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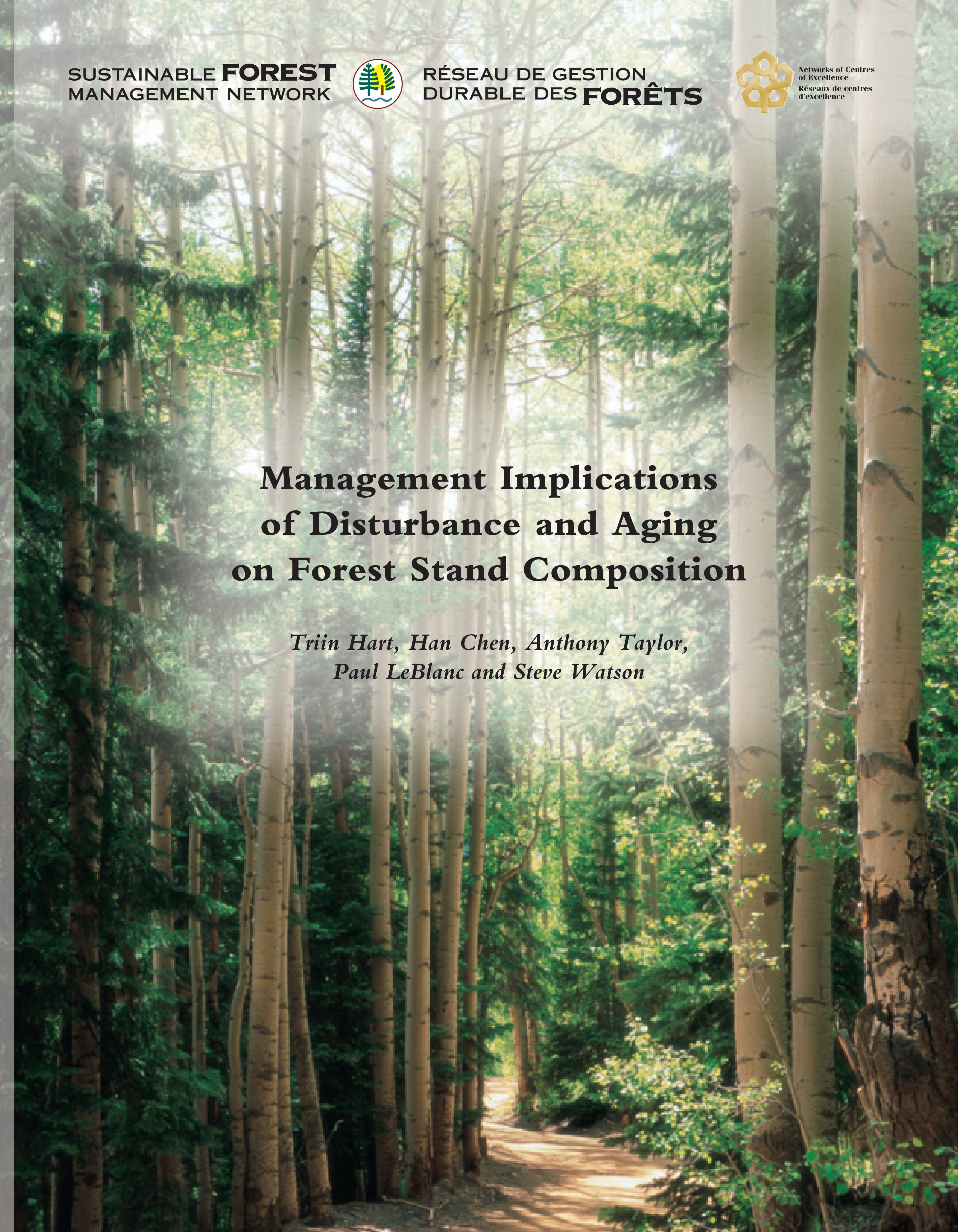

Management Implications of Disturbance and Aging on Forest Stand Composition

Triin Hart, Han Chen, Anthony Taylor,
Paul LeBlanc and Steve Watson

THE SUSTAINABLE FOREST MANAGEMENT NETWORK

Established in 1995, the Sustainable Forest Management Network (SFM Network) is an incorporated, non-profit research organization based at the University of Alberta in Edmonton, Alberta, Canada.

The SFM Network's mission is to:
- Deliver an internationally-recognized, interdisciplinary program that undertakes relevant university-based research;
- Develop networks of researchers, industry, government, Aboriginal, and non-government organization partners;
- Offer innovative approaches to knowledge transfer; and
- Train scientists and advanced practitioners to meet the challenges of natural resource management.

The SFM Network receives about 60% of its $7 million annual budget from the Networks of Centres of Excellence (NCE) Program, a Canadian initiative sponsored by the NSERC, SSHRC, and CIHR research granting councils. Other funding partners include the University of Alberta, governments, forest industries, Aboriginal groups, non-governmental organizations, and the BIOCAP Canada Foundation (through the Sustainable Forest Management Network/BIOCAP Canada Foundation Joint Venture Agreement).

KNOWLEDGE EXCHANGE AND TECHNOLOGY EXTENSION PROGRAM

The SFM Network completed approximately 334 research projects from 1995 – 2008. These projects enhanced the knowledge and understanding of many aspects of the boreal forest ecosystem, provided unique training opportunities for both graduate and undergraduate students and established a network of partnerships across Canada between researchers, government, forest companies and Aboriginal communities.

The SFM Network's research program was designed to contribute to the transition of the forestry sector from sustained yield forestry to sustainable forest management. Two key elements in this transition include:
- Development of strategies and tools to promote ecological, economic and social sustainability, and
- Transfer of knowledge and technology to inform policy makers and affect forest management practices.

In order to accomplish this transfer of knowledge, the research completed by the Network must be provided to the Network Partners in a variety of forms. The KETE Program is developing a series of tools to facilitate knowledge transfer to their Partners. The Partners' needs are highly variable, ranging from differences in institutional arrangements or corporate philosophies to the capacity to interpret and implement highly technical information. An assortment of strategies and tools is required to facilitate the exchange of information across scales and to a variety of audiences.

The KETE documents represent one element of the knowledge transfer process, and attempt to synthesize research results, from research conducted by the Network and elsewhere in Canada, into a SFM systems approach to assist foresters, planners and biologists with the development of alternative approaches to forest management planning and operational practices.

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Knowledge Exchange and Technology Extension Program (KETE)
Sustainable Forest Management Network

Management Implications of Disturbance and Aging on Forest Stand Composition

By

**Triin Hart[1], Han Chen[2], Anthony Taylor[3],
Paul LeBlanc[4] and Steve Watson[5]**

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[1] Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, tilisson@lakeheadu.ca.

[2] Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, hchen1@lakeheadu.ca.

[3] Taylor Lumber Company Limited, 12111 Hwy 224, P.O. 92, Middle Musquodoboit, NS B0N 1X0, Anthony@taylorlumber.ca.

[4] LP Canada Ltd. – Swan Valley Forest Resources Division, 439 Westwood Road, PO Box 998, Swan River, MB R0L 1Z0, Paul.LeBlanc@lpcorp.com.

[5] AbitibiBowater Inc. – Ontario Forest Products, 2001 Neebing Avenue, Thunder Bay, ON P7E 6S3, steve.watson@abibow.com.

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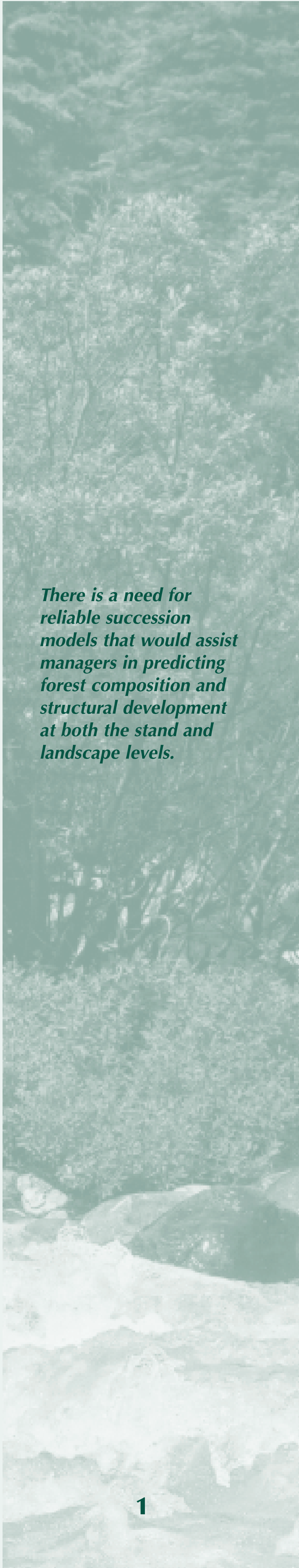
1 Introduction

The concept of sustainable forest management includes finding a balance between society's increasing demands for forest products and benefits, and the conservation of forest health and diversity (Canadian Council of Forest Ministers, 2003). Current management practices in Canadian boreal forests determine potential future forest patterns that are dependent on uncertain interactions among natural disturbances and forest succession. This presents a significant challenge to forest managers who make long-term forest management plans, usually spanning time periods of 150 years or more into the future. To meet sustainable forest management targets, there is a need for reliable succession models that would assist managers in predicting forest composition and structural development at both the stand and landscape levels. Future species composition and structure of forest stands are the key elements affecting future benefits of the forest, including biodiversity, timber supply, productivity, carbon dynamics, ungulate, fur-bearer, bird habitats, recreational opportunities, and non-timber forest products.

Drivers of stand structural and compositional development include regeneration dynamics and processes associated with aging succession and post-disturbance succession. These succession processes are dependent on the interactions of several factors including vegetation type, disturbance regime, local climate conditions, topography and soil type (Mccook, 1994; Chen and Popadiouk, 2002). This synthesis report provides an overview of the factors influencing forest succession and their long-term importance in forest management planning. More specifically, the objectives are to:



There is a need for reliable succession models that would assist managers in predicting forest composition and structural development at both the stand and landscape levels.

A. Present a theoretical model of succession and multiple pathways for boreal forests using boreal mixedwoods as an example,

B. Describe post-disturbance succession after stand-replacing disturbances (fire, logging, insect outbreak and wind throw) in boreal forests of central Canada and other northern forests in North America,

C. Illustrate patterns of forest compositional changes during stand development for boreal forest stand types dominated by jack pine, trembling aspen, white birch, black spruce and white spruce, balsam fir and eastern white cedar, and

D. Discuss application of forest succession models to forest management planning.

2 Conceptual succession pathways of the boreal mixedwood forest

2.1 What are succession pathways?

A **succession pathway** is defined as a temporal change in vegetation composition (trees, shrubs, herbs, and nonvascular plants) over time. It describes the transition of one stage of forest development to another (*e.g.* jack pine dominated stands succeeds to late succession black-spruce-balsam fir dominated stands). Succession pathways are largely driven by succession mechanisms (*e.g.* time, disturbances and species life-history traits), which interact to cause succession.

Various attempts by researchers have been made to describe and predict the rate and direction of succession using succession models (Clements, 1916; Frelich and Reich, 1995; Bergeron, 2000; Mladenoff, 2004). These models combine various ecological factors and specify the relationships between the succession mechanisms and pathways.

Stand dynamics in boreal mixedwoods can be defined as changes in stands' composition and structure during and after disturbances (Oliver and Larson, 1996; Chen and Popadiouk, 2002). Starting from time since stand-replacing disturbance, four phases of development can be distinguished (Figure 1).

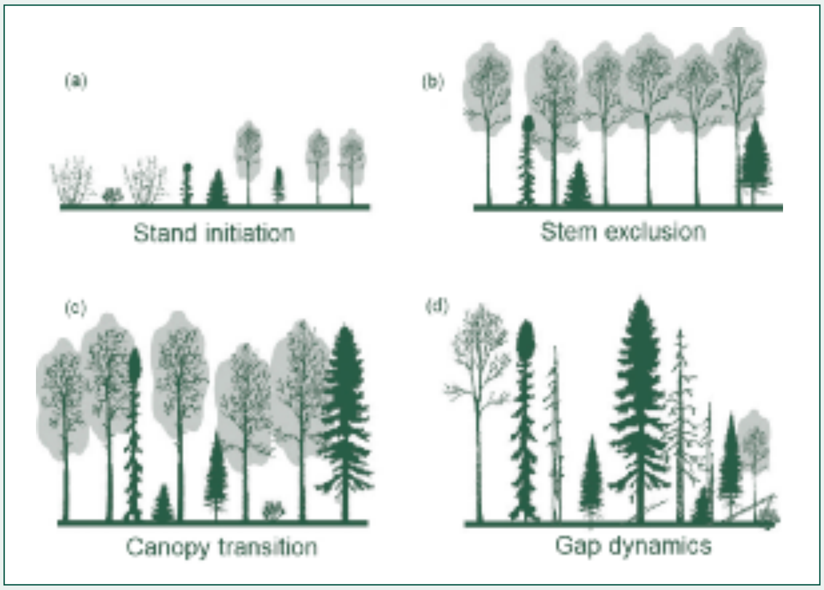
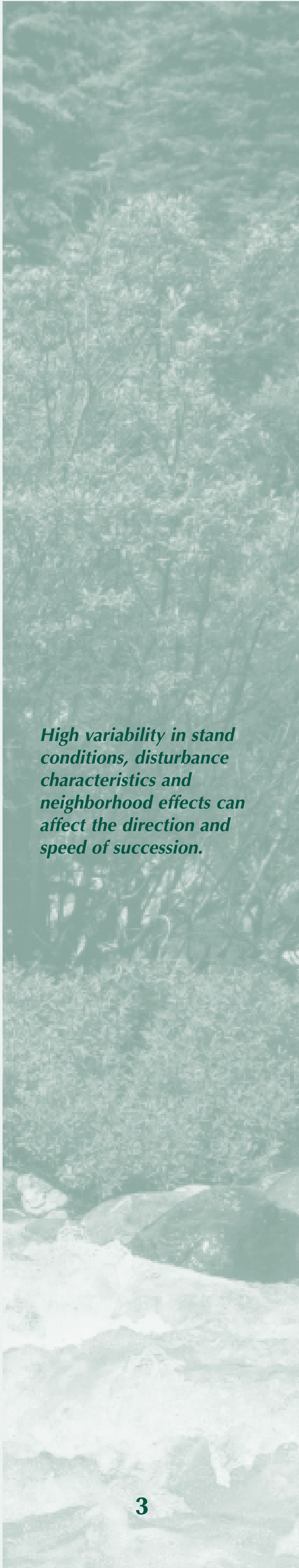


Figure 1. The phases of stand development in boreal mixedwoods (Chen and Popadiouk, 2002).

- **Stand initiation phase –** Stand-replacing disturbances (*e.g.* fire, clearcutting, windthrow) open space for new recruits by killing the overstory. By the end of this stage, a horizontally closed canopy is formed, typically composed of shade-intolerant tree species (*i.e.* aspen, birch, jack pine).
- **Stem exclusion phase –** As trees expand in size, there is intense intra- and inter-specific competition for resources causing self-thinning. At this point, canopy is composed mainly of pioneer species and no new individuals can



enter the canopy. Self-thinning is rapid, but dependent on species composition and density. For example, aspen densities decrease very rapidly, while spruce densities change slowly. Tree mortality is also greater with high initial regeneration densities. The stem exclusion phase ends when shade-tolerant conifers (*e.g.* black spruce, balsam fir) begin to emerge in the upper canopy layer.

- **Canopy transition –** Shade-intolerant canopy dominants (*i.e.* jack pine, aspen, birch) begin to decline. Shade-tolerant trees in the lower canopy layers (*i.e.* black spruce, white spruce, balsam fir) respond to increased light-levels with an accelerated growth rate. This stage lasts until the death of the first cohort pioneer species that established after the initial stand-replacing disturbance.
- **Gap dynamics –** Defined by shifting patterns of small patch disturbances (also referred to as "true old growth" or "steady state"). The senescence of one or more individual trees creates small gaps in the dominant canopy that generally regenerate with shade-tolerant species. Stand composition shifts toward late-succession species (*e.g.* white spruce, balsam fir, and eastern cedar). The canopy is structurally very diverse, often with multiple canopy layers. There is an abundance of dead wood debris.

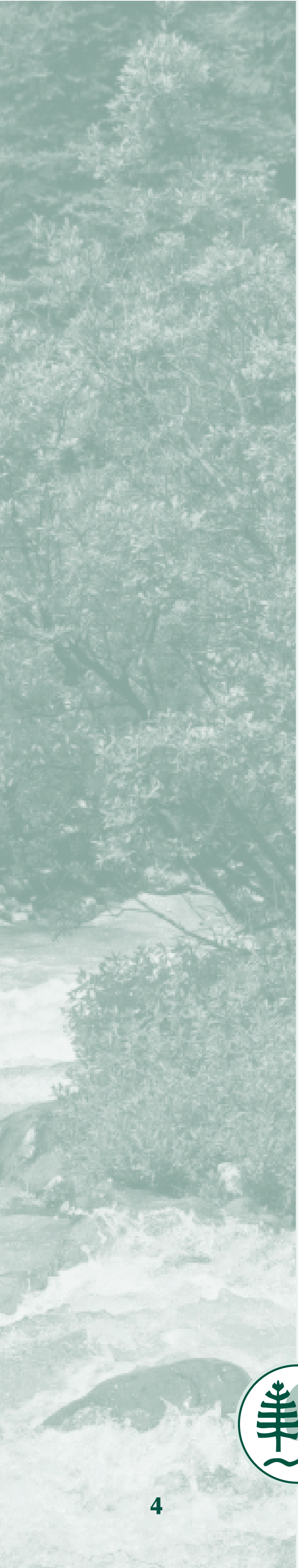
2.2 Multiple pathways

The stand development model of boreal mixedwoods provides a simplified, stage by stage conceptual model of succession development over time. However, high variability in stand conditions (stand age, composition, soil, slope, etc.), disturbance characteristics (type, size, severity), and neighborhood effects (seed sources and inter- and intra-specific interactions such as competition and facilitation) may cause variation in direction and speed of succession development. Chen and Popadiouk (2002) provided various models to illustrate multiple succession pathways that may result under varying conditions, using the boreal mixedwoods as an example (Figures 2 to 6):

High variability in stand conditions, disturbance characteristics and neighborhood effects can affect the direction and speed of succession.

- **Cyclic pathway** – Following fire, shade-intolerant species (*e.g.* aspen, birch, jack pine) invade an area. Shade-tolerant spruce regenerate in the understory and gradually enter the canopy. Shade-intolerant species eventually succumb to age related mortality whereby spruce and balsam fir take over. The community is then sustained by gap creating disturbances (*e.g.* insect outbreaks) until another stand-replacing disturbance converts the stand back to shade-intolerant composition.

Figure 2. Cyclic pathway (modified from Chen and Popadiouk, 2002).



- **Convergent pathway** – Shade-intolerant aspen, birch or jack pine converges over time to shade-tolerant spruce or balsam fir. This is the classic model of Clements (Clements, 1936).

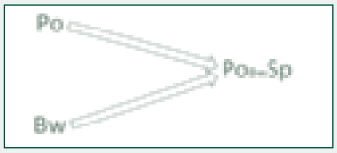


Figure 3. Convergent pathway (modified from Chen and Popadiouk, 2002).

- **Divergent pathway** – Following intermediate disturbance (*e.g.* windthrow, fire, spruce budworm, and forest tent caterpillar) one community diverges into two or more community states. For example, following windthrow, large gaps are created within an aspen stand. Here, old aspen stands may not regenerate well or sprout after stem snap or uprooting. In the case of a sufficient source of birch seeds, birch may become the dominant species after the windthrow. Where there is lack of seed sources of tree species, transitions into temporary shrub field may take place.

Figure 4. Divergent pathway (modified from Chen and Popadiouk, 2002).

- **Parallel pathway** – Each of two or more communities undergoes a disturbance and returns to the same community state shortly after the disturbance. For example, jack pine can regenerate from its aerial seed bank following a crown fire to maintain jack pine dominance. Similarly, aspen and birch can regenerate after fire or clearcutting and maintain their dominance, while mixed species stands of aspen, birch and black spruce may behave the same after fire.

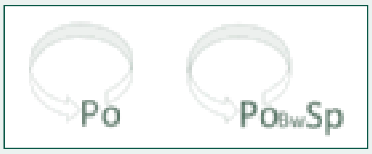


Figure 5. Parallel pathway (modified from Chen and Popadiouk, 2002).

- **Individualistic pathway** – stochastic variables (*e.g.* mast years, disturbances, droughts) lead to multiple pathways at different times at the same locations. There is a continuous change in the stand and no stable end point. For example, after spruce budworm attack in black spruce-balsam fir forest, gap regeneration depends largely on seed source availability. If birch is available in neighboring stands, the gap may likely regenerate as birch dominated. Over time, late-succession species, such as white spruce, black spruce, balsam fir or eastern cedar may replace the birch. If an immediate seed source is not available, the gap will likely regenerate with seeds from surviving spruce. If the spruce budworm attack was very severe (killing both spruce and fir) and a tree species seed source was not available, the stand may become shrub field.

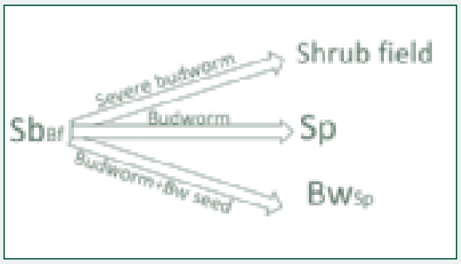


Figure 6. Individualistic pathway (modified from Chen and Popadiouk, 2002).

2.2.1 Case Study: Modeling multiple succession pathways in central Canada

In the prolonged absence of stand-replacing fire, compositionally similar stands undergo multiple succession pathways, depending on time since fire (TSF), soil conditions and intermediate disturbances (Taylor and Chen 2010). The transition starts approximately 50 years after the stand-replacing disturbance. In this case study, multiple pathways were modeled for common stand types of central Canada.

- **Jack pine (PJ) dominated stands –** the succession pathways differed by soil moisture and fertility (Figure 7). Succession was faster on moist and wet fertile soils compared to fresh and dry nutrient poor soils. 100 years after disturbance, more than half of the PJ stands were converted to mixed conifer (MC) or black spruce dominated (SB) stand types on S1, while approximately 70% of the sites sustained pine dominance in S2 sites. This result reflects jack pine's weaker ability to compete on moist fertile sites than on dry sites (Yao *et al.,* 2001). The transition from JP to MC and SB stand types occurs when shade-tolerant understory spruce reaches the main jack pine canopy.

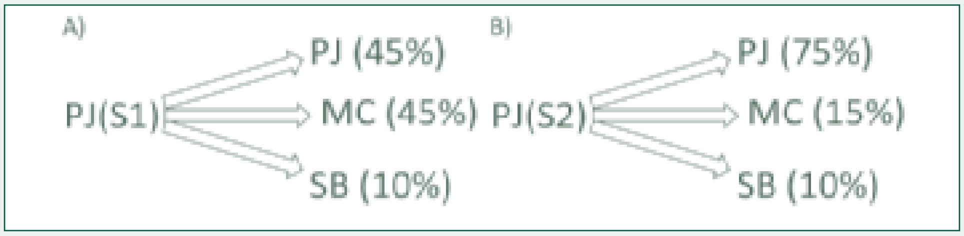


Figure 7. The succession pathways of jack pine dominated stands (PJ) 100 years following disturbance: A) in fine to medium textured soils and moist to wet soil moisture conditions (S1) and B) in medium to coarse textured soils and fresh to dry soil moisture conditions (S2). MC – mixed conifer stands, SB – black spruce dominated stands (modified from Taylor and Chen, 2010).

- **Trembling aspen (PO) and paper birch (BW) dominated stands –** transition of these stand types to late succession species dominated stand types is slower than that for the PJ stand type. After 200 years since disturbance, most of PO and BW stands continued to maintain their dominance through the strong self-replacement ability of these species (Figure 8). However, maintenance of hardwood trees over 200 years may be attributed to the lack of seeding success of late-succession species to establish in the understory.

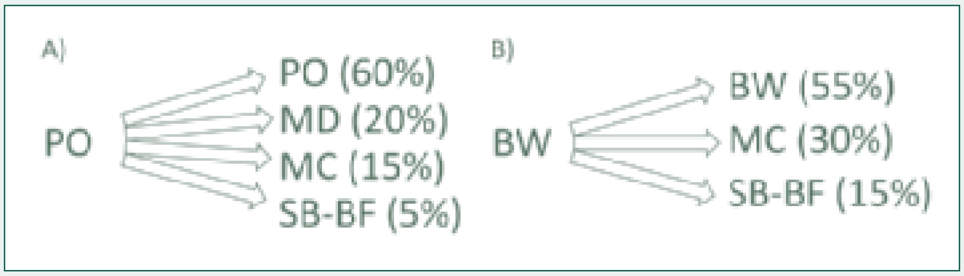
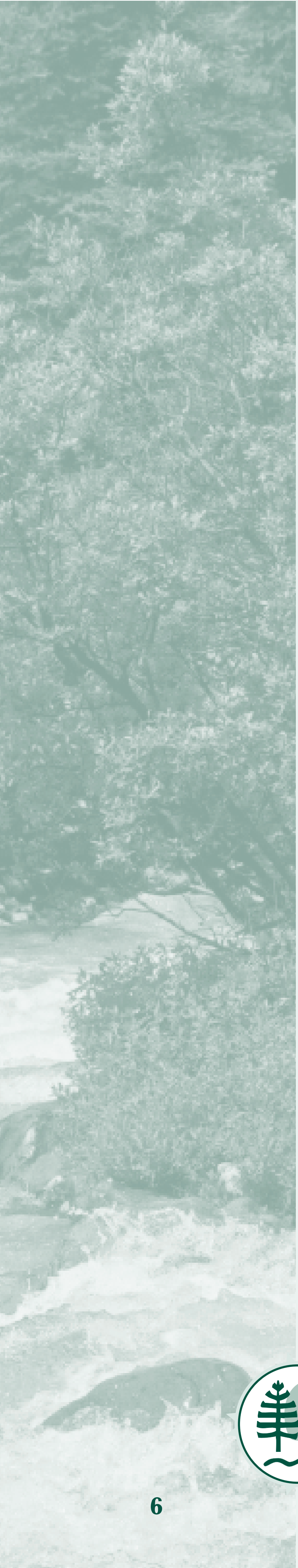


Figure 8. The succession pathways of A) trembling aspen dominated stands (PO) and B) paper birch dominated stands (BW) 200 years following disturbance. MD – mixed deciduous species stands, MC – mixed conifer stands, SB-BF – black spruce and balsam fir dominated stands (modified from Taylor and Chen, 2010).



- **Black spruce (SB) dominated stands –** these are relatively stable stand types where the transition to other species occurs very slowly over time. After a 200 year TSF, black spruce stands in moist to wet sites remained as black spruce stands, except for <10% of the stands changing to eastern white cedar dominated stands (Figure 9). However, on dry to fresh soils black spruce stands largely remained black spruce. Despite eastern white cedar having a broad physiological tolerance to varying moisture levels (Collier and Boyer, 1989), cedar is also a very weak competitor and can only successfully compete on very moist and wet sites where the competition rate is low.

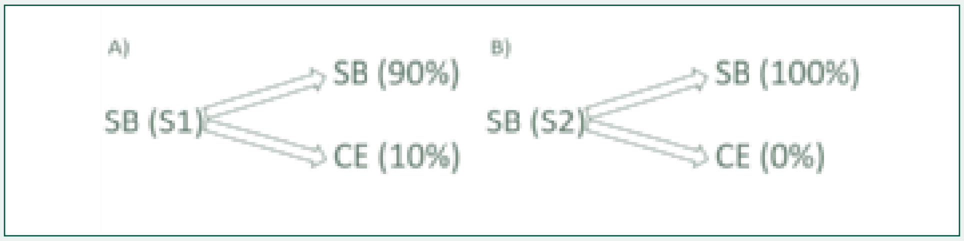


Figure 9. The succession pathways of black spruce dominated stands (SB) 200 years following disturbance A) in fine to medium textured soils and moist to wet soil moisture conditions (S1) and B) in medium to coarse textured soils and fresh to dry soil moisture conditions (S2). CE – eastern white cedar dominated stands (modified from Taylor and Chen, 2010).

- **Balsam fir (BF) dominated stands –** this stand type generally did not experience transition to other stand types until an intermediate disturbance (mainly spruce budworm) took place. The most common transition following an intermediate disturbance event was towards paper birch dominated stand type (Figure 10). However, the degree to which paper birch will establish may vary, depending on the relative abundance of trees present before the disturbance.

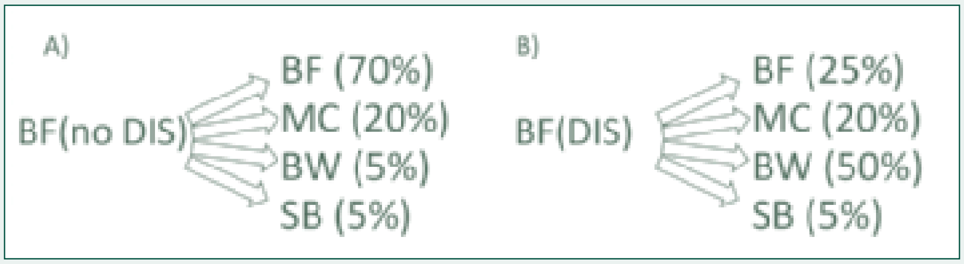


Figure 10. The succession pathways of balsam fir (BF) dominated stands A) without the occurrence of intermediate disturbance (no DIS), and B) with the occurrence of intermediate disturbance (DIS). MC = mixed conifer stands, BW = paper birch dominated stands, SB = black spruce dominated stands (modified from Taylor and Chen, 2010).

Key Messages

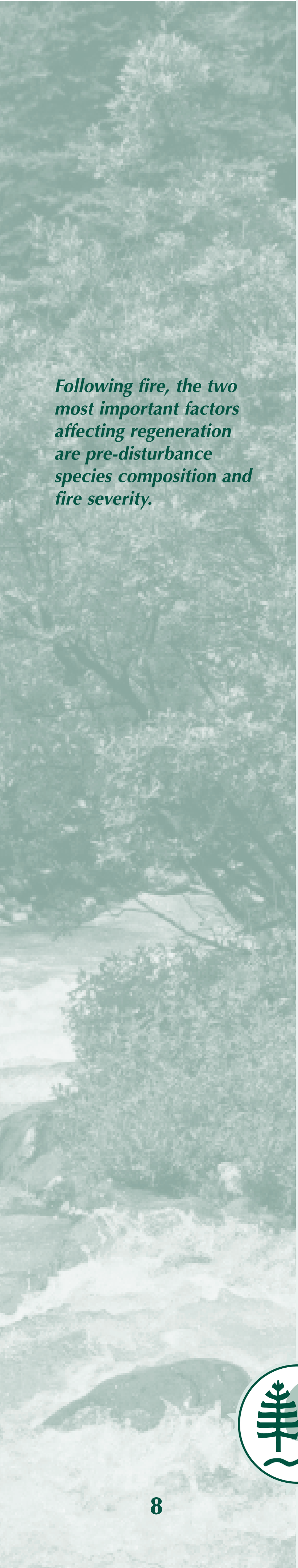
- Succession pathways of stands dominated by shade-intolerant species (*i.e.* trembling aspen, jack pine, paper birch) are most influenced by time since fire. The longer the time since fire, the greater the probability of transitioning to stands dominated by shade-tolerant species (*i.e.* black spruce, white spruce, and balsam fir).
- Succession pathways of stands dominated by shade-tolerant species are less affected by time since fire and are more dependent on soil conditions and disturbances.
- Very dry coarse-textured soils or water-saturated nutrient poor soils favor tree species capable of tolerating limited resources (*e.g.* jack pine on poor, dry soils and black spruce on wet soils).
- Fertile soils permit invasion of competitive species and promote species mixtures during succession.
- Intermediate disturbances affect the direction of succession by reducing overstory competition and promoting recruitment in the understory.
- If boreal stands are undisturbed by stand-replacing agents, they may eventually converge towards stands dominated by shade-tolerant species. This phenomenon is largely due to the ability of shade-tolerant species to progressively recruit and grow in the understory.

3 Post-disturbance succession related to stand-replacing events

3.1 Fire

In the boreal forests of Canada, fire is the most common natural disturbance. Fires vary in size, occurrence frequency, and intensity. Boreal forest fire regimes are generally characterised by high numbers of small fires and few large fires (Stocks *et al.,* 2002). Despite the abundance of small fires, the landscape mosaic is primarily determined by few large fires.

Fire frequency differs across the continent. Generally, fire frequency increases from the east to the west, with the exception of British Columbia and parts of



Alberta where fire suppression is believed to lengthen the fire cycle. On the eastern coast of Canada, the fire cycle is around 200-500 years, even up to 1000 years in some regions (Wein and Moore, 1979). In Ontario, Quebec, Manitoba and Saskatchewan, fire cycles vary from 150 to 250 years and in parts of Alberta, British Columbia and Alaska, the cycle is only 50 to 200 years (Lafontaine-Senici and Chen, unpublished data). The mosaic of stand types in the landscape typically reflects the length of fire cycle. For instance, the shorter the fire cycle, the more prevalent are young and shade-intolerant species dominated stands.

Following fire, the two most important factors affecting regeneration are pre-disturbance species composition and fire severity.

Following stand replacing fire, two key factors influencing post-fire regeneration composition are pre-disturbance species composition and fire severity. For most shade-intolerant boreal tree species, post-fire regeneration densities are positively related to their pre-fire stand basal area (Greene and Johnson, 1999; Greene *et al.,* 2004; Chen *et al.,* 2009; Ilisson and Chen, 2009b), indicating the importance of seed and bud availability to post-fire natural regeneration. In addition, post-fire regeneration tends to vary with fire severity, which can affect microclimate, substrate, competition, and seed and bud availability for natural regeneration (Wang, 2003; Greene *et al.*, 2004; Johnstone and Kasischke, 2005; Greene *et al.*, 2007). Although natural regeneration after harvesting has been less studied, advance regeneration has been shown to be a significant component of post-harvest stands (Greene *et al.,* 2002; Harvey and Brais, 2002).

The direct influences of fire severity affecting post-fire regeneration include effects on seed and bud availability and the indirect influences include preparation of seed beds. Stand-replacing canopy killing fires can be divided broadly as severe ground fires and moderate and high intensity crown fires. Canopy needles are consumed in crown fires but not in severe ground fires.

3.1.1 Severe ground fires

Occurrence: severe ground fires are most common in low or moderate weather conditions (periods without long lasting drought and high temperatures) (Bessie and Johnson, 1995). As ground fuels (duff, organic soil layers, buried decaying logs, roots) have higher bulk density compared to other fuel types (canopy branches, living understory plants and shrubs, downed logs, needles and leaves) the rate of spread of fire is slow causing high heat. Usually, severe ground fires result in a totally consumed organic layer, death of canopy trees and understory vegetation, and exposed mineral soil.

Regeneration: Severe ground fires consume most of the organic layer creating favorable seed beds for boreal forest tree species. Johnstone and Chapin (2006) found that seed establishment and subsequent growth of trembling aspen, lodgepole pine, black spruce and white spruce was highest on burned soils with an organic layer depth of 2.5 cm or less. There was rapid decline in establishment on organic layers thicker than 2.5 cm. Similar results were obtained by Turner *et al.* (1997) regarding lodgepole pine regeneration establishment after fire. High severity ground fires create heat that allows seed release from serotinous cones (*e.g.* jack pine). At the same time, suitable seed beds that are free of competing vegetation and have exposed mineral soil are created, securing abundant regeneration.

Fire positively affects regeneration by creating favorable seedbeds and promoting vegetative reproduction (suckering).

In addition to the type of fire (*i.e.* surface fire versus crown fire), the depth of burnt duff layer affects the regeneration of suckering species such as trembling aspen. Generally, stand-replacing fires advance trembling aspen sucker initiation (Fraser *et al.*, 2003; Fraser *et al.*, 2004; Chen *et al.*, 2009). Although shallow regenerating roots are often burnt, deep roots that are insulated by mineral soil are still capable of sprouting vigorously. Wang (2003) reported a decreased ability to sprout after severe fire but suggested that it was due to the relatively shallow placement of regenerating roots in the soils on the boreal shield.

Paper birch is well adapted to ground fires, since it regenerates both vegetatively and by seed. However, vegetative reproduction is abundant only if the age of the parent trees is in the 40 to 60 year age range. After age 60 years, birch's ability to sprout decreases sharply (Perala and Alm, 1990). Seeds of paper birch are very light weight and can spread over a large area. The seed bed conditions created by high severity fire enhance seed germination and growth.

3.1.2 Moderate and high intensity crown fires

Weather conditions and proportion of conifers in the stand are the two most important factors that determine both the probability of ignition and the burn intensity of crown fires.

Occurrence: Weather conditions and proportion of conifers in the stand are the two most important factors that determine both the probability of ignition of crown fuels from fires spreading on the surface and the burn intensity of crown fires. Extreme weather conditions (long dry periods combined with high temperatures and high winds) usually result in high intensity fires that are independent of the amount and type of fuels (*e.g.* crown fires in pure aspen stands). The fire intensity of intense crown fires is 10-100 times higher compared to moderate crown fires due to increased fuel consumption and faster spread rates (Bessie and Johnson, 1995). With normal weather conditions, fuel type and amount of fuel become more relevant (Bessie and Johnson, 1995; Johnson *et al.*, 2001).

Stands with a high proportion of conifers regularly experience crown fires, due to the morphological properties of the conifer tree species (Wang, 2002). Characteristics of conifer stands that predispose them to crown fires include:

- low crown height;
- dead lower branches;
- small needles on small diameter branches;
- vertical distribution of needle-bearing branches; and
- low moisture content of needles compared with deciduous leaves (Johnson *et al.*, 2001).

The development of sufficient fuels to carry a crown fire occurs in very young conifer stands.

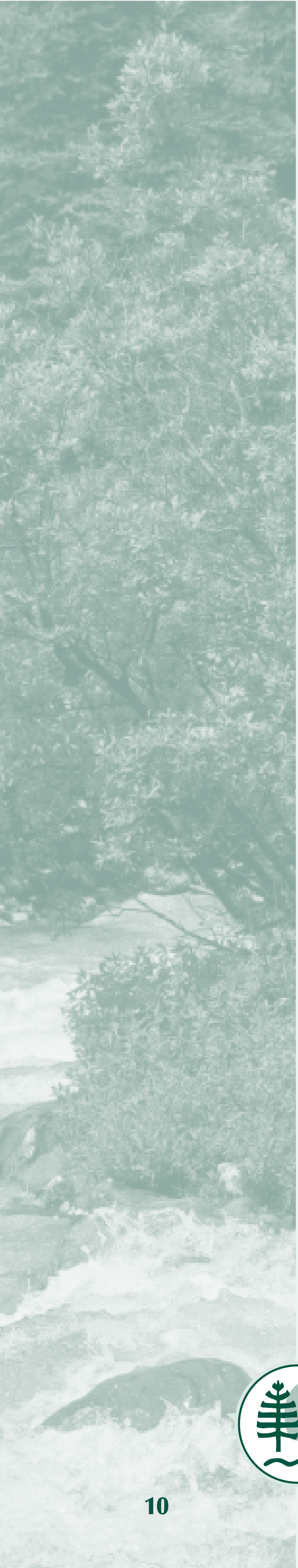


Table 1. Summary of stand-replacing fire effects on post-disturbance succession.

Characteristic	Severe ground fires	Moderate crown fires	Intense crown fires
Occurrence	• Common in moist or moderate weather conditions. • Fire moves slowly within the ground fuels (organic soils, roots, buried rotten logs, etc.) and along the surface, killing overstory trees, burning entire organic layer and understory vegetation, exposing mineral soil.	• Most common with moderate weather conditions in conifer stands with lower crown base height.	• Most common with extreme weather conditions (droughts) when fuel moisture content is very low. • Almost every stand type (including young stands) experiences intense crown fires with extreme weather conditions independently the amount and type of fuels.
Regeneration	• Regeneration of serotinous species abundant due to exposed mineral soil and lack of competing vegetation. • Trembling aspen sucker initiation vigorous from deeper roots. • Paper birch regenerates by both stump suckers and seeds.	• Regeneration of serotinous species abundant due to exposed mineral soil and lack of competing vegetation. • For other species moderate crown fire has similar effect to severe ground fire.	• Regeneration of serotinous species adequate, but less than severe ground fire or moderate crown fire due to decreased seed viability in high intensity fires. • For other species intense crown fire has similar effect to severe ground fire.

Regeneration: The abundance of regeneration from serotinous and semi-serotinous cones depends on the intensity of crown fires. Intense crown fires that occur in drought periods decrease the abundance of regeneration compared to moderate crown fires (Turner *et al.*, 1997; Archambault *et al.*, 1998). The proposed cause of reduced regeneration is that intense crown fires cause cone ignition which decreases seed viability. It is possible that during dry seasons an intense fire may result in total regeneration failure of semi-serotinous and serotinous species. However, the literature on this topic is very limited. For other species regeneration dynamics, crown fires have a similar effect as high severity surface fires.

3.2 Wind

The definition of **stand-replacing windthrow** is a continuous area of five hectares or more in size, where the surviving canopy cover does not exceed 25% of the pre-disturbance cover (Bouchard *et al.,* 2009). Windthrow events less than five hectares in size tend to result in regeneration processes similar to intermediate disturbance dynamics.

Extensive wind disturbances can change the direction and/or speed of succession.

Occurrence: Wind disturbance has been largely overlooked in boreal ecosystems until recently, because it is less frequent than fire and insect outbreaks. Bouchard *et al*. (2009) reported that the disturbance cycle for stand-replacing windthrow is approximately 3900 years (for 1971-2000 period) in the province of Quebec. However, the rarity of extensive wind disturbances does not diminish their potential ecological importance on composition development. In boreal forests, most species are adapted to fire disturbance, therefore, the response of these species to wind disturbance may potentially change the direction and/or speed of succession. In addition, the ecological importance of severe wind storms may increase in the future, due to global climate change.

The complexity of windthrow is related to the highly varying intensity of the disturbance itself and its interaction with physiography (Rich *et al*., 2007). The most distinct characteristic is the influence on soil dynamics. Windthrow exposes mineral soil, mixes it with organic layers, and creates organic soil mounds. The resulting diverse microtopography increases tree species diversity by the establishment of various types of seed beds (Ulanova, 2000). In addition to stand-replacing fire and harvesting, wind disturbance creates abundant light availability, resulting in the release of advanced regeneration and/or establishment and growth of both shade-intolerant and shade-tolerant species.

Regeneration: The regeneration pattern following stand-replacing wind disturbance depends on pre-disturbance stand composition and the intensity of wind. The main factors affecting regeneration are:

1. **How many and what species are left standing alive.** These surviving trees act as seed trees. With increasing diameter, the risk of getting uprooted or broken stems increases (Ilisson *et al.,* 2005; Rich *et al.,* 2007). Among the common boreal tree species, paper birch is the most wind resistant (Rich *et al.,* 2007). In addition, birch is also capable of fast colonization of mineral soil patches, increasing its importance for succession development.

2. **Type and proportion of wind damage** (uprooting or stem breakage). Creation of pits and exposing mineral soil supports seed establishment and germination, while stem breakage leaves ground mostly undisturbed and supports advanced regeneration (Ulanova, 2000). In addition, stem breakage of trembling aspen and paper birch promotes suckering or sprouting.

Advanced regeneration: The rate of advanced regeneration to survive is high following wind disturbance. Shading by fallen trees in the wind disturbed area helps to prevent light shock after loss of overstory. Several studies have reported accelerated succession following wind disturbances due to the survival of a high proportion of late-succession advanced regeneration (Peterson and Pickett, 1995; Ilisson and Chen, 2009a).

Seeds: The importance of seed established regeneration after windthrow is high. Catastrophic wind events usually leave smaller trees standing (Rich *et al.,* 2007), acting as a seed source. At the same time, exposed mineral soil pits are formed as a result of uprooting, which provide excellent seed beds. Although light is less available in windthrow areas compared with fire or harvesting because of the shadowing effect of fallen trees and uprooted root plates, density of seedlings in pits has been found to be high for both deciduous and conifer species (Ulanova, 2000; Vodde *et al.*, 2009).

Vegetative regeneration: Stem-broken hardwoods are prone to suckering or sprouting. However, no studies have examined the rate of vegetative regeneration of trembling aspen or paper birch after windthrow. It may be hypothesized that the rate is similar to that after fire or harvesting, since all of these disturbances kill the parent trees and remove apical dominance.

3.3 Spruce budworm (SBW) outbreak

Occurrence: Spruce budworm *(SBW) (Choristoneura fumiferana* (Clem.)) is a native lepidopteron that exhibits long-term population fluctuations causing epidemic outbreaks at approximately 40-year intervals (Boulanger and Arseneault, 2004). The rate of mortality within a stand during an epidemic outbreak is related to the species composition and stand age. The most susceptible tree species is balsam fir, followed by white spruce and black spruce (Nealis *et al.*, 2004). SBW disturbance is more severe among mature trees compared to immature trees, leaving advanced regeneration trees in the understory often untouched (Nealis *et al.*, 2004). SBW is a stand-replacing disturbance agent only in pure host species stands, since the hardwood component survives in mixedwood stands.

Succession patterns following SBW attack are directly related to the presence and abundance of advanced regeneration.

Regeneration: Since stand-replacing SBW outbreaks take place in stand types that usually have a well established understory tree cohort, the succession patterns are directly related to the abundance of advanced regeneration. Following the death of the overstory, the advanced regeneration trees are released to grow rapidly, giving way to a new cohort of understory species, primarily balsam fir if present, as well as white spruce and black spruce. As a result, a similar species composition to that of pre-SBW will be maintained. However, when advanced regeneration is sparse or advanced regeneration is also affected by SBW, the subsequent regeneration depends on seed and bud availability. Both the invasion of pioneer tree species (*e.g.* paper birch and trembling aspen) and shrubs (*e.g.* raspberry, hazel, mountain maple) may take place, inhibiting the establishment of coniferous species and changing the stand type (Batzer and Popp, 1985).

3.4 Harvesting and silviculture

Forest **harvesting** is a common disturbance in the boreal forest of approximately 900,000 ha per year in Canada (Canadian Council of Forest Ministers (CCFM), 2005). Harvesting involves the removal of dominant vegetation and results in varying degrees of forest floor disturbance that is dependant on the harvest method utilized. The effect of harvesting on succession depends on the disturbance intensity, season of harvest, harvest method, life traits of tree species, and site conditions. Therefore, when deciding which harvest method to use, these key factors must be considered.

Sustainable forest management emphasizes the importance of harvest activities that more closely resemble natural patterns (Bergeron *et al*. 1999). Allowing natural regeneration following harvest is an ecologically valuable and economically feasible alternative compared to conventional artificial regeneration (planting). The establishment of natural regeneration following common harvest methods is described below.

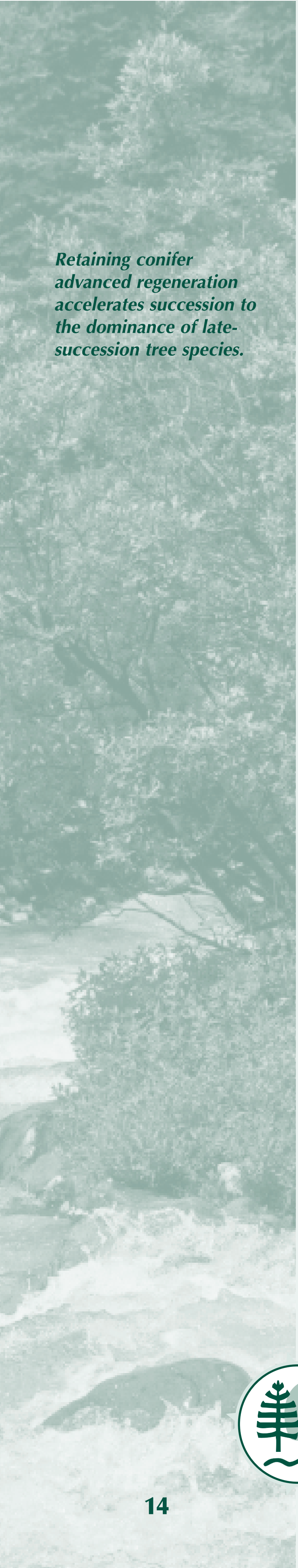
The effect of harvest on succession depends on the disturbance intensity, season of harvest, harvest method, life traits of tree species, and site conditions.

3.4.1 Harvest methods

Harvest method can have an effect on post-harvest stand composition, and therefore affect the succession pathway. **Full tree harvests** cut the trees and drag the limbs, tops and stems to roadside, while **cut to length harvests** and tree length harvests de-limb and top the trees in the cutover, leaving the slash at the stump. Harvest methods influence regeneration dynamics in two ways. First, there is less site disturbance with cut to length and tree length harvests because large loads are not dragged across forest floor. Secondly, in cut to length and tree length harvests the slash is spread across the harvest area reducing mineral soil exposure from machine traffic. Full tree harvests create large piles of slash at roadside and have greater surface soil effects due to machine traffic. As a result, both light and temperature levels are higher, but moisture content is lower with full tree harvests, which influence germination and growth conditions (McInnis and Roberts, 1994). The selection of harvest method should be based on the pre-harvest species composition, and whether or not advanced regeneration will be retained.

The choice of harvest method (full tree, tree length, or cut to length) should depend on the pre-harvest species composition, and whether or not there is protection of advanced regeneration.

Advanced regeneration: Waters *et al.* (2004) found that advanced white spruce, black spruce and balsam fir regeneration growing in the understory suffered less mortality from cut to length harvest operations compared to full tree harvests. McInnis and Roberts (1994) found an opposite trend, but they attributed it to differences in skidding methods and equipment utilized. Advanced regeneration may encounter additional mortality post-harvest due to the changed growing conditions (sudden exposure to light and increased temperatures). In comparison with full tree harvesting, cut to length method leaves a cover of slash on the



ground and prevents exposed trees from light shock and drought due to creation of shading effect and protection of soils from heavy evaporation (McInnis and Roberts, 1994; Waters *et al.,* 2004).

Retaining conifer advanced regeneration accelerates succession to the dominance of late-succession tree species.

If harvesting is done with no attempt to protect advanced regeneration, the estimated survival of the existing conifer understory would be only 10 -30% of stems, depending on harvesting method and the type of machinery used (Harvey and Bergeron, 1989; McInnis and Roberts, 1994). Therefore, in harvest areas, where no attempt was made to protect the understory, initial advanced regeneration likely plays a lesser role in post-disturbance stand composition. However, the importance of these surviving trees may increase over the growing years. Both black spruce and balsam fir are able to disperse seeds and germinate under a closed canopy, which may lead to the establishment of a thick conifer understory layer, accelerating succession towards production targets for conifer species.

Vegetative regeneration: There are few studies comparing the influence of harvest methods on vegetative reproduction success (Murray and Kenkel, 2001; McIsaac *et al,*. 2006). It is likely that vegetative reproduction of trembling aspen is promoted by all harvest methods. Removing the parent tree's stem eliminates apical dominance, increasing the ratio of cytokines (produced by roots) to auxins (produced by shoots), resulting in increased production of root suckers (Farmer, 1962; Eliasson, 1971; Steneker, 1974). Regeneration of paper birch from buds is relatively vigorous after harvest (sprouting from 30-90% of stumps and snags) (Perala and Alm 1990), but is restricted to the location of stumps or snags of parent trees.

Seeds: Waters *et al.* (2004) found that lower slash levels and increased mineral soil seed bed exposure and soil surface temperature facilitated natural jack pine regeneration in full tree harvesting cutovers. However, these authors recommend soil scarification and additional seeding or cone scattering to ensure full stocking. The establishment of other pioneer species has been higher following full tree harvest than cut to length harvest (McInnis and Roberts, 1994). With presence of a nearby seed source, conifer regeneration from seeds has been found to be successful after both harvest methods (Waters *et al.*, 2004).

3.4.2 Season of harvest

Season of harvest influences the development of regenerating species primarily through the degree of soil disturbance caused by harvest equipment (*e.g.* mineral soil exposure, soil compaction), destruction of advance regeneration, and the effects on the suckering ability of trembling aspen. Frozen soils and snow cover during winter harvest decrease mineral soil exposure and the risk of soil compaction (Berger *et al.* 2004) that often have inhibiting effects on the establishment of regeneration species and growth (Lockaby and Vidrine, 1984). Similarly, the survival of advanced regeneration is higher under protective snow cover.

Trembling aspen sucker height growth has been found to be greater after winter harvest compared to spring or summer harvesting (Mulak *et al.*, 2006). This is due to a higher amount of carbohydrate reserves in the root system during winter as a result of a longer period of photosynthesis since the last leaf flush. However, Bates *et al*. (1993) and Mundell *et al*. (2008) did not find any effects of harvesting season on growth or density of aspen suckers caused by fluctuations in carbohydrate reserves. Rather, they found that regeneration establishment and growth were influenced by the degree of soil disturbance.

3.4.3 Understory Protection

Understory protection retains advanced regeneration on protected strips, but can cause greater site disturbance on harvest trails. Regeneration success tends to differ with soil type and shrub competition.

Understory protection, or Careful Logging Around Advance Growth (CLAAG) is a silvicultural approach that conserves advanced conifer regeneration during harvest as a regeneration strategy. It is an alternative to planting conifer seedlings to achieve desirable regeneration after harvest. Advanced growth is retained by limiting machine traffic to designated trails, which should not exceed 25% of the cutover area. The trails are placed parallel to each other with the distance between two trails about twice the operable reach of a feller-buncher's boom or a skidder's boom or cables (Harvey and Brais, 2002; Lieffers and Grover, 2004). Understory protection typically retains advanced regeneration on the areas between trails. However, the trails experience more ground disturbance compared to conventional harvests because of repeated machine traffic.

Succession trajectories following understory protection are dependent on soil texture (Harvey and Brais, 2002) and should be considered in management decisions. For example, research results indicate that for:

- **Fine to medium textured soils** – survival of advanced regeneration was abundant on the strips between skid trails. The densities of black spruce and balsam fir were more than 20,000 trees per hectare each. The vegetation on the trail was mostly dominated by colonizing species, mainly larch, raspberry and graminoids. Conifer stocking seven years after harvest was between 69–74%.
- **Coarse textured soils** – understory protection retained advanced regeneration on the unharvested strips. However, increased mortality and low regeneration establishment rate reduced conifer stocking to 31-51%. The decline was likely due to competition with ericaceous species. Although, the cover of ericaceous shrubs (sheep-laurel (Kalmia angustifolia L.), Labrador-tea (Ledum groenlandicum Oed.), and blueberries (Vaccinium spp.)) decreased initially on the skid trails, ericaceous shrubs increased significantly in the following years.

Harvey and Brais (2002) noted several potential challenges when implementing understory protection. First, growth and yield modeling may be difficult due to the high variability of tree sizes created by dense advanced regeneration between the trails and light-intolerant species composition on the trails. Secondly, the diverse vertical structure of advanced regeneration trees makes it hard to implement pre-commercial thinning. Lastly, if a conifer dominated stand is required, expensive spot planting may be needed to supplement the advanced regeneration.

3.4.4 Single tree and patch retention

Retention of single and patches of trees within a cutover is a common variable retention silvicultural system (Lindenmayer and Franklin, 2002). In addition to the benefits of increased biodiversity, single tree and patch retention provide a well-distributed seed source, and therefore, increases seed availability within the harvest area. This is beneficial to the establishment and growth of natural regeneration.

The main factors that must be considered for successful tree regeneration with the seed tree method are:

i) seed crop year;

ii) seed dispersal radius of specific species;

iii) presence or creation of suitable seed beds; and

iv) competing vegetation.

The seed tree silviculture system has been widely used in European boreal and hemi-boreal forests with two common conifers Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), as well as broadleaves such as silver birch (*Betula pendula* Roth.) and European aspen (*Populus tremula* L.). An additional benefit of seed trees is the increase in biodiversity by increasing stand's structural diversity and providing wildlife habitat before and after tree death (Rosenvald and Lõhmus, 2008), especially if the seed trees are not harvested following regeneration establishment.

Suitable tree species: In the Canadian boreal forest, conifers that regenerate mostly by seed (black spruce, white spruce, balsam fir, white pine and red pine) with an exception of serotinous species such as jack pine could be used as seed trees.

Single tree vs. patch tree retention: Beguin *et al.* (2009) found no significant influence of patch retention size on the regeneration density of balsam fir and black spruce. However, patches of trees are more wind resistant than single trees, and are more likely to secure available seed sources during the first several years after harvest.

Regeneration success using single tree or patch retention is influenced by the seed crop year, seed dispersal radius, suitable seed beds, and competing vegetation.

Distance between single trees or patches: The desirable distance between seed trees depends on seed dispersal ability of each species. The effective seed dispersal radius is about 25-60 meters for balsam fir, and up to 80-90 m for white spruce, black spruce, and white pine (Burns and Honkala, 1990). Prevost (1997) recommended that the distance between the edges of seed tree groups should not exceed 100 meters for balsam fir, and a somewhat longer distance for other boreal tree species.

Seed bed type and preparation: Exposed mineral soil is the preferred seed bed type for most conifers, except black spruce which can also germinate on moist organic soil. Therefore, soil scarification which exposes mineral soil can promote regeneration of most conifers. Exposed mineral soil and high light availability, however, creates more favorable conditions for pioneer tree species than late-succession conifers. For example, depending on the availability of the seed source, paper birch seed establishes more successfully on scarified spots than conifer seed. Birch occupies the microsite faster, and provides serious competition. This is especially problematic in cut stands where paper birch is left standing as commercially undesirable trees. Prevost (1997) found that paper birch seedling density was positively correlated to scarification intensity and recommended only light scarification. It is likely that with the presence of a seed source of pioneer tree species, future stand type will be mixed or pioneer dominated.

Soil scarification also destroys advanced regeneration (Prevost, 1997; Chen and Wang, 2006; Beguin *et al.,* 2009). Prevost (1997) and Chen and Wang (2006) found that seeding soil scarification spots only compensated for the number of destroyed advanced regeneration trees but did not increase the density compared to pre-scarification density. Therefore, it is recommended to retain advanced regeneration without scarification when advanced regeneration density can meet the management objective.

Timing of harvest: Seed tree harvesting should be done during or a year after a heavy seed crop. If seed fall does not happen within first few years following harvesting, the seed beds will be occupied by other species. However, making predictions without a field investigation of seed crops may be difficult because of the temporal variability of seed crop occurrences for most boreal tree species. The heavy seed crop years of occurrence for conifer species are: every 2-4 years for balsam fir, and 2-6 years for black spruce and white spruce (Burns and Honkala, 1990).

3.5 Natural regeneration after fire and harvest: a comparison

Fire and harvesting are two distinctly different processes. Fire chemically kills trees, whereas harvesting physically removes living trees (McRae *et al*., 2001), resulting in different regeneration substrates, coarse woody debris structures, and understory vegetation communities (Brassard and Chen, 2008; Hart and Chen, 2008). Specifically, the differences between fire and harvest that potentially influence regeneration are:

- **Seed bed quality** – fire creates suitable seedbeds in the form of thin humus or exposed mineral soil free from competing vegetation. Harvesting retains the humus layer over mineral soil, retains competing vegetation, and has few exposed mineral soil microsites (Nguyen-Xuan *et al*., 2000);

- **Fire induced heat** – the heat from fire allows seed dispersal from serotinous cones;

- **Damage to advance regeneration** – typical boreal forest fire destroys advanced regeneration completely, while the survival after conventional full tree harvesting is at least 10-30% (Harvey and Bergeron, 1989; McInnis and Roberts, 1994), and potentially much higher if steps are taken to protect the advanced regeneration.

Table 2. Summary table of harvest methods and silvicultural systems to promote natural regeneration.

Harvest method	Recommended stand type	Recommended actions	Pro's	Con's
Full tree harvest	In aspen and pine dominated stands	In jack pine dominated stands additional scarification (and cone distributing) would increase seedling abundance	Resembles severe surface fire and crown fire Helps to cut the regeneration costs	Destroys advanced regeneration
Cut to length and tree length harvest	Aspen or birch dominated with advanced regeneration.		Cutting residuals help to prevent light stress among advanced regeneration trees Seed establishment of pioneers is inhibited	Higher bulk density on harvester trails inhibits seedling growth
Understory protection	In stand types with abundant advanced regeneration Spot planting on the harvesting trails	Herbicide application if aspen, shrubs or birch previously present	Resembles wind disturbance and SBW (partial soil damage, partially sustain advanced regeneration, residuals provide shade)	Fragmented structure and composition - uneven aged shade-tolerant composition between harvester trails and high intolerant composition on the trails Spot planting may be expensive
Single tree or patch retention	Conifer dominated stand types (except jack pine)	Soil scarification Herbicide application if aspen, birch or tall shrubs previously present	Resembles fire with residual patches Increases structural diversity, may decrease regeneration cost	Success dependent on the coordination with mast years Scarification needed, but may lead to the invasion of species with light weight seeds Usually, the outcome is hardwood mixed or dominated Leaving economically valuable trees uncut

- **Soil dynamics** – even though the losses of nitrogen are comparable after both disturbances, harvesting, unlike fire, can remove large amounts of phosphorus, potassium, calcium, and magnesium contained in the tree biomass (McRae *et al.,* 2001). Fire results in increased soil pH and nutrient retention because of charcoal addition (Zackrisson *et al.,* 1996). Vegetative reproduction can be negatively affected by harvesting due to soil compaction (Fraser *et al.,* 2004).
- **Basal area** – Pre-disturbance species-specific basal area is an important factor that influences regeneration density. Post-disturbance species-specific seed production and vegetative reproduction have been reported to be proportional to their pre-disturbance stand basal area (Lavoie and Sirois, 1998; Greene and Johnson, 1999; Wang, 2003; Greene *et al.,* 2004; Johnstone *et al.*, 2004; Johnstone and Chapin, 2006; Chen *et al.,* 2008).

Case Study from Northwestern Ontario

Ilisson and Chen (2009b) and Ilisson and Chen (unpublished data) compared the development of regeneration density and height growth of six boreal tree species after fire and conventional full tree harvesting 5-15 years after disturbance in north-western Ontario. In this study, the tree species examined were: jack pine, trembling aspen, paper birch, black spruce, white spruce and balsam fir.

Post-disturbance regeneration density was positively correlated to the pre-disturbance basal area of trembling aspen, jack pine, paper birch and black spruce (Figure 11). This correlation is useful for regeneration modeling. The influence of disturbance type on regeneration dynamics of each species follows:

Jack pine and trembling aspen – Disturbance type (*i.e.* fire versus harvesting) had no influence on regeneration density or on height growth. It is likely that during logging operations cone drop from slash occurred, and high ground temperatures opened the cones, distributing seed onto microsites that resulted from mechanical harvesting. However, it should be noted that the study areas had sandy and sandy loam soil types, where competition from other vegetation was low. In more fertile soil types, soil scarification may be needed to reduce vegetation competition. Aspen regenerated vigorously after both disturbances, having densities up to 6,000 stems per hectare and developed rapid height growth (Figures 11 and 12). Aspen suckering was promoted equally by both fire and harvesting. **In pine and aspen dominated stand types or in the mixtures of these two species, conventional harvesting is a justified harvest method.**

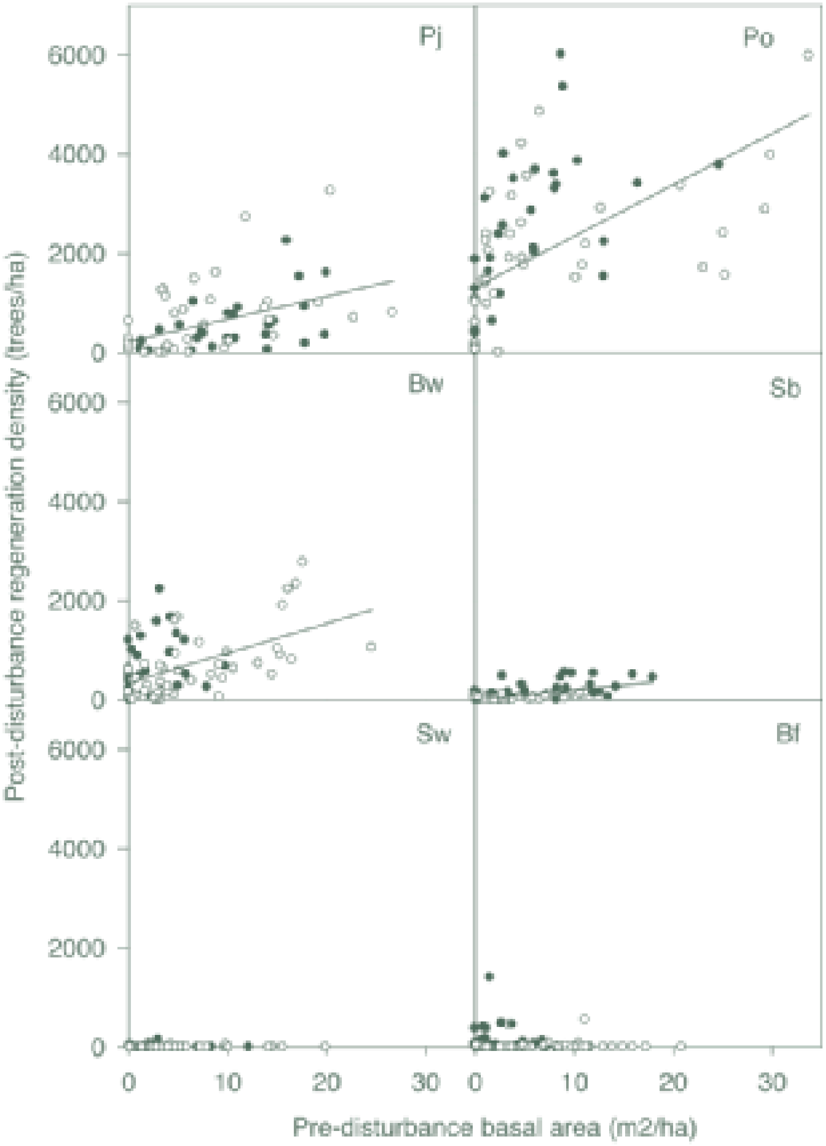


Figure 11. The relationship between post-disturbance regeneration density (trees/ha) and pre-disturbance basal area (m^2/ha). White circles are for post-fire and black circles for post-harvesting. Pj – jack pine, Po – trembling aspen, Bw – paper birch, Sb – black spruce, Sw – white spruce, and Bf – basalm fir.

Case Study from Northwestern Ontario, cont'd.

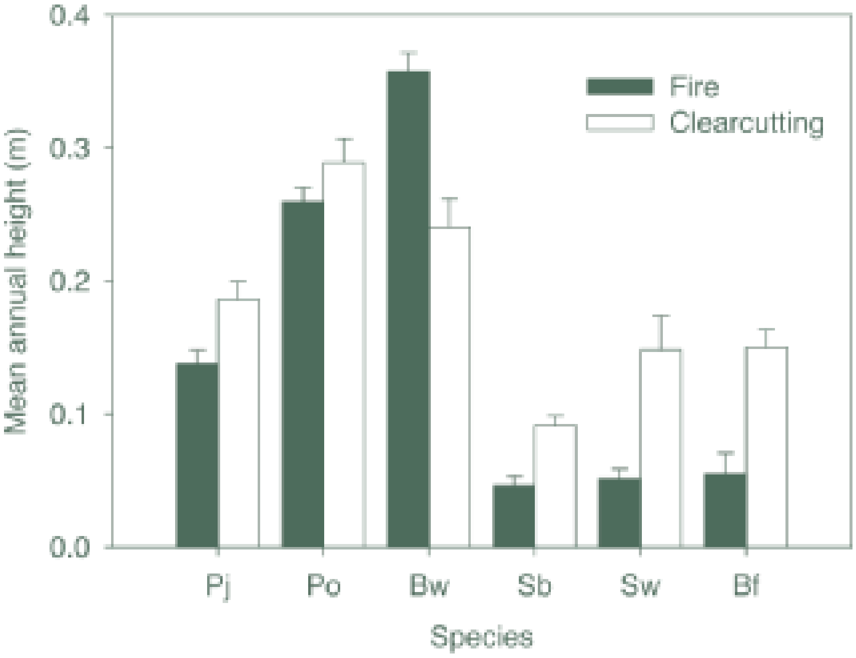
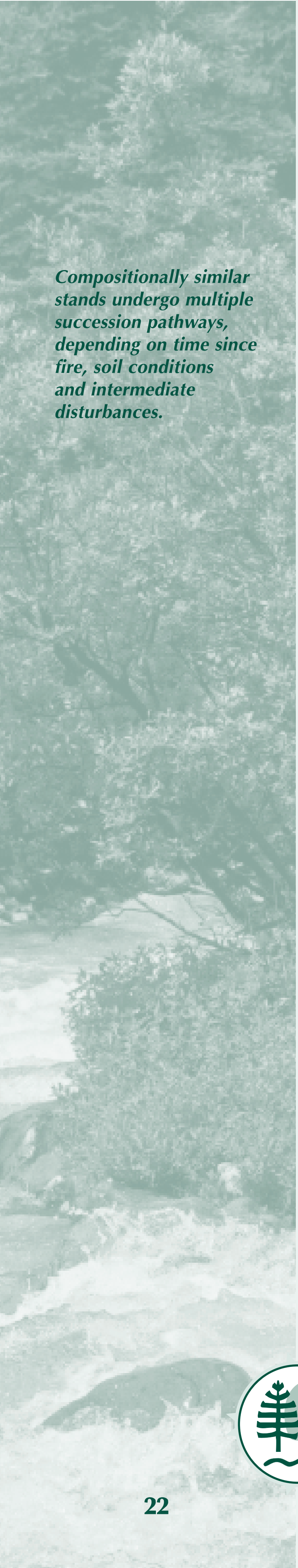


Figure 12. Post-disturbance mean height growth by species. Pj – jack pine, Po – trembling aspen, Bw – paper birch, Sb – black spruce, Sw – white spruce, and Bf – basalm fir.

Paper birch – Post-fire birch densities and height growth were greater than post-harvest (Figures 11 and 12). This difference is attributed to better mineral exposure after fire, promoting regeneration by seed. Although paper birch is considered a very nutrient sensitive species, this was not the case in the central boreal forest sites studied as there were no differences in soil pH, total nitrogen, calcium, potassium, magnesium or phosphorous levels between post-fire and post-harvest sites. The reasons for less regeneration density and slower height growth of birch after harvest need to be further investigated. **Post-fire paper birch stands have greater regeneration density and initial height growth than in harvested stands.**

Black spruce and balsam fir – Fire caused local extirpation of these shade-tolerant species, while harvesting resulted in low densities of surviving advanced regeneration, Harvesting resulted in accelerated succession in forest types with late-succession conifer component. As the proportion of early succession stands in the landscape is expected to increase with increasing fire frequency as a result of human-induced climate change (Wotton *et al*., 2003), **harvesting may be helpful in sustaining late-succession conifers in the area.**

White spruce – White spruce disappeared after both fire and harvesting, showing its late-succession nature. However, in stand types where white spruce advanced regeneration is otherwise abundant, harvesting likely allows partial survival of advanced regeneration. **Harvesting emulates fire in white spruce stands without advanced regeneration.**



4 Factors that influence succession

4.1 Time since disturbance

Compositionally similar stands undergo multiple succession pathways, depending on time since fire, soil conditions and intermediate disturbances.

The effect of time since disturbance on species population dynamics is related to the phase of stand development (Section 2.1). In the stem exclusion phase (approximately up to 50-80 years since disturbance in boreal forests, depending on stand and site conditions), mortality occurs mostly among shade-intolerant species (*e.g.* jack pine, aspen) due to inter and intra-specific competition for light and space. Shade-tolerant species (balsam fir, spruces) experience low mortality as they are capable of suppressed growth. In the stem exclusion phase, the proportion of shade-tolerant species increases gradually as the proportion of intolerant species decreases (Kobe and Coates, 1997).

In the canopy transition phase, the main cause of mortality is aging. The general pattern of mortality is that larger trees begin to die (Yao *et al.*, 2001). Similar to the stem exclusion stage, mortality in the canopy transition phase is higher among intolerant species, while shade-tolerant species have lower mortality (Yao *et al.*, 2001). In mixedwoods, if not disturbed, this leads towards more late-succession composition of shade-tolerant conifers, such as white spruce, black spruce, balsam fir, as well as white birch (Brassard *et al.* 2008).

4.1.1 Soil conditions

The speed and direction of succession along soil nutrient and soil moisture gradients is related to tree species' stress tolerance and competitive ability. Very competitive species (*e.g.* trembling aspen and paper birch) sustain their dominance on fertile and fresh sites, while species with high stress tolerance ability have a competitive advantage on poor and extreme moisture sites (*e.g.* jack pine on dry sands, or black spruce on wet soils). For instance, Yao *et al.* (2001) found that in pine dominated sites, the rate of succession was higher on rich soils compared to poor soils where competition from both trembling aspen and white spruce increased pine mortality. In trembling aspen dominated sites, however, succession was accelerated in dry and nutrient poor sites compared to fresh and rich sites, due to aspen's low tolerance to water and nutrient limitation, which decreased its competitive ability, increased mortality and allowed expansion of other species.

4.1.2 Intermediate disturbances

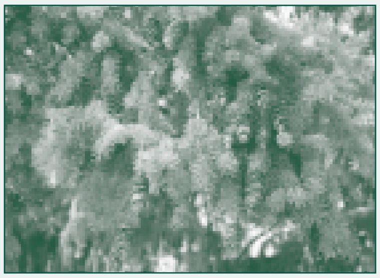
Intermediate disturbances influence stand succession development by weeding out one or more species and making space available for new individuals. The result of disturbance may accelerate, slow or change the direction of succession (Taylor *et al.*, 2009). In the boreal forest of Canada, there are three common intermediate disturbance agents: spruce budworm, forest tent caterpillar, and intermediate severity windthrow (canopy loss less than 75%).

Spruce budworm (SBW) – is a common disturbance agent in balsam fir, white spruce and black spruce forests and also in spruce-aspen mixedwood stands. Since intermediate disturbances rarely cause the death of young understory trees (Nealis *et al.*, 2004), a new canopy is likely formed by the understory of late-succession tree species. In conifer-hardwood stands, where a late-succession understory tree layer may not be present, release of the shrub layer may take place as a response to increased light levels.

Forest tent caterpillar (FTC) *(Malacosoma disstria Hubner)* – is the larvae of the common North American moth, occurring most abundantly in the eastern regions of Canada and the United States. The caterpillars live in deciduous trees, mainly in trembling aspen and paper birch in boreal forests. The outbreaks occur in approximately 10 year cycles and usually last two to four years (Cooke and Roland, 2007). The defoliation of trees reduces photosynthetic ability, and after several years of lasting outbreak, may lead to significantly reduced radial growth and depletion of carbohydrate supplies (Frey *et al.*, 2004). FTC is rarely the cause of aspen stand dieback. However, defoliation can be an inciting factor that weakens the tree's vigor, making the trees more susceptible to wood-boring insects and fungal pathogens, and can further lead to stem breakage or uprooting (Frey *et al.*, 2004). Succession following aspen stand dieback initiated by FTC depends on the abundance of advanced regeneration and seed and bud availability of non-host tree species. Repeated defoliation for several years diminishes aspen's ability to produce suckers, due to the depletion of carbohydrate reserves. Ghent (1958) noted that following a severe FTC outbreak, wind broken aspens did not develop root suckers. Instead, the understory was formed by a thick and "unbreakable" mountain maple shrub layer.

Intermediate severity wind disturbance – selectively kills groups of trees that are similar in species or in size. In early-succession stand types, pioneer species are more likely to be killed than late-succession trees, since they allocate more resources to growth than to wood strength. The prevailing damage type is stem breakage (Rich *et al.*, 2007). Ground disturbance is minimal and if there is advanced regeneration present, the succession will be accelerated towards late-succession composition. In late-succession stand types, conifers tend to form shallow root plates and uproot more easily than broadleaf species. Uprooting creates soil pits with exposed mineral soil that advances establishment of light-seeded pioneer species. Thus, the succession is set back to an early-succession composition.

4.2 Availability of late-succession seed



Succession towards more shade-tolerant composition does not take place if the seed source is either eliminated or too far from the disturbed area. Availability of seeds, especially of late-succession species seeds, differs at the regional and landscape scale. For example, eastern white cedar is quite sparsely distributed in central Canada, but its abundance increases towards the east coast. Likewise, north-facing slopes are moister and cooler and tend to have higher abundance of late-succession conifers (*e.g.* white spruce, black spruce, eastern white cedar) compared to dryer, south facing slopes.

5 Application of forest succession models in long-term forest management planning

Succession is one of the most sensitive inputs of forest management planning.

Succession is commonly embedded in several layers of a forest management plan including:

- tree species yield curves;
- undisturbed forest stand trajectories;
- post-fire and post-harvest trajectories;
- predicted responses to silviculture treatments; and
- habitat elements.

Succession is one of the most sensitive inputs of forest management planning, since a small change to succession assumptions, rules, or modeling typically has large effects on amounts (volume or area) of tree species, which further affects wildlife habitat and biodiversity. Therefore, forest succession and succession modeling needs to be addressed and well-documented in long-term forest management plans and calculations of sustainable harvest levels. Due to the lack of available information regarding forest succession, forest managers have either ignored succession (*i.e.* assumed stand types or species composition do not change with stand development) or used expert opinion models. Since the concept of succession is important to our understanding of the ecological processes in forest ecosystems, practical applications to forest management and habitat availability, various types of forest succession models have been developed.

- **Yield curves** – Succession trends occur naturally within most yield curves (*e.g.* increasing amounts of conifer over time). Additional succession assumptions are almost always added to tree species yield curves as part of the modeling process, but are rarely well-documented. Figure 13 shows a mixedwood yield curve for aspen-spruce stands. The inventory plots commonly range in age from 40 to 120 years (Figure 13 - left). A key assumption used to develop the yield curves involves the extrapolation of yield data beyond what was sampled (*i.e.* ages 120+ years) to predict growth and volume. A second and far more significant modeling assumption is that of **'death age'.** Death age assumes that after the stand begins to 'break-up' (*i.e.* volume begins to decrease) the entire stand dies, and stand volume equals zero (Figure 13-right) at age 160 years. Typically death age is not displayed graphically on the yield curve, but in a separate table instead. A further modeling assumption is that the 'dead' stand immediately regenerates at the modeling age of zero years, with a volume equal to zero. This is theoretical. In reality a stand of age 161+ years since disturbance does in fact have standing trees with volume.

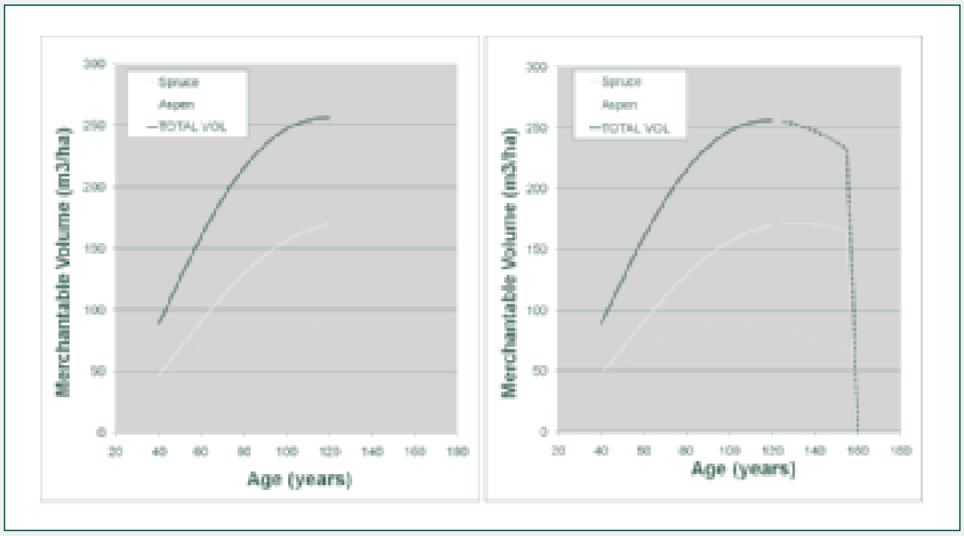


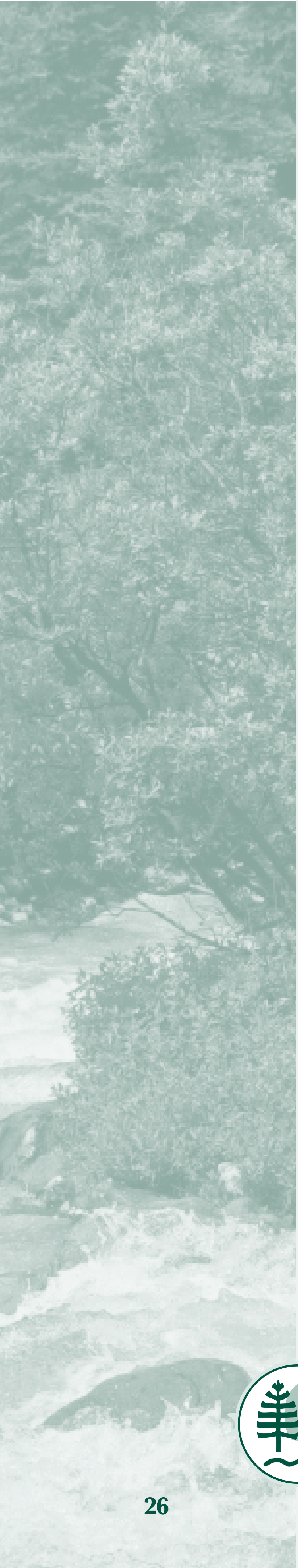
Figure 13. Example of an aspen-spruce yield curve showing the range of data (40-120 years-left), and extrapolation of data beyond 120 years, with an assumed death age where the stand volume crashes to zero (right).

Unfortunately, death age is a commonly used modeling shortcut, instead of accounting for natural succession. Also, there is no evidence to substantiate the phenomenon called death age. Some government agencies and some forest companies have permanent sample plot data (PSP's) for standing trees that exceed stand ages where death age is assumed to occur (120-180 years). Recent analyses of these long term data sets have revealed that gap dynamics occur in these declining stands, creating multi-aged and multi-layered stands with merchantable volumes (Kenkel 2009 – in progress).

Recent analyses of long term data sets have revealed that gap dynamics occur in declining stands, creating multi-aged and multi-layered stands with merchantable volumes.

The consequences of using the modeling shortcut death age include: assuming there is no mature forest canopy when a canopy really does exist; underestimating the biodiversity and habitat values of stands after death age; and excluding future stands from the harvest schedule for an entire rotation.

- **Undisturbed forest stand trajectories** – Many forest stands will not be harvested over the life of the long-term plan. Buffers, core areas, or any other exclusion will not be disturbed by harvesting. However, due to the dynamic nature of boreal forest stands, changes in species composition will occur over the 150-200 year modeling timeframe of long-term plans. Typically, the current forest condition (forest at the beginning of the modeling and planning timeframe) is described with amounts of each forest type, and the habitat and biodiversity metrics that the different forest types create. It is therefore especially important to account for natural succession changes to stands, when describing future forest conditions.
- **Post-fire and post-harvest trajectories** – At the beginning (time zero) of a modeling and planning timeframe, there may be areas that were recently burnt by fire, but not yet inventoried. Likewise, recent cutovers may not yet have regeneration surveys or been inventoried. Therefore it is very important to use succession tools to assign post-fire and post-harvest stands to a stand type, rather than exclude them from the modeling landbase simply because they have not yet been inventoried.



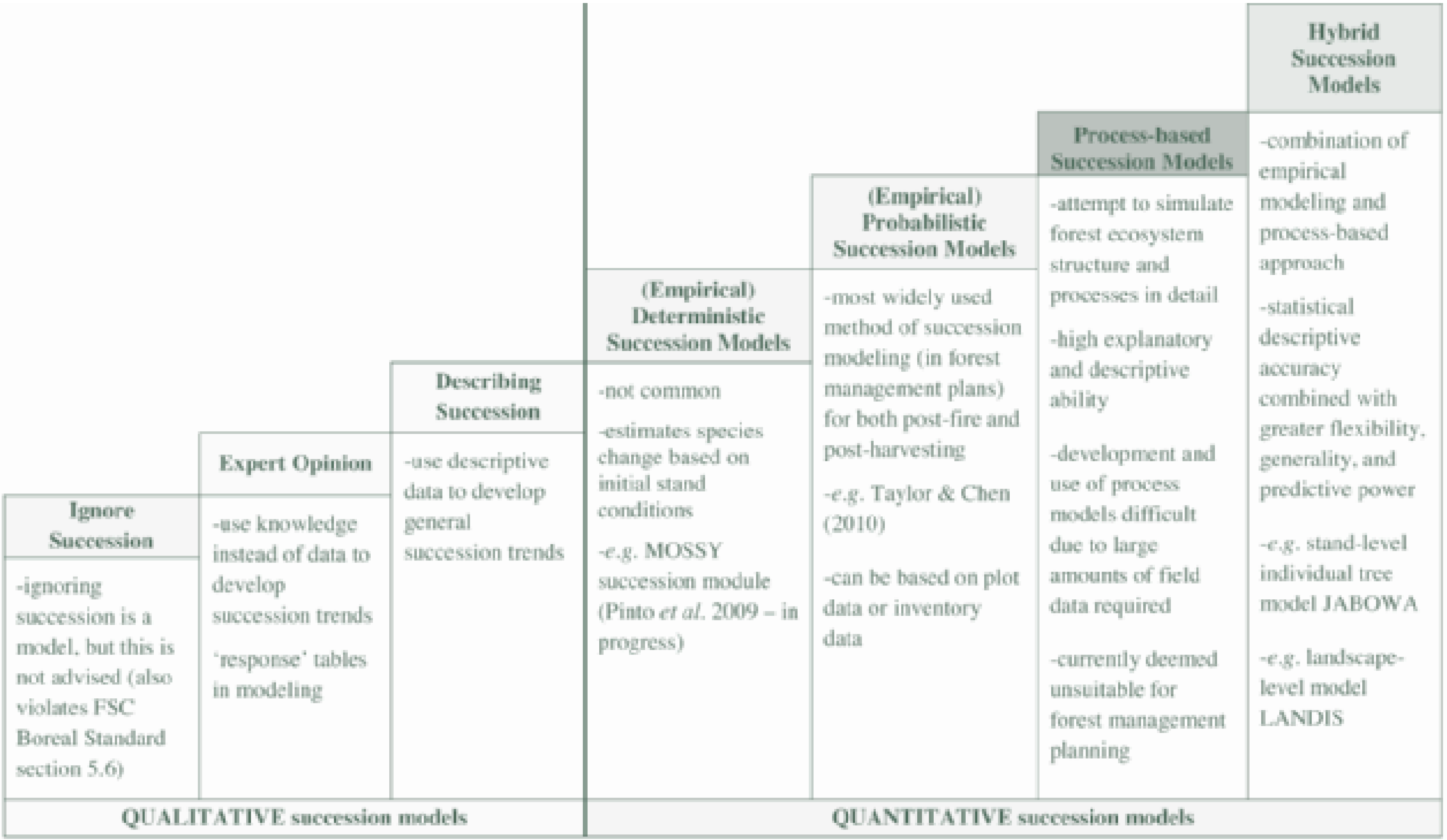
- **Silvicultural responses** – Forest management actions, such as silvicultural treatments, can have a significant effect on forest composition or structure, and therefore affect succession pathways. Most silvicultural treatments, such as understory protection, increase or maintain softwood stocking and species composition. Surprisingly, almost no one accounts for the change in succession pathways due to spraying herbicides, which kill hardwoods, most shrubs and some forb species.

- **Habitat Elements** – Sustainability within a forest management plan includes biodiversity assessments. Habitat suitability or occupancy can be forecasted based on future forest projections as long as some key attributes of forest habitat are included in the modeling framework (*e.g.* habitat elements such as snag density, downed woody debris, canopy cover, etc.). These attributes can be derived from field data as well as the literature to develop relationships that can be forecasted similar to forest growth curves. Habitat elements were described by Bunnell *et al.* (1999) and were applied in forest sustainability assessments undertaken by MacMillan Bloedel in British Columbia in the 1990's. Recently LP Canada, Manitoba used habitat element curves and spatial landscape assessment models in a 20 year Forest Management Plan (Donnelly *et al.*, 2006; Rempel *et al.,* 2006).

The broad classification of succession models that could be used in forest management planning includes qualitative models (*i.e.* conceptual models) and quantitative models (data driven). Below, the description of each model, type and their applicability to forest management planning are outlined (Figure 14).

5.1 Qualitative succession models

Qualitative models (conceptual models) are typically drawn as diagrams with boxes and flow arrows, to show connections and interactions between the model elements. Examples of qualitative models can be found in Figures 2 to 6 (multiple pathways of stand development) and in Figure 15.



Ignore Succession	Expert Opinion	Describing Succession	(Empirical) Deterministic Succession Models	(Empirical) Probabilistic Succession Models	Process-based Succession Models	Hybrid Succession Models
-ignoring succession is a model, but this is not advised (also violates FSC Boreal Standard section 5.6)	-use knowledge instead of data to develop succession trends 'response' tables in modeling	-use descriptive data to develop general succession trends	-not common -estimates species change based on initial stand conditions -*e.g.* MOSSY succession module (Pinto *et al.* 2009 – in progress)	-most widely used method of succession modeling (in forest management plans) for both post-fire and post-harvesting -*e.g.* Taylor & Chen (2010) -can be based on plot data or inventory data	-attempt to simulate forest ecosystem structure and processes in detail -high explanatory and descriptive ability -development and use of process models difficult due to large amounts of field data required -currently deemed unsuitable for forest management planning	-combination of empirical modeling and process-based approach -statistical descriptive accuracy combined with greater flexibility, generality, and predictive power -*e.g.* stand-level individual tree model JABOWA -*e.g.* landscape-level model LANDIS
QUALITATIVE succession models			**QUANTITATIVE succession models**			

Figure 14. Succession modeling 'step' continuum and applicability to forest management planning.

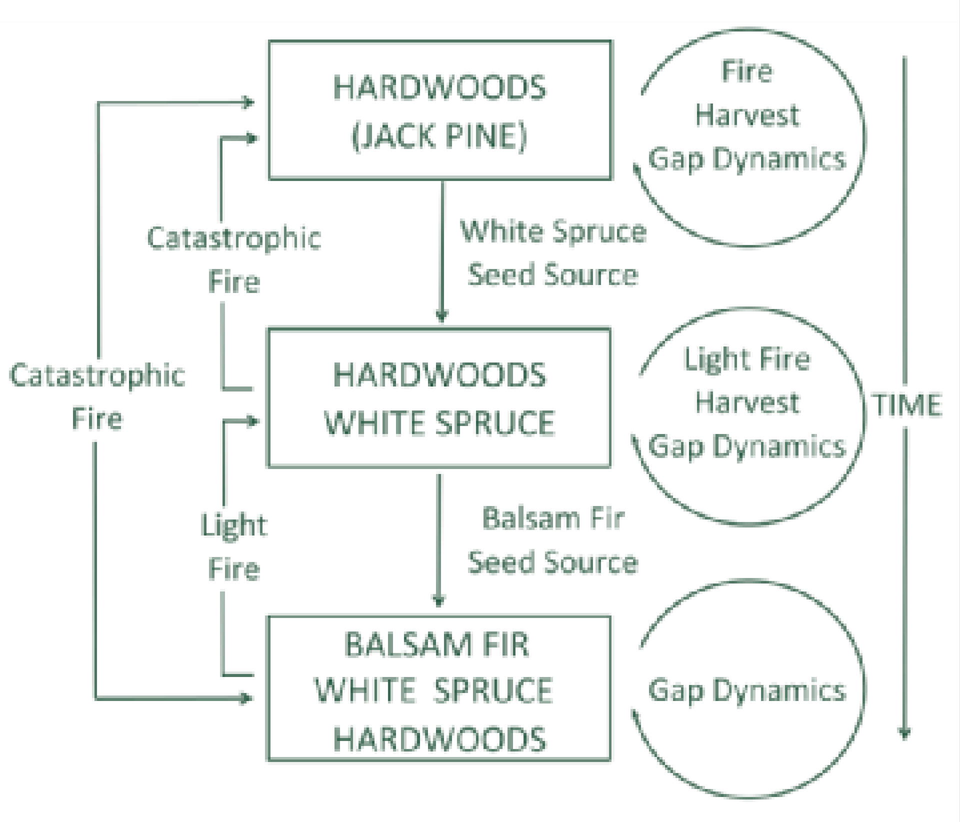


Figure 15. A forest succession model for the Duck Mountain Provincial Forest. This model was recently used to project forest stand development in LP Canada's Forest Management Plan 2006-2026. Lines represent disturbances and rectangles represent succession cohorts (Hamel and Kenkel, 2001).

The ability to incorporate qualitative models in forest management planning is very limited, since they lack details required for predictive modeling.

The qualitative models provide a theoretical understanding of succession processes, but lack quantitative values for predictions. The ability to incorporate qualitative models in forest management planning is very limited as there is a need for more detailed values (absolute versus descriptive) in analysis. However, qualitative models are often critical to the identification of knowledge gaps and help to define research questions. Modeling succession in changing environmental conditions requires input from interdisciplinary parties at different scales. The development process of qualitative models can be used to initiate discussions, reveal hidden and unacknowledged assumptions, and identify areas in which scientists from different fields agree or disagree (Heemskerk *et al.,* 2003).

Qualitative succession models used in the forest management planning can be organized based on the level of knowledge and amount of descriptive data included in models:

- **Ignore Succession** – The default type of succession model is to assume that stands always return to their original stand type, without data to validate.

- **Expert Opinion** – Experienced forest practitioners or a multi-agency working group can draft succession trends based on their experiences. This is a valid starting point if data are not readily available.
- **Describing Succession** – Descriptive data is collected on stand structures, and is combined with expert opinion to describe general succession trends. Usually there is not enough data to quantify succession predictions and it is best used in an adaptive management framework until more is discovered about these systems.

5.2 Quantitative succession models

Quantitative models use data and mathematical techniques that vary in type and complexity depending on available data, and details of the ecosystem being modeled. The model can be a single equation or a series of interacting equations comprising a simulation system (Taylor *et al.*, 2009). Quantitative models are organized into empirical (observed) and mechanistic (process-based) models (Figure 16). The selection and application of quantitative succession models will depend on data availability, analysis techniques, objectives, assumptions and partnerships. There is no perfect model. The suitability of a model type for forest management planning depends directly on the nature of the problem. As Peng (2000) stated, the strength of the mechanistic models is the weakness of the empirical models and vice versa.

The strength of mechanistic models is the weakness of empirical models and vice versa.

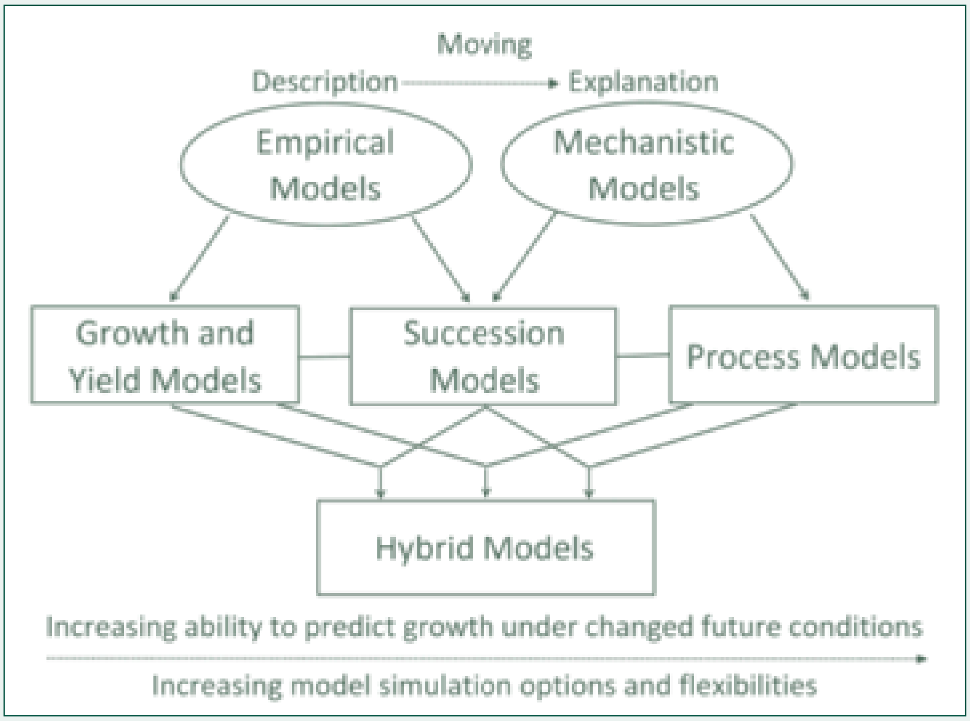
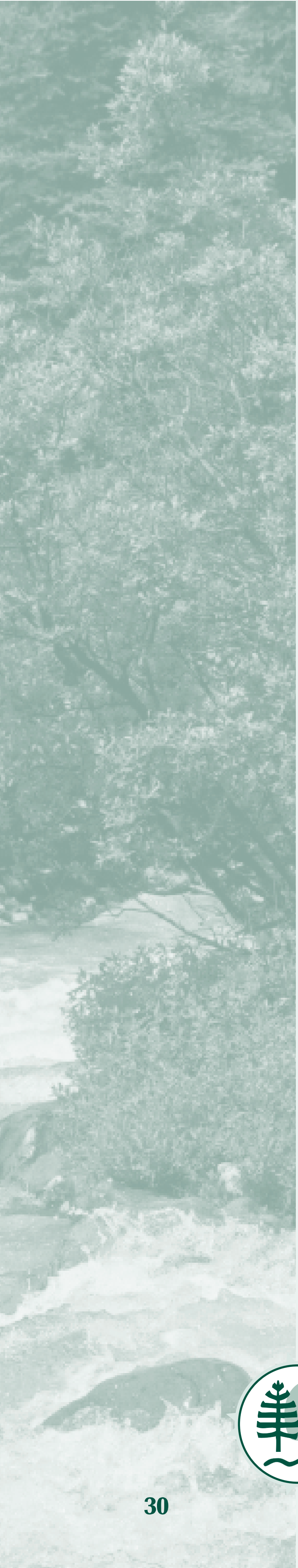


Figure 16. Classification scheme of quantitative forest succession modeling methods (Peng, 2000).



Empirical models

These models are compiled using past data records. The best known and most common empirical models in forest management planning are the growth and yield models (*e.g.* stand density management diagrams (Drew and Flewelling, 1979)). The major strength of empirical models is that they use a mathematical function or curve to describe the best relationship between measured variables. This makes empirical models easy to use, interpret and accurate in predictions. The downside of empirical models is that they are limited only to the sampled sites and climate conditions, and they assume that future growth conditions and management practices remain similar to present ones (Peng, 2000).

For empirical modeling of forest succession, there are two common approaches, **deterministic** and **probabilistic** (Taylor *et al.*, 2009):

- **Deterministic empirical models** estimate species composition change based on given sets of initial conditions (*e.g.* species composition, soil conditions, and disturbance regime). This approach is commonly used to model species abundance and replacement within a community. An example of deterministic succession modeling is Ontario's MOSSY succession module (Pinto *et al.* in progress), where forest inventory stands are assigned succession changes based on their stand characteristics.

- **Probabilistic empirical models** are much more commonly used in forest management planning. They estimate the probability of a succession stage to remain same or change into another succession stage over time. The results can be displayed as a series of succession diagrams (see Section 2.2.1 Figures 7 to 10), or as a matrix table showing all possibilities (Table 3). Shaded cells show stand types that are predicted to remain the same.

Table 3. Example of succession results displayed in a matrix (Taylor and Chen, 2010) for boreal forests in central Canada. PJ – jack pine stands, SB – black spruce dominated stands, BF – balsam fir dominated stands, BW = paper birch dominated stands, CE – eastern white cedar dominated stands, MD – mixed deciduous species stands, MC – mixed conifer stands, SB-BF – black spruce and balsam fir dominated stands, PO – trembling aspen dominated stands.

	Proportion succeeding to stand type (post-disturbance)											
Pre-Disturbance Stand Type	**PJ** (dry sandy)	**PJ** (moist-wet)	**SB** (moist-wet)	**SB** (dry-fresh)	**CE**	**SB**	**BF**	**MC**	**SB-**	**MD** BF	**PO**	**BW**
PJ (dry sandy)	0.75			0.10				0.15				
PJ (moist wet)		0.45	0.10					0.45				
SB (moist-wet)			0.90		0.10							
SB (dry-fresh)				1.00								
CE												
SB												
BF				0.05			0.70	0.20				0.05
MC												
SB-BF												
MD												
PO								0.15	0.05	0.20	0.60	
BW								0.30	0.15			0.55

Applicability to forest management planning: There are two common data sources for developing empirical succession models: 1) plot data (inventory temporary plots, or permanent sample plots); or 2) photo-interpreted inventory. Temporary ground plots can be analyzed by age into a chronosequence time-series to quantify changes in stands structure, but because the chronosequence approach has to assume succession pathways, temporary plots are inadequate for development of succession models. This deficiency may be minimized, but not eliminated, with a large number of sample plots. Permanent sample plot data that has been re-measured are needed for development of forest succession models. The resulting models could be used to directly estimate the succession pathways for the study regions where sample plots were established.

For example, using Table 3, simply apply the succession proportions to the total area of the cover type disturbed. If 10,000 ha of PJ on dry sand will be disturbed, the post-disturbance cover types become 6,500 ha of PJ on dry sand; 2,500 ha of mixed conifer (MC); and the remaining 1,000 ha becomes black spruce (SB). However, for spatial modeling where individual disturbances are tracked spatially, the entire disturbance can only be assigned to one cover type. A common solution to this minor dilemma is to assign succession changes on an area-weighted basis. Please note that over a 200 year modeling horizon, some stands can be disturbed two or even three times, resulting in modeled succession changes two or three times. There may be more stand cover type changes than the modelers and planners expect, resulting in more changes to habitat and biodiversity.

Repeated measured forest inventory data could support the development of empirical succession models for a study region.

Mechanistic models or process-based models

These models attempt to simulate forest ecosystem structure and processes (*e.g.* leaf photosynthesis, carbohydrate allocation, and plant water status) (Landsberg, 2003). The models are very complex and generally realized as computer simulations (Taylor *et al.,* 2009). The main advantage of mechanistic models is their explanatory and descriptive ability as well as flexibility among changing environmental gradients (Peng, 2000). However, mechanistic models require considerably larger amounts of field data, which makes the development and usage difficult and costly.

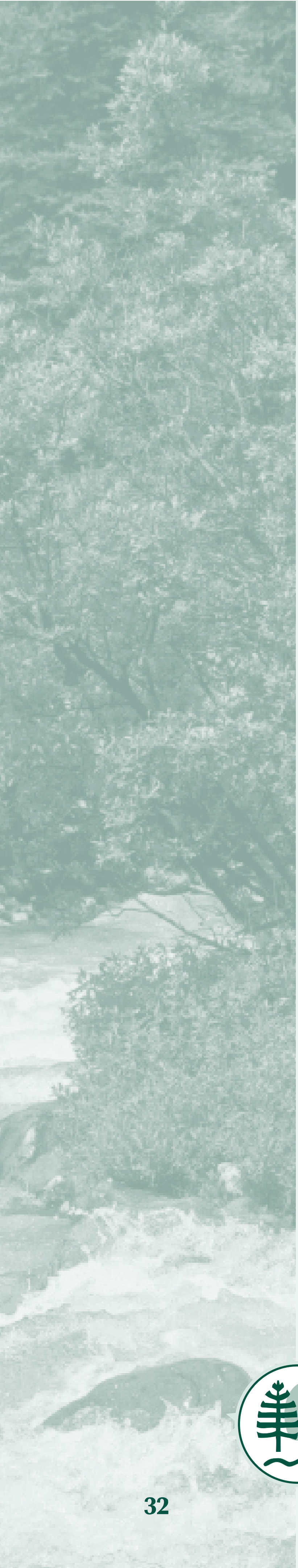
Applicability to forest management planning

Pure mechanistic models are not well suited for succession modeling, particularly at the temporal and spatial scales that are required for forest management planning (Taylor *et al.,* 2009). However they are useful in research applications and to ensure our understanding of processes underlying conceptual models.

A high level of complexity makes mechanistic models unsuitable for forest management planning.

Hybrid models

These models combine empirical modeling techniques with a process-based approach. Empirical models provide descriptive statistical accuracy, while mechanistic models add greater flexibility, generality and predictive power (Landsberg, 2003). Hybrid succession models have been developed at both the stand and landscape levels (Taylor *et al.*, 2009):



- Stand-level hybrid models are mostly gap and tree models that use individual trees as the basic unit to simulate succession (*e.g.* JABOWA (Botkin, 1993)).
- Landscape-level hybrid models simulate succession at larger temporal (decades or more) and spatial resolutions (square meters to hundreds of hectares). The aggregates are often divided based on species composition, age class or management type. A well known example of a landscape model is LANDIS (Mladenoff, 2004).

Applicability to forest management planning: Hybrid models can be modified to deal with changes in management regimes and in environmental conditions making them suitable for scenario planning. The models can be configured to simulate a wide range of anthropogenic and natural effects on succession development and project consequences over relevant time scales. They are suitable for multi-cohort mixedwood management planning due to their capability to incorporate size and species-specific growth and mortality functions. However, it should be noted that hybrid models give realistic predictions only if the ecological processes they are predicting are correctly understood.

6 Conclusions

6.1 Predictions of species composition and density of natural regeneration

There is a strong correlation between pre- and post-disturbance species composition for shade intolerant tree species. In boreal forests, basal area of most fire adapted species (trembling aspen, jack pine, paper birch, and black spruce) is directly related to their seed and bud availability (Lavoie and Sirois, 1998; Greene *et al.,* 2004), making it possible to predict post-disturbance regeneration. However, post-disturbance stands tend to shift to higher proportions of trembling aspen and paper birch. Pre-disturbance stand composition is usually known through both inventory and pre-harvest survey (cruising). Using these data as references, it is possible to predict post-harvest stand composition.

Modifications to the succession pathways may be necessary, based on harvest methods and silvicultural treatments. The species composition of these future stands can be modeled forward in time, within the context of a long-term forest management plan, and the future forest condition of these stands estimated (*i.e.* area by stand type, volume by tree species, amount of habitat, and biodiversity).

6.2 Predictions of aging succession

In the prolonged absence of stand-replacing fire, compositionally similar stands undergo multiple succession pathways, depending on time since fire, soil conditions, intermediate disturbances, presence of advanced regeneration, and seed availability. The transition starts approximately 50 years after the stand-replacing disturbance with the penetration of understory trees into the canopy. Due to the varying ability of tree species to compete within a range of soil moisture and fertility classes, succession is either accelerated or slowed down depending on soil type. Intermediate disturbances interfere with the direction and speed of succession by selectively removing tree species and creating light and space gaps for regeneration. Advanced conifer regeneration generally accelerates succession.

Forest inventory databases need to have information about important succession drivers, such as: initial stand-replacing event; soil moisture and fertility; presence and abundance of advanced conifer understory trees; past disturbance regimes; and climatic conditions. This information could be used to develop regional succession models to assist in long-term forest management planning.

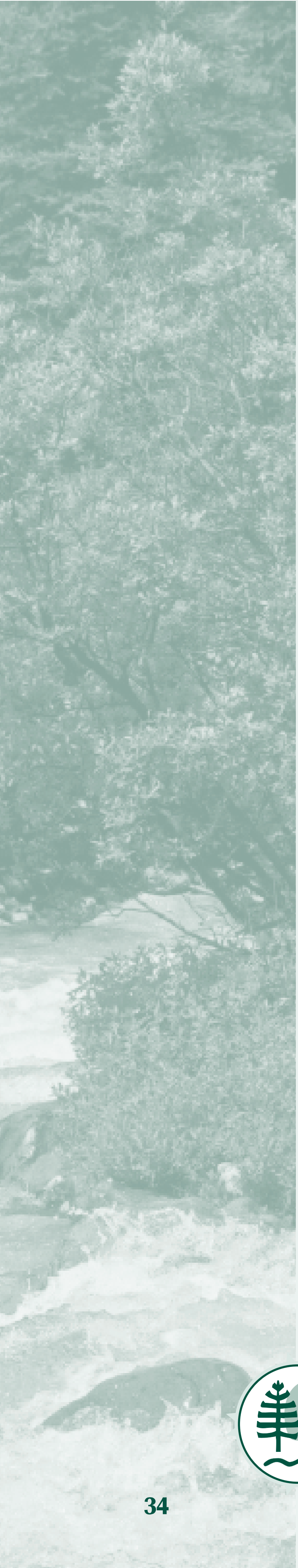
6.3 Policy implications

The results of this report have definite policy implications for forest managers. Forest managers use predictive models to assess whether their planned strategies and activities will allow them to meet their objectives (*e.g.* biodiversity, wood supply). Forest projections affect sustainable harvest levels and habitat availability analyses. As improved tools and new knowledge becomes available, they should assist in making these projections and employed in an adaptive management context.

This report demonstrated that succession rules should be applied to wood supply and habitat modeling analyses to get realistic future forest projections. The current policy of not applying realistic succession rules when modeling future forest states results in a gross misrepresentation of what is occurring and what will occur on the landscape. This can drastically affect stand and landscape planning from both a timber supply and biodiversity conservation perspective.

7 Future directions

- Continuous research on theoretical understanding of the ecological drivers for forest succession is needed. Forest inventory procedures need to include these ecological drivers wherever possible.
- There is a wide range of disturbance types with differing intensities and occurrence intervals that interact with climate and environmental conditions and vegetation properties affecting post-disturbance regeneration establishment as well as aging succession. There is a very limited understanding of the effects of forest harvesting (of various types and intensities on different site conditions) on species and community responses.



- Repeated measures data, both repeated inventory and repeated measures plots, are extremely valuable for quantifying and modeling succession. However, such data is relatively rare. Future forest inventories and plot measurement programs can easily be designed to utilize previous work as the first measurement, and the proposed new work as the second measurement, thus yielding repeated measures data.

- The most challenging limitation in our knowledge of forest succession is the future effect of global climate change. Scientists have only begun to investigate the role of increased CO2 and temperature on individual tree growth and mortality. The response of whole forest ecosystems and their key processes such as forest succession to the global climate change is beginning to be studied. The only attempt in the broad sense of ecology to understand plant community responses to global climate change was made by Reich (2009), based on grassland experiment in Minnesota.

- There is a need to develop research partnerships, data sharing agreements, and cooperative monitoring strategies to capitalize on the discovery of new knowledge and incorporate it into future forest forecasts.

- There is a need to develop predictive models with the realization that our knowledge is limited. Such realization will help determine the best methods to be used and assumptions to be made. Long term targets should be the development of hybrid succession models that could provide predictions based on empirical data, be able to be continuously improved, and be robust and flexible enough to consider long-term effects of climate change, changing management practices and social demands. In the absence of such, the best option would be to rely on the knowledge of past succession and develop empirical succession models to assist long-term management planning.

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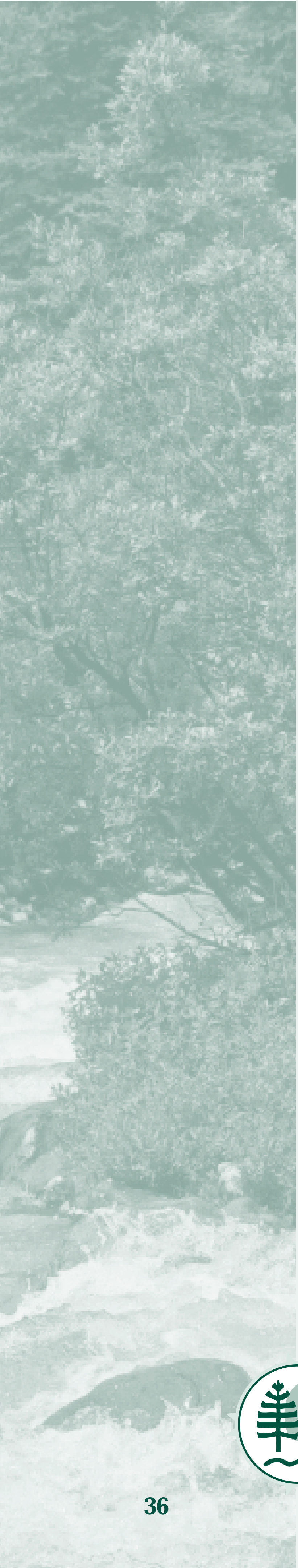

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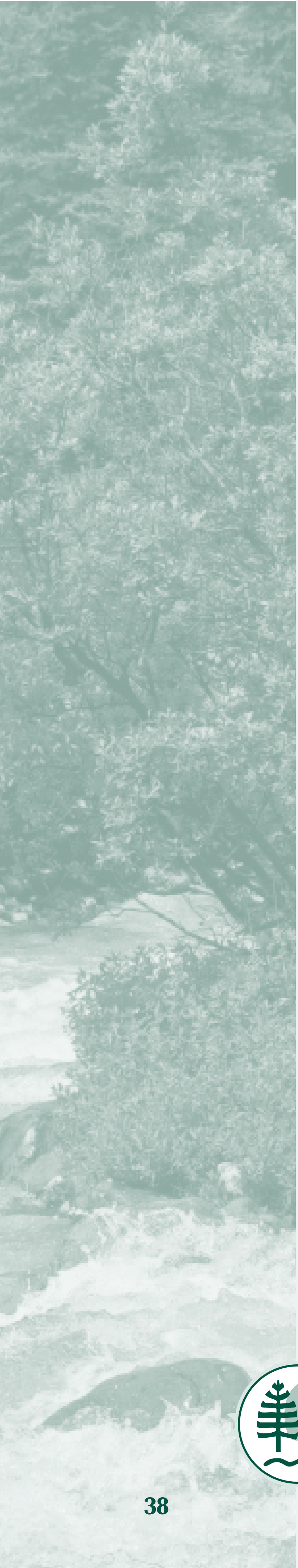

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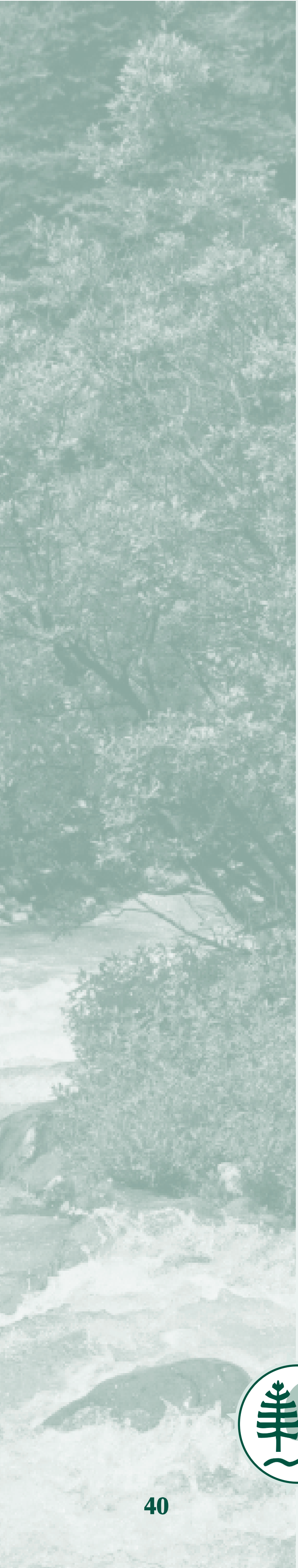

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Sustainable Forest Management Network
3-03 Civil Electrical Engineering Building
University of Alberta
Edmonton, Alberta T6G 2G7
CANADA
Phone: (780) 492-6659
Fax: (780) 492-8160
Email: info@sfmnetwork.ca

www.sfmnetwork.ca