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Stand Structure and Composition Dynamics of Boreal Mixedwood Forest: Implications for Forest Management

Brian W. Brassard and Han Y. H. Chen

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- Offer innovative approaches to knowledge transfer; and
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## Stand Structure and Composition Dynamics of Boreal Mixedwood Forest: Implications for Forest Management

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## **EXECUTIVE SUMMARY**

Forest stand structure and composition are important attributes of forested ecosystems. Wildfire and clearcut harvesting are the most common stand-initiating disturbances in the North American boreal forest. Although these disturbances produce very different stand structures and compositions shortly after disturbance, there is little research that compares their long-term dynamics. This report examines the effects of clearcutting on the post-fire stand structure and composition dynamics of North American boreal mixedwood forest.

Vertical structure and composition change over time is characterized by increased conifer dominance, replacement of early successional pioneering trees by trees of later successional status, and the transition from a unimodal to bimodal to multimodal age and size structure. The death of the pre-fire cohort provides substantial volumes of coarse woody debris (CWD) in the young developing stand. Beyond this initial pulse, however, CWD volume declines until later in stand development when the pioneering cohort succumbs to longevity-related mortality and CWD volume increases. Late in stand development, individual tree replacement dynamics maintain a continuous input of CWD into the stand.

Windthrow and insect outbreaks are also common stand-replacing disturbances in the North American boreal forest, but do not produce similar stand dynamics as wildfire. Clearcut harvesting dramatically reduces the volume of CWD in a young developing stand compared to wildfire. Young post-clearcut stands have a greater proportion of trees of later successional status, lower tree density, and a more heterogeneous vertical structure than respective fire-origin stands. However, evidence suggests that structure and composition eventually converges between the two disturbance origins later in stand development.

Maintaining longer rotation periods and varying harvest block sizes, in conjunction with prescribed burning and the retention of woody residual on site, may be appropriate management options, in certain situations, to better emulate the structure and composition dynamics of fire-origin stands in managed boreal forest. Future climatic change is projected to cause a northward movement of some tree species and alter the fire frequency and overall forest age structure of the landscape. Appropriate management responses to climatic change could include managing for a greater proportion of tree species from more southern forest regions or genotypes of current species that are more adapted to growing in warmer climates.



High intensity wildfire is the most common standreplacing disturbance mechanism in the North American boreal forest.

Justification for the use of clearcutting in the boreal forest is based on the premise that it emulates wildfire. However, whether clearcut harvesting, in its current form, is appropriate for use in the boreal forest is an ongoing debate.

## I. Introduction

Forest stand structure (the arrangement and interrelationships of live and dead trees) and composition (the proportions of live and dead trees by species) are important attributes of forested ecosystems. Forest stand dynamics refers to how stand structure and composition changes over time. Forest stand dynamics are impacted by many factors including:

- stand-initiating disturbances,
- secondary (non-stand-replacing) disturbances,
- pre-disturbance stand structure and composition,
- surrounding seed sources, and
- climatic and edaphic characteristics (Oliver and Larson, 1996; Chen and Popadiouk, 2002; Brassard and Chen, 2006; Hart and Chen, 2006).

In the boreal forest of North America, high intensity wildfire is the most common stand-replacing disturbance mechanism (Johnson, 1992). However, over the past few decades, commercial-level clearcutting has become an increasingly common stand-replacing disturbance, with over 750,000 hectares of forested area harvested annually in the Canadian boreal forest alone (Canadian Council of Forest Ministers, 2009).

Justification for the use of clearcutting in the boreal forest is based on the premise that clearcutting, to some extent, emulates wildfire (Keenan and Kimmins, 1993). Although both disturbances kill most, if not all, of the trees in a stand, clearcutting removes the trees from the site for fiber. Unlike clearcutting, wildfire exposes mineral soil by consuming the duff layer, woody debris, and understory vegetation. This facilitates the recolonization of the site by early successional fireadapted species, and destroys the advanced regeneration of later successional fireavoiding species from the previous stand (McRae et al., 2001). As a result, clearcutting- and fire-origin stands may differ considerably in structure and composition shortly after disturbance (Carleton and MacLellan, 1994; Reich et al., 2001; Pedlar et al., 2002; Brassard and Chen, 2008). This calls into guestion the appropriateness of using clearcut harvesting in the boreal forest, in its current form, to emulate wildfire. However, very little research has compared the longerterm dynamics of post-fire and post-clearcutting stands, and it remains to be seen if stand structure and composition elements converge over time between stands of clearcutting- and fire-origin.

The general purpose of this report is to improve understanding of the effects of natural and anthropogenic disturbances on the stand structure and composition dynamics of boreal forest. Specifically, this review will (*i*) describe the natural stand structure and composition dynamics of North American boreal mixedwood forest and (*ii*) compare these dynamic patterns between post-fire and post-clearcut



harvest stands. Additionally, it will outline some of the potential impacts of future climatic change on forest structure and composition at the landscape-level, and discuss management options for reducing some of the potential negative effects of clearcutting on stand dynamics in managed forest. Similar to Chen and Popadiouk (2002), structure and composition changes are described using discrete stages of stand development (stand initiation, stem exclusion, canopy transition, and gap dynamics). A better understanding of how clearcutting impacts the natural post-fire stand dynamics of the boreal forest will allow forest practitioners to develop better mitigation policies and procedures to reduce some of the undesired effects of forest management on ecosystem integrity.

# II. Structure and composition dynamics of natural boreal forest stands

#### A. Post-fire stand dynamics

#### 1. Stand initiation

Wildfire resets the successional trajectory of a stand by killing overstory and understory trees, and consuming advanced regeneration, shrubs, and herbaceous vegetation, thereby creating desirable conditions for the establishment of a new stand (Brassard and Chen, 2006). Consequently, vertical structure (defined as "the bottom to top configuration of aboveground vegetation within a forest stand" by Brokaw and Lent (1999)), is largely bimodal shortly after stand-replacing fire, with a very dense homogenous layer of small-sized early successional trees (seedlings) of similar age growing beneath a continuous layer of large-sized standing deadwood (snags) (Figure 1a) (Peet and Christensen, 1987; Schulte and Niemi, 1998; Harper et al., 2005; B.W. Brassard, unpublished data). Snag volume is very high following stand-replacing fire (Lee, 1998; Harper et al., 2005; Brassard and Chen, 2008). However, most of these snags, created by the death of the pre-fire cohort, fall to the forest floor within a decade or two after the fire (Sturtevant et al., 1997; Ferguson and Elkie, 2003; Brassard and Chen, 2008). This generates a large amount of downed woody debris (DWD) on the forest floor (Lee et al., 1997; Harper et al., 2005; Brassard and Chen, 2008). Different tree species have different decomposition rates (Harmon et al., 2000; Yatskov et al., 2003; Mäkinen et al., 2006) and snag to DWD conversion tendencies (e.g., uprooting versus breaking along the bole) (Lee, 1998; Siitonen et al., 2000; Hill et al., 2005), that also vary depending on tree size and age. As such, DWD inputs can be quite variable in size, shape, and extent of decay depending on the characteristics of the pre-fire stand.

In the boreal forest, pre-fire stand composition is reflected to a certain extent in post-fire stand composition (Greene and Johnson, 1999; Chen *et al.*, 2009). After wildfire, stands are usually dominated by jack pine (*Pinus banksiana*) (in the eastern boreal forest), lodgepole pine (*Pinus contorta*) (in the western boreal forest), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), and their mixtures. These species have evolved unique reproductive mechanisms that allow them to readily colonize after wildfire (Burns and Honkala, 1990). For example, jack pine has serotinous cones that are held high in the crown and the intense





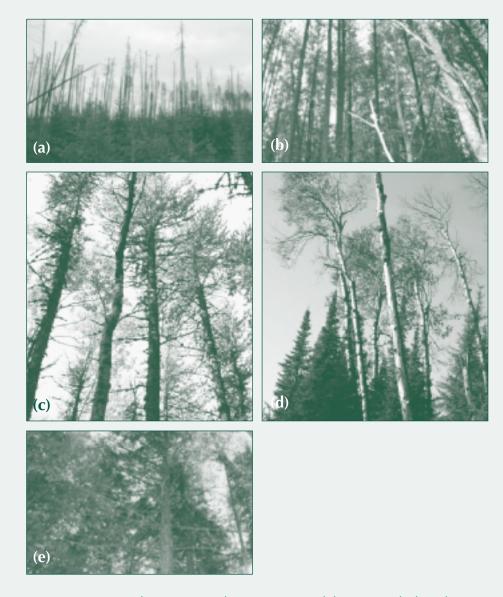


Figure 1. Post-fire structure and composition stand dynamics in the boreal mixedwood forest of northwestern Ontario, Canada, depicted by: *(a)* a 7 year-old stand representing the stand initiation stage of stand development, *(b)* a 25 year-old stand representing the stem exclusion stage of stand development, *(c)* 82 and *(d)* 139 year-old stands representing early and late phases of the canopy transition stage of stand development, respectively, and *(e)* a 201 year-old stand representing the gap dynamics stage of stand development.

heat of fire causes them to open and seeds to fall to the exposed mineral soil where they germinate. Trembling aspen, in contrast, reproduces by root suckering or seeding in from nearby stands. Because of their reproductive mechanisms, if jack pine or trembling aspen are abundant in the pre-fire stand, they will also dominate the post-fire stand.



However, species such as white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and eastern white cedar (*Thuja occidentalis*) which have not evolved reproductive mechanisms that allow them to colonize after stand-replacing fire (Burns and Honkala, 1990), will be almost entirely absent in the post-fire stand, regardless of their abundance in the pre-fire stand. Instead, because of their greater shade tolerance and ability to seed in from nearby stands, these species establish during later stages of stand development (Galipeau *et al.*, 1997; Kneeshaw and Bergeron, 1998; Chen and Popadiouk, 2002).

#### 2. Stem exclusion

Later in stand development, approximately 25 to 35 years after stand initiation, the age, diameter, and height distributions of trees are still relatively homogenous. However, the pioneering trees have grown substantially in size causing tree volume to increase (Figure 1*b*) (Paré and Bergeron, 1995; Lee *et al.*, 1997; Harper *et al.*, 2005). As the stand no longer has enough growing space and soil nutrients to support additional growth of all the trees on the site, intense competition for site resources begins between individuals (self-thinning) (Chen and Popadiouk, 2002; Brassard and Chen, 2006). This results in a decline in tree density (Peet and Christensen, 1987; Oliver and Larson, 1996) and the production of smaller-sized snags (Lee, 1998; Greif and Archibold, 2000; Ferguson and Elkie, 2003; Brassard and Chen, 2008). Because of their smaller size, these snags do not last long and fall to the forest floor quickly, becoming DWD that decays rapidly.

Since most of the fire-generated snags have fallen to the forest floor by this point in stand development, snag volume is relatively low (Lee *et al.*, 1997; Ferguson and Elkie, 2003; Brassard and Chen, 2008). DWD volume, in contrast, is still quite high, since not enough time has passed for the DWD of pre-fire origin to have decayed substantially (Lee *et al.*, 1997; Harper *et al.*, 2005; Brassard and Chen, 2008). DWD in the stem exclusion stage of stand development is highly variable in size and decay extent, since self-thinning generated DWD inputs are smaller in size, from early successional species, and in mid to late stages of decay, while pre-fire DWD is larger in size, from species of early, mid, and late successional status, and of low to medium decay status.

#### 3. Canopy transition

During early stages of canopy transition, approximately 70 to 90 years after stand initiation, members of the colonizing cohort begin to succumb to longevity-related mortality. As the pioneering cohort begins to die off, light, soil resources, and growing space are increasingly freed up (Chen and Popadiouk, 2002; Brassard and Chen, 2006), allowing species such as paper birch, white spruce, and balsam fir to seed in and establish from nearby stands (Kneeshaw and Bergeron, 1998; Bergeron, 2000; Kabzems and Garcia, 2004; Pothier *et al.*, 2004). As a result, the stand begins to transition towards a more bimodal-sized, uneven-aged vertical structure (i.e., young cohort of later successional individuals with small diameters and heights growing underneath a much older cohort of early successional trees with larger heights and diameters) (Figure 1*c*) (Paré and Bergeron, 1995; Brassard *et al.*, 2008).

Vertical structure is still homogenous at the stem exclusion stage of stand development. The intensity of self-thinning is relatively high and reduces the number of trees in the stand, creating small-sized snags in the process.

As most of the firegenerated snags have fallen to the forest floor, snag volume is very low compared to earlier in stand development. However, DWD volume is still high. As the pioneering cohort succumbs to longevityrelated mortality, significant inputs of CWD begin to occur as vertical structure and composition becomes more heterogeneous. DWD volume and piece size and decay variability is relatively low early in canopy transition. Most of the coarse woody debris (CWD; the summation of snag and DWD attributes) generated by the stand-replacing fire and self-thinning has largely decayed, while most of the CWD produced by the death of the pioneering cohort is still standing (Lee *et al.,* 1997; Sturtevant *et al.,* 1997; Brassard and Chen, 2008).

Approximately 120 to 140 years after stand initiation, only a few very large members of the colonizing cohort may persist. The second cohort of later successional trees that established much earlier in canopy transition now begin to occupy canopy and sub-canopy positions, while a third cohort of individuals may also have established in canopy gaps or under the shade of their predecessors. Consequently, vertical structure ranges from bimodal to trimodal during late stages of canopy transition with stand age structure becoming multi-aged (Figure 1*d*) (Paré and Bergeron, 1995; Brassard *et al.*, 2008). The death of almost all the pioneering cohort results in substantial snag and DWD production, and therefore, greater CWD volume and size and decay variability compared to earlier in canopy transition (Lee *et al.*, 1997; Hély *et al.*, 2000; Brassard and Chen, 2008).

#### 4. Gap dynamics

Once all the individuals from the pioneering cohort have completely died off, the stand enters a semi-climax stage of development. The death of individual trees or small groups from insect activity and disease (i.e., non-stand-replacing disturbances) create canopy gaps that facilitate the continuous recruitment of new individuals into the stand (Peet and Christensen, 1987; Chen and Popadiouk, 2002; Hill *et al.*, 2005; Brassard and Chen, 2006). During this stage the stand maintains moderately high snag volumes (Hély *et al.*, 2000; Harper *et al.*, 2005; Brassard and Chen, 2008). The size of the gaps generally determines what types of tree species recruit into them. If gaps are small, they are usually colonized by shade-tolerant tree species such as white spruce and balsam fir. Larger gaps allow greater amounts of sunlight to reach the forest floor, facilitating the recruitment of more shade-intolerant tree species such as paper birch and trembling aspen (Kneeshaw and Bergeron, 1998; Cumming *et al.*, 2000; Pham *et al.*, 2004).

Boreal forest succession is generally characterized by increased conifer dominance as time since stand-replacing fire increases (Frelich and Reich, 1995; Bergeron and Dubuc, 1989; Bergeron, 2000; Gauthier *et al.*, 2000). As such, gaps like those created by spruce budworm (*Choristoneura* spp.) outbreaks, are important for maintaining a broadleaf component late in stand development. Spruce budworm kills mature balsam fir and spruce trees and creates opportunities for tree establishment (Kneeshaw and Bergeron, 1999; Bergeron, 2000; Bouchard *et al.*, 2005; Brassard and Chen, 2006). Consequently, the individual tree replacement dynamics that characterize the gap dynamics stage of stand development result in the production of a diverse multi-layered and multi-aged vertical structure with dominance by later successional coniferous tree species (Figure 1*e*) (Chen and Popadiouk, 2002; Harper *et al.*, 2005; Brassard *et al.*, 2008).



Continuous inputs of DWD of later successional species origin that are small to medium in size and of early to mid decay status result in the maintenance of high volumes of DWD with diverse sizes and extents of decay in this late stage of stand development (Sturtevant *et al.*, 1997; Hély *et al.*, 2000; Brassard and Chen, 2008). Very old stands provide specialized niches for certain species of plants and animals, so that maintaining a certain proportion of these stands, also referred to as old-growth, on the landscape is critical to sustaining biodiversity in the boreal forest (Sturtevant *et al.*, 1997; Frelich and Reich, 2003).

#### B. Other common natural stand-replacing disturbances

Wildfire is not the only stand-replacing disturbance common to the North American boreal forest. Large windthrow events and epidemic insect outbreaks (e.g., spruce budworm and mountain pine beetle (Dendroctonus ponderosae)) are also common stand-replacing disturbance mechanisms (Brassard and Chen, 2006 and references therein). Like fire, these disturbances kill off most of the dominant individuals from the pre-disturbance stand, allowing for the subsequent establishment of a new stand. However, they may result in significantly different post-disturbance stand structures and compositions compared to that following wildfire. These disturbances do not destroy the advanced regeneration and seedbeds of later successional species such as balsam fir, white spruce, and paper birch. Consequently, the regenerating stand following these disturbances will have a much higher proportion of later successional tree species and shrubs such as beaked hazel (Corylus cornuta) and mountain maple (Acer spicatum). The regenerating stand will also have a more heterogeneous vertical structure than that which would occur following stand-replacing fire, resulting in different, albeit still natural, stand structure and composition dynamics.

### III. Effects of clearcutting on structure and composition stand dynamics in boreal forests

#### A. Comparison of fire- and clearcut-origin stand dynamics

#### 1. Stand initiation

Differences between post-fire and post-clearcut stands in structure and composition are most pronounced during the stand initiation stage of stand development. When compared to wildfire, clearcutting results in significantly less CWD volume in the young developing stand. The large snag volume, created by the death of the pre-fire cohort, is absent following clearcutting (Figure 2*a*) (Schulte and Niemi, 1998; Pedlar *et al.*, 2002; Rouvinen *et al.*, 2002; Brassard and Chen, 2008). Given that fire-generated snags will fall to the forest floor and become DWD, young post-clearcut stands are also missing a substantial volume of DWD in comparison to similar-aged post-fire stands (Sturtevant *et al.*, 1997; Pedlar *et al.*, 2002; Martin *et al.*, 2005; Brassard and Chen, 2008). The lack of snags and low DWD volume in young clearcut stands can have detrimental effects on large raptor, cavity nesting bird (Newton, 1994; Imbeau *et al.*, 1999; Delong

Non-stand-replacing disturbances late in stand development maintain a continuous input of CWD and a multi-layered, multi-aged vertical structure dominated by later successional coniferous tree species.

Windthrow and insect outbreaks are also common stand-replacing disturbance mechanisms in the boreal forest but result in different postdisturbance stand structures and compositions compared with wildfire.

Young fire-origin stands contain greater volumes of CWD than young clearcut-origin stands. The low volume of CWD in post-clearcut stands is detrimental to the provision of wildlife habitat on the managed landscape.



Figure 2. Different stand structures and compositions in a (*a*) 7 year-old post-clearcut stand, representing the stand initiation stage of stand development and a (*b*) 25 year-old post-clearcut stand, representing the stem exclusion stage of stand development in the boreal mixedwood forest of northwestern Ontario, Canada.

and Kessler, 2000), and small mammal populations (Moses and Boutin, 2001; Payer and Harrison, 2003; Pearce and Venier, 2005) that rely on larger snags for nesting and hunting and DWD for protection from predators and harsh winter conditions.

In young post-clearcut stands, vertical structure is generally three-layered (Carleton and MacLellan, 1994; Schulte and Niemi, 1998; Reich *et al.*, 2001; B.W. Brassard, *unpublished data*):

- (i) small-sized seedlings of early successional tree species that established after the harvest event,
- (ii) larger-sized advanced regeneration of later successional tree species that established well before harvest, and



 (iii) residual overstory trees from the harvested cohort that are mostly unmerchantable (e.g., undesirable species such as paper birch, unhealthy, smaller-sized, badly formed, or dead).

Although some early successional species such as trembling aspen can propagate equally well after harvest and fire via root suckering, others such as jack pine cannot readily colonize a site after clearcutting. Unlike fire, clearcutting does not produce the high temperatures required to open up jack pine's serotinous cones, nor does it burn away the duff layer and expose mineral soil and available microsites for germination (Keenan and Kimmins, 1993; McRae *et al.*, 2001), both of which are necessary for jack pine recruitment. Since the vertical structure after stand-replacing fire is largely two-layered with dominance by early successional tree species, the vertical structure of young post-clearcut stands is more heterogeneous in size, age, and species composition compared to that after stand-replacing fire.

#### 2. Stem exclusion

Although some structure and composition characteristics of stands of clearcut- and fire-origin are similar by this stage of stand development, most still differ. Trees are generally larger in size but fewer in number in post-clearcut stands and, similar to earlier in stand development, are comprised of a much higher proportion of trees of later successional status. Vertical structure is more heterogeneous in post-clearcut than fire-origin stands due to the size differences between trees that survived the harvest event (i.e., larger-sized advanced regeneration) and the remainder of the stand that recruited after logging (i.e., smaller-sized pioneers) (Figure 2*b*). Because of the lower density of trees in clearcut-origin stands, self-thinning is less intense compared to that in fire-origin stands. This delays the production of snags, and eventually DWD (albeit of smaller-size), further exacerbating the difference in CWD volumes between stands of fire- and clearcut-origin (Sturtevant *et al.*, 1997; Ferguson and Elkie, 2003; Brassard and Chen, 2008).

In European boreal forest, it is common for commercial thinning to be implemented in the stem exclusion stage of stand development in order to extract fiber that would otherwise be lost to self-thinning and increase the growth rates of remaining stems in the process (Smith *et al.*, 1997). However, commercial thinning significantly reduces the volume of CWD in a stand. Declines in biodiversity on the managed landscape in European boreal forest have been directly attributed to a lack of CWD (Linder and Östlund, 1998; Siitonen, 2001; Ecke *et al.*, 2002; Sippola *et al.*, 2005). The implementation of commercial thinning in the North American boreal forest is not widespread, although some forest companies have experimented with it in localized trials (P. Poschmann, *personal communication*). As such, without strong evidence that potential increases in fiber output from commercial thinning would outweigh the negative consequences of CWD losses, especially in previously harvested areas, the use of such practices is not recommended. Young clearcut-origin stands are more heterogeneous in vertical structure and compositionally diverse than young fire-origin stands.

Very few structure and composition characteristics have converged between clearcut- and fire-origin stands by this stage of stand development. While stands of fire- and clearcut-origin should be structurally similar by this stage of stand development, composition differences between the two should still be present.

By this stage of stand development, the legacy of harvesting on the natural stand structure and composition dynamics should have disappeared.

#### 3. Canopy transition

Many structure and composition elements of stands of fire- and clearcut-origin have converged by this stage of stand development, although some differences in both CWD and tree species composition are still present. The density, volume, and sizes of trees should be relatively similar between stands of clearcut- and fireorigin at this stage, however, trees of later successional status may still occupy a greater proportion of the stand in post-clearcut stands compared to stands of fireorigin. Snag characteristics should also be similar between the two disturbance origins, with the exception again, of snags being comprised of a greater proportion of species of later successional status.

Most of the large-sized DWD of pre-disturbance origin and the small-sized DWD created during self-thinning should have largely decayed and been incorporated into the soil by mid- to late- stages of canopy transition (Lee *et al.*, 1997; Sturtevant *et al.*, 1997; Hély *et al.*, 2000; Brassard and Chen, 2008). DWD volume and size and decay characteristics among origins should therefore be relatively similar. However, these predictions are based on available theory and extending known trends from earlier stages of stand development. Conventional commercial-level clearcutting has not occurred long enough in the North American boreal forest for stands of clearcut-origin to have reached the canopy transition stage of stand development. Consequently, it is uncertain whether stands at this point of development will have largely converged in most structure and composition features among the two stand-replacing disturbance mechanisms. It is expected that the legacy of the disturbance event on forest structure, and composition to a lesser extent, should have largely disappeared.

#### 4. Gap dynamics

By the gap dynamics stage of stand development (approximately 180 to 200 years after disturbance, for example, in the mesic upland boreal forest of northwestern Ontario, Canada (Brassard and Chen, 2008; Brassard *et al.*, 2008)), aspects of most structure and composition features should have totally converged among the two disturbance origins, with the exception of possibly a modest increase in the proportion of DWD of later successional species origin among post-clearcut stands. By allowing stands to reach this stage of stand development after clearcutting, natural post-fire stand structure and composition features should be largely restored in managed stands. However, this hypothesis needs to be tested empirically once data becomes available that describes the structure and composition attributes of old post-clearcut boreal forest stands.

## **B.** Management options for emulating natural structure and composition stand dynamics in managed forest

If the primary objective of harvesting guidelines in the boreal forest is to regenerate stands following clearcutting that have similar structure and composition features as those following wildfire (e.g., Ontario Ministry of Natural Resources, 2001), then it is evident that current guidelines are insufficient.



Although not appropriate for all situations, alternative harvesting methods, such as the ones described below, may help reduce the ecological footprint of harvesting on boreal forest ecosystems by resulting in structure and composition dynamics that are more similar to those in un-managed forest.

#### 1. Longer rotation periods for some stands

Currently, a large portion of the boreal forest under tenure (i.e., assigned to forest companies for potential harvest) is generally managed on an 80-year rotation period. However, the generation of significant CWD on post-clearcut stands does not begin until well into the canopy transition stage of stand development. As a result, continuously managing boreal forest on an 80-year rotation period will significantly reduce the volume of CWD on the managed landscape. This will undoubtedly have detrimental effects on plant and animal diversity.

Instead, it has been suggested that management of some areas of boreal forest should move towards a system of three cohort management (Harvey *et al.*, 2002; Bergeron, 2004), which would use clearcutting (to emulate young forest), partial harvesting (to emulate over-mature forest), and selection cutting (to emulate old-growth forest) to better resemble the historical stand age structure distribution on the managed landscape (Van Wagner, 1978).

#### 2. Varying cut sizes

In order to limit the discontinuity of intact forest in an effort to reduce the negative effects of clearcutting on wildlife populations (Matlack and Litvaitis, 1999; McRae *et al.*, 2001; Harper *et al.*, 2004), management guidelines in many jurisdictions have moved towards clearcuts of intermediate size. However, the historical spatial and temporal dynamics of fire events in the boreal forest is such that fire frequency and fire size are inversely related. Very large fires, which can each consume tens of thousands of hectares of forested area are rare, while small fires, each in the order of only a few hectares, are quite common (Weber and Stocks, 1998). As a result, in order to better emulate the natural fire pattern in boreal forest, management practices should strive towards having a few very large clearcuts and many smaller ones.

This approach would better emulate the natural behaviour of fire on the managed landscape, and has the potential for many other ecological and economical benefits as well. For example, the silvicultural costs associated with replanting or seeding and site preparation may be significantly reduced since operations would not need to be moved as often in a single calendar year.

#### 3. Prescribed burning

In very large clearcuts, prescribed burning could also be a useful tool to reduce silvicultural costs even further and increase the proportion of naturally regenerated area, since only a small proportion of the clearcut would need to burn in order to reduce the amount of harvested area that would have to be treated and planted. Prescribed burning can burn away the duff layer and expose mineral soil creating microsites for natural germination and/or increase the ease and success of artificial regeneration. Furthermore, fuel loads on post-clearcut sites would be substantially reduced following prescribed burning, which should markedly decrease the probability of newly regenerating stands burning again in the future (Johnson, 1992).

#### Multi-cohort

management may better emulate the historical stand age distribution on the managed boreal landscape than current practices, and reduce the impact of forest management on natural CWD dynamics in the process.

Current limits on the size and number of allowable clearcuts need to be reevaluated in order to better emulate the natural pattern of fire in the boreal forest.

Prescribed burning after clearcutting is an underutilized silvicultural tool that should be given greater consideration in forest management planning. Leaving woody residual on site after clearcutting may help reduce the negative effects of forest management on biodiversity and nutrient cycling.

Future climate change will affect landscape-level patterns of stand structure and composition by altering disturbance regimes and plant species distributions.



#### 4. Cut to length or slash re-distribution

The significant reduction in DWD after clearcut harvesting compared to wildfire is an obvious reflection of tree removal. By redistributing roadside debris back onto the site post-harvest, or employing cut-to-length harvesting at the stump, however, some of the negative effects that DWD reduction has on some components of biodiversity and nutrient cycling can be mitigated. However, many species depend specifically on larger-sized DWD, and as a result, provision of large size DWD should remain a priority for forest managers.

#### C. Implications of future climatic change

It is predicted that the earth on average will warm between two and four degrees Celsius (relative to 1980 to 1990 levels) by the end of the twenty-first century, with the greatest warming expected in the boreal forest and other high latitude ecosystems (Intergovernmental Panel on Climate Change, 2007). Future climate change is anticipated to have dramatic effects on forest structure and composition at the landscape-level, most notably, by altering tree species distributions and the frequency of stand-replacing fires. It is predicted that future climate change, involving elevated global temperatures and atmospheric carbon dioxide concentrations may cause a northward migration of some tree species and possibly even whole forested regions (Suffling, 1995; Thompson *et al.*, 1998; He *et al.*, 2002). For example, it has been suggested that the boreal forest may shift into the current range of tundra, and that the northern hardwood forest could shift into the current range of boreal forest.

General circulation models predict that the earth's precipitation patterns will also differ substantially in the future from current trends, with coastal areas generally receiving greater amounts of precipitation, while inland areas will have a tendency to be drier overall (Stocks *et al.*, 1998). Consequently, central North American boreal forests may experience a greater frequency of stand-replacing fires through a reduction in annual precipitation, resulting in a greater proportion of grassland and younger forest on the landscape (Thompson *et al.*, 1998; Overpeck *et al.*, 1990; Amiro *et al.*, 2001). However, greater annual precipitation in more coastal boreal forests may reduce the frequency of stand-replacing fires, resulting in a greater proportion of older forest (Bergeron and Flannigan, 1995; Flannigan *et al.*, 1998; Bergeron *et al.*, 2004). Therefore, changes in fire frequency and species distributions are expected to markedly affect the age distribution of stands on the landscape and the range of many boreal forest plant and animal species under predicted future climate change scenarios.

Since climate change will dramatically alter the structure and composition dynamics of the boreal forest, management guidelines need to be adapted to better respond to predicted ecosystem change. For example, a greater proportion of managed boreal forests could be planted or seeded with tree species from more southern forest regions or genotypes of current tree species that are more adapted to growing in warmer climates, in order to help facilitate predicted plant migration patterns. However, trying to determine which tree species and genotypes will grow best within the current range of boreal forest under future climatic conditions will be a challenge because of the tremendous uncertainty associated with current climate models and the wide range of phenotypic variation that exists within many plant species. Adaptive planning, therefore, will require further research.

## IV. Highlights

- Forest stand dynamics are impacted by stand-initiating disturbances, non-stand-replacing disturbances, predisturbance stand structure and composition, surrounding seed sources, and climatic and edaphic characteristics, and have important implications for the provision of wildlife habitat and maintaining biodiversity.
- Under present management practices, vertical structure and composition change in the North American boreal mixedwood forest over time is characterized by an increase in conifer dominance, replacement of early successional pioneering trees by trees of later successional status that seed in from nearby stands, and a transition from unimodal to bimodal to multimodal age and size structure.
- The death of the pre-fire cohort creates a substantial volume of CWD in the young developing stand. Beyond this initial pulse, however, CWD volume steadily declines until later in stand development when the pioneering cohort begins to succumb to longevity-related mortality. At this stage, CWD volume, initially as snags, and later as DWD, begins to increase. Late in stand development, individual tree replacement dynamics, which are driven by secondary disturbances, maintain a continuous input of CWD into the stand.
- Windthrow and insect outbreaks are also common standreplacing disturbances in the North American boreal forest. However, these disturbances do not produce similar stand dynamics as that following wildfire.
- Clearcut harvesting dramatically reduces the volume of CWD in a young developing stand compared to wildfire. Young post-clearcut stands may have a greater proportion of trees of later successional status, lower tree density, and a more heterogeneous vertical structure than respective fire-origin stands. However, structure and composition between stands of fire- and clearcut-origin may converge later in stand development.
- Maintaining longer rotation periods (for some stands) and varying cut sizes, in conjunction with prescribed burning and the retention of woody residual on site, may be appropriate management options, in certain situations, for better emulating the structure and composition dynamics of fire-origin stands in managed boreal forest.





- Burning after harvest may be a necessary management tool in order to encourage the establishment of vegetation communities similar to those resulting from wildfire.
- Management options that facilitate CWD recruitment in postclearcut stands will result in conditions more similar to those resulting from wildfire.
- Projected climatic change may have significant consequences for forest structure and composition at the landscape-level, resulting in a northward movement of some tree species, and altering the fire frequency and overall forest age structure of the landscape. Appropriate management responses to climatic change could include managing for a greater proportion of tree species from more southern forest regions or genotypes of current species that are more adapted to growing in warmer climates.

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## References

- Amiro, B.D., Stocks, B.J., Alexander, M.E., Flannigan, M.D., and Wotton, B.M.2001. Fire, climate change, carbon and fuel management in the Canadian boreal forest. International Journal of Wildland Fire 10, 405-413.
- Bergeron, Y. 2004. Is regulated even-aged management the right strategy for the Canadian boreal forest? Forestry Chronicle 80, 458-462.
- Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81, 1500-1516.
- Bergeron, Y., and Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio 79, 51-63.
- Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., and Lefort, P. 2004. Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. Ambio 33, 356-360.
- Bergeron, Y., and Flannigan, M.D. 1995. Predicting the effects of climate change on fire frequency in the southeastern Canadian boreal forest. Water, Air and Soil Pollution 82, 437-444.
- Bouchard, M., Kneeshaw, D., and Bergeron, Y. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. Forest Ecology and Management 204, 297-313.
- Brassard, B.W., and Chen, H.Y.H. 2006. Stand structural dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25, 115-137.
- Brassard, B.W., and Chen, H.Y.H. 2008. Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. Ecosystems 11, 1078-1090.
- Brassard, B.W., Chen, H.Y.H., Wang, J.R., and Duinker, P.N. 2008. Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada. Canadian Journal of Forest Research 38, 52-62.
- Brokaw, N.V.L., and Lent, R.A. 1999. Vertical structure. In: Hunter, M.L. (Ed.)., Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, pp. 373-399.
- Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. USDA Forest Service, Washington, DC.
- Canadian Council of Forest Ministers. 2009. Canada's boreal forest [online]. Available from http://www.sfmcanada.org/CMFiles/PublicationLibrary/IFPP\_Bro\_US\_Eng(h res)1KGE-11142008-5172.pdf [cited 3 March 2009].
- Carleton, T.J., and MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: a comparative survey in the central Canadian boreal forest. Ecoscience 1, 141-152.



- Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environmental Reviews 10, 137-166.
- Chen, H.Y.H., Vasiliauskas, S., Kayahara, G.J., and Ilisson, T. 2009. Wildfire promotes broadleaves and species mixture in boreal forest. Forest Ecology and Management 257, 343-350.
- Cumming, S.G., Schmiegelow, F.K.A., and Burton, P.J. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecological Applications 10, 744-759.
- Delong, S.C., and Kessler, W.B. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131, 93-106.
- Ecke, F., Löfgren, O., and Sörlin, D. 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. Journal of Applied Ecology 39, 781-792.
- Ferguson, S.H., and Elkie, P.C. 2003. Snag abundance 20, 30, and 40 years following fire and harvesting in boreal forests. Forestry Chronicle 79, 541-549.
- Flannigan, M.D., Bergeron, Y., Engelmark, O., and Wotton, B.M. 1998. Future wildfire in circumboreal forests in relation to global warming. Journal of Vegetation Science 9, 469-476.
- Frelich, L.E., and Reich, P.B. 2003. Perspectives on development of definitions and values related to old-growth forests. Environmental Reviews 11, S9-S22.
- Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecological Monographs 65, 325-346.
- Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Canadian Journal of Forest Research 27, 139-147.
- Gauthier, S., De Grandpré, L., and Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. Journal of Vegetation Science 11, 781-790.
- Greene, D.F., and Johnson, E.A. 1999. Modelling recruitment of *Populus tremuloides, Pinus banksiana,* and *Picea mariana* following fire in the mixedwood boreal forest. Canadian Journal of Forest Research 29, 462-473.
- Greif, G.E., and Archibold, O.W. 2000. Standing-dead tree component of the boreal forest in central Saskatchewan. Forest Ecology and Management 131, 37-46.
- Harmon, M.E., Krankina, O.N., and Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Canadian Journal of Forest Research 30, 76-84.
- Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S., and De Grandpré, L. 2005. Structural development following fire in black spruce boreal forest. Forest Ecology and Management 206, 293-306.



- Harper, K.A., Lesieur, D., Bergeron, Y., and Drapeau, P. 2004. Forest structure and composition at young fire and cut edges in black spruce boreal forest. Canadian Journal of Forest Research 34, 289-302.
- Hart, S.A., and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25, 381-397.
- Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management 155, 369-385.
- He, H.S., Mladenoff, D.J., and Gustafson, E.J. 2002. Study of landscape change under forest harvesting and climate warming-induced fire disturbance. Forest Ecology and Management 155, 257-270.
- Hély, C., Bergeron, Y., and Flannigan, M.D. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Canadian Journal of Forest Research 30, 674-687.
- Hill, S.B., Mallik, A.U., and Chen, H.Y.H. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Canadian Journal of Forest Research 35, 1942-1951.
- Imbeau, L., Savard, J.-P.L., and Gagnon, R. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. Canadian Journal of Zoology 77, 1850-1860.
- Intergovernmental Panel on Climate Change. 2007. Climate change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change.
- Johnson, E.A. 1992. Fire and vegetation dynamics. Studies from the North American boreal forest. Cambridge University Press, New York.
- Kabzems, R., and Garcia, O. 2004. Structure and dynamics of trembling aspenwhite spruce mixed stands near Fort Nelson, B.C. Canadian Journal of Forest Research 34, 384-395.
- Keenan, R.J., and Kimmins, J.P. 1993. The ecological effects of clear-cutting. Environmental Reviews 1, 121-144.
- Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79, 783-794.
- Kneeshaw, D.D., and Bergeron, Y. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. Ecoscience 6, 214-222.
- Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. Forest Ecology and Management 105, 263-272.
- Lee, P.C., Crites, S., Nietfeld, M., Van Nguyen, H., and Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecological Applications 7, 691-701.
- Linder, P., and Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. Biological Conservation 85, 9-19.





- Mäkinen, H., Hynynen, J., Siitonen, J., and Sieväneni, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16, 1865-1879.
- Martin, J.L., Gower, S.T., Plaut, J., and Holmes, B. 2005. Carbon pools in a boreal mixedwood logging chronosequence. Global Change Biology 11, 1883-1894.
- Matlack, G.R., and Litvaitis, J.A. 1999. Forest edges. In: Hunter, M.L. (Ed.)., Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, pp. 210-233.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., and Woodley, S. 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environmental Reviews 9, 223-260.
- Moses, R.A., and Boutin, S. 2001. The influence of clear-cut logging and residual leave material on small mammal populations in aspen-dominated boreal mixedwoods. Canadian Journal of Forest Research 31, 483-495.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds a review. Biological Conservation 70, 265-276.
- Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, Inc., New York.
- Ontario Ministry of Natural Resources. 2001. Forest management guide for natural disturbance pattern emulation, version 3.1. Queen's Printer for Ontario, Toronto, Ontario.
- Overpeck, J.T., Rind, D., and Goldberg, R. 1990. Climate-induced changes in forest disturbance and vegetation. Nature 343, 51-53.
- Paré, D., and Bergeron, Y. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. Journal of Ecology 83, 1001-1007.
- Payer, D.C., and Harrison, D.J. 2003. Influence of forest structure on habitat use by American marten in an industrial forest. Forest Ecology and Management 179, 145-156.
- Pearce, J., and Venier, L. 2005. Small mammals as bioindicators of sustainable boreal forest management. Forest Ecology and Management 208, 153-175.
- Pedlar, J.H., Pearce, J.L., Venier, L.A., and McKenney, D.W. 2002. Coarse woody debris in relation to disturbance and forest type in boreal Canada. Forest Ecology and Management 158, 189-194.
- Peet, R.K., and Christensen, N.L. 1987. Competition and tree death. Bioscience 37, 586-595.
- Pham, A.T., De Grandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Canadian Journal of Forest Research 34, 353-364.



- Pothier, D., Raulier, F., and Riopel, M. 2004. Ageing and decline of trembling aspen stands in Quebec. Canadian Journal of Forest Research 34, 1251-1258.
- Reich, P.B., Bakken, P., Carlson, D., Frelich, L.E., Friedman, S.K., and Grigal, D.F. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82, 2731-2748.
- Rouvinen, S., Kuuluvainen, T., and Karjalainen, L. 2002. Coarse woody debris in old Pinus sylvestris dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Canadian Journal of Forest Research 32, 2184-2200.
- Schulte, L.S., and Niemi, G.J. 1998. Bird communities of early-successional burned and logged forest. Journal of Wildlife Management 62, 1418-1429.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49, 11-41.
- Siitonen, J., Martikainen, P., Punttila, P., and Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management 128, 211-225.
- Sippola, A.-L., Mönkkönen, M., and Renvall, P. 2005. Polypore diversity in the herb-rich woodland key habitats of Koli National Park in eastern Finland. Biological Conservation 126, 260-269.
- Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M. 1997. The practice of silviculture. Applied forest ecology. John Wiley & Sons, Inc., New York.
- Stocks, B.J., Fosberg, M.A., Lynham, T.J., Mearns, L., Wotton, B.M., Yang, Q., Jin, J.-Z., Lawrence, K., Hartley, G.R., Mason, J.A., and McKenney, D.W. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. Climatic Change 38, 1-13.
- Sturtevant, B.R., Bissonette, J.A., Long, J.N., and Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications 7, 702-712.
- Suffling, R. 1995. Can disturbance determine vegetation distribution during climate warming? A boreal test. Journal of Biogeography 22, 501-508.
- Thompson, I.D., Flannigan, M.D., Wotton, B.M., and Suffling, R. 1998. The effects of climate change on landscape diversity: an example in Ontario forests. Environmental Monitoring and Assessment 49, 213-233.
- Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. Canadian Journal of Forest Research 8, 220-227.
- Weber, M.G., and Stocks, B.J. 1998. Forest fires in the boreal forests of Canada. In: Moreno, J.M. (Ed.)., Large forest fires. Backhuys Publishers, Leiden, pp. 215-233.
- Yatskov, M., Harmon, M.E., and Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Canadian Journal of Forest Research 33, 1211-1226.

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