

STAND AGE STRUCTURES OF SINGLE AND MIXED-SPECIES OF FIRE-ORIGIN
BOREAL STANDS IN CENTRAL CANADA

By

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A Thesis Submitted in
Partial Fulfillment of the Requirements for the
Degree of Master of Science in Forestry

Faculty of Forestry and the Forest Environment

Lakehead University

June 2006



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ISBN: 978-0-494-21509-8
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ISBN: 978-0-494-21509-8

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ABSTRACT

Fricker, J.M. 2006. Stand age structures of single and mixed-species of fire-origin boreal stands in Central Canada. 77 pp.

Key Words: biodiversity, bimodal, boreal forest, cover type, developmental stage, old-growth, reverse-J, stand age structure, time since fire, wildlife habitat

Stand age structure has been linked to wildlife habitat and can affect biodiversity. Further, certain stand age structures (such as those associated with old-growth) are valuable from an aesthetic and fiber supply perspective. A review and synthesis of literature indicated that boreal forest stand age structure is influenced by time since stand replacing fire, stand composition, and disturbances such as spruce budworm (*Choristoneura fumiferana*) and wind. Silvicultural options and implications for managing age structure at the stand and landscape level are discussed. My objectives were to examine how stand age structure changes among stand developmental stages and stand cover types.

I sampled living trees in 32 stands representing typical conifer, mixedwood, and hardwood stand types in the central boreal forest region of North America representing the stem exclusion/canopy transition, canopy transition, canopy transition/gap dynamic, and gap dynamic stages of stand development. Using a 400 m² plot in each stand as the sampling unit, the diameter at breast height (DBH) of all canopy trees (DBH ≥ 10 cm) was measured. Five canopy trees in each diameter class ((1) 10-14.9 cm, (2) 15-19.9 cm, (3) 20-24.9 cm, (4) 25-29.9 cm, and (5) ≥ 30 cm) for each species were randomly selected, and the height of each tree was measured and an increment core was taken and aged. Three circular 25 m² subplots were then randomly established within each 400m² plot and the diameter at root collar and height of all seedlings and saplings (DBH < 10 cm) were measured and recorded. A disk was then taken at root collar and aged for 5 seedlings and saplings in each height class. Canopy trees and regeneration were then summed to the plot level and scaled to per hectare.

The results suggest that stand age structure is variable with stand developmental stages and stand cover type. Age distribution in conifer stands was bimodal in the stem exclusion/canopy transition, bimodal in the canopy transition, reverse-J in the canopy transition/gap dynamics, and finally bimodal in the gap dynamics. In the mixedwood stands, similar to the conifers, stand age structure was bimodal in all the stand developmental stages. In the hardwood stands, age structure was bimodal in the stem exclusion/canopy transition, unimodal in the canopy transition stage, reverse-J in the canopy transition/gap dynamics stage and finally bimodal in the gap dynamics stage.

Forest management activities such as partial harvesting, selection harvesting, and seed-tree systems may diversify stand age structures at the stand and landscape levels, benefiting wildlife and creating characteristics of old-growth. It is recommended that quantitative old-growth be defined. I suggest using the following criteria to determine old-growth in the boreal forest: (1) canopy breakdown of pioneering cohort is complete and the stand is dominated by later successional tree species (2) the age structure of the stand is bimodal, with dominating canopy trees that fall within a relatively narrow range of age and height classes and a significant amount of understory regeneration.

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ACKNOWLEDGEMENTS

First and foremost I would like to thank my supervisor Dr. Jian Wang, for his support and guidance throughout this process. I would also like to thank my committee members Dr. Han Chen and Dr. Ken Brown for their constant guidance and assistance. As well, I would like to thank my external reviewer, Dr. Daniel Kneeshaw. Thank you to Mr. Paul Poschmann (Abitibi-Consolidated) for his help in site selection and field assistance. Thank you to my fellow colleagues Brian Brassard and Stephen Hart, as well as our two field assistants Nick Dang and Martina Köhler. I would like to thank Dr. Mathew Leitch for his countless hours in the wood lab helping me construct over 1200 core mounting strips. Thank you to Dr. Peter Dunker for his time reviewing my thesis. I would also like to thank Frank Luckai for his pre-season field training, and Pat Cybulski for his time in the field we spent together collecting tree disks. Lastly, I would like to thank my parents for their never ending support and constant encouragement to accomplish all my goals in life.

CHAPTER 1 GENERAL INTRODUCTION

The boreal forest is one of the largest biomes in the world, encompassing over twelve million square kilometers, and is the largest forested region in Canada (Weber and Stocks 1998). In North America, the boreal forest extends from Newfoundland, Canada in the east to Alaska, USA in the west (Weber and Stocks 1998). Climatically, the area ranges from dry and cold climates with a mean annual temperature of -8°C to a warmer, moist climate with a mean annual temperature of 6°C (Rowe 1972). Fire is the most common stand-replacing disturbance in the boreal forest (Johnson 1992; Weber and Stocks 1998) and the most important factor for controlling vegetation community assemblages and plant succession (Weber and Stocks 1998). The frequency of fire (or its inverse the fire cycle), defined as the “the number of fires per unit area per year” (Bergeron 1991), varies tremendously based on regional climate differences (Johnson 1992; Weber and Stocks 1998). In the western boreal forest, the fire cycle is relatively short, resulting in cyclic succession, where early successional species dominate until being replaced by the next fire due to the frequency of fire in that region (Dix and Swan 1971; Johnson 1992). However, in the eastern boreal forest, the time between fires is relatively long, and succession is directional, leading to species replacement, where early successional species are replaced by later successional species over time (Bergeron and Dubuc 1989; Bergeron and Harvey 1997; Bergeron 2000).

Succession generally brings about changes in stand structure including age structures in the boreal forest (Oliver and Larson 1996; Smith *et al.* 1997; Chen and Popadiouk 2002). As time since stand-replacing fire increases, boreal forests change from an even-aged stand structure (where all trees are the same age), to a two-aged stand

structure (having two age classes occurring within a stand), to an all-aged/uneven-aged stand structure (having three or more age classes) (Oliver and Larson 1996; Smith and Long 2001). While this change has been conceptualized in the literature, few studies to my knowledge have been done on how stand age structure changes with stand development and cover type. Therefore, the goal of my study was to: (1) explore how stand age structure changes with stand development and (2) how stand age structure varies with stand composition (hereafter referred to as stand cover type).

Management decisions surrounding old-growth boreal forests are often hindered by unclear and largely unavailable definitions, as old-growth boreal forest definitions are sparse (Cogbill 1984; Barnard 2004). Due to their importance from an ecological, cultural, economic, and aesthetic perspective (Burton *et al.* 1999; Barnard 2004), research is needed to further describe old-growth forests. Thus, this thesis will describe boreal forest old-growth stand age structure, and investigate how stand age structure differs among stand cover types.

CHAPTER 2 LITERATURE REVIEW

ABSTRACT

The age structure of a stand provides an understanding of important ecological processes taking place during stand development. The age of trees has been estimated by various ageing techniques including historical records, ground level ring and root collar ring counts, dendrochronological cross dating and pithnode counting, and tree size. Each of these methods has inherent advantages and limitations. In the fire-driven boreal forest, stand age structure has been found to shift from a relatively even-aged structure, where all trees establish immediately after fire with a similar height and diameter, to one that is uneven-aged, where trees vary in height and diameter as time since fire increases. The dynamics of age structure differ with stand species composition; however, research surrounding this issue is conflicting. Disturbance events such as spruce budworm outbreaks (*Choristoneura fumiferana*) and blowdown can significantly influence the age structure of a stand. Traditional forest management can shift the age structure at both the stand and landscape level. However, some silvicultural systems and forest management planning techniques are available to mimic natural age structural patterns. Old-growth forests are characterized with uneven-age structure, but the direct influence of climate change and indirect affects through increasing insect outbreaks and the fire frequency on old-growth is poorly understood.

INTRODUCTION

Stand age structure, the distribution of trees by age cohort in a stand, is one of the key structural attributes of a forest stand (Oliver and Larson 1996). The age structure of a

stand allows an understanding of ecological processes such as regeneration and succession that are operating within the stand (Bergeron 2000; Gutsell and Johnson 2002).

In the boreal forest, stands generally proceed from an even- to uneven-aged structure along the successional gradient (Bergeron and Dubuc 1989; Oliver and Larson 1996; Asselin *et al.* 2001; Bergeron 2004). Accordingly, stand structural attributes such as live trees and coarse woody debris (CWD) that are closely associated with stand age structure become more heterogeneous as stand age increases (Oliver and Larson 1996; Chen and Popadiouk 2002; Brassard and Chen 2006). In turn, with the links between the structure of live trees and CWD and wildlife habitat and biodiversity (Payer and Harrison 2003), a better understanding of stand age structure will improve management decisions concerning the protection of wildlife habitat and sustaining biodiversity.

The general purpose of this review is to synthesize the literature surrounding stand age structure, how it changes naturally over time, and how forest management practices may affect the age structure at both the stand and landscape level. More specifically, this review will (1) evaluate different tree ageing techniques, (2) determine how the age structure of stands change with time since fire (TSF), (3) explore how disturbances such as insect outbreaks and blowdown can shape forest stand age structure, and (4) discuss how management activities alter the age structure of a stand in the boreal forest.

AGEING TECHNIQUES

There are several techniques that have been used to age trees with different levels of accuracy. The purpose of this section is to investigate the usefulness and precision of

the ageing techniques that are commonly used in literature, including historical records, using tree size to estimate age, pithnode ring counting at breast height, ground level stem and root collar ring counting, and dendrochronological cross dating and pithnode counting.

Historical records

Historical records of wildfires can be used to estimate stand age. This method can be accurate where detailed fire history information is available (Reed *et al.* 1998). For example, the history of wildfires for areas greater than 200 ha since 1920 is available in Ontario (Perera *et al.* 1998). However, this method can be unreliable when records are incomplete, are lacking needed information, or are collected in a way where the scientific validity is in question (Antos and Parish 2002). Further, historical records of individual tree establishment in natural stands are rarely available. Therefore, historical records are not valid for studying stand age structure of natural stands when the age of each tree within a stand needs to be determined.

Using tree size to estimate age

Tree size such as diameter at breast height (DBH) has often been used to estimate the age of trees in a stand. Lorimer (1980), Takahashi *et al.* (2001), and Stewart *et al.* (2003) all found that tree DBH could be used to estimate tree age. Using tree size to estimate tree age is more advantageous than using increment core ring counts when the tree has heartrot, an accurate pith cannot be retrieved, inaccurate boring techniques are used, or equipment malfunctions or inaccuracies occur (Lorimer *et al.* 1999). However, this technique can produce quite inaccurate results for the following reasons. First, competition can result in different DBHs even though all stems are established

simultaneously. Second, trees that are more susceptible to dying often show a decrease in growth rates (Bigler and Bugmann 2003). Third, some shade tolerant tree species can go through decades of low stationary growth when suppressed (Chen *et al.* 1996; Niklasson 2002; Bigler and Bugmann 2003). The last two cases can result in a significant underestimation of a tree's age. While tree size can provide estimations of tree age under certain stand conditions (Lorimer 1980; Takahashi *et al.* 2001; Stewart *et al.* 2003), tree size as an estimate of tree age can introduce significant errors of tree ages in complex, old-growth stands (Daniels *et al.* 1997).

Pithnode and root collar ring counting

Tree ring counting is a common method in estimating the ages of trees that grow in a climate with distinct seasons, where tree rings form different colors and densities coinciding with the seasonal growing conditions. Cores or disks can be taken for ring counts from tree stems at breast height (approximately 1.3 m from the root collar) (Vasiliauskas and Chen 2002), 30 cm above ground, ground level, or from the root collar (Gutsell and Johnson 2002). Ring counting at breast height or 30 cm above ground is most common for field foresters to estimate the age of a tree. When a core or disk is taken at breast height, a certain number of years can be added to account for the time the tree takes to grow up to breast height (Avery and Burkhart 2002). Vasiliauskas and Chen (2002) reported that it takes 6-7 years for shade intolerant jack pine, trembling aspen, and white birch to reach breast height, while black spruce needs an average of 18 years to grow up to 1.3 m in height after fire in northeastern Ontario. Similarly, Gutsell and Johnson (2002) found the differences in ring counts at 30 cm above ground and at root

collar vary between 0-11 years for shade intolerant species *versus* 0-43 years for shade tolerant species in the boreal forest of Saskatchewan.

Coring at breast height is convenient and efficient, and is often the only suitable means when heartrot occurs or an excessive butt flares up at lower positions of the stem. However, using ring counts at breast height or 30 cm above ground can result in inaccurate estimates of tree ages (DesRochers and Gagnon 1997; Sano 1997; Wong and Lertzman 2001; Stewart *et al.* 2003) because of the error associated with estimating the number of years for the tree to reach breast height from ground level or 30 cm above ground. In addition, it is also prone to underestimation of tree age if the pith is missed when coring a tree (Lorimer *et al.* 1999; Peters *et al.* 2002).

In comparison with ring counts at breast height or 30 cm above ground, ground level and root collar ring counts reduce the error associated with estimating years for the tree to grow up to 30 cm above ground or breast height. These methods can still result in an underestimation of tree age with root collar ring counts being less prone to underestimate tree age (Niklasson 2002). A majority of the error associated with this ageing technique is related to missing rings which can occur following environmental stress and suppression (DesRochers and Gagnon 1997).

Dendrochronological cross dating and pithnode counting

Dendrochronological cross dating has been shown to be an effective ageing technique when information surrounding historical climate and disturbance patterns are available to cross-reference with other ageing techniques. For example, in some studies dendrochronological cross dating has been found to be more accurate than tree ring counting alone (Niklasson 2002). However, DesRochers and Gagnon (1997) found that,

to provide an exact age for some tree species (i.e., black spruce), tree excavation and serial sectioning is required to locate the root collar and detailed dendrochronological analysis of above- and below-ground portions of the stem must be made. This can be quite time consuming and costly. Additionally, this method may not be appropriate for suppressed trees, as close growth rings can make ageing difficult. In turn, diseased trees can have considerable variation in growth ring development, creating conditions where dendrochronological cross dating and pithnode counting may be an inaccurate technique to use.

In conclusion, it is recommended that root collar ring counting be used to age the trees in forest stands. This technique is likely the most accurate ageing technique as the age of the tree from ground level to breast height does not need to be assumed. However, the drawback is that this technique is more time consuming for operational foresters and more destructive on ecosystems. Lieffers and Stadt (2003) state that depending on the nature of the study, different ageing techniques are more accurate and therefore desirable, but acknowledge that cross-dating techniques are more accurate when determining germination ages of trees.

CONCEPTUAL STAND AGE STRUCTURE IN BOREAL FORESTS

The boreal forest is characterized as having large, intense crown fires as the primary stand-replacing disturbance mechanism (Johnson 1992; Groot and Horton 1994). These fires are responsible for resetting successional communities to an earlier stage of development (Flannigan *et al.* 1998). Consequently, stand age structure is largely a reflection of time since fire (Flannigan *et al.* 1998). Age structure can also be influenced by several post disturbance autogenic and allogenic processes that alter age structure such

as individual tree mortality, blowdown, and spruce budworm outbreaks at both the stand and landscape level (Chen and Popadiouk 2002). In this way, tree mortality by natural or catastrophic events can significantly influence the age structure of a stand (Keenan and Kimmins 1993; Carleton and MacLellan 1994). In this section, age structural dynamics will be reviewed for fire origin boreal stands using Chen and Popadiouk's (2002) model of stand development.

Stand initiation

A stand-replacing fire removes canopy and subcanopy trees, destroys advanced regeneration and herbaceous and shrub vegetation, and alters forest floor temperature and light levels (Bergeron and Dubuc 1989), initiating secondary succession and allowing the colonization of early-successional tree species. During the first stage of development called stand initiation, the forest is usually colonized by early-successional tree species if present before fire, such as trembling aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), and lodgepole pine (*Pinus contorta*), depending on site conditions and geographical location (Lieffers *et al.* 1996; Cumming *et al.* 2000). In some areas which are lowland and wet, black spruce (*Picea mariana*) can also colonize a stand shortly after fire (Antos and Parish 2002; Parisien and Sirois 2003). As a result of regeneration mechanisms (i.e., aspen reproducing by root suckering (Antos and Parish 2002; Kabzems and Garcia 2004) and jack pine and lodgepole pine by serotinous cones (White *et al.* 1985; Cumming *et al.* 2000; Delong and Kessler 2000)) and the rapid growth of colonizing species, young stands often develop with single or multiple species forming a single developing cohort (Bartemucci *et al.* 2002). As such, during the stand initiation

stage, the majority of the trees in the stand are developing at the same time, resulting in an age structure that is relatively even-aged (Figure 2.1a).

However, the unpredictability of fire can create situations where some standing trees and even large patches of unburned forest are left alive as fire burns in a very heterogeneous fashion (Day 1972; DeLong and Kessler 2000). Trees that survive fire, mix with the postfire cohort and increase the heterogeneity of the stand's age structure (Oliver and Larson 1996; Smith and Long 2001; Chen and Popadiouk 2002).

Stem exclusion

As a stand continues to develop, all available growing space becomes occupied and intense competition between stems for site resources occurs in a process called self-thinning. In this process, some stems survive and other stems die due to differences in the ability of stems to utilize resources (Oliver and Larson 1996; Chen and Popadiouk 2002). Self-thinning usually kills the weaker, suppressed trees which cannot compete as successfully (Groot and Horton 1994; Cumming *et al.* 2000; Paré *et al.* 2001; Antos and Parish 2002; Chen and Popadiouk 2002). During this stage, the age structure of the stand remains relatively even-aged while the canopy height of trees continues to increase (Peng 2000; Frey *et al.* 2003). This even-aged structure dominates through the end of the stem exclusion stage, until regenerating understory trees can begin to form an important component of the overall age structure of the stand (Oliver and Larson 1996; Chen and Popadiouk 2002) (Figure 2.1b).

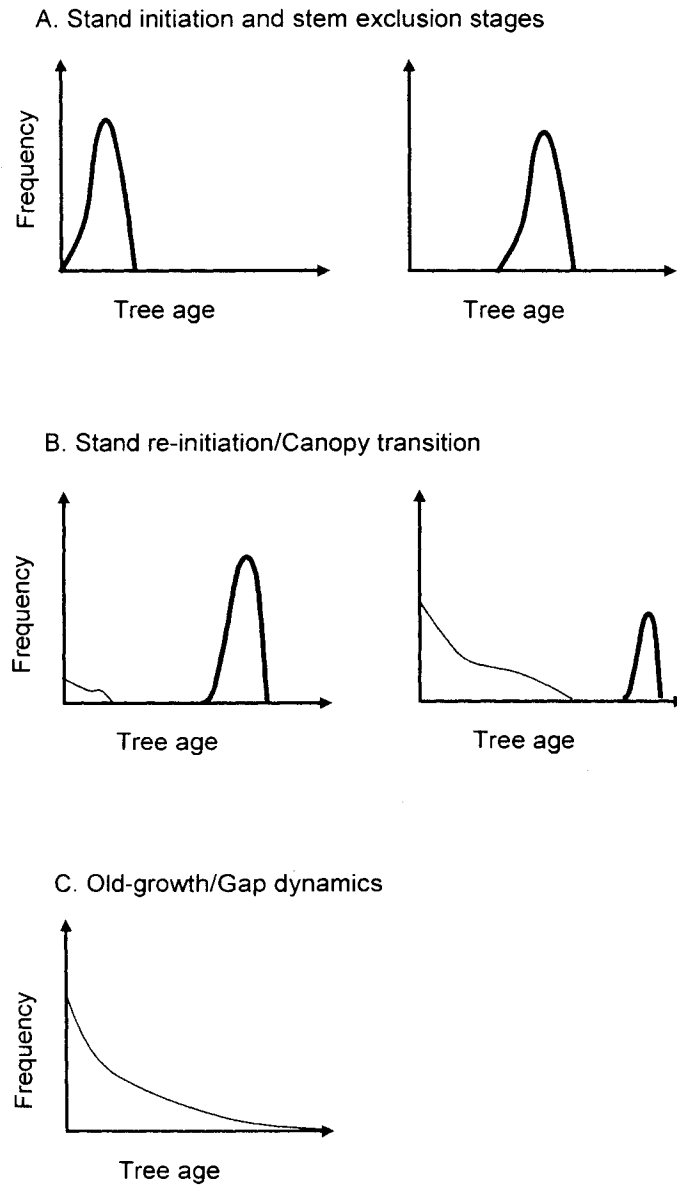


Figure 2.1. Age structural dynamics of a boreal forest stand associated with stand developmental stages defined by Chen and Popadiouk (2004).

The autogenic self-thinning processes that occur in a stand can be influenced by biotic and abiotic factors. For example, in stands where the density of trees is relatively low prior to self-thinning, trees have less competition for resources. This is due to their wider spacing causing the self-thinning process to begin and end later, as vertical stratification of the canopy (indicating all growing space has been utilized) occurs later in less dense stands (Lieffers *et al.* 1996; Pothier *et al.* 2004; Hill *et al.* 2005). For example, White *et al.* (1985) and Johnson and Fryer (1989) found that self-thinning begins in lodgepole pine/Englemann spruce (*Picea engelmanni*) forests around 10-30 years post fire. Environmental variables such as temperature, precipitation and topography can also influence the autogenic processes that occur within a stand.

Canopy transition

During canopy transition, overstory trees from the colonizing cohort begin to die as a result of age related factors (i.e., trembling aspen reaches an age of maturity between 60-80 years (Sano 1997; Cumming *et al.* 2000; Hill *et al.* 2005)), creating gaps in the canopy and freeing up growing space for understory trees to be released into the overstory (White *et al.* 1985; Groot and Horton 1994; Nappi *et al.* 2004; Hill *et al.* 2005).

The increase in light levels caused by canopy gaps promote a new layer of regeneration to occur (Groot and Horton 1994; Bergeron 2004). As a result, the forest stand age structure becomes more uneven and heterogeneous, as both the pioneering cohort of early-successional species and later establishing cohort(s) of late successional species begin to contribute significantly to the age structure of the stand (Groot and Horton 1994; Sano 1997; Delong and Kessler 2000; Stewart *et al.* 2003; Despons *et al.* 2004).

Gap dynamics

When the time between stand-replacing fires is long, the pioneering cohort can completely disappear from the overstory due to the longevity of boreal tree species. When this occurs, the stand develops into the gap dynamics stage (also referred to as old-growth) that is dominated by later established shade tolerant cohorts (Kneeshaw and Bergeron 1998; Takahashi *et al.* 2001; Bartemucci *et al.* 2002; Mori and Takeda 2004). During this stage, succession is driven by tree senescence and non-stand replacing disturbances (i.e., spruce budworm outbreaks and blowdown) that create canopy gaps (Bouchard *et al.* 2005). These canopy gaps are responsible for the self-perpetuation of the stand by creating conditions that are suitable for new seedlings and saplings to recruit by increasing light levels and opening up growing space (Takahashi *et al.* 2001; Mori and Takeda 2004). However, some disturbances including wind that are commonly thought of as non-stand replacing disturbances, can at times be stand-replacing (Hörnberg *et al.* 1995; Kneeshaw and Burton 1997; Linder and Östlund 1998; Delong and Kessler 2000; Stewart *et al.* 2003), causing stand development to revert to a stand initiation phase of development. As such, the gap dynamics stage of development is characterized as having a stand age structure that is quite heterogeneous and composed of various cohorts (Figure 2.1c).

In the gap dynamics stage, it has been found that the trees growing in the stand show reverse-J height and DBH distributions, with many small trees and few large trees with a wide range of ages (Sano 1997). While some researchers have found that the reverse-J curve is relatively continuous (DeLong and Kessler 2000; Stewart *et al.* 2003), Sano (1997) found that the age structure of a stand appears to be a discontinuous reverse-

J. In turn, large, long-lived individuals surviving from the pioneering cohort can be fairly resistant to fire and contribute to the unevenness of the stand age structure even at the old-growth state (Zhang *et al.* 1999).

The shape of the age class distribution curve appears to differ based on cover type. In old-growth conifer forests, the age distribution curve appears to be steeply reverse-J shaped (Hörnberg *et al.* 1995; Kneeshaw and Burton 1997; Linder and Östlund 1998), whereas in old hardwood forests, a multi-aged pattern is seen with trees spread out relatively evenly among age and diameter classes (Leak 1996). At the landscape level, Van Wagner (1978) and Johnson *et al.* (1995) found that the age class distribution of the boreal forest follows a negative exponential distribution with time since fire, where many stands are young and few stands are old.

Soils have been shown to shape successional pathways on various boreal site types. For example, Galipeau *et al.* (1997) has shown that white spruce favours regenerating on sandy to loamy soils. In contrast, black spruce has a competitive advantage regenerating and growing on hydric, nutrient poor soils. As such, successional dynamics and therefore stand age structure is likely to be influenced considerably by site type, climate, and soil composition.

THE EFFECT OF SPRUCE BUDWORM AND WIND AND THEIR EFFECTS ON STAND AGE STRUCTURE

While fire is the main disturbance mechanism in the boreal forest (Johnson 1992), non-stand replacing disturbances can shape the age structure of a stand beyond the initial stand-replacing disturbance (Fleming *et al.* 2000; Kellomäki 2000; Burleigh *et al.* 2002). However, with the great number of disturbances that can alter stand age structure, this

review will focus on the effect of wind and spruce budworm exclusively, as there are many disturbances that can affect stand age structure and an overview of all of them would be a review in itself.

Spruce budworm

Outbreaks of spruce budworm can shape many aspects of forest structure and drive successional processes by causing significant mortality in a stand of host tree species including many spruces and firs (Blais 1981; MacLean and Ostaff 1989; Burleigh *et al.* 2002; Bouchard *et al.* 2005). In areas where spruce budworm outbreaks are common and fires infrequent, budworm outbreaks can create a multiple cohort stand by killing off dominant conifer trees. In turn, this can free up growing space and increase canopy openness while causing higher nutrient allocations and light levels by creating canopy gaps, and allowing the establishment of seedlings and saplings while permitting suppressed individuals to grow up into the canopy (Kneeshaw and Bergeron 1998). Mixedwood management could occur in areas with high incidence of spruce budworm activity, as spruce budworm outbreaks can kill off spruce and fir species and allow for the recruitment of early-successional hardwoods in canopy gaps (Bergeron and Leduc 1998; Kneeshaw and Bergeron 1999; D'Aoust *et al.* 2004).

The susceptibility of trees to spruce budworm may depend on their size and species, as host species have different resistance to budworm outbreaks. For example, white spruce has been found to be less susceptible to budworm attacks than balsam fir (Antos and Parish 2002; Burleigh *et al.* 2002). This can cause the age class distribution of stands 68 years after fire to be bimodal in white spruce dominated forests in contrast to a unimodal stand age distribution in balsam fir stands (Galipeau *et al.* 1997). In turn,

Blais (1958), Baskerville (1975), and Bergeron *et al.* (1995) reported that smaller trees are less prone to budworm damage than larger trees. However, MacLean and Ostaff (1989) reported that larger and smaller trees show similar levels of mortality.

Cover type and stand age appears to affect a stand's susceptibility to spruce budworm outbreaks, as older, more conifer dominated stands tend to suffer greater spruce budworm defoliation than younger stands with a greater hardwood component. In many areas of the boreal forest, stands increase in conifer component as time since fire increases (Morin 1994; Bergeron 2000; Harvey *et al.* 2002). Higher spruce budworm susceptibility with time may be caused by many factors including an increase in host species, a decrease in tree vigour, and an increase in a tree's susceptibility to disease (Galipeau *et al.* 1997).

If the conifer component of susceptible tree species in a stand is high, there tends to be an increase in mortality resulting in stand replacement and cyclical succession by killing most of the canopy trees. This will cause the stand to be largely even-aged and dominated by a single cohort, reverting back to the stand initiation stage of development. Recurrent budworm outbreaks in forests dominated by susceptible conifer species will therefore be relatively young and regenerate in a wave-like fashion (Bergeron *et al.* 1995; Galipeau *et al.* 1997). In this case, the seedling and sapling layer can remain, and will be free to grow up into the canopy and form the next cohort, rather than simply filling available gaps (Morin 1994; Parent *et al.* 2001; Bouchard *et al.* 2005).

The extent of spruce budworm effects seem to differ by geographic and abiotic conditions. For example, some research has shown that abiotic conditions such as soils and temperature affect the susceptibility of a stand to spruce budworm outbreaks

(Burleigh *et al.* 2002; Bouchard *et al.* 2005). However, other research has shown that abiotic conditions have little effect on spruce budworm susceptibility (Bergeron *et al.* 1995). They attributed this contradiction to the extreme severity of the spruce budworm outbreak observed in their study in which even vigorous trees that normally would be more resistant to outbreaks were affected regardless of site and cover types. As well, there appear to be differences in budworm outbreaks from one region of the boreal forest to the next. For example, in eastern Canada, budworm outbreaks are more widespread and occur at shorter intervals compared to the west (Blais 1983). This leads to cyclical patterns of fir mortality in eastern boreal forests and patchy forest structure in the west (Kneeshaw and Bergeron 1999). At the stand level, spruce budworm outbreaks in the eastern boreal forest usually cause the majority of fir to die, and in a balsam fir dominated forest, this results in stand replacement. An entirely new cohort will then occupy the site and will grow until the next spruce budworm outbreak, maintaining a relatively even-aged structure (Kneeshaw and Bergeron 1999). In some parts of the west, however, budworm outbreaks usually do not cause stand replacement, and the death of balsam fir simply causes a patchy structure and leads to a more uneven-aged stand structure (Kneeshaw and Bergeron 1999).

Wind

Extreme wind events can create forces that overcome a tree root's resistance and cause it to be blown over and uprooted or broken at the bole. Depending on the magnitude or intensity of the event, only a few trees can be blown over (non-stand replacing disturbance) or the entire stand can be blown over (stand-replacing). Non-stand replacing blowdown can increase the age structure heterogeneity of the stand by

removing some canopy trees, releasing understory trees, promoting the growth of suppressed trees, and creating microsites that are needed for new regeneration to occur due to less competition from other vegetation, more light, and greater access to nutrients (Webb 1988; Kuuluvainen and Juntunen 1998; Kulakowski and Veblen 2003). In this way, blowdown can allow for the persistence and establishment of many different age cohorts in the stand, thereby increasing age structural diversity. In contrast, severe blowdown can cause a stand-replacing event making the post-disturbance stand relatively even-aged and low in age structural diversity.

The physical characteristics of different tree species appear to affect their susceptibility to blowdown. For example, because they are more flexible, aspen trees are more susceptible to blowdown compared to conifer trees (Baker *et al.* 2002). Further, blowdown tends to affect taller trees more than smaller trees, and a lower tree density has been found to lead to lower levels of blowdown compared to high tree densities (Baker *et al.* 2002). Younger forests in turn are less susceptible to blowdown than older forests (Frelich and Lorimer 1991; Frelich and Graumlich 1994; Meilby *et al.* 2001). It is also important to note that management activities such as thinning and clearcutting can make a stand more likely to experience a blowdown event (Huggard *et al.* 1999; Meilby *et al.* 2001). The effect of forest management on age stand structure will be discussed in greater detail below.

THE IMPLICATIONS OF FOREST MANAGEMENT ON FOREST STAND AGE STRUCTURE

In the boreal forest, clearcutting is the most common type of harvesting system employed. While clearcutting has been found to be better at emulating the patterns

created by fire (Harvey *et al.* 2002; Hebert 2003), it appears that harvesting activities lack the ability to mimic many ecosystem aspects (Brumelis and Carleton 1988; Carleton and MacLellan 1994; Ruel *et al.* 2004). The goal of this chapter is to explore the effect of forest management on forest age structure (at the stand and landscape level) and review old-growth concerns and issues surrounding age structure.

Forest management and effect on stand and landscape age structure

At the stand level, clearcutting and stand-replacing fires create similar age structures soon after the disturbance and likely result in similar age successional dynamics (Bergeron *et al.* 2001; Bergeron *et al.* 2002). However, at the landscape level, forest harvesting is likely to create different age structural dynamics. In the boreal forest, stands could be harvested before the breakup of the pioneering cohort (rotation age between 70-120 years), as in this stage of development, stands have reached their maximum volume (Wardle *et al.* 2004). From an economic perspective focused exclusively on growth and yield, stands should be harvested at or before this time (Smith *et al.* 1997; Seymour and Kenefic 2002). When this occurs, there is the potential for the landscape to be composed of relatively young, even-aged stands (Figure 2.2a) (Frelich and Lorimer 1991; Bergeron *et al.* 2002; Bergeron 2004). However, fire alone usually creates a landscape with many young stands and few old stands following a negative exponential distribution (Bergeron *et al.* 2002; Bergeron 2004) (Figure 2.2b). Further, when a fire burns, it often leaves remnant patches of forest stands on the landscape, further increasing the age structural diversity of the landscape (DeLong and Kessler 2000).

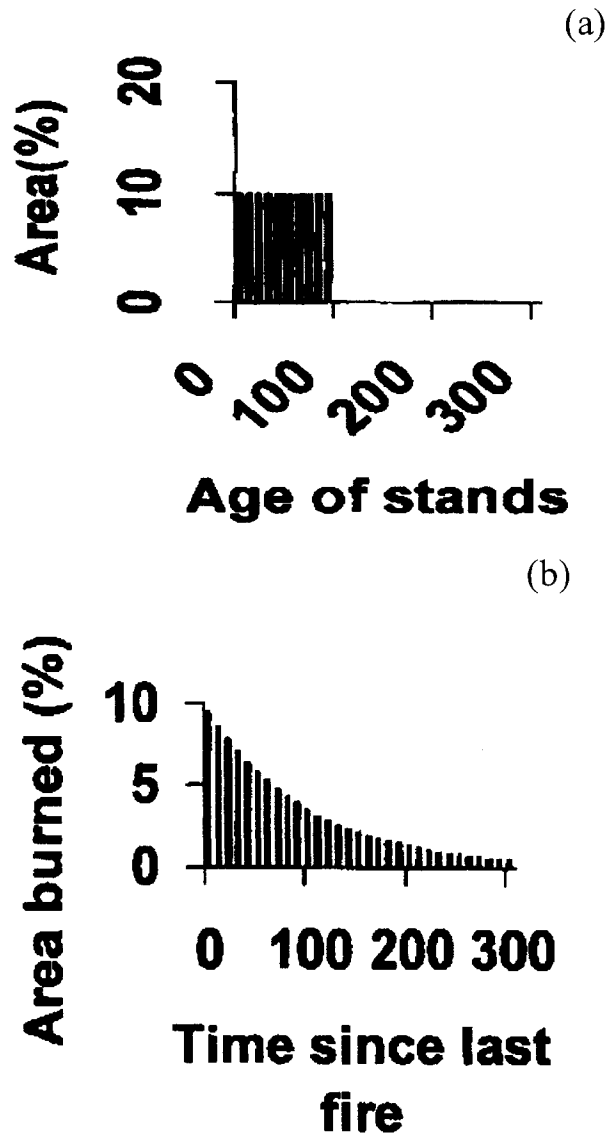


Figure 2.2. Age stand structural composition of the boreal forest (a) when the rotation age is relatively short and (b) under natural conditions (Bergeron 2004).

Nyland (2003) describes silviculture as a long-term process to manage a stand in a way to sustain a set of values and interests that often vary by stand, landscape or region. These values and interests can be biologically, economically, or socially motivated (Smith *et al.* 1997). Traditional forestry has focused largely on extracting wood for its

economic value, placing little value on social (i.e., recreation) or biological (i.e., wildlife habitat) values (Kellomäki 2000). With the increase of public concern surrounding the negative impacts of forestry and the increase in research to understand ecosystem processes and services, the complexities surrounding the implementation of economically viable and ecologically sustainable silvicultural systems are increasing and often conflicting (Kimmins 1997).

It has been suggested that forest management can be used to create a landscape age structure that resembles the natural landscape age structure of the boreal forest (Bergeron *et al.* 2002). Bergeron (2004) recommends using clearcutting to promote young stands, partial cutting to resemble intermediate aged stands, and selective cutting to mimic old stands (Figure 2.3). In turn, Asselin *et al.* (2001) suggests using a combination of strip clearcutting and seed-tree systems to maintain a diverse age structure at the landscape level. Further, Nyland (2003) recommends promoting the development of uneven-aged stands by using partial cutting to ensure an understory cohort of seedlings and saplings is allowed to develop in a stand or by using patch cutting systems to ensure that cutting occurs in a heterogeneous fashion to better represent the natural landscape patterns of the forest.

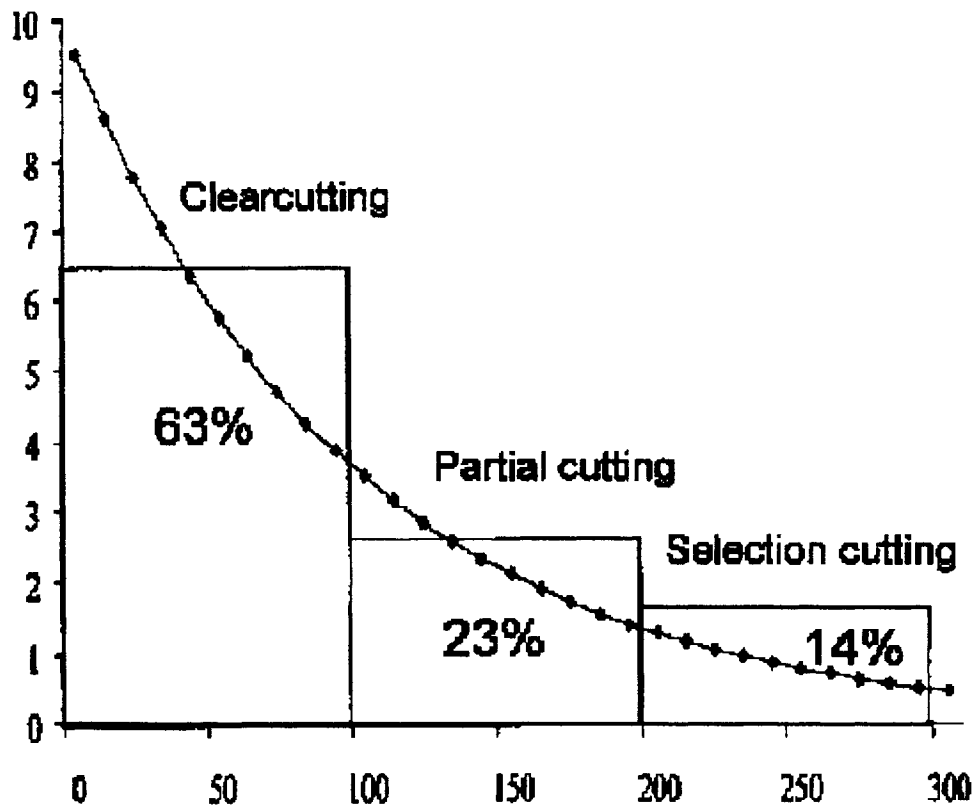


Figure 2.3. A proposed harvesting approach to emulate the natural age structural makeup of stands at the landscape level in the boreal forest (Bergeron 2004).

Old-growth forests: issues and concerns

While foresters agree that old-growth forests are relatively old, there is no consensus on the age at which a forest enters the old-growth state (Gordon 2004; Helms 2004). Helms (2004) describes old-growth stands as “a contiguous group of trees forming a canopy characterized by old-growth trees and in the late successional stage of development”. While an evaluation of old-growth characteristics is still largely incomplete for the boreal forest (Gordon 2004), some researchers have attempted to develop criteria to classify old-growth forests (Kneeshaw and Gauthier 2003). Presently, old-growth forests have been described as having (1) a heterogeneous spatial distribution of trees, (2) dominance of late successional species, (3) multiple canopy layers, (4) a

large CWD component, (5) a subcanopy/canopy ratio of approximately 1.5, and (6) an uneven-aged structure (Lee *et al.* 2000; Stewart *et al.* 2003; Despons *et al.* 2004; Franklin and Van Pelt 2004).

Many old-growth stands are valuable to the forest industry. These stands are highly prized by the forest industry as they contain a high standing volume of commercial fibre, but are prone to disturbances (Burton *et al.* 1999). They are also valuable to society for many ecological, economical, cultural, religious, and aesthetic reasons (Barnard 2004). Further, they have important implications for biodiversity and wildlife habitat, and ecologists are pushing more and more for their protection (Burton *et al.* 1999; Barnard 2004). Old-growth forests have been found to support a variety of unique bird, mammal, epiphytic lichen, and invertebrate species (Linder and Östlund 1998; Niemelä 1999; Despons *et al.* 2004). Timber harvesting that may alter the age structure of the forest and reduce the amount of old-growth found on the landscape may harm these species and deplete biodiversity as a result of habitat loss (Linder and Östlund 1998; Niemelä 1999; Despons *et al.* 2004). As well, human-induced disturbances (i.e., forest harvesting) and natural disturbances (i.e., spruce budworm attacks and blowdown) can set the forest back to a single cohort, even-age structure (Harvey *et al.* 2002).

Some studies suggest that the percentage of old-growth in some areas of the boreal forest is expected to expand as an increase in precipitation brought about by climate change will cause longer fire cycles (Johnson *et al.* 1995; Delong and Kessler 2000). In other areas of the boreal forest, climate change is expected to make areas dryer, causing the fire cycle to shorten and less old-growth to be present (Johnson 1992; Stocks *et al.* 1998). It is likely that a greater percentage of the landscape will be covered by

conifer forests as earlier successional, shade intolerant hardwoods are replaced by late successional, shade tolerant conifers as a part of normal boreal succession (Lesieur *et al.* 2002). However, other studies indicate that fire intensity and frequency will increase with climate change, thereby causing a greater percentage of the landscape to be occupied by early-successional forests and decreasing the amount of old-growth present (Thompson *et al.* 1998).

CONCLUSIONS

- (1) Numerous ageing techniques with varying levels of accuracy have been developed to age trees. Ageing techniques shall be chosen with consideration of the balance of affordability, sample size, and level of tolerance to potential impreciseness.
- (2) Stand age structure is largely a reflection of time since last stand-replacing fire in the boreal forest. In the long term absence of fire, succession leads to a shift in the tree layer, causing the forest stand age structure to shift from a single, even-aged structure to a multi-aged, uneven-aged structure over time.
- (3) Disturbances such as spruce budworm outbreaks and wind influence successional processes and play an important role in shaping the age structure of a stand.
- (4) Traditional forest management can shift the age structure at both the stand and landscape levels. However, silvicultural systems and forest management planning techniques are available to mimic natural stand age structural patterns. Old-growth forests are characterized by uneven-age structure.

CHAPTER 3 STAND AGE STRUCTURAL DYNAMICS OF CONIFER,
MIXEDWOOD, AND HARDWOOD STANDS IN THE BOREAL FOREST OF
CENTRAL CANADA

ABSTRACT

Stand age structure has been linked to wildlife habitat and can affect biodiversity. Further, certain stand age structures (such as those associated with old-growth) are valuable from an aesthetic and fibre supply perspective. My objectives were to examine how stand age structure changes among stand developmental stages and stand cover types.

I sampled living trees in 32 stands representing typical conifer, mixedwood, and hardwood stand types in the central boreal forest region of North America representing the stem exclusion/canopy transition, canopy transition, canopy transition/gap dynamic, and gap dynamic stages of stand development. Using a 400 m² plot in each stand as the sampling unit, the diameter at breast height (DBH) of all canopy trees (DBH ≥10 cm) was measured. Five canopy trees in each diameter class for each species were randomly selected, and the height of each tree was measured and a single increment core was taken at breast height (1.3 m) and aged. Three circular 25 m² subplots were then randomly established within each 400 m² plot and the diameter at root collar and height of all seedlings and saplings (DBH <10 cm) were measured and recorded. A disk was then taken at root collar and aged for 5 seedlings and saplings in each height class. Canopy trees and regeneration were summed to the plot level and scaled to per hectare.

The results suggest stand age structure is variable with stand developmental stages and stand cover type. Age distribution in conifer stands was bimodal in the stem

exclusion/canopy transition, bimodal in the canopy transition, reverse-J in the canopy transition/gap dynamics, and finally bimodal in the gap dynamics. In the mixedwood stands, similar to the conifers, stand age structure was bimodal in all stand developmental stages. In the hardwood stands, age structure was bimodal in the stem exclusion/canopy transition, unimodal in the canopy transition stage, reverse-J in the canopy transition/gap dynamics stage and finally bimodal in the gap dynamics stage.

Forest management activities such as partial harvesting, selection harvesting, and seed-tree systems may diversify stand age structures at the stand and landscape levels, benefiting wildlife and creating characteristics of old-growth. It is recommended that quantitative old-growth be defined. I suggest using the following to determine old-growth in the boreal forest: (1) canopy breakdown of pioneering cohort is complete and the stand is dominated by later successional tree species (2) the age structure of the stand is bimodal, with dominating canopy trees that fall within a relatively narrow range of age and height classes and a significant amount of understory regeneration.

INTRODUCTION

Age structure of natural forest stands changes over time (Daniels *et al.* 1995; Oliver and Larson 1996). Available research has found that forest stands change from an even-aged (all trees are the same age), relatively homogenous tree height structure to a two-aged (having two cohorts established within the stand), bimodal height structure to an all-aged/uneven-aged structure (having three or more age classes) where tree heights are relatively heterogeneous as time since fire (TSF) increases (Oliver and Larson 1996; Smith *et al.* 1997; Pothier *et al.* 2004; Brassard and Chen 2006). Young stands are

primarily composed of early successional species that grow quickly in open areas in full light (Bergeron 2000). However, as stand age increases, stands become increasingly composed of later successional species that can establish under a closed canopy with limited light resources.

Age structure has been examined for conifer (DesRochers and Gagnon 1997), mixedwood (Bergeron 2000), and hardwood forest types (Sano 1997; Lee *et al.* 2000) in a specific successional state. However, few studies thus far have compared age structure for different boreal forest cover types with similar environmental characteristics (i.e., soils, topography, climate) along a successional gradient. As many stand characteristics have been found to differ with stand composition (i.e., productivity, coarse woody debris (CWD) types and amounts) (Hély *et al.* 2000; MacPherson *et al.* 2001; Pedlar *et al.* 2002; Légaré *et al.* 2005), I hypothesize that the different stand cover types and stand developmental stages vary in stand age structural dynamics.

Old-growth forests have potential wildlife habitat and biodiversity benefits that warrant specific management planning. Old-growth forests have higher levels of plant and animal species biodiversity and have unique structural characteristics (i.e., larger trees, a multi-layered canopy, canopy gaps, and higher tree species richness) (Johnson *et al.* 1995) that provide specialized habitats for certain species (Potvin *et al.* 1999). However, few definitions exist to classify old-growth in the boreal forest, and this lack of information and confusion surrounding the old-growth condition is hindering management planning and implementation (OMNR 2003). Therefore, this study may provide meaningful information through age analysis concerning the species and age structure of forest stands in the old-growth state.

Therefore, the goal of this study is to determine how stand age structure changes in the boreal forest over time on similar mesic sites. Specifically, it will address how stand age structure varies with cover type (conifer, mixedwood, and hardwood) and developmental stages (stem exclusion/canopy transition, canopy transition, canopy transition/gap dynamics, gap dynamics (Chen and Popadiouk 2002)).

MATERIALS AND METHODS

Study area

This study was conducted in the northwestern Ontario boreal forests in an area north of Lake Superior in the Superior (B.9) Forest Region (Rowe 1972), approximately 150 km north of Thunder Bay, Ontario (48° 22' N, 89° 19' W, 199 m altitude) (Environment Canada 2005) in the Spruce River Forest (Appendix I). Climatically, the area is influenced by Lake Superior and has a moderately dry, cool climate with short summers. The average annual precipitation for Thunder Bay is 712 mm with an average annual temperature of 2.5 °C. Topographical features were formed during the retreat of the Laurentide Ice Sheet approximately 10,000 years ago (Environment Canada 2005).

The area is characterized as containing tree species of paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), and eastern white cedar (*Thuja occidentalis* L.), with a small component of red and white pine (*Pinus resinosa* Ait. and *Pinus strobus* L.), yellow birch (*Betula alleghaniensis* Britt.), black ash (*Fraxinus nigra* Marsh.), and sugar maple (*Acer saccharum* Marsh.) on certain sites (Rowe 1972).

Common shrubs and herbs found in this area were mountain maple (*Acer spicatum*

Lam.), beaked hazel (*Corylus cornuta* Marsh.), labrador tea (*Ledum groenlandicum* Jacq.), Canada fly honeysuckle (*Lonicera canadensis* Bart. Ex Marsh.), northern star flower (*Trientalis borealis* Raf.), rose twisted stalk (*Streptopus roseus* Michx.), bunchberry (*Cornus canadensis* L.), and wild lily of the valley (*Maianthemum canadense* Desf.). The natural stand-initiating disturbance of the area is predominately stand-replacing fire, which is the most common stand-replacing mechanism in the boreal forest (Johnson 1992).

Sampling design

Three forest types were studied: (1) conifer dominated by jack pine at early stages of development with a mixture of black spruce, white spruce, and balsam fir at later stages of stand development, (2) hardwood dominated by trembling aspen at early stages of development and paper birch at later stages of stand development, and (3) mixedwood dominated by a mixture of jack pine and trembling aspen in early stages of development and a mixture of black and white spruce, balsam fir, and paper birch in later stages of development. Stands were selected using random stratified sampling to represent four developmental stages (stem exclusion/canopy transition, canopy transition, canopy transition/gap dynamics, and gap dynamics (Chen and Popadiouk 2002)). Intermediate stand developmental stages (stem exclusion/canopy transition and canopy transition/gap dynamics) were defined to more accurately capture the effect of time since fire on stand age structure and are defined in Table 3.1.

Table 3.1. Definitions of stand development stages (based upon Chen and Popadiouk (2002)).

Transitional stand development stage	Criteria
Stem exclusion / canopy transition	While the overstory is still dominated by individuals from the colonizing cohort, some individuals from later cohorts are close to reaching the overstory
Canopy transition	Competition of stems come to an end and trees begin to die because of longevity or damage from disturbances. As well, structural attributes such as canopy gaps and stratified canopies may be evident. Canopy trees begin to die and understory individuals start to take over the canopy
Canopy transition / gap dynamics	Only a few individuals from the colonizing cohort remain alive. Several individuals from later cohorts have reached the overstory
Gap dynamics	Pioneering trees such as jack pine and aspen have died off and the overstory is dominated by late successional species.

Stand composition was determined through a modification of methods used by Greif and Archibold (2000). Stand types were assessed as belonging to a specific stand type based on the density (stems/plot) of conifer trees that dominated the overstory of the stand. Stands with greater than 75% conifer component were classified as “conifer type”, stands with 25-75% conifer component were classified as “mixedwood type”, and stands with less than 25% conifer component were classified as “hardwood type”

All sampled stands were fire-origin on prevailing mesic, upland sites in the region to be representative and to limit soil variability. Soil order and texture were determined by excavating one soil pit using methods outlined by British Columbia Ministry of

Environment and British Columbia Ministry of Forests (1998). Soil assessment followed Sims *et al.* (1997) and Soil Classification Working Group (1998) to ensure that sites met the selection criteria described previously. For all sites, soil order was Brunisol while soil texture was sandy loam, sandy clay loam, or clay loam.

In total, 32 stands were sampled (Table 3.4). Despite various efforts, I was unable to find mixedwood stands in the canopy transition/gap dynamics stage of development in the study area. I believe this to be caused by a limited sampling area and more frequent fires. The average fire cycle in northwestern Ontario is 65 years (Li 2000).

Field measurements

Within each stand, a 400 m² circular plot was established to represent the stand. Within each plot, the diameter at breast height (DBH) (1.3 m above the root collar) and species of all live trees (DBH ≥ 10 cm) were measured and recorded and grouped into DBH classes ((1) 10-14.9 cm, (2) 15-19.9 cm, (3) 20-24.9 cm, (4) 25-29.9 cm, and (5) ≥ 30 cm). Diameter at breast height classes were created for the sole purpose of determining which trees should be selected for height and age measurement. Further, five trees (if available) were randomly selected from each 5-cm DBH class. Their heights were measured using a clinometer, and an increment core at breast height using an increment borer was taken. Increment cores were placed in a freezer until they could be processed.

Three circular 25 m² subplots were randomly selected within each 400 m² plot to evaluate natural regeneration. Only trees that were less than 10 cm DBH were considered. This would also include trees that had not yet reached breast height. Within each subplot, diameter at the root collar, height, and species of all trees were measured

and recorded. Further, trees were grouped into height classes ((1) <0.29 m, (2) 0.3-0.99 m, (3) 1.0-1.9 m, (4) 2.0-4.9 m, and (5) ≥ 5 m), and 5 trees were randomly selected from each height class (if available), and a disk was taken at the root collar.

Tree ring counting

In the lab, increment cores from trees $DBH \geq 10$ cm were each mounted on a wood strip and sanded with grit sandpaper until the rings were visible. Growth rings were then counted using a hand-held magnifier. In order to estimate the age of each tree from root collar to breast height, a species-specific number of years was added to each tree's growth ring count as outlined by Vasiliauskas and Chen (2002) (jack pine = 8 years, trembling aspen and paper birch = 7 years, black and white spruce and balsam fir = 18 years). This gave an estimation of tree age. Balsam fir and white spruce were based on a conservative estimate of the ages of trees using black spruce because it is more shade tolerant. For trees $DBH < 10$ cm, the growth rings of each disk were counted using a hand-held magnifier or under a microscope. As the disk was taken at the root collar, no ages had to be added.

Data and analysis

Tree heights for the remaining trees $DBH \geq 10$ cm were estimated using species-specific non-linear regression models developed from the paired height and DBH measurements. The height- DBH models were developed by fitting the Chapman-Richards function (eq. 1) as outlined by Peng *et al.* (2001) and OMNR (2006):

$$[1] \quad H = 1.3 + a(1 - e^{-bDBH})^c$$

where H is tree height (m), a is an asymptote parameter, b is a scale parameter, c is a shape parameter, and DBH is diameter at breast-height (cm) (Table 3.2). Tree heights

were divided into 5-m height classes as follows: (1) 0-4.9 m, (2) 5-9.9 m, (3) 10-14.9, (4) 15-19.9 m, (5) 20-24.9 m, (6) 25-29.9 m, (8) ≥ 30 m.

Table 3.2. Species-specific parameter estimates of non-linear height-diameter at breast-height models using the Chapman-Richards function ($H = 1.3 + a(1 - e^{-b \cdot DBH})^c$) where H is tree height (m), DBH is tree diameter at breast-height (cm), a is an asymptote parameter, b is a scale parameter, c is a shape parameter.

Species	Parameter			MS _(error)	R ²
	a	b	c		
Balsam fir	28.807	0.036	1.021	5.484	0.577
Paper birch	21.770	0.071	0.896	6.332	0.412
Jack pine	20.301	0.149	3.161	7.486	0.610
Trembling aspen	25.909	0.127	2.706	12.238	0.626
Black spruce	25.659	0.047	1.138	3.807	0.687
White spruce	20.461	0.114	2.669	5.103	0.743

Ages for the remaining trees were estimated using species-specific non-linear regression models developed from the (1) paired age and diameter measurements (for trees $DBH \geq 10$ cm, DBH was used in the model; for trees $DBH < 10$ cm, diameter at root collar was used in the model) as outlined by Daniels *et al.* (1995) (eq. 2), and (2) paired age and height measurements as outlined by Wang and Kimmins (2002) (eq. 3):

$$[2] \quad \text{Log}_{10} A = a_0 + a_1 \text{Log}_{10}(\text{diameter})$$

where A is tree age (years), a_0 and a_1 are parameters, and *diameter* is diameter at (a) breast height (if tree $DBH \geq 10$ cm) or (b) root collar (if tree $DBH < 10$ cm).

$$[3] \quad A = 1.3 + a(1 - e^{-b \cdot \text{height}})^c$$

where A is tree age (years), a , b , and c are parameters, and height is tree height (m).

However, as age-diameter relationships were found to be more significant than age-height relationships, diameters were used to determine missing ages, and only the age-diameter models have been presented (Table 3.3).

Table 3.3. Species-specific parameter estimates of non-linear age-diameter at breast height models using Daniels *et al.* (1995) ($A = 10^{(a_0 + a_1 * \text{Log}_{10}(\text{diameter}))}$) where A is tree age (years), a_0 and a_1 are parameters, and diameter is diameter at (a) breast height (if tree DBH ≥ 10 cm) or (b) root collar (if tree DBH < 10 cm). For trees DBH < 10 cm, no jack pine were sampled, while the sample size for trembling aspen was very small. Therefore, no age-diameter models for those species were developed.

Species	Parameter		MS _(error)	R ²
	a ₀	a ₁		
<i>Trees (DBH ≥ 10 cm):</i>				
Balsam fir	1.7265	0.0958	71.6835	0.0496
Paper birch	1.4499	0.3034	101.1264	0.2529
Jack pine	1.4472	0.309	178.5015	0.1715
Trembling aspen	1.2813	0.4364	156.3646	0.3833
Black spruce	1.6816	0.1729	153.9571	0.1015
White spruce	1.5596	0.2406	116.9068	0.3256
<i>Trees (DBH < 10 cm):</i>				
Balsam fir	1.2965	0.459	48.4667	0.5297
Paper birch	1.1645	0.2477	57.9858	0.2668
Jack pine				
Trembling aspen				
Black spruce	1.3301	0.5539	24.2526	0.6614
White spruce	1.2944	0.4908	11.235	0.6537

Trees by species were then grouped into age classes as follows: (1) 0-9 years, (2) 10-19 years, (3) 20-29 years, (4) 30-39 years, (5) 40-49 years, (6) 50-59 years, (7) 60-69

years, (8) 70-79 years, (9) 80-89 years, (10) 90-99 years, (11) 100-109 years, (12) 110-119 years, and (13) ≥ 120 years and a combined system of height classes: (1) 0-4.9 m, (2) 5-9.9 m, (3) 10-14.9 m, (4) 15-19.9 m, (5) 20-24.9 m, (6) 25-29.9 m, and (7) ≥ 30 m and scaled up to per hectare. Bar charts were constructed to show the density of trees (trees/ha) by (a) age class and species and (b) height class in each stand developmental stage and cover type.

RESULTS

Variation in stand age structure with stand developmental stage and cover type

Conifer stands

During the stem exclusion/canopy transition stage of stand development in conifer stands, stand age structure was largely bimodal, having an initial peak in the 2nd and 3rd age classes (10-29 years TSF) and a second peak in the 7th and 8th age classes (60-79 years TSF) (Figure 3.1a). The second peak represents largely jack pine canopy trees with some black spruce, balsam fir and paper birch that established shortly after the stand-replacing fire, therefore falling within a relatively narrow range of age classes. The first peak is attributed to black spruce and balsam fir that had established at various times after the stand-replacing fire (Figure 3.1a). Canopy tree density in this stage was 1217 trees/ha, while regeneration density was 3956 trees/ha (Table 3.4).

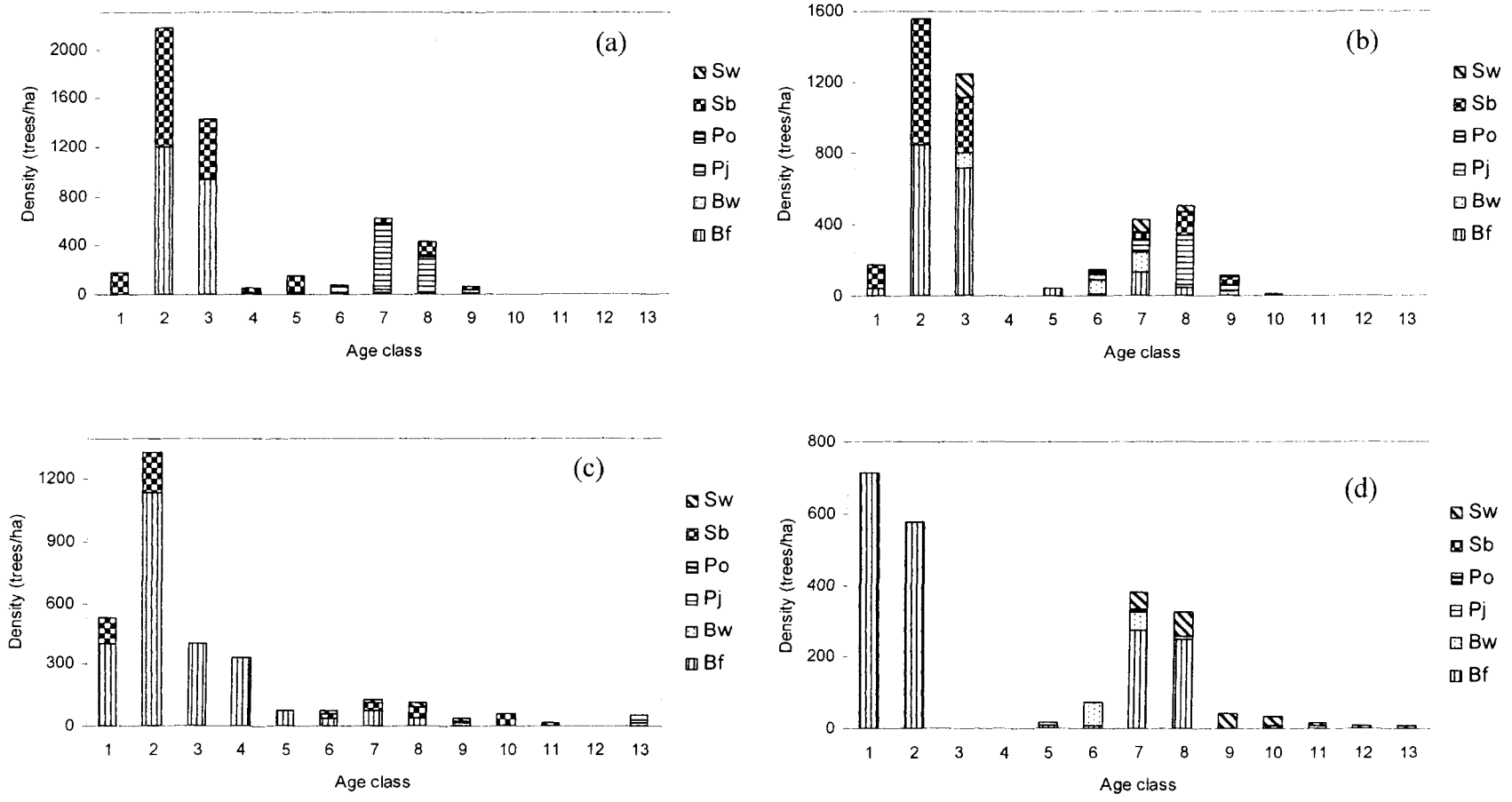


Figure 3.1. Density of trees in conifer stands by age class (1 = 0-9 yrs, 2 = 10-19 yrs, 3 = 20-29 yrs, 4 = 30-39 yrs, 5 = 40-49 yrs, 6 = 50-59 yrs, 7 = 60-69 yrs, 8 = 70-79 yrs, 9 = 80-89 yrs, 10 = 90-99 yrs, 11 = 100-109 yrs, 12 = 110-119 yrs, 13 = 120+ yrs) and species (Sw = white spruce, Sb = black spruce, Po = trembling aspen, Pj = jack pine, Bw = paper birch, Bf = balsam fir) for (a) stem exclusion/canopy transition, (b) canopy transition, (c) canopy transition/gap dynamics, and (d) gap dynamics.

Table 3.4. Description of 32 sampled stands in northwestern Ontario.

Number of stands sampled	Stand type*	Stage [†]	Density (trees/ha)	
			Canopy trees [‡]	Regeneration [‡]
3	C	2-3	1216.7 (253.4) [§]	3955.6 (1142.7)
3	C	3	1208.3 (158.3)	3022.2 (387.5)
2	C	3-4	487.5 (62.5)	2666.7 (133.3)
3	C	4	908.3 (260.3)	1288.9 (437.7)
3	M	2-3	1083.3 (72.6)	2311.1 (823.1)
3	M	3	1108.3 (144.6)	2222.2 (898.8)
3	M	4	1066.7 (96.1)	3777.8 (1646.2)
3	H	2-3	1158.3 (375.4)	1111.1 (512.6)
3	H	3	675.0 (14.4)	177.8 (117.6)
3	H	3-4	716.7 (41.7)	2088.9 (270.3)
3	H	4	1025.0 (203.6)	2866.7 (1404.8)

*Stand type: C = conifer, M = mixedwood, H = hardwood

[†]Stand developmental stage: 2-3 = stem exclusion/canopy transition, 3 = canopy transition, 3-4 = canopy transition/gap dynamics, 4 = gap dynamics

[‡]Canopy trees are ≥ 10 cm diameter at breast height (DBH), regeneration are trees < 10 cm DBH

[§]Numbers in brackets equal one standard error of the mean

The age structure in the canopy transition stage of stand development was similar to the stem exclusion/canopy transition stage with a bimodal age structure as well (Figure 3.1b). The second peak was composed of a mixture of jack pine, black and white spruce, balsam fir, and paper birch canopy trees that fall within the 6 to 9 age classes (50-89 years TSF). The first peak represented regeneration of balsam fir and black spruce with minor components of white spruce and paper birch that were in largely the 2nd and 3rd age classes (10-29 year TSF) (Figure 3.1b). I believe that birch seedlings seeded in to these stands, as the birch I sampled appeared to be distributed randomly throughout the stand and no canopy trees were present for birch seedlings to sprout from. Canopy tree and regeneration density decreased to 1208 trees/ha and 3022 trees/ha respectively (Table 3.4).

During the canopy transition/gap dynamics stage of stand development, the age structure of the stand became largely uneven-aged and the distribution of trees resembles a reverse-J age structure (Figure 3.1c). All age classes from 1 to 13 (0 to ≥ 120 year TSF) were represented with the exception of trees being absent from age class 12 (110-119 year TSF). In conifer stands, canopy trees were largely jack pine, white spruce, black spruce, and balsam fir with minor contributions of paper birch while the understory was black spruce and balsam fir (Figure 3.1c). A few jack pine and paper birch trees are present in the largest age class (13 age class = ≥ 120 years TSF), which may represent trees that survived the last stand-replacing fire (Figure 3.1c). Once again, canopy tree and understory tree density decreased in comparison to the canopy transition stage of conifers to 488 trees/ha and 2667 trees/ha respectively (Table 3.4).

During the gap dynamic stage of stand development, age structure has become largely bimodal once again (Figure 3.1d). There is a significant contribution to stand age structure of exclusively balsam fir regeneration forming the initial peak largely in the 1st and 2nd age classes (0-19 years TSF) while white spruce, balsam fir, and paper birch form the second peak in the 7th and 8th age classes (60-79 years TSF). However, there is a sparse number of white and black spruce and paper birch in larger age classes 9 to 13 (80- ≥ 120 years TSF) (Figure 3.1d). Canopy tree density in this stage increased in comparison to the canopy transition/gap dynamic conifers to 908 trees/ha, while regeneration density decreased to 1289 trees/ha (Table 3.4).

Mixedwood stands

In mixedwood stands during the stem exclusion/canopy transition stage of stand development, stand age structure was bimodal, having a peak in the 2nd and 3rd age

classes (10-29 years TSF) and a second peak in the 6 to 9 age classes (50-89 years TSF). Like with the conifers, the first peak represents the regeneration occurring in the stand while the second peak represents canopy trees (Figure 3.2a). Canopy trees were predominately jack pine and trembling aspen, with some black spruce, paper birch, and balsam fir. Regeneration was mainly black spruce and balsam fir with small amounts of trembling aspen (Figure 3.2a). Canopy tree density during this stage was 1083 trees/ha, while being lower than the density of trees in the conifer stem exclusion/canopy transitions (Table 3.4). Regeneration density was 2311 trees/ha, and also was less than the regeneration occurring in the stem exclusion/canopy transitions conifers (Table 3.4).

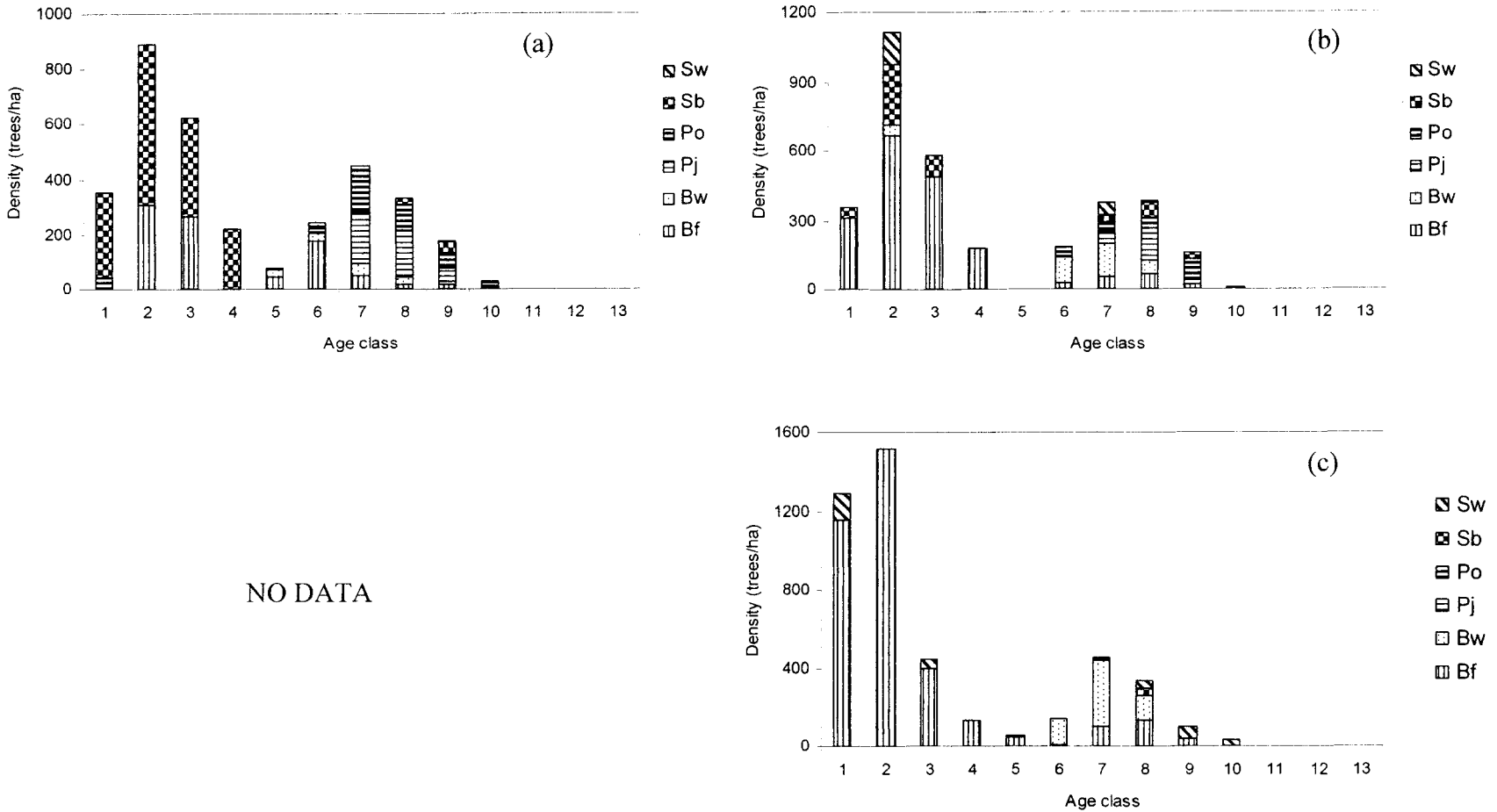


Figure 3.2. Density of trees in mixedwood stands by age class (1 = 0-9 yrs, 2 = 10-19 yrs, 3 = 20-29 yrs, 4 = 30-39 yrs, 5 = 40-49 yrs, 6 = 50-59 yrs, 7 = 60-69 yrs, 8 = 70-79 yrs, 9 = 80-89 yrs, 10 = 90-99 yrs, 11 = 100-109 yrs, 12 = 110-119 yrs, 13 = 120+ yrs) and species (Sw = white spruce, Sb = black spruce, Po = trembling aspen, Pj = jack pine, Bw = paper birch, Bf = balsam fir) for (a) stem exclusion/canopy transition, (b) canopy transition, and (c) gap dynamics.

The age structure in the canopy transition stage of stand development was very similar to the stem exclusion/canopy transition stage, showing a very pronounced bimodal age structure, with an initial peak representing largely balsam fir and black spruce regeneration with minor components of white spruce and paper birch that are largely in the 2nd and 3rd age classes (10-29 year TSF), and a second peak of canopy jack pine, trembling aspen, black spruce, white spruce, balsam fir, and paper birch trees that fall within the 6 to 9 age classes (50-89 years TSF) (Figure 3.2b). The density of canopy trees (1108 trees/ha) is higher than that occurring in the stem exclusion/canopy transition mixedwoods, while being lower than that occurring in the canopy transition conifers (Table 3.4). As well, the regeneration density was lower (2222 trees/ha) compared to both the stem exclusion/canopy transition mixedwoods and the conifer canopy transitions (Table 3.4).

Due to the limited sampling area and the frequent forest fires (Li 2000), I was unable to locate mixedwood stands in the canopy transition/gap dynamics stage of stand development to sample. During the gap dynamic stage of stand development, age structure was relatively bimodal (Figure 3.2c). There was a significant contribution to stand age structure of regeneration forming the initial peak in the 1st and 2nd age classes (0-29 years TSF) and canopy trees forming the second peak in the 7th and 8th age classes (60-79 years TSF) (Figure 3.2c). Canopy trees in the stand were a mixture of paper birch, balsam fir, and white and black spruce. The regeneration was predominantly balsam fir with a small component of white spruce (Figure 3.2c). Canopy tree density decreased in comparison to canopy transition mixedwoods to 1067 trees/ha, while being higher than that in the gap dynamic conifers (Table 3.4). Regeneration density is 3778 trees/ha, and

is lower than the density of regeneration in both the canopy transition mixedwoods and the gap dynamic conifers (Table 3.4).

Hardwood stands

During the stem exclusion/canopy transition stage of stand development in the hardwoods, stand age structure was bimodal, having an initial peak in the 2nd and 3rd age classes (10-29 years TSF) and a second peak in the 6 to 9 age classes (50-89 years TSF). The canopy trees represent the second peak and were largely trembling aspen and black spruce, with some paper birch, and balsam fir, while the regeneration was black spruce and balsam fir (Figure 3.3a). Canopy tree density was 1158 trees/ha, and was higher than the canopy tree density in the stem exclusion/canopy transition mixedwoods but lower than the conifers of this stage (Table 3.4). Regeneration density was 1111 trees/ha, and was lower than both the conifer and mixedwood stem exclusion/canopy transition stands (Table 3.4).

Unlike the age structure in their conifer and mixedwood counterparts, the age structure in the canopy transition hardwoods was unimodal. The single peak represents canopy trees of largely trembling aspen that fell within the 7 to 10 age classes (60-99 years TSF) (Figure 3.3b). Regeneration density was very low (178 trees/ha), thus causing age classes 1 to 5 to be poorly represented (Table 3.4, Figure 3.3b). Canopy tree density is 675 trees/ha, and is lower than the density of canopy trees in the stem exclusion/canopy transition hardwoods and the canopy transition conifers and mixedwoods (Table 3.4).

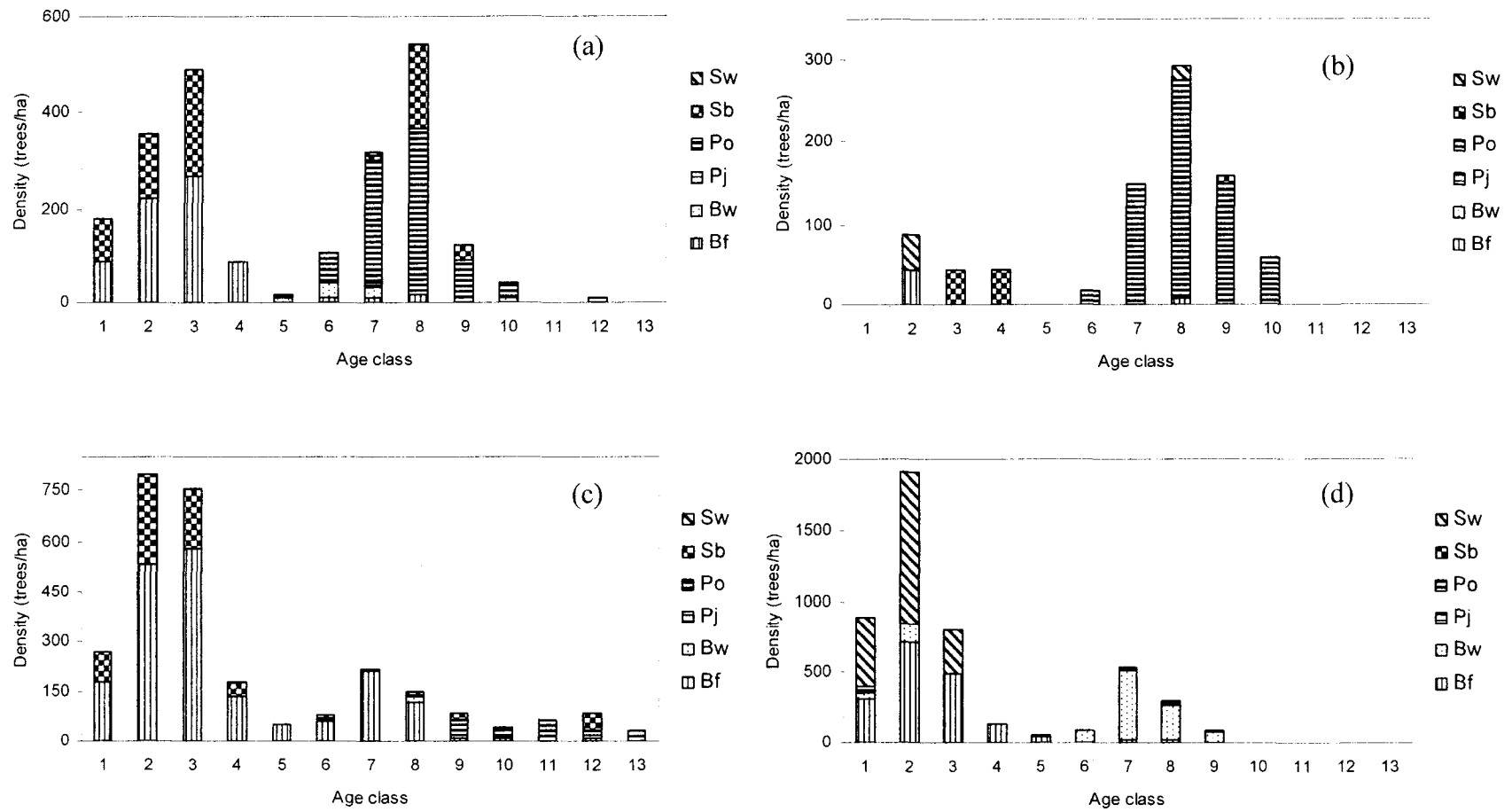


Figure 3.3. Density of trees in hardwood stands by age class (1 = 0-9 yrs, 2 = 10-19 yrs, 3 = 20-29 yrs, 4 = 30-39 yrs, 5 = 40-49 yrs, 6 = 50-59 yrs, 7 = 60-69 yrs, 8 = 70-79 yrs, 9 = 80-89 yrs, 10 = 90-99 yrs, 11 = 100-109 yrs, 12 = 110-119 yrs, 13 = 120+ yrs) and species (Sw = white spruce, Sb = black spruce, Po = trembling aspen, Pj = jack pine, Bw = paper birch, Bf = balsam fir) for (a) stem exclusion/canopy transition, (b) canopy transition, (c) canopy transition/gap dynamics, and (d) gap dynamics.

During the canopy transition/gap dynamics stage of stand development, the age structure of the stand appears to be weakly reverse-J to weakly bimodal, with large peaks in the 2nd and 3rd age classes (10-19 years TSF), minor peaks in the 7th and 8th (60-79 years TSF), and all age classes from 1 to 13 (0 to \geq 120 years TSF) being well represented (Figure 3.3c). The oldest canopy trees were mainly black spruce and trembling aspen, while the younger canopy trees were largely balsam fir with some white and black spruce, paper birch, and trembling aspen. Regeneration was largely balsam fir and black spruce (Figure 3.3c). Canopy tree density increased compared to the canopy transition hardwoods to 717 trees/ha, while being higher than their conifer counterparts (Table 3.4). Regeneration density also increased compared to the canopy transition hardwoods to 2089 trees/ha, but was lower than their conifer counterparts (Table 3.4).

During the gap dynamic stage of stand development, age structure has become largely bimodal once again. There is a significant contribution to stand age structure of white spruce dominated and balsam fir and paper birch regeneration forming the first peak in the 1 to 3 age classes (0-29 years TSF). Canopy trees were largely paper birch with minor components of balsam fir, white spruce, and trembling aspen forming the second peak in the 6 to 8 age classes (50-79 years TSF) (Figure 3.3d). Canopy tree and regeneration density both increased (1025 trees/ha and 2867 trees/ha respectively) compared to the canopy transition/gap dynamics hardwoods (Table 3.4). Canopy tree and regeneration density were both lower than their mixedwood but higher than their conifer respective counterparts (Table 3.4).

Height distributions

In order to better understand stand age structure, height distributions were plotted for all trees, saplings and seedlings. Regardless of stand developmental stage or cover type, the density of trees in the smallest height class (0-4.9 m) was very high and ranged from 1000-4000 trees/ha, with the exception of the canopy transition hardwoods where the density of trees was less than 200 trees/ha (Figure 3.4, 3.5, 3.6). From this point forward, my description of height distributions will not include height class 1 which is mainly understory regeneration. In the stem exclusion/canopy transition and canopy transition conifers, trees were normally distributed from height classes 2 to 5 (5-24.9 m) with a peak in height class 4 (15-19.9 m) (Figure 3.4a, b). Mixedwood stands in the stem exclusion/canopy transition and canopy transition stages of stand development responded similar to the conifer stands, with the exception that the range of the normal distributions extended from height classes 2 to 6 (Figure 3.5a, b). In the stem exclusion/canopy transition hardwoods, trees were represented from height classes 2 to 7 and formed a bimodal distribution with peaks in height class 3 (10-14.9 m) and 5 (20-24.9 m) (Figure 3.6a). There were no trees in height classes 2 (5-9.9 m) and 3 (10-14.9 m) in the canopy transition hardwoods. However, there was an increase in tree density from height class 4 to 6, while height class 7 (≥ 30 m) had very low tree density (Figure 3.6b).

In the canopy transition/gap dynamics conifers, height classes 2 to 5 (5-24.9 m) were well represented while in the hardwoods, classes 2 to 6 (5-29.9 m) were well represented, though class 3 (10-14.9 m) was the highest (Figure 3.4c, 3.6c). In the gap dynamics conifers, trees were present in height classes 3 to 5 (10-24.9 m) with a peak in class 4 (15-19.9 m) (Figure 3.4d), while trees were normally distributed among height

classes 2 to 5 with a peak in height class 4 in mixedwood and hardwood stands during this stage of stand development (Figure 3.5d, 3.6d).

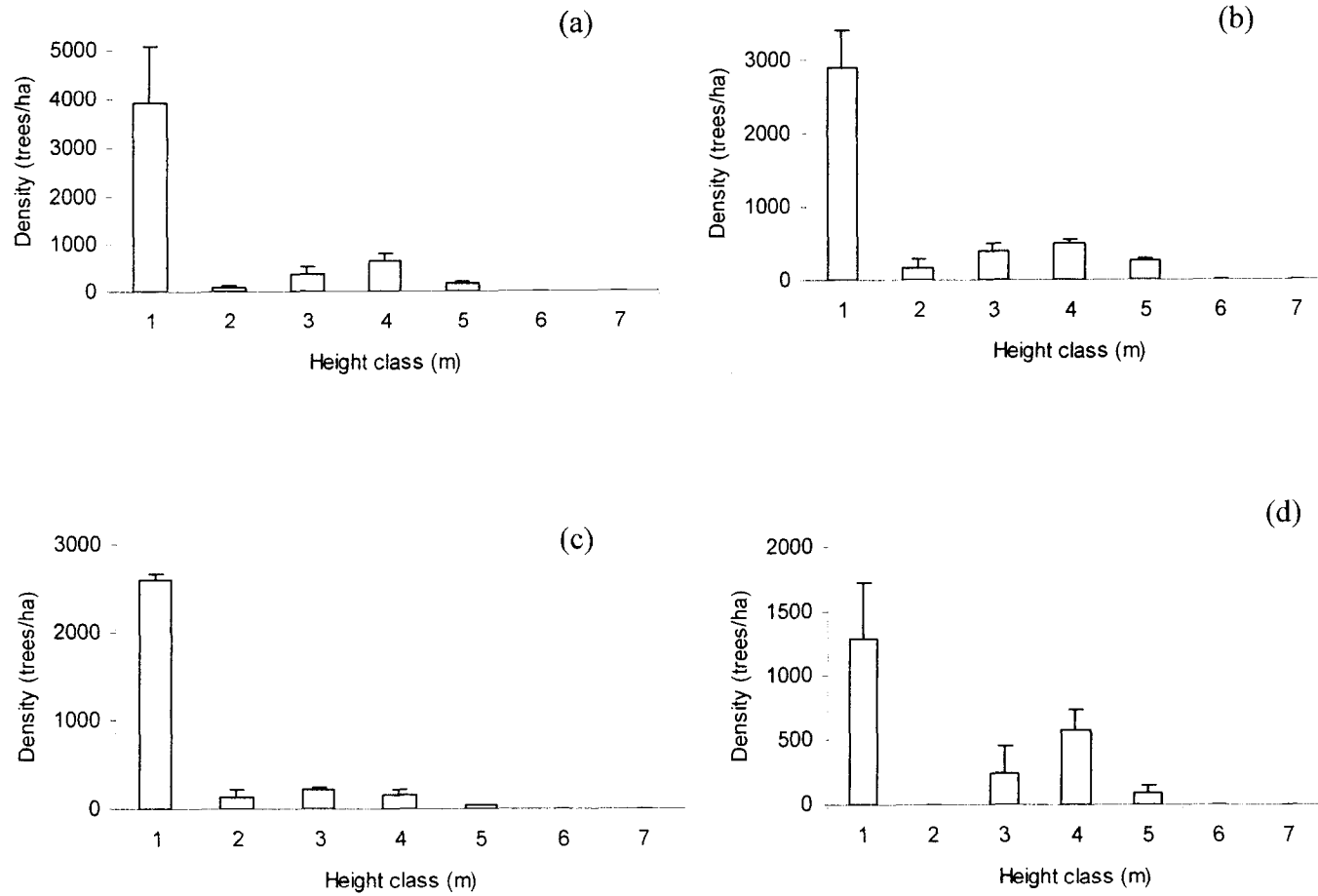


Figure 3.4 Density of trees (trees/ha) in conifer stands by height class (1 = 0-4.9 m, 2 = 5-9.9 m, 3 = 10-14.9 m, 4 = 15-19.9 m, 5 = 20-24.9 m, 6 = 25-29.9 m, 7 = ≥ 30 m) in the (a) stem exclusion/canopy transition, (b) canopy transition, (c) canopy transition/gap dynamics, and (d) gap dynamic stage of stand development.

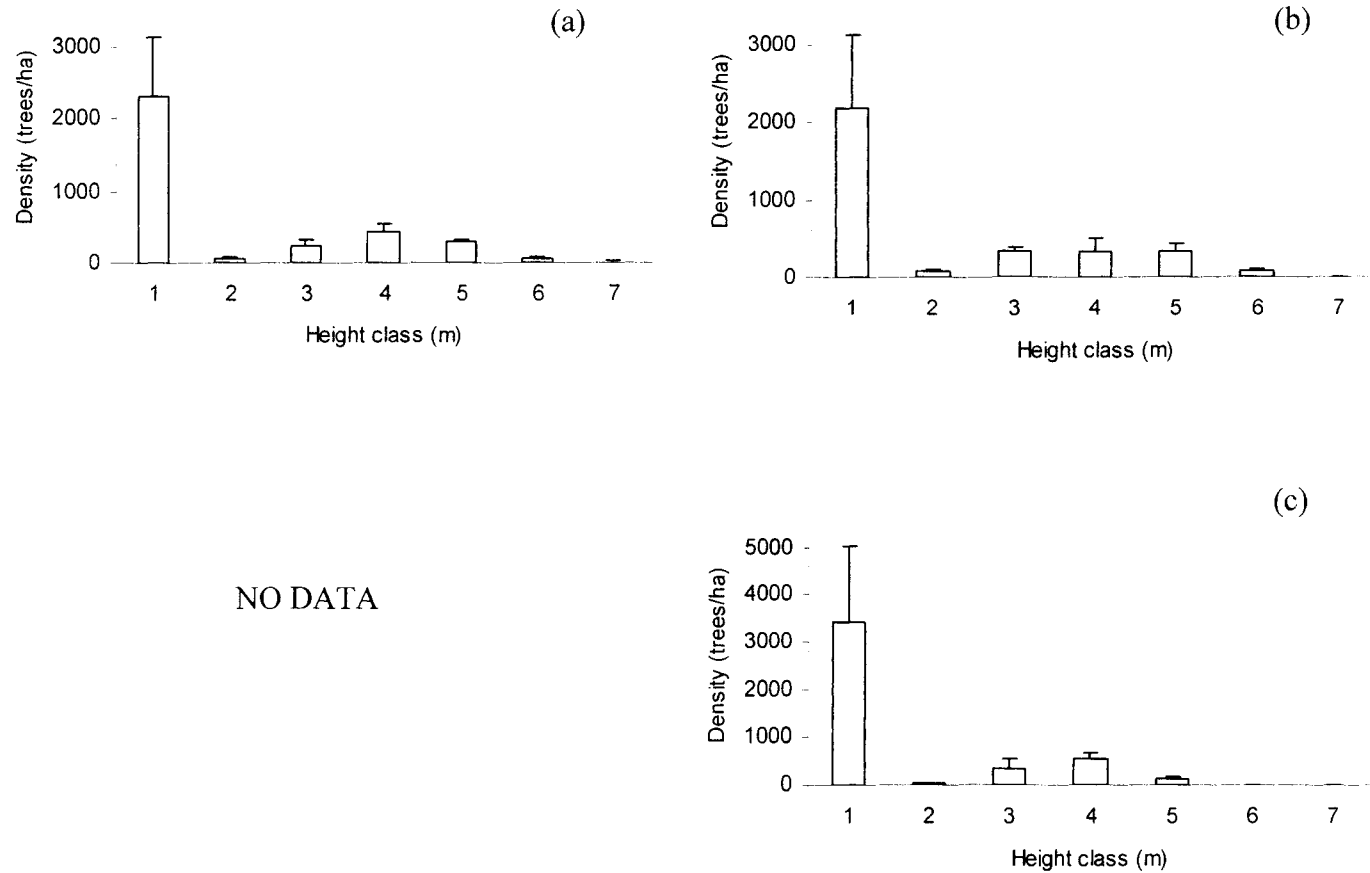


Figure 3.5. Density of trees (trees/ha) in mixedwood stands by height class (1 = 0-4.9 m, 2 = 5-9.9 m, 3 = 10-14.9 m, 4 = 15-19.9 m, 5 = 20-24.9 m, 6 = 25-29.9 m, 7 = ≥ 30 m) in the (a) stem exclusion/canopy transition, (b) canopy transition, and (c) gap dynamic stage of stand development.

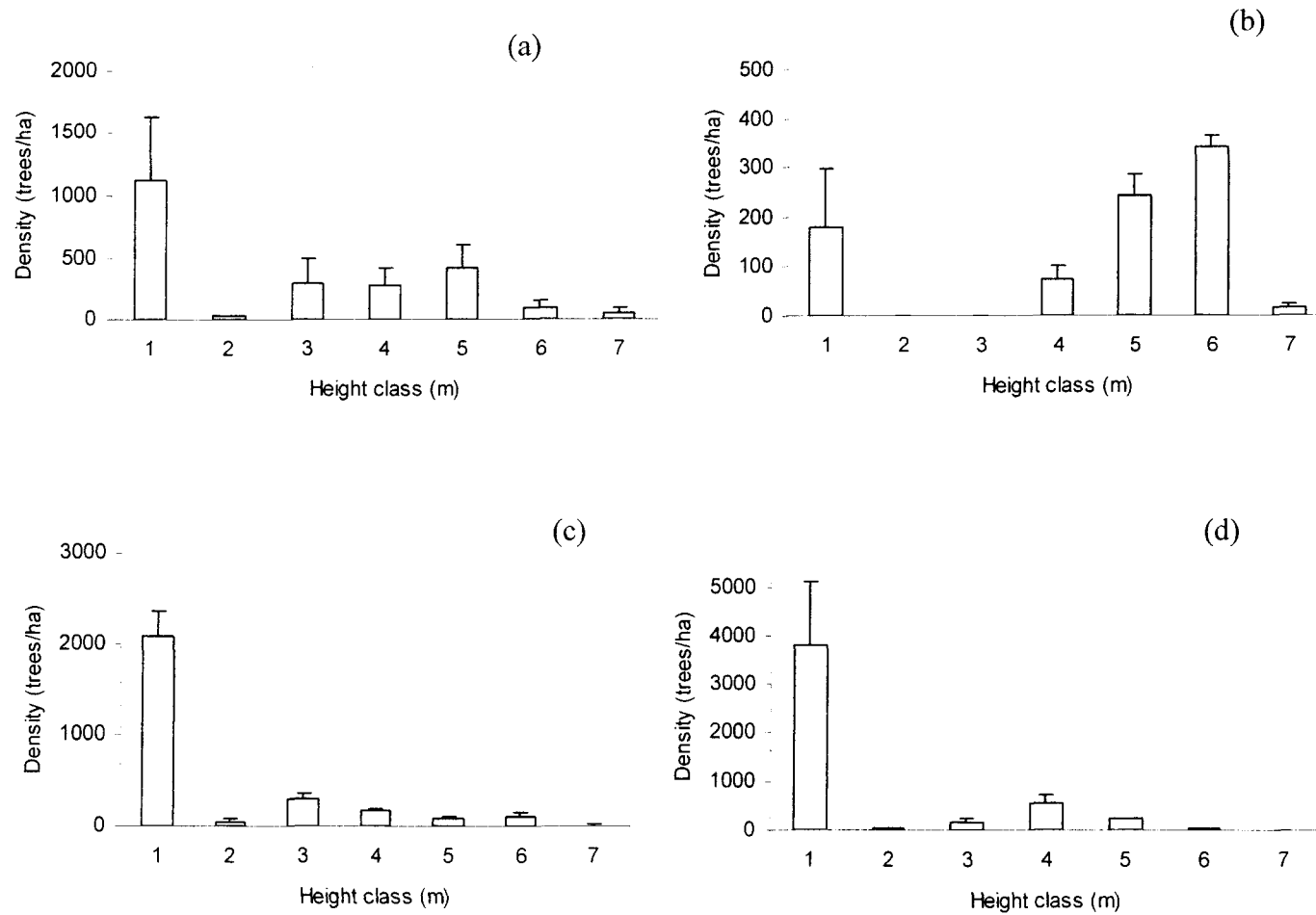


Figure 3.6 Density of trees (trees/ha) in hardwood stands by height class (1 = 0-4.9 m, 2 = 5-9.9 m, 3 = 10-14.9 m, 4 = 15-19.9 m, 5 = 20-24.9 m, 6 = 25-29.9 m, 7 = ≥ 30 m) in the (a) stem exclusion/canopy transition, (b) canopy transition, (c) canopy transition/gap dynamics, and (d) gap dynamic stage of stand development.

DISCUSSION

Variation in stand age structure with stand developmental stage and cover type

My findings suggest that a stand developmental stage and stand cover type effect existed in the study. Because of this, the development of stand age structure with stand developmental stage will be discussed separately for each of the three boreal forest cover types studied even though differences were minimal. Diameter distributions were plotted, but were not significant (see Appendix II).

Stand age structural development in conifer stands proceeded from a bimodal structure in the stem exclusion/canopy transition and canopy transition stages to a reverse-J age structure in the canopy transition/gap dynamics stage to a bimodal structure once again in the gap dynamics stage. In the stem exclusion/canopy transition and canopy transition stages, the canopy is dominated by jack pine that had established immediately after the stand-replacing fire, as significant age-related mortality has not yet occurred. In turn, self-thinning that occurred in earlier stages of development would have opened up growing space and freed up nutrients (Chen *et al.* 1996; Oliver and Larson 1996), thus contributing to the significant regeneration of conifers that was occurring.

By the canopy transition/gap dynamics stage of stand development, most of the pioneer cohort has died off, as only one or two jack pine remain living per plot (average number of pioneering jack pine trees per hectare = 42), as the age of these stands (139 years TSF) are beyond a jack pine's average life span (Farrar 1995). As well, trees that were suppressed in earlier stages of development were released to undergo rapid growth and take position in the canopy and subcanopy. The dieing off of the pioneer cohort of jack pine would free up additional space for further regeneration to establish. This

resulted in a reverse-J age structure occurring in these stands, and is supported by Kneeshaw and Burton (1997), who found that old (>120 year-old) spruce stands in sub-boreal British Columbia show either a reverse-J or bimodal age structure.

By the gap dynamic stage of stand development, the pioneering cohort of jack pine had completely died off, and the canopy is dominated by later successional conifers. These conifers were younger than the jack pine that dominated in the preceding stage, causing the largest age classes to disappear. As such, the age structure was bimodal, with a canopy dominated by later successional tree species and an understory with young regeneration of conifers, largely balsam fir. The very low density of balsam fir in age classes 3 to 6 (20-59 years) may have been caused by periodic spruce budworm outbreaks (the most recent one peaked in 1986 and collapsed approximately ten years later (Paul Poschmann (Abitibi-Consolidated), *personal communication*)), that would have killed a significant amount of host-specific balsam fir (and to a lesser extent white and black spruce) trees (MacLean and Ostaff 1989; Bergeron *et al.* 1995; Parent *et al.* 2001; Burleigh *et al.* 2002).

While differing from conifer stands in that their canopy was dominated by trembling aspen, hardwood stands in the stem exclusion/canopy transition stage of stand development were also bimodal in age structure. The overstory was dominated by trembling aspen trees (with a small spruce component) that established with the stand-replacing fire, while the understory contained largely conifer regeneration. However, hardwoods differed from their conifer counterparts in the canopy transition stage. The stand age structure of these stands were weakly unimodal, dominated largely by a single cohort of trembling aspen trees that established following stand replacing disturbance and

with marginal amounts of conifer regeneration. Stands dominated by trembling aspen often develop very dense shrub layers of mountain maple (*Acer spicatum*) (Bourgeois *et al.* 2004) and beaked hazel (*Corylus cornuta*) (Hill *et al.* 2005). A dense shrub layer was observed to occur in all sampled hardwood stands (except for those in the gap dynamic stage) due to the morphological characteristics of trembling aspen (Burns and Honkala 1990; Farrar 1995) that allowed a substantial amount of light to reach the forest floor. Further, dense shrub layers have been found to hinder regeneration (Wallenius *et al.* 2002; Bourgeois *et al.* 2004; Hill *et al.* 2005), thus contributing to the unimodal age structure that occurred in the canopy transition hardwoods.

In contrast to the conifer stands, hardwood stands had more pioneering trees trembling aspen trees per 400 m² plot still living in the canopy transition/gap dynamic stage of stand development (average number of pioneering trembling aspen trees per 400 m² plot = 6-11; per hectare = 200), even though jack pine is generally a longer-lived tree species compared to trembling aspen (Farrar 1995). This may be due to the hardwood sites in the canopy transition/gap dynamic stage of stand development being more productive than the conifer sites that were sampled. However, as in the conifer stands, hardwoods were also relatively reverse-J. I believe that the dense shrub layer (area coverage at shrub height (1-2 m) = 85%; Jennifer Fricker, *personal observation*) occurring in these stands likely developed recently indicated by a significant amount of later successional conifers and hardwoods in the subcanopy and regeneration in the understory that would have been hindered if a dense shrub layer would have developed earlier in succession.

Paper birch dominated the hardwoods in the gap dynamic stage of development. Paper birch has been shown to be able to live for well over 200 years (Bergeron 2000), and is the only hardwood species in this area of the boreal forest that could form dominant stands by this stand age. Further, the ability of paper birch to allow light to pass through to the forest floor, and the sparse shrub layer that was found, would allow for a significant amount of regeneration to establish. It is possible that (a) the higher density of trees in gap dynamic paper birch dominated stands compared to earlier developed hardwood stands that were dominated by trembling aspen or (b) differences in crown architecture between paper birch and trembling aspen may allow less light to penetrate to the forest floor and reduce the extent of the shrub layer in paper birch dominated stands compared to trembling aspen dominated stands. Therefore, the age structure of gap dynamic hardwoods were similar to that occurring in the gap dynamic conifers, with a bimodal age stand structure caused by a canopy of paper birch trees falling into the older age classes (though not as old as occurring in the canopy transition/gap dynamics hardwoods because of the very old trembling aspen trees) and regeneration of conifers forming the younger age classes.

With the exception of mixedwood stands having canopies composed of a mixture of conifers and hardwoods that met the sampling criteria (25-75% conifer component), and that I was missing mixedwoods in the canopy transition/gap dynamic stage of stand development, stand age structure developed very similar to that in conifer stands. I believe that this was caused by the conifer component limiting light to the forest floor and preventing a dense shrub layer from developing (Bourgeois *et al.* 2004). Without this dense shrub layer, regeneration would have responded similarly to what was

occurring in conifer stands, thus causing a similar age structure to develop. I hypothesize that successional trajectories in mixedwood stands may be headed towards conifer dominance due to the composition, as indicated by the composition of the regeneration layer. However, budworm outbreaks tend to occur every 20 years, therefore making this uncertain Fleming *et al.* 2000). Spruce budworm outbreaks affect both tree layer and understory regeneration.

Regardless of stand cover type or developmental stage, regeneration in all the stands was almost exclusively balsam fir and spruce, indicating that successional trajectories in the study area are likely proceeding towards conifer dominance on most sites. This is likely a consequence of the silvics of these species and the availability of a close seed source. Black spruce is shade tolerant (allowing it to establish under the cover of other trees), while also being able to reproduce by layering (Charron and Greene 2002). Balsam fir is also a shade tolerant species, and has seeds that are readily dispersed by wind (Wang and Kembell 2005) and enter a stand from nearby areas.

Implications for old-growth management

As forest structure has been linked to biodiversity and wildlife habitat (Brassard and Chen 2006), and forest structure has been shown to be related to forest age structure (Moser 1972; Van wagner 1978; Bondarev 1997), it is likely that forest management activities that diversifies forest stand age structures at the landscape level may positively affect forest biodiversity and create specialized wildlife habitat for certain species. For example, Bergeron (2004) recommends using clearcutting in some parts of the boreal forest, partial harvesting in other parts, and selective cutting in other parts to create a landscape that contains young, mature, and old forests. Nyland (2003) recommends

using partial cutting to realize the benefits of an uneven-aged, multi-species stand structure for wildlife habitat, while still benefiting from the economics of fibre extraction. Further, Asselin (2001) recommends seed-tree systems to increase age structure heterogeneity by maintaining some large, older trees in a young developing stand. These large trees left following clearcutting can create wildlife habitat in younger post-clearcut stands for large raptors that need large trees and snags for nesting (Brassard and Chen 2006) and can preserve the superior tree species genetics of that site.

Old-growth forests have been found to provide many values from an ecological, aesthetic/recreational, and economic perspective (Barnard 2004; Brassard and Chen 2006). However, management decisions surrounding old-growth are hampered by the lack of a clear definition on what old-growth is in the boreal forest (Cogbill 1984; Barnard 2004). While some studies (including this study) use the disappearance of the pioneering cohort as the point at which an old-growth structure is reached (Chen and Popadiouk 2002; Brassard and Chen 2006), definitions of old-growth vary depending on the study (Franklin *et al.* 2002). I recommend that old-growth in this region of the boreal forest be considered when the following criteria are met: (1) canopy breakdown of pioneering cohort is complete and the stand is dominated by later successional tree species such as balsam fir and spruce and (2) the age structure of the stand is bimodal, with dominating canopy trees that fall within a relatively narrow range of age and height classes and a significant amount of understory regeneration.

Selection harvesting could be used to hasten the onset of old-growth and/or create a reverse-J stand age structure if applied to stands that are in approximately the stem exclusion/canopy transition stage of stand development or even earlier in the stem

exclusion stage. I suggest removing selective canopy trees that would (a) release suppressed trees to rapid growth, (b) allow canopy trees to grow even faster, and (c) allow trees to establish in gaps created by the removal of canopy trees, which would promote the movement of a unimodal or bimodal age structure into a reverse-J age structure while increasing the later successional component to the stand thereby hastening old-growth onset.

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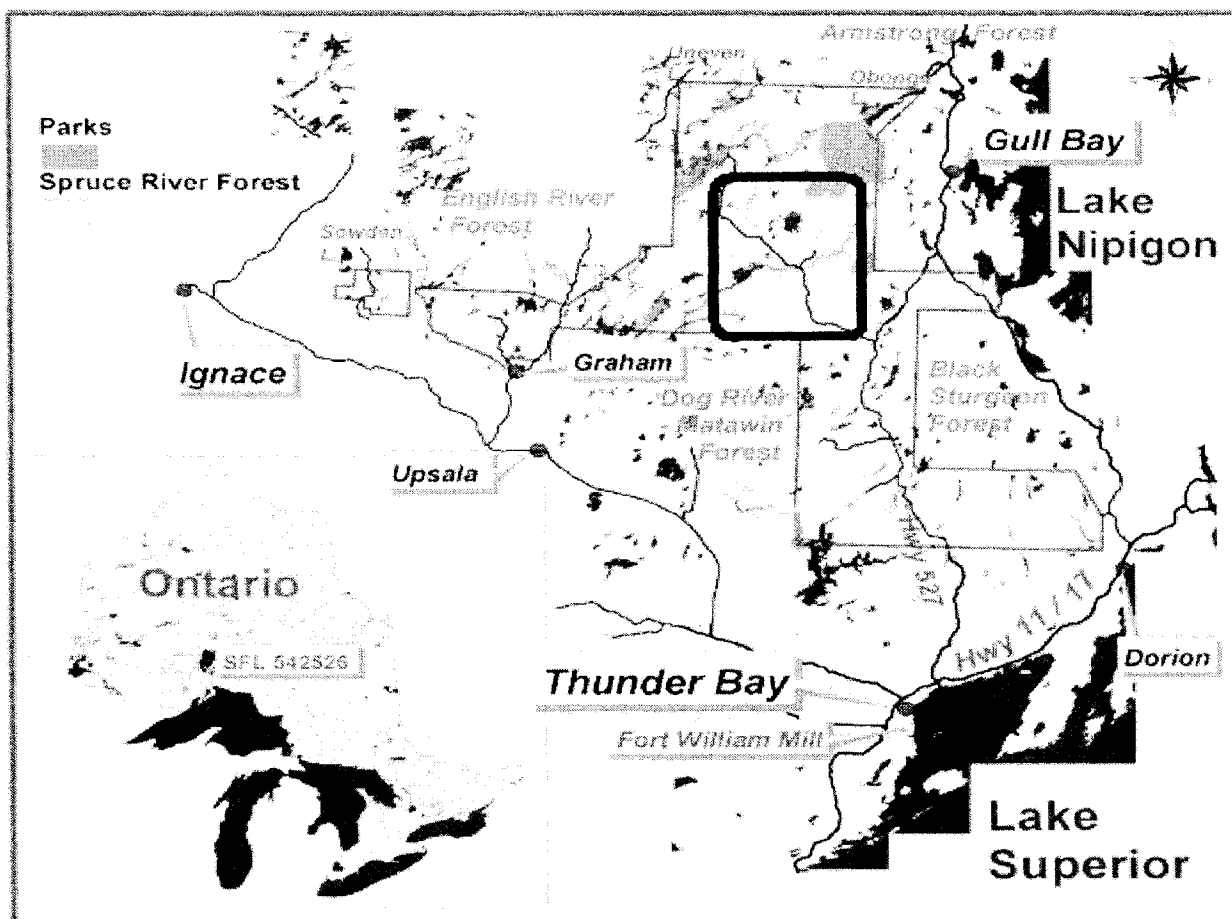
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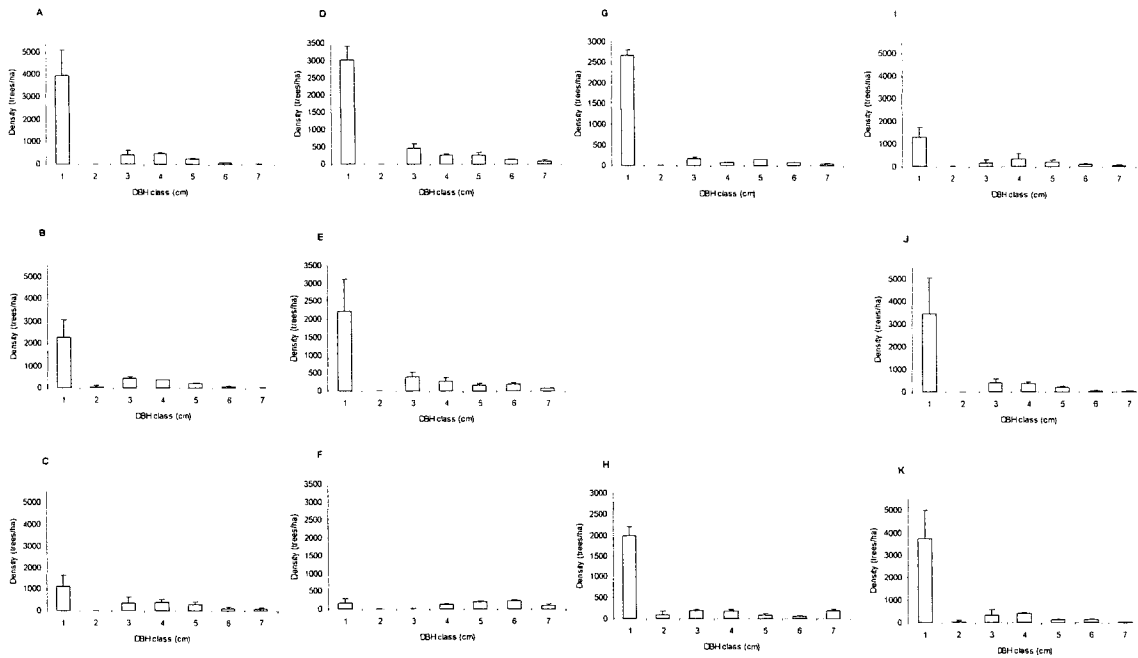
APPENDICES

MAP OF THE STUDY AREA IN NORTHWESTERN ONTARIO, CANADA.



NOTE: Map has been modified from Abitibi-Consolidated (2006).

DIAMETER DISTRIBUTIONS



Density of trees (trees/ha) by diameter class (1 = 0-4.9 m, 2 = 5-9.9 m, 3 = 10-14.9 m, 4 = 15-19.9 m, 5 = 20-24.9m, 6 = 25-29.9 m, 7 = ≥ 30 m) in the (A) stem exclusion/canopy transition for conifer stands, (B) canopy transition for conifer stands, (C) canopy transition/gap dynamics for conifer stands, (D) gap dynamics for conifer stands, (E) stem exclusion/canopy transition for mixedwood stands, (F) canopy transition for mixedwood stands, (G) gap dynamics for mixedwood stands, (H) stem exclusion/canopy transition for hardwood stands, (I) canopy transition for hardwood stands, (J) canopy transition/gap dynamics for hardwoods stands, and (K) gap dynamics for hardwood stands.