Effects of community structure on aboveground net primary productivity (aNPP),
leaf area index (LAI) and light use efficiency (LUE) in a boreal mixedwood forest of
central Alberta, Canada.

by

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Abstract

Management practices, such as the use of herbicides to reduce abundance of deciduous and herbaceous vegetation can have dramatic influences on community structure and composition in regenerating boreal ecosystems. The vertical structure of boreal stands includes different functional groups: trees, shrubs, herbs, grasses and thallophytes. Each group develops its own leaf area contributing to the total leaf area index (LAI) and therefore to net primary productivity (NNP) of the ecosystem in different degree. However, multiple factors affect NPP and its study becomes complicated. An important concept that simplifies the study of biomass production as well as radiation interception is light use efficiency (LUE), which relates production to the amount of light intercepted.

The main purpose of this research was to elucidate the effect of community structure on aboveground net primary productivity (aNPP), LAI and LUE.

This study focussed on the effects of four selected treatments established at the "Judy Creek Mixedwood Experiment" near Whitecourt, Alberta: 1) removal of woody broadleaf vegetation (broadcast woody control; BW), 2) removal of both woody broadleaf and herbaceous vegetation (broadcast complete control; BC), 3) removal of herbaceous vegetation (broadcast herbaceous control; BH), and 4) untreated planted plots (broadcast untreated; BN).Clipped plots and biomass equations were the main methodologies used to evaluate overstory and understory NPP in 2012. Litter traps were used to measure deciduous litter production. A LAI-2000 Plant Canopy Analyzer was used to measure LAI and transmittance (DIFN) that were used to calculate LUE along with aNPP.

Results indicated that applying vegetation control treatments alters vertical structure of young mixedwood forests, causing differences in the LAI and aNPP of the functional groups. All treatments affected the % cover of the understory. Plots with deciduous trees had significantly higher productivity than plots where deciduous trees were removed. Understory contribution ranged between 1 and 86% of total aNPP among treatments. The understory of the BW treatment where deciduous were removed but understory was not controlled developed a thick layer of grasses and had the largest percent contribution by the understory while treatments which removed herbs and grasses (BH and BC) had much lower contributions.

Total LUE was significantly lower for treatments where woody trees were removed and highest efficiency was found in the treatment where herbs were removed but woody vegetation was left intact. Herbs, grasses and shrubs were more efficient in plots where no treatment was applied compared to treatments where any kind of vegetation control was performed. White spruce (*Picea glauca* (Moench) Voss) showed higher light use efficiency in the BC (broadcast complete control) treatment than in the BN (untreated) treatment. Positive linear relationships were found between total LUE and overstory LAI and between total aNPP and overstory LAI. Resulting equations allow estimation of aNPP and LUE of young boreal mixedwood forest from measurements of overstory LAI.

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1. Introduction

1.1 The boreal forest and the importance of its productivity

The world's forests serve a very important role in the global carbon cycle and in the regulation of global climate. Since the industrial revolution, human use of fossil fuels has risen at an accelerated rate. This extensive use of fossil fuel has created considerable emissions of greenhouse gases with carbon dioxide (CO_2) being one of the most important ones. Vegetation, in general, and forest vegetation in particular fix CO_2 from the atmosphere and incorporate it into plant structures through photosynthesis.

Terrestrial carbon (560 Pg in the biotic pool and 2500 Pg in soil carbon) relates to the atmospheric reservoir of carbon (760 Pg) through photosynthesis and plant respiration (Lal, 2007) (Fig. 1).

Forests account for more than half of the carbon kept in the biotic pool stored in terrestrial ecosystems (Hui et al., 2017); therefore, they act as an important tool fighting climate change. Papadopol (2000) and Parker et al. (2000) reaffirmed that managing the forest may potentially increase carbon sequestration; and Canada is considered one of the 12 key forested nations that can significantly contribute to this global capability to sequester carbon (Winjum et al., 1993).

According to Dixon et al. (1994), high-latitude forest (including boreal forest) represent approximately 49% of the carbon of forest vegetation and soil, so their importance in the global carbon cycle resides in their carbon content. The function

of the boreal forest within the terrestrial carbon cycle is very complex and many factors including the age of the stand, disturbance history and forest type influence the extent to which forests act as a sink or source of carbon to the atmosphere. It is also important to consider how different management practices influence carbon fluxes so we can propose strategies that could help to increase the productivity of a forest and its ability to store carbon.

The boreal forest is an extensive area occupying a circumpolar belt in high northern latitudes, it is adjacent to the circumpolar tundra (north) and to the temperate forests and grasslands (south) (Larsen, 1980). The boreal forest is dominated by a restricted number of conifer genera, mainly spruce (*Picea*), pine (*Pinus*), larch (*Larix*) and fir (*Abies*), and a few deciduous genera such as birch (*Betula*) and poplar (*Populus*) (Malhi et al., 1999). The boreal forests of Canada represent about 24% of the world's boreal forests (CFS, 2015). According to Canada's National Forest Inventory (NFI, 2006), more than three-quarters of the forest in Canada are boreal forests and there are more than 56 million of ha of mixedwoods in Canada, but only 38.2 millions of ha are in the boreal region, which represents almost 11% of the total forests in Canada and 14% of the Canadian boreal forest region (Table 1).

The amount of carbon contained in forest vegetation varies widely with latitude (Lal, 2005). In addition, the relationship between the amount of carbon in the vegetation and the amount of carbon contained in the soil change among latitudes (Dixon et al., 1994; Lal, 2005). Activities that disrupt the natural state of the forests, such as harvesting or tending practices, may have different impacts in the boreal forest than in tropical or temperate forests. The large amount of carbon stored in the

boreal is the result of the combination of long days during the summer (growing season) and long winters with cold temperatures that limit decomposition rates (Malhi et al., 1999).

Table 1. Non-boreal and boreal forest land (per forest type) of Canada

Forest Land	Forest Type	Area (1000 ha)
Boreal	Broadleaf	22862.38
Boreal	Coniferous	192343.24
Boreal	Mixedwood	38240.33
Boreal	Non-treed	16971.88
Non-Boreal	Any	80572.76
	Total	350990.59

Source: Canada's National Forest Inventory (NFI, 2006)

Net Primary Productivity (NPP) is a measure related to the absolute amount of carbon being captured by an ecosystem. Knowing the factors affecting NPP can help us understand important processes and aid in selecting or developing management practices that reduce emissions. A review of published work on this topic is a useful starting point. I will begin with a description of the dynamics of mixedwood stands and stand structure and follow this with a review of how much carbon is found in various compartments, and then review the factors influencing carbon distribution and cycling in the boreal.

1.2   Boreal mixedwood forest dynamics

Mixedwood stands are a major component of Canada's boreal forest. CCFM (2006) defines mixedwood stands as stands of trees having a well-mixed composition of deciduous or broadleaf trees (angiosperms) and conifers (gymnosperms). MacDonald (1995) established that no more than 80% of the basal area could be from a single species to be considered a mixedwood stand. According to the National Forest Inventory (NFI, 2006), there are around 350 million hectares of forest land in Canada. The mixedwood forest comprises 56 million hectares (around 16%) of which more than two thirds (38 millions of ha) are in the boreal zone. For the boreal forest itself these 38 million hectares represents 14% of the Canadian boreal forest. This amount of forest definitely can impact the amount of carbon being captured and sequestered in the Earth.

White spruce and trembling aspen (*Populus tremuloides* Michx.) are trees that commonly coexist in the western Canadian mixedwood boreal forest. A mixedwood stand can follow several successional trajectories. Bergeron et al. (2014) described six possible stand dynamics pathways that arise because of different interactions between forest conditions (e.g. initial post-fire regeneration and on-going regeneration). One of these pathways, the classical, was earlier described by Chen and Popadiouk (2002) that based on distinct structures and processes identified four stages of stand dynamics: stand initiation, stem exclusion, canopy transition and gap dynamics.

During stand initiation, following a stand-replacing disturbance, shade intolerant pioneer trees will establish and dominate the site (Chen and Popadiouk,

2002). The most common stand-replacing disturbance in western boreal mixedwoods is fire. If the fire is deep burning, the mineral soil will be exposed and will serve as a seedbed. If the fire is light and burns only the surface, it will allow sprouting of species such trembling aspen and bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) P.Beauv.) (Dyrness et al., 1983). According to Lieffers et al. (1996), spruce can establish naturally under aspen following a very variable system. Spruce seedlings can establish in a single pulse within the first ten years after disturbance or become established over several decades following disturbance (Lieffers et al., 1996).

Approximately 15 to 25 years after stand initiation, aspen leaf area reaches its maximum development (Lieffers et al., 2002) and the second, stem exclusion stage begins. With all the growing space occupied by aspen, intense competition for resources begins between individuals and self-thinning occurs (Chen and Popadiouk, 2002; Brassard and Chen, 2006). During this first 20 years, aspen stands are quite dynamic, presenting very high rates of self-thinning. Bokalo et al. (2007) found that natural aspen stands decrease their mean density from more than 70000 sph to around 20000 sph, a reduction of almost 70% of the original density by year 9. They also highlight the effect of initial stand density, with higher starting densities leading to a drop-in density every year in young stands while at lower starting densities, the mortality exceeds the ingrowth only after year 5, when self-thinning begins. Pitt et al. (2015) also report that aspen stands reduce their densities through self-thinning by 50% (from 59000 sph to 30000 sph) within the first 10 years after establishment.

Self-thinning causes an increment of light levels in the understory and the canopy starts transitioning about 40 years or more after stand initiation because light transmittance at this point is sufficient to support the development of spruce (Lieffers

and Stadt, 1994). There are two possible outcomes of this stage: 1) The stand will become spruce dominated at age 60 to 80 providing there is enough spruce in the stand (Stewart et al., 1998; Stewart et al., 2000; DeLong et al., 1997), or 2) if there are not enough spruce the increased light will allow aspen regeneration in the understory, leading to development of a multi-aged aspen stand (Bergeron et al., 2014).

At the age of 70-120, stands that have abundant spruce become spruce dominated and enter an old growth phase. Gap dynamics occurs when open areas in the canopy develop as old trees fall (Cumming et al., 2000). Canopy gaps create an uneven aged complex ecosystem that rarely persists because in most circumstances (in the absence of human intervention) fire will return stands to an initiation stage (Rowe, 1961).

Regarding the light environment, there are also changes through all successional stages. Right after the disturbance, the site will experience full sun conditions. The light levels near the ground decline as aspen develops and the canopy closes. Transmitted light is lowest at 15-25 years after stand initiation and could be less that 5% of above-canopy light (Lieffers et al., 2002). This level of light in the understory is not enough to allow spruce to survive (Lieffers and Stadt, 1994). During canopy transition and gap dynamics, levels of light are variable, however there is a trend towards increased light transmission, especially when spruce trees reach the height of the aspen canopy (Lieffers et al., 2002). Finally, when conifers overtake aspen and the canopy is completely closed, there will be deep shade (and low light levels) in the understory of the site.

1.3   Vertical structure of a forest

Understory vegetation plays an important role in the dynamics of the boreal forest. The term understory refers to all vegetation growing beneath the overstory tree canopy. In the central boreal mixedwood it includes shrubs, forbs, grasses, mosses and lichens as different functional groups. Yarie (1980) demonstrated that understory biomass could represent from 11% to 48% of the estimated overstory aboveground production and Nilsson and Wardle (2005) stated that the productivity of the understory vegetation is probably comparable to that of the trees. Nilsson and Wardle (2005) also concluded that understory vegetation could drive important ecological processes including regeneration, belowground properties and long-term succession. Even when the total understory biomass might be a small portion of that of the total aboveground biomass, the rate of turnover is often significantly more rapid.

Forests are structured vertically in distinct layers or functional groups: trees, shrubs, herbs, graminoides, thallophytes and epiphytes (Kimmins, 2004). The tree layer constitutes the overstory and the other groups (except the epiphytes) form, all together, the understory of the forest. Through photosynthesis, these vegetation layers each convert CO_2 to carbohydrates and store them in biomass. The carbon contained in each layer contributes to different degrees to the general carbon dynamics.

While each group develops its own leaf area that contributes to the total LAI (tLAI) of the ecosystem, there is little information on how leaf area is partitioned in boreal forest ecosystems and on the factors influencing the partitioning of LAI. Most

of the studies about productivity and LAI are based only on the overstory production, but shrubs and herbs can contribute from 3 to 14% of the tLAI (Gholz et al., 1976). The intensity of light penetrating through a forest decreases exponentially as the leaf area increases. Various studies indicate that both tree size and stand density influence understory light levels (Comeau 2002; Lieffers et al., 2002; Filipescu and Comeau 2007). As tree size and stand density increase, the shorter understory must grow under successively deeper shade and therefore the understory may contribute less and less to net productivity.

1.4 Carbon cycle and forest productivity

Lal (2008) states that the importance of atmospheric concentrations of CO_2 on global temperature was recognized by Arrhenius in 1896, with anthropogenic perturbation of the global carbon cycle becoming an unprecedented phenomenon during the twentieth century has been a historically.

The study of the carbon has always been an important matter in applied forestry, mainly because of the interest in how productivity can be increased and how ecosystems function. However, there is currently an interest in managing forests for carbon sequestration and identifying the best management practices for capturing C. There are five global carbon pools: the oceanic pool, the geological pool, the pedologic pool, the atmospheric pool and the biotic pool. These pools can act as a source or as a sink of carbon. The interchange among these pools is termed carbon flux (Ciesla, 1996). Figure 1 illustrates the carbon in each global pool and fluxes between pools.
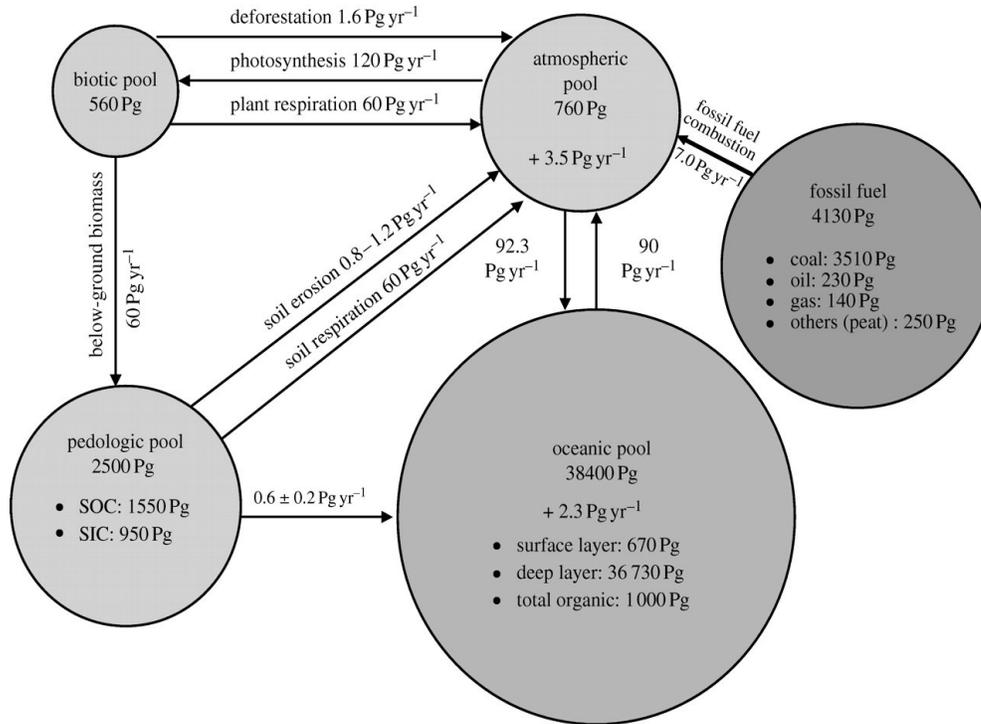
Fig. 1. Principal global carbon pools and fluxes between them (Lal, 2008)

Waring and Running (2007) describe the carbon cycle in the following way: "carbon begins its cycle through forest ecosystems when plants assimilate atmospheric CO_2 through photosynthesis into reduced sugars. Usually about half the gross photosynthetic products produced (GPP) are expended by plants in autotrophic respiration (Ra) for the synthesis and maintenance of living cells, releasing CO_2 back into the atmosphere. The remaining carbon products (GPP − Ra) go into net primary productivity (NPP): foliage, branches, stems, roots, and plant reproductive organs. As plants die and shed leaves and roots, the dead organic matter forms detritus, a substrate that supports animals and microbes, which through their heterotrophic metabolism (Rh) release CO_2 back into the atmosphere. On an annual basis, undisturbed forest ecosystems show a small net gain in carbon exchange with the

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atmosphere, this represents net ecosystem productivity (NEP). An ecosystem may lose carbon if photosynthesis is suddenly reduced, or when organic materials are removed as a result of disturbance."

A forest ecosystem can act as source or sink of carbon (Masera et al., 2000). Decomposition and respiration are the two natural release processes most important in forests. Globally forests release 55GtC y^{-1} through respiration and 54 to 55GtC y^{-1} through decomposition, the amount released adds up a total of approximately 110GtC y^{-1}. Through photosynthesis and other processes terrestrial vegetation through absorbs 110 GtC y^{-1}.

When the amount of carbon released is the same amount of carbon that is absorbed, a forest ecosystem is in balance, has NEP=0 and there is a neutral effect on the atmospheric CO_2 levels. Mature and old-growth forests and mature plant communities have a near neutral balance over the long term, although NEP may fluctuate from year to year. However, when human or natural disturbances occur, this balance is disrupted and then, the ecosystem can become a source or sink of carbon.

The carbon stocks and fluxes are also affected by factors such as age, disturbance history, and forest type. During the development of a stand, NEP is not constant, it changes with time. Grant et al. (2007) modeled this change in a Douglas fir stand after disturbance (clearcutting) and described the changes as follows (Fig. 2):

During the first four years after clearcutting ecosystem respiration (R_e) is elevated and GPP remains low, which leads to a negative NEP because the rapid

losses of soil C, mostly from litter, were not offset by gains in wood C. The annual

GPP and R_e rose slowly during the next decade due to reductions in Rh and soil carbon

losses NEP rose rapidly even though gains in wood carbon were small. The forest

stand was a small source of carbon after 13 years and remained nearly carbon neutral

until the onset of net nitrogen mineralization after 20 years caused NEP to rise

rapidly. After that, declines in soil carbon slowed while gains in wood carbon rose.

(Grant et al., 2007).
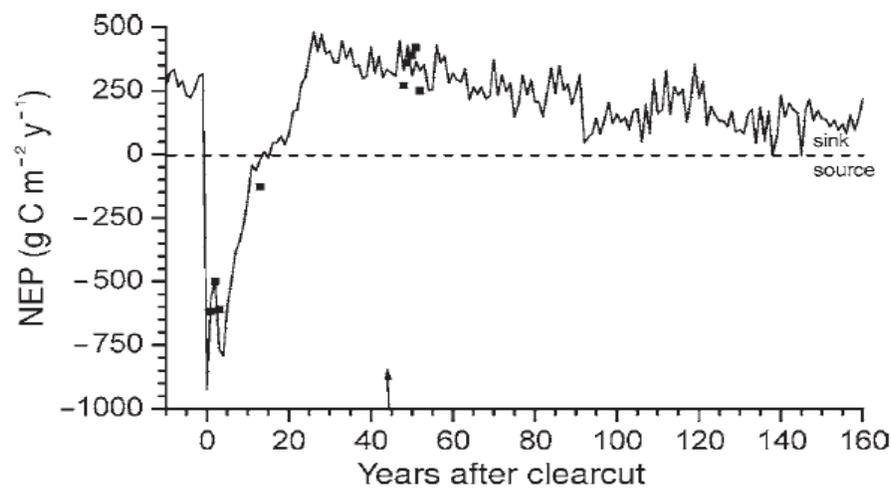
Fig. 2. Net ecosystem productivity (NEP) modeled during 160 years of Douglas fir regrowth following clearcutting (line) and estimates from gap-filled eddy covariance measurements of CO_2 flux in a post-clearcut douglas-fir chronosequence (symbols). (Grant et al., 2007).

Litvak et al. (2003) found different results in boreal black spruce stands in

northern Canada. Using eddy covariance to measure the CO_2 exchange, they

conclude that CO_2 uptake was lowest in the 11-year-old stand, high in the 19 year

old stand, highest in the 36 year old stand, and moderate in the 70 and 130 year old stands. In terms of the carbon balance, they concluded that those boreal stands changed from a slight sink in the 11 year old stand to a modest sink in the 19 year old stand, to a large sink in the 36 year old stand, to a modest sink in the 70 year old stand, and to around zero in the 130 year old stand.

NEP of forests changes with their age, going from being sources at the beginning of their development, then moderate to large sinks, and finally declining to be again sources (when a natural or artificial disturbance happens). However, there is still no consensus or reports that summarize the effect of age on NPP. Nevertheless, it is reasonable to expect that NPP follows the same trend as NEP.

It is also worth mentioning that the amount of stored carbon also varies across disturbance types and forest types. Harmon et al. (1990) examined, compared and assessed the effect of carbon storage of a natural disturbance versus timber harvest and found that harvest of old-growth forest reduced carbon storage for at least 250 years and a natural disturbance such as fire or windthrow also reduced storage but much less drastically (Fig. 3). Their results apply to Douglas fir old-growth forests in the western United States, however, as they state, they may also apply in most forest in which the age of harvest is less than the age required to reach the old-growth stage of succession.

At this point, it is important to recognize that studies about carbon cycling in boreal sites have been focused on the overstory of pure, single-species, forest stands (Baldocchi et al., 2000, 2001; Barr et al., 2002; Blanken et al., 1997; Chen et al.,

2000; Sellers et al., 1997; and Valentini et al., 2000). However, they rely basically

on NEP and do not consider the contribution of the understory.
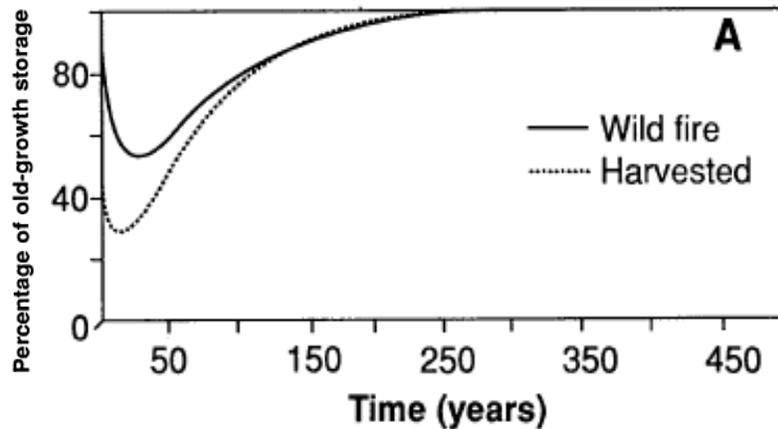
Fig. 3. Carbon storage in a simulation of a Douglas fir and hemlock old-growth ecosystem disturbed by fire or timber harvest (adapted from Harmon et al., 1990).

Boreal understory vegetation is highly dynamic because it is simultaneously

influenced by forest type, canopy succession, and disturbances. Few studies have

considered the role of understory vegetation in carbon dynamics (Blanken et al.,

1997; Sellers et al., 1997; Cavard et al., 2010; Cavard et al., 2011; Kreyling et al.,

2012). Kreyling et al., (2012) concluded that differences in the understory vegetation

could have major implications for the biogeochemistry of boreal forest. Forest

management techniques such as thinning or herbicide application can also affect the

amount and characteristics of the understory vegetation.

1.5 Effects of management practices on the productivity of a forest

Forest management practices influence NPP and carbon dynamics through their effects on rotation length, forest composition, structure, growth rates and processes. These characteristics directly influence the quantity of carbon being captured and stored (Blanken et al., 1997; Sellers et al., 1997; Baldocchi et al., 2000; Chen et al., 2000; Baldocchi et al., 2001; Liski et al., 2001; Barr et al., 2002; Chen and Klinka, 2003; Kaipainen et al., 2004; McCaughey et al., 2006; Seeley et al., 2008; Cavard et al., 2010; Cavard et al., 2011).

Papadopol (2000) and Parker et al. (2000) indicate that managing the forest may potentially increase carbon sequestration. Seedre and Chen (2010) also found that managed forest stands have higher carbon sequestration rates than unmanaged stands at comparable ages up to at least age 27. Management practices can be designed to maximize not only the ecological but also the economic values while reaching targeted productivities.

As mentioned earlier in this chapter, most western boreal mixedwood forests have trembling aspen and white spruce as their main tree species. In young stands competition for light and other resources from aspen may suppress the growth of spruce (Filipescu and Comeau, 2007). In addition, herbaceous vegetation is also very competitive with spruce in young stands (Pitt and Bell, 2005; Man et al., 2008; Pitt et al., 2010; Neufeld et al., 2014; Pitt et al., 2015). Vegetation control, through herbicide applications and/or brushing or pre-commercial thinning, has been used to control this competition in most regions of North America.

Herbicide applications are very common in Alberta. Between 2000 and 2015, an average of 31,320 hectares were treated with herbicides, with glyphosate being the most common herbicide applied in this province (Fig. 4). Glyphosate is a non-selective, broad spectrum herbicide introduced in 1974 by Monsanto and since then has been successfully applied worldwide to control competition in forest ecosystems (Franz et al., 1997).
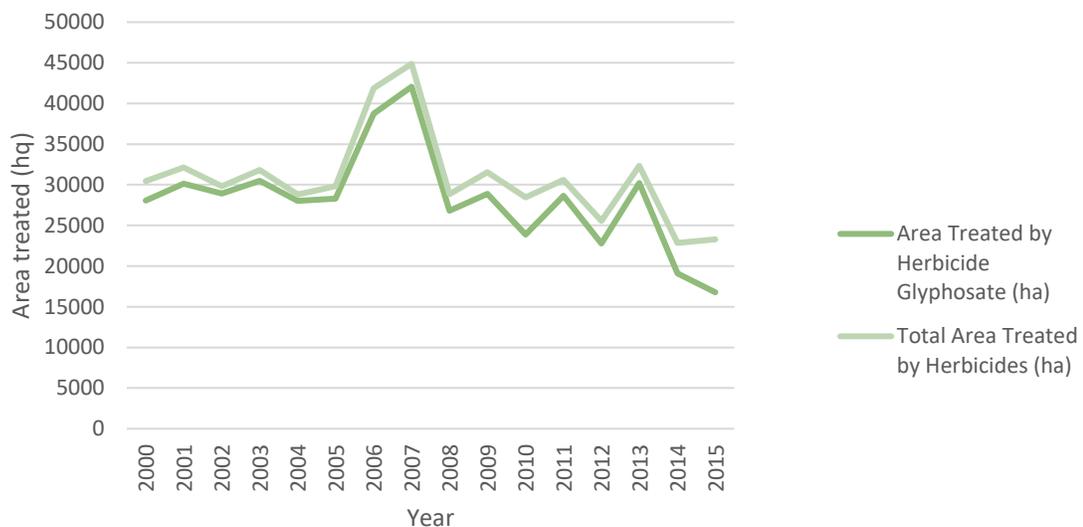
Fig. 4. Total area treated with herbicides versus area treated by glyphosate in Alberta from 2000 to 2015 (from National Forestry Database accessed on June 11, 2018
http://nfdp.ccfm.org/dynamic_report/dynamic_report_ui_e.php).

Herbicide treatments are aimed to control non-desirable vegetation but can lead to substantial changes in plant community composition with the most notable effect being a reduction in aspen and herbaceous and an increase in spruce and grass cover and biomass (Boateng et al., 2000; Maundrell and Hawkins, 2004). Early

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herbicide application was found to be effective in creating softwood-dominated stands over the long term (Olson et al., 2011). The increase in spruce is because early vegetation control provides the optimum environment for the establishment of this species (Groot, 1999) while also reducing the amount of deciduous.

It is important to know the best timing and duration of vegetation control. Wagner et al., (1996) analyzed the effect of different regimes of vegetation control following the establishment of a spruce stand and found differences in vegetation cover, the amount of dry biomass and LAI among treatments and concluded that herbicide application for at least three years after plantation maximize early conifer growth. Wagner et al., (1996) also found that herbicide treatments can result in a reduction of dry biomass; however, as glyphosate is not soil active, biomass often recovers within one to three years after treatment. Their results were validated 15 years after by Hoepting et al. (2011). They found that more intensive vegetation control treatments (4 to 5 years after following planting) results in bigger gains of gross total tree volume per hectare (up to 209%). However, total carbon and nitrogen pools, particularly in the forest floor, are significantly reduced in intensive control treatments. They concluded that two to three years of vegetation control maximize the benefits for conifer growth without adversely affecting soil nutrient pools.

Vegetation management not only changes the structure and composition of a stand in the first years of the stand through the effect on tree growth but also affects the productivity of the stand through effects on biomass accumulation by component species. Böhlenius and Övergaard (2015) found that vegetation control with herbicides increases leaf numbers and leaf sizes in hybrid poplars, resulting in a greater increase in leaf biomass compared to the change in stem biomass.

In summary, vegetation management can impact forest structure and composition and can have profound and long-lasting influences on the carbon cycle due to changes in LAI and therefore in NPP. To understand how these changes in LAI end up affecting the NPP of a forest it is very important to have a clear understanding of how light availability is related to productivity.

1.6   Light and productivity

Light availability in general and light absorption in particular, are some of the most important factors to be considered due to their direct relationship with the production of photosynthates through photosynthesis and consequently with the inputs of carbon into the system. Since photosynthates are the raw material used in building plant tissues, then light availability is a resource affecting biomass production (NPP).

Plants primarily absorb light in the 400-700 nm range, which is termed the Photosynthetically Active Range (PAR) and affect the quality of light that is left available to the understory. As a general rule, understory leaf area is inversely proportional to overstory leaf area and if the overstory captures much of the incoming light, there is only a little left for the development of the understory (Constabel and Lieffers, 1996). Moreover, the heterogeneity of tree canopies also affects the light reaching the understory by creating spatial and temporal variation due to the presence of gaps or dense patches of the canopy (Comeau et al., 1998). Another general rule is that shade intolerant species (e.g. aspen) transmit more light to the understory than shade tolerant species (e.g. spruce) (Lieffers et al., 1999). Latitude

also affects the amount of light reaching the understory. In general, light transmission is higher for boreal forest than for temperate forest: Messier et al. (1996) found that light reaching the understory level in closed boreal forest is very variable but ranges between 2 and 40% of the overstory light in contrast with the less than 5% of light transmitted to the understory of Canadian temperate and coastal forests.

Binkley et al. (2011) reviewed the relationship between leaf area and light absorption and suggest the existence of three categorical types of light absorption in relation to leaf area: 1) the absorption of light through the crown of an individual tree (or canopy of a stand), 2) light absorption in relation to LAI within a set of stands, and 3) light absorption at the scale of a set of whole, individual trees. The primary interest of this review is category 1. Light absorption through the crown of a tree as well as through the canopy of a stand, typically follows a logarithmic trend; each additional layer of leaves absorbs roughly a constant proportion of the light reaching that layer. Given the wide variety of structural differences that are common between stands of differing leaf area indexes, no single a priori expectation would be appropriate for the pattern of light absorption versus leaf area index (Binkley et al., 2011).

Light affects forest dynamics mainly beneath the overstory, where levels of light could act as the factor limiting growth and production. According to Stadt et al. (2001), light is the most limiting resource to the growth of white spruce in the boreal mixedwood, especially at early stages of establishment. Many studies have evaluated the effects of light on the composition and structure of the understory compartment (Camham et al., 1990; Bartemucci et al., 2006, DeRömer et al., 2007; Bartels,

2010). Other studies have considered the effects of light on stand development and tree growth (Comeau et al., 1993; Lieffers et al., 1999; Lieffers et al., 2002; Filipescu and Comeau 2007). However, no studies have related light availability with biomass production in the understory.

Some studies have evaluated the effects of light on the composition and structure of the understory in temperate forests (Canham et al., 1990; Bartemucci et al., 2006, DeRömer et al., 2007; Bartels, 2010) as well as the effects of stand development on light in boreal forests (Lieffers et al., 1999; Comeau 2002; Lieffers et al., 2002; Comeau et al., 2006; Ye and Comeau 2009).

1.7 Leaf area index (LAI) and light use efficiency (LUE)

Monteith and Unsworth (2013) defined leaf area index as the total one-sided leaf area per unit ground surface area. Chen and Black (1992) modified this definition for the needles of conifers, making it more convenient assuming their close to cylindrical shape. For conifer needles LAI is one half of the total leaf area per unit ground surface area. All integrated ecosystem models have as a prerequisite the inclusion of seasonal changes of LAI in addition to general site descriptors (Waring and Running, 2007) because LAI is a factor in predicting productivity and biomass (Pope and Treitz, 2013). However, there are multiple factors influencing LAI as stand composition, structure, site conditions and management practices (Jonckheere et al., 2004). Lieffers et al. (2002) provided a comprehensive description of changes in LAI and light transmission in young boreal aspen dominated stands and concluded that

LAI reaches a maximum of about 6 m^2m^{-2} at 15 to 25 years, while the light transmitted declined to as low as 2% at these LAI values.

Two of the most important plant ecosystem processes are radiation interception and biomass production. Radiation interception depends on leaf area index and canopy structure, while biomass production is influenced by several factors including the photosynthetic characteristics of the foliage, stomatal behaviour, nitrogen distribution, radiation, temperature, vapor pressure deficit and leaf nutrient status (Brix, 1971; Dang et al., 1997; Atkin et al., 2005; Landsberg and Sands, 2011; Stinziano and Way, 2014; Ouimet and Moore, 2015). To be able to predict biomass production requires the integration of multiple equations describing photosynthesis over time and space as well as how all environmental factors are affecting it.

An important concept that contributes to the study of biomass production and radiation interception is light use efficiency (LUE), a useful measurement of productivity (Monteith, 1972) which relates production with intercepted light. Accurate measurements of LUE can improve the estimates of the productivity of a stand. Gilmanov et al. (2013) and John et al. (2013) describe the importance of LUE in the determination of NPP and GPP in ecosystem production models.

According to the Light use efficiency model, the relationship between NPP and aPAR (absorbed PAR) is linear when factors other than light are non-limiting:

$$NPP= \varepsilon\ aPAR$$

Since levels of light decrease through the forest canopy, it is also important to consider how different functional groups located in different vertical layers in the forest utilize the light that is available to them. Excluding components of the forest

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production (e.g. understory) can lead to erroneous estimates of light use efficiency (Gower, 1999). Hence the importance of considering all functional groups and components that contribute to the total NPP and their particular LAI and efficiency. One of the less considered and many times ignored component of total NPP is the understory vegetation.

Thus, considering the understory vegetation contribution as well as their relationships with total aNPP, LAI and light use efficiency may significantly improve our understanding of the carbon dynamics of boreal forest.

1.8   Objectives and hypothesis

The main purpose of this research is to elucidate the effect of community structure on aboveground net primary productivity, LAI and LUE. A secondary objective is to evaluate the contribution of the understory to aboveground NPP of central Alberta boreal forests, through understanding the effects that vertical structure has on LAI and light use efficiency. In addition, effects of selected vegetation management treatments on early carbon accumulation in white spruce and mixedwood stands are examined. For this study I examine effects of selected treatments established at the "Judy Creek Mixedwood Experiment" near Whitecourt Alberta in 2003/2004 as described by Pitt et al. (2015).

Objectives:

1. To estimate the contribution of understory vegetation to aboveground net primary production and compare this contribution among plant communities with different vertical structure

2. To evaluate the effect of community vertical structure on light utilization.

3. To elucidate the relationship between LAI and NPP as well as between LAI and LUE.

The hypotheses tested are:

1. **Total aNPP is related to community structure and composition created by different treatments applied**. Total aNPP will be highest in the untreated plots followed by plots where herbaceous control was performed, then plots with complete vegetation control and finally plots with woody control treatments. This is due to: 1) vigorous early growth of aspen in combination with understory vegetation will result in the largest biomass accumulation in untreated; 2) Broadcast Herbaceous Control will be second due to rapid growth of aspen and lack of understory; 3) Broadcast Complete control will be third due to good growth of spruce; and 4) Broadcast Woody Control will be lower due to reduced growth of spruce.

2. **The contribution of the understory to aNPP is variable depending on treatments applied that created specific community vertical**

structures. Most carbon dynamics studies do not consider the understory when analyzing aNPP. If the vertical structure includes a well-developed understory it may contribute significantly to aNPP. The significance of including understory NPP will be related to the abundance (and biomass) of understory resulting from treatments (understory aNPP follows this pattern for the treatments being examined in the Judy Creek Mixedwoods Experiment: Broadcast Woody Control > Untreated> Broadcast Complete Control >Broadcast Herbaceous Control).

3. **Light use efficiency is affected by treatments applied that created differences in the vertical community structure.** Since the light reaching each functional group is different, they develop different light use efficiencies. The light use efficiency of a functional group is affected by the presence of another functional group (e.g. the presence of shrubs can make the herb layer more or less efficient).

4. **There is a positive relationship between NPP and LAI.** NPP rises if LAI increases. This applies to the NPP of the overstory as well as the NPP of the understory

5. **There is a positive relationship between LUE and LAI.** Light use efficiency improves if LAI increases. This applies to the LUE of the overstory as well as the LUE of the understory.

2. Methods

2.1   The study site and experimental design

The "Judy Creek Mixedwood Study" provides a unique opportunity to explore the influence of overstory and understory vegetation on carbon cycling because treatments applied in this experiment provide contrasting levels of both overstory and understory vegetation cover creating very unique community vertical structures.

The site is situated in Western Canada, close to Swan Hills, Alberta (83: 54°22' N, 115°35' W; elevation 1000 m). The site was harvested in March-April of 2002 and white spruce seedlings were planted in June 2002. Aspen were 75 years old at the time of harvesting and had regenerated naturally from root suckering. The original design of the Judy Creek Mixedwood Experiment consisted in eight treatments (with three replicates each). For this study, only four of those eight treatments were used.

The four chosen treatments are benchmark treatments; all of them were applied to white spruce planted at 2.5 m spacing. The selected treatments are: 1) removal of woody broadleaf vegetation (BW), 2) removal of both woody broadleaf and herbaceous vegetation (BC), 3) removal of herbaceous vegetation (BH), and 4) untreated planted plots (BN). Each of these four treatments was replicated 3 times, providing 12 plots for this study (4 treatments X 3 replicates). Treatment plots are 35 m x 35 m in size and treatments were assigned randomly to plots within the

site. Measurement plots are 25 m X 25 m. For a complete description of the experimental design, site and treatments see Pitt et al. (2010). See Table 2 for complete treatment definitions and their characteristics.

Table 2. Treatment definitions and major characteristics at the time of establishment of the experiment

Code	Plot #	Definition	Tree layer	Understory	Sw density (sph)
BC	11	Broadcast complete control - Woody and herbaceous removed	White spruce	Low cover of willow herb and *Crepis*	1600 sph
BC	29	Broadcast complete control - Woody and herbaceous removed	White spruce	Low cover of willow herb and *Crepis*	1600 sph
BC	32	Broadcast complete control - Woody and herbaceous removed	White spruce	Low cover of willow herb and *Crepis*	1600 sph
BW	10	Woody(aspen) removed	White spruce	High cover of *Calamagrostis canadensis*	1600 sph
BW	16	Woody(aspen) removed	White spruce	High cover of *Calamagrostis canadensis*	1600 sph
BW	34	Woody(aspen) removed	White spruce	High cover of *Calamagrostis canadensis*	1600 sph
BH	15	Broadcast herbaceous control (Herbaceous removed)	Aspen and white spruce	none	1600 sph
BH	30	Broadcast herbaceous control (Herbaceous removed)	Aspen and white spruce	none	1600 sph
BH	40	Broadcast herbaceous control (Herbaceous removed)	Aspen and white spruce	none	1600 sph
BN	4	No vegetation control (spruce planted)	Aspen and white spruce	*Calamagrostis*, *Epilobium*, …	1600 sph
BN	33	No vegetation control (spruce planted)	Aspen and white spruce	*Calamagrostis*, *Epilobium*, …	1600 sph
BN	35	No vegetation control (spruce planted)	Aspen and white spruce	*Calamagrostis*, *Epilobium*, …	1600 sph

2.2 Data collection

Data were collected to determine carbon content and NPP in the aboveground compartment. This study considered the carbon contained in overstory, understory and litterfall. In addition, light measurements were taken to evaluate light absorption, transmittance and light use efficiency.

a) Biomass components

Overstory data

Diameter and height of all spruce within the 25 x 25 m measurement plots were measured in 2009 and 2012.

Every plot contains four 5 x 5 m subplots (Fig. 5). Aspen were measured within these subplots in 2010 and were re-measured in October 2012 for diameter (dbh) and height.

Tree biomass (stem and branches) was calculated based on the equations provided by Ung et al. (2008) for trembling aspen and on the equations provided by Ter-Mikaelian and Parker (2000) for white spruce. Carbon content was considered to be a fraction of 0.5 of the dry biomasses.

Tree biomass increments were calculated based on the difference between calculated plot level biomass for 2012-2009 for spruce and 2012-2010 for aspen.

Understory data

Understory vegetation biomass was determined using 1 x 1 m clip-plots (Goodman and Hungate, 2006). Tall shrubs, low shrubs, herbs, grasses and mosses

were collected from 8 systematically located 1 X 1m subplots established in each treatment plot (Fig. 5). These subplots were located at the outside edge of each measurement plot, two on each side (N, S, E and W). All samples were oven-dried at 70ºC to constant mass. Carbon contained in the understory vegetation was assumed to be 50% of the oven-dried weight. Sampling understory vegetation happened only once, at the peak of vegetation development (late July), to calculate biomass and understory NPP (uNPP). Prior to clipping percent cover of each species group (tall shrubs, low shrubs, herbs, grasses and mosses) was assessed visually.
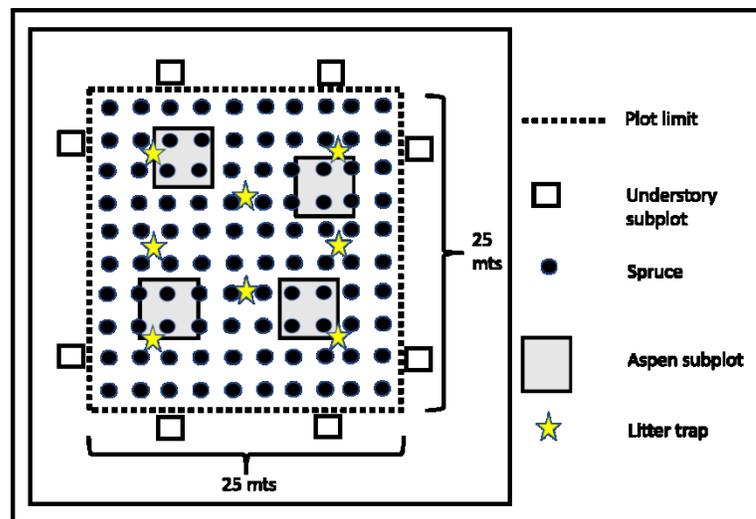
Fig. 5. Sampling design.

Litter fall

Aboveground litterfall measurements were collected to document detritus production as part of the aboveground NPP. To sample litterfall, eight plastic litter traps (milk crates with internal dimensions of 30.5 x 30.5 x 26.7 cm and lined with

fibreglass window screening) were secured inside every plot. Traps were set out systematically within each plot and the litterfall was collected monthly from June to October 2012. The litterfall collected was oven-dried and weighed to calculate dry-biomass.

b) Light absorption, transmittance, light use efficiency and LAI

There are several direct and indirect methods to measure light in forest (Comeau, 2000). One of the most common and reliable methods is the use of plant canopy analyzers (e.g. LAI-2000). LAI-2000 measures diffuse non-interceptance light (DIFN) which is correlated with growing-season transmittance in canopies (Comeau, 2000). According to Gendron et al. (1998), Comeau et al. (1998), and Comeau (2000), DIFN can be considered as an unbiased estimate of this transmittance. Then fractional absorption by the plant canopy was calculated as:

$$A = 1 - T$$

Where A is the amount of absorbed light in $\mu mol/m^2/y$ and T is the transmittance obtained from LAI-2000 as DIFN.

Once we have the absorbed light we can calculate aPAR:

$$aPAR = A \cdot (\int open\ PPFD - \int reflected\ PPFD)$$

where aPAR is the fraction of absorbed photosynthetically active radiation, A is the absorbed light by the vegetation canopy and PPFD is photosynthetic photo flux density in $\mu mol/m^2/s$ at open sky and reflected under the canopy.

Using the LAI-2000 plant canopy analyzer (LI-COR INC., Lincoln, Nebr.), light absorption and transmittance were determined from paired readings of open sky

and understory. Open sky PAR (PPFD) data provided by a climate station installed on site was used to calculate aPAR. Estimates were validated against data from PAR sensors installed in the understory of 6 plots.

To differentiate the contribution of functional group (trees, herbs, shrubs, grasses, and moss), readings were taken over the grass-herb-shrub cover and at the ground level. LAI-2000 measurements were taken at 4 systematically located points in each plot. Readings were taken in two directions (west and east) at two times of day, with matching open sky readings being taken by a separate LAI-2000 sensor place in an open area. These data were used to calculate aPAR for each functional group. As herbs, shrubs and grasses were approximately at the same height, they were considered as having the same level of aPAR.

To calculate aPAR of the overstory we used the sum of all monthly PAR minus albedo of the overstory species and then multiplied this by the absorption of the overstory.

To calculate the aPAR of the understory we used monthly PAR minus the overstory albedo minus aPAR absorbed by overstory. Then, I summed the calculation for every month of the growing season (May to August for herbs, grasses, shrubs and mosses and May to September for spruce). Once we knew the annual PAR reaching the understory we calculated the aPAR using the absorption values that we got from LAI-2000 (A=1-DIFN).

To calculate total aPAR we added aPAR absorbed by overstory, aPAR of herbs and aPAR absorbed by spruce.

As the results of aPAR were in µmol/m^2/y a conversion to MJ/m^2/y was done as follows.

Assuming green light has an average of 550 nm of wavelength and using the velocity of light, the frequency of green photos was calculated as follow:

$$v \; \lambda = c$$

Where v is the frequency (in s-1) of green photons, λ is the known wavelength (5.5E-7 m) and c is the velocity of light (2.99E8 m/s). That results in a frequency of 5.45E14 s-1.

To calculate the energy per green photon this formula was used:

$$E = h \; v$$

Where E is the energy per photon in joules/photon, h is Plank's constant (6.626E-34 J*s) and v is the calculated frequency at 550nm (5.45E14 s-1). The result is 3.611E-19 J/photon. Using the Avogadro's number of 6.022E23 we can affirm that there are 0.217MJ/mol. This result is very similar to the value used by Amthor (2010). Amthor (2010) used a conversion factor of 4.57 mol photons/MJ which equals 0.218MJ/mol.

After transforming all the aPAR values to MJ/mol, light use efficiency (ε) per functional group was calculated by dividing net primary production of each group by the aPAR at the height at which each group is located.

$$\varepsilon_i = NPP_i \; / \; aPARh_i$$

Where εi is the light use efficiency of the functional group i, NPPi is the net primary productivity of the functional group i and aPARhi is the absorbed photosynthetically active radiation at the height of the functional group i.

Total LUE (tLUE) was calculated diving total aNPP by total aPAR at each plot.

Leaf area index (LAI) was also obtained using the LAI-2000 plant canopy analyzer (LI-COR INC., Lincoln, Nebr.). LAI total (tLAI) was based on measurements taken at 10 cm above ground. Overstory LAI (oLAI) was based on measurements collected above the herb/low shrub layer so it includes "LAI" of both trees and tall shrubs that are taller than the understory (readings generally taken at 80 cm). Understory LAI (uLAI) was calculated as the difference between tLAI and oLAI.

2.3   Calculation of total aNPP

As one of the main objectives of this research is to elucidate the contribution of understory vegetation to the aboveground net primary production (aNPP) and compare this contribution among plant communities with different vertical structure, aNPP was calculated as:

aNPP= oNPP + uNPP + L

where oNPP is the increment production at the overstory level, uNPP is the production of the understory layer and L is the production of litterfall.

Overstory net primary productivity (oNPP) was calculated as the tree biomass for spruce and/or aspen using allometric equations. With this information the average oNPP per treatment was estimated (See table 2 for the four treatment definitions).

To calculate uNPP I assumed that all understory plants were annuals and then all the biomass present at the peak of vegetation development equals uNPP. Using the 1m X 1m clipped plot, the biomass of moss, herb, grass and shrub layers were obtained and the sum of all of them was considered as the uNPP.

The dry-weight of the litterfall collected by litter traps was used to calculate the average litter production per treatment.

2.4   Data analysis

All data was processed with the aim of calculating aNPP, aPAR, light use efficiency (LUE) and leaf area index (LAI) per functional group and per treatment. Statistical analyses were done using the SAS system for Windows (SAS Institute Inc., Cary, NC) considering the significance set at $P<0.05$. Before all ANOVA analyses, data were tested to verify they met the assumptions of homogeneity of variance and normality of distribution.

1) To test hypothesis 1: **"Total aNPP is related to community structure and composition created by different treatments applied."** To know if there are differences in total aNPP among treatments, used one-way ANOVA to determine

whether there are differences between treatments. When any significant difference was detected ($p \leq 0.05$) they were compared using a Tukey HSD test.

2) To test hypothesis 2: "**The contribution of the understory to aNPP is variable depending on treatments applied that created specific community vertical structures".** After calculating the percent of understory contribution per treatment, a one-way analysis of variance was applied to determine if there was any difference among treatments. When any significant difference was detected ($p \leq 0.05$) the treatments were compared using a Tukey HSD test.

3) To test hypothesis 3: **"Light use efficiency is affected by treatments applied that created differences in the vertical community structure."** After LUE per functional group are calculated, a one-way analysis of variance was applied to determine if there was any difference among functional groups. For example, if there is any difference between the LUE of grasses versus the LUE of shrubs versus the LUE of trees. When any significant difference was detected ($p \leq 0.05$) the functional groups were compared using a Tukey HSD test.

Differences among functional groups per treatments were also analyzed. For example, whether the LUE of grasses is different or equal between the treatments applied. For this a one-way analysis of variance was applied to determine if there were differences among treatments for each functional group. When significant differences were detected ($p \leq 0.05$) they were compared using Tukey HSD tests.

4) To test hypothesis 4: "**There is a positive relationship between LUE and LAI".** To analyze the relationship between LUE and LAI regression analysis

was applied. For this regression analysis, LAI was considered the independent variable and LUE the dependent variable.

5) To test hypothesis 5: "**There is a positive relationship between NPP and LAI".** To analyze the relationship between NPP and LAI regression analysis was applied. For this regression analysis, LAI was considered the independent variable and NPP the dependent variable.

3. Results

3.1 Community vertical structures developed after treatments

The 12 treatment plots located at the "Judy Creek Mixedwood Study" provided contrasting levels of overstory and understory vegetation cover resulting in four distinct and unique community vertical structures (Table 3).

Broadcast complete control treatment resulted in an overstory layer of spruce and an understory component with grasses (mostly *Calamagrostis canadensis*), herbs (usually *Equisetum* sp.) and occasional shrubs. The average of total cover on this treatment was 44% (Fig. 6a).

Broadcast woody control treatment resulted in an overstory layer of spruce and a well-developed understory with abundant *Calamagrostis canadensis*, various herbs and few shrubs (Fig. 6b). The average total cover was 79%.

Broadcast herb control treatment caused a well established overstory layer of aspen. Spruce has not developed very well and remains in the understory along with very scarce herbs and very little cover of shrubs or grasses (Fig. 6c). The average total cover for this treatment was 8%.

The untreated produced a well developed overstory layer of aspen. However, spruce remains in the understory (not well developed) and we can also find herbs, shrubs and grasses (Fig. 6d). The average total cover for the untreated was 54%.

Table 3. Characteristics of community vertical structure for the four treatments and 12 plots included in this study.

Treatment	Plot #	Definition	Overstory tree layer	Understory total % cover
BC	11	Broadcast complete control - Woody and herbaceous removed	White spruce	35
BC	29	Broadcast complete control - Woody and herbaceous removed	White spruce	39.125
BC	32	Broadcast complete control - Woody and herbaceous removed	White spruce	46.875
Mean %cover (S.D.)				40.33 (4.92) b
BW	10	Woody(aspen) removed	White spruce	66.875
BW	16	Woody(aspen) removed	White spruce	83.75
BW	34	Woody(aspen) removed	White spruce	85
Mean %cover (S.D.)				78.54 (8.27) a
BH	15	Broadcast herbaceous control (Herbaceous removed)	Trembling aspen	2.3125
BH	30	Broadcast herbaceous control (Herbaceous removed)	Trembling aspen	0.375
BH	40	Broadcast herbaceous control (Herbaceous removed)	Trembling aspen	15.625
Mean %cover (S.D.)				6.10 (6.78) c
BN	4	No vegetation control (spruce planted)	Trembling aspen	36.25
BN	33	No vegetation control (spruce planted)	Trembling aspen	48.75
BN	35	No vegetation control (spruce planted)	Trembling aspen	75
Mean %cover (S.D.)				53.33 (16.15) ab
r^2				0.872
Pr>F				**0.0006**

Note: The % value between parentheses following a species name represent the average percent cover for that species among the 8 sampling sites on each plot. ND means that functional group was not developed on that plot. Values in parentheses after the mean % cover indicate the standard deviation (S.D.) and letters in the same column indicate differences detected using Tukey HSD test. BC=complete control treatment, BW=woody control treatment BH=herbaceous control treatment, and BN=untreated.

Table 3. (Continued)

Understory (% cover)		
Shrubs	**Herbs**	**Grasses**
Rubus idaeus (1%)	*Equisetum sp.* (40%) and *Epilobium glandulosum* (4%)	*Calamagrostis canadensis* (4%)
ND	*Fragaria virginiana* (14%), *Equisetum sp.* (10%) and *Galeopsis tetrahit* (3%)	*Calamagrostis canadensis* (39%) and *Agrostis scabra* (10%)
Rubus idaeus (15%)	*Equisetum sp.* (25%), *Crepis sp.* (7%) and *Hieracium umbellatum* (6%)	*Poa sp.* (30%) and *Calamagrostis canadensis* (12%)
0.67 (0.86) b	29.92 (9.42)	23.38 (15.02) ab
Rubus pubescens (17%)	*Senecio vulgaris* (30%), *Chamerion angustifolium* (19%) and *Fragaria virginiana* (14%)	*Calamagrostis canadensis* (53%) and *Deschampsia cespitosa* (10%)
Rubus idaeus (14%)	*Chamerion angustifolium* (22%), *Galeopsis tetrahit* (13%) and *Aralia nudicaulis* (3%)	*Calamagrostis canadensis* (61%)
Rubus idaeus (20%) and *Amelanchier alnifolia* (10%)	Fragaria virginiana (28%), *Chamerion angustifolium* (24%) and *Petasites palmatus* (23%)	*Calamagrostis canadensis* (51%) and *Poa sp.* (5%)
8.9 (3.18) ab	52.25 (25)	55.58 (4.09) a
Rubus pubescens (<1%) and *Viburnum edule* (<1%)	*Petasites palmatus* (2%) and *Galium sp.* (1%)	*Agrostis scraba* (<1%) and *Elymus innovatus* (<1%)
ND	*Petasites palmatus* (<1%)	ND
Viburnum edule (25%)	*Galium sp.* (7%), *Mitella nuda* (7%) and *Epilobium glandulosum* (7%)	*Calamagrostis canadensis* (2%)
1.13 (1.42) b	5.15 (5.63)	0.33 (0.43) b
Rubus pubescens (7%) and *Viburnum edule* (5%)	*Aralia nudicaulis* (18%), *Cornus canadensis* (6%) and Rosa acicularis (5%)	*Calamagrostis canadensis* (8%)
Viburnum edule (23%) and *Rubus pubescens* (5%)	*Aster cilliolatus* (18%), *Aralia nudicaulis* (4%) and *Petasites palmatus* (3%)	*Calamagrostis canadensis* (13%)
Viburnum *edule (26%) and Rubus pubescens* (12%)	*Aralia nudicaulis* (16%), *Chamerion angustifolium* (13%) and *Galium triflorum* (8%)	*Calamagrostis canadensis* (46%)
20.79 (7.83) a	26.17 (6.06)	22.48 (16.97) ab
0.782	0.588	0.745
0.005	0.058	**0.009**

a)

b)

c)

d)

Fig. 6. Photographs illustrating differences between the four treatments: a) Broadcast complete control treatment (BC), b) Broadcast woody control treatment (BW), c) Broadcast herb control treatment (BH) and d) Broadcast non-control treatment (BN).

In general, vegetation control treatments did have a significant effect on total % cover of the understory (r^2=0.872 and P>F 0.0006). Understory cover

ranged from 6 to 79%. Tukey test identified three significantly different groups (where ANOVA indicated a p value<0.05). The first group included BW (%cover=78.5) and BN (%cover=53.3). The second group included BN (%cover=53.3) and BC (%cover=40.3). Lastly, the third group included only BH (%cover=6.1).

Analysing cover of each layer among treatments showed a marginally non-significant effect of treatments on the %cover of herbs (p=0.058). However, differences among treatments for % cover of grasses (p=0.0092) and shrubs (p=0.0051) were strongly significant.

Treatment effect on % cover of grasses was significant and Tukey test resulted showed clear differences between BW (% grass cover =55.6%) and BH (% grass cover = 0.3%), while BN and BC were intermediate and did not differ significantly from either BW or BH.

Shrub cover was also affected by treatment and resulted in two groups. BN (%shrub cover=20.8) had significantly higher cover than BH (% shrub cover=1.1%) and BC (% shrub cover=0.7%) while BW (%shrub cover=8.9) had intermediate cover and did not differ significantly from other treatments.

3.2 Aboveground net primary productivity is affected by community vertical structure

Total aboveground biomass in 2012 ranged from 1.714 to 21.353 TC/ha among all plots. The highest values were found in treatments where aspen was

present while treatments where aspen was not present developed the lowest total

aboveground biomass. BH and BN aboveground standing biomasses were 18.999

and 16.405 TC/ha respectively and they were not statistically different. BC and BW

aboveground standing biomasses were significantly lower with 4.700 and 1.918

TC/ha (Table 4).

Table 4. Results of Tukey HSD test for total aboveground biomass (TC/ha) among treatments (alpha 0.05).

Tukey Grouping	Mean biomass (S.D.) TC/ha	N	Treatment
A	18.999 (2.914)	3	BH
A	16.405 (5.713)	3	BN
B	4.700 (1.381)	3	BC
B	1.918 (0.214)	3	BW

Note: Means (Standard Deviation) in the same group are not significantly different. BH=herbaceous control treatment, BN=untreated, BC=complete control treatment, and BW=woody control treatment. N=number of replicates.

Total Aboveground Net Primary Productivity (aNPP) ranged from 119 to 627

gC/m^2/y. Highest values of total aNPP were found in BH treatment plots (average of

551 gC/m^2/y) followed by BN treatments (507 gC/m^2/y in average). The BC

treatment produced an average aNPP of 151 gC/m^2/y, just a little bit above the less

productive BW treatment which had an aNPP of 142 gC/m^2/y on average (Table 5).

Table 5. Aboveground net primary productivity (gC/m²/y) per plot.
BC=complete control treatment, BH=herbaceous control treatment,
BN=untreated, and BW=woody control treatment.

Plot	Treatment	Overstory NPP (gC /m²/y)	Understory NPP (gC/m²/y)	Litterfall NPP (gC/m²/y)	Total aNPP (gC/m²/y)
11	BC	108.6	34.3	0	142.9
29	BC	92.2	27.1	0	119.3
32	BC	172.3	19.8	0	192.2
15	BH	318.8	10.3	106.0	435.1
30	BH	477.6	7.5	142.3	627.5
40	BH	461.4	9.0	118.5	589.0
4	BN	204.4	56.6	133.1	394.1
33	BN	398.4	41.6	151.1	591.1
35	BN	366.4	40.1	130.1	536.5
10	BW	10.1	135.5	0	145.6
16	BW	25.5	122.9	0	148.4
34	BW	22.9	109.2	0	132.2

The differences in total aNPP among treatments were significant (F=26.52 and p=0.0002) (Fig. 7). Tukey HSD test detected significant differences between two groups of treatments (Table 6).

The first group included BH and BN treatments with higher values of aNPP compared to second group that included BC and BW treatments.

These results make sense because the presence of aspen increased the production of biomass as well as the litterfall. Despite the development of grasses in BW and spruce in BC, productivity was not as high as in those treatments where aspen was present.
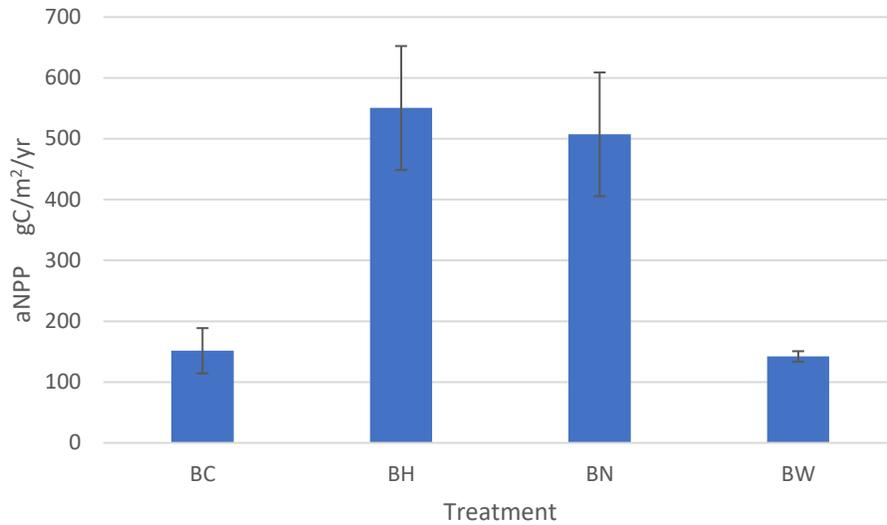
Fig. 7. Differences in total aboveground net primary productivity (aNPP)(gC/m^2/y). The error bars indicate the 95% confidence intervals. BC=complete control treatment, BH=herbaceous control treatment, BN=untreated, and BW=woody control treatment.

Table 6. Results of Tukey HSD test for total aboveground net primary productivity (aNPP) among treatments (alpha 0.05).

Tukey Grouping	Mean aNPP (S.D.) (gC/m^2/y)	N	Treatment
A	550.53 (101.8)	3	BH
A	507.23 (1001.7)	3	BN
B	151.46 (37.19)	3	BC
B	142.07 (8.66)	3	BW

Note: Means (Standard Deviation) in the same group are not significantly different. BH=herbaceous control treatment, BN=untreated, BC=complete control treatment, and BW=woody control treatment. N=number of replicates.

The same trend is followed when oNPP is analyzed. The means of oNPP among treatments were significantly different (p=0.0005) (Fig. 8). Tukey HSD test resulted in the same two groups, which again reflected the contribution of aspen to NPP in BH and BN treatments.
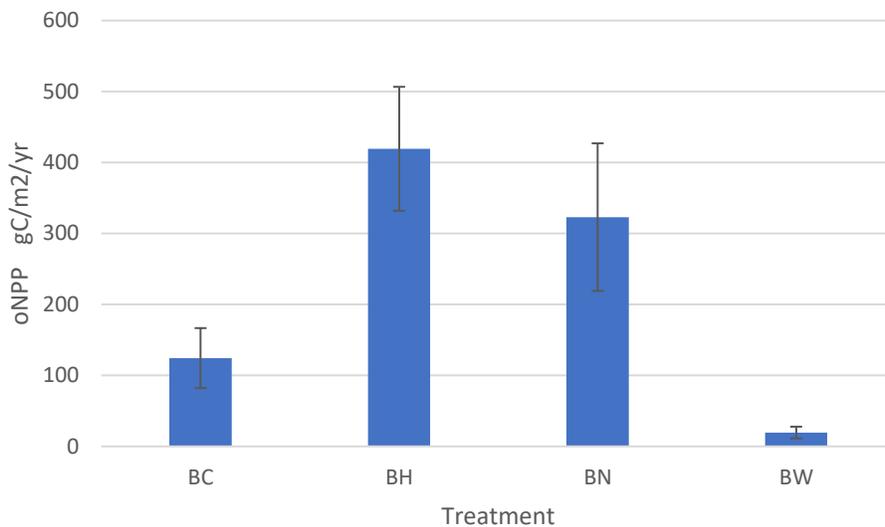
Fig. 8. Treatment effects on overstory net primary productivity (oNPP)(gC/m²/y). Error bars indicate 95% confidence intervals. BC=complete control treatment, BH=herbaceous control treatment, BN=untreated, and BW=woody control treatment.

However, when we analyzed uNPP the results differ. The uNPP among treatments was again statistically different (F=96.31 and P>F <0.0001) (Fig.9). Tukey HSD arranged the treatments in three different groups (Table 7) for uNPP. The first group separated BW with the highest uNPP (122.53 gC/m²/y).

The Tukey group B included BN. BN plots present well defined functional groups that result in a good understory productivity (mean of 46.1 gC/m²/y) but they were not significantly higher than BC, which had uNPP intermediate between BN and BH.

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The last group comprised the uNPP of plots with BH treatments. They have the lowest productivity (8.9 gC/m^2/y); however, their mean uNPP was not significantly different of the mean of uNPP on plots with BC treatments.
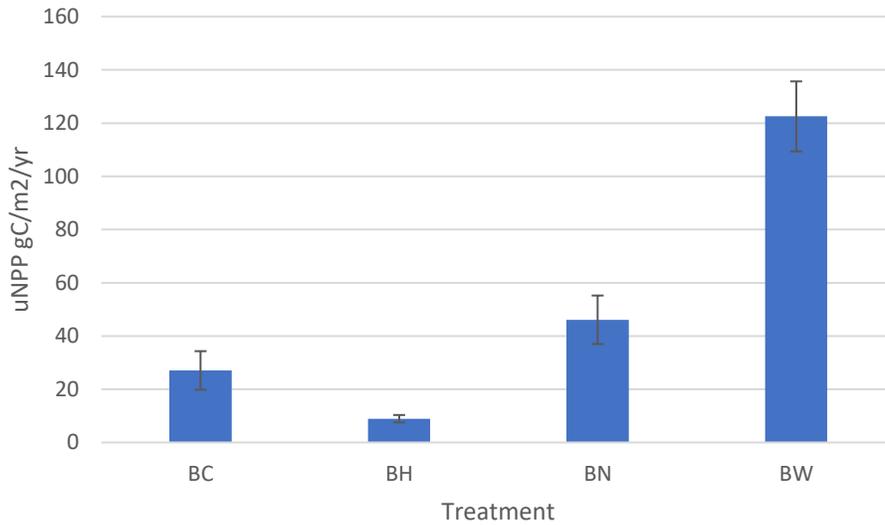
Fig. 9. Treatment effects on understory net primary productivity (uNPP)(gC/m^2/y). Error bars indicate the 95% confidence intervals. BC=complete control treatment, BH=herbaceous control treatment, BN=untreated, and BW=woody control treatment.

Table 7. Results from Tukey HSD test for understory net primary productivity (uNPP) among treatments (alpha 0.05).

Tukey grouping		Mean uNPP (gC/m^2/y)	N	Treatment
	A	122.533	3	BW
	B	46.10	3	BN
C	B	27.067	3	BC
C		8.933	3	BH

Note: Means (Standard Deviation) in the same group are not significantly different. BW=woody control treatment, BN=untreated, BC=complete control treatment, and BH=herbaceous control treatment. N=number of replicates.

3.3 Understory contribution to aNPP is determined by the composition and structure of the community

When aNPP was analyzed, the contribution of each of its components was calculated as a percent. Overstory contribution to total aNPP ranged from 7 to 90% among all treatments while understory contribution to total aNPP varied from 1 to 93%. Aspen litter production contributed to aNPP only in those treatments where aspen was present (BH and BN) and it ranged from 20 to 34% of the total productivity of those plots (Fig. 10).
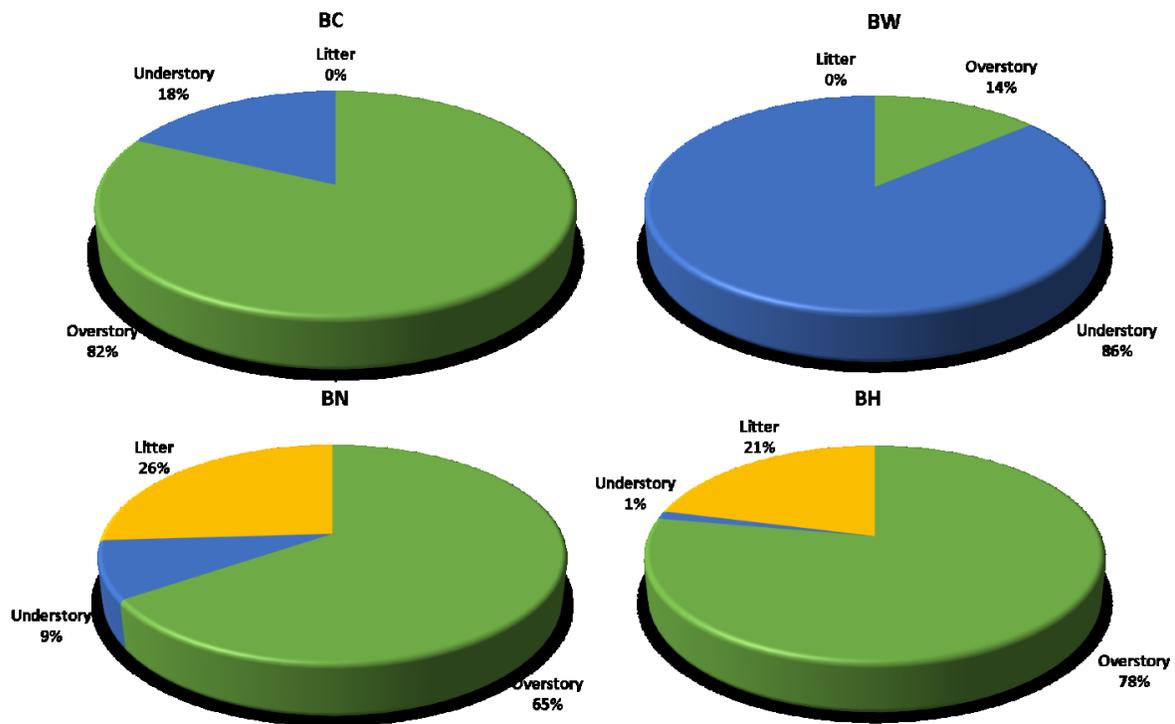
Fig. 10. Contributions of each component (overstory, understory and litter) to total aboveground net primary productivity (aNPP) per component for each of the four treatments. BH=herbaceous control treatment, BN=untreated, BC=complete control treatment, and BW=woody control treatment.

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It was expected that uNPP would follow a pattern like this: Broadcast Woody Control > Untreated> Broadcast Complete Control >Broadcast Herbaceous Control (BW>BN>BC>BH). This is correct for BW treatments, where the mean understory contribution was 86%. However, the results show that understory contribution on BN treatments was not greater than in BC (9% and 18% respectively). BH treatments did show lower contribution of their understory, as expected, with only 2% of total aNPP coming from the understory.

One-way ANOVA detected a significant difference among treatments ($F=161.64$ and $Pr>F<0.0001$). A Tukey HSD test determined three distinct groups (Table 8).

Table 8. Results from Tukey HSD test for percent of contribution of understory to total aNPP among treatments (alpha 0.05).

Tukey grouping		Mean contribution to total aNPP (S.D.) %	N	Treatment
	A	86.16 (6)	3	BW
	B	19.03 (7.6)	3	BC
C	B	9.63 (4.1)	3	BN
C		1.7 (0.6)	3	BH

Note: Means (Standard Deviation) in the same group are not significantly different. BW=woody control treatment, BC=complete control treatment, BN=untreated, and BH=herbaceous control treatment. N=number of replicates.

The first group A included only the BW treatment (as mentioned before with a mean of 86% of understory contribution to total aNPP). BW had a very well developed *Calamagrostis* layer that resulted in the highest productivity of the understory.

BC formed group B with contribution of 19%. BN was intermediate between BC and BH and did not differ significantly from them. The contribution of the understory in BC treatments (total aNPP=151.5 gC/m^2/y) was similar to the contribution of understory in BN (total aNPP=507.23 gC/m^2/y) because even when the production of understory layers was low in BC overstory production was also low.

Tukey group C included BH. In BH plots the understory was not developed and contributed very little to total aNPP because in BH all herbs were removed, shade and litterfall from aspen inhibited regrowth of the understory, and aspen is the functional group that contributed the most to aNPP.

3.4   Community vertical structure affects light use efficiency

Total light use efficiency is the result of total aNPP divided by total aPAR. Total LUE varied from 0.19 to 0.94 gC/MJ across all treatments (Table 9). The differences among means of treatments were statistically significant (p=0.0041) (Fig. 11).

Table 9. Total light use efficiency (tLUE) (gC/MJ) on each plot

Plot	Treatment	tLUE (gC/MJ)
4	BN	0.60
10	BW	0.25
11	BC	0.22
15	BH	0.68
16	BW	0.22
29	BC	0.44
30	BH	0.94
32	BC	0.69
33	BN	0.85
34	BW	0.19
35	BN	0.77
40	BH	0.89

Note: BH=herbaceous control treatment, BN=untreated, BC=complete control treatment, and BW=woody control treatment.
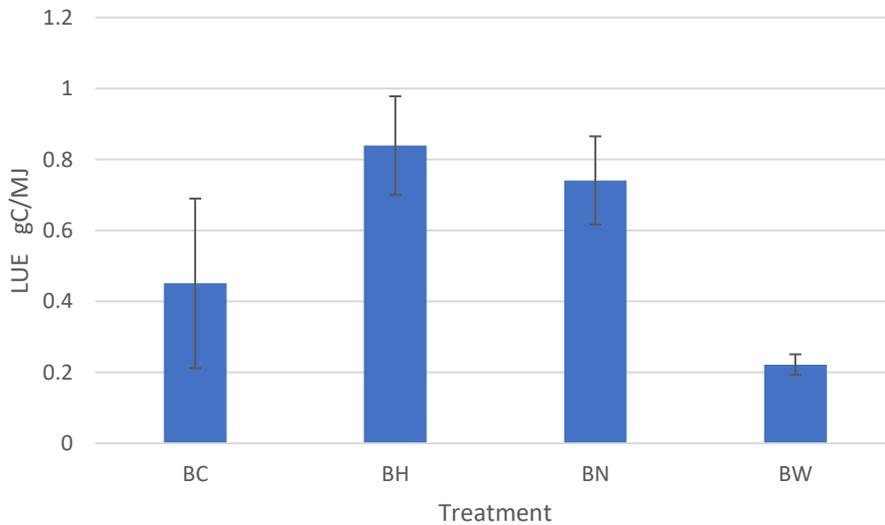
Fig. 11. Treatment effects on total light use efficiency (LUE) (gC/MJ) for each of the four treatments. Error bars indicate the 95% confidence intervals. BC=complete control treatment, BH=herbaceous control treatment, BN=untreated, and BW=woody control treatment.

The most efficient treatment was BH (LUE=0.84 gC/MJ) followed by BN (LUE=0.74 gC/MJ), BC (LUE=0.45 gC/MJ) and the less efficient was BW (LUE=0.22 gC/MJ). However, further analyses with a Tukey HDS test separated the treatments in only two groups that were significantly different. The first one included BH and the second one BC and BW (Table 10), while BN was intermediate between BH and BC and did not differ significantly from other treatments.

Table 10. Results from Tukey HSD test for total light use efficiency (LUE) (alpha 0.05).

Tukey grouping		Mean LUE (S.D.) (gC/MJ)	N	Treatment
	A	0.84 (0.14)	3	BW
	A	0.74 (0.12)	3	BC
B	A	0.45 (0.24)	3	BN
B		0.22 (0.03)	3	BH

Note: Means (Standard Deviation) in the same group are not significantly different. BW=woody control treatment, BC=complete control treatment, BN=untreated, and BH=herbaceous control treatment. N=number of replicates.

Analysis of light use efficiency (LUE) for each functional group results in values ranging between 0.22 and 0.76 gC/MJ in average (Table 11).

Aspen was present only on BH and BN treatments. The average of LUE for aspen was 0.58 gC/MJ. Even when LUE is greater on BH (0.65 gC/MJ) than on BN (0.48 gC/MJ), they were not statistically different (F value=2.25 and Pr>F 0.2079).

Table 11. Light use efficiency (LUE) (gC/MJ) for each functional group and total for each treatment.

Functional Group	LUE (gC/MJ) per treatment					
	BC	BH	BN	BW	Average	p value
Aspen	0.0 b	0.66 a	0.5 a	0.0 b	0.58	0.2079
Spruce	0.44 a	0.33 ab	0.02 b	0.1 ab	0.22	0.0193
Grasses	0.21 a	0.01 a	1.56 b	0.18 a	0.49	<0.0001
Herbs	0.18 a	0.07 a	1.09 b	0.07 a	0.35	0.0001
Shrubs	0.09 a	0.1 a	2.79 b	0.06 a	0.76	<0.0001
Mosses	0.38 a	1.89 b	0.12 a	0.01 a	0.6	0.6591
Total	0.45 ab	0.84 a	0.74 ab	0.22 b	0.56	0.0041

Note: Different letters indicate a significant difference between treatments (Tukey's test at alpha 0.05). BC=broadcast complete control, BH=broadcast herbaceous control, BN=untreated, and BW=broadcast woody control.

The overall LUE for spruce was 0.22 gC/MJ. There was a significant treatment effect among LUE of spruce (F value=5.98 and Pr>F 0.0193). There was a Tukey group formed among those treatments where vegetation control was performed, BC, BH and BW; and another group that excluded the complete control treatment (BH, BW and BN).

Overall LUE for herbs was 0.35 gC/MJ. There was a significant treatment effect on LUE for herbs (p=0.0001). Tukey test identified two complete separate groups. The first one includes treatments where vegetation control was applied (BW, BC and BH). In them, LUE was very low with an average of 0.11 gC/MJ. The other group included only plots where no control was done, and the efficiency of herbs reached an average of 1.09 gC/MJ.

There was also a treatment effect on the LUE of grasses (p<0.0001). According to the Tukey test grasses were also most efficient in plots were no control was applied (BN treatment) with a LUE of 1.56 gC/MJ. If vegetation control was applied, their efficiency declined to 0.19 gC/MJ in those treatments where aspen was removed (BW and BC). The lowest LUE for grasses is found at 0.01 gC/MJ on those plots where they were controlled along with other herbs (BH treatments). However, there was no significant difference among the means of treatments where vegetation control was performed.

Maximum LUE for shrubs was found in plots were no control was applied (BN) with an average LUE of 2.79 gC/MJ. On those plots where vegetation control treatments were applied the average LUE for shrubs was significantly different with an average of 0.09 gC/MJ.

Mosses also presented a high LUE with an average of 0.6 gC/MJ. They were more efficient where herbs were controlled (BH) with LUE of 1.89 gC/MJ. This treatment was separated by the Tukey test from the other three treatments that averaged a LUE of 0.17 gC/MJ. BC treatments had a LUE of 0.38 gC/MJ and where no treatments were applied the LUE was 0.12 gC/MJ. The lowest efficiency for mosses was found where aspen was removed (BW) with a LUE of 0.01 gC/MJ.

One-way ANOVA did not detect a significant difference in mean LUE between functional groups (p= 0.6591). (Fig. 12).
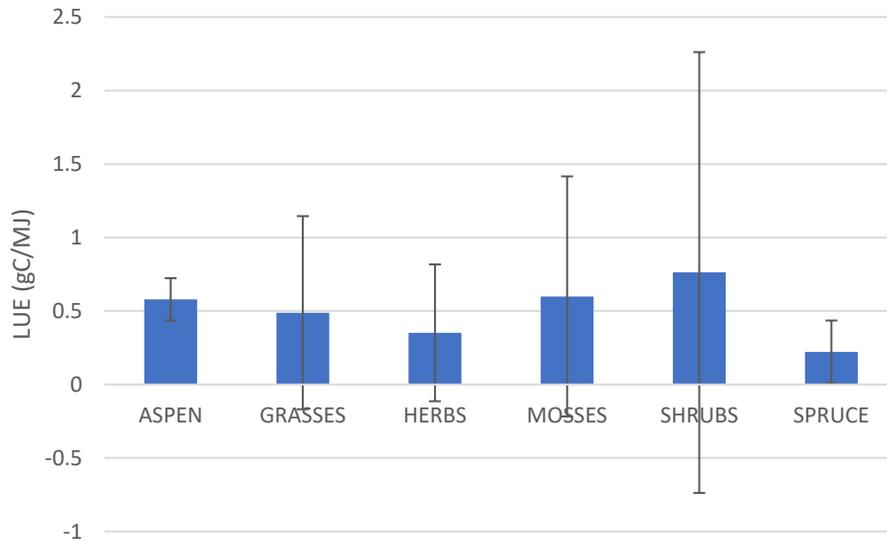
Fig. 12. Differences in light use efficiency (LUE) (gC/MJ) between functional groups across all treatments (+/-1 S.D.).

3.5   Relationship between LUE and LAI

Regression and correlation analysis were used to examine the relationship between LUE and LAI. The relationship between tLUE and tLAI was not significant using linear or non-linear models ($p > 0.05$) (Table 12). However, a Pearson correlation analysis showed that while there was no correlation between tLUE and tLAI, tLUE is well correlated to oLAI ($p < 0.05$) (Table 13).

Table 12. Results from linear and non-linear regressions of total leaf area index (tLAI) versus total light use efficiency (tLUE)

Y	X	p	r²	Equation
tLUE	tLAI	0.1428	0.1226	$y = 0.0633x + 0.3528$
		0.2647	0.2550	$y = 0.014x^2 - 0.0376x + 0.48$
		0.0701	0.5660	$y = -0.0307x^3 + 0.339x^2 - 0.899x + 0.875$
		-	0.1434	$y = 0.3293e^{0.1152x}$
		-	0.0539	$y = 0.0688\ln(x) + 0.5006$

Table 13. Pearson correlation coefficients for total light use efficiency (tLUE) with total leaf area index (tLAI), overstory leaf area index (oLAI) and understory leaf area index (uLAI)

	tLUE	tLAI	oLAI	uLAI
tLUE	1	0.449	**0.785**	-0.455
		0.143	**0.003**	0.137

Note: tLUE=total light use efficiency, tLAI=total leaf area index, oLAI=overstory leaf area index, uLAI= understory leaf area index. N = 12 Prob > |r| under H0: Rho=0

Regression analysis showed a significant positive relationship between tLUE and oLAI (p=0.003, adj-r^2=0.578). There were also positive but weak significant relationships between oLUE and oLAI (p=0.0423, adj-r^2=0.286) but no significant relationship between understory LUE and uLAI (p=0.8737, adj-r^2=-0.097) (Fig. 13, 14 and 15 and Table 14).

Table 14. Results from linear regressions of leaf area index (LAI) versus light use efficiency (LUE).

Y	X	p	Adj r²	Equation
tLUE	oLAI	0.0025	0.578	y=0.119x + 0.298
oLUE	oLAI	0.0080	0.286	y=0.0801x + 0.245
uLUE	uLAI	0.8737	-0.097	y=-0.019x + 0.494

Note: tLUE=total light use efficiency, oLUE=overstory light use efficiency, uLUE=understory light use efficiency, oLAI=overstory leaf area index, uLAI= understory leaf area index.
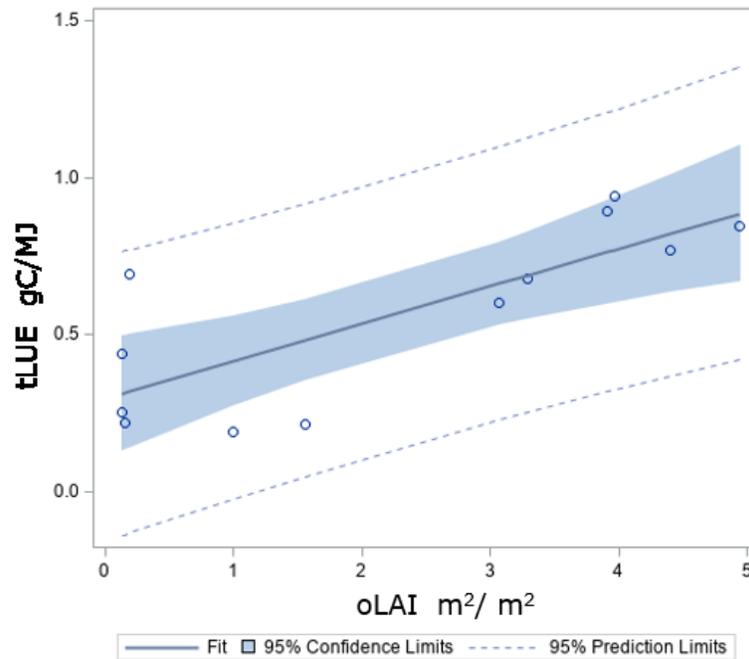
Fig. 13. The linear relationship between total light use efficiency (tLUE) (gC/MJ) and overstory leaf area index (oLAI) (m²/m²) and scatter of datapoints (the equation for the linear relationship is shown in Table 13).
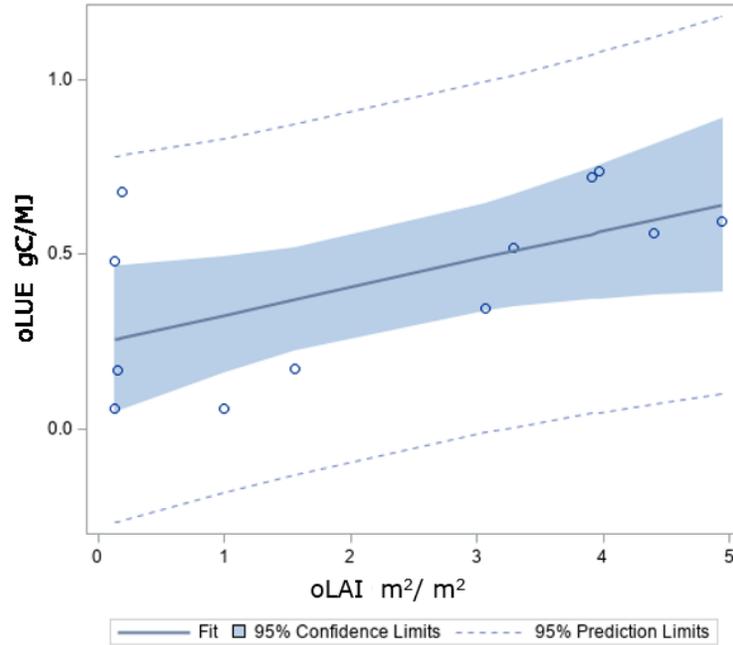
Fig. 14. The linear relationship between overstory light use efficiency (oLUE) (gC/MJ) and overstory leaf area index (oLAI) (m^2/m^2) and scatter of datapoints (linear equation is shown in Table 13).
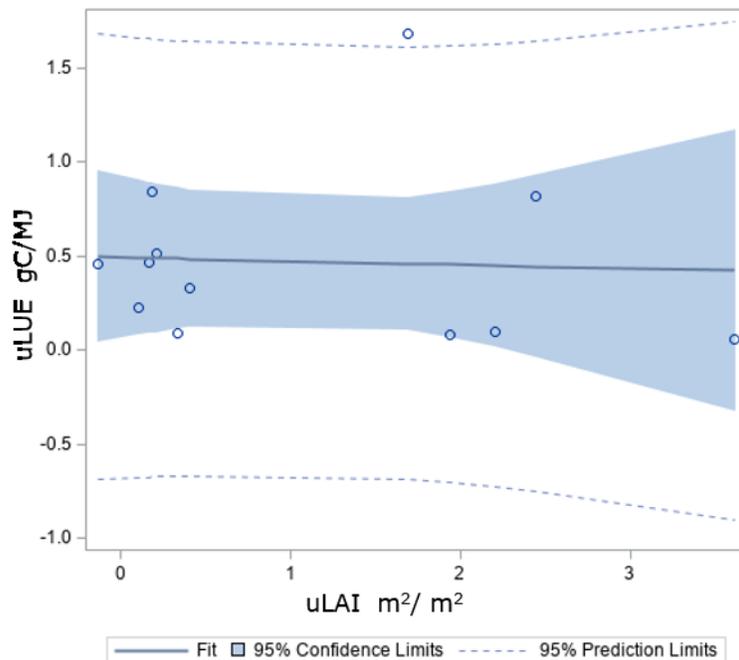
Fig. 15. The linear relationship between understory light use efficiency (uLUE) (gC/MJ) and understory leaf area index (uLAI) (m^2/m^2) and scatter of datapoints (linear equation is shown in Table 13).

3.6   LAI and aNPP

tLAI ranged from 0.3 to 6.8. There was a treatment effect on tLAI that separated the treatments into two groups (p=0.0093). From that separation we conclude that tLAI is significantly different between BC (0.9) and BN (5.56). BW (3.03) and BH (3.8) are intermediate and not different from the other two groups (Table 15).

Overstory LAI also differed significantly between treatments (p=0.0002). Tuckey test identified two separate groups. The first group includes treatments where aspen was removed (BW=0.43 and BC=0.63) and the second group includes treatments where aspen was present (BH=3.72 and BN=4.14).

A Tukey test also identified two groups for uLAI. Group A included BW (2.59) and group B included BC (0.28) and BH (0.19). BN (1.44) presented intermediate values of LAI between these two groups.

Table 15. Leaf area index (LAI) (m^2/m^2) per treatment. Different letters indicate a significant difference between treatments (Tukey's test at alpha 0.05)

	Mean LAI (S.D.) (m^2/m^2) per treatment				
	BC	**BH**	**BN**	**BW**	**p value**
Total	0.91 (0.91) b	3.8 (0.36) ab	5.58 (2.01) a	3.01 (0.86) ab	0.0093
Overstory	0.63 (0.8) b	3.72 (0.37) a	4.14 (0.96) a	0.43 (0.49) b	0.0002
Understory	0.28 (0.16) b	0.08 (0.19) b	1.44 (1.15) ab	2.59 (0.9) a	0.0110

A regression analysis to evaluate aNPP in relationship with tLAI showed a significant positive relationship between both parameters (p=0.007, adj-r^2=0.490) (Fig. 16). Positive significant relationships were also found between oNPP and oLAI (p <.0001, adj-r^2=0.790) and uNPP and uLAI (p=0.003, adj-r^2=0.560) (Fig. 17 and 18). However, the best fit relationship found was between aNPP and oLAI with a p<0.0001 and an adj-r^2=0.890 (Table 16) (Fig. 19).

Table 16. Results from linear regressions of leaf area index (LAI) (m^2/m^2) versus net primary productivity (NPP) ($gC/m^2/y$).

Y	X	P	Adj r²	Equation
aNPP	tLAI	0.0071	0.4853	y = 75.6x + 86.49
oNPP	oLAI	<0.0001	0.7908	y = 84.04x +34.32
uNPP	uLAI	0.0029	0.5666	y = 29.12x + 19.22
aNPP	oLAI	<0.0001	0.8920	y = 106.01x + 101.64

Note: aNPP=total aboveground NPP, oNPP=overstory NPP, uNPP=understory NPP, tLAI=total leaf area index, oLAI=overstory leaf area index, uLAI= understory leaf area index.
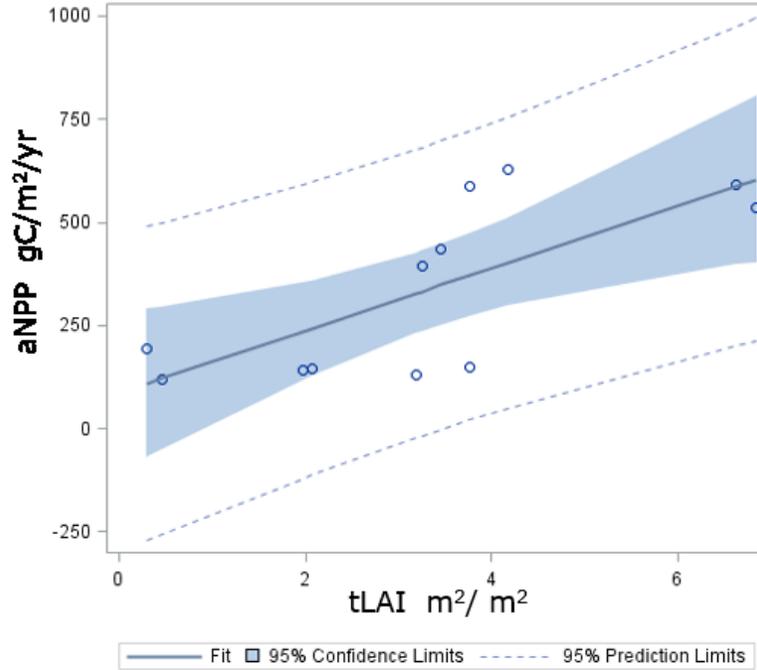
Fig. 16. The linear relationship between total aboveground net primary productivity (aNPP) (gC/m²/y) and total leaf area index (tLAI) (m²/m²) and scatter of datapoints (the linear equation is shown in Table 15).
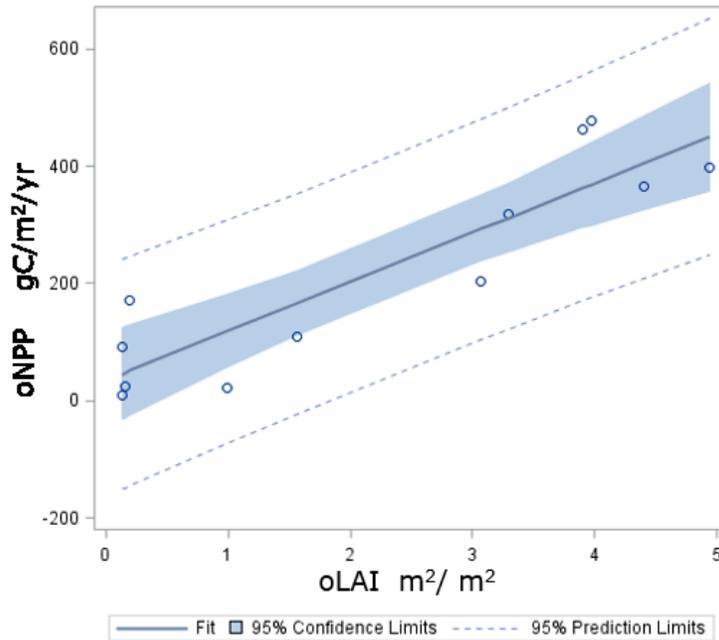
Fig. 17. The linear relationship between overstory net primary productivity (oNPP) (gC/m²/y) and overstory leaf area index (oLAI) (m²/m²) and scatter of datapoints (the equation for the line is shown in Table 13).
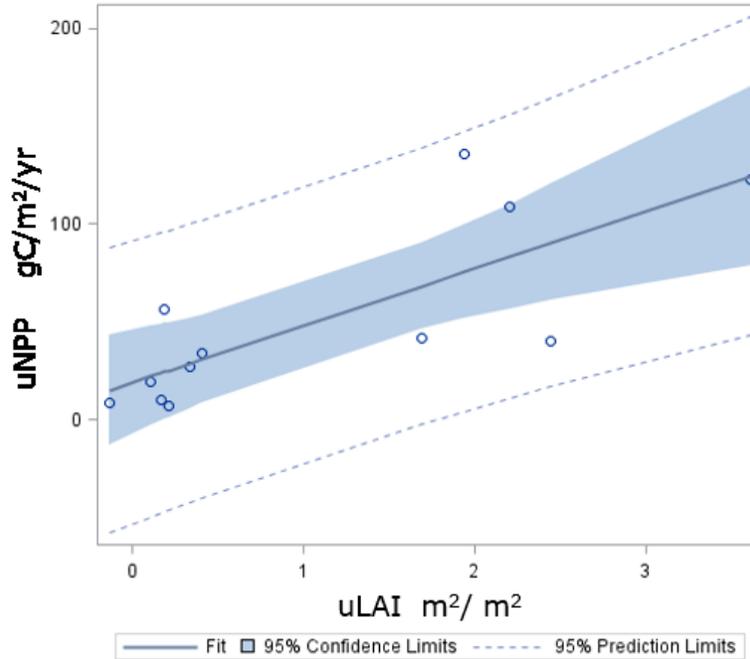
Fig. 18. The linear relationship between understory net primary productivity (uNPP)(gC/m²/y) and understory leaf area index (uLAI)(m²/m²) and scatter of datapoints (the equation for the line is shown in Table 13).
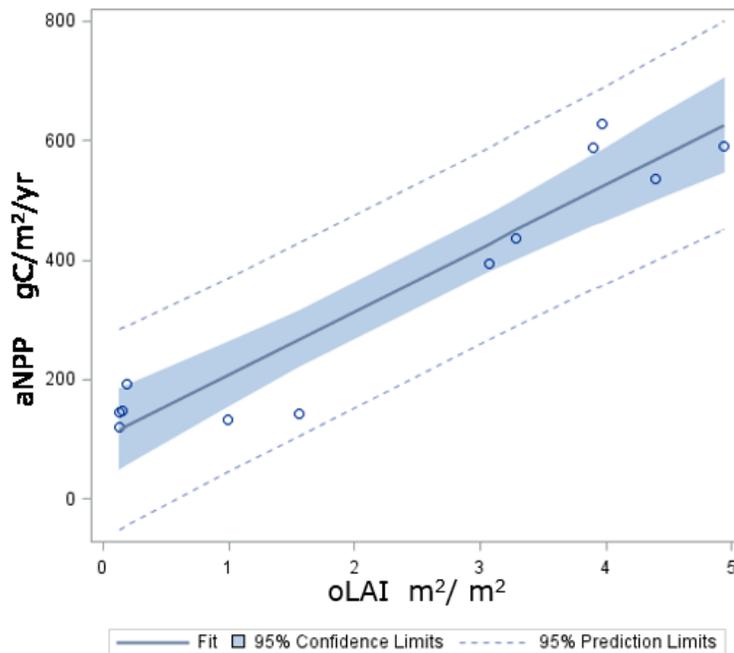
Fig. 19. The linear relationship between total aboveground net primary productivity (aNPP) (gC/m²/y) and overstory leaf area index (oLAI) (m²/m²) and scatter of datapoints (the equation for the line is provided in Table 13).

4. Discussion

4.1 Effect of community vertical structure on the productivity of a forest

Results from this study show that applying vegetation control treatments changes the vertical structure of young mixedwood communities and influences net primary productivity.

In boreal forest, aNPP has been reported to range from 51 to 938 gC/m^2/y (Table 17). In this study aNPP is compatible with these results ranging from 119 to 627 gC/m^2/y.

Table 17. Comparison of productivity (gC/m^2/y) reported in several studies from 1997 to 2011.

Type of forest	Years	aNPP (gC/m^2/y)	Study
Aspen	1993-1994	249-352	Gower et al. (1997)
Black spruce	1993-1995	111-166	Gower et al. (1997)
Young Jack pine	1993-1995	51-92	Gower et al. (1997)
Old Jack pine	1993-1995	98-122	Gower et al. (1997)
Old aspen	1994	342-361	Ryan et al. (1997)
Canadian forests	1895-1996	250-350	Chen et al. (2000)
Young aspen	1995-1997	460	Reich et al. (2001)
Young Black spruce	1995-1997	160	Reich et al. (2001)
Canadian forests	1920-1995	105-330	Li et al. (2003)
Boreal evergreen forest	varies	211	Zheng et al. (2003)
Boreal mixed forest	varies	251	Zheng et al. (2003)
Mixed forest	1997-1999	810	Lagergren et al. (2005)
Deciduous forest	1994-1996	505	Kang et al. (2006)
Coniferous forest	1994-1996	157	Kang et al. (2006)
Boreal broadleaf deciduous	1982-2000	596	Kimball et al. (2006)
Boreal coniferous forest	1982-2000	441	Kimball et al. (2006)
Canadian managed forest	1990–2008	352	Stinson et al. (2011)

Studies report that aNPP is greater in managed forest than unmanaged forest. Stinson et al. (2011) reports an average aNPP of 352 $gC/m^2/y$ for managed forest in Canada, which is higher than the values reported by Chen et al. (2000) and Li et al. (2003) that report aNPP for Canadian forest in general without differentiating between managed and unmanaged. Seedre and Chen (2010) also agreed that managed forests have higher productivity than unmanaged. Noormets et al. (2015) explain that more of the assimilated carbon is allocated to aboveground pools in managed than in unmanaged forests, and less allocation of carbon goes to fine roots and rhizosymbionts. This shift in allocation patterns in managed forest is promoted by increasing plant size and by increased nutrient availability (Noormets et al., 2015).

Aboveground NPP is the result of the productivity of the overstory, the understory and the litter production. The treatments applied in this study result in different vertical structures that impact the overall aNPP, not only at the overstory level but also in the understory and litter components.

In aspen dominated stands (BH and BN treatments) at my study site aNPP ranges from 460 to 661 $gC/m^2/y$ with an average of 560 $gC/m^2/y$ while aNPP ranges from 119 to 192 $gC/m^2/y$ with an average of 147 $gC/m^2/y$ in spruce dominated stands (BC and BW treatments). These results show much higher productivity in stands where deciduous trees are the dominant species versus stands where deciduous trees are not present, and the conifers are the dominant trees. This is a consistent pattern that has also been reported by other authors (Cleve et al., 1983; Ruess et al., 1996; Gower et al., 1997, 2001; Reich et al., 2001; Zheng et al., 2003; Kang et al., 2006).

Gower et al. (1997) reports values of 349-352 $gC/m^2/y$ for deciduous stands and 117-122 for conifers stands and mention that possible causes of this greater aNPP in deciduous forest are the greater capacity to absorb light (i.e. LAI) and the greater intrinsic capacity to convert solar radiation to dry matter (i.e. LUE).

Indeed, LAI in stands dominated by aspen (BN and BH) is greater than LAI in stands with spruce as dominant overstory species (BW and BC). This is not only true respecting tLAI but is even clearer when comparing oLAI. BN has an average of oLAI of 4.14 and BH of 3.72 while BC oLAI is only 0.63 and BW is 0.43. Greater LAI gives the stand a greater capacity of absorb light.

The other cause of greater aNPP in deciduous forest is related to the capacity to convert absorbed light into actual biomass. LUE explains this concept. Aspen uses light in a more effective way than spruce. In this study aspen presents an average LUE of 0.58 gC/MJ while LUE of spruce is only 0.22 gC/MJ.

Kang et al. (2006) explain that deciduous forests exhibit a more rapid productivity response to nutrient availability (i.e. nitrogen availability) because they have a shorter leaf canopy turnover rates relative to coniferous forests. Despite this, Reich et al. (2001) concluded that deciduous forests have higher aNPP than conifers even when growing on comparable soils.

Other possible causes of the greater aNPP in aspen dominated plots are:

1) Photosynthetic rates of aspen compared to spruce. Trembling aspen is a shade intolerant species, and as such it has an intrinsic higher photosynthetic rate than shade-tolerant species as white spruce (Boardman, 1977).

2) Higher tissue percentage of nitrogen than white spruce. Trembling aspen leaves have a 2.76% of nitrogen compared to only 1.51% of nitrogen in white spruce needles (unpublished field data).

3) Greater litterfall nitrogen and better litter quality in aspen plots which lead to greater nitrogen mineralization rates (Paré, D. & Bergeron, Y., 1996; Côté L. et al., 2000).

Gower et al. (2001) found poor correlations between climate variables (such as mean annual temperature, mean annual precipitation and latitude) and aNPP and they suggest that environmental conditions influence NPP of boreal forests, but only at the continental to biome scale.

Another aspect to consider when analyzing aNPP among treatments is the way that these treatments affected understory productivity. uNPP was significantly different among treatments. The effect of treatments on the productivity of the understory and its contribution to the total aNPP will be further discussed in the next section (4.2).

In this study, litter production in conifer stands was negligible and difficult to estimate accurately so litter input to aNPP was only considered in BN and BH treatments. However, even in those treatments, the litter traps did not capture herbaceous and shrubs litterfall so in general, aNPP was slightly underestimated.

After evaluating how aNPP changes between the treatments applied we can certainly assume that there is a clear effect of the different treatments on the total productivity of the forest, at least in the first 10 years after establishment.

There are general and consistent patterns that relate aNPP with the age of the stand, with an initial increase of aNPP up to a peak value followed by a decline (He et al., 2012). Leaf area also changes with stand age (Bond-Lamberty et al., 2002, Goulden et al., 2011). We can see in Figure 20 that evergreen species have a low LAI at young age and rapidly increase around age 20 (Goulden et al., 2011). On the other hand, aspen LAI shows a sharp increase with stand age and reaches a maximum around 15 to 25 and then starts declining. This being the case, we would expect that stands where spruce dominates the overstory will increase their LAI and then increase their productivity. However, we do not know if this increase will be enough to equal the productivity of the aspen dominated stands. More research will be needed to determine how conifer and deciduous LAI change in the future on this site.
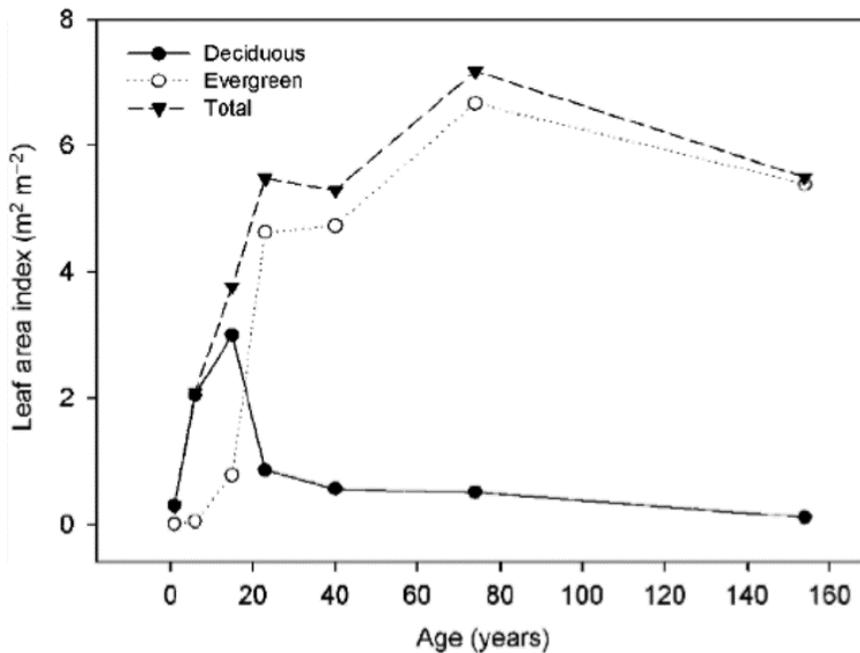
Fig. 20. Deciduous, evergreen and total LAI as a function of stand age (Goulden et al., 2011).

4.2   Importance of considering understory contribution to NPP

Several studies suggest the importance of understory contribution to NPP, particularly to aNPP (Yarie, 1980; Nilson and Wardle, 2005). Vegetation control treatments applied at this study site affected the composition and vertical structure of the plots resulting in changes to growth rates and productivity of the whole system.

After analyzing total aNPP two groups of treatments were defined: the first one where aspen was the dominant tree and the second one where spruce was dominating the overstory layer. However, when these groups were analyzed further, differences in the understory productivity also emerged.

On those treatments where aspen is the dominant tree, the understory productivity between them is significantly different. BN presented a much higher uNPP compared to BH. Leaf area index of the understory can explain this difference. As herbicide treatments were applied to control the growth of herbs, grasses and shrubs, the LAI of the understory is very low in the BH treatment (0.07) compared to the LAI of the understory on those plots where no control (BN) was applied (1.44). Lower LAI means less area for radiation interception and results in less biomass production (Leverenz and Hinckley, 1990 and Gholz 1976).

In treatments where aspen was removed, the uNPP was also significantly different. On those plots where herbs and woody plants were controlled (BC) the uNPP was lower than on those where they were not controlled (BW). It is worth to emphasize that the maximum understory productivity was reached in treatments

where aspen was removed but herbs and grasses were not controlled (BW), causing a large growth of *Calamagrostis* and other grasses. In absence of aspen, *Calamagrostis* took over and became very productive, explaining the highest uNPP in this treatment.

As already mentioned, BW developed the largest uNPP, in fact it also presented the largest contribution to the total aNPP with 86% of the total. The understory productivity in this treatment was certainly higher than in the rest of the treatments, however this highly developed understory was not enough to offset the productivity of a missing layer of overstory aspen found in the BH and BN treatments.

The contribution of the understory in BW treatments is well above of the range reported in other studies, where understory contributes from 11 to 50% of the estimated aNPP (Yarie, 1980; and Nilsson and Wardle, 2005). In the rest of the treatments, the understory contribution to NPP ranged from 1 to 18%, close to the range reported by these other authors.

BH not only presented the lowest of all understory productivity, its contribution to total aNPP was also the lowest with no more than 1% of the total aNPP. This can be explained because the application of herbicides to control any growth in the understory was very effective with virtually no herbs, grasses or shrubs growing on those plots. It is worth to mention that in terms of contribution of the understory to the total aNPP, the contribution in BH (<1%) was not statistically different than the contribution of the understory in BN treatments (9%), even when the amount of total understory productivity was different between these treatments. This BH treatment is unusual and is not used operationally in forestry,

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but was done only for the purposes of research aimed at examining effects of woody and herbaceous competition on growth of white spruce.

Plots where no vegetation control treatment was applied (BN) developed a forest with a well-defined vertical structure where the understory contributed an average of 9% to the total aNPP. Statistically BN and BC were not different in terms of their understory contribution. BN plots had well defined functional groups that result in reasonable understory productivity (mean of 46.10 $gC/m^2/y$) but they were not significantly higher than those plots where complete control of the understory and deciduous was performed, even when the understory contributed 18% of the total aNPP in those treatments.

In plots where complete control of vegetation was applied some grasses (*Poa spp*) and *Equisetum spp* had established. These species are growing very well in these plots were glyphosate was applied because they were resistant to this herbicide (Binkholder et al., 2011; Torstensson, L and Börjesson, 2004), or established from seed after herbicide treatment. In addition, some *Calamagrostis* and other species remained underneath the spruce following treatment since treatment was directed to avoid applying herbicide to conifer foliage. Following cessation of herbicide application some of these plants have expanded into the treated area of the plots. It should be noted that the BC treatment is also not representative of operational forestry applications of glyphosate herbicide. For forest vegetation management in a spruce plantation glyphosate is commonly applied once, and occasionally twice. In contrast, the BC treatment in this study involved broadcast herbicide application during the first year of the study, followed

by targeted application to control any shrubs, herbs or grasses over the following 8 years.

As we can see from these results, the understory is highly dynamic and contributes significantly to the productivity of forest ecosystems (Kreyling et al., 2012) with the magnitude of their contribution being influenced by the vegetation management treatments applied.

4.3   Differences in the light use efficiency among communities with different vertical structure.

This study showed that light use efficiency is affected by the treatments applied that created different community vertical structures. The difference of LUE between treatments is especially significant between BH and BW treatments. BH has aspen dominating the overstory while BW presents spruce as the overstory tree along with a thick layer of *Calamagrostis* in the understory. BH presents the highest efficiency of all treatments (0.84 gC/MJ), while BW showed the lowest one (0.22 gC/MJ). This pattern can be explained by the particular efficiencies of the dominant species present on each of these treatments. Aspen LUE is in average 0.58 gC/MJ while spruce LUE is only 0.22 gC/MJ.

LUE has been reported to be different for different species (Table 18). In this study, as mentioned earlier, results showed that aspen has a higher LUE than spruce, which is similar to what has been reported by other authors (Goetz and Prince, 1996; Gower et al., 1998; Liu et al., 1999). For example, Liu et al. (1999)

reports that LUE is about 1.5-2 times higher for deciduous than for coniferous

forest.

Table 18. Comparison of light use efficiency (LUE) (gC/MJ) reported in several studies

Species or forest type	Location	LUE gC/MJ	Study
Coniferous forest	Boreas study region	0.2	Lui et al. (1999)
Picea spp.	Central Canada	0.25-0.40	Hunt and Running (1992)
Picea mariana	Northeast Minessota	0.24	Goetz and Prince (1996)
Picea mariana	Boreas study region	0.34	Gower et al. (1999)
Picea spp.	Northeast Minessota	0.17	Goetz and Prince (1997)
Picea abies	Czechia	0.23-0.33	Bellan et al. (2017)
Deciduous forest	Boreas study region	0.4	Lui et al. (1999)
Populus tremuloides	Central Canada	0.17-0.39	Hunt and Running (1992)
Populus tremuloides	Northeast Minessota	0.45	Goetz and Prince (1996)
Populus spp.	Wisconsin USA	0.53-1.1	Green et al. (2001)
Populus spp.	Scotland, UK	0.75	Canell et al. (1988)
Populus tremuloides	Northeast Minessota	0.46	Goetz and Prince (1997)
Crop	Boreas study region	0.33	Lui et al. (1999)

Note. Values reported as gWDM/MJ were transformed to gC/MJ considering that 50% of the dry matter weight is carbon. Values considering total NPP were considered to be 60% overstory in order to get the efficiency for aNPP.

Goetz and Prince (1996) reported average values of LUE of 0.46 gC/MJ in

aspen versus values of 0.24 gC/MJ in spruce. They mentioned that the difference of

LUE between these two species can be explained by differences in life history,

particularly differences in the energy requirements associated with different

resources allocation strategies.

However, other studies have reported exactly the opposite. Boardman (1977) reports that spruce has higher LUE than aspen and Kaufmann and Ryan (1986) concluded that understory trees may be as efficient as dominant trees. They explain that the foliage of shade tolerant species has lower compensation and saturation points for photosynthesis, and then higher light use efficiency than shade intolerant species. However, my results suggest that spruce in the understory was less efficient than overstory aspen. It is possible that this may reflect impacts of browsing by snowshoe hare on the white spruce growing in the understory of the BH and BN treatments.

Treatment effects on LUE differed between functional groups. Aspen was not significantly different in terms of LUE between the two treatments where we found them as dominant in the overstory. Spruce had significantly higher LUE in BC treatments than in untreated plots. As Olson et al. (2011) mention, early herbicide application is effective in creating softwood-dominated stands as this early vegetation control provides the optimum environment for the establishment and growth of spruce (Groot, 1999) while also reducing the amount of aspen. Having better conditions to grow with no competition in the understory, spruce thrive reaching the maximum LUE among all treatments.

For herbs, grasses and shrubs we found no difference among the treatments where vegetation control was applied, however they were significantly less efficient than in untreated plots. These three functional groups reached the highest LUE when left untreated. Reasons for this could be that there was no presence of any kind of herbicide that could cause a detriment in the productivity of any of these functional groups.

Bryophytes showed a relatively low LUE with the exception of plots where all herbs were controlled through the application of herbicides. Newmaster et al. (1999) explain that colonizers and drought-tolerant species of mosses begin to recover 1 year after a disturbance (e.g. application of herbicides). The higher availability of light in BH plots along with the lack of competition with other understory species can explain how those plots treated with herbicides (BH) showed a higher productivity and efficiency of bryophyte following treatments.

Several factors have been found to influence light use efficiency including light absorption, light penetration, length of the growing season, and nutrient availability. In general, in the absence of any other limiting factor, the low values of LUE can be explained by a low radiation absorption (Phillips and Riha, 1993) that could be the result of either a lower capacity of light absorption of the species or a lower amount of light reaching that species. The length of the growing season has also been reported to affect LUE (Linder, 1987; McMurtrie et al., 1994; Bartelink et al., 1997). However, in this study it is not possible to analyze if there is such effect since all plots were located at the same site with the same length of growing season. Some studies report that nitrogen concentration can affect the values of LUE because LAI is highly nutrient dependent and LAI directly affects the determination of aPAR (Vose et al., 1994), but this is not consistent and other authors found this relationship was not significant (McMurtrie et al., 1994).

LUE values are often used for modelling of forest stands NPP or even GPP (Bartelink et al., 1997; Landsberg and Waring, 1997; Ahl et al., 2004; Wirth et al., 2004; Smith et al., 2008; Hilker et al., 2012). However, many of these studies extract values of LUE from look-up tables based on biomes which can cause

inaccuracies inherent to this way of estimation (Drolet et al., 2005). This inaccuracy has an effect in the estimation of productivities that use the LUE model to calculate NPP.

Gower et al. (1999) suggested that another important source of error in most estimates of LUE is the exclusion of important components of forest production such as the understory production. Ahl et al. (2004) concluded that LUE models should consider species-specific efficiency measurements rather than biome-specific ones. Direct measurements, like the ones that were done in this study, can contribute to the improvement of estimations of carbon fluxes from terrestrial ecosystems at regional and global scales (Drolet et al., 2005).

A weakness of this study is the lack of information of belowground NPP (bNPP) to calculate total NPP and calculate total LUE. Gower et al. (1999) suggested that biomass allocation to belowground components can range from 20% to 75% and therefore it should not be ignored. Since a greater fraction of NPP is allocated to roots in evergreen conifer than deciduous broad-leaved forests (Gower et al., 1999), it can directly influence NPP and LUE.

4.4   Relationship between LAI, LUE and productivity

The relationship between LAI and forest productivity and aboveground net primary productivity has been shown by numerous studies (e.g. Gholz 1982, Linder 1985, Vose and Allen 1988, Vose et al., 1994). This relationship is the result of

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leaves being the primary site of fluxes of CO_2, water and energy (Vose et al., 1994).

LAI is an integrated measure of environmental constraints on resource availability and should be correlated to NPP (Grier and Running 1977, Gholz 1982, Fassnacht and Gower 1997). In fact, several studies have used LAI to correlate or estimate biomass and productivity (Leverenz and Hinckley, 1990; Friedl e al., 1994; Gower et al., 1997, 2001; Green et al., 2001; Bond-Lamberty et al., 2004; Pope and Treitz, 2013)

In this study aNPP was significantly related to tLAI. Moreover, aNPP has a strong positive relationship with oLAI. These results agree with other studies that also found relationships between these two parameters that range from weak correlations to strong relationships (Gower et al., 1997 and 2001, Bond-Lamberty et al., 2004, Pope and Treitz, 2013).

According to this study oNPP = 84.04 oLAI +34.32. Bond-Lamberty et al. (2004) found a very similar relationship for mixedwood forests: NPP_{TREE} = 80.0 LAI_{TREE} (Fig. 21). We can see that LAI of the tree layer (overstory) is significantly and directly affecting the aNPP. Liu et al. (1999) also found that NPP was strongly correlated to LAI and that this relationship is linear when LAI is below 4 and then becomes asymptotic (saturated) as LAI increases further. They explained that this saturation occurs because at large LAI values, the increase in canopy radiation absorption becomes small. My results show a linear relationship for these young stands due to their relatively low LAI, but it would be interesting to implement future research that can evaluate what happens at higher levels of LAI.

Gower et al. (2001) observed a weak positive correlation between LAI and aNPP ($r^2 = 0.200$, $P < 0.05$) for conifer boreal forests, but found that the relationship was insignificant for boreal deciduous forest. However, these positive significant relationships have not always being found. Green et al. (2001) report that the aboveground biomass gain in poplar species is unrelated to canopy light interception.
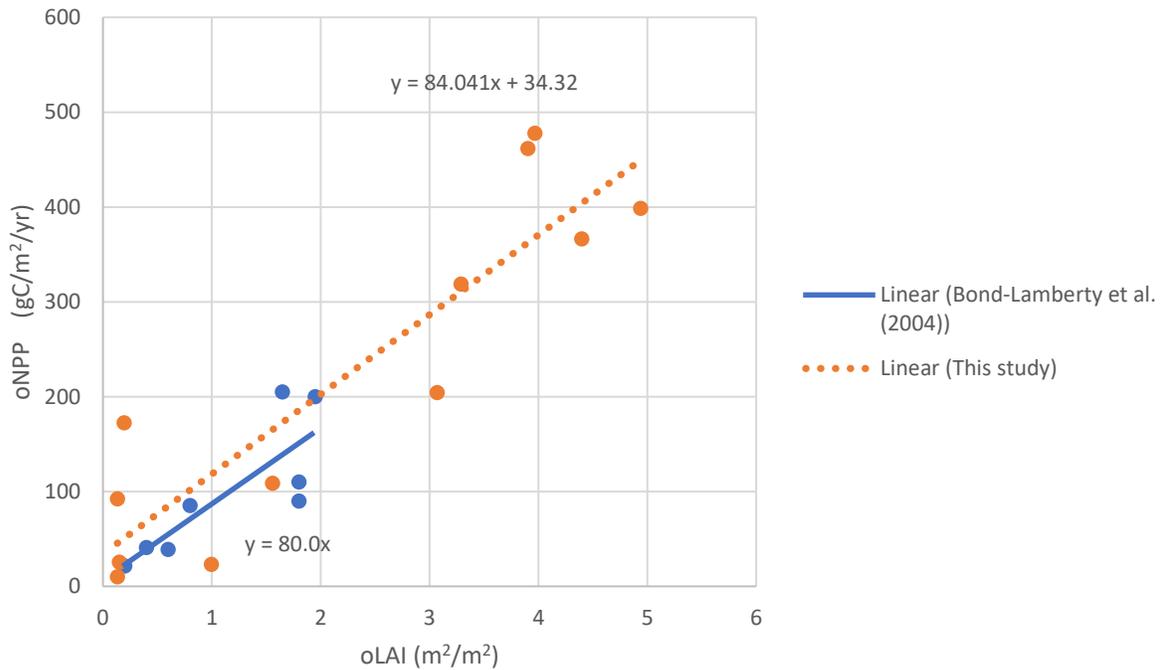
Fig. 21. Comparison between the relationship overstory leaf area index (oLAI) (m^2/m^2) versus overstory net primary productivity (oNPP) (gC/m^2/y) found in boreal mixedwoods by Bond-Lamberty et al. (2004) and the relationship found in this study.

These differences in results from studies examining relationships between aNPP and LAI likely arise because these parameters can be affected by the range of

stand age, and may also be influenced by stand origin, stand management, climate, site, and other factors.

According to the Light use efficiency model (Monteith, 1972), the relationship between NPP and aPAR is linear and the LUE is the coefficient between both and is expressed as the amount of carbon produced per unit of absorbed PAR (gC/MJ).

Developing a relationship that allows us to estimate LUE with more precision could be beneficial in other fields like remote sensing. Prince (1991) concluded that if LUE is a constant for the vegetation under consideration, remotely sensed measurements can be used to measure NPP over large areas and at high temporal frequencies, making the value of LUE of considerable significance for remote sensing of primary production.

We can also relate LUE to LAI. In the present study we found a correlation between LUE and oLAI. The relationship between these two was positive and significant (p=0.0025, adj-r^2=0.578). We also found a positive but weakly significant relationship between oLUE and oLAI and no significant relationship between uLUE and uLAI. These results suggest that the efficiency of a stand is affected by the oLAI but not by the uLAI.

Goetz and Prince (1997) found highly significant relationships between LAI and LUE in spruce and young aspen but conclude that despite the fact that much of the variability in NPP was driven by variables like LAI, the measurement of it would not be sufficient to be used in models to predict LUE or NPP in some boreal forest.

4.5 Contribution of this research to the study of the carbon cycle in young mixedwood forest

With increasing interest in managing forests for carbon sequestration, a knowledge of how management practices can improve carbon capture has become a priority. There are numerous factors that directly affect the productivity of a forest (Bonan and Shugart, 1989; Lloyd, 1999; Boisvenue and Running, 2006; Kljun et al., 2007; LeBauer and Treseder, 2008; Paquette and Messier, 2011). Furthermore, it is not only the amount of resources available but also the ability of the forest to use them and also the efficiency on how those resources are being used (Forrester, 2014).

Moreover, there are numerous studies that demonstrate that productivity is highly affected by the age of the stand (Litvak et al., 2003; Grant et al., 2007; Goulden et al., 2011; He et al., 2012). Houghton et al. (2009) suggested that rapid tree growth at the beginning of the stand development increases the potential of the forest to sequester a large amount of carbon.

Influencing the LAI and LUE of trees directly affects the net carbon production and therefore terrestrial carbon flux. The study of how LAI changes overtime and how that affects the productivity of a forest is strongly linked to the terrestrial carbon cycle. He et al. (2012) suggested that NPP in young forest rapidly increase reaching a peak in middle ages and then slowly declining in mature forest and concluded that forest management can affect this pattern. It is important to apply the right management strategies in order to favor the forest acting as a sink instead of source. That means that we need to maximize the productivity of a forest

in order to contribute to make the NEP positive. However, when seeking to maximize productivity it is important to include understory vegetation in the determination of NEP.

My results indicate that at least in this study, vegetation control as a management practice, affects not only the development of LAI but also the productivity and the efficiency at which the forest uses the intercepted light. This study contributes to the knowledge of LAI and productivity in young mixedwood and spruce stands.

Most models of carbon dynamics use general information about the productivity of a forest and do not consider the influences of age or stand structure on efficiency (e.g. Sitch et al., 2003; Yuan et al., 2007; Kurz et al., 2009). This study contributes with information on LUE in young stands and also provides information on how these values are affected by management practices such as vegetation control.

5. Conclusions

Vegetation management treatments applied in young mixedwood stands have a considerable impact on the vertical structure of a forest. Such vertical structure affects LAI, LUE and aNPP. One of the main effects of these treatments is in the development of the understory layer that can significantly contribute to the total productivity of the forest.

Total aNPP varies significantly among vegetation management treatments and is clearly higher in treatments where aspen is present, and the herbs are removed. This is the recommended treatment if we want to maximize the total aNPP of a stand without focus on the species growing on them. If there is an interest in maximizing the productivity of spruce along with the total aNPP of the stand, the recommended treatment would be the removal of all herbs and woody plants.

Total aNPP was highest in the Broadcast Herbaceous control followed by untreated, Broadcast Complete Control and finally Broadcast Woody Control treatments. This was due to the rapid growth of aspen and lack of competition in the understory. Untreated plots were second due to a vigorous early growth of aspen in combination with understory vegetation that resulted a large biomass accumulation. Broadcast Complete control was third due to good growth of white spruce and at the end Broadcast Woody Control was the lower due to reduced growth of spruce.

The contribution of the understory to aNPP was also variable depending on the treatments applied that created specific community vertical structures. If the

vertical structure includes a well-developed understory it contributes significantly to aNPP. The significance of including uNPP was related to the abundance (and biomass) of understory resulting from treatments. In the treatments being examined in the Judy Creek Mixedwood Experiment the highest contribution of understory was observed in Broadcast Woody Control followed by Broadcast Complete Control, then Untreated and finally Broadcast Herbaceous Control (where all the understory was removed by the treatment and so it contributed to less than 1% of the total aNPP).

Light use efficiency was also affected by treatments that created differences in the vertical community structure. The efficiency of aspen was not affected by the removal of the understory; however, the efficiency of spruce was different (higher) when a complete control of vegetation was applied to the forest compared to untreated plots. The efficiency of herbs, grasses and shrubs was affected by vegetation control treatments, being always higher in plots untreated. Mosses were significantly more efficient in plots where herbs were removed probably due to colonizing and herbicide-resistant species that thrive in those conditions.

I found a positive relationship between tLUE and oLAI. tLUE improves if oLAI increases. This also applies to the LUE of the overstory but not for the LUE of the understory.

There was also a positive linear relationship detected between total aNPP and tLAI. This relationship is consistent with the expectation that aNPP rises if LAI increases. Beside this relationship we also detected that the best relationship fit was in fact between total aNPP and oLAI.

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