Forest Dynamics and the Application of a Natural Disturbance-Based Management Model in Duck Mountain Provincial Forest, Manitoba

By

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A Thesis submitted to the Faculty of Graduate Studies of the
University of Manitoba
in partial fulfillment of the requirements of the degree of

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ABSTRACT

The forest industry has been moving towards the adoption of ecosystem-based forest management techniques to achieve sustainable forest management. Different models have been developed in an attempt to incorporate increasingly diverse management goals. This study utilizes data from a pilot Forest Land Inventory (FLI) i) to identify major successional pathways in Duck Mountain Provincial Forest of western Manitoba, ii) to analyze tree species cover variability within each pathway, iii) to assess the successional variability of forest stands originating from large, catastrophic fires that occurred in the 1880s and 1890s, and iv) to assess the applicability of the three structural cohort natural disturbance based management (NDBM) model, developed for the mixed boreal forest of Quebec. Cluster analyses were performed to classify the upper forest canopy into 3 major successional pathways: Trembling aspen-white spruce, jack pine-black spruce, and black spruce-eastern larch. Ordination analysis was used to determine the relationship among vegetation, environmental, and structural variables within each major pathway. Results suggested that the FLI environmental variables distinguish well among the three major pathways primarily along a moisture/slope gradient, but explain little of the species and structural variability within each pathway. Forest stands originating from large fires in the 1880s and 1890s were analyzed to assess successional variability within each major pathway. Results showed that despite being of similar age, there was a large amount of variability in structural development, but 2-layered canopies with a continuous to discontinuous upper canopy tended to dominate in these stands. The landscape was then classified into structural cohorts. Globally, 59.5%, 34.5%, and 6.0% of the landscape was in cohort 1, 2, and 3, respectively. The three structural cohort management model was applied to the forest under three different scenarios: (1) the current distribution of cohorts, (2) a 110-year fire cycle (current), and (3) a 60-year fire cycle (pre-European settlement). Results suggest that, in terms of forest structure, the current distribution of cohorts in DMPF is closest to the expected distribution under a 60-year fire cycle. The results are compared to findings in other regions of the mixed boreal forest, and the implications for forest management in DMPF are discussed.

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DEDICATION

This thesis is dedicated to Davian, who has always believed in me.

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1. INTRODUCTION

1.1 The mixed boreal forest

The boreal forest is the world's largest terrestrial biome, representing approximately 32% (14 million km^2) of the planet's forest cover (Burton et al., 2003). Boreal forests comprise about 83% of Canada's total forest and 35% of Canada's total land area (CCFM, 2000), and boreal forest-related industry is estimated to make up approximately 60% of Canada's overall forest economy (Burton et al., 2003). Although the boreal ecosystem as a whole is generally similar in appearance and shares similar dominant canopy species, there are important regional differences in terms of which species attain dominance (Larsen, 1980). These differences are primarily determined by changes in physiography and climate (Wiken, 1986; Elliott-Fisk, 1988; Barnes et al., 1998), and in Canada the boreal forest is subdivided into seven ecozones as defined by Wiken (1986) (Fig. 1a). Often the boreal forest is classified according to the dominant form of vegetation cover, or the physiognomic-structural classification (Scott, 1995; Barnes et al., 1998). According to the relative dominance of coniferous and broadleaf species, Canada's boreal forest can be classified into (1) coniferous forest; (2) mixed forest, dominated by both coniferous and broadleaf-deciduous species; and (3) deciduous forest (Fig. 1b). A fourth forest type, the transitional forest, corresponds to the boreal forest–tundra ecotone, which represents a transitional zone between the northern coniferous boreal forest and the shrub-dominated tundra (Scott, 1995).

The mixed boreal forest is a dynamic system, and may be defined as forests that are dominated by both broadleaf species and coniferous species at some point throughout

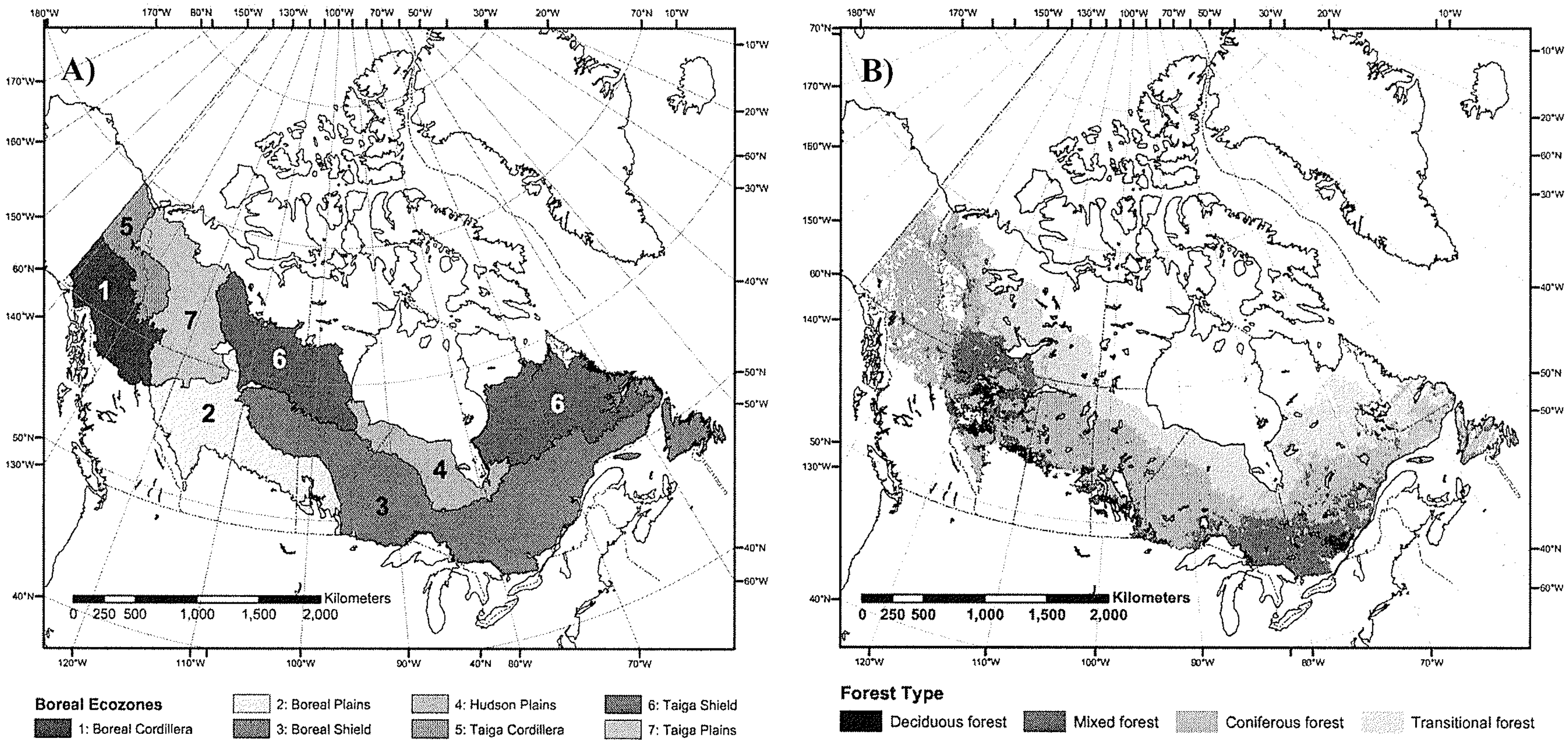


Figure 1. A) The boreal forest ecozones of Canada (data source: Schut, 2005), and B) the boreal forest types of Canada (data source: St-Laurent et al., 1995).

the forests' successional stages, and where no single species comprises greater than 80% of the basal area (MacDonald, 1995). The mixed boreal forest constitutes approximately 18% of the Canadian boreal forest region (St-Laurent et al., 1995). This forest type is concentrated along the southern fringes of the boreal shield and boreal plains ecozones, as well as in the southern portion of the taiga plains (Scott, 1995) (Fig. 1a, b). Compared to the more northern, conifer-dominated forests, the mixed boreal forests tend to be richer and more diverse in terms of species as well as in soil conditions (MacDonald 1995; Côté et al., 2000). Dominant coniferous tree species in the mixed boreal forest include black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), eastern larch (*Larix laricina* (Du Roi) K. Koch), and northern white-cedar (*Thuja occidentalis* L.). The dominant broadleaf species include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), and willow (*Salix* spp.) (Rowe, 1972; Larsen, 1980; Gauthier et al., 2000).

The biological and environmental conditions associated with the mixed boreal forest vary across Canada. The eastern region (eastern Ontario and Quebec) of the mixed boreal forest tends to be somewhat richer in species compared to the western regions (Manitoba, Saskatchewan, and Alberta), as it is part of the Boreal-Broadleaf Ecotone, which is a transition zone possessing environmental conditions suitable to both the coniferous trees of the north, and the increasingly dominating broadleaf deciduous trees to the south as growing conditions improve (Rowe, 1972; Scott, 1995). In contrast, the western mixed boreal is part of a transition between the northern boreal forest and the drier grasslands and aspen parklands to the south (Rowe, 1972; Wiken, 1986; Scott, 1995). Rather than a transition to better growing conditions dominated by broadleaf forests as is the case in the east, the mixedwood state in this region is determined by a combination of factors, including moisture stress and shorter fire cycles which help to define the southern limit of the boreal conifer species in this region (Rowe and Scotter, 1973; Scott, 1995).

1.2 Dynamics of the mixed boreal forest

The process of succession and its interruption by disturbances drives the dynamics of a forest landscape. Forest stand dynamics encompasses the changes in forest composition and structure over time during and after disturbances (Chen and Popadiouk, 2002). Environmental differences across the range of the mixed boreal forest have important implications for the development of the forest and the factors affecting forest dynamics (i.e. disturbances, growth). Girardin and Tardif (2005) have shown that in Manitoba, the growth of boreal tree species are not only responding to variation in temperature and precipitation, but also reflect variation in atmospheric pressure heights as well. Climatic trends have a strong influence on the frequency and severity of disturbances such as fire (Flannigan and Van Wagner, 1991; Johnson and Larsen, 1991; Carcaillet et al., 2001). Atmospheric circulation patterns have been linked to differences in drought severity patterns in historical reconstructions, which in turn strongly influence the potential for fire initiation (Girardin et al., 2004a). Climate also determines conditions that may be favourable or unfavourable to other types of disturbances such as insect outbreaks which also play an important role in forest dynamics (Hogg et al., 2002; Sutton and Tardif, 2005; in press). As a consequence of the climatic variability existing across the mixed boreal forest of Canada, there is a significant amount of variability in the regional disturbance regime, and consequently, in forest dynamics.

1.2.1 Disturbances

There are three major factors that determine the forest mosaic over a landscape: geomorphology and regional climate, both of which affect vegetation composition at the regional level (Bridge and Johnson, 2000), and disturbances, which can be either endogenous (from within the system) or exogenous (from outside the system). Disturbances can affect vegetation composition on a stand or landscape level (Attiwill, 1994). Fire and insect outbreaks, such as spruce budworm, are some of the most important natural disturbances in the mixed boreal forest ecosystem, largely determining the age distribution and composition of the forest mosaic over the landscape (Morin, 1994; Gauthier et al., 1996; Bergeron et al., 2002b; Wallenius et al., 2004).

The fire cycle of a given region can be defined as the number of years required to burn an area equal to the size of the study area (Johnson and Gutsell, 1994), and it varies spatially, temporally, and in intensity (Bergeron et al., 2004a). With the global increases in temperature, it is believed that the frequency and severity of fires will increase. Using general circulation models, Flannigan and Van Wagner (1991) have predicted a potential 40% increase in seasonal fire severity and area burned under a $2 \times CO_2$ climate scenario. Flannigan et al. (2001) have, however, reported variable trends in fire weather indexes (FWI) between western and eastern Canada as global temperature increases. Evidence suggests that the length of fire cycles in the mixed boreal forest of eastern Canada has increased since the end of the Little Ice Age (~1850) despite global warming (Bergeron et al., 2001; Lesieur et al., 2002; Bergeron et al., 2004a). The increase in temperature in this region is likely offset by an increase in precipitation resulting from a shift in atmospheric circulation (Girardin et al., 2004a, b).

Based on fire history work done in the eastern mixed boreal forest by Bergeron et al. (2001) and Gauthier et al. (2002), estimates of the average fire cycle in the past century ranges from >190 years to >400 years. In the western mixed boreal forest, dendroecological evidence suggests that there was also an increase in the fire cycle at the end of the Little Ice Age (Larsen, 1997; Weir et al., 2000). Historically, the fire cycle in the western mixed boreal forest has been shorter than in the east, ranging from 52 to 118 years over the past century (Larsen, 1997; Bergeron et al., 2004a; Tardif, 2004). Anthropogenic influences such as active fire suppression have made estimates of the current "natural" fire cycle difficult in many study areas throughout the mixed boreal forest, as this activity may potentially influence apparent fire return intervals (Bergeron et al., 2004a; Tardif, 2004). It has been shown that there are potentially one or more shifts (increases or decreases) in fire frequency possible within the period of a stand's development, and as a consequence the forest mosaic, which is governed by this system, is unlikely to achieve a developmental equilibrium with the fire cycle (Weir et al., 2000).

Insect outbreaks also play an important role in the mixed boreal disturbance regime (Johnson et al., 2003; Brassard and Chen, 2006). While fire disturbances have the potential to damage and cause mortality to all vegetation in a given area, insect outbreaks are host-specific. With respect to conifer species, the most important insect disturbance on the landscape is spruce budworm (*Choristoneura fumiferana* Clem.) which tends to occur in large, cyclical outbreaks (Johnson et al., 2003). As stand age surpasses the fire cycle, shorter-lived intolerant species tend to give way to longer-lived tolerant species in the dominant canopy layer (De Grandpré et al., 2000). Spruce budworm plays an important role in recycling late-successional species on the landscape, particularly balsam fir and white spruce (Morin, 1994; Bergeron, 2000; Nealis and Régnière, 2004). Morin (1994) found that the spruce budworm outbreaks and balsam fir forests tend to form an interdependent, self-regulating system in the absence of stand-replacing fires. However, mortality and openings caused by outbreaks can also increase light penetration and favour the recruitment of early-successional species such as trembling aspen into the stand (Nealis and Régnière, 2004). Spruce budworm outbreaks tend to play a more important role in the eastern mixed boreal forest compared to that in the west, because the forest is generally older in the east, and there is a greater proportion of balsam fir, which is spruce budworm's primary host (Su et al., 1996; Bergeron et al., 2004a; Pham et al., 2004).

One of the most important defoliators of broadleaf trees in the mixed boreal forest is the forest tent caterpillar (*Malacosoma disstria* Hbn.), whose primary host is trembling aspen (Peterson and Peterson, 1992). Forest tent caterpillar (FTC) is not necessarily a direct cause of mortality in aspen, but acts as a stressor that, when combined with other stressors such as drought, can reduce growth and predispose the trees to damage from pathogens, eventually leading to mortality (Hogg et al., 2002). Like spruce budworm, FTC outbreaks are also cyclical in nature (Hogg et al., 2002; Sutton and Tardif, 2005; in press). There are many factors that influence the dynamics of FTC outbreaks. The severity and duration of FTC outbreaks tend to be greater in forests that have been fragmented to some degree, which may be due to a reduction of the mortality agents that lead to the collapse of FTC populations (Cooke and Roland, 2000; Roland, 2000). A higher severity of forest tent caterpillar outbreaks has been associated with warmer, drier conditions which favour the insect (Hogg et al., 2002). Because of the drier conditions in the western region of the mixed boreal forest, it follows that FTC disturbances are potentially more severe in this region when compared to the east. Mechanical disturbances such as wind also play an important role within the mixed boreal forest (Brassard and Chen, 2006). Windthrow contributes to the supply of coarse woody debris (CWD), and can alter substrate and microsite conditions which influence regeneration and structural changes in the stand (Brassard and Chen, 2006).

Disturbances create structural variability over the landscape by interrupting the development of the established vegetation, or by making a site available for the establishment of new individuals or communities depending on the type and severity of the disturbance (Pickett and Cadenasso, 2005). Disturbances occur on many different scales, and as a consequence can have very different effects on the development of a forest stand ranging from landscape-level, stand replacing fires, to individual tree mortality due to windthrow, insects, or disease (Barnes et al., 1998). Variability in the degree of disturbance and its interaction with specific site and microsite conditions can lead to multiple successional trajectories for a particular stand, and result in the development of different stand types over a landscape (Lieffers et al., 2003).

1.2.2 Secondary succession in the mixed boreal forest

There are many factors dictating temporal vegetation change at a given site, including type and severity of disturbances, pre-disturbance conditions, abiotic characteristics, vegetation characteristics, and soil (seedbed) characteristics (Bergeron and Dubuc, 1989; Leiffers et al., 1996b; Galipeau et al., 1997; Chen and Popadiouk, 2002). Successional pathways in a particular area can be grouped according to similar abiotic conditions, specifically substrate and drainage characteristics, which partly determine the composition of the post-disturbance cohort (Bergeron and Dubuc, 1989; Gauthier et al., 2000; Chen and Popadiouk, 2002). Compositional changes along a successional pathway are accompanied by a variety of structural changes as well. Following stand replacing disturbances, there tends to be a gradual change from even structured canopies, to a heterogeneous, multilayered canopy with time (Brassard and Chen, 2006).

The overall development of mixed boreal stands can be placed into stages based on structural and compositional changes. Chen and Popadiouk (2002) differentiated between four developmental stages, which are also similar to the stages outlined by Oliver and Larson (1996). These include: (1) **Stand initiation**, following a stand-replacing disturbance. This stage usually involves the domination of fast growing pioneer (intolerant) species such as trembling aspen or jack pine. (2) **Stem exclusion** is observed where individual tree competition becomes important and vertical canopy stratification occurs. (3) **Canopy transition** occurs when mortality due to age or competition begins to break up the pioneer canopy species, and shade tolerant trees in the understory begin to penetrate into the canopy. (4) **Gap dynamics** characterizes the stage where tolerant trees tend to self perpetuate in canopy gaps following individual or small group mortality. This stage is characterized by a complex vertical canopy structure. It is important to note that there are possible variations in the definition of these stages, depending on specific site and forest characteristics (Barnes et al., 1998). Several studies have evaluated the process of secondary succession within the mixed boreal forest across Canada, and there is a large amount of variability across the region (Bergeron and Dubuc, 1989; Bergeron, 2000; Hamel and Kenkel, 2001; Stewart et al., 2001; Green et al., 2002).

In the mixed boreal forest, the dominant early successional species forming the initial cohorts after a stand replacing disturbance often include trembling aspen on fine-textured deposits, and jack pine and paper birch on coarse textured deposits, while black spruce communities dominate on organic peat sites (La Roi, 1992; Hamel and Kenkel, 2001; Lecomte and Bergeron, 2005). Post-disturbance communities of white spruce and balsam fir may also occur on finer textured, moister soils (Lieffers et al., 1996a; Galipeau et al., 1997; Bergeron, 2000; Hamel and Kenkel, 2001; Kenkel et al., 2003). Important late-successional species include black spruce, white spruce, balsam fir, and northern white-cedar, with balsam fir being more abundant in the eastern than the western mixed boreal forests, and northern white-cedar being nearly absent in the west (Bergeron, 2000; De Grandpré et al., 2000; Hamel and Kenkel, 2001).

In the absence of any additional stand replacing disturbance there is a tendency for mixed boreal stands to evolve toward a conifer-dominated stand, initially containing a mosaic of post-disturbance and later successional species, with late-successional conifers becoming more abundant with time, and the accumulation of CWD and snags becoming a major element of stand structure (Bergeron and Dubuc, 1989; Bergeron, 2000; De Grandpré et al., 2000; Hamel and Kenkel, 2001; Brassard and Chen, 2006). Because of the shorter fire cycle in the west, late successional species, particularly balsam fir and northern white-cedar, are less abundant in the western than the eastern mixed boreal forest (Weir and Johnson, 1998; Bergeron et al., 2002b). Subsequently, deciduous species tend to remain more important as time-since-last-fire increases in the western mixed boreal forests (Weir and Johnson, 1998; Hamel and Kenkel, 2001). Studies in this region of the mixed boreal have shown that in the absence of conifer seed sources, pure aspen stands can potentially achieve a self-perpetuating, gap dynamic system (Cumming et al., 2000; Hamel and Kenkel, 2001).

The initial dominance of deciduous species following a stand replacing disturbance is often a function of differential growth rates between early- and late-successional species (Lieffers et al., 1996a; Bergeron, 2000). Using dendroecological analysis, Bergeron and Charron (1994) found that white spruce and balsam fir were recruited into the post-fire cohort within five years following the recruitment of aspen and birch. It was noted that this may partially have been possible because of the pre-fire and surrounding stand composition, which was coniferous, and the small size of the fire may have provided an abundant seed source for regeneration. In the eastern mixed boreal forests, the peak establishment of northern white-cedar, however, does not usually occur until decades after the dismissal of the post-disturbance cohort (Bergeron, 2000). The regenerating density of white spruce and balsam fir are influenced by several factors, including proximity to a seed source, and the soil (seedbed) characteristics, particularly surface till-type deposits as opposed to clay soils (Galipeau et al. 1997; Kenkel et al., 2003).

With time, the initial post-disturbance cohort is gradually dismissed from the canopy starting about 100 to 150 years following stand-replacing disturbance (Bergeron, 2000; De Grandpré et al., 2000). This is primarily a function of the longevity of the early successional, shade-intolerant species, and the density of late successional species such as white spruce and balsam fir will increase if a seed source is available (Bergeron and Harvey, 1997; Bergeron, 2000; Hamel and Kenkel, 2001). Insect disturbances, such as FTC, may also play an important role by contributing to the break-up of the aspen canopy and favouring the release of understory spruce and balsam fir, but recruitment of trembling aspen, balsam poplar, and white birch may continue to occur in gaps (Hamel and Kenkel, 2001; Bergeron et al., 2002a; Hogg et al., 2002). At this stage a forest mosaic consisting of patches of deciduous and coniferous trees in the canopy tends to form (Bergeron, 2000). After about 175 to 200 years without fire, conifer species may continue to increase in abundance and spruce budworm disturbances and windthrow become the most important disturbance initiating the gap dynamic pattern (Bergeron and Harvey, 1997; De Grandpré et al., 2000). Because of the shorter fire cycle and lower mean forest age of the western mixed boreal forest compared to the east, secondary disturbances such as windthrow and spruce budworm outbreaks play a less important role in structuring the landscape, as do late successional conifer species such as balsam fir and northern white-cedar. Other types of insect disturbances, such as FTC outbreaks, may play a more important role in the development of western mixed boreal stands where conditions for these disturbances are more favourable; particularly with respect to promoting canopy transition to the next cohort (Chen and Popadiouk, 2002; Ghent, 1958). Because of a longer fire cycle in the eastern mixed boreal forest compared to the west, there is a relatively larger proportion of old-growth forest in the east compared to the west (Bergeron, 2000; Weir et al., 2000; Gauthier et al., 2002; Lesieur et al., 2002).

1.3 Natural disturbance based management

In response to social and economic pressures, and increasing knowledge of forest ecosystems, the forest industry has been directed towards a more sustainable forest management approach, including ecologically-based management encompassing a broad range of values over a large spatial and temporal scale (Galindo-Leal and Bunnell, 1995). Within ecological management there is an emphasis on maintaining biodiversity within the ecosystem. Several authors have suggested that one way to achieve this is to maintain a forest mosaic, in terms of age, structure, and dynamics, similar to one that is left by natural disturbances (Franklin, 1993; Bondrup-Nielsen, 1995; Gauthier et al., 1996). By preserving these elements over the landscape, one may help to preserve the natural range of habitats and ecological niches. Because of the importance of fire and other disturbances' influence on the composition and structure of the forest landscape, there has been interest in the adoption of natural disturbance based management (NDBM) which attempts to emulate the effects of disturbances such as fire through silviculture (Rempel, 1999; Bergeron et al., 2002b; Harvey et al., 2003). Implementation of NDBM is, however, difficult because forest landscapes managed under commercial licence do not produce forest age-class distributions similar to that produced under a natural disturbance regime (Figure 2A) (Bergeron et al., 1999). Many forest managers erroneously equate rotation age with the natural disturbance cycle, and under such a management regime the average stand age across a landscape would be greatly reduced (Figure 2B) (Bergeron et al., 2002b; Harvey et al., 2002).

Because of the variability of the mixed boreal forest across Canada, the development of any NDBM plan should reflect the natural conditions specific to the region being managed. Several studies conducted in the eastern mixed boreal forest have investigated and recommended silvicultural strategies based on the natural balance of disturbances over the landscape, with the goal of maintaining the mosaic's natural variability of composition and structure (Gauthier et al., 1996; Bergeron et al., 1999; Bergeron et al., 2001; Bergeron et al., 2002b; Harvey et al., 2002). In a NDBM setting managers seek to apply silvicultural techniques that emulate the effects of natural processes on the age structure of landscape (Rempel, 1999; Bergeron et al., 2002b; Harvey et al., 2003) (Figure 2A). Any NDBM system requires an understanding of the disturbance patterns influencing the landscape of interest, as well as their interactions with the forest (Attiwill, 1994). One such system proposed for the mixed boreal forest suggests that forest managers should employ a combination of even-aged and uneven-

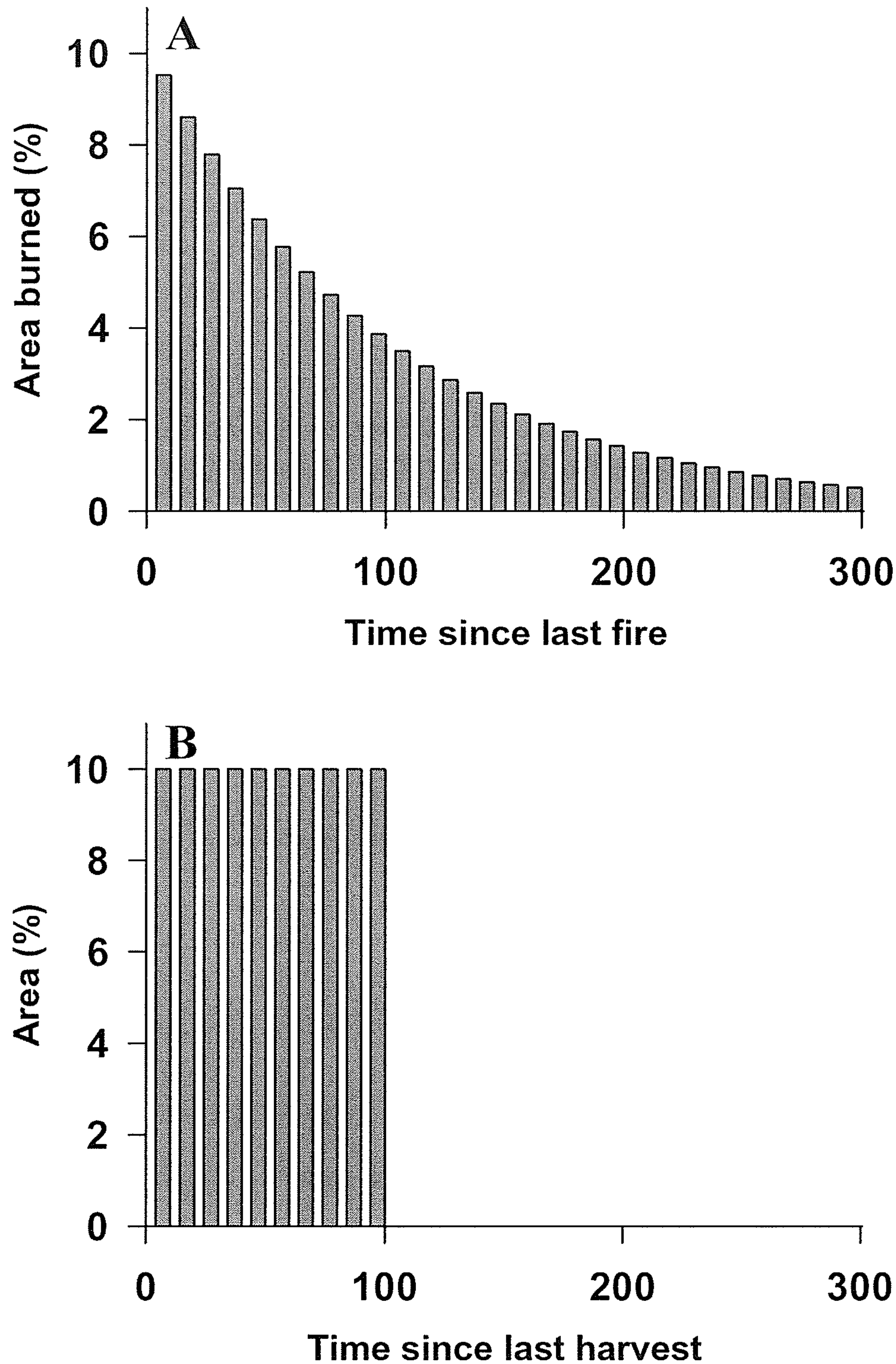


Figure 2. Theoretical forest age class distribution for forest stands based on (A) a 100 year fire cycle, and (B) a fully-regulated landscape under a 100 year even-aged rotation.

aged silvicultural techniques to maintain the structure of forests that have escaped burning, and are older than the local fire cycle (Bergeron et al., 2001; Harvey et al., 2002; Bergeron et al., 2004a) (Figure 2A). Even-aged silviculture would be used to emulate the effect of a stand-replacing disturbance, such as fire; while uneven-aged silviculture, such as partial and selective cutting may be used to facilitate canopy transition and emulate the gap-dynamic cycle of older stands. This model is theoretically adaptable to any number of situations as long as one knows the natural fire cycle, secondary disturbance impacts (such as insect and host relationships), and maximum rotation age in the area of interest (Bergeron et al., 1999). Because of the greater importance of older, gap-dynamic driven stands in the eastern region of the mixed boreal forest compared to the west, management plans employing primarily even-aged silviculture may be inappropriate for maintaining the full range of landscape variability in the east (Bergeron et al., 2001; Bergeron et al., 2004a). In the eastern mixed boreal forest, NDBM systems should incorporate a balance of silviculture that employs a greater emphasis on uneven-aged techniques relative to the west in response to the greater mean age of the forest (Bergeron et al., 2001). Because of the shorter fire cycle in the western region of the mixed boreal compared to the eastern region, the balance of silvicultural techniques employed in NDBM strategies should reflect the lesser importance of gap dynamics and their associated disturbances. The shorter a fire cycle in a region is, the more NDBM strategies should focus on even-aged management techniques such as clearcutting in order to maintain the natural age and structure over the landscape (Bergeron et al., 2002b; Bergeron et al., 2004a). In addition, a smaller proportion of late-successional conifers in the west means that there is less seed source available for their natural regeneration in situations where conifer regeneration following harvest is required (Greene et al., 2002). Studies have suggested that more intensive silvicultural treatments such as planting may be required more often in the western mixed boreal forest compared with the east in order to meet stocking requirements (Leiffers et al., 1996a; Greene et al., 2002).

One of the main problems to overcome in the implementation of NDBM is that the natural fire cycle of a region is generally longer than the relatively short commercial rotation ages (Bergeron et al., 2001). The 3-structural cohort model addresses this issue by dividing the natural landscape into three cohorts based on the natural structural and compositional changes occurring in time given a specific disturbance regime, and by varying silvicultural practices to artificially maintain the structural and compositional flux between the three structural cohorts within the commercial rotation period (Figure 3b) (Bergeron et al., 2001; Bergeron et al., 2002b). Silvicultural techniques such as clearcutting (fire), and shelterwood and selection cuts (succession), can be used to both imitate the natural transition between cohorts, and recreate the stand structure and composition associated with these stages of development (Figure 4) (Harvey et al, 2002; Lieffers et al., 2003). In this fashion forest managers may approximately maintain the natural proportion of, and transition between cohorts over the landscape, thereby satisfying the goals of NDBM.

1.4 Disturbances and succession in Duck Mountain Provincial Forest

There has been extensive work done on the disturbance regime of Duck Mountain Provincial Forest (DMPF) in Manitoba (Tardif, 2004; Sutton and Tardif, 2005; in press), as well as on forest succession (Hamel and Kenkel, 2001; Kenkel et al., 2003; Locky, 2005; White et al., 2005). Tardif (2004) has developed a 300-year fire history reconstruction for the DMPF region. Results of this study showed a forest landscape with a mean age of 108 ± 38 years in 2002. A large portion of the DMPF landscape originated between 1880 and 1889, during which approximately 83% (283,580 ha) of the forest area was affected by large "catastrophic" fires. This was followed by numerous small fires along the southwest periphery of DMPF in the early 20th century, and a large fire in 1961 where about 6% of the forest area burned. Despite the increase of fire activity due to European settlement, the fire cycle has lengthened over time, particularly after 1961 presumably due to active fire suppression and/or inappropriate climatic conditions. This study suggested that the DMPF fire cycle could be divided into three periods: (1) Pre-European settlement (prior to 1880), which was characterized by a short fire cycle punctuated by large fires, (2) European settlement (1880–1961), and (3) fire suppression (1962–present). The catastrophic fires of the 1880's coincided with a period of severe drought (Girardin et al., 2004b), and the peripheral fires of the early 20th century may be due to European agricultural activity adjacent to DMPF.

Sutton and Tardif (in press) reconstructed FTC outbreaks in DMPF over the past century using dendrochronological analysis and found that tree species directly affected by the insect included trembling aspen, balsam poplar, and paper birch. Four major outbreaks were identified in DMPF since the 1870's. These occurred during the periods 1875–1880, 1939–1948, 1961–1965, and 1982–1985. A more recent outbreak in the late 20th and early 21st century was also noted but not studied in detail (Sutton and Tardif, in press). The most intense of these outbreaks was in the 1960's, where it was associated with a high degree of growth suppression in the affected trees. This outbreak immediately followed an extreme drought year and the large fire in 1961. The 1940's and 1980's outbreaks appeared to be similar in their spatial patterns and slower development, however Sutton and Tardif (in press) suggested that severe frosts in the spring of 1984 may have reduced FTC populations and arrested the development of a larger outbreak. All of the three major outbreaks of the 20th century appear to have originated in the northern vicinity of DMPF.

Hamel and Kenkel (2001) characterized stand dynamics in DMPF and developed a general successional model for DMPF as a whole. The study identified five post-fire stand types, each characterized by a dominant species. These include: (1) trembling aspen, (2) balsam poplar, (3) white spruce, (4) jack pine, and (5) black spruce stand types. The dynamics of trembling aspen stands are characterized by extensive suckering, and may be nearly self perpetuating without a nearby white spruce seed source. If a seed source is available, white spruce density will slowly increase over time; however recruitment of trembling aspen, balsam poplar, and white birch may continue to occur in gaps. Depending on the site, balsam poplar stands contain a primary advance regeneration of white spruce or trembling aspen, and sometimes balsam fir on nutrient-rich slopes. Advance regeneration of trembling aspen in these stands may be less important as the density of the conifer component increases and is more restricted to gaps, because light is a limiting factor (Paré et al., 2001; Greene et al., 2002). Succession in these stands tends to proceed to balsam fir dominated stands. White spruce dominated stands show primarily balsam fir advance regeneration when density is high, and when density is low advance regeneration tends to be dominated by white spruce, with some trembling aspen and white birch. These stands tend to occur adjacent to unburned areas, and tend to self-perpetuate, with balsam fir becoming more important with increasing density. Trembling aspen in these stands is limited to recruitment in gaps. Hamel and Kenkel (2001) found four major regeneration trends in jack pine stands depending on abiotic conditions and seed sources. Advanced regeneration can consist of combinations of white spruce, black spruce, trembling aspen, white birch, and balsam fir. Balsam fir, white spruce, and black spruce becomes more important in moist stands rather than sandy, well-drained sites. Black spruce stand types tend to be very dense on mineral soil, with very little advanced regeneration. Trembling aspen or white birch may occur sporadically in gaps, but are usually suppressed. In the absence of major disturbance, black spruce stands are generally self-perpetuating. On organic substrates black spruce is much less dense and eastern larch may also exist in the initial cohort. Black spruce tends to self-perpetuate through layering in these stands.

1.5 Forest Land Inventory of DMPF

In 1999, the Manitoba Forest Lands Inventory Technical Advisory Committee (FLITAC) recommended the development of a new, ecologically-based Forest Lands Inventory (FLI) (The Forestry Corp., 2003). A pilot of the proposed FLI process was initiated by Manitoba Conservation and Louisiana-Pacific Canada Ltd., and carried out in FMU's 13 (Duck Mountain Provincial Forest) and 14 (Porcupine Provincial Forest). Data for the pilot inventory was gathered by The Forestry Corp. in 2000 and 2001, after which specifications on the FLI process were provided (The Forestry Corp., 2003). This inventory includes a wide range of information including location information, stand composition and structure (overstory and understory), abiotic environment, disturbance, and silvicultural treatment information. The goal of this inventory was to provide a tool for regional and stand level planning including: harvest planning, timber supply analysis, wildlife habitat management, and biodiversity management (The Forestry Corp., 2003). This inventory provides continuous ecological data over the entire landscape of DMPF.

1.6 Objectives

Most studies focusing on implementing the 3-structural cohort approach to NDBM have occurred in the eastern boreal forest of Canada, particularly in the mixedwood boreal forest of the Abitibi region of Quebec (Bergeron and Harvey, 1997; Bergeron et al., 2002b; Harvey et al., 2002). Studies have suggested that the 3-structural cohort approach is applicable to any boreal forest region where the natural disturbance regime allows for even-aged forest management (Bergeron et al., 2002b). There is a need to test the applicability of this approach in other regions of the Canadian boreal forest. In DMPF, the development of the new FLI project provided an opportunity to further assess the applicability of the NDBM model by employing the type of data that is generally available to forest managers. In addition, because much of the DMPF landscape originates from the fires of the 1880's and 1890's (~83%), there is an opportunity to analyze successional variability over a broad land base of similar age.

The objectives of this project are to analyze the DMPF landscape using the information available in the FLI database and fire history data from Tardif (2004), and to apply the 3-structural cohort model to DMPF. These include assessing how well the FLI land base can be used to:

1. Characterize the upper canopy, abiotic environment, and stand structure of the DMPF landscape and determine the major successional pathways.
2. Analyze the full canopy profile (divided into height classes) of the major successional pathways, and assess the relationship between stand composition, abiotic characteristics, and structure.
3. Isolate all stands that originated from the fires of the 1880's and 1890's, and characterize the variability within each major pathway by isolating individual successional trajectories.
4. Define structural cohorts over the DMPF, and apply the 3-structural cohort model to DMPF based on the current mean forest age (110 year), and comparing it to alternate disturbance scenarios (Tardif, 2004).

2. METHODOLOGY

2.1 Study area

The DMPF is located in western Manitoba about 300 km northwest of Winnipeg, between 51°N and 52°N, 100°W and 102°W, adjacent to the Manitoba-Saskatchewan border (Figure 3). DMPF covers an area of about 376,000 ha, and within the forest is Duck Mountain Provincial Park (DMPP) which covers an area of 142,400 ha (Figure 3). DMPF is part of the mid-boreal uplands ecoregion which makes up part of the Manitoba Escarpment – a series of uplands that includes Riding Mountain to the south, and Porcupine Hills to the north, which all fall within the greater boreal plains ecozone (Environment Canada, 2004a).

The escarpment is characterized by its bedrock, primarily composed of Odanah shale, and higher elevation compared to the plains to the east, with a maximum elevation of 831 m at Baldy Mountain (Manitoba Conservation, 2004a). The eastern boundary is made up of the escarpment, a steep 245 m drop to the Manitoba plains (Sauchyn and Hadwen, 2001), and to the west the elevation decreases more gradually, at a rate of approximately 3.1 m/km (Smith et al., 1998) (Figure 4). The current landscape of Duck Mountain emerged as the last glacier receded 10 to 12 thousand years ago, and is covered by glacial deposits of clay, gravel, sand, and boulders (Manitoba Conservation, 2004a), as well as stratified deposits of outwash sediments (Sauchyn and Hadwen, 2001). The landscape is uneven, with slopes ranging from 10 to 15%, but can be much steeper at a local scale (Smith et al., 1998). Soils in the region are primarily composed of well-drained Gray Luvisols associated with glacial till. There are also localized areas of Dark

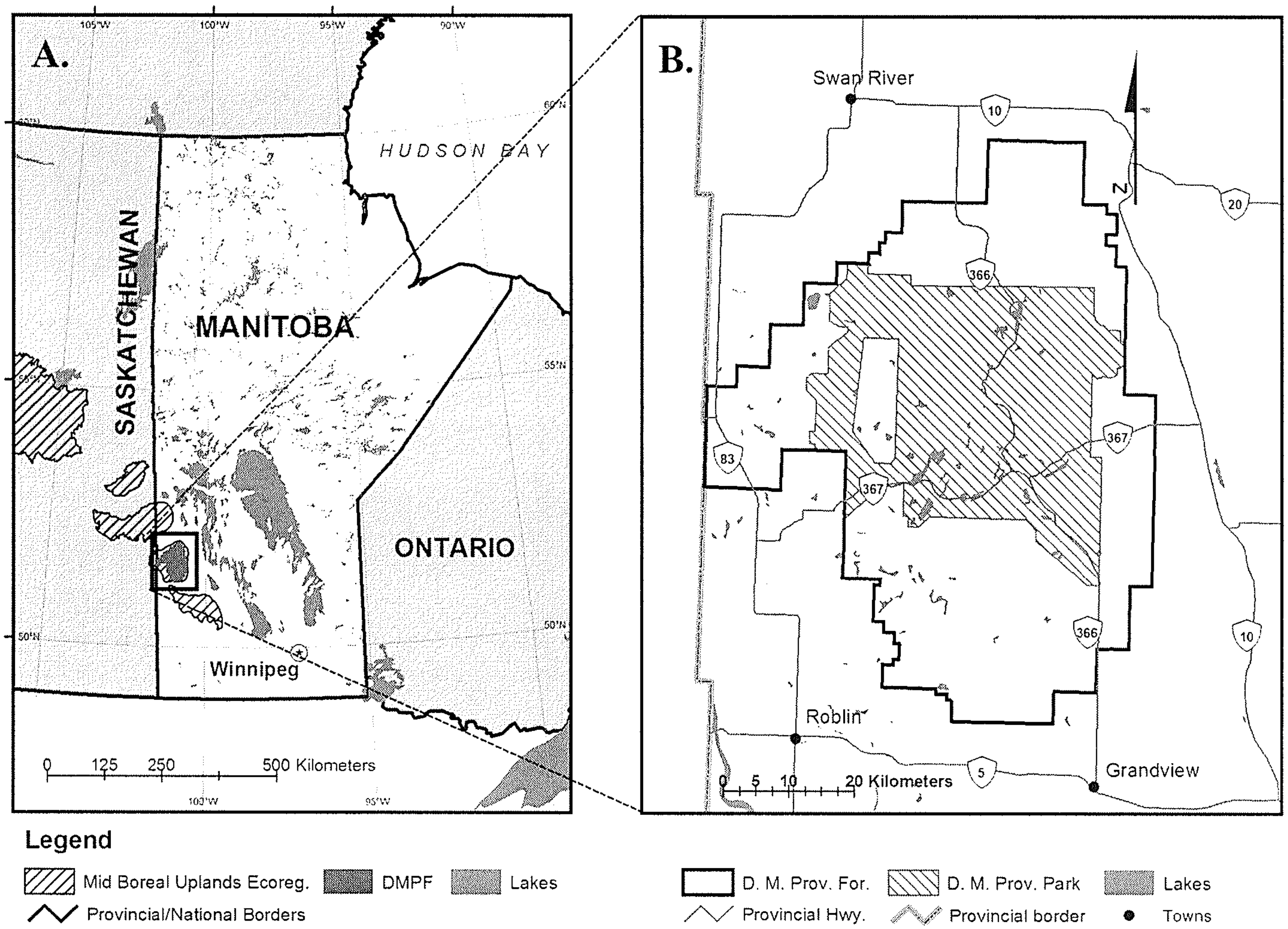


Figure 3. Map of study area showing location of DMPF and the Mid Boreal Uplands Ecoregion (data source: Schut, 2005) (A), and the provincial forest and provincial park boundaries (data source: Manitoba Conservation, 2000) (B). The meteorological station used for climate data is located at Swan River.

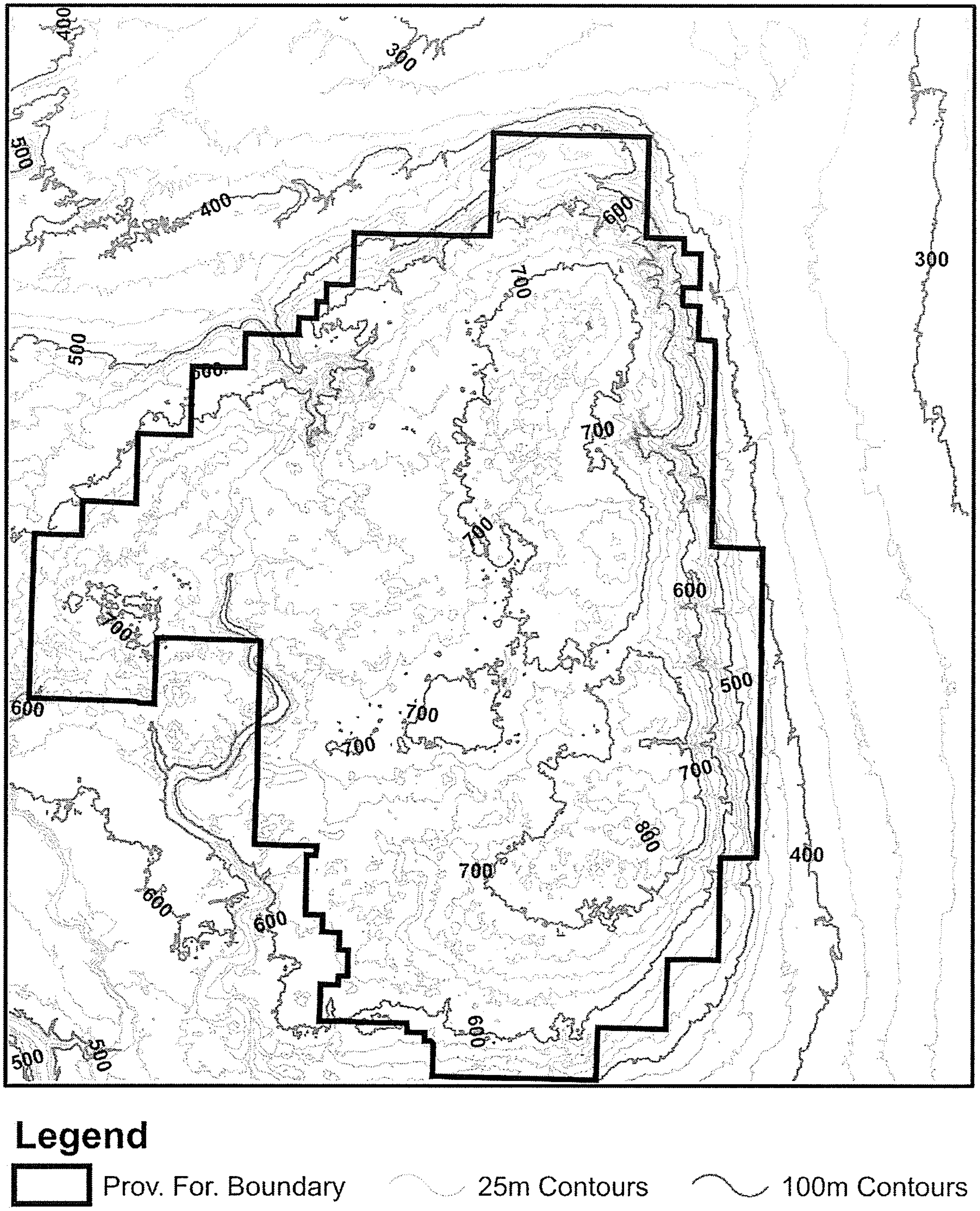


Figure 4. Topography of the DMPF landscape. Contours represent elevation isolines drawn at 25 m intervals. Bold isolines are labelled and occur at 100 m intervals (data source: Louisiana Pacific Canada, Ltd.).

Gray Chernozems, and poorly drained Luvic Gleysols associated with depressions (Smith et al., 1998).

The Mid-boreal Uplands Ecoregion is part of the Subhumid Mid-boreal Ecoclimatic Region (MBs), with predominantly short, cool summers and cold winters (EWG, 1989). In the MBs, the period of mean daily temperatures above 0°C extends from April to October, with up to 120 frost-free days. Maximum precipitation occurs in July for this region (EWG, 1989). Climate data from the meteorological station located at Swan River (Figure 6; 52° 03' N and 101° 13' W; elevation 346.6 m a.s.l., approx. 17 km from the NW border of DMPF) indicates that the temperature ranges from an average daily minimum of -23.0°C in January to average daily maximum of 24.4°C in July, and the average annual precipitation is 530.3 mm (Environment Canada, 2004b). The Duck Mountains plateau is, however, cooler than the surrounding lowlands, and could receive up to 50% more precipitation (MPB, 1973).

The forest cover in the upland area is dominated by mixed wood and conifer stands consisting primarily of trembling aspen, balsam poplar, white birch, jack pine, white spruce, and balsam fir in the uplands (Hamel and Kenkel, 2001; Sauchyn and Hadwen, 2001). Stands of black spruce and eastern larch occur in smaller patches in depressions and on gentle slopes, usually associated with organic substrates (Locky et al., 2005). The surrounding region is dominated by agricultural activity including crop production in the Swan River valley, and grazing and hay land near the base of the escarpment (Sauchyn and Hadwen, 2001).

The Duck Mountain area was first surveyed and mapped during the 1880's (Tyrrell, 1888). During this time the presence of Aboriginal settlements was noted in the surrounding area, as well as some agricultural activity. The DMPF was established as a forest reserve in 1906 and it was considered at the time to be the most valuable forest in the province with regards to its timber (Harrison, 1934). In 1961 the DMPP was established with a goal of protecting the natural integrity of the park while providing recreational activities and honouring existing resource commitments (Manitoba Conservation, 2003). The DMPF has provided a source of timber for European settlers as they settled the surrounding plains, and forestry continues to play an important role in this forest (Sauchyn and Hadwen, 2001). Since 1994 this land has been included in Louisiana-Pacific Canada's (LP's) management license (FML #3), and harvesting and silvicultural activities are ongoing within the DMPF. Louisiana-Pacific primarily utilizes hardwood fibre in this region, including trembling aspen, balsam poplar, and paper birch (LP, 2006a). There are also about 27 quota holders operating in the forest, primarily utilizing softwood fibres. The largest quota holder operating in the region is Spruce Products Ltd., with approximately 59.6% of the total softwood quota volume (LP, 2006b).

2.2 Forest Land Inventory of Duck Mountain Provincial Forest

The FLI was initiated by Louisiana-Pacific Canada Ltd. and Manitoba Conservation, and carried out by The Forestry Corp. between 2000 and 2003. The DMPF was initially stratified using 1:15,000 black and white infrared photography flown in

1998 (The Forestry Corp., 2003). Understory information was obtained using leaf-off color photography. Initial stratification of the forest was based on variability of forest cover. Adjacent polygons of similar vegetation composition were considered distinct if the minimum height difference was at least 3 metres. The minimum size allowed for forested polygons was 2 hectares, and the largest forested polygon in the database was 745 hectares.

Interpretation of the aerial photography was verified and calibrated using a series of truthing plots, which involved sampling stands at ground level to gather accurate data for the attributes, as well as air calls, where attributes were assigned from just above the canopy level from a helicopter. Potential truthing plots were selected by photo interpreters during the initial delineation and interpretation process. The goal for ground-truthing was 15 ground plots and 35 air calls per 100 km^2 map sheet. Ground plots and air calls were interspersed, allowing for calibration of the aerial height estimates. The raw FLI database consists of 60,334 polygons, with 444 ground truthing polygons, and 1096 air truthing calls. For quality control, 2-3% of the polygons were audited by an interpreter not involved in the original process. Externally, the audited polygons were re-interpreted by Manitoba Conservation staff. Stands from the audited group were selected by Manitoba Conservation for field verification visits by Manitoba Conservation and Forestry Corp. interpreters, and a representative from Louisiana-Pacific. Detailed information outlining the FLI process is documented in the *Forest Lands Inventory Specifications* (The Forestry Corp., 2003).

2.3 FLI database preparation

2.3.1 Correction of the FLI GIS vector database

Raw data from the FLI database had to be prepared so that it would be in a format suitable for analysis. The original GIS vector file for the entire DMPF landscape consisted of 60,334 treed and non-treed polygons that had been merged from 53 separate map sheets. As a result of the merge, many polygons at the edge of a map sheet were split between two map sheets and recorded as separate polygons with identical biological and abiotic attributes. To correct this, all of the split polygons were identified and dissolved into single polygons using ArcView GIS 3.3 (ESRI, 2002). The resulting database was reduced to a total of 46,603 treed polygons, with 404 ground checks and 1,041 air calls.

2.3.2 Conversion of FLI attributes

Attributes from the corrected database were classified into one of three categories based on the type of information they contained, including: (1) vegetation, (2) environmental, and (3) structural attributes. In the FLI, vegetation and structural attributes are divided into separate canopy layers if tree height varies by 3m or more, and the information for each layer is stored in a separate database. For our analysis, these separated databases had to be combined and each polygon was allowed a separate row for each canopy layer present. For ease of analysis, the original FLI attributes codes were modified and used as variable identifiers. Definitions of the codes are included in Appendix 1A, as well as in the *Forest Lands Inventory Specifications* (The Forestry Corp., 2003). Attributes from the three categories were then converted into a total of six matrices (Table 1), that were in a format suitable for statistical analysis. Any attributes

Table 1. The six matrices derived from the corrected FLI database and their characteristics. Included are the objectives, and specific analyses in which each of the matrices were used. Further details on the variables within each matrix are outlined in Appendix 1.

Information	Matrix No.	Data Type	No. Var.	Analysis
Vegetation	1	Cover values: upper canopy layer	8	Objective 1 (TWINSPAN, CCA)
	2	Cover values: 6m height classes	40 (5/spp.)	Objective 2 (RDA)
	3	Cover values: upper, intermediate, lower canopy levels	24 (3/spp.)	Objective 3, 4 (TWINSPAN)
Environmental	1	Quantitative/binary	14	Objective 1, 2 (CCA, RDA)
	2	Binary	11	Objective 1 (TWINSPAN)
Structural	1	Binary	10	Objective 1 (TWINSPAN)

that were defined by the FLI, but not represented in the converted matrices were eliminated. The converted matrices were cross-checked with the corrected FLI for validation.

Vegetation data:

Vegetation attributes were converted into three matrices to meet the different requirements for each objective (Table 1). For each matrix, the raw percent composition for each tree species was multiplied by the layer's percent crown closure to obtain a crown closure-weighted species cover value. For example, if a given layer of a polygon had a crown closure of 50%, and the corresponding percent composition of trembling aspen was 80%, then the cover value for trembling aspen in that layer would be recorded as 0.40. This provided greater weight to species with higher abundance (as inferred by crown closure) when comparing canopy layers as well as polygons. The first matrix (objective 1) consisted of species cover values for the dominant, upper canopy layer. For the second matrix (objective 2), species cover values for all layers were used, and using tree height, we created variables corresponding to 6-metre height classes (e.g. 6m height classes for trembling aspen: TA[1-6], TA[7-12],...TA[25-30]). For the third matrix (objectives 3 & 4) we used tree height to create another set of variables corresponding to the understory (1-6 m), intermediate (7-18 m), and overstory (19-30 m) tree height classes. This was done to reduce noise created by a large number of height classes, and to simplify the analysis and the interpretation for objectives 3 and 4.

Environmental data:

Environmental attributes were converted into two matrices (Table 1). For the first, categorical (nominal) attributes such as landform or soil type data were converted into binary variables, with a separate column for each category (Appendix 1C). Where possible, quantitative variables, such as moisture regime (class 1 to 5, dry to wet), and soil texture (fine to coarse), were converted into a single numeric ordinal variable. Quantitative variables representing actual ranges of values (e.g. percent slope) were converted to their native units, using the midpoint value of the corresponding class (Appendix 1C). Three additional variables not included in the inventory were appended to this matrix. The first two included elevation (m a.s.l.), derived from a digital elevation model (DEM) of the landscape, and log-transformed polygon size (ha) derived from the GIS database. The third was time-since-last-fire (TSLF), acquired from the fire history study by Tardif (2004). The resulting environmental matrix consisted of 14 variables, including 4 binary, and 10 quantitative variables (Appendix 1C). The second matrix was similar to the first, but all quantitative variables were retained as binary variables representing a range of values, which were determined from the distributions of histograms (e.g. low elevation = ELE_L (421–553 m); mid elevation = ELE_M (554–685 m); high elevation = ELE_H (686–816 m). This matrix was used solely with two-way indicator species analysis (TWINSPAN), which requires that all variables be of the same scale.

Structural data:

Structural attributes were converted into a single matrix of binary variables in the same format as environmental matrix 2 (Table 1; Appendix 1D). One new variable (CPAT_Cplx) was created as a general measure of the degree of vertical and horizontal canopy arrangement complexity. This variable represents the number of unique horizontal cover arrangements (CAPAT) among all layers of a given canopy (Appendix 1D). For example, if a given stand has three layers, and each layer has a different cover arrangement, then CPAT_Cplx = 3. However, if two layers have the same arrangement and one layer is different, then CPAT_Cplx = 2. The resulting structural matrix consisted of 10 binary variables (Appendix 1D).

2.3.3 Extraction of data subsets for analysis

To complete the first, second, and fourth objectives, data pertaining to the 1445 truthing polygons (404 ground checks and 1,041 air calls) were used. This subset was used because the full dataset (46,603 polygons) exceeded the maximum number of data rows analyzable for CANOCO v. 4.52 (ter Braak and Smilauer, 2003) and PC-ORD v. 4.36 (McCune and Mefford, 1999), and the truthing polygons were believed to represent the most accurate data in the inventory due to their closer scrutiny. Any group assignments that resulted from the classification of the truthing polygons were later applied to the remaining (non-truthing) polygons using a multiple discriminant analysis (MDA) classification function.

For the analysis of successional trajectories from stands originating in the 1880's and 1890's fires (objective 3), the time-since-last-fire (TSLF) map developed by Tardif (2004) for DMPF (Appendix 1F) was used. First, a total of 15,085 polygons contained within the extent of these fires were extracted. These polygons were further screened to eliminate stands that were identified in the FLI as having been more recently disturbed or treated in any way. Next, FLI inventory dates were used to eliminate any other polygons in which the age greatly deviated from the 1880–1900 range. Comparison of the FLI ages with sampling point dates obtained from the TSLF analysis (Tardif, 2004) showed that there was a significant but poor correlation (adjusted $r^2 = 0.1018$, $P = <0.0001$, $n = 283$) between FLI origin dates and the TSF study ages, obtained by cross-dated wood samples. Based on this comparison, the FLI stand ages for polygons corresponding to the 1880-90 fires were underestimated by nearly 20 years on average. To minimize uncertainty, all polygons with an inventory origin prior to 1880 were eliminated, and no polygon was allowed with an origin later that 1910. All polygons with a cross-dated age available (from Tardif, 2004) were flagged, and this age was used rather than the FLI age. The resulting 1880-90 matrices consisted of 11,228 polygons covering an area of 73,015 ha. For classification and ordination analyses, randomly selected subsets of 693 polygons were taken from each major successional pathway identified in objective 1. This number corresponded to the successional pathway (see section 2.6 below) with the lowest number of polygons. Subsets were taken in order to place all successional pathways on equal footing for analysis and comparison. The final matrix consisted of 2,079 polygons.

2.4 Statistical procedures

Classifications in objectives 1, 3, and 4 were carried out with Two-way Indicator Species Analysis (TWINSPAN) in PC-ORD v. 4.36 (McCune and Mefford, 1999). This method was chosen because it identifies characteristic species for each group, as well as the relationship between groups. Although some problems have been identified with the application of this classification method (Legendre and Legendre, 1998), the presence of a strong, simple gradient in our data, and a low number of divisions partially alleviate these problems. For species cover values, pseudospecies cut levels were set at 0, 0.05, 0.15, 0.25, 0.35, 0.45, 0.55, 0.65, and 0.75. For the environmental and structural matrices the "presence/absence" option was selected. The final number of groups selected was based on differences in terms of composition, group size, and the accuracy of re-classification following a multiple discriminant analysis (MDA) of the candidate groups (see below). Multiple discriminant analysis (objectives 1 and 3) was carried out with SYSTAT v. 11 (SSI, 2004). For all MDAs, a stepwise classical discriminant analysis was used with backward selection (Probability to enter and remove = 0.05) to identify the best discriminating variables for the model. Prior group membership probabilities were computed from group size. Jack-knifed re-classification tables were used to assess the accuracy of the models.

Canonical correspondence analysis (CCA) and redundancy analysis (RDA) in objectives 1 and 2, respectively, were carried out with CANOCO v. 4.52 (ter Braak and Smilauer, 2003). Co-linear variables were eliminated according to inflation factors ($\geq$10.0), and forward selection was used to identify significant environmental variables (*P*

< 0.05 after 999 Monte-Carlo permutations). Elimination of co-linear and non-statistically significant variables greatly reduced the number of candidate variables in each analysis, simplifying interpretation of the results. Log-transformed species cover values were used for both the CCA and RDA. For the RDA, the covariance association matrix was used. For the CCA, any species represented in less than 5% of the polygons in the analysis were eliminated to reduce the impact of outliers. All eliminated variables were retained as passive variables in the analyses. Pearson chi-square tests were carried out in SYSTAT v. 11 (SSI, 2004) under a two-way table analysis.

2.5 Characterization of the upper canopy, environment, and structure

Upper canopy species cover values belonging to the truthing polygons were used to identify canopy types after a TWINSPAN. Environmental and structural attributes were also respectively classified using TWINSPAN to identify environmental and structural types. These groups were retained as passive variables in subsequent analyses. This approach helped simplify interpretation of the results. Classification functions were also derived from MDA to allocate each of the remaining 45,158 polygons in the DMPF (that were not part of the truthing ground checks and air calls) into a canopy, environmental, and structural type. The MDA classification functions were in the form of:

(Eq.1) $Score_{ji} = C_j + b_{j1}x_{i1} + b_{j2}x_{i2} + \ldots + b_{jn}x_{in}$

Where $Score_{ji}$ is the score for group j for object i, C_j is a constant for group j, b_{jn} is the weight for the variable x, and x_{in} is the value for variable n of object i. For each object, the group score was calculated, and the group with the highest score was the group the object was assigned to.

The result of the TWINSPAN was used to identify the major successional pathways in DMPF. A distribution map of the successional pathways and canopy types was created, and the relative landscape area for each group was calculated to obtain an importance value. Canonical correspondence analysis was used to determine the relationship between the successional pathways and environmental variables, with the environmental and structural types included as passive variables. The CCA method was chosen after examining the upper canopy species cover values and finding that the dominant species exhibited species turnover, indicating a unimodal distribution of tree species (ter Braak and Prentice, 1988; Legendre and Legendre, 1998; Kenkel, 2006).

2.6 Analysis of major successional pathways (6m height class)

Detailed analysis of the variability within each major successional pathway was carried out using the species cover data described for objective 2 (Section 2.3.2). Redundancy analysis was performed on the species cover values and the environmental matrices with environmental and structural types included as passive variables. The RDA approach was used in this case because examination of the data did not suggest turnover of the dominant species within pathways (Legendre and Legendre, 1998; Kenkel, 2006).

2.7 Analysis of 1880-90's fire-originated stands

To characterize variability in stands originating from the 1880-90 fires, TWINSPAN was performed on the random subset of species cover values described for objective 3 (Section 2.3.2). The resulting groups were used to define successional trajectories within each pathway at 100-120 years after stand initiation. The remaining 8,207 polygons were assigned to trajectories using MDA. The distribution of structural types was compared between trajectories and pathways to characterize structure for stands originating from approximately the same time. For each trajectory, significant deviations from the expected distribution of structural types were identified using a Pearson chi-square test.

2.8 Definition of structural cohorts and application of the management model

A similar approach to that of Harvey et al. (2002) was used to assign polygons to one of three structural cohorts. Assignments were based on information obtained from objective 3 regarding the relationship between stand age, species composition, and structural types, as well as literature regarding mixed boreal forest stand development (Hamel and Kenkel, 2001; Chen and Popadiouk, 2002; Brassard and Chen, 2006). After all polygons were assigned to a cohort, the proportion of each cohort over the landscape was calculated and a distribution map was created. To illustrate the composition and structure of stands within each cohort, diagrams of stand profiles were created. This was accomplished by performing TWINSPAN on the species cover data described for objective 4 (section 2.3.2) pertaining to the 1445 truthing polygons to identify species assemblages for each pathway. The distribution of cohorts was calculated for each assemblage, and a stand profile (based on species cover and structural type) was constructed for each cohort represented in ≥10% of a given assemblage. Three management scenarios were presented. The first was based on maintaining the current distribution of cohorts in the landscape, the second was based on maintaining the current mean forest age of 110 years, and the third was based on maintaining a pre-European settlement fire cycle of ~60 years. The proportions of the forest to be managed under even-aged and uneven-aged silviculture were calculated with respect to the different management goals.

3. RESULTS

3.1 Characterization of the upper canopy, environment, and structure

Of the total 376,916.5 ha, 84.1% (316,971.5 ha) of DMPF was treed, and six canopy types were identified by TWINSPAN (Table 2; Figure 5). These canopy types include: (1) trembling aspen dominated; (2) trembling aspen dominated with a white spruce and balsam poplar component; (3) trembling aspen dominated with a balsam poplar component; (4) white spruce dominated; (5) jack pine dominated with a black spruce and trembling aspen component; and (6) black spruce dominated canopy with an eastern larch component. The MDA model successfully re-classified 84% of the cases into the correct canopy type (Appendix 3A). After applying the model to the remaining 45,158 polygons, canopy type 1 was found to be the most common, composing 26.3% of the treed area, and canopy type 5 was the least common, composing 6.2% of the treed area (Figure 6).

Based on the TWINSPAN division of canopy types and their dominating tree species, three major successional trajectories were identified: (1) a trembling aspen-white spruce pathway (canopy types 1-4); (2) a jack pine-black spruce pathway (canopy type 5); and (3) a black spruce-eastern larch pathway (canopy type 6). The trembling aspen-white spruce pathway comprised 79.7% of the treed landscape, followed by the black spruce-eastern larch pathway at 14.1%, and the jack pine-black spruce pathway at 6.2% (Figure 6).

Table 2. Characteristics of the six canopy types identified using TWINSPAN with the 1445 truthing plots. Shown are the percent frequency (F%), and the mean weighted percent species cover values (C%) and standard deviation (SD) for each species (TA = trembling aspen; BA = balsam poplar; WB = paper birch; WS = white spruce; BS = black spruce; JP = jack pine; BF = balsam fir; TL = eastern larch). Mean percent cover values are derived from all polygons in the group.

	1. TA (*n* = 305)			2. TA(WS,BA) (*n* = 163)			3. TA(BA) (*n* = 214)			4. WS (*n* = 342)			5. JP(BS,TA) (*n* = 161)			6. BS(TL) (*n* = 260)		
Spp	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD
TA	100	62	19	100	41	10	97	17	12	26	2	6	55	4	6	5	<1	1
BA	36	2	3	58	5	7	73	8	14	6	<1	1	1	0	0	2	<1	<1
WB	11	1	3	10	1	2	47	5	12	2	<1	1	7	1	3	1	<1	1
WS	18	1	2	73	4	5	41	2	4	100	19	16	25	2	4	6	<1	1
BS	2	<1	1	1	<1	<1	20	1	3	15	1	3	78	11	11	98	38	23
JP	5	<1	2	25	2	5	23	4	10	4	1	3	98	36	19	19	2	5
BF	<1	<1	1	3	<1	1	1	<1	1	8	1	4	1	0	1	<1	<1	<1
TL	<1	<1	1	—	—	—	1	<1	<1	2	<1	1	6	0	2	61	6	11

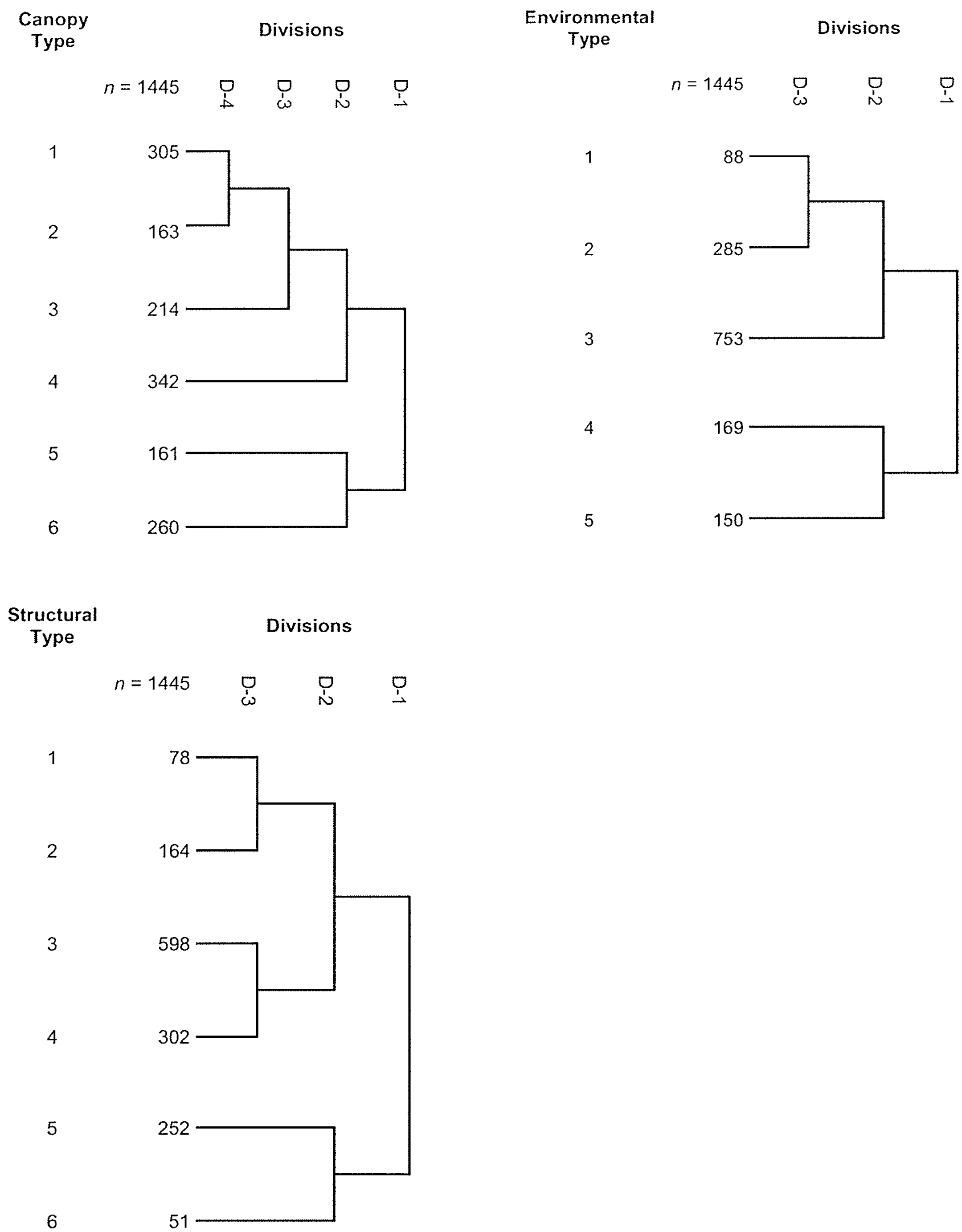


Figure 5. Dendrograms outlining the groups resulting from TWINSPAN for the upper canopy species cover values (canopy types), environmental variables (environmental types), and structural variables (structural types). Detailed descriptions for each group are presented in the text. Included at the end of each branch are the number of individuals in each group, out of a total of 1445 truthing polygons.

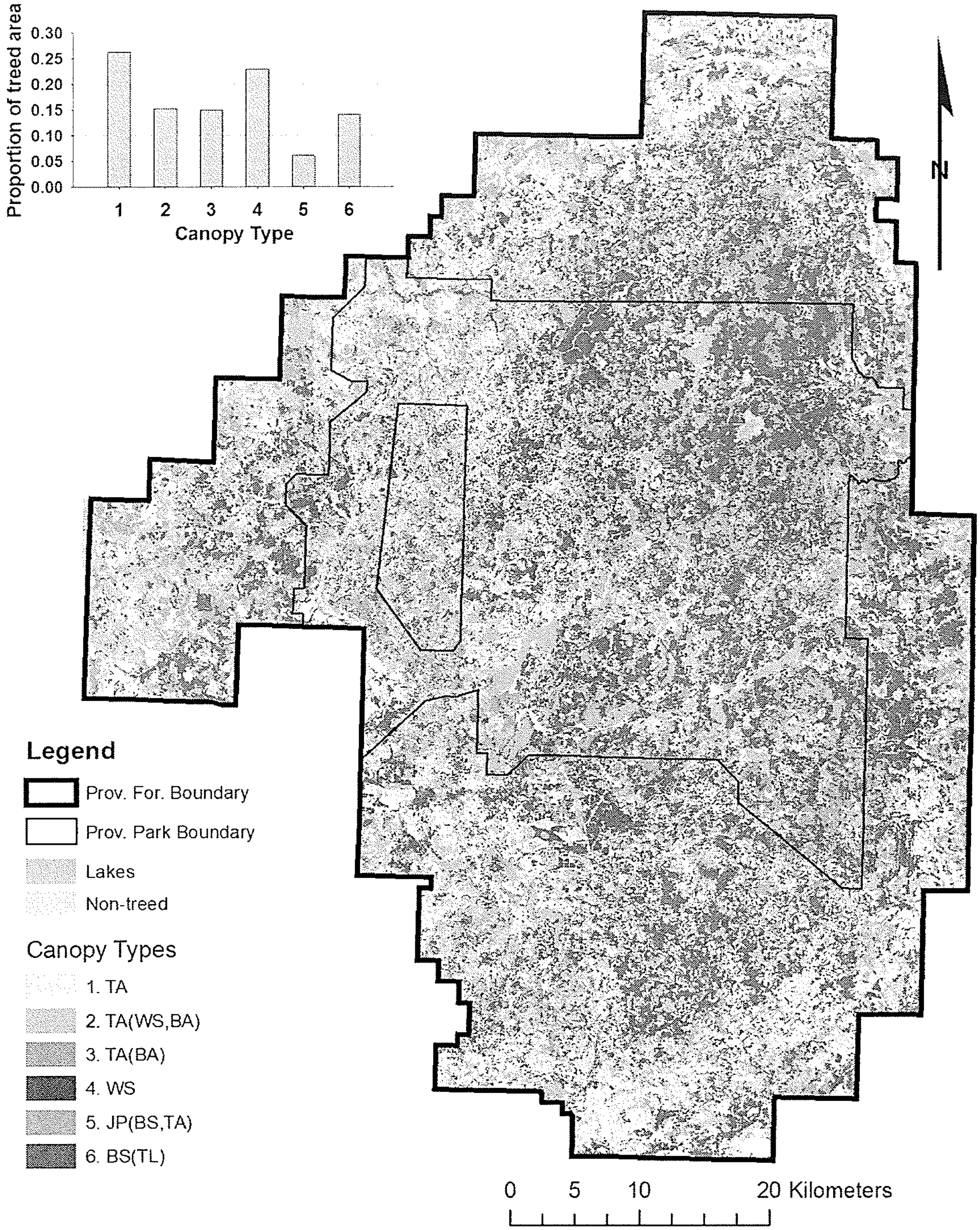


Figure 6. Distribution map of the canopy types classified over the Duck Mountain landscape. The bar chart shows the proportion of treed area represented by each canopy type (numbered 1 to 6 in legend). Green shades represent the trembling aspen-white spruce pathway, pink represents the jack pine-black spruce pathway, and brown represents the black spruce-eastern larch pathway.

Classification of the environmental data produced five environmental types (Figure 5; Appendix 4A). These include: (1) steep, upper slopes, dominated by medium soil textures, and a predominately very fresh to fresh moisture regime (E1); (2) middle slopes, hummocky, and complex topography dominated by medium soil textures and a very fresh to fresh moisture regime (E2); (3) middle to lower slopes, undulating and planar topography, predominately fine soil texture and a very fresh moisture regime (E3); (4) lower slopes and flat, level topography, dominated by fine soil textures and a moist moisture regime (E4); and (5) flat and depressed sites, dominated by peat and organic substrates, with a wet moisture regime (E5). The MDA classification functions successfully re-classified 89% of the polygons into their correct environmental type (Appendix 3B). Following landscape classification, the environmental type 3 (middle to lower slopes, undulating landscape) was found to be the most common, occurring with 47.04% of the forested polygons. Environmental type 5 (wet, organic) was the least common, occurring with 8.49% of the forested polygons (Appendix 4B).

Classification of structural data produced six structural types (Figure 5; Appendix 4C). These include: (1) a two- to three-layered group (with intermediate layers) with moderately variable cover arrangement and some conifer recruitment, up to 30 m tall, with a non-continuous canopy but more continuous intermediate layer (S1); (2) a three-layered group with highly variable cover arrangement, often with conifer recruitment in the understory, usually up to 24 m tall, often with a veteran layer, the main canopy is usually more continuous than intermediate layers (S2); (3) a two-layered group (usually overstory and understory layers) with moderately variable cover arrangement and conifer recruitment in the understory, 18- 24 m tall, with a more continuous overstory than understory (S3); (4) a two-layered group with a less variable cover arrangement, sometimes with an intermediate layer and conifer recruitment, 18-24 m tall, with a less continuous overstory layer (S4); (5) a single, usually continuous layer, with a height range up to 24 m (S5); and (6) a complex canopy of variable heights, with an average height of 6-12 m (S6). The discriminant analysis model successfully re-classified 94% of the polygons into their correct structural type (Appendix 3C). Following landscape classification, structural type 3 was found to be the most common, comprising 41.42% of the total treed polygons, while structural type 6 was the least common comprising 2.18% (Appendix 4D).

Canonical correspondence analysis of the upper canopy species cover values and environmental variables revealed that the later explained a total of 23.7% of the variation in the upper canopy cover data on all canonical axes. The first and second environmental axes were significantly correlated with the first and second species axes (r = 0.833 and 0.463, respectively; $P = 0.001$). Most of the variation (17.5%) was explained by the first axis, which primarily reflected an environmental gradient from steeper upper slopes with a fresh moisture regime, mineral, and till substrates (F_TILL, TILL), to flat landforms with a wet moisture regime and organic substrates (Figure 7). The trembling aspen-white spruce pathway tended to be associated with the drier, sloping sites and larger polygons. The black spruce-eastern larch pathway tended to be associated with the flat, wet sites. The second CCA axis explained 3.8% of the variation in species cover data and primarily

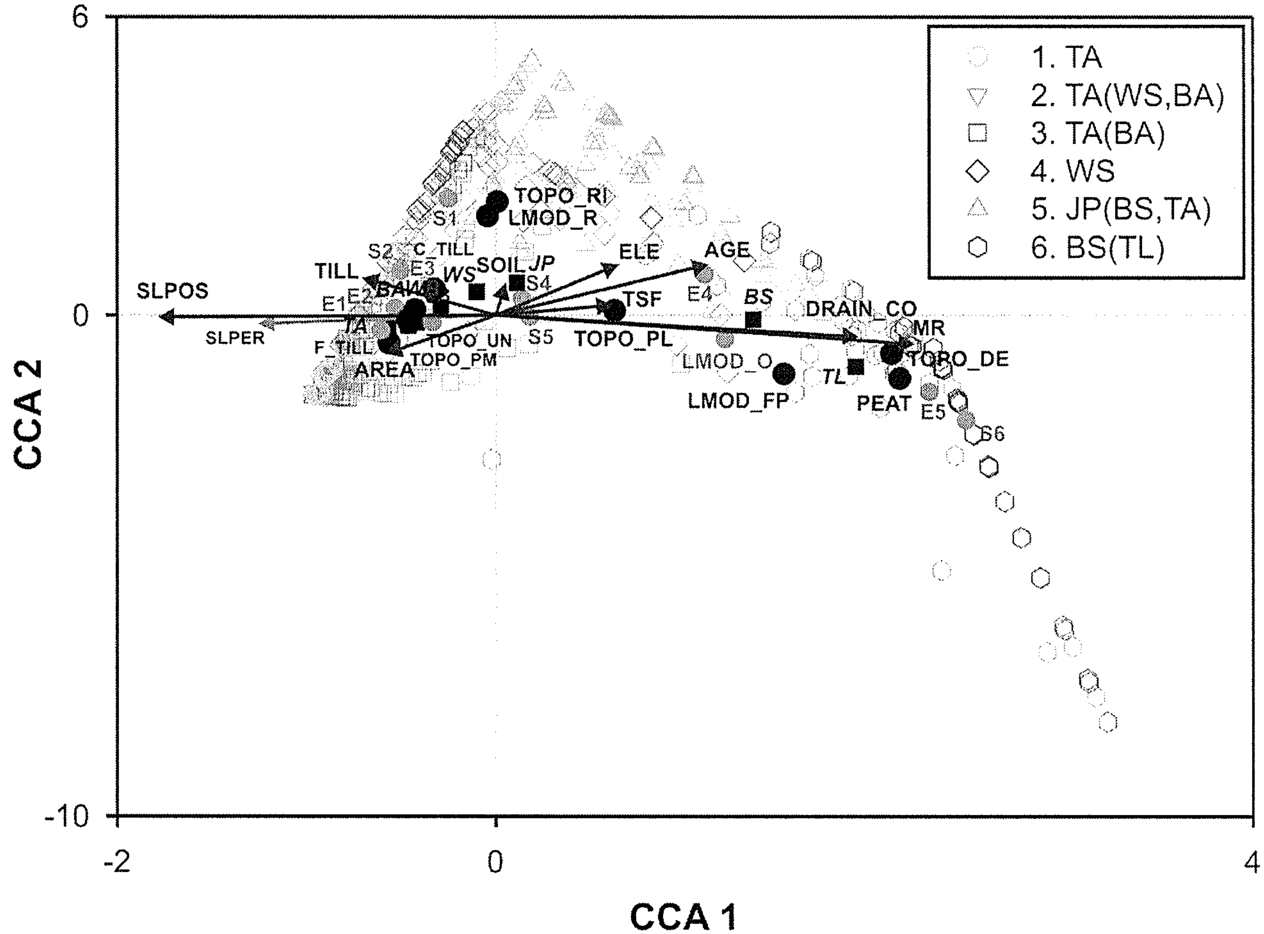


Figure 7. Canonical correspondence analysis of upper canopy species cover and environmental attributes corresponding to the 1445 ground truthing plots. Black squares represent species, black vectors and circles represent significant quantitative and binary variables, respectively. Dark gray vectors and circles are passive. The six canopy types identified by TWINSPAN are represented by different coloured empty symbols. Labels for the variables are identified in Appendix 1. Included are the environmental types (E1-5) and structural types (S1-5).

reflected a gradient from lower to higher elevation sites, with the jack pine-black spruce pathway associated more strongly with the higher elevations.

3.2 Analysis of major successional pathways (6m height class)

3.2.1 Trembling aspen-white spruce pathway

Redundancy analysis of the trembling aspen-white spruce successional pathway indicated that 13.1% of the variation in species cover was explainable by the environmental variables on all canonical axes (Figure 8). The first and second environmental axes were significantly correlated to the first and second species axes ($r = 0.502$ and 0.480, respectively; $P = 0.001$). The first RDA axis reflected a gradient from older stands to younger stands and explained 6.9% of the total variance in species cover. Older stands tended to be associated with the taller height classes, while smaller height classes tended to be associated with younger stands and recently burned sites (MOD_BU). The second RDA axis was related to a moisture and slope gradient, and explained 4.4% of the total species variance. Broadleaf species tended to dominate on the drier upper slopes, and were associated with larger polygons, while conifer species tended to dominate on wetter sites and the lower and flat slopes. The more complex structural types, particularly structural type 1, were associated with the coniferous species, while structural types 3 and 5, which are least complex, were associated with trembling aspen (Figure 8). Overall, although the environmental and species axes were significantly correlated, the predictive power of environmental variables with respect to species variance was fairly low, suggesting that within this pathway environment plays

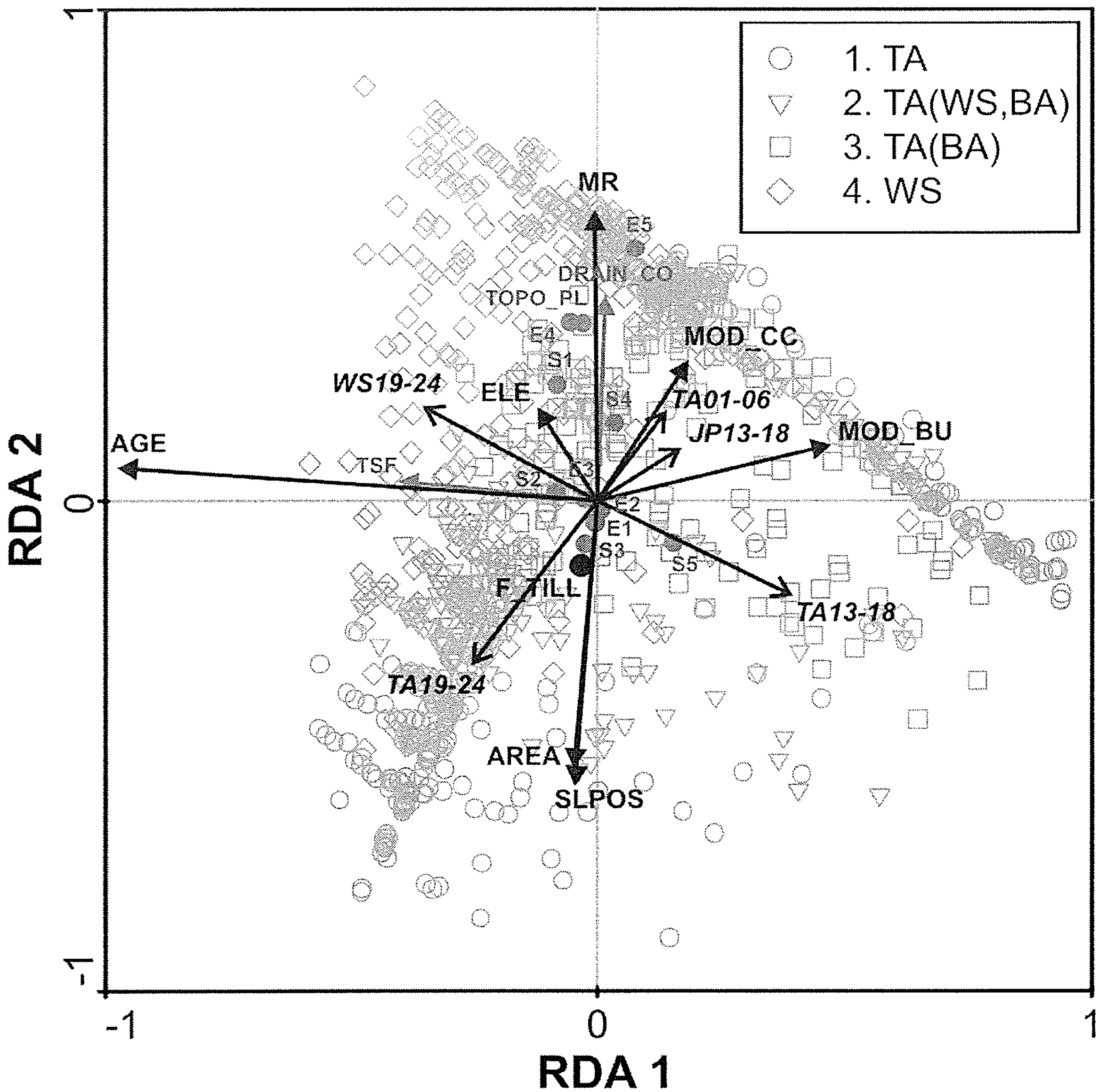


Figure 8. Redundancy analysis of the trembling aspen-white spruce pathway 6m height class species cover data and environmental variables ($n = 1024$). Open gray symbols represent the 4 canopy types in this pathway. Black vectors with open arrows represent species height classes. Black vectors with closed arrows and circles represent significant quantitative and binary environmental variables, respectively. Dark gray vectors and circles are passive. Only the species with a fraction of total species variance explained ≥ 10% are presented to simplify interpretation. Labels for the variables are identified in Appendix 1.

only a minor role in determining the composition of the canopy profile.

3.2.2 Jack pine-black spruce pathway

Redundancy analysis of the jack pine-black spruce pathway indicated that 19.8% of the variation in species cover was explainable by the environmental variables on all canonical axes (Figure 9). The first and second environmental axes were significantly correlated to the first and second species axes (r = 0.709 and 0.325, respectively; P = 0.001). The first axis explained most of the variance in species cover (12.5%) and represented a gradient from older to younger stands in terms of FLI stand origin. The species in taller height classes tended to be associated with the older sites, while the shortest height classes (1–6 m) were rare, occurring in less than 10% of the sites analyzed, and they tended to be associated with recently burned (MOD_BU) or clearcut (MOD_CC) sites (Figure 9). The second RDA axis explained only 3.2% of the variance in species cover, and was primarily associated with till texture and moisture, with the 19–24 m height classes tending to occur on coarser tills (TILL), and with black spruce and eastern larch associated with the wetter sites. Younger sites in terms of FLI age and shorter height classes tended to be associated with simpler structural types, particularly structural type 5, which consists of single layer canopies.

3.2.3 Black spruce-eastern larch pathway

Redundancy analysis of the black spruce-eastern larch pathway indicated that 14.4% of the variation in species cover was explainable by the environmental variables

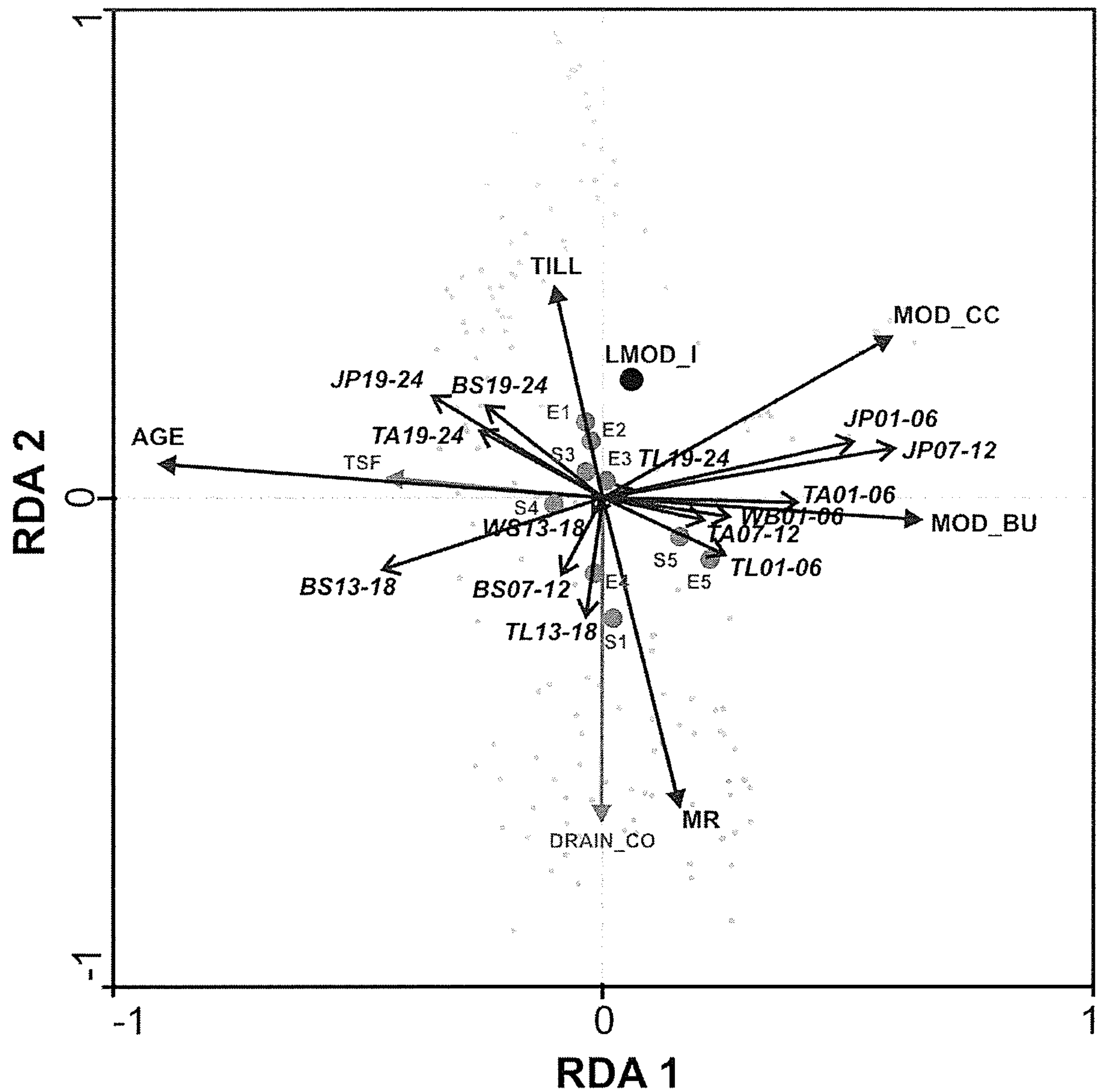


Figure 9. Redundancy analysis of the jack pine-black spruce pathway 6m height class species cover data and environmental variables (n = 161). Black vectors with open arrows represent species height classes. Black vectors with closed arrows and circles represent significant quantitative and binary environmental variables, respectively. Dark gray vectors and circles are passive. Only the species with a fraction of total species variance explained ≥ 10% are presented to simplify interpretation. Labels for the variables are identified in Appendix 1.

on all canonical axes (Figure 10). The first and second environmental axes were significantly correlated to the first and second species axes (r = 0.561 and 0.209, respectively; $P = 0.001$). The first axis explained most of the variance of species cover (13.4%), and was primarily related to a gradient of moisture and age. The taller height classes tended to be associated with drier moisture regimes, steeper slopes, and mineral soils (SOIL), and were somewhat older in terms of FLI age (Figure 10). The second RDA axis explained only 1.0% of the species variance and was most strongly correlated with FLI age. Wetter sites tended to be more strongly associated with structural type 6 (S6), which has a complex height structure. While FLI age is correlated with the first RDA axis, in this pathway moisture appears to dominate the environmental gradient.

3.3 Analysis 1880-90's fire-originated stands

3.3.1 Trembling aspen-white spruce pathway

Of the 11,228 polygons originating from the 1880-90 fires, this pathway represents approximately 73.8% (53,841 ha) of the total area. TWINSPAN resulted in the identification of five successional trajectories (Table 3; Appendix 2A). The upper canopies of trajectories 1–3 were trembling aspen-dominated. Trajectories 1 and 3 had white spruce-dominated and mixed intermediate layers, respectively, and trajectory 2 had an infrequent intermediate layer with low species cover values. Trajectory 4 was dominated by white spruce in the upper and intermediate canopy layers, and trajectory 5 was a mixture of black spruce and white spruce in the intermediate layer, with an infrequent upper canopy layer of white spruce. The MDA model used to classify the remaining 1880-90 polygons successfully re-classified the polygons into their correct

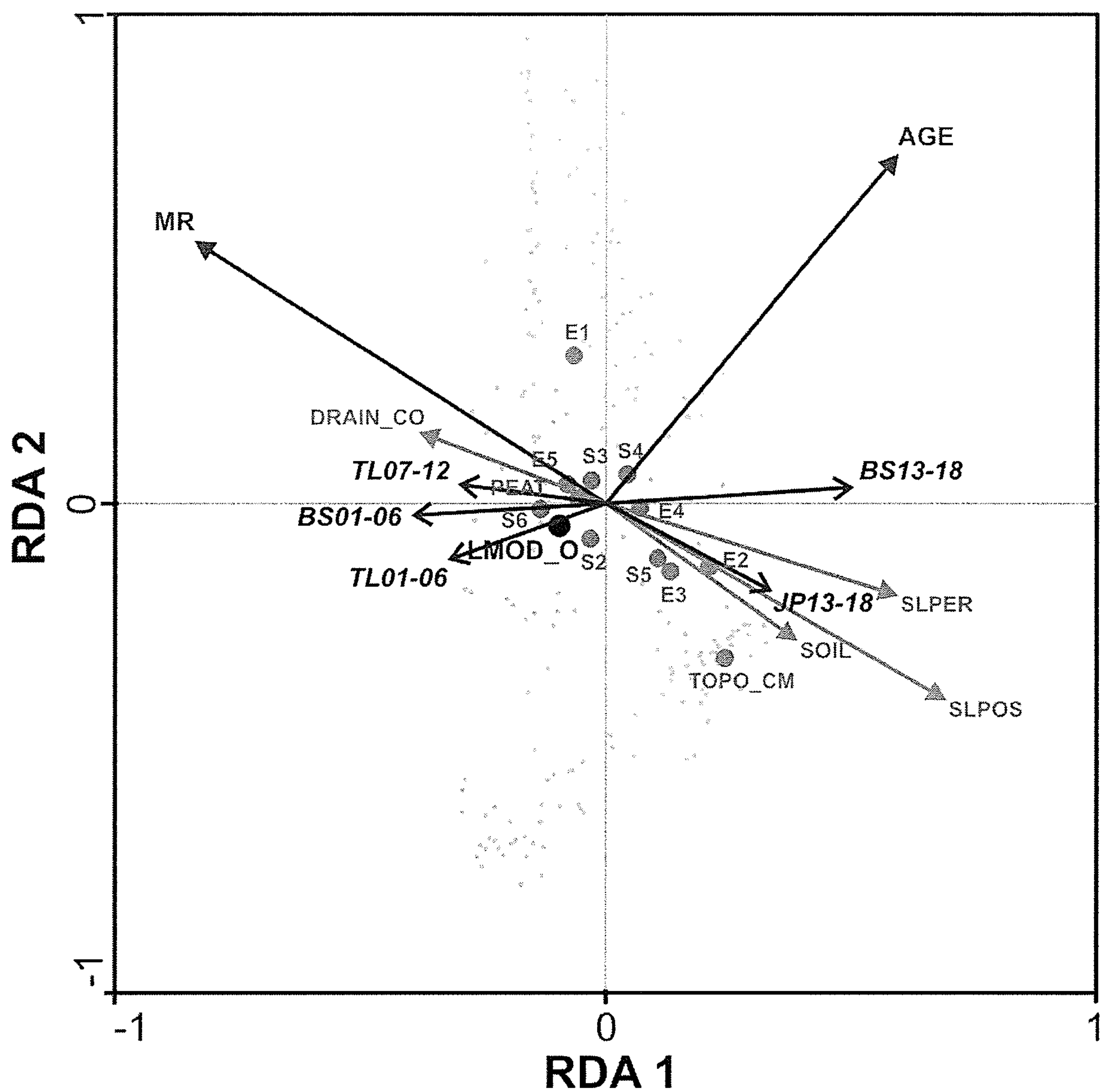


Figure 10. Redundancy analysis of the black spruce-eastern larch pathway 6m height class species cover data and environmental variables (n = 260). Black vectors with open arrows represent species height classes. Black vectors with closed arrows and circles represent significant quantitative and binary environmental variables, respectively. Dark gray vectors and circles are passive. Only the species with a fraction of total species variance explained ≥ 10% are presented to simplify interpretation. Labels for the variables are identified in Appendix 1.

Table 3. Characteristics of the five trajectories identified using TWINSPAN with the random subset of the 1880-90 fire-originated polygons (n = 693) from the trembling aspen-white spruce pathway. Shown are the percent frequency (F%), and the mean weighted species cover values (C%) and standard deviation (SD) for each species by height class (see Appendix 1B for species codes).

	Trajectory 1 (n = 51)			Trajectory 2 (n = 158)			Trajectory 3 (n = 178)			Trajectory 4 (n = 120)			Trajectory 5 (n = 186)		
Spp[ht.class]	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD
TA[19-30]	100	61	13	100	62	13	95	24	14	78	12	13	32	4	10
BA[19-30]	63	4	4	46	3	4	80	8	10	26	2	6	13	1	4
WB[19-30]	2	0	1	11	1	2	25	1	3	6	0	2	4	0	1
WS[19-30]	69	4	3	51	4	7	66	4	6	94	24	20	51	7	11
BS[19-30]	2	0	1	5	0	2	15	1	2	12	1	2	32	2	4
JP[19-30]	4	0	1	8	1	2	13	1	4	9	1	3	20	2	5
BF[19-30]	—	—	—	1	0	0	1	0	0	10	1	5	—	—	—
TL[19-30]	—	—	—	—	—	—	1	0	0	—	—	—	2	0	0
TA[7-18]	2	0	0	13	1	4	60	12	17	44	4	8	41	10	19
BA[7-18]	8	0	1	7	0	0	35	2	4	24	1	3	27	2	5
WB[7-18]	2	0	0	8	0	2	53	5	9	11	0	1	22	2	8
WS[7-18]	100	51	20	47	6	8	68	10	13	86	29	21	65	8	12
BS[7-18]	16	1	3	13	1	4	36	3	5	33	2	5	85	26	25
JP[7-18]	—	—	—	—	—	—	3	0	1	3	0	1	16	1	5
BF[7-18]	2	0	1	3	0	1	2	0	0	16	2	5	2	0	1
TL[7-18]	2	0	1	0	0	0	1	0	0	1	0	0	9	0	2
TA[1-6]	—	—	—	—	—	—	—	—	—	1	0	0	2	0	3
BA[1-6]	—	—	—	—	—	—	1	0	0	—	—	—	—	—	—
WB[1-6]	—	—	—	1	0	0	1	0	0	1	0	0	3	1	5
WS[1-6]	2	0	2	4	1	6	3	0	3	2	0	2	4	0	1
BS[1-6]	—	—	—	—	—	—	2	0	1	—	—	—	4	1	5
JP[1-6]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
BF[1-6]	—	—	—	—	—	—	—	—	—	1	0	1	—	—	—
TL[1-6]	—	—	—	—	—	—	—	—	—	—	—	—	1	0	0

trajectory for 84% of cases (Appendix 3D). The most common trajectory with respect to landscape area was trajectory 3, comprising 27.8% of the land base in the pathway. Overall, trembling aspen-dominated trajectories were most common, comprising a total of 66.3% of the land base, followed by trajectory 5 at 18.3%, then trajectory 4 at 15.4%.

The distribution of structural types within the trembling aspen-white spruce pathway trajectories illustrates a range of structural characteristics (Table 4). Globally, structural type 3 is most strongly represented in this pathway, followed by structural type 4 and 5. Structural type 1, representing the highest level of complexity, is least represented in this pathway. The Chi-square test showed that there was a significant deviation from the expected distribution of structural types (df = 16; $\chi^2 = 194.85$; $P = <0.001$), indicating that there may be some association between the trajectories and structural types. The largest deviation was associated with trajectory 2, which is composed primarily of trembling aspen with little understory development, and structural types 5 (simple, even-aged stands) and 4 (multi-layered stands), which were higher and lower than expected, respectively. Trajectory 4, which is conifer dominated with lower species cover values for the upper canopy, and structural type 1, which describes stands with a high degree of structural complexity, was associated with the next largest deviation which was higher than expected (Table 4).

Table 4. Contingency table for the 1880-90 trajectories by successional pathway. Included are the observed frequencies (O), expected frequencies (E), and the standardized deviates* (D). Standardized deviates in boldface type are those referred to in the text.

Trajectory		Structural Type S1	S2	S3	S4	S5	S6
Trembling aspen-white spruce pathway							
1	O	2	7	34	8	0	—
	E	2.4	5.3	23.6	13.3	6.4	—
	D	-0.3	+0.7	+2.2	-1.5	-2.5	—
2	O	0	12	85	6	55	—
	E	7.5	16.4	73.0	41.3	19.8	—
	D	-2.7	-1.1	+1.4	**-5.5**	**+7.9**	—
3	O	5	17	79	65	12	—
	E	8.5	18.5	82.2	46.5	22.3	—
	D	-1.2	-0.3	-0.4	+1.9	-1.8	—
4	O	17	24	29	42	8	—
	E	5.7	12.5	55.4	31.3	15.1	—
	D	**+4.7**	+3.2	-3.5	+1.9	-1.8	—
5	O	9	12	93	60	12	—
	E	8.9	19.3	85.9	48.6	23.4	—
	D	0.0	-1.7	+0.8	+1.6	-2.3	—
Jack pine-black spruce pathway							
1	O	—	3	224	142	90	—
	E	—	2.0	205.3	142.4	109.3	—
	D	—	+0.7	**+1.3**	0.0	**-1.8**	—
2	O	—	0	86	73	75	—
	E	—	1.0	104.7	72.6	55.7	—
	D	—	-1.0	**-1.8**	0.0	**+2.5**	—
Black spruce-eastern larch pathway							
1	O	0	0	38	7	6	1
	E	0.4	0.3	16.1	12.2	19.0	4.1
	D	-0.6	-0.5	**+5.4**	-1.5	**-3.0**	-1.5
2	O	4	2	124	117	241	46
	E	3.9	3.1	165.7	124.8	195.0	41.6
	D	+0.1	-0.6	**-3.2**	-0.7	**+3.3**	+0.7
3	O	1	2	53	38	6	7
	E	0.8	0.6	33.2	25.0	39.1	8.3
	D	+0.3	+1.8	**+3.4**	+2.6	**-5.3**	-0.5

* Standardized deviates are computed as: (Observed-Expected)/√(Expected)

3.3.2 Jack pine-black spruce pathway

This pathway represents approximately 6.9% (5,049 ha) of the 11,228 polygons originating from the 1880-90 fires. TWINSPAN resulted in the identification of two successional trajectories (Table 5; Appendix 2B). The first trajectory was characterized by taller trees, with an average canopy height of about 20 m., while the second trajectory had an average canopy height of about 15 m. All 1880-90 fire-originated polygons within the jack pine-black spruce pathway were analyzed because it was the pathway with the smallest number of polygons (n = 693). As a result, there were no remaining polygons to allocate with a MDA model. The most common trajectory with respect to landscape area was trajectory 1, comprising 69.4% of the land base in the pathway.

The distribution of structural types for this pathway was similar to that for the trembling aspen-white spruce pathway (Table 4). Structural type 3 was the most common, followed by structural types 4 and 5. Again, the most complex structural types (1 and 2) are least represented in this pathway. The Chi-square test showed that there was a significant deviation from the expected distribution (df = 3; $\chi^2 = 16.64$; $P = 0.001$) indicating that there may be some association between the trajectories and structural types. The largest deviations were associated with structural types 3 and 5 for both trajectories (Table 4). Structural type 3 was higher and lower than expected for trajectory 1 and 2, respectively, and the inverse was observed with respect to structural type 5.

Table 5. Characteristics of the two trajectories identified using TWINSPAN with the random subset of the 1880-90 fire-originated polygons (n = 693) from the jack pine-black spruce pathway. Shown are the percent frequency (F%), and the mean weighted species cover values (C%) and standard deviation (SD) for each species by height class (see Appendix 1B for species codes).

	Trajectory 1 (n = 459)			Trajectory 2 (n = 234)		
Spp[ht. class]	F%	C%	SD	F%	C%	SD
TA[19-30]	69	7	9	—	—	—
BA[19-30]	6	0	1	—	—	—
WB[19-30]	2	0	1	—	—	—
WS[19-30]	28	2	5	—	—	—
BS[19-30]	78	8	7	—	—	—
JP[19-30]	100	37	13	—	—	—
BF[19-30]	—	—	—	—	—	—
TL[19-30]	1	0	1	—	—	—
TA[7-18]	4	0	2	46	4	7
BA[7-18]	1	0	0	3	0	1
WB[7-18]	9	0	2	6	0	3
WS[7-18]	16	1	4	11	1	4
BS[7-18]	77	28	22	96	43	23
JP[7-18]	4	0	3	100	33	13
BF[7-18]	—	—	—	—	—	—
TL[7-18]	—	—	—	9	1	3
TA[1-6]	0	0	1	—	—	—
BA[1-6]	—	—	—	—	—	—
WB[1-6]	—	—	—	—	—	—
WS[1-6]	0	0	1	—	—	—
BS[1-6]	1	0	2	0	0	2
JP[1-6]	—	—	—	—	—	—
BF[1-6]	—	—	—	—	—	—
TL[1-6]	—	—	—	—	—	—

3.3.3 Black spruce-eastern larch pathway

This pathway represents approximately 19.3% (14,114 ha) of the 11,228 polygons originating from the 1880-90 fires. TWINSPAN resulted in the identification of three successional trajectories (Table 6, Appendix 2C). The trajectories 1 and 2 primarily differ in terms of percent species cover, with the second trajectory having a higher percent cover of black spruce and less eastern larch. Trajectory 3 is generally two-layered, with the 7-18 m layer having a lower percent species cover than the 1-6 m layer. The MDA model used to classify the remaining 1880-90 polygons successfully re-classified the species cover data 95% of the time (Appendix 3E). The most common trajectory with respect to landscape area was trajectory 2, comprising 73.1% of the land base in the pathway. Trajectory 3 was the second most common covering 19.4%, followed by trajectory 1 covering 7.5% of the land base.

The distribution of structural types showed similar trends to the other two pathways (Table 4). Structural type 5 was the most common, followed by structural types 3 and 4. Structural types 1 and 2 were very uncommon, however this pathway is the only one to represent structural type 6, which is highly complex in terms of height structure, but only occurs in 7.8% of the polygons analyzed. The Chi-square test was strongly significant for this pathway (df = 10, χ^2 = 116.30, P = <0.001) indicating there may be association between the trajectories and structural types. The highest two deviations were found in trajectories 1 and 3, respectively. Both trajectories 1 and 3 had a higher than expected frequency of structural type 3, and a lower than expected frequency of structural type 5. The inverse was true for trajectory 2 (Table 4).

Table 6. Characteristics of the three trajectories identified using TWINSPAN with the random subset of the 1880-90 fire-originated polygons (n = 693) from the black spruce-eastern larch pathway. Shown are the percent frequency (F%), and the mean weighted species cover values (C%) and standard deviation (SD) for each species by height class (see Appendix 1B for species codes).

	Trajectory 1 (n = 52)			Trajectory 2 (n = 534)			Trajectory 3 (n = 107)		
Spp[ht. class]	F%	C%	SD	F%	C%	SD	F%	C%	SD
TA[19-30]	—	—	—	2	0	1	—	—	—
BA[19-30]	—	—	—	0	0	1	—	—	—
WB[19-30]	—	—	—	—	—	—	—	—	—
WS[19-30]	—	—	—	2	0	1	—	—	—
BS[19-30]	—	—	—	5	1	6	—	—	—
JP[19-30]	—	—	—	2	0	1	—	—	—
BF[19-30]	—	—	—	—	—	—	—	—	—
TL[19-30]	—	—	—	2	0	2	—	—	—
TA[7-18]	—	—	—	8	0	2	4	0	0
BA[7-18]	—	—	—	4	0	1	3	0	0
WB[7-18]	4	0	2	5	0	2	1	0	0
WS[7-18]	—	—	—	14	1	3	6	0	0
BS[7-18]	92	12	11	99	60	18	82	17	14
JP[7-18]	—	—	—	25	2	5	7	0	1
BF[7-18]	—	—	—	1	0	1	—	—	—
TL[7-18]	100	19	20	36	2	5	60	3	7
TA[1-6]	—	—	—	—	—	—	—	—	—
BA[1-6]	—	—	—	—	—	—	—	—	—
WB[1-6]	—	—	—	0	0	1	4	0	1
WS[1-6]	—	—	—	—	—	—	1	0	0
BS[1-6]	—	—	—	4	1	5	100	45	20
JP[1-6]	—	—	—	—	—	—	—	—	—
BF[1-6]	—	—	—	0	0	1	—	—	—
TL[1-6]	—	—	—	1	0	0	70	6	7

3.4 Definition of structural cohorts and application of management model

3.4.1 Definition of structural cohorts

Structural cohorts are defined on the basis of the structural characteristics of stands within different age ranges, or stages of development. Comparison of the cross-dated TSLF dates (Tardif, 2004) and the corresponding FLI dates revealed that there was a significant but poor correlation between both variables ($r^2 = 0.1018$, $P = <0.0001$, $n = 283$) (Figure 11). As a consequence, the photo-interpreted FLI origin dates were not considered accurate enough to confidently assign polygons to a structural cohort. It should be noted, however, that the two origin dates were not obtained by the same methods, and the trees sampled for the FLI truthing polygons were not necessarily the same trees sampled in the TSLF study. Comparison of cross-dated TSLF dates (Tardif, 2004) with structural types also revealed that there may be some trends with respect to structure as TSLF increases (Figure 12). Overall, there is a decrease in structural types 3 and 5, and a general increase in structural types 4, 2, 1, and 6. This needs to be interpreted with caution, however, due to the low *n*-values for the youngest and oldest age classes (Figure 12). Most of the stands used in objective 3 were assumed to be greater than 100 years in age, which is generally the age where mixed boreal stands are identified as being in a transitional stage from the first to second cohort (Bergeron et al., 2002b; Harvey et al., 2002). In terms of structure, this stage is characterized by the break-up of the initial cohort in the upper canopy, with the second cohort beginning to take over as the dominant canopy (Chen and Popadiouk, 2002; Brassard and Chen, 2006). Since the polygons analyzed in objective 3 originate from a similar time, they provide an age reference for the structural types defined earlier. Additionally, the structural types

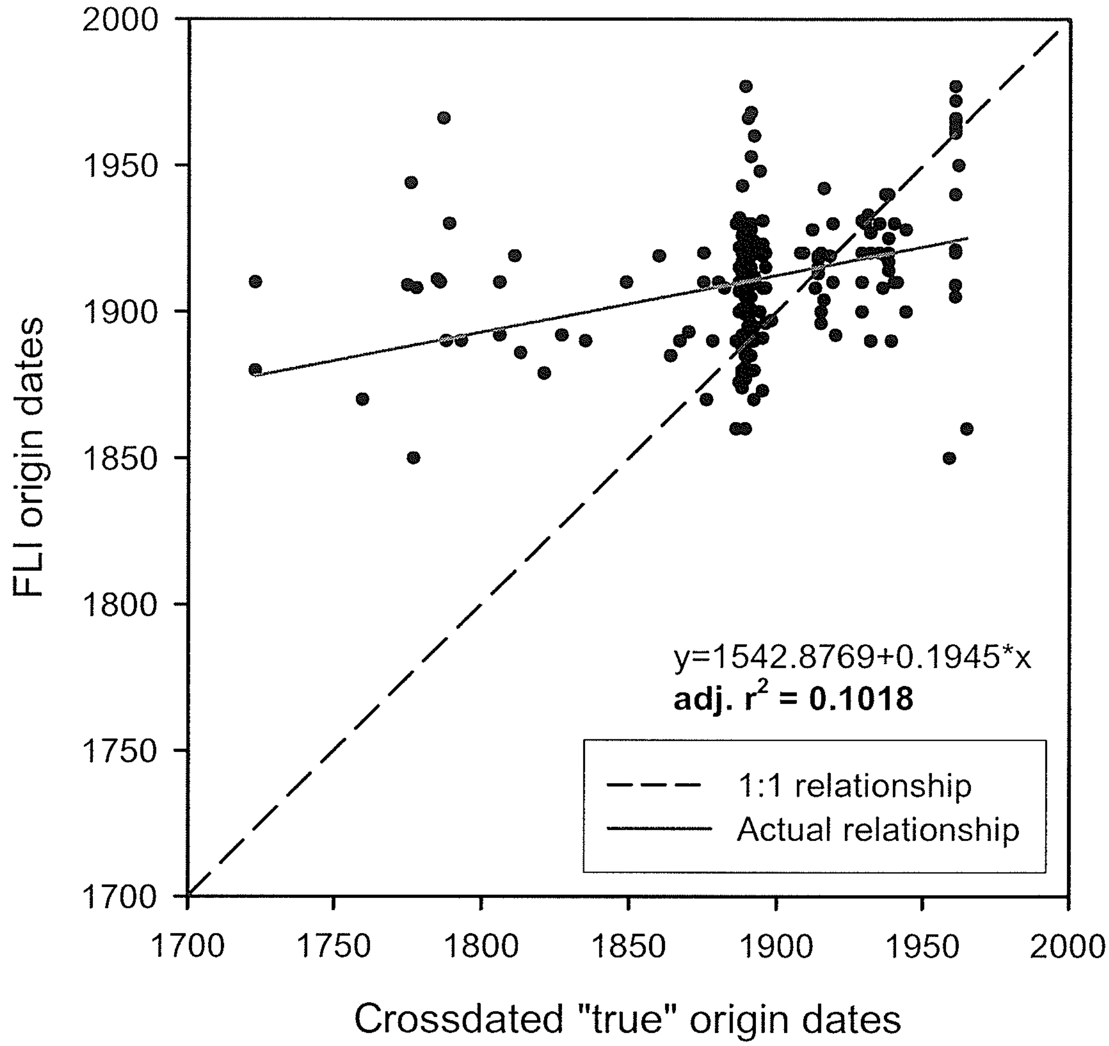


Figure 11: Linear regression depicting the association between cross-dated stand origin dates from the TSLF study (Tardif, 2004), and the corresponding photo-interpreted origin dates from the FLI (n = 283). Included are the regression model and the r^2 value adjusted for degrees of freedom. Recently harvested polygons were excluded from the analysis since cross-dated ages refer only to time-since-fire. In cases where single polygons contained more than one site from the TSLF study, the mean crossdated origin date was calculated to compare with the FLI origin date.

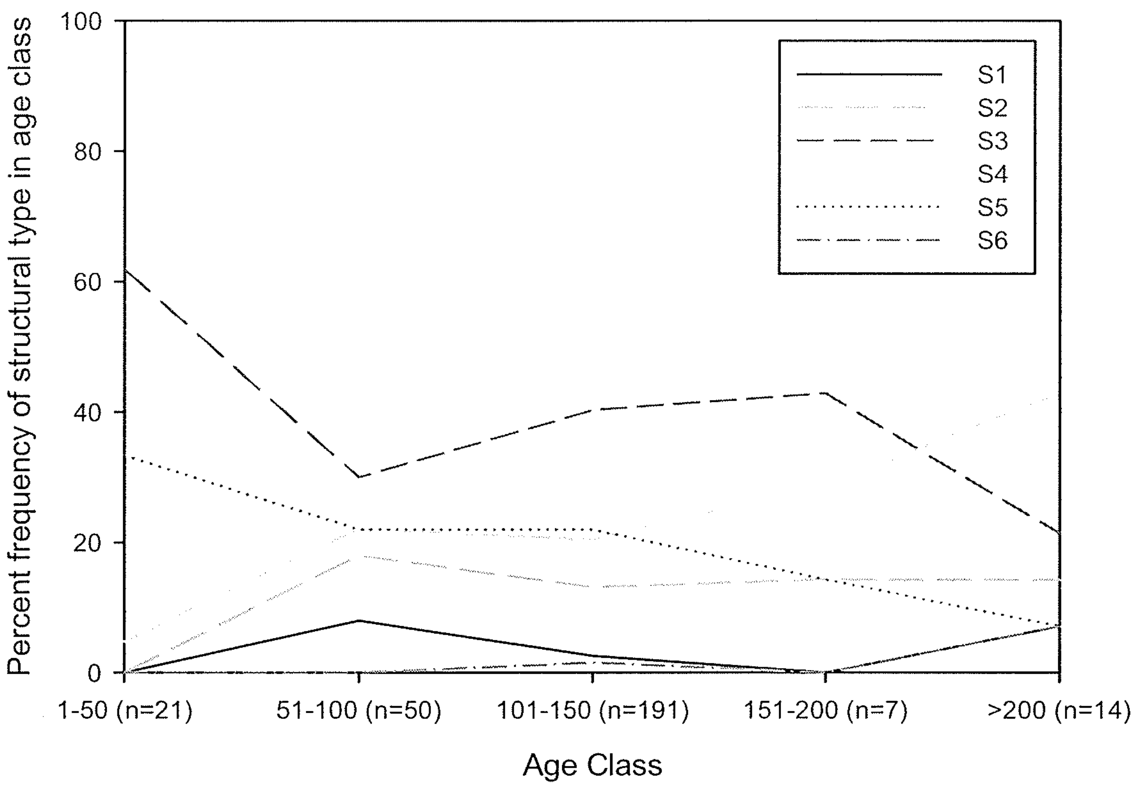


Figure 12: Relative percent frequency of the 6 TWINSPAN structural types by crossdated age class (n = 283) (Tardif, 2004). Recently harvested polygons were excluded from the analysis since cross-dated ages refer only to time-since-last-fire. In cases where single polygons contained more than one site from the TSLF study, the mean crossdated origin date was calculated to assign an age class.

provide a reference point for distinguishing between the first and second cohorts based on the literature pertaining to the structural development of mixed boreal stands (above).

As previously shown in section 3, structural types 3 and 4 were the most strongly represented structural types in the trajectories identified for the 1880-90 fire-originated stands. The former characterizes stands with a continuous overstory, and an established understory or intermediate layer, while the latter characterizes stands with a relatively discontinuous overstory and an established intermediate layer. On this basis, structural type 3 was considered to be characteristic of the first cohort (since the canopy remains relatively unbroken), and structural type 4 was considered be characteristic of the second cohort. Structural type 5, which is defined by an even-aged, single-layered stand structure was also considered to be representative of the first cohort. Structural type 2, which is more complex than structural type 4 but still fairly well represented in the 1880-90 trajectories, was also considered to be representative of the second cohort. The upper canopy is strongly associated with white spruce (canopy type 4), and is often relatively continuous (Appendix 4C). Structural type 1 was not strongly represented in the 1880-90 trajectories. This structural type is very complex, with a discontinuous canopy of two or more layers, and almost exclusively occurs in stands with a white spruce-dominated upper canopy (Appendix 4C). Trajectory 4 (trembling aspen-white spruce pathway) in objective 3, however, had a higher than expected proportion of structural type 1 and it is characteristic of late successional stands, as it is composed primarily of conifer species, and has a upper canopy layer with relatively lower percent species cover values. As a result, this structural type was considered to represent the third structural cohort.

Similarly, the complex height structure of structural type 6 in the black spruce-eastern larch pathway is characteristic of old black spruce stands (Harper et al., 2003), and was also considered to be representative of structural cohort 3.

Using this information, all treed polygons in DMPF were assigned to a structural cohort based on their structural type (Table 7). Approximately 59.5% (188,492 ha) of the treed landscape area is in structural cohort 1; 34.5% (109,404 ha) is in structural cohort 2; and 6.0% (19,075 ha) is in structural cohort 3 (Figure 13). With respect to individual pathways, approximately 58.8% (148,684 ha) of the trembling aspen-white spruce pathway area was in structural cohort 1, 36.4% (91,915 ha) was in cohort 2, and 4.8% (12,119 ha) was in cohort 3. In the jack pine-black spruce pathway, approximately 76.0% (14,881 ha) was in structural cohort 1, 23.9% (4,674 ha) was in cohort 2, and 0.1% (25 ha) was in cohort 3. In the black spruce-eastern larch pathway, approximately 55.8% (24,928 ha) was in structural cohort 1, 28.7% (12,814 ha) was in cohort 2, and 15.5% (6,932 ha) was in cohort 3 (Figure 13).

To illustrate the characteristics of the stands within each cohort, we used TWINSPAN with the species cover values described for objectives 3 and 4 (Section 2.3.2) corresponding to the 1445 truthing polygons. This resulted in the identification of six species assemblages for the trembling aspen-white spruce pathway; three species assemblages for the jack pine-black spruce pathway; and four species assemblages for the black spruce-eastern larch pathway (Appendix 2G–I; Appendix 4E–G). These assemblages were similar to the trajectories identified in section 3, but encompassed the

Table 7: The three structural cohorts and descriptions of their structural characteristics, including the structural types (S-Types) used to assign individual polygons to a structural cohort.

Structural cohort	S-Types	Description
1	S3, S5	1 to 2-layered stands, with a relatively continuous upper canopy layer. Upper canopy dominated by early-successional species, such as trembling aspen and jack pine. On wet, organic sites, early successional species primarily consist of black spruce and eastern larch.
2	S2, S4	Canopy usually 2-layered, with the upper canopy breaking up (usually less continuous than the lower layers). Upper canopy increasingly dominated by conifers such as white spruce.
3	S1, S6	2 to 3-layered canopy, or a canopy of variable height (undefined layers). Usually a multi-layered over story with a conifer understory. Canopy openings are common.

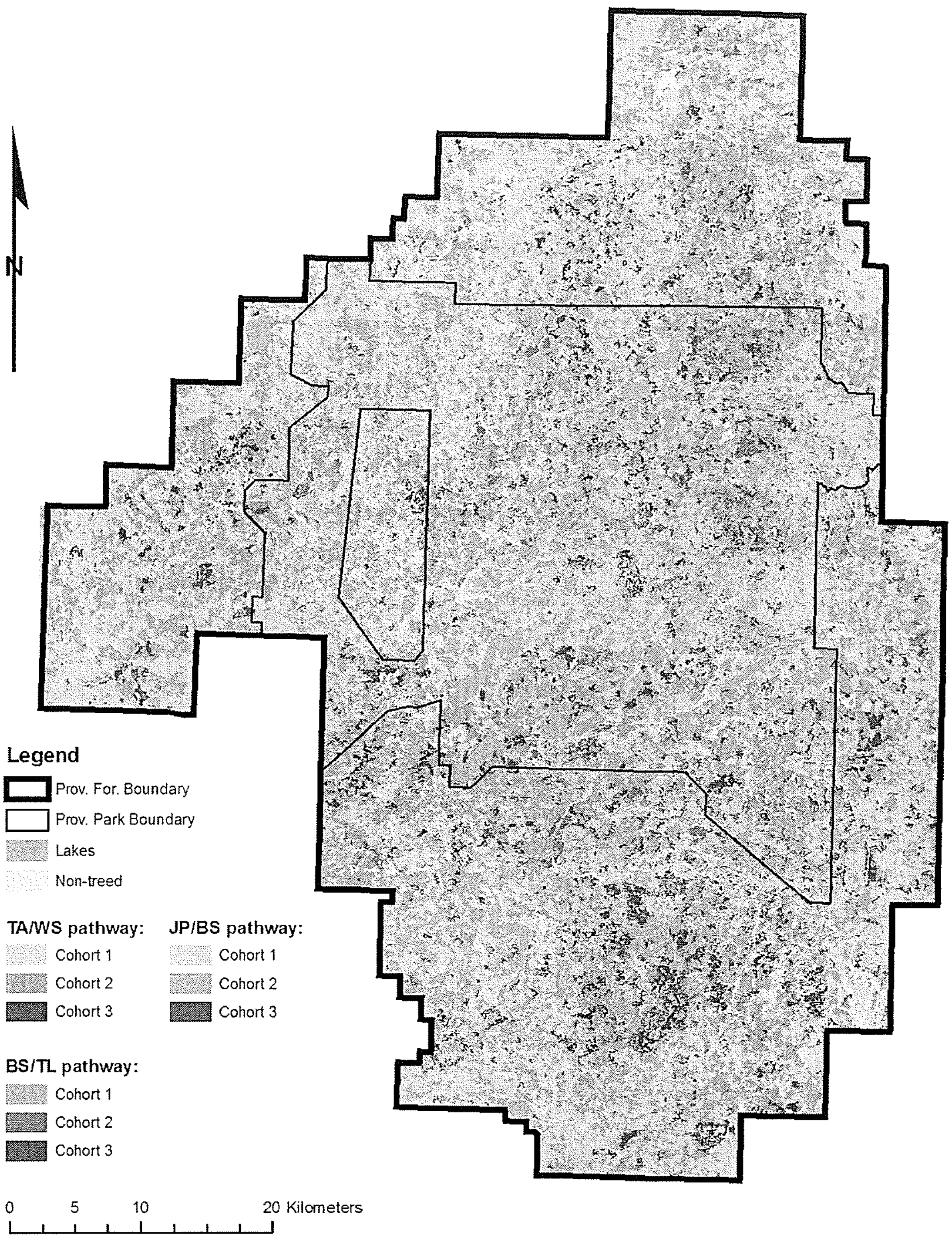


Figure 13: Map showing the distribution of structural cohorts over the DMPF landscape. Different colours represent different pathways, and within the pathways, different shades represent different structural cohorts.

entire range of stand ages in DMPF. Based on the distribution of cohorts for each assemblage, in the trembling aspen-white spruce pathway cohort 1 was most strongly represented in assemblages 3, 5, and 2; cohort 2 was most represented in 1 and 4; and cohort 3 was most represented in assemblage 1 (Appendix 4H). A large amount of assemblage 6 was associated with the second cohort, however, most of these polygons (n = 20) were recently harvested, and subsequently associated with cohort 1. In the jack pine-black spruce pathway, cohort 1 was strongly represented in all three species assemblages, and cohort 2 was most strongly represented by assemblage 3 and 1. Assemblage 3, however, was also associated with recently harvested polygons, and was subsequently entirely associated with cohort 1. Cohort 3 was not well-represented in this pathway (Appendix 4H). In the black spruce-eastern larch pathway cohort 1 was most strongly represented in species assemblages 2, 1, and 4, cohort 2 was most represented by assemblages 1 and 2, and cohort 3 was most represented by assemblages 3 and 4 (Appendix 4H). Stand profiles suggest a general increase in the dominance of conifer species from the first to third cohort for the trembling aspen-white spruce pathway, and an increase in dominance of black spruce in the jack pine-black spruce pathway (Figure 14). In the black spruce-eastern larch pathway, black spruce remains dominant from the first to third cohort, but structural complexity increases. Similarities in environmental conditions between the jack pine-black spruce pathway, and assemblage 2 of the black spruce-eastern larch pathway suggest that the jack pine-black spruce pathway and a portion of the black spruce-eastern larch pathway occurring on upland sites may converge in the third+ cohort (Figure 14).

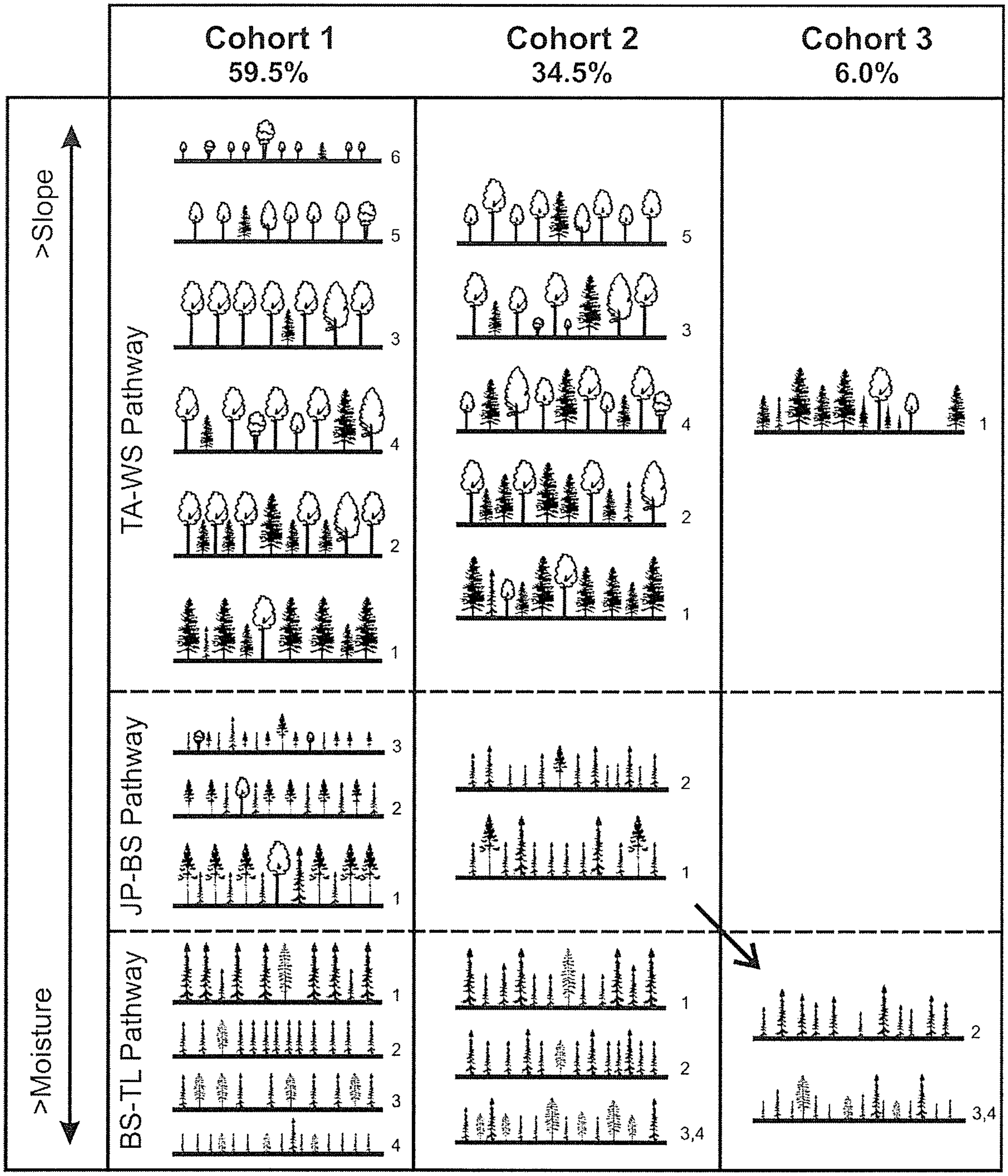


Figure 14: Stand profile diagrams for the three structural cohorts described for DMPF, and the proportion of each cohort with respect for landscape area. Diagrams are based on the species assemblages identified by TWINSPAN (Appendix 2D–F; 4E–G) and their structural characteristics for each cohort they represented (Appendix 4H). Assemblages are identified by the number to the right of the diagrams. The scale to the left reflects the relative position of the pathways along the slope-moisture gradient. The black arrow represents possible successional convergence between the jack pine-black spruce pathway, and the upland component of the black spruce-eastern larch pathway.

3.4.2 Application of NDBM model

To apply the three cohort model to DMPF, the forest must be divided into units under which different silvicultural treatments will be applied to maintain the structural characteristics expected in a landscape under a specific disturbance regime (Figure 15). If the forest management goal is to maintain the current distribution of structural cohorts over the DMPF land base (Figures 14, 15A), globally about 40.5% of the DMPF landscape would need to be managed under uneven-aged silvicultural techniques (UAS), and 59.5% would need to be managed under even-aged silvicultural techniques (EAS) within the period of one commercial rotation (Figure 15A). Applying UAS techniques, such as partial or selection cuts, would emulate succession to the next structural cohort. Applying EAS techniques (clear-cuts) would return a stand to a post-disturbance state, emulating the effects of stand-replacing disturbances such as fire. This model is assuming an average maximum commercial rotation age of 75 years after pooling all tree species. This age is based on the species rotation ages established for this forest management unit by Manitoba Conservation (2004b). Under this status-quo scenario, about 58.0% of Cohort 1 should be treated with UAS to emulate succession to the next structural cohort, while 42.0% should be treated with EAS to return the stands to a post-disturbance state. Similarly, 10.4% and 89.6% of Cohort 2 should be treated with UAS and EAS, respectively. A portion of Cohort 3 may also be treated with UAS, such as selection cutting, in order to emulate the effects of gap dynamics. Here, about 40.0% of this cohort is treated with UAS, and 60% is returned to the first cohort with EAS (Figure 16).

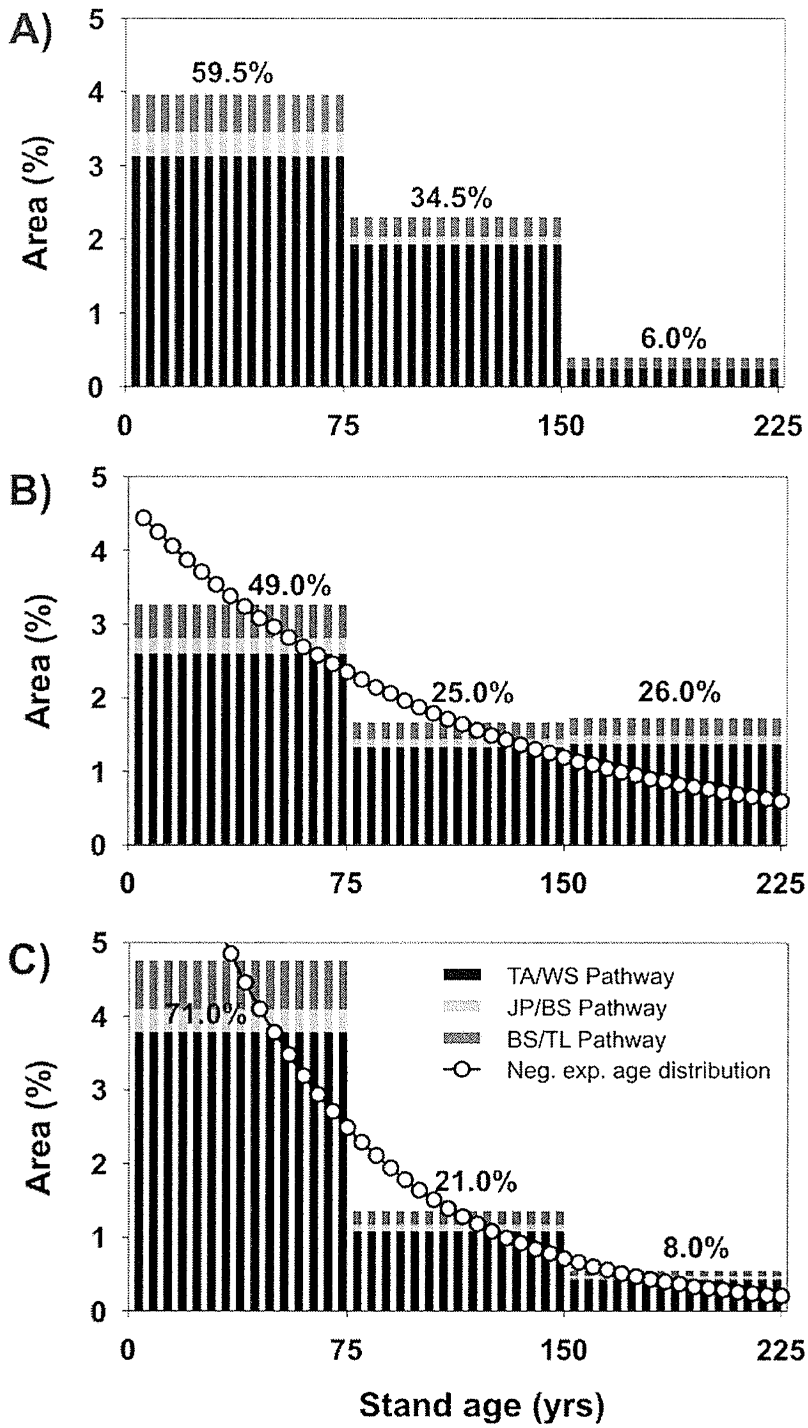


Figure 15: Proportion of landscape to be managed for each of the three cohorts in 5-year increments. Proportions are based on an average commercial rotation age of 75 years. Three scenarios are presented for maintaining: A) The current distribution of cohorts; B) the distribution based on a 110-year fire cycle; and C) the distribution based on a 60-year fire cycle. The expected natural age-class distribution is represented by the negative exponential curve. Cumulative percent area managed for each cohort is given inside the graphs.

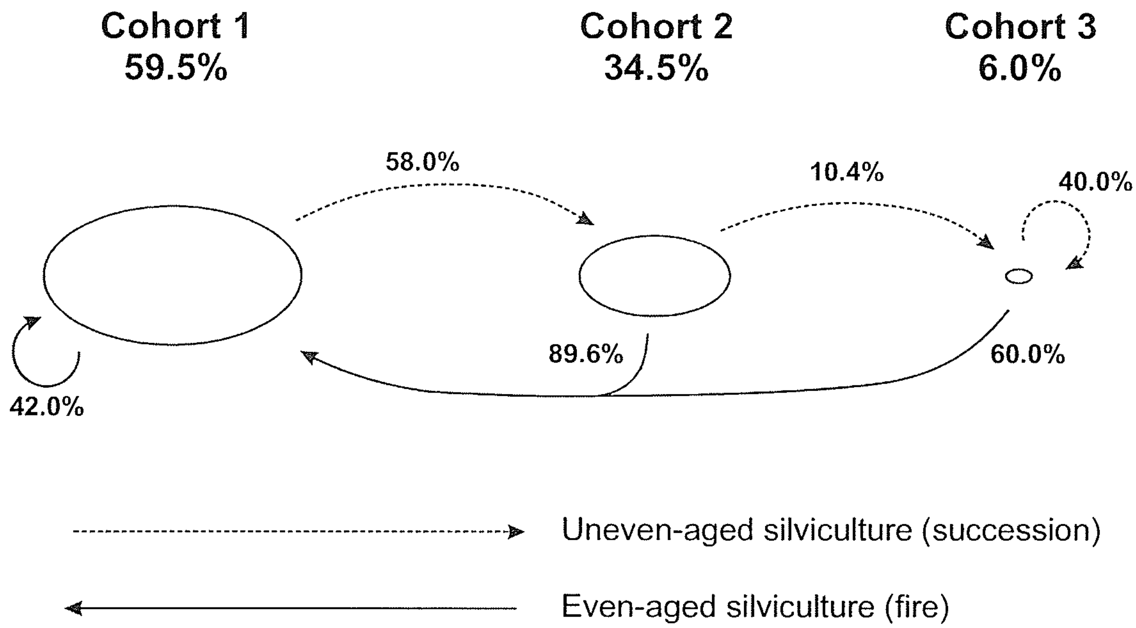


Figure 16: Silvicultural model depicting the balance of silvicultural treatments required to maintain the current distribution of structural cohorts over a mean 75-year commercial rotation. Ellipse size reflects the relative area occupied by the cohort, and arrows represent the silvicultural techniques for each cohort used to emulate the natural flux between the cohorts.

The current distribution of structural cohorts does not reflect the negative exponential distribution model expected in a natural landscape under a 110-year fire cycle (Figure 15A & B). Theoretically, under this model approximately 49% of the landscape should be in Cohort 1, 25% of the landscape should be in Cohort 2, and 26% of the landscape should be in Cohort 3 or greater. One management scenario may be to shift the landscape structure to more closely reflect this theoretical age-class distribution in terms of structure. In order to shift the actual global distribution of structural cohorts to the desired distribution, during the first rotation period the balance of UAS and EAS for each cohort must be such that the landscape structure shifts toward the desired result, and in the following rotations, the UAS/EAS balance must be changed again in order to maintain the new distribution (Figure 17A). However, the global landscape balance of UAS and EAS remains the same for all rotations, with 51% and 49% of the landscape being managed under UAS and EAS, respectively. A third scenario may be to shift the landscape structure to more closely reflect the structure of a landscape under a 60-year fire cycle (Figure 15C). Assuming a 75-year mean commercial rotation, approximately 71% of the landscape should be in Cohort 1, 21% of the landscape should be in cohort 2, and 8% of the landscape should be in cohort 3 (Figure 17B).

The above proportions represent a global model for the entire managed landscape. In practice, however, the proportions of UAS and EAS should be further subdivided to reflect the proportions of individual successional pathways within each cohort, and the different rotation ages associated with individual species. Figure 18 represents a generalized example of how silvicultural treatments could be subdivided between the

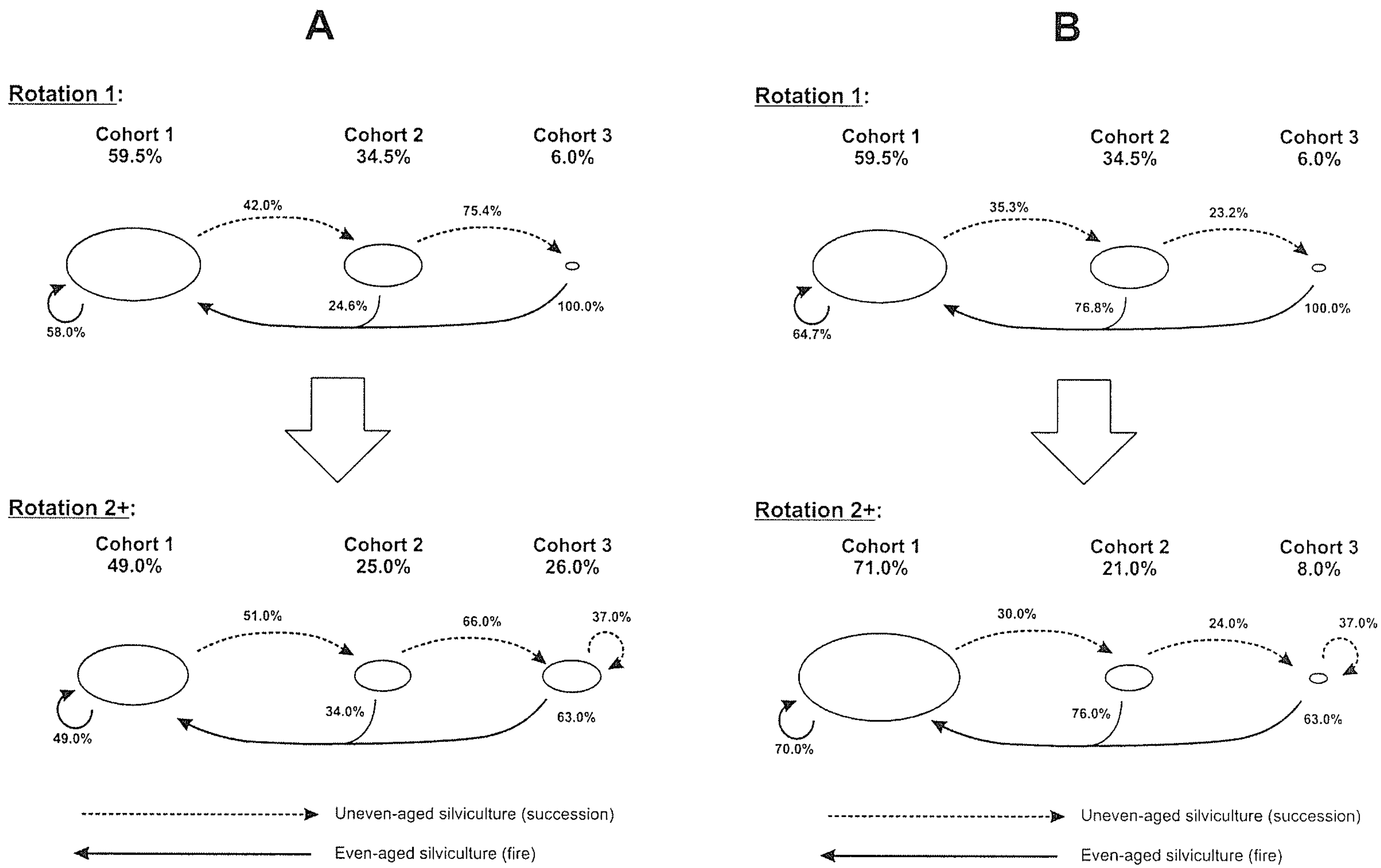
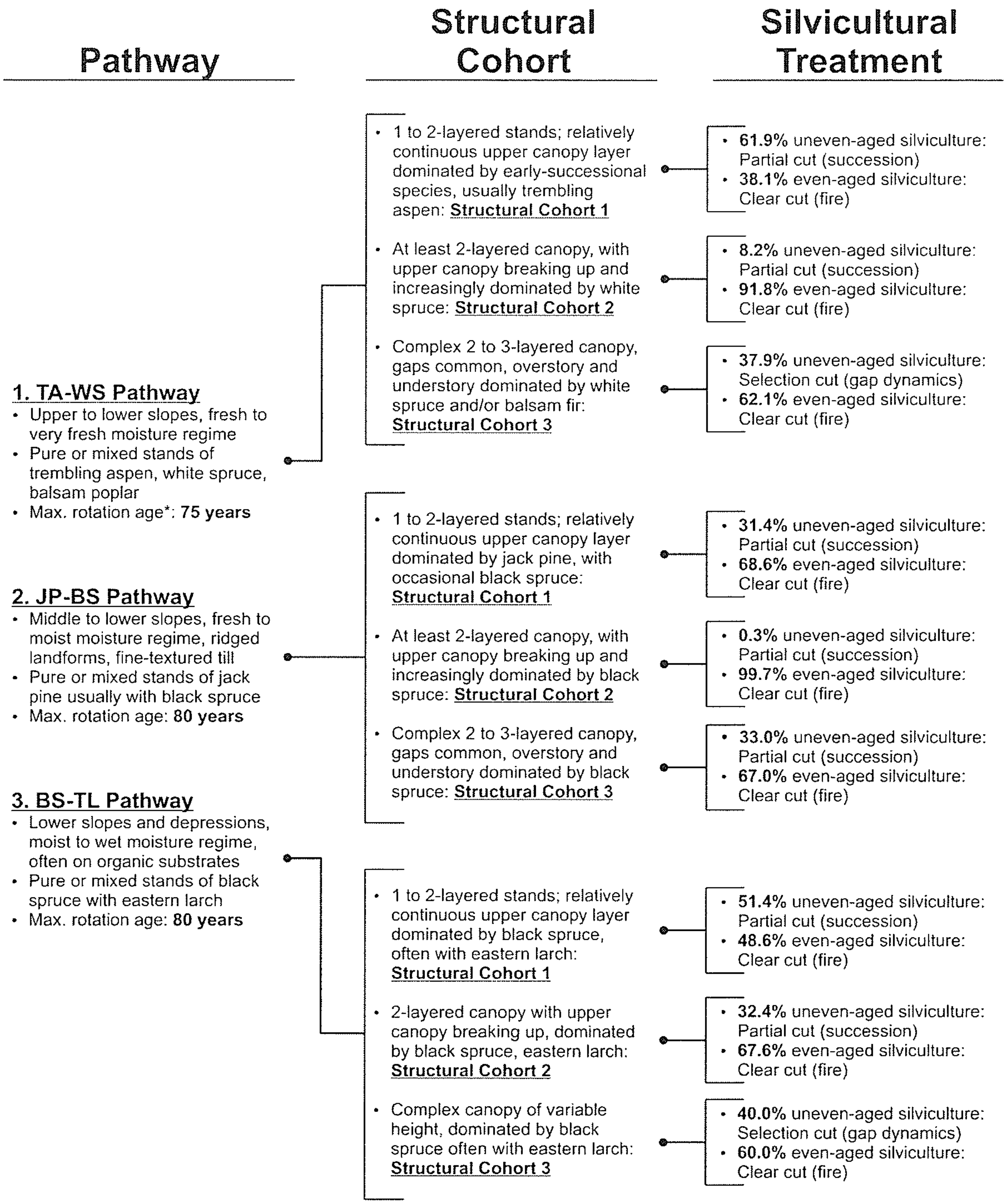


Figure 17: Silvicultural models depicting the balance of treatments required to shift the current cohort distribution to the theoretical distribution under A) a 110-year fire cycle, and B) a 60-year fire cycle. Depending on management goals, the proportion of the third cohort harvested in rotation 1 (A & B) can be varied from 0–100%.



* Rotation ages are based on a wood supply analysis report for DMPF (Manitoba Conservation, 2004b)

Figure 18: Fictitious example of a silvicultural key outlining the process by which the balance of uneven- and even-aged silviculture may be prescribed to each pathway in order to maintain the current balance of structural cohorts over the landscape.

individual pathways for the "current distribution" scenario. Further considerations should be made for incorporating park boundaries, protected areas, and areas managed for non-timber purposes (not presented here).

4. DISCUSSION

4.1 Major successional pathways in DMPF

The trembling aspen-white spruce pathway, which primarily consists of mixed stands of deciduous and conifer species in varying proportions, is the dominant forest type in DMPF, followed by the black spruce-eastern larch pathway. Trembling aspen, white spruce, and black spruce are the three dominant species in DMPF, occurring in 71.7%, 62.1%, and 52.7% of all forest stands, respectively. Only 7.8% of forest stands could be considered "pure" with only one tree species, and these were mostly found in the black spruce-eastern larch pathway which is less rich in tree species overall. This is consistent with the definition of mixed boreal forest ecosystems (MacDonald, 1995). The canopy types described in this study are also consistent with the species mixtures of five post-fire stand types described by Hamel and Kenkel (2001) for DMPF. Jack pine-dominated stands made up a relatively small component of DMPF. Some are concentrated within the area of the large fire of 1961 (Tardif, 2004), and other stands in this pathway appear to occur within the regions originating from the large fires of the late 19^{th} century, and tend to have a much larger black spruce component. Jack pine stands tend to be favoured by the occurrence of larger, less frequent fires (Rudolph and Laidly, 1990; Bergeron et al., 2000) which characterized the fire history in DMPF (Tardif, 2004). If, however, the fire interval is long enough, black spruce would become more dominant, and given a long enough interval jack pine could become locally extinct (Le Goff and Sirois, 2004). Active fire suppression in the latter half of the 20^{th} century may partially determine the proportion of jack pine in DMPF. Since the fire cycle has artificially lengthened, much of the stands in the jack pine-black spruce pathway are changing in composition, sometimes being replaced by trembling aspen, or becoming increasingly dominated by black spruce (Tardif, 2004).

The successional pathways identified in the DMPF were distinguishable based on differences in moisture regime, landform, and substrate characteristics, with the trembling aspen pathway occurring on drier, more sloping landforms and tills, and the black spruce-eastern larch pathway occurring on wet, organic sites. Elevation distinguished the jack pine-black spruce pathway from the others, but the relationship was relatively weak. Hamel and Kenkel (2001) found that in DMPF hardwood stands tended to occur on richer soils and slopes, while softwood stands tended to occur at higher elevations and with deeper organic layers. Jack pine and black spruce were associated with more well-drained sandy upland sites, and black spruce with eastern larch was found on poorly drained organic sites (Hamel and Kenkel, 2001). Although many of the environmental variables used by Hamel and Kenkel (2001) were unavailable in the FLI, in terms of landform, our results are in concordance with the results from their study. Other studies throughout the boreal and mixed boreal forest that have identified the importance of soil moisture and growing substrate gradients in determining tree composition (Bergeron and Dubuc, 1989; La Roi, 1992; Gauthier et al., 1996; Gauthier et al., 2000; Lecomte and Bergeron, 2005). In the boreal forest of Quebec, Gauthier et al. (1996) found that deciduous and mixed deciduous forests tended to dominate on mineral substrates, while coniferous forests dominated on organic sites. La Roi (1992) and Gauthier et al. (2000) found strong associations between jack pine stands and sandy and rocky substrates, but this wasn't evident in DMPF based on the data used in this study.

This may be due to differences in the way that the FLI characterizes the growing substrates, or a lack of significant environmental differences in this case.

When examining the species cover of the entire canopy profile within the trembling aspen-white spruce pathway, there was a considerable amount of variability with respect to both tree height and tree composition in the upper and intermediate canopy layers. This variability wasn't strongly correlated with the FLI environmental attributes, but the underlying trend in the ordination was primarily related to FLI age. This must be interpreted with caution since these age values were found to be inaccurate, but they do appear to reflect tree height. Gauthier et al. (2000) found that time-since-last-fire was the most important variable explaining the variation in forest composition after environmental characteristics have been accounted for. However, according to the ordinations FLI age was associated with tree height, not composition. A secondary gradient in the ordination was related to environmental characteristics. Although the amount of variance explained by this gradient was low, it may reflect a divergence in successional trajectories associated with differences in slope and moisture regimes. Other studies also found that environmental characteristics, particularly slope and growing substrate, explained some of the differences between successional trajectories (Bergeron and Dubuc, 1989; De Grandpré et al., 2000). The remaining variability in composition with respect to all canopy layers may be related to variability associated with successional change. Mixed boreal stands tend to proceed from intolerant deciduous species-dominated stands, to tolerant conifer-dominated stands with time (Bergeron and Dubuc, 1989; Bergeron, 2000; Hamel and Kenkel, 2001), but the rate and timing of this process varies according to many different small-scale factors, such as local disturbances and proximity to seed sources (Lieffers et al., 1996a; Galipeau et al., 1997; Bergeron, 2000; Kenkel et al., 2003). Another element associated with the secondary gradient in the ordination was the association between trembling aspen-dominated stands and larger polygon area. The differences in polygon size, and the differences in relative dominance of white spruce along the secondary gradient may be a function of proximity to a white spruce seed source. Several studies have shown that proximity to seed source is an important factor for white spruce establishment, and large, trembling aspen-dominated forest stands would be more resistant to compositional change than smaller stands near a white spruce seed source (Galipeau et al., 1997; Hamel and Kenkel, 2001; Kenkel et al., 2003). In the absence of fire, stands such as these may develop an uneven-aged structure while remaining dominated by shade-intolerant hardwoods (Cumming et al., 2000). The more complex structural types in the trembling aspen-white spruce pathway were associated with conifer species, while the simplest structural type was associated with the shorter height classes of trembling aspen. This association is supported by evidence that as stands age, structural complexity increases along with the relative importance of conifer species (Bergeron and Dubuc, 1989; Bergeron, 2000; De Grandpré et al., 2000; Hamel and Kenkel, 2001; Brassard and Chen, 2006).

Both the jack pine-black spruce and black spruce-eastern larch pathways were less variable in terms tree species composition. FLI age was the most important explanatory variable, particularly in the jack pine-black spruce pathway, and the shortest height classes were associated with recently disturbed sites. The black spruce-eastern larch pathway appeared to be more strongly influenced by moisture compared to the other pathways, but this is not surprising considering that on organic sites, moisture plays a more limiting role on tree growth (Lavoie et al., 2005). There also appeared to be a trend related to soil textures, separating taller and shorter height classes among the older stands. This suggests that site quality may play a role explaining height variation within these pathways, particularly with the black spruce-eastern larch pathway which appears to be separated into a drier stand types on slopes, and wetter stand types on flat organic substrates. Many studies throughout the boreal forest describe black spruce stands in terms of upland (drier) and lowland (organic) types, which certainly seems to be the situation in DMPF (La Roi, 1992; Gauthier et al., 2000; Harper et al., 2003; Lecomte and Bergeron, 2005). Studies have shown that in general, stands dominated by jack pine and black spruce tend to become increasingly dominated by black spruce, while stands initially dominated by black spruce tend to remain black spruce-dominated through time, while stand structure changes (De Grandpré et al., 2000; Gauthier et al., 2000; Harper et al., 2003; Lecomte and Bergeron, 2005). This would explain the smaller amount of compositional variability within these pathways, because there is more of a change in relative dominance over time, rather than a turnover in species communities.

Overall, the results of this study suggest that a gradient of moisture, slope, and organic-mineral soil textures in the FLI are useful for discriminating between the major successional pathways in DMPF, but within the pathways, FLI age appears to be the dominant explanatory variable. However, this needs to be interpreted with caution because of the error associated with the photo-interpreted dates. Further investigation is required to assess the true accuracy of the FLI ages, and their relationship to stand characteristics. Other studies have also found that age, or time-since-fire takes on the dominant explanatory role with respect to species variation (De Grandpré et al., 2000; Gauthier et al., 2000; Lecomte and Bergeron, 2005). Gauthier et al. (2000) found that after vegetation differences between organic and non-organic deposits were accounted for, time-since-fire was the most important explanatory variable, which supports the findings in this study.

4.2 Variability of 1880-90's fire-originated stands

A commonly used method for studying succession involves a chronosequence approach, grouping sites with similar abiotic characteristics, and comparing stands at different stages of development (Bergeron and Dubuc, 1989; De Grandpré et al., 2000; Gauthier et al., 2000). However, a major drawback associated with this approach is that differences in forest composition between sites are not necessarily only related to time-since-last-fire, but other site-specific factors and events (Bergeron, 2000; De Grandpré et al., 2000). A large sample size can help to reduce the degree of uncertainty. Because of the large number of stands in DMPF originated from the fires of the late 19^{th} century, this study was able to benefit from a very large sample size of stands that are presumably of a similar age.

Within the trembling aspen-white spruce pathway, there remained a considerable amount of variability in terms of structure and species cover. Others studying succession in the mixed boreal forest also observed compositional and structural variability in stands of similar age (Bergeron, 2000; Hamel and Kenkel, 2001). Furthermore, results suggested that within each successional pathway, environmental factors may not play an important role in determining tree composition. The structural variability between similarly-aged stands suggests that age is not the only factor determining the development of canopy structure. Evidence suggests that variability in terms of successional trajectories may be more of a function of landscape context than environmental differences (Fastie, 1995). There are other factors besides time that contribute to variability as a stand develops. Several studies have found that the proximity of seed source plays an important role in the development of a stand, particularly in terms of white spruce establishment (Galipeau et al., 1997; Hamel and Kenkel, 2001; Kenkel et al., 2003). Galipeau et al. (1997) found that the distance to unburned zones was an important predictor of white spruce regeneration density. Similarly, in DMPF Kenkel et al. (2003) found that the distance to seed source was important for the establishment of second cohort white spruce in the understory. Unburned stands could have potentially provided a white spruce seed source for the early establishment and recruitment of white spruce in stands regenerating nearby. Additional factors contributing to variability in stand development include fire intensity, which influences the characteristics of the growing substrate and the seed and vegetative banks (Wang, 2002; Lee, 2004; Wang and Kemball, 2005). More intense fires tend to favour the establishment of seed-regenerating conifers, while the least intense fires favour tree species that establish vegetatively (Wang and Kemball, 2005). In turn, variations in the abundance of different species following stand-replacing disturbance can strongly influence future stand development (Bergeron, 2000).

The jack pine-black spruce and black spruce-eastern larch trajectories exhibited much less variability in tree species cover than the trembling aspen-white spruce pathway. This is not surprising considering that these pathways exhibited comparatively less variability when the full age-class range is considered. Examination of species cover and environmental characteristics suggest that there may be some overlap between the jack pine-black spruce and black spruce-eastern larch pathways resulting in successional convergence to black spruce in continued absence of fire. Jack pine and black spruce convergence was also modelled by Le Goff and Sirois (2004) and Lecomte and Bergeron (2005) for jack pine and black spruce on similar substrates. Trajectories 2, of both the jack pine-black spruce and black spruce-eastern larch pathways had similar environmental characteristics, mostly differing in terms of the relative dominance of jack pine and black spruce. Jack pine and black spruce frequently occur together on well-drained sites, and both species can act as pioneers after a stand-replacing disturbance (Zoladeski and Maycock, 1990; Gauthier et al., 2000; Hamel and Kenkel, 2001; Lecomte and Bergeron, 2005). The proportion of these species establishing after fire would have an effect on the species composition after ~100 years, since the initial cohort composition is a very important factor in compositional development (Zoladeski and Maycock, 1990; Bergeron, 2000).

As a forest stand ages, many small-scale, unpredictable events and disturbances such as windthrow and insect outbreaks strongly influence the structural development of the canopy profile (Morin, 1994; De Grandpré et al., 2000; Brassard and Chen, 2006). Spatial patterns of individual tree mortality due to competition or senescence also may increase structural variability between sites (Senecal et al., 2004). The timing of different phases of structural development is also not consistent from stand to stand. Kneeshaw and Gauthier (2003) found that the time elapsed since fire until replacement of the initial cohort was highly variable across the boreal forest region, and even within regions. Brassard and Chen (2006) outlined other factors besides age affecting structural development, including canopy composition and non-stand replacing disturbances. However, the occurrence of these events is not always entirely random. For example, spruce budworm outbreaks specifically affect balsam fir and white spruce, and tend to be more severe in areas that have a greater concentration of these species (Su et al., 1996). Similarly with early successional broadleaf species, Hogg et al. (2002) found a correlation between FTC outbreaks and the incidence of wood-boring insects and pathogens, which contribute to trembling aspen stem dieback and stem mortality. Sutton and Tardif (2005; in press) found that in DMPF, trembling aspen, balsam poplar, and paper birch experienced growth reduction associated with FTC outbreaks. The spatial dynamics and timing of these outbreaks may play a role in determining the timing of transition between successional stages and structural development. Subsequently, this may also contribute to the overall structural variability observed in the stands originating from the 1880-90 fires. Hill et al. (2005) also found that gap development was common in trembling aspen stands between 60 and 120 years of age. Infections by fungal pathogens were the most common cause of gap-maker mortality, and they were not related to stand age (Hill et al., 2005). In undisturbed stands, variability in the rate of understory development can also influence structural development. For example, initial spruce recruitment in the understory can occur sporadically or continuously for a period greater than 20 years, the rate of which is somewhat governed by the distribution and proximity of seed sources (Lieffers et al., 1996a; Galipeau et al., 1997). Overall, these factors emphasize the unpredictable nature of structural development, and would explain why a high degree of structural variability is present in these similarly-aged stands.

4.3 Application of the 3-structural cohort model

Assignment of polygons to one of the three structural cohorts was challenging. In the context of this NDBM model, cohorts are defined as conceptual ecological units defined by particular age, compositional, and structural characteristics (Bergeron et al., 1999; Bergeron et al., 2002b; Harvey et al., 2002). Others investigating the application of this method in the mixed boreal forest of Quebec have assigned stands to cohorts based on composition and structure using inventory data, and associated these compositional and structural attributes with an age range based on information from other ecological studies in the region (Harvey et al., 2002). A similar approach was utilized in this study, however linking these characteristics to a specific age range was difficult. This was because the photo-interpreted stand origin dates in the FLI were found to be associated with a large degree of error when compared to cross-dated origin dates from the fire history study conducted in DMPF (Tardif, 2004). Cumming et al. (2000) also pointed out the limitations of forest inventory stand age estimates with respect to their accuracy, suggesting that they should not directly be used in natural disturbance models. It should be noted, however, that even with respect to ground truthing plots, it is unlikely that stand origin dates were based on the same location and trees within the polygon. As a result, some discrepancies should be expected, but these should be minor if dates were taken from within the same polygon. Structural associations with age were also unreliable considering the degree of structural variability associated with stands of similar age, however, despite a low *n*-value for the youngest and oldest age classes corresponding to the TSLF sites (Tardif, 2004), there appeared to be a weak structural trend from older to younger stands. A better correspondence between structure and age may have been possible with more detailed structural information in the FLI. Studies characterizing old growth and structural development of stands in the mixed boreal forest have emphasized the importance of the accumulation of snags and coarse woody debris (CWD) (Brassard and Chen, 2006). These attributes are missing from the FLI, but they may be the key to characterizing structural types that are more indicative of stand age. Kneeshaw and Gauthier (2003) have, however, defined a method of characterizing old-growth based on ratio of overstory (post-disturbance cohort) and understory basal areas. This gives merit to the approach utilized in this study, because the structural types are partly defined and associated with cohorts based on the stem arrangement for the different canopy layers.

Currently in DMPF about 59.5% of the area is in the first structural cohort, 34.5% is in the second, and 6.0% was in the third. The amount of first cohort stands is comparable to what is expected in the eastern mixed boreal forest, under a 140-year fire cycle (Harvey et al., 2002), but there is a higher proportion of second cohort stands. However, it was found that DMPF has a significantly lower proportion of third cohort stands. This supports Kneeshaw and Gauthier's (2003) findings, in which the expected amount of old growth forest in western and central Canada was less than in eastern Canada. With respect to individual pathways, the jack pine-black spruce pathway had the highest proportion of first cohort stands, while the black spruce-eastern larch pathway had the highest proportion of third cohort stands. This is supported by the findings of Tardif (2004), who found that black spruce and eastern larch had the oldest mean ages, after white spruce, while jack pine had the second youngest mean age. From the distribution map, there is a high concentration of first cohort jack pine-black spruce stands in the central uplands of DMPF, and trembling aspen-white spruce stands around the southwest periphery of the forest. These regions roughly correspond with the extent of 1961 fire, and the fires of the early 20th century (Tardif, 2004).

Several fire history studies have shown that the fire cycle in a given region varies within the time-frame of a single forest rotation (Weir et al., 2000; Bergeron et al., 2001; Tardif, 2004). Frequent, shorter-term changes in fire cycle would be difficult to compensate for in forest management practices. Natural disturbance based management studies have suggested that mean age is an appropriate figure to use in lieu of the current fire cycle because it has greater inertia, and encapsulates all variations in fire cycles that have occurred over the living history of the landscape (Bergeron et al., 2001; Bergeron et al., 2004b). The mean forest age at the time of this study was approximately 110 years (Tardif, 2004), however the distribution of structural cohorts in DMPF does not reflect the distribution expected under a natural landscape with this mean age. Under such a regime, based on the negative exponential age-class model (Johnson and Van Wagner, 1985), one would expect to find a much larger proportion of cohort 3, and a smaller amount of cohort 1 and 2. Aside from a relatively large amount of cohort 2, the current distribution of structural cohorts is in fact closer to the distribution expected under a 60-

year fire cycle; which is reflective of the estimated fire cycle prior to European settlement around the turn of the century (Tardif, 2004). This distribution is largely the result of the influence of the large, catastrophic fires of the late 19^{th} century, followed by active fire suppression in the latter half of the 20^{th} century (Gill, 1930; Tardif, 2004). As a result, we see a landscape where much of the area originates from those large fires, and much of the first cohort is at or near a transitional phase toward the second cohort. The influence of large, infrequent catastrophic disturbances (LIDs) on the forest mosaic and succession has been studied in many forest landscapes. Studies have suggested that LIDs show a lasting, persistent impact on the landscape and successional processes compared to smaller fires, whether more or less frequent (Turner and Dale, 1998; Turner et al., 1998).

The specific balance of even- and uneven-aged silviculture used in DMPF largely depends on the long-term management goals for the forest. The three scenarios presented in this study are global scenarios based on maintaining the current structure of DMPF, imposing a structure expected in a natural landscape with a mean age of 110 years, and imposing a structure based on a fire cycle of about 60 years. Some advantages to 60-year fire cycle scenario include the fact that the landscape is structurally closer to the expected 60-year fire cycle distribution, it uses a fire cycle unaffected by European influence, and climate change scenarios generally predict a shortening of the fire cycle for this region of the mixed boreal forest (Flannigan and Van Wagner, 1991; Flannigan et al., 2001). Actual implementation of the 3-structural cohort silvicultural model will need to be implemented at stand-level, with the balances of silviculture considered separately for each major pathway and individual species rotation ages. This is important because compositional diversity reflective of a natural landscape is just as important as structural diversity (Gauthier et al., 1996). The example outlined in this study suggests that about 76% of the jack pine/black spruce pathway is managed under even-aged management because it contains a larger proportion of cohort 1 than the other pathways. In addition, these models would also need to be adjusted to take into account non-productive forested land, protected areas, and forest under other types of non-timber supply management. The presence of a provincial park in DMPF will be an important factor limiting or influencing the choice of silvicultural methods, however, protected forest within the park may provide a means to manage for older, third cohort stands without employing silvicultural techniques which would be an economically attractive alternative. Harvey et al. (2003) outlined a two-level dispersion strategy, in which the managed area was divided into three types of management zones: (1) even-aged (clear-cut harvesting), (2) uneven-aged (partial harvesting), and (3) light management (limited harvesting). Within each zone, different silvicultural strategies were dispersed to recreate the heterogeneity of natural disturbance events. This mixed management approach would help to accommodate different cultural values, as well as ecological requirements. Additionally, studies suggest that this type of mixed strategy does not significantly affect the annual allowable cut (AAC) (Harvey et al., 2003). Such a mixed approach may be suited for the DMPF, since the forest supports a wide range of use and interests and contains a provincial park in which harvesting activity is already limited.

With respect to maintaining the current structure in DMPF, the overall ratio of even- to uneven-aged management required confirms what Bergeron et al. (2002b) suggested for the application of this model in western Canada. Younger forest on average in this region requires a greater proportion of even-aged management due to a greater proportion of cohort 1 on the landscape. Applying this model to the eastern mixed boreal forest under a 140-year fire cycle, Harvey et al. (2002) estimated that approximately 55% and 45% of the management zone should be under even-aged and uneven-aged management, respectively, while in DMPF about 60% should be under even-aged management, and if the 60-year fire cycle scenario were to be adopted, about 70% should be under even-aged management.

Actual silvicultural prescriptions for individual stand types and cohorts were beyond the scope of this study, but the techniques used should be applied on the basis of individual stands in such a way that they reflect site-specific natural dynamics (Harvey et al., 2002). For example, in terms of even-aged management, the fire size and severity characteristic of the managed area would be important in determining the appropriate size and distribution of clear cuts, as well as the retention seed trees versus the use of planting and seeding for regeneration (Bergeron et al., 1999; Bergeron et al., 2002b). Similarly, there is a variety of even and uneven-aged techniques that could be specifically applied to emulate cohort transition, and stand-level disturbances of varying sizes (e.g. windthrow events, spruce budworm, and FTC outbreaks) that characterize the gap dynamic cycle of old-growth stands (Lieffers et al., 1996b; Bergeron et al., 1999; Lieffers et al., 2003). These include shelterwood systems, which may be utilized to simulate natural die off of the first cohort, increasing light penetration and favouring the development of the understory, as well as single and group selection systems, which remove individuals or groups of trees, simulating small to larger scale disturbances like windthrow and spruce budworm outbreaks (Lieffers et al., 2003). Stocking requirements also play an important role in silvicultural considerations. Greene et al. (2002) suggested that in the eastern mixed boreal forest, conifer basal area is usually high enough that natural seeding and regeneration will meet stocking requirements. But in the western mixed boreal forest this is not usually the case, and understory planting would be more applicable (Greene et al., 2002). On the other hand, since proximity to seed source plays an important role in the establishment of conifers such as white spruce, planting seedlings in areas that are not near a seed source for natural regeneration would not respect the principles of NDBM. There are also factors other than ecological considerations that determine the types of silvicultural techniques employed. Managers must also consider technological and safety limitations regarding the application of silviculture, and there are also socio-economic considerations to be addressed (Lieffers et al., 2003).

4.4 Implications for forest management

The FLI has proven to be a useful tool for classifying the forest cover and structure of DMPF. It was also useful for determining important compositional-environmental relationships that distinguish between the major successional pathways. Indeed, LP has already utilized the FLI for this purpose in their recent 20-year management plan (LP, 2006a). However, managers using this data should be aware that there is a large degree of error associated with photo-interpreted stand origin dates. The classification of the forest canopy in this study corresponds fairly closely with classifications carried out by Louisiana-Pacific Ltd. using the same inventory data (LP, 2006a). Louisiana-Pacific Ltd. (2006a) did not identify major successional pathways, but did identify nine species groups based on canopy composition, which were further delineated into 24 groups according to ecosite classifications (abiotic characteristics). These groupings were based on more detailed sampling plot-derived data, which was used to develop an ecosite key that was used with the FLI to classify the landscape. The resulting groups, however, separated most strongly along a moisture gradient, with trembling aspen, white spruce, and jack pine broadly dominating on the drier sites and slopes, and black spruce dominating the wet, organic sites, which is fairly consistent with this study (LP, 2006a).

Different approaches have been proposed to maintain a natural age-class distribution through forest management, including varying rotation lengths to allow portions of the landscape to naturally develop second and third cohort structures (Seymour and Hunter, 1999). One major difficulty to this approach is that commercial rotation ages are relatively short, averaging about 75 years (Manitoba Conservation, 2004b), making long rotations unfeasible in certain situations since this could potentially reduce the annual allowable cut (Bergeron et al., 2002b). The presence of a provincial park within the forest may provide an opportunity to maintain an appropriate portion of the landscape beyond the rotation age. However, one drawback to this is that it constrains the spatial distribution of second and third cohorts, and may not respect the natural distribution of age classes over the forest as a whole, which is an important component of NDBM (Harvey et al., 2003). Conversely, allowing longer rotation ages may help to account for structural variability and different rates of structural development observed in this study. However, in a fully regulated system the 3-structural cohort approach may be advantageous from an economical point of view, because it relies primarily on structure and compositional knowledge, and all silvicultural treatments are carried out within the commercial rotation time-frame. It also provides the opportunity to control the distribution of "older" structural cohorts over the entire landscape, provided that the differences between a natural and artificially produced old-growth stand structure can be accepted from an ecological and social perspective.

There are some challenges regarding the implementation of the 3-structural cohort NDBM approach in DMPF. The landscape is dominated by the effects of the large fires of the late 19th century, and active fire suppression in the latter half of the 20th century (Tardif, 2004). As a result of fire suppression, it is difficult to assess the natural length of the fire cycle in this system, and the current age structure of the landscape does not necessarily reflect that in the absence of fire suppression. Tardif (2004) estimated that in the latter half of the 20th century, the fire cycle has been lengthened and if this trend continues (not accounting for forest harvests), within the next century, a large portion of the stands currently in the first cohort will have moved on to later cohorts. Disregarding harvesting activity, even-aged structural characteristics would be removed from the landscape. If this model was to be implemented, forest managers must consider the implications of adopting a strategy that accepts the current structure of the landscape as a benchmark for management, accepts a benchmark reflecting the expected natural structure for forest with a mean age of 110 years, or one that is based on a fire cycle characteristic of pre-European settlement. Further challenges arise from DMPF's past history of large, infrequent catastrophic fires (Gill, 1930). These fires have been linked with extended periods of drought (Girardin et al., 2004b), and if climatic trends in the future increase the risk of extreme drought events the risk for future catastrophic fires would also increase (Flannigan et al., 2001). Large, infrequent disturbance events are usually impractical to emulate in a forest management situation, yet because of their historical importance in DMPF and their influence on the landscape, they cannot be ignored (Turner et al., 1998; Tardif, 2004). Dale et al. (1998) suggested that forest managers can reduce the risk of such catastrophic events. For example, the landscape can be managed to reduce the impacts of large fires by creating breaks in fuel source, or re-introducing larger fires into the landscape, but in a more controlled fashion (Dale et al., 1998).

The employment of NDBM is part of the mandate of Louisiana-Pacific's and Manitoba Conservation's operations in DMPF. Part of Louisiana-Pacific's long-term management plan is to maintain the current compositional and structural diversity of the forest (LP, 2006a). The current NDBM strategy involves even-aged management techniques that vary the size and distribution of cutblocks to reflect the natural distribution and size variability of fires, but uneven-aged silviculture is generally not utilized, as LP primarily utilizes early successional hardwoods, primarily trembling aspen (LP, 2006a) which are usually maintained through even-aged management (Lieffers et al., 2003). LP's current strategy for maintaining structure involves targeting stands in younger age classes (first cohort) for harvest, while preserving stands older than 120 years (LP, 2006a). In the absence of fire, such a strategy would result in an overall increase in second and third cohort stands on the landscape, moving it toward a structure characteristic of a longer fire cycle. In the regulated landscape, however, the process of cycling of these older stands back to the first cohort would be lost, and as these stands continue to age, pathogens and insect disturbances may become an issue (Morin, 1994; Bergeron, 2000; Hill et al., 2005). Management of second and third cohort stands is of less interest to LP, again, because LP primarily utilizes early successional hardwoods, primarily trembling aspen (LP, 2006a), which are less important in the older stands. There are other quota holders operating in DMPF that utilize later-successional softwood species that may be able to employ a balance of even- and uneven-aged silviculture that would help to achieve the goals of a 3-structural cohort NDBM strategy.

At the stand level, the current silvicultural practices employed by Louisiana Pacific in DMPF are almost exclusively even-aged techniques (modified clearcut with protection of softwood understory if present) with a dispersion of single tree and patch retention, followed by natural regeneration (LP, 2006a). Trees that are retained for structure and wildlife (about 8-12 trees per hectare) are usually dispersed throughout the cut-block, and riparian buffer zones are incorporated when applicable. In larger cut-blocks, patches of mature trees are retained for wildlife cover and to break line-of-sight. Cut-block size ranges from 4.1 to 134.6 hectares (ave = 42.8 ha). In the case of LP operations, the adoption of the pre-settlement fire cycle scenario (60 years) may be a favourable option, as it calls for a greater proportion of even-aged silviculture which is generally more appropriate for maintaining their target tree species (Lieffers et al., 2003). Other challenges may arise at the operational level if the 3-structural cohort model were to be adopted by LP. Harvests are generally carried out with large equipment, such as feller-bunchers and skidders. The results of this study and others suggested that trembling aspen-dominated stands can develop complex structures and gap dynamics in the absence of fire and a white spruce seed source (Cumming et al., 2000; Hamel and Kenkel, 2001). This situation would require incorporating some proportion of uneven-aged silviculture in trembling aspen stands, but this would be difficult to carry out with the current harvesting equipment employed by LP. However, there may be opportunities for smaller forest operators to incorporate some uneven-aged silviculture in trembling aspen stands.

Other management requirements need to be accounted for in the overall management plan as well. For example, watershed management and the health of aquatic ecosystems need to be incorporated within the framework of sustainable forest management, and intensifies the complexity of forest management. Donnelly (2003) outlines current and future initiatives for riparian management in DMPF. Current requirements limit cumulative harvest within a watershed to protect aquatic health, primarily by maintaining riparian buffer zones. However, one of the remaining issues identified by Donnelly (2003) relates to how these practices fit within the NDBM approach to forest management. The maintenance of riparian buffer zones do not necessarily adhere to typical disturbance behaviour since large fires would not always leave preserved patches around aquatic zones, and generally affect stream flow levels and water chemistry (Kimmins, 1997). The overall management of riparian zones within the framework of NDBM warrants further investigation in order to achieve an acceptable compromise between ecological and social values.

Manitoba Conservation developed Duck Mountain Provincial Park to be managed for multiple uses. These include backcountry use, where harvesting and landscape manipulation are not permitted; recreational development, where harvests are only permitted for park maintenance; resource management, and access, both in which harvesting may be permitted (Manitoba Conservation, 2003). The resource management area is the largest use by area, covering 86,719 ha. The second largest area (46,851 ha) is allocated to backcountry use, and is protected from harvest activities. This provides a significant amount of opportunity for forest management within the park. The protected area makes up approximately 15% of the total treed area of DMPF, which exceeds the expected proportion of 3+ cohort stands in DMPF for the status-quo and 60-year fire cycle scenarios presented above. This may provide managers with sufficient area in which the forest could be allowed to develop into 3+ cohort stands naturally. However, this protected area is confined to a specific, continuous region, and this would need to be considered when developing the spatial aspect of any mixed management strategy, and for maintaining representative proportions of the three cohorts for DMPF overall. According to the draft management plan for the park (Manitoba Conservation, 2003), forest planning within DMPP is primarily the responsibility of Louisiana-Pacific Ltd., but with some additional restrictions to accommodate other activities in the park. These include operation timeframes, access limitations and road closure, and imposed buffers for certain natural features, historic, and recreation sites (Manitoba Conservation, 2003).

In terms of harvesting practices, current legislation for the Province of Manitoba also does not incorporate standards for the development of a representative range in structure over the managed landscape. Guidelines for cutting practices in mixedwood stands focus on preserving the un-utilized tree species, and prioritizes harvests in the oldest stands, and stands that are at high risk for disturbance (Manitoba Conservation, 1996). This does not necessarily reflect disturbance behaviour, particularly fires, which are not necessarily or age-specific disturbances (Johnson and Van Wagner, 1985). Forest renewal standards focuses primarily on the immediate restoration of clearcut stands to pre-harvest composition and stocking conditions (Manitoba Conservation, 2001). These standards currently do not reflect the structural and compositional development and processes of a disturbed stand in a natural system. If management for biodiversity and the principles of NDBM become a priority for sustainable forest management legislation, and if uneven-aged silviculture were to be more strongly utilized, then the current forest renewal standards would need to be revised to incorporate these processes.

4.5 Conclusions

The results of this study have shown that the FLI is a useful tool for characterizing canopy composition and structure in DMPF, as well as for determining it's relationship to abiotic characteristics. The successional characteristics and structural development between the three cohorts generally agree with the findings of other studies conducted in this region using plot-based data (Hamel and Kenkel, 2001; Kenkel et al., 2003; Tardif, 2004). However, it was found that photo-interpreted stand origin dates are unreliable, and have limited use in applications where accurate knowledge of stand ages are required. Including coarse-woody debris and snags in future inventories may result in better characterization of stand development, and may be a better than "correct" age with respect to managing stands from a structural perspective. Similar-aged stands originating from the fires of the late 19th century exhibit a large degree of structural and compositional diversity, which suggests structure does not develop evenly with age. This is in line with other research, which identifies many random and unpredictable factors that contribute to the structural development of a forest stand (Brassard and Chen, 2006). Because of the error associated with photo-interpreted stand origin dates in forest inventories, the 3-structural cohort model may be an appropriate NDBM strategy because it relies primarily on composition and structure to classify landscape development. In comparison to the eastern mixed boreal forest, there is a smaller proportion of third cohort stands in DMPF. This supports the proposal that the 3-structural cohort model is applicable in the western mixed boreal forest, and that it would require a greater relative proportion of even-aged silviculture due to a younger mean forest age resulting from a shorter fire cycle (Bergeron et al., 2001; Bergeron et al., 2004a). However, the presence of a provincial park within the forest, and multiple interests in the area, may also facilitate the adoption of strategies that allow for longer rotation periods. The latter may represent a more socially acceptable option, since the landscape would not need to be fully regulated. Overall, a balance between ecological sustainability, economical, and social requirements is the goal of sustainable forest management.

The current distribution of structural cohorts in DMPF is reflective of a history of large, catastrophic fires, followed by active fire suppression in the latter half of the 20th

century (Tardif, 2004). Because the "true" fire cycle is difficult to estimate, forest managers must choose a management scenario that would best serve ecological requirements, as well as management objectives and socio-economic needs. Potential scenarios include maintaining the current distribution of cohorts in DMPF, imposing a structure that reflects the "natural" cohort distribution expected for a landscape with a mean age of 110 years, or imposing a structure that reflects that expected under a 60-year fire cycle, which characterized the landscape prior to European settlement. These choices would also have an impact on the major successional pathways in the forest. For example, adopting a longer fire cycle would mean that the amount of jack pine would be reduced in DMPF, since they tend to be replaced by black spruce as time-since-fire increases (Le Goff and Sirois, 2004). Regardless of the scenario considered, it must be applied with consideration for the effect future trends in climate will have on the disturbance regime, and a potential increase in the risk of large, catastrophic fires (Flannigan et al., 2001). In a natural system, a shorter fire cycle would mean an increase in the proportion of first cohort stands on the landscape. The potential for increased fire risk would need to be monitored in the future, and if a natural disturbance-based management strategy were adopted, the silvicultural practices would need to be shifted to reflect this dynamic fire cycle in the long term.

Finally, it is important to note that silvicultural practices cannot fully replicate the natural processes that create diversity across the forest (Lieffers et al., 2003). For this reason it is important to preserve natural forests and processes in DMPF at some sustainable and representative level. One possibility may be to adopt some form of a “triad” approach, that would zone the forest into areas subjected to varying levels of management intensity that range from preserved areas, with little or no human activity allowed, to areas of intensive resource management (Andison, 2003; Messier et al., 2003), or a dispersion strategy for silvicultural practices, such as that outlined by Harvey et al. (2003) mentioned earlier in this paper. Specific application of these management strategies to DMPF at the stand level, while incorporating all ecological, social, and economic considerations, would require further research and analysis. The current distribution of structure in DMPF is a product of the effects of the 1880-90 fires and active fire suppression in the 20th century. Because of long-term fire suppression, the current landscape cannot be assumed to represent a natural mosaic. Consequently, basing the 3 structural cohort model on a 60-year fire cycle, which is representative of the estimated pre-settlement situation, would best fit the requirements of NDBM. Although the current mean age of the landscape is older (110 years), the high likelihood of a shorter fire cycle in this region as global warming continues further supports this stance.

REFERENCES

Andison, D.W., 2003. Tactical forest planning and landscape design. Chapter 12. *In* Towards sustainable management of the boreal forest. *Edited by* Burton, P.J., Messier, C., Smith, D.W. and W.L. Adamowicz, NRC Research Press, Ottawa, Ontario, Canada. pp.433–480.

Attiwill, P.M., 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manage. 63, 247–300.

Barnes, B.V., Zak, D.R., Denton, S.R., Spurr, S.H., 1998. Forest ecology. 4th ed. John Wiley & Sons, Inc., New York.

Bergeron, Y., 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81, 1500–1516.

Bergeron, Y., Charron, D., 1994. Postfire stand dynamics in a southern boreal forest (Quebec): A dendroecological approach. Écoscience 1, 173–184.

Bergeron, Y., Dubuc, M., 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio 79, 51–63.

Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. 92, 235–242.

Bergeron, Y., Denneler, B., Charron, D., Girardin, M.P., 2002a. Using dendrochronology to reconstruct disturbance and forest dynamics around Lake Duparquet, northwestern Quebec. Dendrochronologia 20, 175–189.

Bergeron, Y., Gauthier, S., Flannigan, M., Kafka, V., 2004b. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85, 1916–1932.

Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. For. Chron. 75, 49–54.

Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002b. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn. 36, 81–95.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., Lefort, P. 2004a. Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. Ambio 33, 356–360.

Bergeron, Y., Gauthier, S., Carcaillet, C., Flannigan, M., Richard, P.J.H., 2000. Reconstruction of recent and Holocene fire chronologies and associated changes in forest composition : A basis for forest landscape management. Project Report 2000-39, Sustainable Forest Management Network. University of Alberta, Edmonton, Alberta.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31, 384–391.

Bondrup-Nielsen, S., 1995. Forestry and the boreal forest: maintaining inherent landscape patterns. Water Air Soil Poll. 82, 71–76.

Brassard, B.W., Chen, H.Y.H., 2006. Stand structural dynamics of North American boreal forests. Crit. Rev. Plant Sci. 25, 37–59.

Bridge, S.R.J., Johnson, E.A., 2000. Geomorphic principles of terrain organization and vegetation gradients. J. Veg. Sci. 11, 57–70.

Burton, P.J., Messier, C., Weetman, G.F., Prepas, E.E., Adamowicz, W.L., Tittler, R., 2003. The current state of boreal forestry and the drive for change. *In* Towards sustainable management of the boreal forest. *Edited by* P.J. Burton, C. Messier, D.W. Smith, W.L. Adamowicz. NRC Research Press, Ottawa, Ontario, Canada.

Canadian Council of Forest Ministers (CCFM), 2000. Criteria and indicators of sustainable forest management in Canada. National Status 2000. Natural Resources Canada, Canadian Forest Service, Ottawa, Ont.

Carcaillet, C., Bergeron, Y., Richard, P.J., Fréchette, B., Gauthier, S., Prairie, Y.T., 2001. Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? J. Ecol. 89, 930–946.

Chen, H.Y.H., Popadiouk, R.V., 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. 10, 137–166.

Cooke, B.J., Roland, J., 2000. Spatial analysis of large-scale patterns of forest tent caterpillar outbreaks. Ecoscience 7, 410–422.

Côté, L., Brown, S., Paré, D., Fyles, J., Bauhus, J., 2000. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. Soil Biol. Biochem. 32, 1079–1090.

Cumming, S.G., Schmiegelow, F.K.A., Burton, P.J., 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecol. Appl. 10, 744–759.

Dale, V.H., Lugo, A.E., MacMahon, J.A., Pickett, S.T.A., 1998. Ecosystem management in the context of large, infrequent disturbances. Ecosystems 1, 546–557.

De Grandpré, L., Morissette, J., Gauthier, S., 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. J. Veg. Sci. 11, 791–800.

Donnelly, M., 2003. Ecologically-based forest planning and management for aquatic ecosystems in the Duck Mountains, Manitoba. J. Environ. Eng. Sci. 2, S35–S40.

Ecoregions Working Group (EWG), 1989. Ecoclimatic regions of Canada, first approximation. Ecological Land Classification Series, No. 23. Sustainable Development Branch, Canadian Wildlife Service, Conservation and Protection, Environment Canada, Ottawa, Ont.

Elliott-Fisk, D.L., 1988. The boreal forest. *In* North American terrestrial vegetation. *Edited by* M.G. Barbour, W.D. Billings. Cambridge University Press, New York.

Environment Canada, 2004a. Narrative descriptions of terrestrial ecozones and ecoregions of Canada. Available from: http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/TOC.cfm [cited November, 2004].

Environment Canada, 2004b. Canadian climate normals 1971-2000. Available from: http://www.climate.weatheroffice.ec.gc.ca/climate_normals/results_e.html [cited March, 2006].

Environmental Systems Research Institute, Inc (ESRI), 2002. ArcView GIS 3.3. Redlands, California.

Fastie, C. L., 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology, 76, 1899–1916.

Flannigan, M.D., Van Wagner, C.E., 1991. Climate change and wildfire in Canada. Can. J. For. Res. 21, 66–72.

Flannigan, M., Campbell, I., Wotton, M., Carcaillet, C., Richard, P., Bergeron, Y., 2001. Future fire in Canada's boreal forest: paleoecology results and general circulation model – regional climate modes simulations. Can. J. For. Res. 31, 854–864.

Franklin, J.F., 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecol. Appl. 3, 202–205.

Galindo-Leal, C., Bunnell, F.L., 1995. Ecosystem management: implications and opportunities of a new paradigm. For. Chron. 71, 601–606.

Galipeau, C., Kneeshaw, D., Bergeron, Y., 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. 27, 139–147.

Gauthier, S., De Grandpré, L., Bergeron, Y., 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. 11, 781–790.

Gauthier, S., Leduc, A., Bergeron, Y., 1996. Vegetation modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. Environ. Monit. Assess. 39, 417–434.

Gauthier, S., Lefort, P., Bergeron, Y., Drapeau, P., 2002. Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Natural Resources Canada, Canadian Forest Service, Laurentian forest Centre, Sainte-Foy, Quebec. Information Report LAU-X-125.

Ghent, A.W., 1958. Mortality of overstory trembling aspen in relation to outbreaks of the forest tent caterpillar and the spruce budworm. Ecology 39, 222–232.

Gill, C.B., 1930. Cyclic forest phenomena. For. Chron. 6, 42–56.

Girardin, M.P., Tardif, J., 2005. Sensitivity of tree growth to the atmospheric vertical profile in the Boreal Plains of Manitoba, Canada. Can. J. For. Res. 35, 48–64.

Girardin, M.P., Tardif, J., Flannigan, M.D., Bergeron, Y., 2004a. Multicentury reconstruction of the Canadian Drought Code from eastern Canada and its relationship with paleoclimatic indices of atmospheric circulation. Clim. Dynam. 23, 99–115.

Girardin, M.P., Tardif, J. Flannigan, M.D., Wotton, B.M., Bergeron, Y., 2004b. Trends and periodicities in the Canadian Drought Code and their relationships with atmospheric circulation for the southern Canadian boreal forest. Can. J. For. Res. 34, 103-119.

Greene, D.F., Kneeshaw, D.D., Messier, C., Lieffers, V., Cormier, D., Doucet, R., Coates, K.D., Groot, A., Grover, G., Calogeropoulos, C., 2002. Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). For. Chron. 78, 281–295.

Hamel, C., Kenkel, N., 2001. Structure and dynamics of boreal forest stands in the Duck Mountains, Manitoba. Final Project Report 2001-4, Sustainable Forest Management Network. University of Alberta, Edmonton, Alberta.

Harper, K., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S., Bergeron, Y., 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environ. Rev. 11, S79–S98.

Harrison, J.D.B., 1934. The forests of Manitoba. Forest Service Bulletin 85, Department of the Interior, Ottawa, Canada.

Harvey, B.D., Leduc, A., Gauthier, S., Bergeron, Y., 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. 155, 369–385.

Harvey, B.D., Nguyen-Xuan, T., Bergeron, Y., Gauthier, S., Leduc, A., 2003. Forest management planning based on natural disturbance and forest dynamics. Chapter 11. *In* Towards sustainable management of the boreal forest. *Edited by* Burton, P.J., Messier, C., Smith, D.W. and W.L. Adamowicz, NRC Research Press, Ottawa, Ontario, Canada. pp.395–432.

Hill, S.B., Mallik, A.U., Chen, H.Y.H., 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Can. J. For. Res. 35, 1942–1951.

Hogg, E.H., Brandt, J.P., Kochtubajda, B., 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Can. J. For. Res. 32, 823–832.

Johnson, E.A., 1978. Fire recurrence in the subarctic and its implications for vegetation composition. Can. J. Bot. 57, 1374–1379.

Johnson, E.A., Gutsell, S.L., 1994. Fire frequency models, methods and interpretations. Adv. Ecol. Res. 25, 239–287.

Johnson, E.A., Larsen, C.P.S., 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. Ecology 72, 194–201.

Johnson, E.A., Van Wagner, C.E., 1985. The theory and use of two fire history models. Can. J. For. Res. 15, 214–220.

Johnson, E.A., Morin, H., Miyanishi, K., Gagnon, R., Greene, D.F., 2003. A process approach to understanding disturbance and forest dynamics for sustainable forestry. Chapter 8. In Towards sustainable management of the boreal forest. Edited by Burton, P.J., Messier, C., Smith, D.W. and W.L. Adamowicz, NRC Research Press, Ottawa, Ontario, Canada. pp.261–306.

Kenkel, N.C., 2006. On selecting an approprate multivariate analysis. Can. J. Plant Sci. 86, 663–676.

Kenkel, N., Foster, C., Caners, R., Lastra, R., Walker, D., 2003. Spatial and temporal patterns of white spruce recruitment in two boreal mixedwood stands, Duck

Mountains, Manitoba. Project Reports 2003/2004, Sustainable Forest Management Network. University of Alberta, Edmonton, Alberta.

Kimmins, J.P., 1997. Forest ecology, 2nd ed. Prentice Hall, Inc. Upper Saddle River, New Jersey.

Kneeshaw, D., Gauthier, S., 2003. Old growth in the boreal forest: a dynamic perspective at the stand and landscape level. Environ. Rev. 11, S99–S114.

La Roi, G.H., 1992. Classification and ordination of southern boreal forests from the Hondo – Slave Lake area of central Alberta. Can. J. Bot. 70, 614–628.

Larsen, C.P.S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr. 24, 663–673.

Larsen, J.A., 1980. The boreal ecosystem. Academic Press, Inc., New York.

Lavoie, M., Paré, D., Fenton, N., Groot, A., Taylor, K., 2005. Paludification and management of forested peatlands in Canada: a literature review. Environ. Rev. 13, 21–50.

Le Goff, H., Sirois, L., 2004. Black spruce and jack pine dynamics simulated under varying fire cycles in the northern boreal forest of Quebec, Canada. Can. J. For. Res. 34, 2399–2409.

Lecomte, N., Bergeron, Y., 2005. Successional pathways on different surficial deposits in the coniferous boreal forest of the Quebec Clay Belt. Can. J. For. Res. 35, 1984–1995.

Lee, P., 2004. The impact of burn intensity from wildfires on seed and vegetative banks, and emergent understory in aspen-dominated boreal forests. Can. J. Bot. 82, 1468–1480.

Legendre, P., Legendre, L., 1998. Numerical Ecology, Second English edition. Elsevier Scientific Publishing Co., Amsterdam, The Netherlands.

Lesieur, D., Gauthier, S., Bergeron, Y., 2002. Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada. Can. J. For. Res. 32, 1996–2009.

Lieffers, V.J., Stadt, K.J., Navratil, S., 1996a. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26, 1002–1007.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K., Stewart, J.D., 1996b. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72, 286–292.

Lieffers, V.J., Messier, C., Burton, P.J., Ruel, J.-C., Grover, B.E., 2003. Nature-based silviculture for sustaining a variety of boreal forest values. Chapter 13. *In* Towards sustainable management of the boreal forest. *Edited by* P.J. Burton, C. Messier, D.W. Smith, W.L. Adamowicz. NRC Research Press, Ottawa, Ontario, Canada. pp. 481–530.

Locky, D.A., Bayley, S.E., Vitt, D.H., 2005. The vegetational ecology of black spruce swamps, fins, and bogs in southern boreal Manitoba, Canada. Wetlands, 25, 564–582.

Louisiana-Pacific Canada, Ltd. (LP), 2006a. 20 year sustainable forest management plan (2006 – 2026) [Online]. Louisiana Pacific Canada, Ltd., Swan River, Manitoba. Available at http://www.swanvalleyforest.ca/planning/LongTermPlan.html [cited December, 2006].

Louisiana-Pacific Canada, Ltd. (LP), 2006b. 2006-2007 annual operating plan [Online]. Louisiana Pacific Canada, Ltd., Swan River, Manitoba. Available at http://www.swanvalleyforest.ca/documents.html#AR_2005.

MacDonald, G.B., 1995. The case for boreal mixedwood management: an Ontario perspective. For. Chron. 71, 725–734.

Manitoba Conservation, 1996. Timber harvesting practices for forestry operations in Manitoba. Manitoba Natural Resources, Forestry Branch. Available at http://www.gov.mb.ca/conservation/forestry/forest-practices/practices/fpp-guideline-pdfs.html [cited January, 2007].

Manitoba Conservation, 2000. Park boundaries in Manitoba – Outlines [Vector digital data, online]. Manitoba Conservation, Winnipeg, Manitoba. Available at http://web2.gov.mb.ca/mli/adminbnd/index.html [cited October, 2004].

Manitoba Conservation, 2001. Forest renewal standards. Manitoba Conservation, Forestry Branch, Winnipeg, Manitoba. Available at http://www.gov.mb.ca/conservation/forestry/forest-renewal/fr2-standards.html [cited October, 2006].

Manitoba Conservation, 2003. Duck Mountain Provincial Park, Draft Management Plan, Draft Management Plan [Online], Parks and Natural Areas Branch, Winnipeg, Manitoba. Available at http://www.manitobaparks.com [cited October, 2004].

Manitoba Conservation, 2004a. Duck Mountain Provincial Park, Park Information and Maps [Online], Parks and Natural Areas Branch, Winnipeg, Manitoba. Available at http://www.gov.mb.ca/conservation/parks/popular_parks/duck_mtn/info.html [cited October, 2004].

Manitoba Conservation, 2004b. Wood Supply Analysis Report for Forest Management Unit 13 and 14 [Online], Forestry Branch, Manitoba Conservation, Winnipeg, Manitoba. Available at http://www.swanvalleyforest.ca/planning/LongTermPlan.html [cited January, 2007].

Manitoba Parks Branch (MPB), 1973. Outdoor recreation master plan: Duck Mountain Provincial Park. Manitoba Department of Tourism, Recreation and Cultural Affairs, Parks Branch, Winnipeg.

McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.36. MjM Software, Gleneden Beach, Oregon, U.S.A.

Messier, C., Bigué, B., Bernier, L., 2003. Using fast-growing plantations to promote forest ecosystem protection in Canada. Unasylva, 54, 59–63.

Morin, H., 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the Boreal Zone of Quebec. Can. J. For. Res. 24, 730–741.

Nealis, V.G., Régnière, J., 2004. Insect–host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. Can. J. For. Res. 34, 1870–1882.

Oliver, C.D., Larson, B.C., 1996. Forest stand dynamics. Update ed. John Wiley and Sons, Inc., New York, N.Y.

Paré, D., Bergeron, Y., Longpré, M., 2001. Potential productivity of aspen cohorts originating from fire, harvesting, and tree-fall gaps on two deposit types in northwestern Quebec. Can. J. For. Res. 31, 1067–1073.

Peterson, E.B., Peterson, N.M., 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Canada. Forestry Canada, Northwest region, Northern Forestry Centre, Edmonton, Alberta. Special Report 1.

Pham, A.T., De Grandpré, L., Gauthier, S., Bergeron, Y., 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. 34, 353–364.

Pickett, T.A., Cadenasso, M.L., 2005. Vegetation dynamics. Chapter 7. *In* Vegetation ecology. *Edited by* E. van der Maarel. Blackwell Science Ltd., Malden, MA, USA. pp. 172–198.

Rempel, R.S., 1999. Natural disturbance analysis and planning tools. Project Report 1999-3, Sustainable Forest Management Network. University of Alberta, Edmonton, Alberta.

Roland, J., 2000. Predator-prey dynamics of forest tent caterpillar as an indicator of forest integrity. Final Project Report, 2000-31, Sustainable Forest Management Network. University of Alberta, Edmonton, Alberta.

Rowe, J.S., 1972. Forest regions of Canada. Publication No. 1300, Department of the Environment, Canadian Forest Service. Ottawa, Canada.

Rowe, J.S., Scotter, G.W., 1973. Fire in the boreal forest. Quaternary Res. 3, 444–464.

Rudolph, T.D., Laidly, P.R., 1990. *Pinus banksiana* Jack Pine. *In* Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. Volume 2. Technical coordinators, Burns, R. M., and B. H. Honkala.

Sauchyn, D.J., Hadwen, T., 2001. Forest ecosystems and the physical environment, Duck Mountains, west central Manitoba. Final Project Report 2001-29, Sustainable Forest Management Network. University of Alberta, Edmonton, Alberta.

Schut, P., 2005. A national ecological framework for Canada, GIS data. Canadian Soil Information System, Agriculture and Agri-food Canada. Available from: http://sis.agr.gc.ca/cansis/nsdb/ecostrat/gis_data.html [cited March, 2006].

Scott, G.A.J., 1995. Canada's vegetation: a world perspective. McGill-Queen's University Press, Montreal, Quebec.

Senecal, D., Kneeshaw, D., Messier, C., 2004. Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Can. J. For. Res. 34, 396–404.

Seymour, R.S., Hunter, M.L. Jr., 1999. Principles of ecological forestry. *In* Maintaining biodiversity in forest ecosystems. *Edited by* Hunter, M.L. Jr. Cambridge University Press. Cambridge, UK. pp. 22–61.

Smith, R.E., Veldhuis, H., Mills, G.F., Eilers, R.G., Selby, C., Santry, M., 1998. Terrestrial ecozones, ecoregions and ecodistricts of Manitoba: and ecological stratification of Manitoba's natural landscapes. Manitoba Land Resource Unit, Brandon Research Centre, Research Branch, Agriculture and Agri-Food Canada, Winnipeg, Manitoba.

St-Laurent, L., Palko, S., Huffman, T, Eric Unrau, E., 1995. The Canada Vegetation and Land Cover: A Raster and Vector Data Set for GIS Applications - Uses in Agriculture. Ninth Annual Symposium on Geographic Information Systems, GIS 95, Vancouver British Columbia, Canada. pp. 613–619.

Stewart, J.D., Landhäusser, S.M., Stadt, K.J., Lieffers, V.J., 2001. Predicting natural regeneration of white spruce in boreal mixedwood understories. For. Chron. 77, 1006–1013.

Su, Q., MacLean, D.A., Needham, T.D., 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. Can. J. For. Res. 26, 1620–1628.

Sutton, A., Tardif, J., 2005. Distribution and anatomical characteristics of white rings in Populus tremuloides. IAWA Journal, 26, 221–238.

Sutton, A. , Tardif, J., in press. Dendrochronological reconstruction of forest tent caterpillar outbreaks in time and space, western Manitoba, Canada. Can. J. For. Res. 0, 00–00.

Systat Software Inc. (SSI), 2004. SYSTAT Version 11.00.01. Point Richmond, CA, U.S.A.

Tardif, J., 2004. Fire history in the Duck Mountain Provincial Forest, western Manitoba. Project Reports 2003/2004, Sustainable Forest Management Network. University of Alberta, Edmonton, Alberta.

ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. Adv. Ecol. Res. 18, 271–317.

ter Braak, C.J.F., Smilauer, P., 2003. Canoco for Windows Version 4.52. Biometris – Plant Research International, Wageningen, The Netherlands.

The Forestry Corp., 2003. Forest Lands Inventory Specifications. The Forestry Corp., Edmonton, Alberta, Canada.

Turner, M.G., Dale, V.H., 1998. Comparing large, infrequent disturbances: what have we learned? Ecosystems 1, 493–496.

Turner, MB., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1, 511–523.

Tyrrell, J.B., 1888. Notes to accompany a preliminary map of the Duck and Riding Mountains in North-Western Manitoba. Dawson Brothers, Montreal.

Wallenius, T.H., Kuuluvainen, T., Vanha-Majamaa, I., 2004. Fire history in relation to site type and vegetation in Vienansalo wilderness in eastern Fennoscandia, Russia. Can. J. For. Res. 34, 1400–1409.

Wang, G.G., 2002. Fire severity in relation to canopy composition within burned boreal mixedwood stands. For. Ecol. Manage. 163, 85–92.

Wang, G.G., Kemball, K.J., 2005. Effects of fire severity on early development of understory vegetation. Can. J. For. Res. 35, 254–262.

Weir, J.M.H., Johnson, E.A., 1998. Effects of escaped settlement fires and logging on forest composition in the mixedwood boreal forest. Can. J. For. Res. 28, 459–467.

Weir, J.M.H., Johnson, E.A., Miyanishi, K., 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. Ecol. Appl. 10, 1162–1177.

White, C., Tardif, J., Adkins, A., Staniforth, R., 2005. Functional diversity of microbial communities in the mixed boreal plain forest of central Canada. Soil Biol. Biochem. 37, 1359–1372.

Wiken, E., 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series No. 19. Lands Directorate, Ottawa.

Zoladeski, C.A., Maycock, P.F., 1990. Dynamics of the boreal forest in northwestern Ontario. Am. Midl. Nat. 124, 289–300.

APPENDIX 1

A) Original attribute codes from the FLI database and brief descriptions. Attribute type refers to the type of data (i.e. Identifier, vegetation information, abiotic information, and structural information), and subsequently, which matrix it contributed to.

Attribute	Description	Attribute Type	Attribute	Description	Attribute Type
ID	I.D. #: Unique to each record within a mapsheet	Identifier	MAPSHEET	6 - digit mapsheet # corresponding to the tile # [e.g., 360586(0)]	Identifier
SEQ	Identifies the vegetation layer (1 - 5)	Identifier	POLYNUM	Polygon #, unique within a mapsheet	Identifier
MER	Meridian # (arbitrarily assigned, doesn't refer to actual coordinates)	Identifier	TWP	Township # (arbitrarily assigned, doesn't refer to actual coordinates)	Identifier
RGE	Range # (arbitrarily assigned, doesn't refer to actual coordinates)	Identifier	SACOV1	Largest stand ground cover type within polygon	Structural
SACLASS1	% coverage of SACOV1 (classes 0 - 9)	Structural	SACOV2	Second largest stand ground cover type within polygon (if applicable)	Structural
SACLASS2	% coverage of SACOV2 (classes 0 - 9)	Structural	COVARR	Stand ground cover arrangement (P0 - P5) based on SACOV1	Structural
CANLAY	Canopy layer code describing the specific vegetation layer in the polygon (e.g., V = "Veteran")	Structural	CANRANK	Canopy rank identifying the vegetation layer the vegetation attributes refer to (1 - 5)	Structural
CANPAT	Canopy pattern structure of the specific vegetation layer in the polygon (1 - 5)	Structural	COMHT	Complex stand height range (only has value when CANLAY = "C"). E.g., Height ± X meters (where X = COMHT)	Structural
SPH	Stems per hectare class (only for conifer stems in understory: <15m. high)	Structural	CC	Crown closure code (0 - 9, treed layers only). Percent coverage relative to total polygon area	Vegetation
HT	Average tree height of the vegetation layer of interest	Structural	SP1	Main species in the vegetation layer	Vegetation
SP1PER	Composition percent class of SP1 (1 - 10)	Vegetation	SP2	Secondary species in vegetation layer	Vegetation
SP2PER	Composition percent class of SP2 (1 - 10)	Vegetation	SP3	Third highest contributing species in vegetation layer	Vegetation

Attribute	Description	Attribute Type	Attribute	Description	Attribute Type
SP3PER	Composition percent class of SP3 (1 - 10)	Vegetation	SP4	Fourth highest contributing species in vegetation layer	Vegetation
SP4PER	Composition percent class of SP4 (1 - 10)	Vegetation	SP5	Fifth highest contributing species in vegetation layer	Vegetation
SP5PER	Composition percent class of SP5 (1 - 10)	Vegetation	SP6	Sixth highest contributing species in vegetation layer	Vegetation
SP6PER	Composition percent class of SP6 (1 - 10)	Vegetation	ORIGIN	Origin year of treed vegetation layer	Environmental
LANDMOD	General landscape model (e.g., dunes = D)	Environmental	LMODNO	Landscape model number (details on LANDMOD, e.g., longitudinal dunes = D1) which follows LANDMOD letter	Environmental
SOILTEX	Parent material texture (letter followed by number providing further detail)	Environmental	TOPO	Topographic form of landscape code (landscape shape)	Environmental
SLOPEPOS	Slope position on landscape (e.g., upper slope)	Environmental	SLPER	Slope percent class (1 - 8)	Environmental
ASP	Aspect class of slope (cardinal point code, e.g. NW = North West)	Environmental	DRAINPAT	Drainage pattern code (0 - 5)	Environmental
MR	Moisture regime code (letter code). D = Dry; F = Fresh; V = V. Fresh; M = Moist; W = Wet	Environmental	NNF_ANTH	Code describing naturally non-forested/vegetated or anthropogenic areas	Environmental
MOD1	Primary stand modifier (disturbance) code	Environmental	EXT1	Extent class of MOD1 (1 - 5), referring to % of land area or crown closure affected	Environmental
ORIG1	Year of disturbance (MOD1)	Environmental	MOD2	Secondary stand modifier (disturbance) code	Environmental
EXT2	Extent class of MOD2 (1 - 5), referring to % of land area or crown closure affected	Environmental	ORIG2	Year of disturbance (MOD2)	Environmental
TREATMOD	Code describing prescribed silvicultural treatment within polygon	Environmental	TREATEXT	Extent class of TREATMOD (1 - 5), referring to % of land area affected	Environmental
TRORIG	Year of treatment	Environmental	WETECO1	Code for wetland classification (predominant)	Environmental
WETECO2	Code for wetland classification (secondary within polygon)	Environmental	INTER	Initials of interpreter	Identifier
DTYPE	Code identifying additional data sources used in interpretation	Identifier	MONTH_	Month # of origination of DTYPE	Identifier

Attribute	Description	Attribute Type	Attribute	Description	Attribute Type
YEAR_	Year of origination of DTYPE	Identifier	FORESTKEY	Forest key: unique identifier for polygon in database (combination of POLYNUM and MAPSHEET)	Identifier

B) Species Codes and their descriptions. Values for each code in the converted matrices are derived from the percent cover values multiplied by crown closure.

Code	Descripton
TA	*Populus tremuloides* (trembling aspen)
BA	*Populus balsamifera* (balsam poplar)
WB	*Betula papyrifera* (paper birch)
WS	*Picea glauca* (white spruce)
BS	*Picea mariana* (black spruce)
JP	*Pinus banksiana* (jack pine)
BF	*Abies balsamea* (balsam fir)
TL	*Larix laricina* (eastern larch)

C) Environmental codes for the converted environmental matrix, their descriptions, and data format. Variables converted to classes for the matrix used with TWINSPAN are presented in italics under the corresponding quantitative variable.

Code	Description	Data Type	Code	Description	Data Type
LMOD_FP	floodplain	binary	LMOD_H	hummocky	binary
LMOD_I	inclined	binary	LMOD_O	organic	binary
LMOD_M	rolling (inclined slopes > 400m, multi-directional	binary	LMOD_SC	valley	binary
LMOD_R	ridged	binary	LMOD_U	undulating	binary
LMOD_W	water body basin, channel sloughs and ponds	binary	SOIL	mineral substrate texture (fine to coarse: 1 – 3)	quantitative
TILL	till substrate texture (fine to coarse: 1 – 3)	quantitative	*STEX_C*	*coarse textured substrate*	*binary*
STEX_M	*medium textured substrate*	*binary*	*STEX_F*	*fine textured substrate*	*binary*
C_TILL	layered, coarse material over till	binary	F_TILL	layered, fine material over till	binary
PEAT	peat substrate	binary	TOPO_PM	topography: planar - moderate to steep slope	binary
TOPO_PL	topography: planar - level to gentle slope	binary	TOPO_CX	topography: convex side slope	binary
TOPO_CC	topography: concave side slope	binary	TOPO_TX	topography: straight or convex trough	binary
TOPO_RI	topography: ridge	binary	TOPO_HU	topography: hummock	binary
TOPO_TC	topography: concave trough	binary	TOPO_DE	topography: depression	binary
TOPO_UN	topography: undulating	binary	TOPO_CM	topography: complex	binary
SLPOS	slope position: 0 (lowest) to 5 (highest)	quantitative	*SLPOS_C*	*slope position: crest*	*binary*
SLPOS_U	*slope position: upper*	*binary*	*SLPOS_M*	*slope position: middle*	*binary*
SLPOS_L	*slope position: lower*	*binary*	*SLPOS_T*	*slope position: toe*	*binary*
SLPOS_V	*slope position: level*	*binary*	*SLPOS_D*	*slope position: depression*	*binary*
SLPER	percent slope (midpoint value of 8 classes dividing 0-130% slope)	quantitative	*SLP1*	*percent slope (0–5%)*	*binary*
SLP2	*percent slope (6–10%)*	*binary*	*SLP3*	*percent slope (11–20%)*	*binary*
SLP4	*percent slope (21–30%)*	*binary*	*SLP5*	*percent slope (31–45%)*	*binary*
SLP6	*percent slope (>46%)*	*binary*	ASPECT	aspect of slope expressed as deviation from north	quantitative

Code	Description	Data Type	Code	Description	Data Type
				(1=N; 2=NW,NE; 3=E,W; 4=SW,SE; 5=S)	
ASP_D	level aspect	binary	ASP_V	variable aspect	binary
ASP_N	north aspect	binary	ASP_NE	north east aspect	binary
ASP_E	east aspect	binary	ASP_SE	south east aspect	binary
ASP_S	south aspect	binary	ASP_SW	south west aspect	binary
ASP_W	west aspect	binary	ASP_NW	north west aspect	binary
DRAIN_COM	drainage pattern complexity: 0 (no pattern) to 5 (most complex)	quatitative	DPAT0	no drainage pattern (MR=1, 2, or 3)	binary
DPAT1	no patterned form	binary	DPAT2	interspersed drainage pattern (net-like)	binary
DPAT3	simple linear drainage pattern	binary	DPAT4	complex linear drainage, closed canopy	binary
DPAT5	complex linear drainage, open canopy	binary	MR	moisture regime (1=dry; 2=fresh; 3=very fresh; 4=moist; 5=wet)	quantitative
MRD	dry moisture regime	binary	MRF	fresh moisture regime	binary
MRV	Very fresh moisture regime	binary	MRM	Moist moisture regimi	binary
MRW	Wet moisture regime	binary	AGE	stand origin date, from the FLI	quantitative
TSLF	Time-since-last-fire (expressed to the nearest decade) data source: Tardif, 2004	quantitative	SLOPE_DEM	measure of slope from the digital elevation model (% slope)	quantitative
SLP_DEM1	percent slope (0–1.4%)	binary	SLP_DEM2	percent slope (1.5–2.8%)	binary
SLP_DEM3	percent slope (2.9–4.2%)	binary	SLP_DEM4	percent slope (4.3–5.6%)	binary
SLP_DEM5	percent slope (5.7–6.9%)	binary	SLP_DEM6	percent slope (>6.9%)	binary
ELE	measure of elevation from the digital elevation model (metres above sea level)	quantitative	ELE_L	low elevation (421–553 m)	binary
ELE_M	mid elevation (554–685 m)	binary	ELE_H	high elevation (686–816 m)	binary
AREA	log-transformed area of polygon in hectares	quantitative	MOD_BU	fire disturbance (% cover in polygon)	quantitative
MOD_CL	clearing (% cover in polygon)	quantitative	MOD_CC	clearcut disturbance (% cover in polygon)	quantitative
MOD_SF	seasonally flooded land (upland occurrence) (% cover in polygon)	quantitative	MOD_WF	windthrow disturbance (% cover in polygon)	quantitative

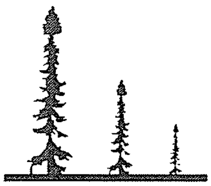
Code	Description	Data Type	Code	Description	Data Type
TREAT_SC	treatment: seedbed prepared (% cover in polygon)	quantitative	MOD_BF	beaver flood (% cover in polygon)	quantitative
TREAT_PL	treatment: planted or seeded (% cover in polygon)	quantitative	MOD_SN	snags (% cover in polygon)	quantitative

D) Structural codes for the converted structural matrix. Variables converted to classes for the matrix used with TWINSPAN are presented in italics under the corresponding quantitative variable

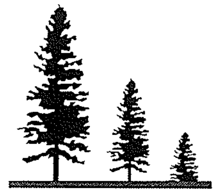
.Code	Description	Data Type	.Code	Description	Data Type
MAXHT6	1–6 m stand height	binary	MAXHT12	7–12 m stand height	binary
MAXHT18	13–18 m stand height	binary	MAXHT24	19–24 m stand height	binary
MAXHT30	25–30 m stand height	binary	NOLAY1	single layer	binary
NOLAY2	two layers	binary	NOLAY3	three layers	binary
NOLAY4	four layers	binary	COMHT	complex stand (only has value when CANLAY = "C"). E.g., Height ± X meters (where X = COMHT)	binary
SHBHT1	1 m shrub height	binary	SHBHT2	2 m shrub height	binary
SHBHT3	3 m shrub height	binary	SHBHT4	4+ m shrub height	binary
SPH1	1–500 stems/hectare	binary	SPH2	501–1000 stems/hectare	binary
SPH3	1001–2000 stems/hectare	binary	SPH4	>2000 stems/hectare	binary
CVARR_P0	single stems cover arrangement	binary	CVARR_P1	single patch cover arrangement	binary
CVARR_P2	a few patches cover arrangement	binary	CVARR_P3	several patches cover arrangement	binary
CVARR_P4	continuous cover, openings common	binary	CVARR_P5	continuous cover, openings uncommon	binary
CPAT_Cpl1	single canopy arrangement	binary	CPAT_Cpl2	two canopy arrangements	binary
CPAT_Cpl3	three canopy arrangements	binary	Vlayer	veteran canopy layer	binary
Ulayer	understory canopy layer (< or =15 m tall)	binary	Slayer	single canopy layer (alone or with veteran and/or understory layer)	binary

.Code	Description	Data Type	.Code	Description	Data Type
Mlayer	part of a multi-layered canopy (>15 m tall)	binary	CAPAT1_0	canopy pattern of the vegetation layer (CAPAT#_$, where #=layer [top-down], and $=arrangement [see CVARR_P#])	binary
CAPAT1_1	see description for CAPAT1_0	binary	CAPAT1_2	see description for CAPAT1_0	binary
CAPAT1_3	see description for CAPAT1_0	binary	CAPAT1_4	see description for CAPAT1_0	binary
CAPAT1_5	see description for CAPAT1_0	binary	CAPAT2_0	see description for CAPAT1_0	binary
CAPAT2_1	see description for CAPAT1_0	binary	CAPAT2_2	see description for CAPAT1_0	binary
CAPAT2_3	see description for CAPAT1_0	binary	CAPAT2_4	see description for CAPAT1_0	binary
CAPAT2_5	see description for CAPAT1_0	binary	CAPAT3_0	see description for CAPAT1_0	binary
CAPAT3_1	see description for CAPAT1_0	binary	CAPAT3_2	see description for CAPAT1_0	binary
CAPAT3_3	see description for CAPAT1_0	binary	CAPAT3_4	see description for CAPAT1_0	binary
CAPAT3_5	see description for CAPAT1_0	binary	CAPAT4_0	see description for CAPAT1_0	binary
CAPAT4_1	see description for CAPAT1_0	binary	CAPAT4_2	see description for CAPAT1_0	binary
CAPAT4_3	see description for CAPAT1_0	binary	CAPAT4_4	see description for CAPAT1_0	binary
CAPAT4_5	see description for CAPAT1_0	binary	CAPAT5_0	see description for CAPAT1_0	binary

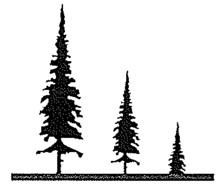
E) Description of tree profiles used for constructing stand profiles, including common name (abbreviation in brackets) and scientific name.



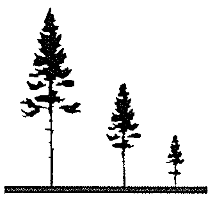
Black Spruce (BS)
Picea mariana



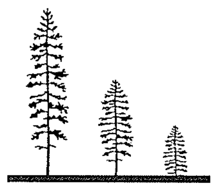
White Spruce (WS)
Picea glauca



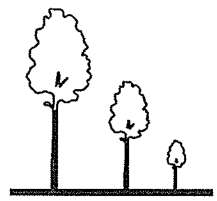
Balsam Fir (BF)
Abies balsamea



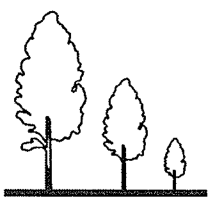
Jack Pine (JP)
Pinus banksiana



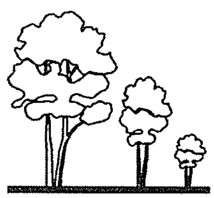
Eastern Larch (TL)
Larix laricina



Trembling Aspen (TA)
Populus tremuloides

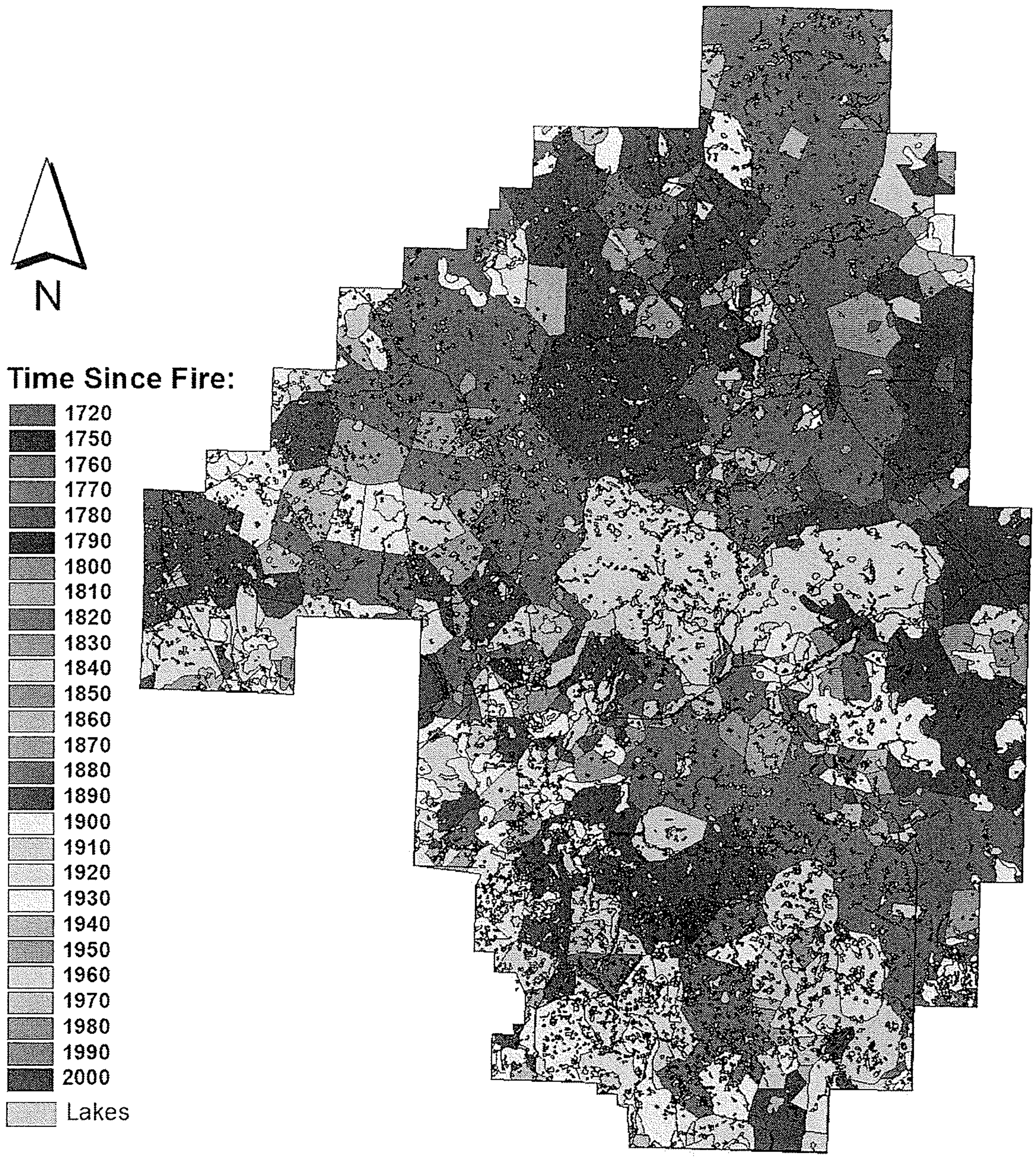


Balsam Poplar (BA)
Populus balsamifera



Paper Birch (WB)
Betula papyrifera

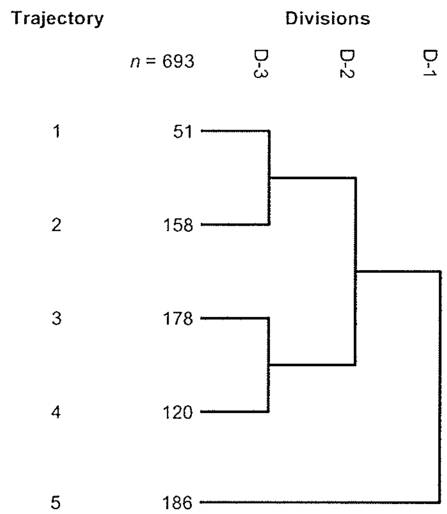
F) Time since fire map for DMPF. Different coloured areas identified on the scale to the left represent date of last fire. Spatial information from this study was used to help isolate polygons originating from the catastrophic fires of the 1880's and 1890's (data source: Tardif, 2004).



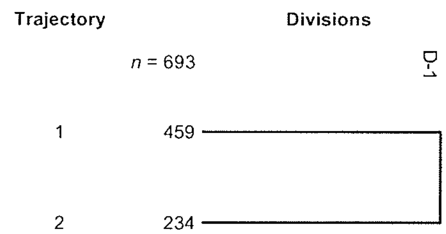
APPENDIX 2

Dendrograms representing the subdivision of groups identified by TWINSPAN:

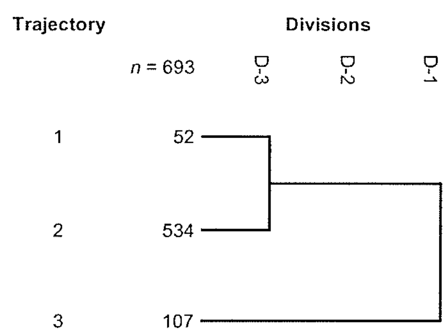
A) Trembling aspen-white spruce pathway trajectories (1880-90 fire-originated polygons)



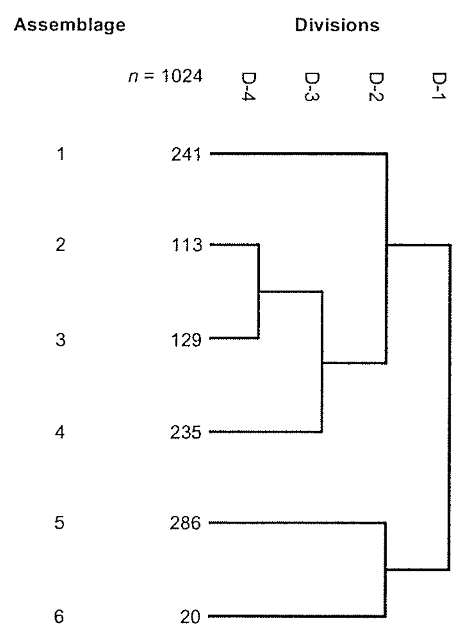
B) Jack pine-black spruce pathway trajectories (1880-90 fire-originated polygons)



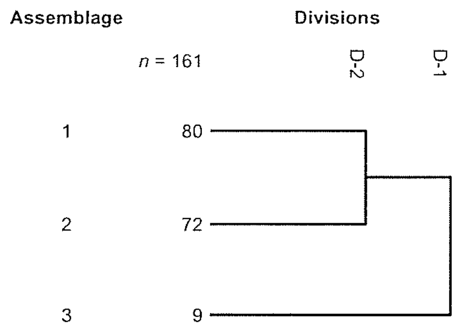
C) Black spruce-eastern larch pathway trajectories (1880-90 fire-originated polygons)



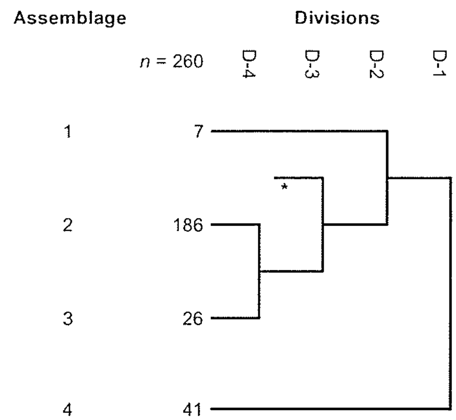
D) Trembling aspen-white spruce pathway species assemblages



E) Jack pine-black spruce pathway species assemblages



F) Black spruce-eastern larch pathway species assemblages



*Outlier (n = 1) excluded as a potential group and regrouped with assemblage 2

APPENDIX 3

A) Multiple discriminant analysis jackknifed re-classification of the 6 canopy types for the 1445 truthing plots using the upper canopy species cover data. Cases in row categories are classified into columns. Numbers in bold typeface are correctly re-classified.

Canopy Type	1	2	3	4	5	6	%correct
1	**261**	25	14	5	0	0	86
2	31	**122**	9	1	0	0	75
3	1	23	**149**	24	17	0	70
4	0	6	0	**335**	1	0	98
5	0	1	10	13	**124**	13	77
6	0	0	1	30	4	**225**	87
Total	293	177	183	408	146	238	**84**

B) Multiple discriminant analysis jackknifed re-classification of the 5 environmental types for the 1445 truthing plots using the environmental variables. Cases in row categories are classified into columns. Numbers in bold typeface are correctly re-classified.

Environmental Type	1	2	3	4	5	%correct
1	**81**	6	1	0	0	92
2	18	**254**	9	4	0	89
3	27	39	**662**	25	0	88
4	0	0	8	**149**	12	88
5	0	0	0	8	**142**	95
Total	126	299	680	186	154	**89**

C) Multiple discriminant analysis jackknifed re-classification of the 6 structural types for the 1445 truthing plots using structural variables. Cases in row categories are classified into columns. Numbers in bold typeface are correctly re-classified.

Structural Type	1	2	3	4	5	6	%correct
1	**70**	8	0	0	0	0	90
2	16	**140**	5	3	0	0	85
3	0	7	**552**	38	1	0	92
4	1	0	7	**294**	0	0	97
5	0	0	0	0	**252**	0	100
6	0	0	0	0	0	**51**	100
Total	87	155	564	335	253	51	**94**

D) Multiple discriminant analysis jackknifed re-classification of the 5 trajectories for the trembling aspen-white spruce pathway 1880-90 random subset polygons (n = 693) using the three-height class species cover data. Cases in row categories are classified into columns. Numbers in bold typeface are correctly re-classified.

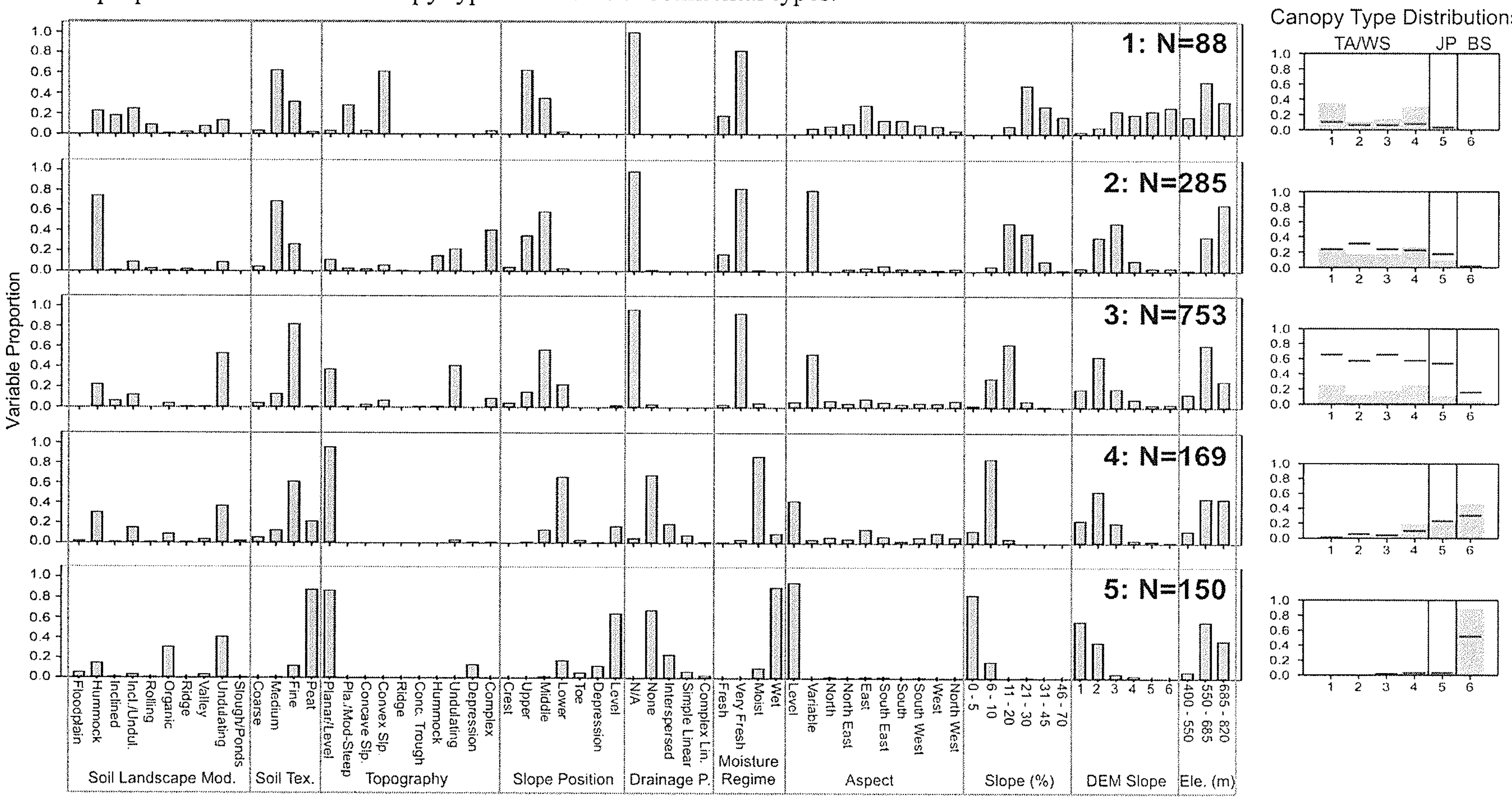
Trajectory	**1**	**2**	**3**	**4**	**5**	**%correct**
1	**41**	6	3	1	0	80
2	0	**148**	10	0	0	94
3	3	9	**148**	7	11	83
4	3	4	12	**95**	6	79
5	0	2	17	19	**148**	80
Total	47	169	190	122	165	**84**

E) Multiple discriminant analysis jackknifed re-classification of the 3 trajectories for the black spruce-eastern larch pathway 1880-90 random subset polygons (n = 693) using the three-height class species cover data. Cases in row categories are classified into columns. Numbers in bold typeface are correctly re-classified.

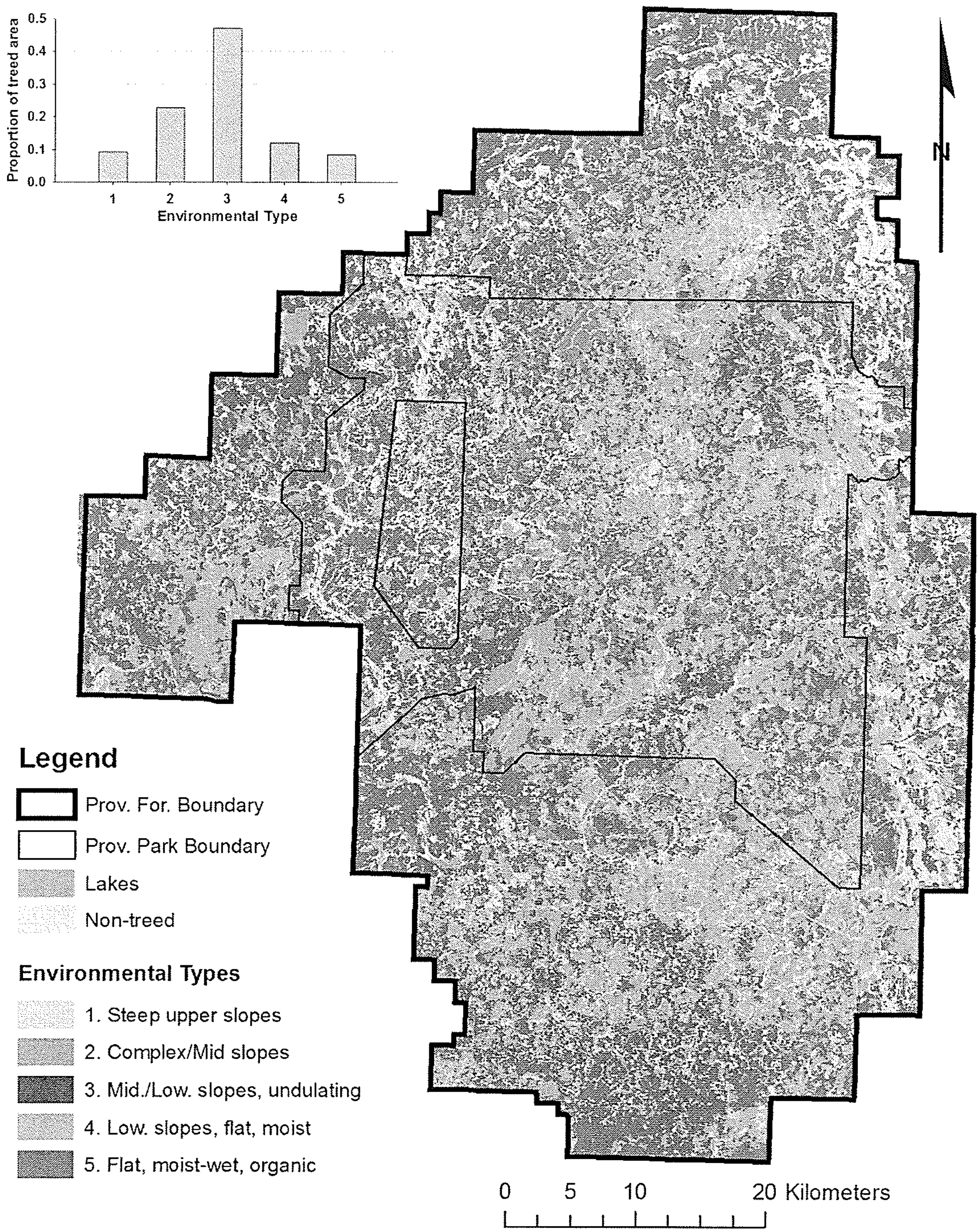
Trajectory	**1**	**2**	**3**	**%correct**
1	**48**	4	0	92
2	18	**510**	6	96
3	5	5	**97**	91
Total	71	519	103	**95**

APPENDIX 4

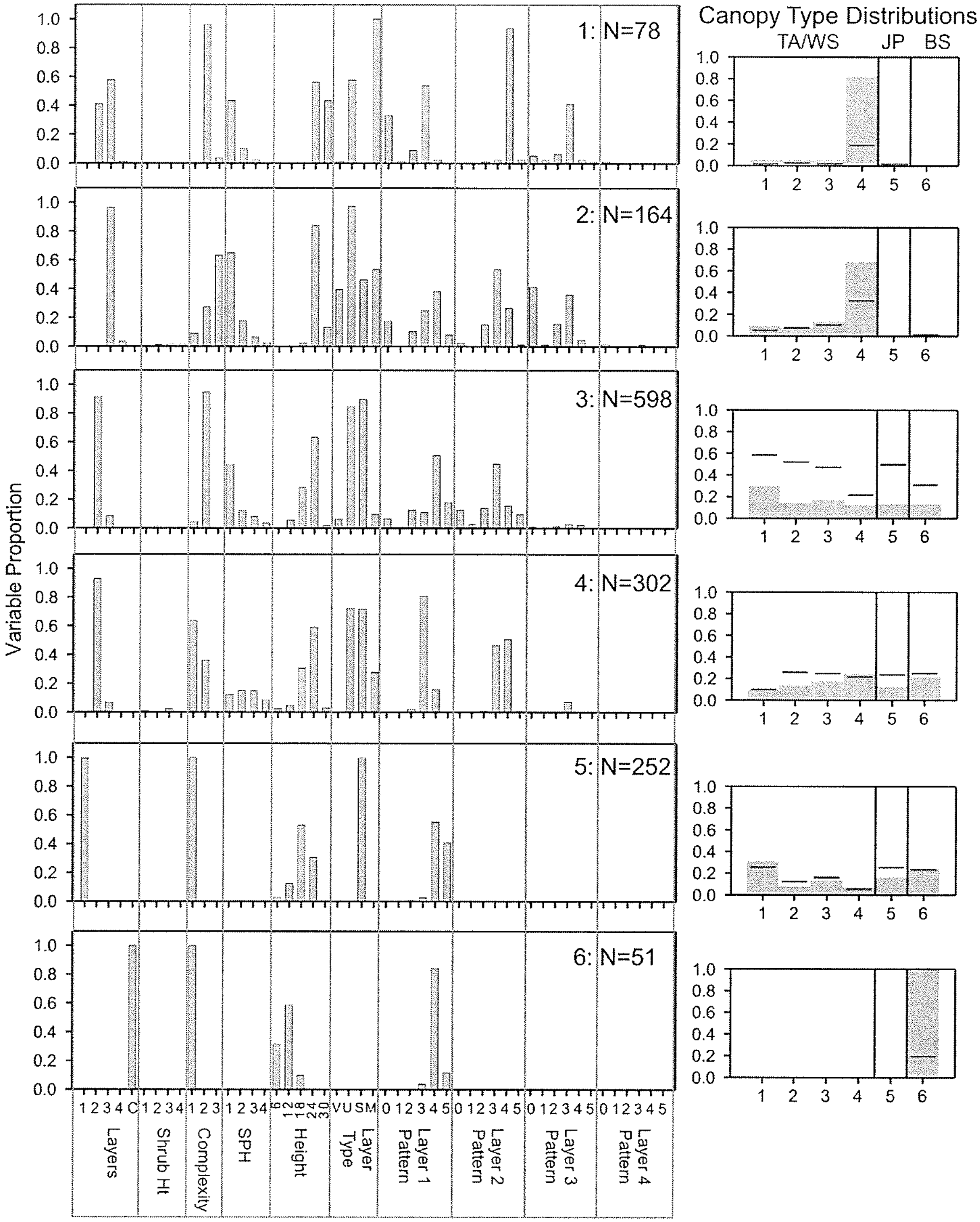
A) Characteristics of the five environmental types (left) showing the proportion of the truthing polygons (n = 1445) in which each environmental variable is present. Figures to the right show the distribution of canopy types within each environmental type. Vertical bars represent the relative proportion of different canopy types within the environmental type, and horizontal dashes represent the relative proportion of the same canopy type between environmental types.



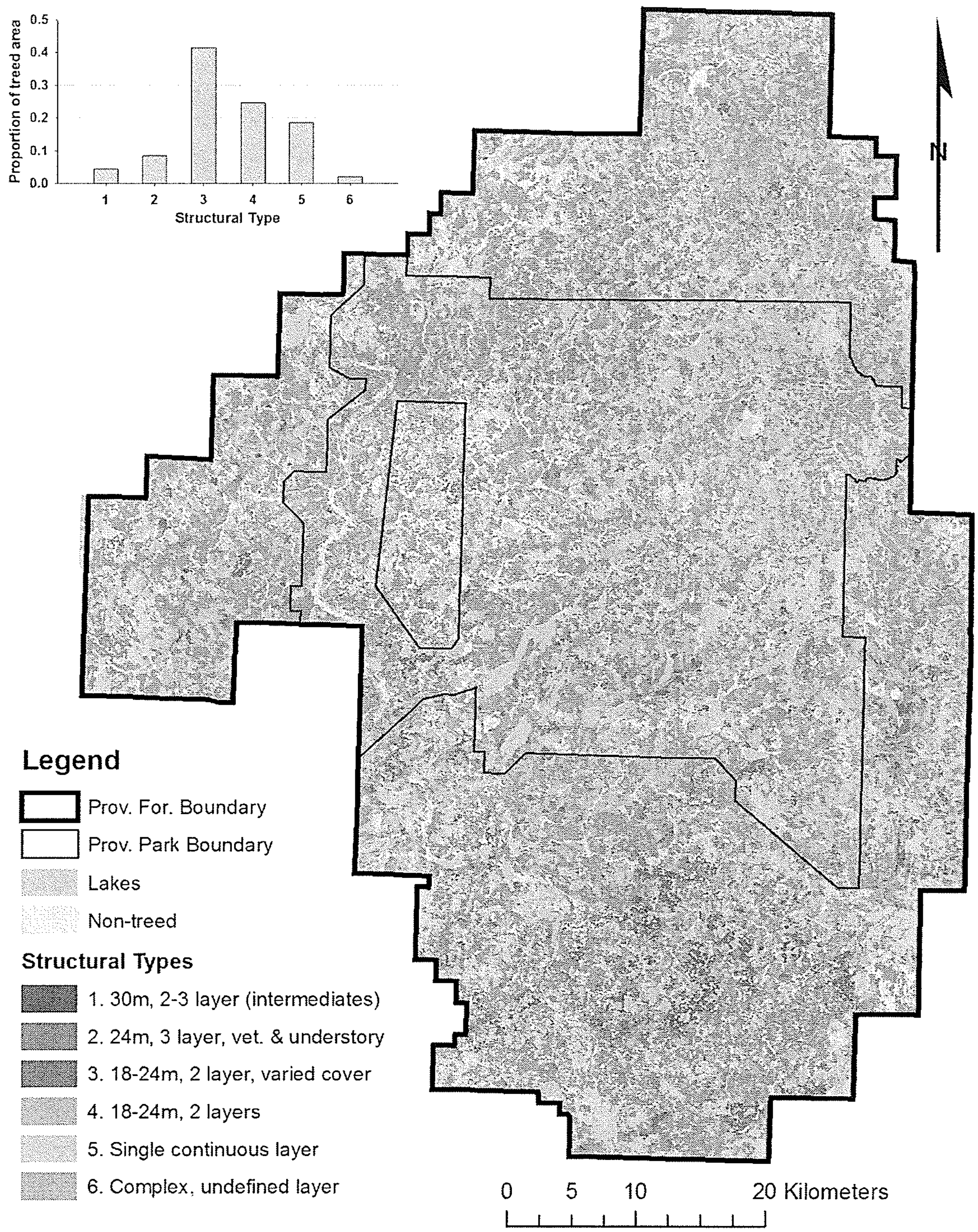
B) Distribution of the TWINSPAN environmental types classified for the Duck Mountain landscape using the MDA model. The bar chart shows the proportion of treed area represented by each environmental type (numbered 1 to 5 in legend).



C) Characteristics of the six structural types (left) showing the proportion of the truthing polygons (n = 1445) in which each structural variable is present. Figures to the right show the distribution of canopy types within each structural type. Vertical bars represent the relative proportion of different canopy types within the structural type, and horizontal dashes represent the relative proportion of the same canopy type between structural types.



D) Distribution of the structural types classified over the Duck Mountain landscape using the MDA model. The bar chart shows the proportion of treed area represented by each structural type (numbered 1 to 6 in legend).



E) Characteristics of the six assemblages identified using TWINSPAN with the three-height class species cover values for the truthing polygons (n = 1024) from the trembling aspen-white spruce pathway. Shown are the percent frequency (F%), and the mean weighted species cover values (C%) and standard deviation (SD) for each species by height class.

	Assemblage 1 (n = 241)			Assemblage 2 (n = 113)			Assemblage 3 (n = 129)			Assemblage 4 (n = 235)			Assemblage 5 (n = 286)			Assemblage 6 (n = 20)		
Spp[ht.class]	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD
TA[19-30]	61	10	14	99	53	13	100	66	14	98	33	17	24	5	10	30	3	6
BA[19-30]	13	1	3	39	2	3	43	3	5	77	8	10	14	0	2	15	0	1
WB[19-30]	11	1	5	8	1	3	8	1	2	29	2	6	2	0	0	10	0	1
WS[19-30]	92	28	23	85	6	6	12	1	2	60	5	7	14	1	5	—	—	—
BS[19-30]	28	3	7	4	0	1	5	0	1	10	0	1	1	0	0	—	—	—
JP[19-30]	12	1	5	26	3	6	10	1	3	15	2	6	3	0	1	—	—	—
BF[19-30]	11	1	6	—	—	—	—	—	—	2	0	1	1	0	0	—	—	—
TL[19-30]	1	0	0	1	0	0	—	—	—	—	—	—	—	—	—	5	0	0
TA[7-18]	38	3	6	12	1	4	11	1	4	68	9	11	97	47	25	40	2	3
BA[7-18]	20	1	3	13	0	1	3	0	0	29	1	4	49	6	11	20	1	2
WB[7-18]	18	2	6	8	0	2	9	0	2	59	6	10	37	5	11	35	4	11
WS[7-18]	68	17	18	85	28	20	44	5	8	64	8	11	53	8	12	10	0	1
BS[7-18]	40	8	16	28	3	5	16	2	7	31	2	5	16	1	5	10	1	5
JP[7-18]	7	1	4	—	—	—	1	0	0	1	0	0	19	3	10	—	—	—
BF[7-18]	19	5	13	4	0	1	3	1	4	6	1	4	2	0	3	—	—	—
TL[7-18]	6	0	1	1	0	0	—	—	—	—	—	—	2	0	1	—	—	—
TA[1-6]	0	0	1	—	—	—	8	1	5	—	—	—	1	0	1	95	25	20
BA[1-6]	—	—	—	1	0	0	2	0	1	—	—	—	1	0	2	5	0	1
WB[1-6]	—	—	—	—	—	—	4	0	2	—	—	—	2	0	1	60	8	10
WS[1-6]	2	0	2	4	1	6	8	1	5	1	0	1	10	3	10	40	5	15
BS[1-6]	2	0	1	—	—	—	1	0	0	—	—	—	5	1	4	30	2	6
JP[1-6]	—	—	—	—	—	—	1	0	0	—	—	—	2	0	3	10	1	2
BF[1-6]	4	1	7	—	—	—	2	0	0	—	—	—	—	—	—	5	0	1
TL[1-6]	—	—	—	—	—	—	—	—	—	—	—	—	1	0	1	20	1	3

F) Characteristics of the three assemblages identified using TWINSPAN with the three-height class species cover values for the truthing polygons (n = 161) from the jack pine-black spruce pathway. Shown are the percent frequency (F%), and the mean weighted species cover values (C%) and standard deviation (SD) for each species by height class.

	Assemblage 1 (n = 80)			Assemblage 2 (n = 72)			Assemblage 3 (n = 9)		
Spp[ht. class]	F%	C%	SD	F%	C%	SD	F%	C%	SD
TA[19-30]	61	5	6	—	—	—	—	—	—
BA[19-30]	—	—	—	—	—	—	—	—	—
WB[19-30]	10	0	2	—	—	—	—	—	—
WS[19-30]	23	2	4	1	0	0	—	—	—
BS[19-30]	80	9	9	1	0	1	—	—	—
JP[19-30]	99	38	16	—	—	—	—	—	—
BF[19-30]	1	0	1	—	—	—	—	—	—
TL[19-30]	4	0	2	—	—	—	—	—	—
TA[7-18]	8	1	3	47	3	5	11	3	10
BA[7-18]	—	—	—	3	0	1	—	—	—
WB[7-18]	13	1	4	7	1	4	—	—	—
WS[7-18]	16	2	5	33	4	10	—	—	—
BS[7-18]	84	30	20	83	33	26	22	1	3
JP[7-18]	9	0	2	97	36	22	33	6	14
BF[7-18]	3	0	1	3	0	2	—	—	—
TL[7-18]	6	0	1	11	1	4	—	—	—
TA[1-6]	—	—	—	—	—	—	89	6	4
BA[1-6]	—	—	—	—	—	—	—	—	—
WB[1-6]	1	0	0	1	0	0	33	2	4
WS[1-6]	1	1	6	3	0	1	11	2	5
BS[1-6]	—	—	—	6	2	9	89	7	5
JP[1-6]	—	—	—	1	0	0	100	22	6
BF[1-6]	—	—	—	1	0	0	—	—	—
TL[1-6]	—	—	—	—	—	—	22	1	1

G) Characteristics of the four assemblages identified using TWINSPAN with the three-height class species cover values for the truthing polygons (n = 260) from the black spruce-eastern larch pathway. Shown are the percent frequency (F%), and the mean weighted species cover values (C%) and standard deviation (SD) for each species by height class.

	Assemblage 1 (n = 7)			Assemblage 2 (n = 186)			Assemblage 3 (n = 26)			Assemblage 4 (n = 41)		
Spp[ht.class]	F%	C%	SD	F%	C%	SD	F%	C%	SD	F%	C%	SD
TA[19-30]	14	0	1	1	0	2	—	—	—	—	—	—
BA[19-30]	14	1	1	—	—	—	—	—	—	—	—	—
WB[19-30]	—	—	—	1	0	0	—	—	—	—	—	—
WS[19-30]	29	2	4	2	0	1	—	—	—	—	—	—
BS[19-30]	100	44	18	4	0	2	—	—	—	—	—	—
JP[19-30]	43	6	11	1	0	0	—	—	—	—	—	—
BF[19-30]	—	—	—	—	—	—	—	—	—	—	—	—
TL[19-30]	29	3	7	3	0	3	—	—	—	2	0	2
TA[7-18]	—	—	—	9	0	2	4	0	1	2	0	0
BA[7-18]	—	—	—	2	0	0	—	—	—	2	0	0
WB[7-18]	14	2	6	2	1	4	12	1	2	—	—	—
WS[7-18]	—	—	—	9	0	2	—	—	—	—	—	—
BS[7-18]	57	19	22	99	65	16	96	26	13	49	9	13
JP[7-18]	—	—	—	25	3	6	4	1	5	—	—	—
BF[7-18]	—	—	—	1	0	2	—	—	—	—	—	—
TL[7-18]	29	1	2	56	4	5	96	34	17	41	4	8
TA[1-6]	—	—	—	—	—	—	—	—	—	2	0	2
BA[1-6]	—	—	—	1	0	0	—	—	—	—	—	—
WB[1-6]	—	—	—	1	0	0	—	—	—	5	0	1
WS[1-6]	—	—	—	1	0	0	—	—	—	—	—	—
BS[1-6]	14	1	3	5	2	8	4	1	6	100	45	22
JP[1-6]	—	—	—	—	—	—	—	—	—	5	1	4
BF[1-6]	—	—	—	1	0	1	—	—	—	—	—	—
TL[1-6]	14	1	3	1	0	1	4	0	0	78	10	13

H) Percent distribution of structural cohorts for the species assemblages identified using TWINSPAN for each successional pathway.

	Structural Cohort		
Assemblage	1	2	3
Trembling aspen-white spruce pathway (*n* = 1024)			
1	31	49	20
2	68	27	5
3	89	10	1
4	49	48	3
5	70	26	4
6	45	55	0
Jack pine-black spruce pathway (*n* = 161)			
1	70	29	1
2	82	17	1
3	67	33	0
Black spruce-eastern larch pathway (*n* = 260)			
1	57	43	0
2	59	30	11
3	31	15	54
4	46	15	39