analysis showed that two species (*Pyrola asarifolia* Michx. (p=0.005) and *Mitella nuda* L. (p=0.025) were significant indicators of thinning treatments. *Mitella* was a significant indicator for the 4000 stems/ha plot (IV=37.2) and *Pyrola* was a significant indicator for aspen-free plots (IV=30.0).

There were five introduced species found in the plots: *Taraxacum officinale* Weber, *Trifolium hybridum* L., *Trifolium repens* L., *Trifolium pretense* L., and *Phleum pratense* L.(refer to Appendix A). Analysis of the cover of introduced species indicated that aspen treatment density had a significant effect on the cover of *Taraxacum officinale* Weber (dandelion) using Friedman's test ($p<0.01$) (Fig. 3.20). However, *Taraxacum* cover was highest in the natural aspen density, 4000 stems/ha, and aspen free plots and lowest in the 500 stems/ha plot. Covers of the three clover species and *Phleum pratense* L. were not significantly affected by aspen treatment density ($p>0.05$).

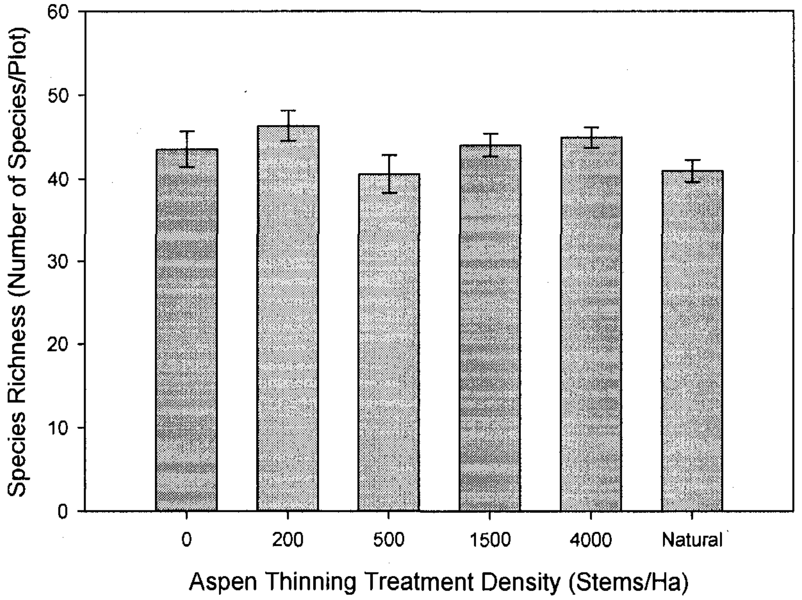


Figure 3.15. Richness (# of species) per plot for each aspen thinning treatment. Aspen density did not have a significant effect on species richness (mixed model ANOVA, see Table 3.1). Each bar represents the mean (95% confidence intervals) of all plots in the three blocks.

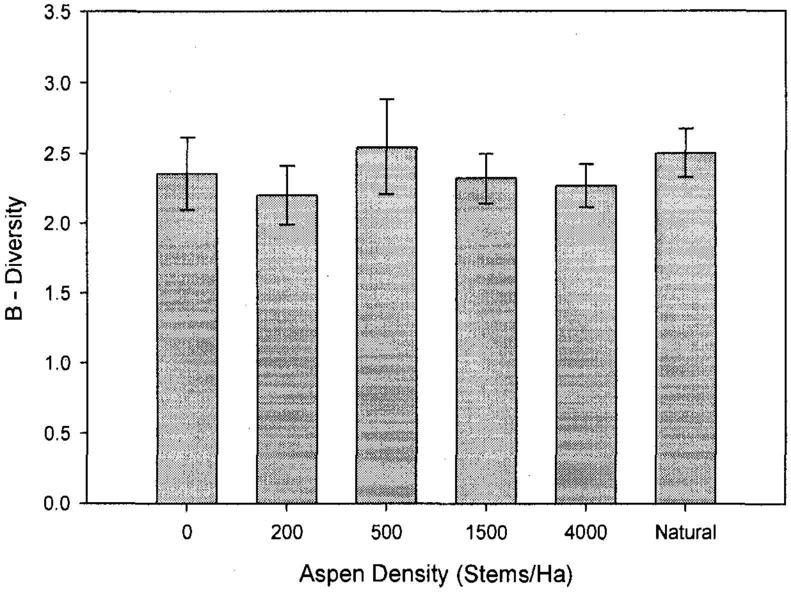
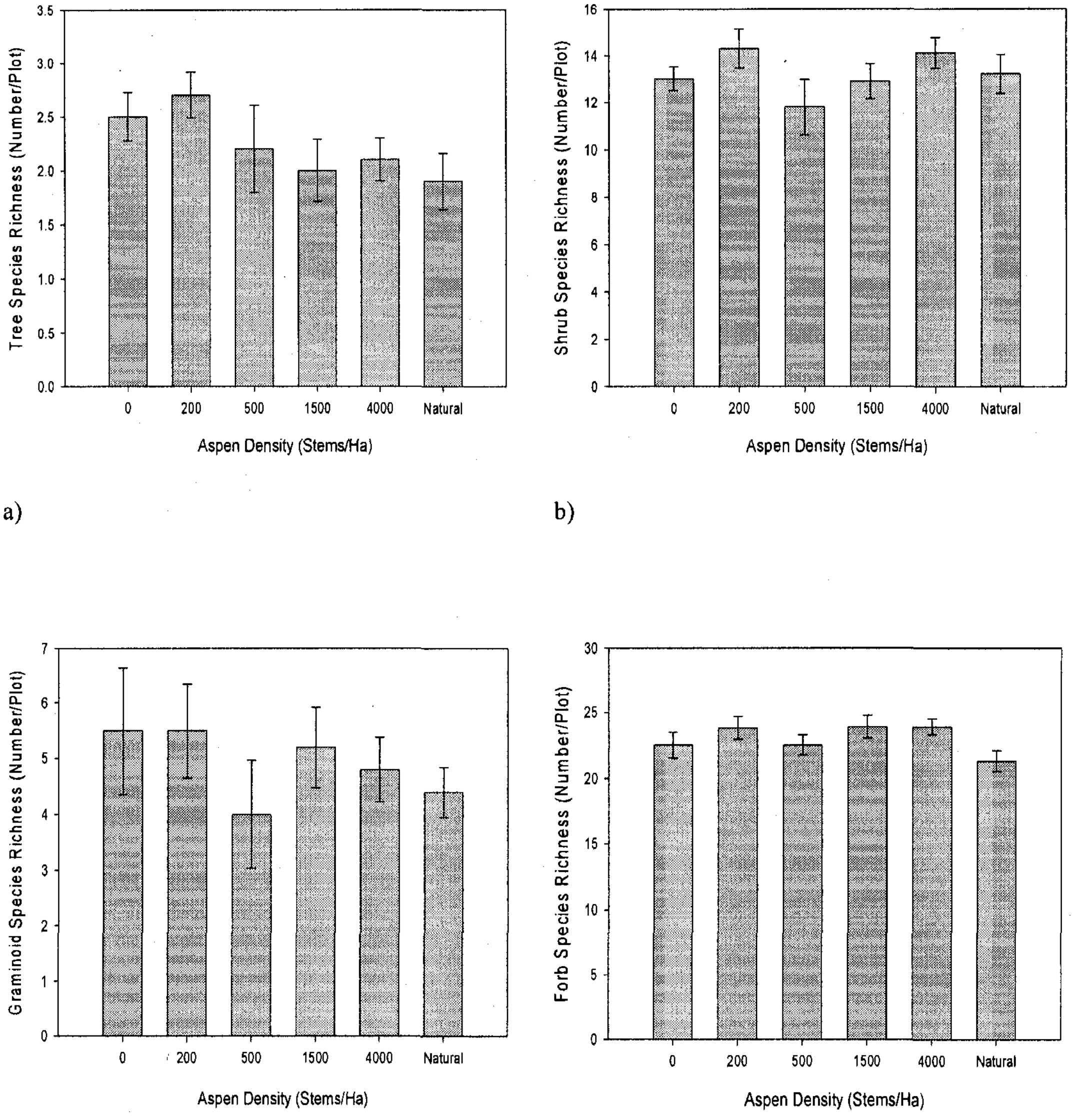


Figure 3.16. Whittaker's beta diversity for each aspen thinning treatment. Aspen density did not have a significant effect on beta diversity (mixed model ANOVA, see Table 3.1). Each bar represents the mean (95% confidence interval) of all plots in the three blocks.



a) b)

c) d)

Figure 3.17. Measures of species richness (number of species per plot) for a) trees, b) shrubs, c) grasses, d) forbs for each aspen thinning treatment. The thinning treatment did not have a significant effect on species richness (mixed model ANOVA, see table 3.1). Each bar represents the mean (95% confidence interval) of all plots.

Table 3.4. Results from linear regressions of measures of PAI using a) hemispherical photographs, b) LAI-2000 overall PAI, c) LAI-2000 overstory and d) LAI-2000 understory, versus measures of understory diversity (species richness (S), evenness (E), Shannon's diversity index (H) and Simpson's diversity index (D)).

a)

Y	X	p	r^2	Equation
S	Hemispherical Photograph Overstory PAI (m^2/m$^{2)}$	0.64	0.005	Y=44.00-0.30x
E		037	0.02	Y=0.84+0.0060x
H		0.50	0.01	Y=3.16+0.019x
D		0.29	0.03	Y=0.92+0.0042x

b)

Y	X	p	r^2	Equation
S	LAI-2000 Overall PAI (m^2/m^2)	0.53	0.009	Y=45.49-0.66x
E		**0.03**	**0.10**	**Y=0.78+0.02x**
H		0.11	0.06	Y=2.97+0.07x
D		0.06	0.08	Y=0.89+0.012x

c)

Y	X	p	r^2	Equation
S	LAI-2000 Overstory PAI (m^2/m^2)	0.81	0.0014	Y=43.67-0.21x
E		0.08	0.07	Y=0.83+0.015x
H		0.14	0.05	Y=3.12+0.054x
D		0.07	0.07	Y=0.91+0.0096x

Table 3.4 (continued)

d)

Y	X	p	r^2	Equation
S	LAI-2000 Understory LAI (m^2/m^2)	0.52	0.0095	Y=45.36-1.22x
E		0.95	0.0001	Y=0.85+0.0012x
H		0.78	0.002	Y=3.24-0.023x
D		0.60	0.006	Y=0.94-0.0063x

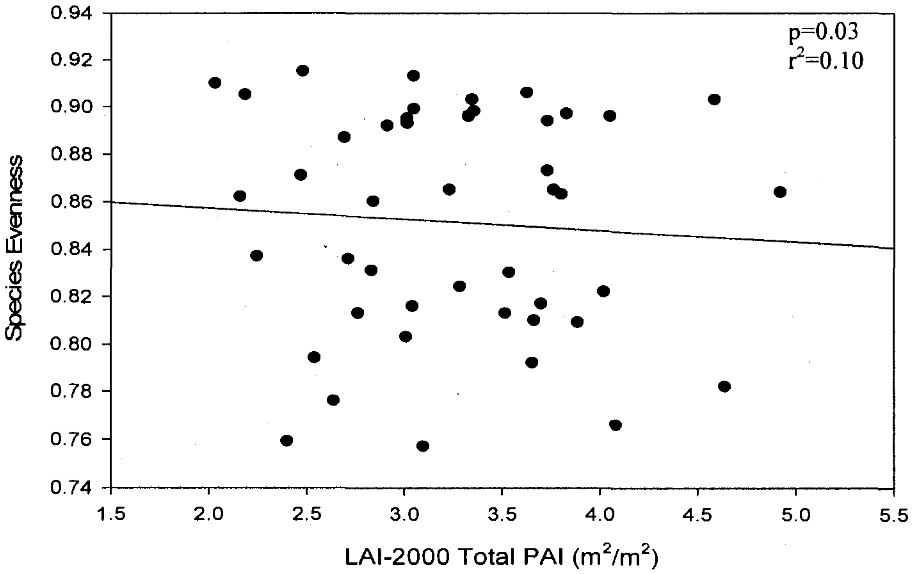


Figure 3.18. The linear regression relationship between LAI-2000 total PAI and total species evenness. The solid line is the regression described in Table 3.3.

Table 3.5. Results from linear regressions of aspen basal area versus measures of understory diversity (species richness (S), evenness (E), Shannon's diversity index (H), Simpson's diversity index (D)).

Y	X	p	r^2	Equation
S	Aspen Basal Area (m^2/ha)	0.26	0.03	Y=43.95-0.062x
E		0.28	0.03	Y=0.86-0.00061x
H		0.16	0.05	Y=3.24-0.0033x
D		0.23	0.03	Y=0.93-0.00041x

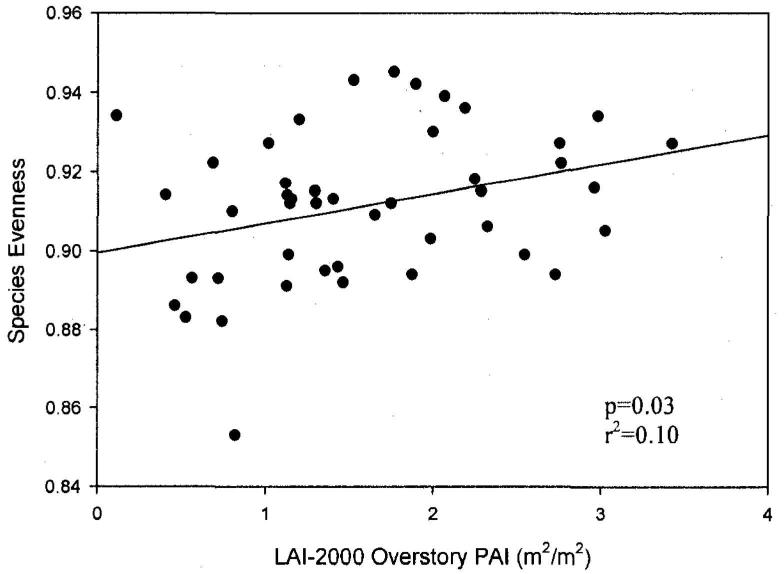


Figure 3.19. The linear regression relationship between LAI-2000 overstory PAI and forb species evenness. The solid line is the regression y=0.90+0.0074x.

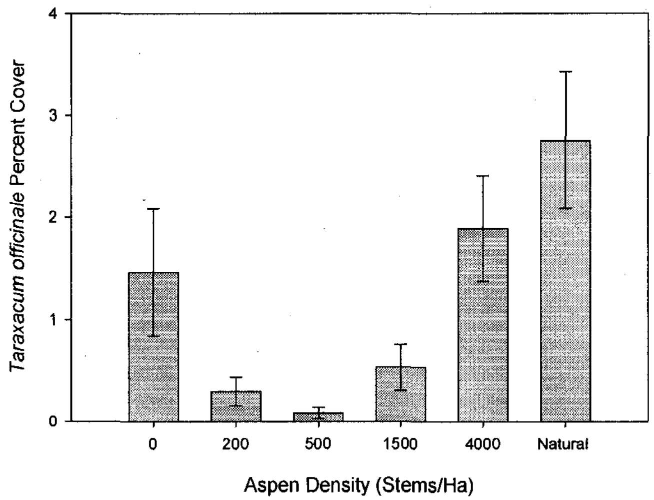
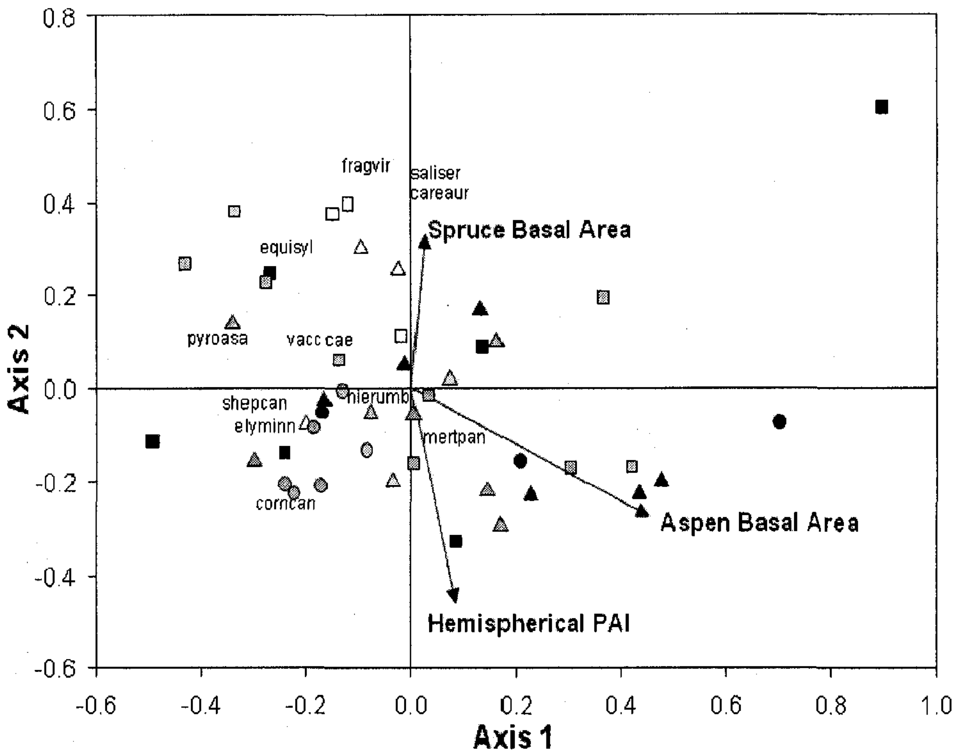


Figure 3.20. Measure of percent cover for *Taraxacum officinale* Weber versus aspen thinning treatment density. Aspen density had a significant effect on *T. officinale* cover using Friedman's test. Each bar represents the mean (95% confidence intervals) of all plots for a given thinning treatment.

Aspen and spruce basal areas were found to have a significant relationship with understory composition using RDA ($p<0.05$) (Figure 3.21). The first ordination axis of the RDA was insignificant ($p=0.13$), but all three ordination axes together were significant ($p=0.0004$) and species environment correlations were strong (axis 1=0.64, axis 2=0.81) (Table 3.6). However, only some of the variation in understory species was explained by the ordination (24.7%). Hemispherical photograph overstory PAI, spruce height, aspen basal area and spruce basal area were significant environmental vectors ($p<0.05$).

High values of aspen basal area were associated with the higher density aspen treatments and high values of spruce basal area were associated with greater spruce density plots. A decrease in aspen basal area was associated with higher cover of *Pyrola asarifolia* Michx, *Equisetum sylvaticum* L., *Vaccinium caespitosum* Michx. and *Frageria virginiana* (Duchesne). Plots with greater spruce basal area were associated with higher cover of *Fragaria virginiana* (Duchesne), *Salix serissima* (Bailey) Fern and *Carex aurea* Nutt..



Aw Density / Sw Density	Natural	4000	1500	500	200	0
1000	■	▩	▨	▧	■	□
500	▲	▲	△	△	▲	△
0	●	◉	◍			

Fig 3.21. Results of redundancy analysis (RDA) showing the relationship of understory species composition to environmental variables. Each point represents one plot. Arrows indicate vectors for significant environmental variables at 3 times their value (Hemispherical PAI: hemispherical photograph overstory PAI). Species with greater than 50% inter-set correlation with axes are included at 1/3 values. Species are identified by seven letter codes: the first four letters of the genus followed by the first three letters of the species (refer to Appendix A).

Table 3.6. Summary of results for constrained ordinations (RDA) of understory species composition. Presented are: eigenvalues (representing the percent variance of Sørenson species matrix explained) for the first three canonical axes along with the trace (sum of all canonical eigenvalues; **, significant with P<0.005); species-environment correlations for the first three axes; cumulative percentage variance of species data, and species-environment relation; and correlation coefficients for each significant environmental variable with the first three axes (bolded environmental correlation coefficients correspond with the placement of the environmental variables in the RDA).

	Axis 1	Axis 2	Axis 3	Trace
Eigenvalue	0.033	0.030	0.023	0.19**
Species-Environment Correlation	0.642	0.814	0.741	
Cumulative percentage variance of species data	4.2	8.0	10.8	
Cumulative percentage variance of species-environment relation	10.3	15.9	21.1	
Environmental Variable Correlation Coefficient				
Aspen Basal Area	**0.49**	-0.22	0.11	
Spruce Basal Area	0.19	**-0.47**	-0.10	
Hemispherical Photograph Overstory PAI	0.03	**0.30**	-0.60	

3.4 Discussion

This study indicates that pre-commercial thinning has a small but significant effect on the structure and composition of the overstory and understory plant communities in boreal mixedwood forest stands. Thinning had significant effects on the size of overstory aspen and spruce as well as on the understory cover, height and composition. The change in overstory density had a direct impact on overstory and understory leaf area which was significantly related to understory cover, height and diversity.

Pre-commercial thinning is applied in boreal mixedwood stands to reduce competition so that the understory conifer and remaining broadleaf trees accelerate their growth. Studies have shown variable effects of pre-commercial thinning on stem diameter, crown size, survival, and merchantable volume of the remaining trees (Brissette et al. 1999; Lindgren and Sullivan 2001; Penner et al. 2001; Rice et al. 2001; Sullivan et al. 2001; Sullivan et al 2002; Bokalo et al. 2007). Rice et al. (2001) found that pre-commercial thinning increased individual tree growth of aspen fifteen to seventeen years post treatment but did not increase the gross merchantable volume. In contrast, Penner et al. (2001) found that pre-commercial thinning did not have long term effects on the height, basal area or DBH because the aspen had outgrown the competitors prior to the thinning application.

Ten years after the initial thinning and five years following the final thinning, our results indicate that treatment had an expected negative effect on aspen basal area. Selective thinning of the aspen resulted in a significant increase in aspen stem diameter and height compared with the trees in the natural sites.

Several studies have shown that pre-commercial thinning treatments accelerate the growth of white spruce by increasing the light levels to the understory (Biring et al. 1999; Pitt et al. 2004). There appeared to be a strong but insignificant positive effect of pre-commercial thinning on spruce root collar diameter, but no effect was seen on spruce height. Conifer height growth is relatively insensitive to competition except in extreme competition stress because the priority for allocation of photosynthate is to height growth, presumably so the trees can outcompete neighboring plants (Larcher 1995; Jobidon 2000; Wagner 2000; Bokalo 2007). Spruce density also had no effect on spruce height or root color diameter, but there was the expected change in spruce basal area.

Understory Cover

Effect of Pre-commercial Thinning

Many pre-commercial thinning studies have found a significant increase in understory vegetation cover with thinning (Thomas et al. 1999; Lindgren et a. 2006). However, Alaback and Herman (1988) and Sullivan et al. (2002) found that thinning increased the variability in cover rendering the treatment effect insignificant. In the Grande Prairie WESBOGY LTS, pre-commercial thinning had a significant impact on understory cover, with the highest cover values in the most intense thinning treatment. This positive response has been well documented and is attributed to the increase in light, water and nutrients available to the understory resulting from the reduced canopy (Thomas et al. 1999; Lindgren et al. 2006).

Relationship with Overstory Variables

The positive relationship between canopy openness and understory cover has been strong in several studies (Malcolm 1994; Klinka et al. 1996; Stone and Wolfe 1996; McKenzie et al. 2000). However, Thomas et al. (1999) found the relationship between light levels and understory vegetation cover to be weak. I found a significant negative relationship between LAI-2000 overstory PAI and understory PAI, but a significant relationship was not found between total understory percent cover and measures of overstory leaf area. There are several possibilities for this disconnect. One reason could be a time lag in the response of the understory vegetation to the redevelopment of the overstory canopy after thinning. Thomas et al. (1999) suggested that over time since thinning, the relationship becomes more complex as other resources become limiting. In the boreal, the leaf area of the overstory drops in the spring and fall allowing for exposure of the understory to periods of high understory light. Messier et al. (1998) found that aspen canopies in the drier western provinces are smaller and have greater light penetration, perhaps indicating competition for light is not as strong.

Graminoid cover had a significant negative relationship with both aspen basal, and overstory measures of plant area index, and a positive relationship with spruce basal area. Forb, moss and shrub cover had no such relationship. Graminoid species such as *Calamagrostis canadensis* are shade intolerant pioneer species that establish readily by rhizome growth in disturbed sites and may be more able to quickly respond to changes in the overstory (Lieffers et al 1993; Naumber and DeWald 1999; Peltzer et al. 2000).

Understory Height

Effect of Pre-commercial thinning

Simard and Hamman (2000) found that thinning did not have a significant effect on understory modal height. In this study, pre-commercial thinning had a significant negative effect on graminoid and willow height but herb and shrub height did not respond. Graminoid and willow height growth appear to be stimulated by competition for resources such as light in the higher density plots compared with the aspen free plots. In the aspen free plots, competition for light is diminished, allowing for lateral as well horizontal growth.

Relationship with Overstory Variables

Shropshire et al. (2001) found that the dominant understory species showed increased height with increasing light to the understory. In contrast, I found that graminoid and willow height were positively correlated with aspen basal area, and grass and shrub height increased with increasing overstory PAI. This supports the above suggestion that the height of these species is stimulated by competition.

Understory Diversity

Effect of Pre-commercial thinning

Several studies have found that understory diversity increased with thinning treatments due to the rise in resource availability and space for the establishment of species (Alaback 1988; Thomas et al. 1999; Lindgren et al. 2006). However, other studies have found that pre-commercial thinning does not have significant effects on understory community composition and richness (Lautenschlager 1997; Bauhus et al. 2001; Sullivan et al. 2002; Lindh and Muir 2004; Heineman et al. 2007).

In the Grande Prairie WESBOGY LTS, pre-commercial thinning did not have an effect on understory diversity ten years after the initial treatment. Bauhus et al. (2001) suggested that the thinning treatments in their study did not increase niche availability for new species. Another possibility for the lack of response could be the high light levels found under unthinned aspen canopies, and spring and fall periods of high understory light in the western boreal broadleaf forests. The fraction of full sunlight or diffuse non-intercepted light (DIFN) ranged from 0.10 to 0.61 in the unthinned plots with an average of 0.24. These understory light conditions may not be limiting to understory vegetation survival and growth.

It has been suggested that after thinning, the increase in resources allows for shade intolerant ruderal species to establish causing a spike in species richness (Fredericksen et al. 1999; Haeussler et al. 2002; Lindgren et al. 2006). However, in these plots, shade intolerant species such as *Epilobium angustifolium* L., *Achillea millefolium* L. and shade tolerant species such as *Viburnum edule* (Michx.) Raf. and *Mitella nuda* L. were present in the both the control and thinned plots.

Introduced weedy species were expected to be more abundant in the more highly disturbed (more intensively thinned) treatments (Bell and Newmaster 2002; Battles et al. 2001). There was no significant effect of thinning on the cover of clover (*Trifolium sp.* L) and timothy (*Phleum pratense* L.). There was a significant effect of thinning on dandelion (*Taraxacum officinale* Weber) but contrary to previous findings (Roberts and Zhu 2002; Lindgren et al. 2006), it was most abundant in the natural plots. Hansen and

Clevenger (2005) found that although non-native plant species abundance increased with disturbance from transportation corridors, that dandelion and *Trifolium repens* were common in both their control and disturbance plots. The Alaska weed ranking program does not consider any of the five introduced species found in these plots to be a significant risk for invasion based on the invasive traits of the species (dispersal capability, range of habitat and reproductive strategy) (ANHP 2006).

Relationship with Overstory Variables

The relationship between understory plant diversity and the overstory is extremely variable (Gilliam and Roberts 2003; Thomas et al. 1999; Bartemucci et al. 2006). Thomas et al. (1999) found a positive but weak relationship between understory species richness and light availability, while Bartemucci et al. (2006) failed to find a relationship between overstory light transmission and understory species composition and diversity. Species richness, Shannon or Simpson's index were not significantly related to overstory estimates of PAI or basal area in this study. The fact that species richness did not change in response to varying overstory PAI and thinning treatment indicates that the boreal understory species are resilient and may remain on disturbed sites. Bartemucci et al. (2007) suggests that the reason for the lack of relationship between richness and light may be because boreal understory species are adapted for growth in a wide range of light conditions (Constabel and Lieffers 1996).

In addition, there are limitations to using a single measurement of light availability and species composition. The understory community captured in a single measurement is the result of past and present conditions with the majority of the species capable of resprouting, germinating from seedbank or clonal growth, allowing them to persist in the community (Hubbell and Foster 1986; De Grandpré et al. 1993; Bartemucci et al. 2007). Therefore, the understory vegetation community may not be in equilibrium with the canopy conditions measured at a single point in time.

Forb species evenness had a significant positive relationship with overstory estimates of PAI. High species evenness is often considered desirable for forest ecosystems because it indicates that a few species are not dominating the understory. Reducing the overstory canopy seems to have increased the abundance of a few species while decreasing the abundance of others, leading to the increase in evenness. *Pyrola asarifolia* cover was greatest in the complete removal plot but in the past has been seen as sensitive to disturbance (Dyrness 1973; Halpern and Spies 1995). *Mitella nuda* was most abundant in the lowest intensity thinning treatment and has been shown to decrease in cover in response to disturbance as well (Harper and Macdonald 2001; Macdonald and Fenniak 2007).

The RDA analysis indicated the important influence of aspen basal area, spruce basal area and overstory PAI on understory community composition. There appears to be some separation among plots by treatment with the heavily thinned plots clustered with decreasing aspen basal area, but there is no clear segregation between thinning treatments. Composition appeared to shift with pre-commercial thinning. Shade intolerant species such as *Salix serissima* (Bailey) Fern., *Carex aurea* Nutt., *Frageria virginiana* Duchesne and *Equisetum sylvaticum* L. were associated with the lowest aspen density plots and highest spruce density plots.

3.5 Conclusions

Pre-commercial thinning had some small but significant effects on the overstory and understory community of boreal mixedwood forests ten years after treatment. Thinning increased spruce root collar diameter and through selective thinning retained the largest aspen trees. Understory cover declined exponentially with retained aspen basal area, leveling off at $7m^2$/ha. Contrary to the findings of Lieffers and Stadt (1994), *Calamagrostis canadensis* did not have a significant relationship with overstory aspen basal area or leaf area. Removing or reducing the overstory aspen to low densities improved spruce growth, indicating that in this study, high levels of pre-commercial thinning did not lead to inhibitive levels of competition to spruce growth from understory vegetation.

Pre-commercial thinning also had a significant effect on the understory community. Overstory leaf area estimates were significantly lower in thinned stands while understory cover was greater. Pre-commercial thinning did not have a significant effect on species richness but thinning did shift community composition towards greater abundance of shade intolerant species and reduced the cover of some shade tolerant understory species. Invasive species abundance did not increase with thinning.

This shift towards increased cover of ruderal, shade intolerant species indicates a departure from the successional pathway towards old growth forests with late-seral shade tolerant species. Thinning appeared to maintain shade intolerant species that would have likely declined with canopy closure. This finding is contrary to other studies such as Alaback and Herman (1986) and Lindh and Muir (2004) who found that thinning accelerated succession towards older forest conditions and increased the cover of shade tolerant species. Conservation efforts are often concerned with the effect of silvicultural techniques on the reduction of old-growth species or attributes (Cole 1996). However, the forb-shrub stage is the most dynamic successional stage with a unique set of understory species that provide forage and cover for mammals (Schoonmaker and McKee 1988; Lindgren et al. 2006). Pre-commercial thinning maybe a useful tool in maintaining early-successional boreal forests.

Our results should be applied with caution and I recommend that future studies be undertaken that consider the longer term (>10 year) impacts of these thinning treatments on the understory community, and the dynamics of the understory development under these different regimes. Further studies of the effect of overstory leaf area and other factors on vascular and non vascular plant communities over the long term are required.

3.6 References

Alaback, P.B., and Herman, F.R. 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. Canadian Journal of Forest Research **18**:1522-1530.

Alaska Natural Heritage Program (ANHP). 2006. Weed Ranking Project. http://akweeds.uaa.alaska.edu/akweeds_ranking_page.htm. Accessed August 12, 2008.

Alberta Environmental Protection. 1998. The boreal forest natural region of Alberta. Natural Resources Service, Recreation and Protected Areas Division, Edmonton, AB.

Bartemucci, P., Messier, C., and Canham, C.D. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Canadian Journal of Forest Research **36**:2065-2079.

Battles, J.J., Shliski, A.J., Barrett, R.H., HEald, R.C., and Allen-Diaz, B.H. 2001. The effect of forest management on plant species diversity in a Sierran conifer forest. Forest Ecology and Management **146**:211-222.

Bauhus, J., Aubin, I., Messier, C., and Connell, M. 2001. Composition, structure, light attenuation and nutrient content of the understory vegetation in a *Eucalyptus sieberi* regrowth stand 6 years after thinning and fertilization. Forest Ecology and Management **144**:275-286.

Bauhus, J., Paré, D., and Côté, L. 1998. Effect of tree species, stand age and soil type on soil microbial biomass and its activity in southern boreal forest. Soil Biology & Biochemistry **30**:1077-1089.

Bell, F.W., and Newmaster, S.G. 2992. The effects of silvicultural disturbances on the diversity of seed-producing plants in the boreal mixedwood forest. Canadian Journal of Forest Research **32**:1180-1191.

Bergeron, Y. 2000. Species and stand dynamics in the mixed-woods of Quebec's southern boreal forest. Ecology **81**:1500-1516.

Biring, B.S., Hays-Byl, W.J., Hoyles, S.E. 1999. Twelve-year conifer and vegetation responses to discing and glyphosate on a BWBSmw backlog site. B.C. Ministry of Forest, Research Branch, Victoria. Working Paper 43.

Boateng, J.O., Haeussler, S., and L. Bedford. 2000. Boreal plant community diversity 10 years after glyphosate treatment. Western Journal of Forestry **15**:15-26.

Bokalo, M., Comeau, P.G., and Titus, S.J. 2007. Early development of tended mixtures of aspen and spruce in western Canadian boreal forests. Forest Ecology and Managment **242**(2-3):175-184.

Brais, S., Camiré, C., Bergeron, Y., and Paré, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. Forest Ecology and Management **76**:181-189.

Brissette, J.C., Frank, R.M., Stone, T.L., Skratt, T.A. 1999. Precommercial thinning in a northern conifer stand: 18 year results. The Forestry Chronicle **75**:967-972.

Berger, A.L., and Puettman, K.J. 2000. Overstory composition and stand structure influence plant diversity in mixed aspen forest of northern Minnesota. American Midland Naturalist **143**(1):111-125.

Carleton, T.J., and Maycock, P.F. 1981. Understory-canopy affinities in boreal forest vegetation. Canadian Journal of Botany **59:**1709-1716.

Chapin, F.S., Vitousek, P.M., and Van Cleve, K. 1986. The nature of nutrient limitation in plant communities. American Naturalist. **127**:48-58.

Cole, E.C. 1996. Managing for mature habitat in production forests of Western Oregon and Washington. Weed Technology Journal **10**:422-428.

Collins , B.S., Dunne, D.P., and Pickett, S.T.A. 1985. Responses of forest herbs to canopy gaps. Page 218-234 *in* Pickett, S.T.A., and White, P.S., editors. The ecology of natural disturbances and patch dynamics. Academic Press, Orlando, Florida, USA.

Comeau, P.G., Kabzems, R., McClarnon, J., and Heineman, J.:. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. The Forestry Chronicle **81**:559-574.

Connell, J.H. 1978. Diversity in tropical forests and coral reefs. Science. **199**:1302-1310.

Constabel, A.J., and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Canadian Journal of Forest Research **26**:1008-1014.

De Grandpré, L., Gagnon, D., and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. Journal of Vegetation Science **4**:803-810.

Doerr, J.G., and Sandburg, N.H. 1986. Effects of precommercial thinning on understory vegetation and deer habitat utilization on Big Level Island in Southeast Alaska. Forest Science **32**:1092-1095.

Dyrness, C.T. 1973. Early stages of plant succession following logging and burning in the western cascades of Oregon. Ecology **54**(1):57-69.

Easton, W.E., and Martin, K. 2992. Effects of thinning and herbicide treatments on nest-site selection by songbirds in young managed forests. The Auk **119**(3):685-694.

Fredericksen, T.S., Ross, B.D>, Hoffman, W., Morrison, M.L., Beyea, J., Johnson, B.N., Lester, M.B., and Ross, E. 1999. Short-term understory plant community response to timber-harvesting intensity on non-industrial forestlands in Pennsylvania. Forest Ecology and Management **116**:129-139.

Gagnon, D., and Bradfield, G.E. 1986. Relationships amoung forest strata and environment in southern coastal British Columbia. Canadian Journal of Forest Research **16**:1264-1271.

Gilliam, F.S., and Roberts, M.R. 2003. The herbaceous layer in forests of eastern north America. Oxford University Press, Oxford, UK.

Gilliam, F.S., Turril, N.L., and Adams, M.B. 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. Ecological Applications **5**:947-955.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews **52**:107-145.

Haeussler, S., Bartemucci, P., and L. Bedford. 2004. Succession and resilience in boreal mixedwood plant communities 15-16 years after silvicultural site preparation. Forest Ecology and Management. **199**:349-370.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., and Kranabetter, M. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fennica **36**(1):307-327.

Halpern, C.B., and Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications **5**(4):913-934.

Hannam, K.D., Quideau, S.A., Oh, S.-W., Kishchuk, B.E., and Wasylishen, R.E. 2004. Forest floor composition in aspen- and spruce-dominated stands of the boreal mixedwood forest. Soil Science Society of America Journal **68**:1735-1743.

Hansen, M.J., and Clevenger, A.P. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biological Conservation **125**(2):249-259.

Harper, K.A., and Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. Ecology **82**(3):649-659.

Heineman, J.L., Simard, S.W., Sachs, D.L., and Mather, W.J. 2007. Ten year responses of Engelmann spruce and a high-elevation Ericaceous shrub community to manual cutting treatments in southern interior British Columbia. Forest Ecology and Management **248**:153-162.

Homyack, J.A., Harrison, D.J., and Krohn, W.B. 2004. Structural difference between precommercially thinned and unthinned conifer stands. Forest Ecology and Management **194**:131-143.

Host, G.E., and Pregitzer, K.S. 1992. Geomorphic influences on ground-flora and overstory composition I upland forests of northwestern lower Michigan. Canadian Journal of Forest Research **22**:1547-1555.

Hubbell, S.P., and Foster, R.A. 1986. Biology, chance and history and the structure of tropical rain forest tree communities. *In* Community ecology. *Edited by* J. Diamond and T.J. Case. Harper & Row, New York. pp. 314-329.

Hunter, M.L. 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, New York.

Huston, M.A. 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

Jerabkova, L., Prescott, C.E., and Kishchuk, B.E. Nitrogen availability in soil and forest floor of contrasting types of boreal mixedwoods. Canadian Journal of Forest Research **36**:112-122.

Jobidon, R. 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition, and stand structural development- a 5-year study. Forest Ecology and Management **130**(1):77-97.

Johnson, D., Kershaw, L., MacKinnon, A., and Pojar, J. 1995. Plants of western boreal forest and aspen parkland. Lone Pine Press.

Kevan, P.G., Greco, C.F., and Belaoussoff, S. 1997. Log-normality of biodiversity and abundance in diagnosis and measuring ecosystemic health: pesticide stress on pollinators on blueberry health. Journal of Applied Ecology **34**(5):1122-1136.

Klinka, K., Chen, H.Y., Wang, Q., and de Montigny, L. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on west Vancouver Island. Northwest Science. **70**:193-200.

Larcher, W. 1995. Physiological plant ecology: ecophysiology and stress physiology of functional groups. 3rd Ed. Springer, Berlin. 506p.

Lautenschlager, R.A., Bell, F.W., Wagner, R.G., Reynolds, P.E. 1998. The Fallingsnow Ecosystem Project: Documenting the consequences of conifer release alternatives. Journal of Forestry **96**(11):20-27.

Lemenih, M., Gidyelew, T., and Teketay, D. 2004. Effects of canopy cover and understory environment of tree plantations on richness, density and size of colonizing woody species in southern Ethiopia. Forest Ecology and Management **194**:1-10.

Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Canadian Journal of Forest Research **23**(10):2070-2077.

Lieffers, V.J., and Stadt, K.J. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis,* and *Epilobium angustifolium* in relation to overstory light. Canadian Journal of Forest Research **24**:1193-1198.

Lindgren, P.M.F., Randsome, D.B., Sullivan, D.S., and Sullivan, T.P. 2006. Plant community attributes 12 to 14 years following precommercial thinning in a young lodgepole pine forest. Canadian Journal of Forest Research **36**:48-61.

Lindgren, P.M.F., and Sullivan, T.P. 2001. Influence of alternative vegetation management treatments on conifer plantation attributes: abundance, species diversity, and structural diversity. Forest Ecology and Management **142**:163-182.

Lindh, B.C., and Muir, P.S. 2004. Understory vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? Forest Ecology and Management **192**:285-296.

Macdonald, S.E., and Fenniak, T.E. 2007. Understory plant communities of boreal mixedwood forests in western Canada: Natural patters and response to variable-retention harvesting. Forest Ecology and Management **242**:34-48.

Malcolm, J.R. 1994. Edge effects in central Amazonian forest fragments. Ecology **75**:2438-2445.

McConnell, B.R. and Smith, J.G. 1970. Response of understory vegetation to ponderosa pine thining in eastern Washington. Journal of Range Management **23**:208-212.

McCune, B., and Mefford, M.J. 1999. PC-ORD Multivariate analysis of ecological data, version 5 ed. MJM Software Design, Glenedon Beach, Oreg.

McKenzie, D., Halpern, C.B., Nelson, C.R. 2000. Over-story influences on herb and shrub communities in mature forests of western Washington, USA. Canadian Journal of Forest Research **30**:1655-1666.

Messier, C., Parent, S., and Bergeron, Y. 1998. Characterization of understory light environment in closed mixed boreal forests: effects of overstory and understory vegetation. Journal of Vegetation Science **9**:511-520.

Naumburg, E., and DeWald, L.E. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. Forest Ecology and Management **124**:205-215.

O'Hara, K.L. 1989. Stand growth efficiency in a Douglas-fir thinning trial. Forestry. **62:** 409-418.

O'Neill, R.V., DeAngeles, D.L., Waide, J.B., and Allen, T.F.H. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, NJ, 263 pp.

Paré, D., Bergeron, Y., and Camiré,C. 1993. Cahnges in the forest floor of Canadian southern boreal forest after disturbance. Journal of Vegetation Science **4**:811-818.

Pasto, J.P., and Bockheim, J.G. 1984. Distribution and cycling of nutrients in an aspen-mixed hardwood-spodosol ecosystem in northern Wisconsin. Ecology **65**:339-353.

Peltzer, D. A., Bast, M.L., Wilson, S.D., and Gerry, A.K. 2000. Plant diversity and tree responses following contrasting disturbances in boreal forest. Forest Ecology and Management **127**:191-203.

Penner, M., Robinson, C., and Woods, M. 2001. The response of good and poor aspen clones to thinning. The Forestry Chronicle 77:874-884.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology **13**:131-144.

Pitt, D.G., Mihajlovich, M., and Proudfoot, L.M. 2994. Juvenile stand responses and potential outcomes of conifer release efforts on Alberta's spruce-aspen mixedwood sites. The Forestry Chronicle **80**:583-597.

Prescott, C.E., Zabek, L.M., Staley, C.L., and Kabzems, R. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Canadian Journal of Forest Research **30**:1742-1750.

Rapport, D.J., Costanza, R., and McMichael, A.J. 1998. Assessing ecosystem health. Trends in Ecology and Evolution. **13**(10):397-402.

Rice, J.A., MacDonald, G.B., and Weingartner, D.H. 2001. Precommercial thinning of trembling aspen in northern Ontario. Part I. Growth responses. The Forestry Chronicle 77:893-901.

Roberts, M.R., and Zhu, L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. Forest Ecology and Management **155**(1-3):17-31.

Schaffer, D.J., Herricks, E.E., Kerster, H.W. 1988.Ecosystem Health: I. Measuring Ecosystem Health. Environmental Management **12**(4):445-455.

Schoonmaker, P., and McKee, A. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. Forest Science **34**:960-979.

Shannon, C.E., and Weaver, W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, III.

Shropshire, C., Wagner, R.G., Bell, F.W., and Swanton, C.J. 2001. Light attenuation by early successional plants of the boreal forest. Canadian Journal of Forest Research **31**:813-823.

Simard, S.W., Blenner-Hassett, T., and Cameron, I.R. 2004. Pre-commercial thinning effects on growth, yield and mortality in even-aged paper birch stands in British Columbia. Forest Ecology and Management. **190**:163-178.

Simard, S.W., and Hannam, K.D. 2000. Effects of thinning overstory paper birch on survival and growth of interior spruce in British Columbia: implications for reforestation policy and biodiversity. Forest Ecology and Management **129**(1-3): 237-251.

Simpson, E.H. 1949. Measurement of diversity. Nature **163**:688.

Ste-Marie, C., and Paré, D. 1999. Soil, pH and N availability effects on net nitrification in the forest floor of a range of boreal forest stands. Soil Biology & Biochemistry **31**:1579-1589.

Stone, W.E., and Wolfe, M.L. 1996. Response of understory vegetation to variable tree mortality following mountain beetle epidemic in lodgepole pine stands in orthern Utah. Vegetatio **122**:1-12.

Sullivan, T.P., and Sullivan, D.S. 2003. Vegetation management and ecosystem disturbance: impact of glyphosate herbicide on plant and animal diversity in terrestrial systems. Environmental Reviews **11**:37-59.

Sullivan, T.P., Sullivan, D.S. and Lindgren, P.M.F. 2001. Stand structure and small mammals in young lodgepole pine forests: 10-year results after thinning. Ecological Applications **11**:1151-1173.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., and Boateng, J.O. 2002. Influence of conventional and chemical thinning on stand structure and diversity of plant and mammal communities in young lodgepole pine forest. Forest Ecology and Management **170**:173-187.

Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., and Austin, K.A. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. Ecological Applications **9**(3):864-879.

Wagner, R.G. 2000. Competition and critical-period thresholds for vegetation management decisions in young conifer stands. 2000. The Forestry Chronicle **76**(6):961-968.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon **21**(2/3):213-251.

Chapter 4. Research Summary, implications and future research

Chapter 1 Conclusions:

- Retaining less than 1500 trees/ha on site will reduce overstory PAI 10 years after initial thinning
- Spruce root collar diameter (RCD) and height were greater when aspen density was below 1500 trees/ha but difference was not significant
- Aspen diameter and height were greater in thinned plots due to selective thinning
- Litter trap LAI, LAI-2000 PAI and hemispherical photograph PAI were extremely variable
- Hemispherical photograph PAI estimates had the strongest relationship with stand basal area

Chapter 2 Conclusions:

- Total cover and graminoid cover increased with a decrease in aspen overstory
- Graminoid, shrub and willow height decreased with a decrease in aspen overstory
- Forb species evenness decreased with a decrease in aspen overstory
- The understory community composition shifted with changes in aspen basal area, spruce basal area and overstory PAI

In this thesis I examined the effect of pre-commercial thinning on young boreal mixedwoods ten years after the initial treatments were applied. In Chapter 2, the objective was to examine the impact of thinning on overstory leaf area, and the relationship between basal area and leaf area index (LAI) using three leaf area measures:

litter traps, hemispherical photographs and LAI-2000 PCAs. In Chapter 3, I studied the response of the understory community to thinning treatments and changing overstory density and LAI.

Pre-commercial thinning significantly reduced estimated overstory leaf area. Pre-commercial thinning was applied to increase light transmittance to the understory white spruce by reducing crown closure of the overstory aspen. I found a significant exponential relationship between aspen basal area and plant area index (PAI) whereby at basal areas above 7m^2/ha (1500 trees/ha), the PAI was constant (approximately 2.8 m^2/m^2). In order to reduce overstory leaf area, a pre-commercial thinning treatment that leaves fewer than 1500 trees/ha should be prescribed. White spruce is capable of achieving maximum photosynthesis when light levels are above 40% (Lieffers and Stadt 1994). Light levels ranged from 10% to 90% in the Grand Prairie site with an average light transmittance of 41% in the 1500 trees/ha plot and 57% in the 500 trees/ha plot. Comeau (2001) estimated that the radial increment of white spruce is at 70% of maximum when aspen basal area is 8 m^2/ha. In these sites, white spruce had greater diameters in the lower density plots, but spruce height and diameter were not significantly different between treatment densities. Aspen diameter and height were greater in the pre-commerically thinned plots, but this can be attributed to the fact that the largest trees were left after thinning.

Hemispherical photograph estimates of PAI provided the strongest relationship with measures of stand density compared with LAI-2000s and litter traps. A negative nonlinear relationship was significant for all three methods, but the indirect methods greatly underestimated the PAI as compared to estimates obtained by the litter traps. All three methods had large variation in their estimates of leaf area. Leaf area, especially in young, pre-commercially thinned stands is spatially variable. Of the three methods compared, litter traps are the most direct method and are widely considered the most reliable method for measuring LAI (Fassnacht et al. 1994; Wilhelm et al. 2000; Mussche et al. 2001; Jonckheere et al. 2004). However, I found great variation in the litter trap estimates within plots and between replicates. Direct methods such as litter traps maybe more accurate but only if the litter trapped is representative of the overstory, which often requires a large number of traps (Jonckheere et al. 2004). Power analysis indicated that over one hundred replicates of each treatment are needed to achieve a power of 0.90 for detection of differences among thinning treatments using this method. It was also the most time consuming in set-up, data collection and analysis.

A significant relationship was found between LAI-2000 estimates of PAI and hemispherical photograph PAI and litter trap LAI estimates, but there was no significant relationship between hemispherical photographs and litter trap estimates of leaf area. These indirect methods also had large variation in their estimates, but require only about half the number of replicates as litter traps. They are also much easier to use in the field and faster to analyze, but greatly underestimated leaf area as defined by the litter traps. Using a correction value of 70° to account for the angle at which leaves hang from trees in calculations of the LAI-2000 estimates of leaf area reduced the underestimation to 18% from 48%. Improvements to the models are needed to improve the accuracy by taking into account the non-random distribution of leaves in the canopy.

Concern over the impacts of intensive forest management practices, such as pre-commercial thinning, on stand diversity are widespread (Seymour and Hunter 1999). By removing part or all of the overstory, pre-commercial thinning can reduce the spatial and structural heterogeneity of the stand and increase the abundance of introduced weedy species (Spies and Turner 1999). Also, pre-commercial thinning could have a negative effect on spruce growth, if the thinning encourages the growth of the competing understory vegetation, introducing competition from the understory instead of the overstory. Alaback and Herman (1998) assumed that thinning would have a significant effect on species richness with the greatest richness found at intermediate levels of disturbance.

My study showed that the understory vegetation community was influenced slightly by pre-commercial thinning. Ten years after the initial treatment, thinned stands had greater understory cover and also showed a shift in the vegetation community towards shade intolerant species. The increase in understory cover and the negative relationship between graminoid cover and aspen basal area suggest that thinning provided more resources for the understory. However, spruce growth did not appear to be delayed by this increase, as the spruce had overtopped the understory vegetation and were not competing with the understory for light. Thinning did not have a significant impact on species richness but had a negative impact on forb species evenness. The introduced species found at this site did not increase with thinning, as had been predicted, but were found in both the disturbed and undisturbed sites. The introduced species are widespread across the boreal in severely disturbed areas (e.g. roadsides, logging trails and well sites) and traffic through the control plots to the treated plots and for measurements as well as animal movement may have allowed for their introduction.

Aspen and spruce densities, as well as overstory leaf area, were shown to play a significant role in differentiating community composition among the thinning levels. Thinned stands had a greater abundance of shade intolerant species than the unthinned plots.

In summary, results from this study indicate that in order to reduce the leaf area of the overstory for a 10 year period, thinning should reduce aspen density to less than 1500 trees per hectare. The understory vegetation community will increase in cover with the reduction in overstory basal area, but species richness will not be affected. The understory community will shift with the increase in light and other resources to a community with more abundant shade intolerant species.

Suggestions for future research

Further research is required to evaluate the application of these results to other sites. The power analysis indicated that additional replication and measurements per site were critical for precise and accurate direct and indirect leaf area measurements. In addition, it would be useful to continue measurements of the understory and overstory as the stand continues to age. I recommend in future studies that a chronosequence of leaf area and understory measures be taken before and after thinning to provide a more complete picture of the temporal dynamics of thinning effects. These short- term responses provide useful information but without long term data, it is difficult to determine how these stands will continue to develop. Landscape level research that examines effects of forest management practices on the spatial patterning of plant populations in forest landscapes is also needed. A comprehensive understanding of the impacts of these practices is needed at a provincial or ecosystem scale instead of stand by stand.

Management Implications

Examination of sites ten years after the initial pre-commercial thinning treatment indicated that this treatment can have a significant effect on the overstory leaf area and understory community. Pre-commercial thinning reduced the overstory leaf area when 1500 trees per hectare or less were left on site, the remaining overstory aspen are larger and the white spruce have bigger root collar diameters. Pre-commercial thinning did not increase the abundance of weedy introduced species, or lead to the loss of diversity. The alteration of the understory plant community abundance and cover by the thinning treatments, however, indicates that this treatment is changing the forest structure at least over a 10 year period.

4.1 References

Alaback, P.B., and Herman, F.R. 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. Canadian Journal of Forest Research **18**:1522-1530.

Comeau, P.G. 2001. Relationships between stand parameters and understory light in boreal aspen stands. B.C. Journal of Ecosystems and Management **1**: 1-8.

Fassnacht, K.S., Gower, S.T., Norman, J.M., and McMurtrie, R.E. 1994. A comparison of optical and direct methods for estimating foliage surface area index in forests. Agricultrual and Forest Meteorology **71**:183-207.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B. and Coppin, P. 2004. Methods for leaf area index determination. Part I: Theories, Techniques and Instruments. Agricultural and Forest Meteorology **121**:19-35.

Lieffers, V.J., and Stadt, K.J. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis,* and *Epilobium angustifolium* in relation to overstory light. Canadian Journal of Forest Research **24**:1193-1198.

Mussche, S., Samson, R., Nachtergale, L., DeSchrijver, A., Lemeur, R., and Lust, N.A. 2001. Comparison of optical and direct methods for monitoring the seasonal dynamics of leaf area index in deciduous forests. Silva Fennica 35:373-384.

Seymour, R.S. and Hunter, M.L. 1999. Principles of ecological forestry, In: Hunter, M.L. (Ed.), Maintaining biodiversity in forest ecosystems. Cambridge University Press, New York.

Spies, T.A., and Turner, M.G. 1999. Dynamic forest mosaics. In: Hunter, M.L. (Ed.), Maintaining biodiversity in forest ecosystems. Cambridge University Press, New York.

Wilhelm, W.W., Ruwe, K and Schlemmer, M.R. 2000. Comparison of three leaf area index meters in a corn canopy. Crop Science 40:1179-1183.

Appendix A. List of abbreviations.

Basal area: cross-sectional area (over the bark) at breast height (1.3m) measured in squared meters per hectare (m^2/ha).

DBH: diameter of the stem (over the bark) measured at breast height (1.3m) (cm).

LAI: leaf area index is the ratio of leaf area to ground area (m^2/m^2).

PAI: plant area index is the ratio of vegetative area (leaves, stems, branches) to ground area (m^2/m^2).

RCD: root collar diameter (over the bark) measured at the root collar (cm).

WAI: woody plant area index is the ratio of woody vegetative area (stems and branches) to ground area (m^2/m^2).

Appendix B. List of taxa for vascular plants found in the sample plots

(Moss, E.H., 1983. In: Packer, J.G. (Ed.), Flora of Alberta. second ed. University of Toronto Press, Toronto.)

Code	Name	Common Name
Forbs		
Achimil	*Achillea millefolium* L.	Common yarrow
Achisib	*Achillea sibirica L.*	Siberian yarrow
Actarub	*Actaea rubra* (Ait.) Willd.	Red and white baneberry
Allisch	*Allium schoenoprasum* L.	Wild chives
Aralnud	*Aralia nudicaulis L.*	Wild sarsaparilla
Arenlat	*Arenaria lateriflora*	Blunt-leaved sandwort
Astecil	*Aster ciliolatus* (Lindl.)	Fringed aster
Astecon	*Aster conspicuus* (Lindl.)	Showy aster
Astepur	*Aster puniceus* L.	Purple-stemmed aster
Botrvir	*Botrychium virginianum* (L.) Sw.	Grape Fern
Castmin	*Castilleja miniata* Dougl. Ex Hook.	Common red paint-brush
Castrau	*Castilleja raupii* Pennell	Purple paint-brush
Corncan	*Cornus canadensis* L.	Bunchberry
epilang	*Epilobium angustifolium* L.	Fireweed
equiarv	*Equisetum arvense* L.	Common horsetail
equipra	*Equisetum pratense* Ehrh	Meadow horsetail
equisyl	*Equisetum sylvaticum* L.	Woodland horsetail
fragves	*Fragaria vesca* L.	Woodland strawberry
fragvir	*Fragaria virginiana* Duchesne	Wild strawberry
galibor	*Galium boreale* L.	Northern bedstraw
galitri	*Galium triflorum* Michx.	Sweet scented bedstraw
geumale	*Geum aleppicum* Jacq.	Yellow avens
geumriv	*Geum rivale* L.	Purple avens
habehyp	*Habenaria hyperborea* (L.) R.Br.	Northern green orchid
habevir	*Habenaria viridis* (L.) R.Br.	Bracted orchid
haledef	*Halenia deflexa* (Sm.) Griseb.	Spurred gentian
heralan	*Heracleum lanatum* Michx.	Cow parsnip
hierumb	*Hieracium umbellatum* L.	Narrow-leaved hawkweed
lathoch	*Lathyrus ochroleucus* Hook.	Creamy peavine
linnbor	*Linnaea borealis* L.	Twin-flower
maiacan	*Maianthemum canadense* Desf.	Wild lily of the valley
mertpan	*Mertensia paniculata* (Ait.) G. Don.	Tall lungwort
mitenud	*Mitella nuda* L.	Bishop's-cap
orchrot	*Orchis rotundifolia* Banks ex Pursh	Round-leaved orchid
osmodep	*Osmorhiza depauperata* Philippi	Spreading sweet cicely
petapal	*Petasites palmatus* (Ait.) A. Gray	Palmate-leaved coltsfoot
pyroasa	*Pyrola asarifolia* Michx.	Common pink wintergreen
rhinbor	*Rhinanthus borealis* (Sterneck) Chab.	Yellow rattle

rubupub	*Rubus pubescens* Raf.	Dewberry
seneere	*Senecio eremophilus* Richards	Cut-leaved ragwort
senepau	*Senecio pauperculus* Michx.	Balsam groundsel
solican	*Solidago canadensis* L.	Canada goldenrod
taraoff	*Taraxacum officinale* Weber*	Common dandelion
trifhyb	*Trifolium hybridum L.**	Alsike clover
trifrep	*Trifolium repens L.**	White clover
Trifpra	*Trifolium pratense* L*.	Red clover
viciame	*Vicia americana* Muhl.	Wild vetch
violcan	*Viola canadensis* L.	Western Canada violet
violren	*Viola renifolia* A.Gray	Kidney-leaved violet
zigaele	*Zigadenus elegans* Pursh	White camas
Graminoids		
agrotra	*Agropyron trachycaulum* (Link) Malte.	Slender wheat grass
bromine	*Bromus inermis* Leyss.	Awnless brome
calacan	*Calamagrostis canadensis* (Michx.) Beauv.	Bluejoint
careaen	*Carex aenea* (Fern.)	Bronze sedge
careaur	*Carex aurea* Nutt.	Golden Sedge
carebru	*Carex brunnescens* (Pers.) Poir.	Brownish Sedge
carecur	*Carex curta* Good.	Short sedge
caredef	*Carex deflexa* Hornem	Bent sedge
caredew	*Carex deweyana* Schwein.	Dewey's sedge
caredis	*Carex disperma* Dewey	Two-seeded sedge
careint	*Carex interior* Bailey	Inland sedge
caresic	*Carex siccata* Dewey	Hay sedge
careten	*Carex tenuiflora* Wahlenb.	Thin-flowered sedge
caretin	*Carex tincta* Fern.	Slender sedge
descces	*Deschampsia cespitosa* (L.) Beauv.	Tufted hair grass
elyminn	*Elymus innovatus* Beal	Hairy wild rye
phlepra	*Phleum pratense* L.*	Timothy
poapalu	*Poa palustris* L.	Fowl bluegrass
poapra	*Poa pratensis* L.	Kentucy bluegrass
schipur	*Schizachne purpurascens* (Torr.) Swallen	False melic
Shrubs and Trees		
amelaln	*Amelanchier alnifolia* Nutt.	Saskatoon berry
cornsto	*Cornus stolonifera* Michx.	Red osier dogwood
lonidio	*Lonicera dioica* L.	Twining honeysuckle
loniinv	*Lonicera involucrata* (Richards.) Banks	Bracted honeysuckle
lonivil	*Lonicera villosa* (Michx.)	Fly honeysuckle
ribehud	*Ribes hudsonianum* Richards	Wild black currant
ribelac	*Ribes lacustre* (Pers.) Poir.	Bristly black currant

ribeoxy	*Ribes oxyacanthoides* L.	Wild gooseberry
ribetri	*Ribes triste* Pall.	Wild red currant
rosaaci	*Rosa acicularis* Lindl.	Prickly rose
rosawoo	*Rosa woodsii* Lindl.	Common wild rose
rubuida	*Rubus idaeus* L.	Wild red raspberry
shepcan	*Shepherdia canadensis* (L.) Nutt.	Canadian buffalo-berry
spiralb	*Spiraea alba* Du Roi	Narrow-leaved meadowsweet
sympalb	*Symphoricarpos albus* (L.) Blake	Snowberry
sympocc	*Symphoricarpos occidentalis* Hook.	Buckbrush
vacccae	*Vaccinium caespitosum* Michx.	Dwarf bilberry
vacculi	*Vaccinium uliginosum* L.	Bog bilberry
vibuedu	*Viburnum edule* (Michx.) Raf.	Low-bush cranberry
vibuopu	*Viburnum opulus* L.	High-bush cranberry
betupap	*Betula papyrifera* Marsh.	Paper birch
picegla	*Picea glauca* (Monech) Voss	White Spruce
poputre	*Populus tremuloides* Michx.	Aspen
salibar	*Salix barclayi* Anderss.	Willow
salibeb	*Salix bebbiana* Sarg.	Beaked willow
saliboo	*Salix boothii* Dorn	
salimac	*Salix maccalliana* Rowlee	Velvet-fruited willow
salimel	*Salix melanopsis* Nutt.	
saliser	*Salix serissima* (Bailey) Fern.	Autumn willow

*Introduced species.