

# Stand Structural Dynamics of North American Boreal Forests

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Stand structure, the arrangement and interrelationships of live and dead trees, has been linked to forest regeneration, nutrient cycling, wildlife habitat, and climate regulation. The objective of this review was to synthesize literature on stand structural dynamics of North American boreal forests, addressing both live tree and coarse woody debris (CWD) characteristics under different disturbance mechanisms (fire, clearcut, wind, and spruce budworm), while identifying regional differences based on climate and surficial deposit variability. In fire origin stands, both live tree and CWD attributes are influenced initially largely by the characteristics of the stand replacing fire and later increasingly by autogenic processes. Differences in stand structure have also been observed between various stand cover types. Blowdown and insect outbreaks are two significant non-stand replacing disturbances that can alter forest stand structure through removing canopy trees, freeing up available growing space, and creating microsites for new trees to establish. Climate and surficial deposits are highly variable in the boreal forest due to its extensive geographic range, influencing stand and landscape structure by affecting tree colonization, stand composition, successional trajectories, CWD dynamics, and disturbance regimes including regional fire cycles. Further, predicted climate change scenarios are likely to cause regional-specific alterations in stand and landscape structure, with the implications on ecosystem components including wildlife, biodiversity, and carbon balance still unclear. Some stand structural attributes are found to be similar between clearcut and fire origin stands, but others appear to be quite different. Future research shall focus on examining structural variability under both disturbance regimes and management alternatives emulating both stand replacing and non-stand replacing natural disturbances.

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**Keywords** stand structure, live trees, coarse woody debris, snags, downed logs, time since fire, stand cover type, wind, spruce budworm, climate change, timber harvesting

## I. INTRODUCTION

Stand structure, the arrangement and interrelationships of live and dead trees, is one of the key attributes of forest ecosystems. Stand structure has important implications for forest ecosystems including the maintenance of wildlife habitat (Sturtevant *et al.*, 1997; Kolström, 1998; Lee, 1998; Ecke *et al.*, 2002), the regulation of climate through carbon storing (Harmon and Hua, 1991; Gower, 2003), and the prevalence of forest regeneration (Siitonen *et al.*, 2000). Forest stand dynamics refers to the changes in forest stand structure over time (Oliver and Larson, 1996; Chen and Popadiouk, 2002). These changes are driven by various stand-initiating disturbances, partial disturbances and autogenic processes (Delong and Kessler, 2000). For the purpose of this paper, the study of forest stand structure will include

an examination of the physical and temporal characteristics of both live trees and dead wood (CWD).

This paper will review the stand structural dynamics of boreal forests in North America. The topics that will be covered in this review include (1) tree species compositional dynamics, (2) structural changes with time since fire, (3) the effect of canopy composition on stand structure, (4) the role of non-stand replacing disturbances in altering forest structure, (5) variability of stand structure related to climate and geography, and (6) a comparison of stand structure in natural forests and managed forests.

## II. TREE SPECIES COMPOSITIONAL DYNAMICS IN THE NORTH AMERICAN BOREAL FOREST

Boreal forests account for 30 percent of the world's terrestrial phytomass (Bailey, 1996). In North America, four major boreal ecozones (Atlantic Maritime, Boreal Shield, Boreal Plains, and Boreal Cordillera) form a continuous forest belt from east to west between 45° and 65° north. Of Canada's 417.6 million hectares of forest, nearly 90 percent of the productive forest area is boreal, which represents more than 30 percent of the global boreal forest. The boreal forest varies greatly in climate and disturbance regimes. Climates range from dry and cold climates with a mean annual temperature of only -8°C and a mean annual precipitation of 300 mm to relatively warm and moist climates with a mean annual temperature of 6°C and a mean annual precipitation of 1350 mm (Rowe, 1972). The boreal forest ecosystems today host 291 plant species distributed among 147 genera and 47 families (La Roi, 1967).

Forest stands develop by changing in composition and structure over time (Finegan, 1984). Successional trends in the boreal forest depend upon differences in fire frequency (Bergeron and Dubuc, 1989). An important process, for example, is cyclic succession, and occurs when the fire frequency is short enough that species replacement does not occur, and the same species that colonized the stand after disturbance dominate until the next stand-replacing disturbance (Dix and Swan, 1971; Carleton and Maycock, 1978; Johnson, 1992; Chen and Popadiouk, 2002). This leads to the persistence of sites dominated by shade-intolerant species such as jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.) (Carleton and Maycock, 1978; Cumming, 2001; Chen and Popadiouk, 2002). In contrast, directional succession involves species replacement and lead to stands dominated by shade-tolerant white and black spruce

(*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) BSP, respectively), balsam fir (*Abies balsamea* (L.) Mill.), and eastern white cedar (*Thuja occidentalis* L.) when time since a stand-replacing fire is significantly long (Bergeron and Dubuc, 1989; De Grandpré *et al.*, 2000; Harper *et al.*, 2002; Lesieur *et al.*, 2002). Species replacement is controlled by differences in a species' ability to reproduce under a closed canopy (Bergeron and Dubuc, 1989), and the ability of a species to persist in the forest as succession proceeds is related to its unique ability to successfully reproduce within the changing conditions that succession creates (Suffling, 1995).

Surficial deposits and landscape configuration are important contributors in determining which species colonize certain areas of forest and how succession proceeds (Vancleve *et al.*, 1991; Gauthier *et al.*, 2000; Harper *et al.*, 2002; Chen and Popadiouk, 2002). Mixedwood or deciduous stands tend to be more abundant on mesic, modal sites while coniferous stands are more abundant on hydric and xeric sites (Bergeron and Dansereau, 1993; Timoney, 2003), reflecting long-term evolutionary trends. Mesic sites are colonized usually by trembling aspen (Gauthier *et al.*, 2000), whereas rocky and sandy drier sites are usually dominated by jack pine or paper birch (De Grandpré *et al.*, 2000; Gauthier *et al.*, 2000; Timoney, 2003). Acidic soils create conditions where black spruce can thrive and other species are excluded due to their intolerance of acidic soils (Parisien and Sirois, 2003). Over time, succession brings about a change in stand species composition, resulting in a decrease in the proportion of shade-intolerant species, i.e., paper birch, trembling aspen, and jack pine in favor of an increase in the proportion of shade-tolerant conifers, i.e., balsam fir, black spruce, white spruce, and eastern white cedar (Bergeron and Dubuc, 1989; Bergeron and Dansereau, 1993; Bergeron and Harvey, 1997; Bergeron, 2000; De Grandpré *et al.*, 2000; Gauthier *et al.*, 2000; Harper *et al.*, 2002). The succession on mesic, boreal sites can be summarized as follows (Bergeron, 2000; De Grandpré *et al.*, 2000; Gauthier *et al.*, 2000; Harper *et al.*, 2002):

1. Domination of the post-fire cohort by trembling aspen and paper birch. Many boreal tree species rely on fire as a mechanism for propagation (Thompson *et al.*, 1998). Paper birch and trembling aspen are early successional species that have adapted to frequent fires and open conditions by evolving regeneration mechanisms that make them well suited to quickly colonize habitats disturbed by fire (Harper and Macdonald, 2002). Paper birch and trembling aspen can reproduce by stem sprouts and suckering respectively, or by seeds (Bergeron and Dubuc, 1989; Suffling, 1995; Bergeron and Harvey, 1997; Bergeron, 2000; Harper and Macdonald, 2002; Vasiliauskas and Chen, 2002). Paper birch is especially successful at colonizing early after fire in the absence of trembling aspen (Bergeron, 2000).
2. Deciduous (most noticeably trembling aspen) stands break up from age-related factors and the formation of mixedwoods through an increase in conifer abundance. Trembling aspen

decline has been found to occur at an age as early as 60 years after a stand-replacing disturbance (Pothier *et al.*, 2004). In turn, Paré and Bergeron (1995), Cumming *et al.* (2000), and Kabzems and Garcia (2004) all revealed that trembling aspen can dominate forest stands for a considerable length of time due to its ability to recruit new individuals in gaps created during stand break up and therefore foster the development of more than one dominating cohort. Structural heterogeneity therefore increases as stand age increases, indicating that structural development as a result of gap dynamics is not exclusive to forests composed largely of shade-tolerant trees (Cumming *et al.*, 2000).

3. Increasing abundance and dominance of shade-tolerant coniferous species (white spruce, balsam fir, eastern white cedar) and the prevalence of eastern spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks maintain a deciduous component in the forest due to the superior competitive ability of deciduous trees when sufficient light is available. Some species such as eastern white cedar and white spruce have not evolved unique adaptations to fire, and therefore are usually present predominantly late in succession in areas where time since fire is very long (Kneeshaw and Bergeron, 1998; Asselin *et al.*, 2001; Parisien and Sirois, 2003).

In the North American boreal forest, jack pine and black spruce are the two most extensively distributed coniferous species (Arseneault, 2001). When jack pine establishes as the pioneering cohort on xeric sites, it is usually replaced by black spruce when the fire return interval is long enough (De Grandpré *et al.*, 2000; Gauthier *et al.*, 2000; Harper *et al.*, 2002). The pre-fire abundance of jack pine largely determines its presence in the post-fire landscape. However, long fire intervals can cause jack pine to disappear through succession to more shade-tolerant species (Bergeron and Dansereau, 1993). Both black spruce and jack pine use seeds as their main mechanism for reproduction (Suffling, 1995; Vasiliauskas and Chen, 2002) and have evolved heat-opening semiserotinous and serotinous cones respectively (Arseneault, 2001; Parisien and Sirois, 2003), although black spruce can also reproduce by layering (Suffling, 1995).

Organic and hydric sites are predominantly colonized by black spruce, tamarack (*Larix laricina* (Du Roi) K. Koch), and eastern white cedar (Bergeron and Dubuc, 1989; Gauthier *et al.*, 2000; Harper *et al.*, 2002). Large, extremely intense fires can create situations where large areas are burned and the establishment of jack pine or black spruce is hindered due to the large distance from a seed source or by the destruction of seeds on sites that were available for propagation before the fire (Arseneault, 2001). On organic sites dominated by black spruce, species replacement is virtually absent, and the structure of the stand changes over time from a single layered canopy to one that is multilayered (Gauthier *et al.*, 2000; Harper *et al.*, 2002). However, balsam fir can occasionally be found in very old black spruce stands suggesting that changes in stand composition of black spruce

dominated stands can occur on upland sites (De Grandpré *et al.*, 2000). On xeric sites in the southern part of the boreal forest at the limit of its northern distribution (Timoney, 2003), red pine can be the dominant post-fire cohort (Bergeron and Gagnon, 1987; Bergeron and Dubuc, 1989). Many species such as white pine (*Pinus strobus* L.), red pine, sugar maple (*Acer saccharum* Marsh.), eastern white cedar, and yellow birch (*Betula alghaniensis* Britt.) reach their northwestern limits in southeastern Manitoba and northwestern Ontario (Timoney, 2003).

The successional trends described above apply to eastern, central and west-central North American boreal forests. In Alaska, topography is even more important in controlling stand composition and structure while soil parent materials and disturbance regimes all contribute to tree species compositional dynamics (Viereck *et al.*, 1983; Vancleve *et al.*, 1991, 1996). In the sub-boreal forest of British Columbia, stands are usually colonized by lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (an early successional species with serotinous cones) following fire, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and hybrids of white spruce and Engelmann spruce (late successional species) can form dominant stands as well (Clark *et al.*, 2003). Even when the establishment densities of lodgepole pine are low, this species usually dominates due to its ability to grow more rapidly than its associated more shade-tolerant species (Chen *et al.*, 1996; Chen, 1997; Clark *et al.*, 2003). Like jack pine, however, lodgepole pine can disappear from the landscape due to its inability to establish itself beyond stand replacement (Chen, 1997; Antos and Parish, 2002) especially when fire return intervals are long, very intense fires destroy seed sources, and/or recruitment from distant stands is difficult (Clark *et al.*, 2003). Over time, the ability of subalpine fir and white spruce and Engelmann hybrids to grow in the understory and subcanopy will result in their increased abundance at the expense of lodgepole pine (Clark *et al.*, 2003). Subalpine fir dominates older forests due to its efficient seed bank and shade tolerance (Antos and Parish, 2002). Although old stands are largely dominated by subalpine fir, white spruce and Engelmann hybrids can establish in the understory and be an important component of the overstory in even the oldest stands (Varga and Klinka, 2001; Clark *et al.*, 2003).

### III. STRUCTURAL CHANGES IN THE BOREAL FOREST WITH TIME SINCE FIRE

Stand structure includes characteristics of both live trees and snags and downed logs as CWD (Table 1). In this section, we evaluate stand structural dynamics through the changes of both live trees and CWD in stand basal area, volume, density, abundance, spatial and size distribution, decay state (CWD only), and species composition along chronosequences.

#### A. Living Tree Dynamics

Young stands contain trees with small tree heights and small diameters although large, live, residual trees do often survive

stand replacing fires and continue to grow in the post-disturbance stand (Greif and Archibold, 2000). The density of trees in a stand decreases while tree size increases with stand age (Lee *et al.*, 1997; DeLong and Kessler, 2000; Popadiouk *et al.*, 2003). Therefore, older forest stands contain larger trees than younger stands, but have less overall trees per unit area (DeLong and Kessler, 2000). This is a result of the self-thinning process, as competition between stems and unequal success at utilizing resources allows some stems to survive and continue to grow while others perish (Oliver and Larson, 1996; Chen and Popadiouk, 2002). Consequently, the stand changes from having a largely uniform, single-layered canopy with stems that are relatively homogeneous in diameter and height to having a bimodal or multimodal canopy structure with a broad, multi-sized diameter and height distribution with dominance of shade-tolerant tree species (Paré and Bergeron, 1995; Linder *et al.*, 1997; Kuuluvainen *et al.*, 1998; Varga and Klinka, 2001; Clark *et al.*, 2003).

In forest stands, the spatial pattern of live trees is a reflection of initial establishment patterns, sunlight and climatic variables, interspecific and intraspecific competition, microenvironment, and chance (Moeur, 1993). In boreal and temperate forests, the spatial arrangement of live trees has been reported as shifting from a clumped distribution in young stands to a relatively regular distribution in older stands (Kenkel, 1988; Moeur, 1993; Szwagrzyk and Czerwczak, 1993; Kenkel *et al.*, 1997; Chokkalingam and White, 2001; Gratzner and Rai, 2004), a consequence of density-dependent intraspecific competition between neighboring stems during self-thinning. However, other studies suggest that the establishment of trees on microsites and canopy gaps and the regeneration strategies of some tree species (i.e., vegetative reproduction such as stem sprouting, limited seed dispersal ability, and preferential establishment on downed logs) in intermediate aged and older stands can cause the structural patterns of trees to become relatively clumped (Payandeh, 1974; Taylor and Halpern, 1991; Peterson and Squiers, 1995; Camarero *et al.*, 2000; Manabe *et al.*, 2000; Takahashi *et al.*, 2001; Hou *et al.*, 2004). A random spatial arrangement of trees in intermediate aged and old stands may be attributed to weak competition or clumping processes (Szwagrzyk, 1990; Wallenius *et al.*, 2002). Further, disturbances beyond stand replacement (i.e., insect outbreaks, blowdown, and pathogen infections) (Szwagrzyk and Czerwczak, 1993) and environmental heterogeneity (Antonovics and Levin, 1980) can mask expected spatial patterns. It is unclear how the spatial arrangement of trees affects or is affected by ecological processes such as productivity, disturbance dynamics, and interrelationships among tree species.

Popadiouk *et al.* (2003) reported that stand basal area increases with stand aging in eastern boreal mixedwoods. Similarly, Paré and Bergeron (1995) reported that, along a chronosequence, biomass increased steadily before decreasing and stabilizing. This biomass accumulation pattern appears to be a reflection of both the contribution of trembling aspen to stand composition and spruce budworm outbreaks (Paré and

TABLE 1  
Dynamics of live trees and coarse woody debris (CWD) in boreal forests

Study	Stand age (years)	Stand type*	Stand origin*	Live trees				CWD				Location	
				Volume (m <sup>3</sup> /ha)	Density (stems/ha)	Basal area (m <sup>2</sup> /ha)	Total volume (m <sup>3</sup> /ha)	Snags		Downed logs			
								Volume (m <sup>3</sup> /ha)	Density (stems/ha)	Basal area (m <sup>2</sup> /ha)	Volume (m <sup>3</sup> /ha)		Density (stems/ha)
North American boreal forests:													
Clark <i>et al.</i> (1998)	0–50	C	F					32				>100	Sub-boreal, British Columbia
Reich <i>et al.</i> (2001)	25–40	C	F			23							Southern boreal, Minnesota
DeLong and Kessler (2000)	40–70	C	F	2597					268			262	Sub-boreal, British Columbia
Clark <i>et al.</i> (1998)	51–100	C	F									60	Sub-boreal, British Columbia
Clark <i>et al.</i> (1998)	51–200	C	F						460			174	Sub-boreal, British Columbia
DeLong and Kessler (2000)	71–140	C	F	1910									Sub-boreal, British Columbia
Ruel <i>et al.</i> (2004)	77–90	C	F	263–376	1967–2850	37–47							Central Quebec
Reich <i>et al.</i> (2001)	70–100	C	F			27							Southern boreal, Minnesota
Pedlar <i>et al.</i> (2002)	88	C	F				18						Northwestern Ontario
DeLong and Kessler (2000)	>140	C	F	984					170			193	Sub-boreal, British Columbia
Stewart <i>et al.</i> (2003)	164–214	C	F	540–563	497–520	56–58	110–148	40–57	47–149			71–91	Nova Scotia
Clark <i>et al.</i> (1998)	201–250	C	F										Sub-boreal, British Columbia
Hély <i>et al.</i> (2000b)	236	C	F			35						34	Northwestern Quebec
Clark <i>et al.</i> (1998)	≥400	C	F						1–2			143	Sub-boreal, British Columbia
Ferguson and Archibald (2002)	0–60	C	M	14–17									Northwestern Ontario
Brumelis and Carleton (1988)	1–56	C	M	3050									Northwestern Ontario
Reich <i>et al.</i> (2001)	25–40	C	M			20							Southern boreal, Minnesota
Sturtevant <i>et al.</i> (1997)	36	C	M										Newfoundland
Ruel <i>et al.</i> (2004)	49–55	C	M	75–173	1250–1608	14–27						32	Central Quebec
Ferguson and Archibald (2002)	61–80	C	M	26–31					2–4				Northwestern Ontario
Sturtevant <i>et al.</i> (1997)	64	C	M										Newfoundland
Reich <i>et al.</i> (2001)	70–100	C	M			31							Southern boreal, Minnesota
Sturtevant <i>et al.</i> (1997)	80	C	M										Newfoundland
Ferguson and Archibald (2002)	81–100	C	M	25–30					3–5				Northwestern Ontario
Ferguson and Archibald (2002)	>100	C	M	22–25					3–6				Northwestern Ontario
Pedlar <i>et al.</i> (2002)	1	M	F				343						Northwestern Ontario
Pedlar <i>et al.</i> (2002)	75	M	F				161						Northwestern Ontario
Hély <i>et al.</i> (2000b)	175–205	M	F			26–37						45–52	Northwestern Quebec
Ferguson and Archibald (2002)	0–60	M	M	17–18					4				Northwestern Ontario

(Continued on next page)

TABLE 1  
Dynamics of live trees and coarse woody debris (CWD) in boreal forests (*Continued*)

Study	Stand age (years)	Stand type*	Stand origin*	CWD										
				Live trees					Downed logs					
				Volume (m <sup>3</sup> /ha)	Density (stems/ha)	Basal area (m <sup>2</sup> /ha)	Total volume (m <sup>3</sup> /ha)	Volume (m <sup>3</sup> /ha)	Density (stems/ha)	Basal area (m <sup>2</sup> /ha)	Volume (m <sup>3</sup> /ha)	Density (stems/ha)	Location	
Ferguson and Archibald (2002)	61–80	M	M	23–28	4									Northwestern Ontario
Ferguson and Archibald (2002)	81–100	M	M	21–25	4–6									Northwestern Ontario
Ferguson and Archibald (2002)	>100	M	M	18–21	5–6									Northwestern Ontario
Lee <i>et al.</i> (1997)	20–30	D	F	278	33					109	36			Northeastern Alberta
Lee (1998)	20–39	D	F		18									Alberta
Reich <i>et al.</i> (2001)	25–40	D	F	1247	73	22				109	32			Southern boreal, Minnesota
Lee <i>et al.</i> (1997)	50–65	D	F											Northeastern Alberta
Pedlar <i>et al.</i> (2002)	67	D	F			26	105							Northwestern Ontario
Reich <i>et al.</i> (2001)	70–100	D	F											Southern boreal, Minnesota
Lee (1998)	≥100	D	F			46					62–100			Alberta
Hély <i>et al.</i> (2000b)	117	D	F											Northwestern Quebec
Lee <i>et al.</i> (1997)	≥120	D	F	535	66					40				Northeastern Alberta
Stewart <i>et al.</i> (2003)	178–197	D	F	366–461	11–100	33–38	62–84	17–25	11–100	124	31			Nova Scotia
Ferguson and Archibald (2002)	0–60	D	M	14	3					45–58				Northwestern Ontario
Reich <i>et al.</i> (2001)	25–40	D	M			19								Southern boreal, Minnesota
Ferguson and Archibald (2002)	61–80	D	M	27	4									Northwestern Ontario
Reich <i>et al.</i> (2001)	70–100	D	M	30	5	31								Southern boreal, Minnesota
Ferguson and Archibald (2002)	81–100	D	M	25	5									Northwestern Ontario
Ferguson and Archibald (2002)	>100	D	M											Northwestern Ontario
European and Asian boreal forests:														
Linder <i>et al.</i> (1997)	117–270	C	F	108–511	1106–2889			12–70	167–334	31–166	88–366			Boreal Sweden
Sitonen <i>et al.</i> (2000)	129–198	C	F	396	725	35	111							Southern Finland
Rouvinen <i>et al.</i> (2002)	187–210	C	F	151–333			59–92	24–47		20–52				Boreal Fennoscandia
Kuuluvainen <i>et al.</i> (1998)	>200	C	F	216	2064		145	28	263	117				Northeastern Europe
Karjalainen and Kuuluvainen (2002)	>250	C	F				70	27	75	43				Russian Viena Karelia
Narukawa <i>et al.</i> (2003)	>300	C	F											Taishetsu, Japan
Jonsson (2000)	Old-growth	C	F					1–13		17–65	176			Northern Sweden
Sippola <i>et al.</i> (1998)	Old-growth	C	F				19–60	7–11		11–47				Finnish Lapland
Rouvinen <i>et al.</i> (2002)	111–179	C	M	156–169			7–22	2		5–20				Boreal Fennoscandia
Sitonen <i>et al.</i> (2000)	124–145	C	M	331	801	31	22							Southern Finland
Sitonen <i>et al.</i> (2000)	95–118	C	M	299	605	28	14							Southern Finland
Sippola <i>et al.</i> (1998)	15	C	M				8	1		7				Finnish Lapland
Takahashi <i>et al.</i> (2001)	≥120	M	F	1071		26								Kamchatka peninsula, Russia
Linder <i>et al.</i> (1997)	88–108	D	F	87–218	1154–1981			12–31	318–621	16–80	135–223			Boreal Sweden

Note: \*Stand type: C = coniferous, M = mixedwood, D = deciduous.

\*\*Stand origin: F = fire, M = managed.

Bergeron, 1995). In an interregional study of boreal, temperate, and tropical biomes using long-term chronosequences, Wardle *et al.* (2004) found that stand basal area and ecosystem biomass increased, reached a maximum, and then declined in all ecosystem types. For each of the chronosequences, the decline phase was associated with an increase in the substrate nitrogen-to-phosphorus ratio, indicating increasing phosphorus limitation over time. Wardle *et al.* (2004) further concluded that the maximal biomass phase during succession cannot be maintained in the long-term absence of major disturbance in forested ecosystems spanning the tropical, temperate, and boreal zones.

The species composition and size distributions of CWD reveals the past history of a stand (Linder *et al.*, 1997), which is the premise of so-called stand reconstruction approach that has been extensively used in the study of successional dynamics (Johnson and Fryer, 1989; Bergeron, 2000). A lesser amount of live tree volume than CWD volume of a certain tree species indicates that this species was more abundant in an earlier successional stage and is currently experiencing a decline in its contribution to stand composition (De Grandpré *et al.*, 2000; Pham *et al.*, 2004).

It has been reported that there is a positive relationship between the volume and basal area of CWD and that of living trees (Sippola *et al.*, 1998; Ferguson and Archibald, 2002; Stewart *et al.*, 2003). This relationship does not appear to be influenced by forest age or cover type (Ferguson and Archibald, 2002). Ratios of CWD to living trees vary across a wide range. For example, Nilsson *et al.* (2002) calculated a ratio of dead to live standing stems of 1:9 in the boreal forest. Siitonen *et al.* (2000) found that CWD comprises about one quarter of the total stand volume, while Kuuluvainen *et al.* (1998) found this value to be approximately 40 percent. Linder *et al.* (1997), Sippola *et al.* (1998), and Karjalainen and Kuuluvainen (2002) reported that CWD comprises between 19 percent and 30 percent of the total volume of timber in old-growth forests. However, Rouvinen *et al.* (2002) did not find a relationship between CWD and live tree volume. It is unclear how competition and longevity induced mortality and species-specific rates of CWD decomposition contribute to the discrepancies in the ratio of CWD to live tree volume.

## B. CWD Dynamics

The CWD in a stand can influence nutrient cycling, productivity, and species composition (Spies *et al.*, 1988; Greif and Archibald, 2000; Karjalainen and Kuuluvainen, 2002). The CWD dynamics is largely a reflection of the time since the last stand-replacing fire (Arseneault, 2001), as fire is the main disturbance factor in the boreal forest (Johnson, 1992; Linder *et al.*, 1997; Amiro *et al.*, 2001, 2002; Karjalainen and Kuuluvainen, 2002) for both producing and eliminating dead organic material in forests under natural conditions (Sippola *et al.*, 1998). Fires in the boreal forest can be either lethal, killing most of the trees in a stand and initiating a new stand, or non-lethal, killing some of the trees in the stand (Johnson, 1992).

Living trees, upon death, add to the CWD component in forest ecosystems (Hély *et al.*, 2000a). The life history of a tree typically consists of (1) living tree, (2) snag, (3) fall of snag to the forest floor, and (4) decomposition of the downed log (Storaunet and Rolstad, 2002). The processes that influence CWD are inputs through mortality and breakage (which control accumulation) and decomposition and combustion (which affect losses from the system). Inputs of CWD come from both the pre-disturbance and current stand, and the inputs from each to the total CWD pool varies with the age of the stand (Siitonen *et al.*, 2000).

In the boreal forest (Sturtevant *et al.*, 1997; Clark *et al.*, 1998; Hély *et al.*, 2000a; Ferguson and Archibald, 2002) and subalpine forest (Spies *et al.*, 1988; Feller, 2003), the pattern of CWD accumulation over time has been shown to follow a U-shaped distribution (Figure 1), where large, pre-fire in origin inputs of CWD decreases logarithmically while post-fire inputs increase exponentially (before decreasing slightly) (Figure 1) (Spies *et al.*, 1988; Sturtevant *et al.*, 1997; Delong and Kessler, 2000). This translates to high amount of CWD in young, early successional forests and old, late successional forests and low levels in mature, intermediate-aged forests, with levels in very old forests being lower than old forests (Spies *et al.*, 1988; Sturtevant *et al.*, 1997).

Coarse woody debris (pre-disturbance debris) and live trees (residual standing trees) can survive fire and contribute significantly to post-disturbance structure (Lee *et al.*, 1997; Fraver *et al.*, 2002). Residual snags will slowly deteriorate as the forest ages and fall to the ground (Greif and Archibald, 2000). In young stands, the amount of CWD contributed by the pre-disturbance stand is high (Spies *et al.*, 1988; Sturtevant *et al.*, 1997; Clark *et al.*, 1998; Delong and Kessler, 2000). This includes both pre-disturbance debris that is not consumed by the stand-replacing fire and disturbance-generated debris (Sturtevant *et al.*, 1997). However, as the stand ages, this dead material decomposes and is incorporated into the soil (Sturtevant *et al.*, 1997; Pedlar *et al.*, 2002).

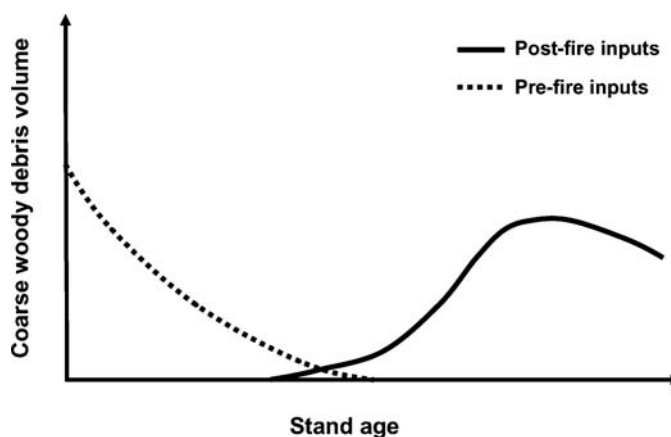


FIG. 1. Dynamics of pre-disturbance and post-disturbance CWD patterns in a forest stand with time since fire (adapted from Sturtevant *et al.* (1997)).

Coarse woody debris of post-disturbance origin is very low in young stands (Spies *et al.*, 1988; Sturtevant *et al.*, 1997), as trees that establish are growing to fill available growing space. During this stage of development, called *stand initiation* (Oliver and Larson, 1996; Chen and Popadiouk, 2002), the low competition induced mortality between stems results in little inputs of CWD. In early, intermediate aged forests, all available growing space is occupied and the trees undergo intense competition for space and resources (stem exclusion stage, Oliver and Larson, 1996; Chen and Popadiouk, 2002) in a process called self-thinning, which brings about tree mortality and causes the levels of CWD with post-disturbance origin to begin to increase (Sturtevant *et al.*, 1997; Fraver *et al.*, 2002). In dense, regenerating forests, there is intense competition for space, soil nutrients, moisture and light by young trees (Greif and Archibold, 2000). Through self-thinning, many small snags are created as weaker trees are killed off, creating improved growing conditions for remaining trees that survive (Greif and Archibold, 2000). At this point, a large proportion of CWD from the pre-disturbance stand may have disappeared while the production of CWD from the current stand has yet to occur significantly (Spies *et al.*, 1988), which can explain the low levels of CWD during this stage of production.

As succession and stand development continues, stem competition ends and the colonizing cohort of trees that dominate the canopy begin to reach their maximum life expectancy and die (Chen and Popadiouk, 2002). In this stage, called *canopy transition* (Chen and Popadiouk, 2002), CWD accumulation continues to increase and the input of CWD that is post-disturbance in origin rises (Sturtevant *et al.*, 1997) in these late, intermediate-aged stands. At the end of this stage when the final trees from the colonizing cohort die (Chen and Popadiouk, 2002), the amount of CWD reaches its maximum while the stand undergoes a transition from an even-aged to an uneven-aged structure (Sturtevant *et al.*, 1997; Hély *et al.*, 2000a). After this, the stand enters the stage of old growth when gap dynamics are predominant (Chen and Popadiouk, 2002), and the amount of CWD begins to decline slightly (Sturtevant *et al.*, 1997). However, new inputs of CWD continue to occur due to non-stand replacing disturbances such as insect damage, disease, injury that is caused by neighboring trees falling, ice, snow, and wind (Greif and Archibold, 2000). These will be discussed in greater detail later. In this way, high tree mortality in intermediate-aged forests (as a result of high tree densities, insects, blowdown, or disease) or very severe stand-replacing events (which can cause a low input of post-disturbance CWD as well as consuming pre-disturbance CWD) may partially modify the U-shaped distribution of CWD along the chronosequence (Clark *et al.*, 1998; Feller, 2003).

As the majority of the literature breaks down the chronosequence into young/mature, intermediate/overmature, and old/old-growth forest classes when discussing forest stand structure, this paper will do the same. For the remainder of this section, an overview of how CWD characteristics change along the chronosequence will be undertaken.

### 1. Snags

During the different stages of succession, snags have different size distributions and decay characteristics. Snags produced by a stand-replacing fire are often large (Lee *et al.*, 1997). In contrast, snags produced later in succession through competition-induced stem death (self-thinning) during the stem exclusion development stage (Chen and Popadiouk, 2002) tend to be smaller (Lee *et al.*, 1997). Still later in succession, during the canopy transition stage of development (Chen and Popadiouk, 2002), snags are a result of age-related tree mortality (Chen and Popadiouk, 2002) and are once again larger in size. In old stands (gap dynamics development stage (Chen and Popadiouk, 2002)), snags are produced by non-stand replacing disturbances such as insect attacks, disease, or damage by ice, snow, and wind that may affect overmature individuals (Clark *et al.*, 1998; Greif and Archibold, 2000; Hély *et al.*, 2000a). Unlike competition and suppression, which create small diameter snags in young stands, these factors are not size specific, and a greater range of snag diameters occurs in older stands (Greif and Archibold, 2000).

The stand basal area (i.e., the sum of cross-sectional area at breast height per hectare,  $m^2/ha$ ) and density (stems/ha) of snags both follows a bimodal distribution over stand age, where basal area and density are highest in young post-fire stands, lowest in young intermediate-aged stands, higher in older intermediate-aged stands, and reach another maximum in old stands before decreasing slightly in very old stands (Lee *et al.*, 1997; Clark *et al.*, 1998) (Figure 2). The high values for snag basal area and density reported for young stands is attributed to large inputs from the pre-fire, whereas the low values that occur in young intermediate-aged stands are a consequence of snags falling to the forest floor where they become downed logs and before significant post-fire inputs can occur (Clark *et al.*, 1998). Beyond a young intermediate age, values of snag basal area and density once again increase, induced by stem competition mortality (Oliver and Larson, 1996; Chen and Popadiouk,

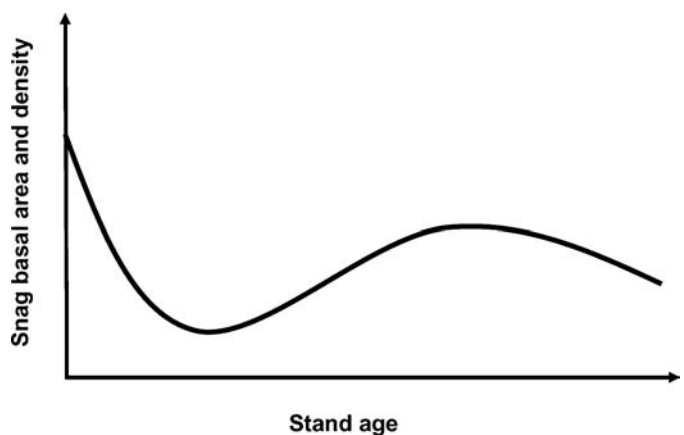


FIG. 2. Dynamics of stand basal area and density of snags with time since fire.



2002), trees reaching their maximum life expectancy and dying, as is the case for trembling aspen (Pothier *et al.*, 2004) and lodgepole pine (Clark *et al.*, 1998), or from non-stand replacing disturbances (Clark *et al.*, 1998; Greif and Archibold, 2000; Hély *et al.*, 2000a).

## 2. Downed Logs

Downed logs are important for many reasons including recycling nutrients into the ecosystems following disturbances (Harmon and Hua, 1991; Karjalainen and Kuuluvainen, 2002), storing water (Fraver *et al.*, 2002; Karjalainen and Kuuluvainen, 2002), fostering tree regeneration (Hofgaard, 1993; Takahashi, 1994; Parent *et al.*, 2003; Lampainen *et al.*, 2004), and sheltering and feeding small mammals (Tallmon and Mills, 1994; Pearce and Venier, 2005). Downed logs create conditions where light and moisture requirements are favorable for tree regeneration while plant competition is limited (Kuuluvainen and Juntunen, 1998; Parent *et al.*, 2003). The amount of decayed downed logs on the forest floor has been positively correlated to spruce, fir, and pine seedling occurrence (Webb, 1988; Hofgaard, 1993; Takahashi, 1994; Kuuluvainen and Juntunen, 1998; Narukawa *et al.*, 2003; Parent *et al.*, 2003; Lampainen *et al.*, 2004). However, Kuuluvainen *et al.* (1998) reported that sapling density was not related to the amount of downed logs on the forest floor, suggesting the downed logs are favorable substrates for tree germination, but not necessarily the best medium for tree growth and survival.

Substrate quality (soil moisture and temperature), in addition to light availability (Chen *et al.*, 1996; Chen, 1997; Kolström, 1998; Messier *et al.*, 1999), is important for tree seedlings to establish. More decayed downed logs show a greater occurrence of seedlings and samplings than less decayed downed logs, as seedlings have difficulty establishing on young logs that are relatively intact (Narukawa *et al.*, 2003). Freshly fallen spruce logs take approximately 50 years to decompose to a point where spruce seedling establishment is possible (Hofgaard, 1993). This is likely because freshly fallen logs have bark and wood that is too hard and cannot be utilized by tree seedlings, whereas more decomposed wood is often softer, which allows for penetration of the log by seedling roots (Narukawa *et al.*, 2003). Further, some tree species (e.g., paper birch) have a persistent papery bark that makes colonization difficult (Webb, 1988). Log size is also related to regeneration, as seedlings were found to be more abundant on larger logs than smaller logs because of their difference in available surface areas to seeds (Takahashi, 1994).

The cross-sectional area of downed logs has been found to be U-shaped in distribution, where it is highest in young stands, lowest in intermediate-aged stands, and increased to another maximum in old stands (Clark *et al.*, 1998). In contrast to snag basal area, the basal area of downed logs continues to increase in very old stands (Clark *et al.*, 1998).

The density of downed logs (stems/ha) changes over time, but its pattern depends on the size of the downed logs. Lee *et al.* (1997) found that the density of large diameter downed

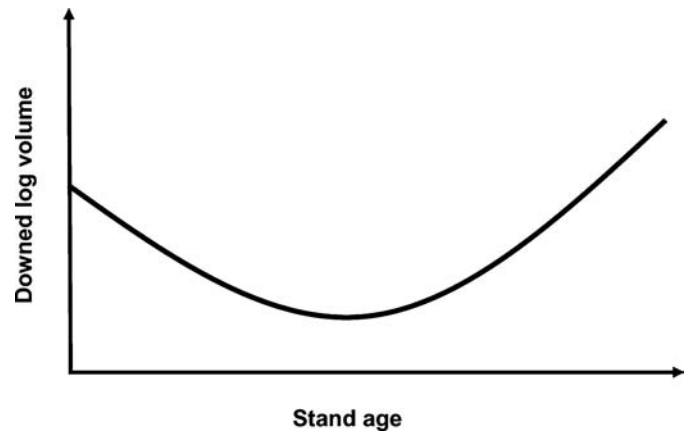


FIG. 3. Dynamics of stand volume of downed logs with time since fire.

logs displays a U-shaped pattern along the chronosequence, the density of medium diameter downed logs decreases with stand age, and the density of small diameter downed logs shows an inverse U-shaped pattern as time since fire increases.

The volume of downed logs has been found to follow a U-shaped distribution along the chronosequence, where levels are high in young and old stands and low in intermediate-aged stands (Lee *et al.*, 1997; Sturtevant *et al.*, 1997; Clark *et al.*, 1998) (Figure 3). Further, in old forests, the volume of large downed logs is significantly higher than the volume of small downed logs (Edman and Jonsson, 2001), and by the old-growth stage, the volume of downed logs has been shown to be higher than the volume of snags (Siitonen *et al.*, 2000).

## 3. Decomposition of CWD

The decomposition of CWD has been shown to occur in two successive stages: (1) time from the death of the tree until it falls, and (2) time after fall until decomposition is complete (Storaunet and Rolstad, 2002). In young stands, there is generally a high proportion of CWD biomass, volume, and density (Spies *et al.*, 1988; Delong and Kessler, 2000; Yatskov *et al.*, 2003) that occurs in advanced states of decay compared to early states of decay. In contrast, old stands have more CWD biomass, volume, density, and basal area in early decay classes compared to late decay classes (Spies *et al.*, 1988; Clark *et al.*, 1998; Delong and Kessler, 2000; Yatskov *et al.*, 2003). Coarse woody debris in old forests is also more often evenly distributed among the decay classes (DeLong and Kessler, 2000; Jonsson, 2000; Karjalainen and Kuuluvainen, 2002), although Edman and Jonsson (2001) found that the majority of downed logs in old-growth coniferous forests were in intermediate to late decay classes.

The size of CWD has an effect on the volume and decay state of CWD in a stand. The volume of CWD that is large and showing little decay is higher in older stands compared to younger stands (DeLong and Kessler, 2000). Consequently, the volume of CWD that is small and highly decayed is higher in younger stands compared to older stands, likely because as time since fire increases, the size of dying trees also increases (DeLong

and Kessler, 2000). Large diameter downed logs appear to decay slower than small diameter downed logs due to their larger size (Storaunet and Rolstad, 2002), although it has been noted that the opposite occurs, attributed to large diameter downed logs being in greater contact with the ground than small diameter downed logs (Næsset, 1999).

Decomposition of downed logs is affected by substrate quality, temperature, moisture, and type and amount of decomposing organisms (Storaunet and Rolstad, 2002). For example, temperature affects decay-susceptible species but not decay-resistant species (Yatskov *et al.*, 2003). For decay-susceptible species, decomposition increases exponentially with increases in temperature (Yatskov *et al.*, 2003). Further, decomposition rates for downed logs have been reported as being higher on moist soils than drier soils (Næsset, 1999). Snags in general have slower rates of decomposition than downed logs (Karjalainen and Kuluvainen, 2002; Storaunet and Rolstad, 2002; Yatskov *et al.*, 2003), attributed to insufficient moisture in snag tissues (Yatskov *et al.*, 2003). In summary, Yatskov *et al.* (2003) highlights the variations in CWD decay patterns for various species, and identifies four patterns of CWD loss (based on a 5 decay class system where decay extent increases from decay class 1 to decay class 5):

1. For *Betula* spp., a linear, gradual decrease in wood density occurs from decay class 1 to 5 which is likely caused by the prolonged retention of bark that hinders decomposition of sapwood and to the absence in the heartwood of decay-suppressing substances (Webb, 1988; Yatskov *et al.*, 2003). For example, European white birch (*Betula pendula* Roth) does not lose its bark during decomposition, which prevents sloughing of heartwood and sapwood cells (Yatskov *et al.*, 2003).
2. For some *Pinus* spp. and *Larix* spp., very little change in wood density occurs until a decay class of 4 is reached due to the presence of dense, decay-resistant heartwood, and because bark and less resistant sapwood fall off during decomposition (Yatskov *et al.*, 2003).
3. For *Picea* spp. and other *Pinus* spp., decomposition and a decrease in density proceeds through a slow, rapid, and moderately slow phase (Harmon *et al.*, 2000) as the breakdown of woody debris goes through the 5 decay classes. The little change in wood density that is observed in the "slow phase" (occurring between decay classes 1 and 2) is attributed to the slow colonization by decomposing organisms or to drying due to shrinkage. The large loss of density in the "rapid phase" (occurring between decay classes 3 and 4) and slight density decline (occurring between classes 4 to 5) is the result of the slow decay of remnant decay-resistant tissues (Yatskov *et al.*, 2003).
4. For *Quercus* spp. and *Acer* spp., decomposition is usually complex, as decay of snags and downed logs is from the log circumference towards the center. CWD of these species generally have fast initial losses of wood density due to their

susceptibility to heartwood rot (Yatskov *et al.*, 2003). *Acer* spp. and *Quercus* spp. lose their bark swiftly during the process of decomposition (Yatskov *et al.*, 2003).

Decay characteristics are likely to have important implications for seedling establishment. In spruce forests, once the sapwood rots and thick bark falls off, available nutrients may provide ideal conditions for the establishment and growth of seedlings (Sollins, 1982). However, for trees those have thinner bark (such as balsam fir), bark that remains intact long after the sapwood and heartwood rots may result in poorer conditions for seedling establishment (Sollins, 1982).

#### IV. THE EFFECT OF CANOPY COMPOSITION ON STAND STRUCTURE

Stand structure may differ significantly among stand cover types as canopy composition influences ecosystem productivity (Chen and Klinka, 2003; Chen *et al.*, 2003), carbon and nutrient dynamics (Simard *et al.*, 1997; Prescott *et al.*, 2000), and susceptibility to natural disturbances (Su *et al.*, 1996; Cumming, 2001). Some studies of boreal forests have characterized stand structure over time of live and dead material in exclusively coniferous forests (Linder *et al.*, 1997; Clark *et al.*, 1998) or exclusively deciduous forests (Lee *et al.*, 1997; Lee, 1998), but no study has examined changes in mixedwood structure along a chronosequence in the boreal forest. The studies that have explored differences among cover types have occurred under different environmental conditions (i.e., soils, topography, geography, climate, etc.) and/or have only examined forests that are in a specific successional stage (i.e., old-growth) (Harmon and Hua, 1991; Greif and Archibald, 2000; Pedlar *et al.*, 2002; Stewart *et al.*, 2003), although Ferguson and Archibald (2002) reported changes in snag and live tree density along the chronosequence in various boreal cover types.

While the abundance of coniferous species increases with time since fire at the expense of deciduous species (Bergeron and Dubuc, 1989; Bergeron and Dansereau, 1993; Bergeron and Harvey, 1997; Bergeron, 2000; De Grandpré *et al.*, 2000; Gauthier *et al.*, 2000; Harper *et al.*, 2002), old mixedwood stands are still maintained in some areas due to outbreaks of spruce budworm and other disturbances that kill late successional shade tolerant coniferous species and favor the recruitment of early successional, shade-intolerant deciduous species within the canopy openings (Bergeron and Dansereau, 1993). Stands dominated by deciduous trees may be maintained if fires are relatively frequent. However, with the increase in the fire cycle that is expected to occur due to climate change for some areas of the boreal forest (Bergeron and Flannigan, 1995; Flannigan *et al.*, 1998; Bergeron *et al.*, 2004), there is concern that pure deciduous stands will dramatically decrease in abundance (Bergeron and Dansereau, 1993). Therefore, there is a need to explore stand structural characteristics (e.g., CWD and live tree abundance, volume, density, height, DBH, and arrangement) along successional gradients for the various cover types that occur within

the boreal forest. This section will synthesize information on differences in live tree and CWD structural characteristics between different boreal cover types and explore how these aspects change along a chronosequence.

### A. Living Tree Dynamics

The basal area of living trees differs among cover types (Plonski, 1974; Chen and Popadiouk, 2002; Popadiouk *et al.*, 2003). Hély *et al.* (2000b) reported that the basal area of live trees is higher in deciduous forests than coniferous forests with mixedwood forests being intermediate. Linder (1998) also reported that live tree basal area is higher in mixedwood stands compared to coniferous stands. The higher basal area of live trees in deciduous and mixedwood forests compared to coniferous forests may be explained by the superior height of aspen and by the decrease in above-ground biomass that is observed to occur as a stand succeeds from deciduous dominance to coniferous dominance (Paré and Bergeron, 1995; Bergeron and Harvey, 1997). However, Stewart *et al.* (2003) conversely reported that the basal area of live trees was higher in coniferous stands compared to deciduous stands.

The density and volume of live trees appears to be variable with cover type. In young stands, the density of live trees was found to be highest in coniferous stands followed by mixedwood stands and deciduous stands (Ferguson and Archibald, 2002). In old forests, coniferous stands have been reported as having a higher density of live trees than deciduous and mixedwood stands (Linder, 1998; Stewart *et al.*, 2003; Table 1). In turn, live tree volume has been found to be lower in old deciduous stands than old mixedwoods and coniferous stands (Linder, 1998; Stewart *et al.*, 2003).

The conflicting results may reflect the confounding effects of stand cover type and site quality. The broad classification of coniferous *versus* deciduous stand types may further cloud the effect of tree species dominance on stand basal area and stem density. For example, these stand attributes differ significantly between deciduous trembling aspen and paper birch dominated stand types (Plonski, 1974; Chen and Popadiouk, 2002) and among coniferous stand types (Varga *et al.*, 2005). Future research may require consideration of site quality and individual species dominance.

Variability of tree size within a stand is an important structural attribute as it affects forest productivity, plant diversity, and wildlife habitat (Berger and Puettmann, 2000; Staudhammer and LeMay, 2001; Sullivan *et al.*, 2001; Pommerening, 2002). Tree size diversity has been measured by using Shannon-Weiner's index (Shannon and Weaver, 1949), variance, and coefficient of variation of tree heights and diameters (Staudhammer and LeMay, 2001; Varga *et al.*, 2005). After studying three types of coniferous mixtures in western Canada, Varga *et al.* (2005) reported that tree size diversity did not only differ with tree species dominance and stand age, but also increased in mixtures of shade-intolerant and shade-tolerant species.

### B. Mortality Mechanisms, Canopy Gaps, and Regeneration Patterns

The kind of mortality that a tree undergoes appears to be linked to cover type. Trees in coniferous forests are more likely to be snapped than uprooted, attributed to the heavy snow loading that conifers experience (Clark *et al.*, 1998; Storaunet and Rolstad, 2002). However, Siitonen *et al.* (2000) and Antos and Parish (2002) found that pines usually form intact snags when they die. In contrast, spruce has been found to uproot or snap close to the ground and form downed logs upon death (Siitonen *et al.*, 2000). In deciduous forests, trees have a tendency to die and remain as snags rather than being uprooted or breaking (Lee, 1998), although Siitonen *et al.* (2000) has reported that deciduous trees have a tendency to snap and break. A recent study of trembling aspen gap dynamics 60 to 120 years since fire in eastern boreal forests reported that snags were most frequent in young stands, whereas snapped snags were most frequent in old stands (Hill *et al.*, 2005). Infection by fungal pathogens was the most frequent cause of mortality (56%), followed by blowdown (16%), and all other causes including mammals, insects, and those unidentified (28%) (Hill *et al.*, 2005).

Gaps appear to be important in seedling establishment, as recruitment has been found to be very poor (restricted to the most shade tolerant species) under a closed canopy (Coates, 2002). The species of gap makers and gap fillers differ between coniferous and deciduous stands (Cumming *et al.*, 2000; Takahashi *et al.*, 2001; Pham *et al.*, 2004) (Table 2), highlighting a reciprocal replacement pattern in canopy gaps for coniferous forests (Pham *et al.*, 2004). In aspen dominated forests, gaps are usually large, created by largely trembling aspen and balsam poplar tree mortality, and are usually filled by trembling aspen and other shade intolerant tree species (Cumming *et al.*, 2000). In mixedwood forests (dominated by birch and spruce), spruce can establish itself under the shading of overstory trees, and will grow up into the canopy when space is made available (Takahashi *et al.*, 2001). As well, fir appears to grow well in the shaded conditions created by a mixed fir and birch canopy (Mori and Takeda, 2004). Although the canopy is closed, the increased light levels in northern microsites create conditions suitable for fir regeneration (Mori and Takeda, 2004). Birch regeneration on the other hand has been reported as being clumped around canopy birch trees (Takahashi *et al.*, 2001). This is common for birch, which is known to regenerate by seed after fire, while maintaining itself by sprouting in the absence of fire (Takahashi *et al.*, 2001). In coniferous forests, due to the small and infrequent nature of gaps (Bartemucci *et al.*, 2002; Pham *et al.*, 2004) and the limited germination sites that are suitable for shade-intolerant deciduous tree establishment, regeneration is largely restricted to shade-tolerant conifers that can establish under the canopy of other trees where light is limited (Bartemucci *et al.*, 2002).

It has been reported that in large gaps, the density of seedlings is higher in the shady southern portion of the gap than in the sunny northern portion of the gap in high latitude boreal

TABLE 2  
Gap makers and gap fillers in different boreal cover types

Cover type	Gap makers	Gap fillers
Trembling aspen dominated	Trembling aspen, balsam poplar	Trembling aspen, balsam poplar, paper birch
Balsam fir dominated	Balsam fir, paper birch, white spruce, black spruce	Balsam fir
Black spruce dominated	Balsam fir, paper birch, white spruce, black spruce	Black spruce
Birch and spruce mixedwood	Birch	Spruce and birch
Aspen and spruce mixedwood	Aspen	Spruce, balsam fir, and birch
Balsam fir and black spruce dominated	Balsam fir and black spruce	Balsam fir and black spruce

forests (Coates, 2002). Kneeshaw and Bergeron (1998) found that gap size increases and is more variable with forest age, driven by spruce budworm outbreaks that kill balsam fir and create gaps. Gaps allow for not only the regeneration of shade-tolerant species such as balsam fir and eastern white cedar, but also for the maintenance of shade-intolerant deciduous species (Kneeshaw and Bergeron, 1998). It is possible then that gap size may be controlling the species that can regenerate and the patterns of regeneration. However, after studying the influence of small gaps (<350 m<sup>2</sup>) on understory regeneration and canopy transition probabilities of the trembling aspen forest in eastern Canada, Hill *et al.* (2005) reported that understory tree species composition and growth were independent of gap size and age, indicating that the relationship between overstory structure and understory regeneration founded in coniferous stands may not be applicable in deciduous stands, where light availability is much higher (Chen, 1997; Messier *et al.*, 1999; Chen and Popadiouk, 2002).

### C. CWD Dynamics

There is less overall CWD in deciduous old-growth forests than coniferous old-growth forests (Harmon and Hua, 1991; Stewart *et al.*, 2003). However, in mature, intermediate-aged boreal forests, the opposite trend has been found, in which mixedwood stands were discovered to have a greater amount of CWD than deciduous stands, which in turn had more CWD than coniferous stands (Pedlar *et al.*, 2002). Little information has been unearthed that contrasts CWD dynamics in different cover types for young forests. The distribution of CWD among size classes is similar for mixedwood and deciduous forest types, while coniferous forests differ in that they lack CWD in large size classes (Pedlar *et al.*, 2002). In mixedwood, deciduous, and coniferous forests, the majority of CWD is in the form of logs, followed by snags and then stumps (Siitonen *et al.*, 2000; Pedlar *et al.*, 2002; Stewart *et al.*, 2003).

#### 1. Snags

The basal area of snags in old boreal forests has been found to be higher in coniferous forests than deciduous forests (Stewart *et al.*, 2003). No research, however, has compared the basal area

of snags among conifer, mixedwood, and deciduous young and intermediate-aged boreal forest stands. The volume of snags is likely to be greater in coniferous forests than in deciduous forests because deciduous species generally have faster decomposition rates of snags than coniferous species do (Yatskov *et al.*, 2003). Stewart *et al.* (2003) confirmed that the volume of snags was higher in old coniferous forests than old deciduous forests. However, little information is available comparing young and intermediate-aged conifer, mixedwood, and deciduous stands.

The diameter distribution appears to change with time for both coniferous and deciduous stands. In young deciduous stands, the diameter distribution of snags is a reverse J shape. However in old deciduous stands, snags become present in larger diameter classes and the distribution of snags becomes more evenly spread out among the diameter classes as the reverse J distribution becomes less and less prominent (Lee, 1998). In contrast, the diameter distribution of snags in old coniferous stands has been shown to follow a reverse J distribution with many smaller individuals and fewer larger ones (Kuuluvainen *et al.*, 1998).

#### 2. Downed Logs

While no studies have been found that compare the volume of young and intermediate aged coniferous and deciduous forests with respect to downed log volume, the volume of downed logs has been reported to be higher in old coniferous boreal forests than in old deciduous boreal forests (Stewart *et al.*, 2003). However, Hély *et al.* (2000b) found a contrasting trend, where old boreal mixedwood stands had the highest volume of downed logs followed by deciduous stands and then coniferous stands. Snag falldown rates for deciduous forests are lower than those for coniferous forests, suggesting that deciduous forests may contain a greater volume of downed logs (Lee, 1998). However, deciduous species generally have faster decomposition rates of downed logs than coniferous species (Yatskov *et al.*, 2003), indicating that downed logs may persist for longer on the forest floor in coniferous forests.

The size of downed logs, number of downed logs, projected ground cover of downed logs, and total mass of downed logs

has been found to be significantly higher in coniferous forests than deciduous forests (Harmon and Hua, 1991). However, this study did not compare forests in similar geographic regions, and the differences between cover types may be highly confounded with the differences in site characteristics.

## V. THE ROLE OF NON-STAND REPLACING DISTURBANCES IN ALTERING STAND STRUCTURE

While fire is the major stand renewing disturbance mechanism controlling species distributions and assemblages in the boreal forest (Amiro *et al.*, 2001), the importance of other disturbances in shaping forest structure is also evident (Blais, 1981; Bergeron *et al.*, 1995; D'Aoust *et al.*, 2004; Bouchard *et al.*, 2005). Non-stand replacing disturbances help to maintain a heterogeneous forest structure (Antos and Parish, 2002). In this section, the effects of these disturbances on forest structure will be explored.

Small-scale disturbances generate conditions for new trees to establish (De Grandpré *et al.*, 2000), and for suppressed trees to be released into the canopy (Antos and Parish, 2002). As boreal successional trajectories lead to a change from deciduous dominance to coniferous dominance without disturbances (Bergeron and Dubuc, 1989; Bergeron, 2000; Gauthier *et al.*, 2000; Harper *et al.*, 2002), non-stand replacing disturbances are essential to maintain the deciduous component in forests, and can often lead to the maintenance of mixedwood stands for a very long period of time (Harper *et al.*, 2002). Due to the extensive amount of non-stand replacing disturbances that can affect forest structure in the boreal forest, this review will focus on wind-caused and insect-caused damage (exclusively the spruce budworm) and their effects on stand structure.

### A. Wind

Extremely windy conditions can damage forests in a phenomenon called blowdown or windthrow. Wind can damage trees by uprooting them, snapping their trunks, or causing bending to occur (Webb, 1988), resulting in blowdown, which largely affects the dominant canopy trees in a forest stand by blowing them to the ground (Kuuluvainen and Juntunen, 1998; Kulakowski and Veblen, 2003). In this way, blowdown is an important mechanism to allow a continuous supply of CWD to forest ecosystems (Huggard *et al.*, 1999). Trees that are the colonizing cohort and usually early successional are most susceptible to blowdown (Kuuluvainen and Juntunen, 1998). Following blowdown, canopy space is made available for suppressed, later successional species to grow up into the canopy from the subcanopy (Kulakowski and Veblen, 2003). As well, blowdown can create microsites for new seedlings to establish by removing canopy closure and allowing light to penetrate to the forest floor, by creating a tremendous amount of downed logs, and by raising substrate and exposing mineral soil, making sites drier and reducing competition by creating sites largely free of herbaceous vegetation (Kuuluvainen and Juntunen, 1998;

Kulakowski and Veblen, 2003). Both early successional trees (Kuuluvainen and Juntunen, 1998) and late successional trees (Kulakowski and Veblen, 2003) have been shown to recruit in openings created following blowdown.

Many species in the boreal forest (including spruce and fir) have a tendency to be uprooted instead of breaking at the bole (Webb, 1988; Kulakowski and Veblen, 2003), creating ideal regeneration conditions (Kulakowski and Veblen, 2003). True firs also appear to be less susceptible to blowdown than spruce (Huggard *et al.*, 1999). In contrast, other species such as trembling aspen have a tendency to be snapped, breaking at the bole (Webb, 1988). Aspen dominated forests have been reported to have lower levels of blowdown (due to flexible stems with reduced wind drag), while spruce/fir forests have been shown to have higher levels of blowdown (as a result of denser tree canopies and shallower root systems) (Baker *et al.*, 2002). Blown over trees have been found to have higher height/diameter ratios, attributed to trees with smaller diameters being more likely to be blow over than thicker trees (Cremer *et al.*, 1982; Wonn and O'Hara, 2001), whereas Huggard *et al.* (1999) have reported that wind-thrown trees had lower height/diameter ratios in a partial harvesting experiment. Huggard *et al.* (1999) suggests that topography may be confounding blowdown susceptibility in their study, which might help to explain their contradictory findings. Trees growing in rocky, exposed topography may be exposed to higher wind speeds and have lower height/diameter ratios. Further, lower levels of blowdown occur in stands with lower tree densities (Baker *et al.*, 2002). While the effects of forest harvesting on stand structure will be discussed in a later section, it is important to note that harvesting can lead to an increase in blowdown (Huggard *et al.*, 1999).

### B. Spruce Budworm

Spruce budworm is a significant insect pest in the boreal forest from an economical perspective, affecting millions of hectares of forests and resulting in major losses of merchantable timber (MacLean and MacKinnon, 1997). Outbreaks of spruce budworm can shape the forest structure tremendously on sites dominated by tree species including balsam fir, white spruce, red spruce (*Picea rubens* Sarg.), black spruce, and the red-black spruce hybrid in the east (Morin, 1994; MacLean and MacKinnon, 1997; Bergeron and Leduc, 1998; Gordon *et al.*, 2001; Bouchard *et al.*, 2005) and subalpine fir and the white spruce/Engelmann spruce complex in the west (Antos and Parish, 2002). Spruce budworm infestations weaken and defoliate balsam fir trees and create conditions where forest trees are more susceptible to being blown over (Morin, 1994). If large older trees survive the insect attack and subsequent blowdown, then the forest may have a more uneven structure (Morin, 1994). An outbreak that occurs over a number of years can lead to high tree mortality (Kneeshaw and Bergeron, 1999) and CWD inputs into the overall CWD pool that lag slightly behind the actual timing of the outbreak (Fraver *et al.*, 2002).

Outbreaks of spruce budworm are an important mechanism in creating canopy gaps in both subalpine (Antos and Parish, 2002) and boreal (Kneeshaw and Bergeron, 1999; Harper *et al.*, 2002; D'Aoust *et al.*, 2004) mixedwood and coniferous forests. The patches of open canopy created allow for the release of suppressed individuals (balsam fir can be suppressed for quite a long time) into the canopy (Morin, 1994; Antos and Parish, 2002), and promotes growth into the overstory (Morin, 1994). Spruce and fir prefer regenerating in the southern part of gaps while trembling aspen prefers the northern part, likely due to the increased levels of light (Kneeshaw and Bergeron, 1999). The gaps created by spruce budworm outbreaks may be essential for the persistence of shade-intolerant species such as trembling aspen in the landscape in areas where the fire cycle is long (Baskerville, 1975). In contrast, shade-tolerant species such as eastern white cedar, white spruce and balsam fir may prefer the southern part of the gap due to their preference for shade and higher moisture levels (Kneeshaw and Bergeron, 1999).

Cover type plays a role in the extent of spruce budworm mortality and the impact on stand structure. In balsam fir dominated forests, spruce budworm outbreaks can be stand replacing (Bouchard *et al.*, 2005), creating a unimodal or bimodal structure (depending on the severity and duration of the outbreak) (Morin, 1994). In balsam fir dominated forests, an increase in spruce budworm outbreaks occurs as time since fire (and therefore stand age) increases, attributed to an increase in the proportion of host coniferous species that make up the stand as succession proceeds (Bergeron and Leduc, 1998; Harper *et al.*, 2002; D'Aoust *et al.*, 2004). These outbreaks lead to tree mortality in host species and are reflected as changes in canopy openness (D'Aoust *et al.*, 2004). In contrast, mixedwood stands have been observed to have lower mortality levels than coniferous stands (Su *et al.*, 1996; Bouchard *et al.*, 2005). In these stands the development of a multilevel canopy structure is common (Bouchard *et al.*, 2005).

Stands dominated by deciduous trees (because they contain a low proportion of host species), show little change in canopy openness following spruce budworm outbreaks, while coniferous stands show a significant increase in canopy openness following an attack, with mixedwood stands being intermediate (D'Aoust *et al.*, 2004). In contrast, Blais (1981) reported that budworm induced mortality for white spruce and balsam fir trees are approximately the same in coniferous and mixedwood forests. Bergeron *et al.* (1995), however, found that the mortality rates of balsam fir were higher in coniferous stands than deciduous stands with mixedwood stands being intermediate. The lower mortality rates of balsam fir stems in deciduous stands may be related to overstory deciduous trees creating situations where female spruce budworms experience difficulty finding subcanopy or understory balsam fir (Bergeron *et al.*, 1995).

Outbreaks result in an increase in canopy gaps and influence gap distribution, depending on spatial arrangement of susceptible trees in a stand. D'Aoust *et al.* (2004) reported that before

outbreaks, gaps are relatively uniformly distributed, whereas after an outbreak, gaps become patchy and heterogeneous in distribution, and gap size increases with an increase in the coniferous component. Spruce budworm outbreaks often have detrimental effects on the white spruce component of a stand, as the forest environment following a spruce budworm outbreak does not encourage white spruce regeneration (Bergeron and Dubuc, 1989). A severe spruce budworm outbreak can result in mortality levels of approximately 90 percent for balsam fir and 50 percent for white spruce (Blais, 1981), and it is possible that severe outbreaks can lengthen the interval between outbreaks due to the high mortality of balsam fir and white spruce that severe outbreaks cause (Blais, 1981).

Mortality levels appear to differ with tree sizes and site condition. Bergeron *et al.* (1995) reported that balsam fir tree mortality (number of stems killed) increases as (1) the diameter of trees increases (indicating that smaller trees suffer less mortality than larger trees), (2) the percentage of coniferous stands that dominate the forest landscape increases, (3) stand age increases, and (4) balsam fir basal area and abundance increases. While Bergeron *et al.* (1995) revealed that abiotic factors did not significantly affect balsam fir mortality rates caused by spruce budworm, MacLean and MacKinnon (1997) reported that defoliation by spruce budworm was higher on well-drained, more productive sites than less well-drained sites, possibly due to variation in egg-laying behavior of the spruce budworm females and higher foliage nutrient levels on richer sites. In contrast, Bouchard *et al.* (2005) found that balsam fir dominated stands suffered the greatest mortality on imperfectly drained soils.

Although spruce budworm outbreaks last longer in western Canada, they usually cause less mortality (Timoney, 2003). Mortality levels have been directly related to the fire cycle, as mortality of balsam fir has been shown to increase with an increase in fire cycle, likely due to an increase in overall balsam fir abundance in the stands (Bergeron and Leduc, 1998). Therefore, it is likely that in areas where climate change leads to a longer fire cycle, spruce budworm induced mortality will increase, while areas that experience a shorter fire cycle will have a decrease in spruce budworm induced mortality (Bergeron and Leduc, 1998). In particular, spruce budworm outbreaks may be responsible for maintaining mixedwood stands in areas of the boreal forest with longer fire cycles (Kneeshaw and Bergeron, 1999).

## VI. THE IMPACT OF CLIMATE AND GEOGRAPHY ON BOREAL STAND STRUCTURE

Due to its circumpolar distribution and extensive geographic range, the boreal forest is subject to highly variable climatic conditions from one region to the next (Weber and Stocks, 1998; Amiro *et al.*, 2001). In North America, the boreal forest forms an uninterrupted transcontinental band that extends from Alaska in the west to Newfoundland in the east (Weber and Stocks,

1998), and Canadian boreal forests themselves are approximately 340 million ha in size (Amiro *et al.*, 2001). The dynamics of a stand are impacted tremendously by climatic conditions, as climate plays an important role in determining fire regimes (Overpeck *et al.*, 1990; Bergeron, 1991; Suffling, 1995; Lesieur *et al.*, 2002), tree species and other vegetation distributions (Bonan *et al.*, 1992; Hogg, 1994; Suffling, 1995; Flannigan and Bergeron, 1998), and successional pathways (Overpeck *et al.*, 1990; Chen and Popadiouk, 2002). In this section, we will discuss (1) how fire cycle varies regionally and how fire cycle and geography impact structure, (2) how the fire cycle has changed since the termination of the Little Ice Age, (3) how climate change is projected to affect the fire cycle and how this might impact structural dynamics, species distributions and wildlife, and (4) the implications of climate change on the earth's carbon balance.

### A. Geography and Fire Cycle and Their Influence on Species and Structural Dynamics

In the Canadian boreal forest, the fire cycle, defined as "the number of years required to burn over an area equal to the whole area of the forest" (Van Wagner, 1978) decreases from Newfoundland in the east to Alberta in the west (Johnson, 1992; Suffling, 1995; Bergeron *et al.*, 2001). This decrease in fire cycle from east to west can be attributed to many factors including probability of lightning strikes and climate, both of which affect the fire weather and the fire regime (Bergeron *et al.*, 2001; Kneeshaw and Gauthier, 2003). The west-central portion of the country is characterized as having relatively dry and severe fire weather which contributes to the high incidence of fires (Amiro *et al.*, 2001; Kneeshaw and Gauthier, 2003).

In areas where the fire frequency, i.e., "the number of fires per unit area per year" (Bergeron, 1991) is high, frequent fires can result in cyclic succession maintaining intolerant colonizing species as the dominant tree species until the next fire (Dix and Swan, 1971; Carleton and Maycock, 1978; Johnson, 1992), whereas long fire cycles can produce directional succession, leading to species replacement of shade-intolerant tree species by shade-tolerant ones (Bergeron *et al.*, 2001; Lesieur *et al.*, 2002). With long fire cycles, the importance of secondary disturbances such as insects, disease, and blowdown with respect to shaping forest structure increases in importance (Bergeron and Leduc, 1998; Bergeron *et al.*, 2001). The fire regime is also responsible for controlling species distributions (Bergeron and Brisson, 1990; Flannigan and Bergeron, 1998; He *et al.*, 2002). For example, the fire regime appears to limit the northward distribution of red pine due to the higher intensity of fires that occurs in the northern boreal forest compared to the south (Bergeron and Brisson, 1990; Flannigan and Bergeron, 1998), although highly frequent fires of low intensity promote red pine abundance (Engstrom and Mann, 1991).

Disturbance regime, climatic conditions, successional stage, activity of decomposing organisms, composition of tree species, and soil productivity are largely responsible for determining the amount of CWD in a stand (Linder *et al.*, 1997). Moist sites generally have higher volumes of CWD than drier sites (Feller, 2003). This is likely due to higher productivity (more tree biomass production) on moist sites, but may also be a consequence of longer fire cycles that generate larger pre-disturbance production of CWD or by slower downed log decomposition (Spies *et al.*, 1988; Feller, 2003). Indeed, productive sites have higher living and dead timber volumes than less productive sites (Sippola *et al.*, 1998). In contrast, it has been suggested that areas with less precipitation and colder temperatures have slower microbial activity and reduced decomposition rates (Harmon and Hua, 1991; Hély *et al.*, 2000a), resulting in a build-up of downed logs on the forest floor (Hély *et al.*, 2000a).

Northern boreal forests have been found to be structurally different from southern boreal forests (Fridman and Walheim, 2000; Siitonen *et al.*, 2000; Rouvinen *et al.*, 2002). Old-growth forests in Fennoscandia and Russia were reported to contain higher CWD volumes in hemiboreal and southern boreal regions than northern boreal regions (Siitonen *et al.*, 2000). In contrast, Fridman and Walheim (2000) and Rouvinen *et al.* (2002) reported that the volume of CWD increases from the south to the north, attributed to a harsher climate in the northern areas that favor slower decomposition rates and added CWD accumulation. The contrasting results of these studies may be attributed to differences in study regions, cover type, or site type. Nilsson *et al.* (2002) reported that the density of large, living trees in northwestern North American old-growth boreal forests is several times higher than that in other boreal regions in Europe and North America.

### B. Changes in the Fire Cycle Since the Little Ice Age

North American boreal forests have holistically experienced an increase in fire cycle since the end of the Little Ice Age (approximately 1850 AD) (Clark, 1988; Flannigan *et al.*, 1998; Bergeron *et al.*, 2001; Lesieur *et al.*, 2002), where the number of fires and area per year that is burned has decreased since about 1850 to present (Bergeron, 1991; Bergeron *et al.*, 2001). This temporal change in fire cycle and the variation in fire cycle among regions is likely driven by climate rather than by direct human involvement (including suppression) (Flannigan *et al.*, 1998; Bergeron *et al.*, 2001; Lesieur *et al.*, 2002). This is supported by Timoney (2003) who concluded that fire suppression has had little effect on decreasing the annual area burned in the prairies of western Canada. However, Linder *et al.* (1997) and Linder (1998) found that fire suppression has been effective in significantly altering the natural forest structure in some areas of the boreal forest by almost completely eliminating fires, thereby reducing the heterogeneous nature of the landscape. By suppressing fire, old-growth conditions created may increase the likelihood of larger, more detrimental fires in the future (Hendrickson, 2003).

### C. The Potential Impacts of Climate Change on the Disturbance Regime and Forest Stand Structure

A changing climate has the potential to impact species distributions. It is predicted that higher CO<sub>2</sub> levels will continue to bring about an increase in the earth's temperature (Stocks *et al.*, 1998). With an increase in CO<sub>2</sub> and resulting warmer temperatures, species distribution will change, as some species will advance northward (Bonan *et al.*, 1992; Suffling, 1995; Thompson *et al.*, 1998; He *et al.*, 2002). However, for other species a northward movement will be difficult due to changes in abiotic conditions, such as soil properties, that will hinder advancement (Suffling, 1995).

Bonan *et al.* (1992) suggests that climatic warming may initiate a positive feedback response where a warmer climate would cause the northward migration of the boreal forest, which would in turn result in further warming. While boreal species may move northward, it is likely that southern tree species will also move northward into the current boreal range (He *et al.*, 2002). The consequence of this within the current boreal forest range may be a decrease in abundance of northern temperate deciduous and boreal tree species (Suffling, 1995; He *et al.*, 2002), and an increase in the abundance of more southern temperate species such as white ash (*Fraxinus americana* L.), bur oak (*Quercus macrocarpa* Michx.), black oak (*Quercus velutina* Lam.) and white oak (*Quercus alba* L.) (He *et al.*, 2002) and fire avoiders such as white spruce and balsam fir (Suffling, 1995; Flannigan *et al.*, 1998). However, Overpeck *et al.* (1990) predicted a greater proportion of the landscape being occupied by early successional species in the boreal as the consequence of global warming.

In the western boreal and temperate forests, predicted climatic warming will likely alter disturbance regimes, leading to less precipitation and an increase in fire frequency and intensity, which has the potential to cause a homogenization of the forest landscape with reduced diversity and complexity and leading to the decline of some forest tree species (Clark, 1988; Overpeck *et al.*, 1990; Thompson *et al.*, 1998; Amiro *et al.*, 2001). If general circulation models (GCM) hold true (Stocks *et al.*, 1998), North American boreal forests will be more subject to fire danger, especially in the west-central portion (Stocks *et al.*, 1998), where large portions of the boreal landscape may be transformed into grassland and early successional forests (Flannigan *et al.*, 1998; Amiro *et al.*, 2001), resulting in loss of forest cover and forest fragmentation (Hogg, 1994; He *et al.*, 2002). However, higher temperatures do not necessarily indicate that fire disturbances will be larger and more frequent (Bergeron and Flannigan, 1995; Flannigan *et al.*, 1998). In the eastern portion of the boreal forest, it is predicted that the fire cycle will continue to increase under projected warming trends (Bergeron and Flannigan, 1995; Flannigan *et al.*, 1998; Bergeron *et al.*, 2004). This decrease is driven by the precipitation regime of the region, which is quite different from that in the west (Bergeron and Flannigan, 1995; Bergeron *et al.*, 2004).

### D. Climate Change and Carbon Ecosystem Stores

The processes that influence and are influenced by CWD are essential in managing carbon retention in boreal forest ecosystems (Yatskov *et al.*, 2003). The input of carbon dioxide (CO<sub>2</sub>) to the atmosphere as a consequence of CO<sub>2</sub> flux from CWD and CO<sub>2</sub> soil surface flux appears to be important in fire-prone boreal forests (Krankina and Harmon, 1995; Mäkipää *et al.*, 1999; Wang *et al.*, 2002, 2003). Soil surface CO<sub>2</sub> fluxes increase with increasing soil temperature and deciduous forest component while decreasing with increasing forest stand age (Mäkipää *et al.*, 1999; Wang *et al.*, 2003). As well, CWD CO<sub>2</sub> flux increases as the temperature of air and CWD rises (Wang *et al.*, 2002). However, under warmer climatic conditions, it is predicted that the carbon stores in vegetation will increase as net primary productivity increases (Mäkipää *et al.*, 1999), which may offset some of the releases of carbon by soil surface and CWD CO<sub>2</sub> flux.

At the stand level, younger stands have the potential to sequester more carbon annually than older stands because of their higher production rates (i.e., photosynthetic rates) (Goulden *et al.*, 1998). However, at the landscape level, it is likely that an increase in fire frequency in some areas of the boreal forest, as a consequence of global warming, may lead to an increase in overall CO<sub>2</sub> flux to the atmosphere and an increase in the percentage of young forests on the landscape (Krankina and Harmon, 1995; Thompson *et al.*, 1998; Mäkipää *et al.*, 1999; Amiro *et al.*, 2001). The increase in CO<sub>2</sub> emissions may in turn bring about a positive feedback where higher rates of CO<sub>2</sub> emissions cause more fires and greater CO<sub>2</sub> emissions (Amiro *et al.*, 2002). Consequently, it is possible that the boreal forest may turn from an important carbon sink into an important carbon source (Mäkipää *et al.*, 1999; Amiro *et al.*, 2001). However, in some areas of the boreal forest, longer fire cycles may accompany the warmer temperatures (Bergeron and Flannigan, 1995; Flannigan *et al.*, 1998), and under these conditions, the slower rates of decomposition in older forests and reduced releases of carbon through combustion (due to less fires) (Wardle *et al.*, 2003) may cause the boreal forest to continue to be a carbon sink (Flannigan *et al.*, 1998; Wardle *et al.*, 2003). This highlights the complexities surrounding this issue and stresses the need for further investigation.

## VII. A COMPARISON OF STAND STRUCTURE IN NATURAL AND MANAGED BOREAL FORESTS

Clearcutting is the most common harvesting method used in many areas of the boreal forest. The use of clearcutting to emulate the conditions created by natural disturbances is at best well-intentioned naïveté but in reality is a misleading interpretation of many known ecological processes (Keenan and Kimmins, 1993; Gordon, 1994; McRae *et al.*, 2001). While both clearcutting and fire remove the tree canopy and bring about changes in ground microclimate (Keenan and Kimmins, 1993; Carleton and MacLellan, 1994), it appears that CWD dynamics of burned



stands are different from that of clearcut stands (Brumelis and Carleton, 1988; Linder and Östlund, 1998; Sippola *et al.*, 1998; Krankina *et al.*, 2002). Forest fires are responsible for creating new dead organic material by killing the stems of trees, burning root systems and scorching crowns (Sippola *et al.*, 1998). These dead trees remain as snags for a variable length of time before eventually falling to the forest floor (Sippola *et al.*, 1998). In contrast, clearcut harvesting removes organic material from the forest, and results in a disruption in the production and availability of CWD for a substantial length of time (Sippola *et al.*, 1998).

For the remainder of this section, “natural stands” will refer to stands that were disturbed by a stand replacing fire, whereas “managed stands” will refer to stands that have undergone harvesting activities such as clearcutting, selective cutting and thinning. While studies have explored the differences between natural and managed stand structure (Pedlar *et al.*, 2002; Rouvinen *et al.*, 2002; Storaunet and Rolstad, 2002; Ruel *et al.*, 2004), a study that characterizes the differences between the living tree and CWD dynamics of natural and managed stands along a chronosequence with similar abiotic conditions is needed for better understanding of long-term impacts of clearcutting on forest stand structure. Because of this, an accurate comparison of stand structural dynamics in fire origin stands versus clearcut harvested stands is difficult. This section will investigate the dynamics of CWD and living trees in natural and managed boreal forest stands. It will also outline the impacts of clearcutting and selective cutting on biodiversity with special reference to old-growth forests.

### A. Living Tree Dynamics

Forests that are logged differ considerably from natural forests with respect to some of their live tree characteristics (Brumelis and Carleton, 1988; Linder and Östlund, 1998; Rouvinen *et al.*, 2002; Ruel *et al.*, 2004), while other characteristics appear to be similar (Reich *et al.*, 2001). It has been reported that the volumes of live trees, numbers of large living trees, and deciduous tree component is lower while the density of live trees is higher in logged stands compared with natural stands in the old-growth state (even though a considerable length of time had passed since logging occurred) (Linder and Östlund, 1998; Rouvinen *et al.*, 2002; Ruel *et al.*, 2004). However, Reich *et al.* (2001) found that the basal area of trees in young and old post-fire stands was similar to those post-logged, indicating that stand origin has no significant effect on the basal area of trees in a stand in the southern boreal forest. Ferguson and Elkie (2003) found that the density of live trees was lower in young managed stands when compared to young natural stands, with no significant differences in basal area between the two. Moreover, the density of live trees was higher in natural stands compared with clearcut stands in black spruce dominated forest (Brumelis and Carleton, 1988). As well, tree height has been found to be lower in younger logged black spruce stands compared with burned

black spruce stands (Ruel *et al.*, 2004). This is possibly due to trees in logged stands having to acclimate to new growing conditions or because of lower nutrient levels (Ruel *et al.*, 2004). However, the difference in height between logged and natural stands faded after the stands reached an age of approximately 50 years (Ruel *et al.*, 2004). Further, Ruel *et al.* (2004) also found that black spruce in logged stands allocated more biomass to the development of branches and leaves than to their stems, but it is unclear why different stand origins resulted in different allocation patterns.

Logging can lead to a temporary nutrient flush, and as deciduous trees have a competitive advantage over conifers on nutrient-rich sites, the composition of species may change in favour of an increased deciduous component at the expense of conifers after disturbance (Brumelis and Carleton, 1988; Carleton and MacLellan, 1994). Coniferous regeneration may also be poorer on logged sites than natural sites due to a greater abundance of ericaceous shrubs on logged sites that hinders coniferous growth (Ruel *et al.*, 2004). As well, seedling recruitment is poor in the large open areas created by clearcuts, except for shade intolerant deciduous trees such as trembling aspen (Coates, 2002). Logging also has been shown to destroy advanced regeneration, which may also be hindering coniferous regeneration in logged areas (Ruel *et al.*, 2004).

The spatial configuration of live trees is different in areas that are burned, as compared to areas that are clearcut (Niemelä, 1999). Fire burns in a heterogeneous fashion and leaves patches of unburned trees on the landscape. In contrast, clearcutting removes most of the trees from harvested areas (Niemelä, 1999; Gordon *et al.*, 2001). However, guidelines have been written in an attempt to promote live tree retention during harvesting operations (Ontario Ministry of Natural Resources, 2001). There is little information available that compares live tree characteristics along a chronosequence for stands that are harvested versus burned and allowed to develop without additional human intervention such as partial or selective cutting and thinning. The need for this kind of study is crucial if forest management decisions are going to be made that more effectively reflect the natural stand structure of boreal forest ecosystems.

### B. CWD Dynamics

Following clearcutting, less residual material is left behind than what is left following a natural disturbance (Fleming and Freedman, 1998; Niemelä, 1999; Krankina *et al.*, 2002). In young forests, CWD volume, snag abundance, snag basal area, and volume of large snags and logs is significantly higher in natural stands than in clearcut stands (Fridman and Walheim, 2000; Krankina *et al.*, 2002; Pedlar *et al.*, 2002). While volumes of logs are similar, the snags that contribute a large proportion of CWD in natural stands are largely absent in managed stands (Pedlar *et al.*, 2002), as stand replacing fire leaves many large snags (killed during the fire) while clearcutting does not (Pedlar *et al.*, 2002; Rouvinen *et al.*, 2002). Instead, clearcutting

produces small logging slash in early states of decay that breaks down quickly (Fraver *et al.*, 2002). The distribution of CWD in natural forests has been found to be fairly even among small, medium, and large classes, whereas the CWD in managed stands was largely skewed towards small diameter classes (Fridman and Walheim, 2000; Fraver *et al.*, 2002; Pedlar *et al.*, 2002). Even in intermediate-aged and old forests, the volume of CWD appears to be higher in natural forests than forests where the stand initiating disturbance was clearcutting (Krankina *et al.*, 2002). Therefore, managed stands differ remarkably from natural stands in the amount, type, and size of CWD that is produced (Fridman and Walheim, 2000; Pedlar *et al.*, 2002; Rouvinen *et al.*, 2002), and the ability of clearcutting to effectively emulate the forest structure of burned stands is seriously questionable.

Both timber harvesting and fire create forest edge that fragments the boreal forest, but unlike fire, clearcuts create forest edges that are narrower, have less snags, a less extensive structural change, an increase in tree mortality and snag breakage, and a sudden edge-to-interior forest transitional gradient (Gordon *et al.*, 2001; Harper *et al.*, 2004). It is therefore evident that forest edge created by clearcut harvesting does not mimic the edge created by fire, and because of this, clearcut edge may not be able to fulfill the necessary habitat requirements for some species that rely on forest edge created by fire (Harper *et al.*, 2004). Selective cutting and thinning also have significant impacts on forest structure. These activities lower the overall CWD volume, decrease the number of large downed logs and snags, diminish the overall snag abundance, and increase the decomposition rates while decreasing landscape heterogeneity and the unevenness of a stand (Kolström, 1998; Siitonen *et al.*, 2000; Jantunen *et al.*, 2002; Storaunet and Rolstad, 2002).

### C. The Impacts of Timber Harvesting on Biodiversity

In recent years, the effect of harvesting on biodiversity and ecosystem sustainability has been closely scrutinized. Maintaining biodiversity has many benefits, including the ability to buffer ecosystems against unforeseen perturbations (Niemelä, 1999). Biodiversity in the boreal forest may be maintained by mechanisms that create secondary succession at both small and large scales such as forest fires and gap phase dynamics, that can affect a few square meters (e.g., death of a single tree) or several thousand hectares (e.g., forest fire) (Niemelä, 1999).

Wildlife can be severely affected by harvesting activities, and in many areas, intensive logging has resulted in the loss or decline of forest species including Gapper's red-backed vole (*Clethrionomys gapperi* Vigors) (Moses and Boutin, 2001) and the woodland caribou (*Rangifer tarandus caribou* Gmelin) (Chubbs *et al.*, 1993). The American marten (*Martes americana* Turton) appears to prefer sites with diverse stand structure including tall trees, a high density of tall snags, large diameter downed logs, a high basal area of deciduous trees, and a suitable subnivean habitat to forage for small animals (Sturtevant *et al.*, 1997; Payer and Harrison, 2003). Harvesting usually occurs at

an age that corresponds to the lowest volumes of CWD in stands (Sturtevant *et al.*, 1997), and consequently, the lower volumes of CWD that remains following harvesting may be detrimental to marten populations by limiting habitat availability (Payer and Harrison, 2003). Further, managed forests contain less large diameter snags and trees, which has the potential to negatively impact many cavity dwelling animals, cavity nesting birds, and large raptors (Linder and Östlund, 1998; Imbeau *et al.*, 1999; Delong and Kessler, 2000).

It has been suggested that alternative forest harvesting techniques can be used in an attempt to lessen the impact of forest harvesting. Asselin *et al.* (2001) suggests using strip clearcutting and seed-tree systems to help in the effective regeneration of some coniferous species such as white spruce and eastern white cedar, when clearcutting would create situations where seeds banks are far away. Moses and Boutin (2001) in turn suggest that implementing live tree patch retention can lessen the negative impacts on some small mammal populations. As well, alternative harvesting methods, such as "harvesting with advance regeneration protection" (HARP), can be used to increase the retention and redevelopment of old-growth features more effectively than traditional harvesting methods (clearcutting) in the boreal forest (Deans *et al.*, 2003). Finally, with the increase in fire cycle that is expected to occur in some areas of the boreal forest (Flannigan *et al.*, 1998; Bergeron *et al.*, 2004), the use of clearcutting may not be appropriate for all areas. As such, Bergeron (2004) recommends clearcutting some areas (followed by seeding or planting), partially cutting other areas (to resemble overmature forests), and using selective cutting in still others (to retain old-growth characteristics) in an attempt to emulate a heterogeneous forest structure at the landscape level.

While harvesting is the most significant anthropogenic disturbance mechanism in the boreal forest, other human activities such as farming and the oil and gas industry (especially in the western boreal) are continuing to expand and further fragment the landscape, contributing more and more to habitat loss and degradation (Timoney, 2003), which will likely put additional pressure on boreal species. Further, harvested sites are occasionally planted with tree species that are different from the ones that used to inhabit the site, thereby changing tree species assemblages and impacting biodiversity (Timoney, 2003).

### D. The Impacts of Timber Harvesting on Old-Growth Forest Structure

The characteristics that define boreal forest old-growth state are still widely debated and with the public's concern over the perceived decline in old-growth forest (Mosseler *et al.*, 2003), criteria must be established that can be used to identify old-growth boreal forest. In an attempt to develop structural criteria to identify old-growth forest, Lee *et al.* (2000), Nilsson *et al.* (2002), Kneeshaw and Gauthier (2003), Mosseler *et al.* (2003), and Zenner (2004) made the following generalizations regarding boreal forests that are in an old-growth state:

1. About 10 percent of all stems are dead.
2. The percentage of dead trees that are standing is between 20 percent and 40 percent of total CWD volume and basal area.
3. High structural complexity exists.
4. An intricate combination of large, old trees and young, small trees can be found.
5. A 1.5 subcanopy/canopy tree stem ratio is common.
6. Individuals from the original cohort are beginning to die while stems in the understory are beginning to be recruited.
7. The cohort basal area ratio (CBAR) is between 0.3–0.4. The CBAR increases (with a maximum value of 1 and a minimum value of 0) as time since fire increases.

Old-growth forests provide a variety of ecosystem services including storing large amounts of carbon, habitat protection, preserving a reservoir of genetic diversity, and improving water quality (Frelich and Reich, 2003; Mosseler *et al.*, 2003). There is much concern in forestry today over the loss of old-growth forests, as the loss of these forests will influence the species that require them for forest habitat (Niemelä, 1999). Numerous species of predatory arthropods, small and large mammals, fungi, birds, amphibians, reptiles, and vascular plants require forests with old-growth characteristics (Niemelä, 1999; Delong and Kessler, 2000; Edman and Jonsson, 2001; Mosseler *et al.*, 2003). Many of these species are endangered (Edman and Jonsson, 2001), stressing the need for protection of existing old-growth forest and using forest management to promote the development of old-growth forest in the future.

The loss of old-growth forests from the landscape as a result of timber harvesting and other anthropogenic causes has the potential to impact the earth's CO<sub>2</sub> levels, as young and mature clearcut stands have lower deadwood carbon stores than old-growth forests (Krankina and Harmon, 1995). Therefore, the loss of old-growth forests may cause an input of CO<sub>2</sub> to the atmosphere and influence climate change through global warming. Also, as forests age, they increase in reproductive fitness and genetic diversity, thereby serving as important gene pools (Mosseler *et al.*, 2003). The loss of these older forests may be harmful from a genetic standpoint for boreal forest trees (Frelich and Reich, 2003; Mosseler *et al.*, 2003).

Following harvesting, the slowest component to recover in attaining natural structure is CWD, and therefore, management practices that try to emulate the structure of old-growth characteristics in forest management are desirable (Siitonen *et al.*, 2000). While old-growth forests have traditionally been thought of as forests that have not been harvested (Hendrickson, 2003), there are many who believe that second growth forests that have been harvested could in time develop to be old-growth forests (Mosseler *et al.*, 2003). If young harvested stands have the same structure as young natural stands, then it is likely that provided the young harvested stand is allowed to develop without anthropogenic influences, it will develop to resemble a natural stand (Frelich and Reich, 2003).

## VIII. SUMMARY

1. Stand structure has important implications for forest ecosystems including the maintenance of wildlife habitat, sustaining and indicating biodiversity, nutrient cycling, regulating climate through carbon storage, and affecting forest regeneration.
2. Surficial deposits and landscape configuration are important contributors in determining which species will colonize which areas of forest and in influencing successional pathways.
3. Fire is the dominant stand replacing disturbance in the North American boreal forest, as stand structure is largely a reflection of the time since last stand replacing fire. Fire origin stands are characterized as having a U-shaped CWD accumulation pattern with stand age.
4. Research is lacking that compares and contrasts CWD and live tree dynamics in different cover types within similar environmental conditions and in mixedwood forests in general along the chronosequence.
5. Over time, a forest stand changes from having a largely even-structured canopy to developing a canopy that is heterogeneous and multilayered in structure. As forests age, they develop larger CWD that is more evenly spread out among diameter and height classes and decay states. However, following a stand replacing fire, the production of large sized CWD can be significant. This CWD originates from the pre-disturbance stand (trees killed during the fire and CWD from the pre-disturbance stand that survives the fire).
6. Downed logs are important regeneration microsites for many species as well as being an important habitat requirement for wildlife. In turn, snags also have important wildlife value.
7. Non-stand replacing disturbances such as blowdown and spruce budworm outbreaks play an important role in altering forest structure and maintaining a deciduous component for many forests when time since fire is long, by removing canopy trees, freeing up available growing space, reducing the coniferous component of dominating trees, and creating microsites for new trees to establish.
8. The Canadian boreal forest has a fire cycle that increases in general from the west to the east. The North American boreal forest is highly variable in climate across its geographic range, and it is still unclear how predicted climate change scenarios will affect tree species dynamics and distributions, the regional fire cycle, and overall carbon ecosystem stores. As a result, at the landscape level, the boreal forest may turn from a CO<sub>2</sub> sink into a CO<sub>2</sub> source.
9. Clearcutting is a common harvesting practice throughout the North American boreal forest. It has been employed under the assumption that it effectively emulates boreal natural disturbances, specifically a stand replacing fire. However it appears that CWD characteristics are considerably different between fire origin and clearcut stands. Little study has been done to compare the stand structure of the two origins along a

chronosequence where both have been allowed to develop without further anthropogenic influences. If effective forest management decisions are going to be made, this type of study must be undertaken.

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