

**STRUCTURE AND DYNAMICS OF BOREAL FOREST STANDS IN
THE DUCK MOUNTAINS, MANITOBA**

BY

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A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

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ABSTRACT

No single process seems to characterize succession in the boreal forest; accumulating evidence suggests that it is subject to considerable variation resulting in multiple successional pathways. This study was undertaken to elucidate the structure and dynamics of major boreal forest stands in the Duck Mountain Provincial Park and Forest.

Detailed tree size and age data were obtained from each of 70 sampled stands located throughout the study area. Our approach involved reconstructing the initial post-fire composition of these stands, and classifying them into five stand types (Trembling Aspen, Balsam Poplar, White Spruce, Jack Pine, and Black Spruce). Successional pathways within these stand types were inferred through the careful examination of major stand dynamic features in 80-130 year old stands. A novel multivariate approach was used to examine the relationship between the initial cohort and the composition of the subsequent advance regeneration cohort. Variation in patterns of regeneration were examined universally and within each stand type. Timing of recruitment and major factors affecting secondary recruitment were also examined.

Our results reveal that landscape-scale succession in Duck Mountain does not result in convergence to a single self-perpetuating 'climax' forest community. Historically, many stands burned with sufficient frequency that canopy succession did not occur, resulting in long-term reestablishment of pre-fire canopy composition. In the absence of disturbance, the initial post-fire cohort composition may be maintained by gap dynamic processes. More often, however, recruitment of other species along with regeneration of the initial cohort species results in increased canopy diversity and complexity over time.

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CHAPTER 1

INTRODUCTION AND OBJECTIVES

1.1 Introduction

The Duck Mountain Provincial Park and Forest is a complex forested landscape that incorporates elements of the Manitoba Escarpment, the Manitoba and Saskatchewan Plains, and the Grandview and Swan River Valleys. These underlying landforms, combined with Holocene glacial activity, have contributed to the complex and variable topography of the region. Largely as a result of this complex physiography, the area supports a remarkably diverse assemblage of forest communities. Other than a descriptive summary by Rowe (1956), few successional studies have been undertaken in the boreal mixedwood forests of western Manitoba (but see Caners & Kenkel 1998).

The boreal forest is one of the largest biomes in the world, occupying approximately 8% of the global continental landmass. Although it has been described as a ‘simple’ ecosystem (Larsen 1980), the dynamic of these forests is poorly understood (Bonan & Shugart 1989). The boreal is a disturbance-driven ecosystem: catastrophic forest fires are so frequent that the classic Clementsian notion of forest succession is largely meaningless (Rowe 1961). Most studies of boreal forest succession in North America suggest that Egler’s (1954) ‘initial floristic composition’ model is broadly relevant. For example, in the boreal forest of east-central Québec “apparent succession is simply an expression of differential longevity and conspicuousness of species” (Cogbill 1985). In other words, changes in canopy composition and structure are simply a manifestation of differential growth rates of contemporaneously-established trees (the ‘complete’ Egler model, cf. Wilson et al. 1992). Bergeron & Dubuc (1989) concluded that both the ‘initial floristic composition’ model and Connell and Slatyer’s (1977) ‘passive tolerance’ model are applicable to boreal forest

ecosystems. According to the 'passive tolerance' model, succession is a reflection of subordinate species remaining in a suppressed state until more resources (e.g. light) are made available by the removal of an adjacent dominant individual.

A number of studies have indicated that young stands of 'pioneer' species such as jack pine, trembling aspen and white birch are, at least in theory, transitional stages toward forests dominated by balsam fir, black spruce and/or white cedar (*Thuja occidentalis*) (Dix & Swan 1971; Carleton & Maycock 1978; Cogbill 1985; Bergeron & Dubuc 1989; Bergeron & Dansereau 1993; Bergeron 2000; Zoladeski & Maycock 1990) (N.B.: Common plant species names are used throughout this report, following Johnson et al. 1995. Scientific nomenclature is utilized for species not listed in Johnson et al. 1995, and for most mosses.). However, older upland stands are often "decadent", and display "rapid deterioration and degeneration" and limited advance regeneration (Cogbill 1985). Zoladeski and Maycock (1990) found evidence that early-successional stands often develop toward mixed black spruce and balsam fir stands, but hypothesized that fire would normally halt such a trend (see also Dix & Swan 1971). In the absence of fire, Bergeron and Dubuc (1989) hypothesized that mesic and hygric upland sites will eventually be dominated by balsam fir and white cedar, while white cedar and black spruce will dominate xeric sites. However, they also recognized that patch dynamic disturbances (e.g. pest outbreaks) may alter these 'ideal' successional pathways. Boreal hardwood stands may become increasingly dominated by late-successional softwoods, but this trend is periodically interrupted by outbreaks of spruce budworm (Bergeron & Dansereau 1993). The result is a complex patchwork mosaic of mixed hardwood-softwood forest at the landscape level.

Accumulating evidence suggests that succession in boreal forest stands is subject to considerable variation, resulting in multiple successional pathways (e.g. Carleton & Maycock 1978; Cogbill 1985; Zoladeski & Maycock 1990; Kenkel et al. 1998). Factors

contributing to this variation include propagule availability, soil nutrient status and physical structure, ungulate herbivory, granivory, insect pest and fungal pathogens, light availability, rooting space, and seedbed quality (Heinselman 1973; DeGrandpré et al. 1993; Galipeau et al. 1997). The accumulation of organic litter and/or high feathermoss cover can limit tree recruitment by retarding germination and seedling establishment (Cogbill 1985). A dense shrub layer may have a similar effect (Zoladeski & Maycock 1990; Caners & Kenkel 1998).

Attempts have also been made to describe boreal forest dynamics in terms of vital attributes and life-history characteristics of major tree species (cf. Noble & Slatyer 1980; Huston & Smith 1987). Dix and Swan (1971) proposed that most boreal tree species are 'pioneers', defined as species that do not normally regenerate beneath themselves. Included in this category are trembling aspen, jack pine, white birch and balsam poplar (see also Bergeron & Dubuc 1989). Black and white spruce are deemed 'chiefly pioneer', since they may occasionally form an advance regeneration layer beneath an existing canopy. Balsam fir was considered the only late successional boreal forest species in western Canada. Rowe (1961), however, suggests that no western Canadian boreal tree possesses all the attributes required for a self-perpetuating climax species. In eastern Canada, both balsam fir and white cedar have vital attributes typical of late-successional species. These attributes include longevity, shade tolerance, and the ability to germinate and establish on organic substrates (Bergeron & Dubuc 1989).

Repeated observations in the same stand over time are required to unequivocally describe forest stand dynamics, but such data are rarely available. An alternative approach is chronosequencing, which involves the enumeration of stands of various ages to infer successional trajectories. This approach assumes minimal confounding of environmental factors (e.g. differences in soil conditions among the stands sampled), and the existence of a

single underlying successional trajectory. If environmental variation exists, or if multiple successional pathways are possible, chronosequencing may produce meaningless or overly-simplistic trajectories. Another approach involves using the size- and age-class distributions of trees in established stands to infer successional trajectories, under the assumption that individuals in the advance regeneration layer will eventually reach the canopy. An approach combining chronosequencing and size-age class analysis has been widely used to infer successional processes in the boreal forest (e.g. Dix & Swan 1971; Carleton & Maycock 1978; Cogbill 1985; Bergeron & Dubuc 1989; Zoladeski & Maycock 1990).

1.2 Objectives

This study was undertaken to elucidate the structure and dynamics of major boreal forest stands in the Duck Mountain Provincial Park and Forest. The objective was to determine successional trajectories for major forest stand types, and to identify the major biological and non-biological processes that determine stand composition, structure and dynamics. The data used to achieve these objectives were acquired through detailed, intensive sampling of forest stands located throughout the study area. Successional pathways were inferred by aging trees in the canopy and regenerating layers, and by carefully examining stand dynamic processes such as canopy mortality and advanced recruitment in the regeneration layer and overstory. Variation in patterns of regeneration in relation to initial post-fire composition were examined universally and within each of five initial stand types (Trembling Aspen, Balsam Poplar, White Spruce, Jack Pine, and Black Spruce). Timing of recruitment and major factors affecting secondary recruitment (advance regeneration) were also examined. Based on these data, a synoptic model was developed to predict long-term successional dynamics of forest stands in the Duck Mountains.

Our model will be useful in determining conditions most favourable for maintaining and promoting biodiversity in the region, and in predicting the likely outcomes of various forest management decisions. Knowledge of natural forest successional processes is critical to the long-term sustainable management and environmental stewardship of our boreal forests.

CHAPTER 2

LITERATURE REVIEW

2.1 Structure and Dynamics of the Boreal Forest

2.1.1 The Boreal Forest

2.1.1a Introduction

The boreal forest is circumpolar in extent (Pojar 1996) and covers nearly 30% of the landmass of North America north of Mexico (Barbour & Christensen 1993). In North America the boreal forest stretches from Newfoundland, across central and northern Canada, to Alaska (Rowe & Scotter 1973). A forest-tundra ecotone characterizes the northern boundary of the boreal forest (Larsen 1980). The southern edge of the boreal forest borders the aspen parkland region in the Prairie Provinces and deciduous forest in eastern Canada (Swan & Dix 1966).

The dominant vegetation of the boreal forest is characterized by evergreen coniferous forest, but deciduous broadleaf hardwood and mixedwood forests are also common and can be extensive (Pojar 1996). Both white spruce and black spruce have a transcontinental range (Pojar 1996), but white spruce is more abundant in central and western Canada while black spruce is more abundant in the north (Rowe & Scotter 1973). As fire frequency and the occurrence of peaty or shallow, cold substrates increase northward in the boreal forest, so does the dominance of black spruce (Rowe & Scotter 1973). While tamarack has a distribution nearly as widespread as the spruces, its distribution is patchier (Pojar 1996) and predominance greater in the central and eastern boreal forest (Payette 1992). The abundance of balsam fir is greatest in eastern Canada, especially on well-drained sites (Rowe & Scotter

1973). The range of jack pine extends from Cape Breton Island, Nova Scotia to the Mackenzie River in the Northwest Territories, but its abundance is greatest in Ontario (Rudolph & Laidly 1990). The range of lodgepole pine and subalpine fir includes the extreme western boreal forest (Alberta foothills, northern British Columbia, the Yukon and Alaska)(Farrar 1995). Trembling aspen, white birch, and balsam poplar, the three most important hardwood tree species in the boreal forest, are widespread transcontinental species (Pojar 1996).

2.1.1b Climate

The boreal forest is characterized by a northern, continental (-50° to +35° C extremes of temperature) climate with long, very cold winters (Pojar 1996). Maximum precipitation occurs during the short and relatively cool summers. The Canadian Interior Plains are influenced by polar continental air for most of the year (Klassen 1989). Occasionally, however, warm, moist Pacific air extends into Alberta and southwest Saskatchewan. Summer incursions of warm and moist tropical air from the Gulf of Mexico into southeastern Manitoba also occur. The distinct seasonality, storminess, and changeability observed in the Interior Plains are a result of the movements of these air masses (Smith 1989).

It has been suggested that precipitation and air temperature can be used to determine the dominance distribution of major boreal tree species (Lenihan 1993). Lenihan (1993) suggests that species assemblages are primarily controlled by climate, as evidenced by the relationship between the geographic distribution of boreal forest types and seasonal airmass dynamics. A major exception to this principle, however, may be the observed shift in relative dominance from trembling aspen on Cretaceous bedrock to jack pine on Precambrian bedrock in the Central Interior (Lenihan 1993).

Soil thermal regime and moisture content, which determine decomposition and nutrient cycling rates, are also influenced by climate (van Cleve et al. 1983; Prescott et al. 1989). In addition, climate determines both the frequency and intensity of forest fires, and so also affects stand dynamics and the evolution of fire adapted life-history strategies (Kenkel et al. 1997a).

Locally, topographic features can significantly modify general climatic conditions (Kendrew & Currie 1955). The highground along the Manitoba Escarpment in Riding Mountain National Park, for example, receives an average of 40% more summer precipitation than the adjacent uplands (Environment Canada 1993). Wind direction, wind speed, and air temperature can also be affected by local landforms (Kendrew & Currie 1955).

2.1.1c Quaternary Ecology

The chronology of glacial recession and re-advance set the spatial and temporal framework for revegetation processes (Ritchie 1987). As the Late Wisconsin Cordilleran and Laurentide ice sheets and glacial lakes receded, much of the exposed land surface was occupied by an early, spruce dominated version of the boreal forest (Ritchie & Yarranton 1978). This forest lacked pine or tree birch components. Ritchie & Yarranton (1978) suggest that the boreal forest observed in the Western Interior today is a result of modifications and adjustments to this "primeval, late-glacial spruce forest".

This ice-margin forest spread north and east as deglaciation continued, and was present across the southern part of the region approximately 12 000-14 000 years before present (BP). Grassland began replacing this spruce forest in its southwest range as the climate became warmer and drier ca. 10 500 years BP. The much warmer and drier climate of the

hypsothermal (beginning 7400 BP) resulted in the northern expansion of tree species with a Great Lakes-St. Lawrence affinity in eastern Canada, while in the west the grasslands continued to expand (Delcourt & Delcourt 1987). By ca. 6500 BP, spruce forest was restricted mainly to the Canadian Shield and northern Saskatchewan and Alberta (Klassen 1989). A southern shift of the boreal forest occurred between ca. 5500-2000 BP due to a cooler, moister climate (Payette 1992). This climate change also resulted in the cessation of northward boreal migration. A slight southward expansion of the boreal forest has occurred in the last 2000-3000 yrs. (Payette 1992), with the boreal ecotone reaching its present position about 1000 BP (Lui 1990).

The recolonization of the post-glacial boreal landscape has been affected by a number of interacting factors, including the location of glacial refugia and barriers to species movement (Kenkel et al. 1997a). For example, a number of species reach their western distributional limit in northwestern Ontario and southeast Manitoba, including red and white pine, white cedar, black ash, bigtooth aspen, mountain ash, and numerous understory species. Kenkel et al. (1997a) note that this distribution corresponds roughly to the shore of glacial Lake Agassiz, to a shift in substrate type from granite to limestone, to increased fire frequency, and to a drier environment.

2.1.1d Landscape and Landform

While climate largely determines species distributions, it is landform, in combination with fire and other disturbances, that results in the variety of ecosystems and communities observed in the boreal forest (Pojar 1996). The parent materials and surficial topography of a particular region make up that region's landform. Local insolation and drainage patterns, in turn, are determined by this landform, as are soil development and species establishment and growth (Host et al. 1987). The leaching potential of soils, and water movement through

them, are both influenced by physiography and microrelief (Fuller & Anderson 1993). The distribution, abundance, and regeneration dynamics of boreal forest species are influenced by landform, as well (Kenkel et al. 1998).

Landform can strongly influence wildfire spread and intensity (Heinselman 1996). As surface moisture is controlled by physiography, convex surfaces are more prone to burning because they quickly shed water and dry swiftly (Rowe & Scotter 1973). South-facing forest stands are drier, and therefore more susceptible to burning than are more moist, north-facing stands (Rowe & Scotter 1973). Heinselman (1996) identifies a number of landform features that can influence the spread and intensity of fire: the location, size, shape, and compass alignment of lakes, and the abundance of islands in them; the location, size, shape, and alignment of streams and wetlands; the location, size, height, and alignment of bedrock ridges, glacial moraines, and eskers; and the location size, relative depth, and alignment of fault lines, valleys, troughs, and other lowlands.

The development of both topography and soil in the boreal forest region is strongly influenced by bedrock and overlying glacial deposits (Klassen 1989). Early-Precambrian granitic bedrocks dominate the Canadian Shield, while Cretaceous rocks, mostly shales and siltstones, occur throughout the southern Interior Plains. The Manitoba Escarpment (extending in a roughly north-south direction through western Manitoba and eastern Saskatchewan) generally forms the easternmost edge of Cretaceous bedrock on the prairies (Manitoba Department of Energy, Mines, and Resources 1987). Lying between the eastern Precambrian and western Cretaceous bedrocks is a belt of Paleozoic rock (mostly limestone, as well as dolomite, sandstone, and shale)(Klassen 1989).

The Manitoba Escarpment (separating the Manitoba Plain from the Saskatchewan Plain) and the Missouri Coteau (separating the Saskatchewan Plain from the Alberta Plain) are two

abrupt rises in elevation lying between the Precambrian shield and the Rocky Mountains. These areas resisted glaciation due to the fact that they consist of resistant bedrock overlaying weaker beds (Klassen 1989). A series of uplands are found along the Manitoba Escarpment, including Riding and Duck mountains and the Porcupine Hills. At Duck Mountain, the height of the escarpment ranges from 170-370 m above the Manitoba Plain (Neilsen 1988). Where older, softer rock lay close to the surface, drainage from the west cut deep channels into the escarpment (Neilsen 1988). These broad preglacial valleys have undergone extensive deposition of Quaternary sediments.

The general physiography of the Interior Plains is dictated by its underlying bedrock, but it is Quaternary glacial deposits (glacial tills, glacial lake deposits, and glaciofluvial deposits) that most local landforms are influenced by. Glacial tills in the region are quite uniform and contain approximately equal amounts of sand, silt and clay along with minor amounts of coarser material (Klassen 1989). Glacial lake deposits can be a locally significant component of the drift in hummocky moraine complexes, such as those found bordering the Manitoba Escarpment. Clay and silt dominate glacial lake deposits, with sands being locally important as well. Coarse textured substrates (sand and gravels) dominate glaciofluvial deposits, which at the surface are usually expressed as distinct landforms (Klassen 1989). Kames, eskers, deltas, fans, outwash trains, and kame and kettle complexes are examples of glaciofluvial landscape features.

2.1.1e Edaphic Factors

Cold soil temperatures, poor drainage, thick insulating feathermoss/lichen/surface organic layers, low available nutrients, and permafrost are key edaphic features of the boreal forest (Pojar 1996). The distribution and regeneration dynamics of boreal forest species are strongly influenced by edaphic factors (Kenkel et al. 1998). Heinselman (1996) indicates

that the texture and rockiness of soil influences the spread and intensity of wildfires. Soils in the boreal forest can be altered physically or chemically by processes such as organic matter addition, decomposition and transformation, mineral weathering, and the precipitation of secondary products (Fuller & Anderson 1993).

The western boreal forest is dominated by Brunisolic, Regosolic, Gleysolic, Organic, Crysollic, Podzolic, and Luvisolic soils (Pojar 1996). Luvisolic soils are especially common in the Interior Plains. Chernozemic soils dominate the southwestern reaches of the boreal forest in the Interior Plains (Acton 1989). The acidic bedrock of the Precambrian shield is overlain by Luvisols, Brunisols, and Podzols.

2.1.2 Disturbance

2.1.2a Introduction

The landscape-scale spatial patterns of vegetation observed in the boreal forest are largely the result of two overlapping spatial mosaics (Weir et al. 1999). The first is a reflection of surficial geology and geomorphic processes (species sorting by moisture and nutrient gradients) (Bridge & Johnson 1999). The second is a reflection of the forest landscape age, or time since last fire of the various stands observed on the landscape (Weir et al. 1999). At the landscape level, fire is widely accepted as the most important disturbance feature in the boreal forest (Ritchie 1956, Dix & Swan 1971, Heinselman 1973, Carleton & Maycock 1978, Wein & MacLean 1983, Payette 1992, Englemark et al. 1993, Caners & Kenkel 1998, Kenkel et al. 1998, Johnson et al. 1998, Carcaillet et al. 1999). Fire, climate and soils form a multifactorial complex that defines the boreal ecosystem (Larsen 1980). A number of other disturbance factors, including herbivores, pests and pathogens, and human activity can also significantly impact forest structure and dynamics.

2.1.2b Fire

The Physics of Fire

Fire Weather, Fire Behavior, and Season of Burn

Fuel moisture content, and therefore weather, are of “prime importance” when determining fire behaviour because of the level of heat energy needed to dry fuels (Johnson & Miyanishi 1995). The process of combustion requires a number of steps, the first ones being the heating of fuels to 100°C and the resulting evaporation of water present in the fuels. Local climatic conditions for a year or more before a fire influence the nature of the fire (Heinselman 1996). Large, high-intensity burns often accompany severe drought. Prolonged drought conditions can convert many plant materials that normally would not burn into ready fuels, adding to total available fuels. For example, the green leaves and stems of many understory shrubs and herbs, and even the leaves of broadleaf trees such as aspen and birch may dry out and become fuel.

Despite the recharge of soil moisture that occurs in spring due to snowmelt, spring fires can occur. Heinselman (1996) gives a number of reasons for this phenomenon: the needles of living conifers are very dry until growth begins; and the dead needles, leaves, and grasses from the previous year's growth dry quickly on the long, warm, sunny days that often accompany spring dry spells.

Summer fires in most vegetation types require a longer drought buildup and more severe fire weather than spring or fall fires (Heinselman 1996). Actively growing understory vegetation can act as a heat sink, as can deciduous overstory trees. Summer fires are possible however. Under a prolonged summer drought, evapotranspiration dries out the litter and humus layers, and they become part of the fuel load. Heinselman (1996) states that deciduous forests are fuel breaks in most summers, but can burn under extreme conditions,

especially if they contain balsam fir or spruce in the understory to act as fire ladders, carrying ground fires up into the canopy. During extreme fire weather conditions (drought and high winds), the relative importance of different fuel (forest) types diminishes because the conditions in all stands reach the critical point where crown fires can develop (Bessie & Johnson 1995).

Very rapid fire spread can occur in the fall, as most trees, shrubs, and herbs have completed growth by mid-August and are beginning to go into dormancy (Heinselman 1996). After October 1, however, the daily burning period is shorter due to decreasing day length and nightly frost or dew, and so fires are less likely to burn vigorously.

Some pure coniferous stands are much less affected by seasonal variations in fuel availability. Heinselman (1996) states that the jack-pine and black spruce-feathermoss communities found in the Boundary Waters Region of northern Minnesota are examples. The sparse herb and shrub cover and few broadleaf trees in the canopy reduce the number of heat sinks to slow down fire advance. As well, coniferous needles do gain moisture content in the summer, but are easily dried out under drought conditions. A number of other factors contribute to the inherent flammability of these communities, including the fact that coniferous species contain significant amounts of resins, tars, and other easily ignitable compounds in their wood, bark, and needles. In addition, the feathermosses and dead needles found on the forest floor in these communities are considered “short time-lag fuels”, and dry out very quickly, even after short periods without rain.

The weather conditions during a fire can also strongly influence its behaviour (Rowe & Scotter 1973; Johnson 1992; Engelmark et al. 1993; Heinselman 1996). Key factors include humidity, wind speed and direction, temperature, sky conditions, day length, and time of day (Heinselman 1996). The most severe fire activity occurs when humidity is

below 20%, winds that are greater than 20 miles per hour and are blowing towards large areas of heavy fuels and highly flammable stands, temperatures are high (usually > 80 °F), skies are clear, and at midday when days are long (generally before late September). In conditions such as these fires can run several kilometres in a single day, aided by long-distance spotting, and complicated by fire-induced winds, whirls, and strong convection columns. It is also likely that it is during fire weather like this that fires are able to jump lakes and streams and other possible fire barriers. Wind shifts can also bring about rapid increases in fire size, as a long fire flank can become a new, wide flaming front.

Fuel Buildup in Older Stands

Heinselman (1996) maintains that a number of factors work together to tend to increase the fuels, and hence the flammability, of stands as they age. These factors include increasing total aboveground plant biomass up to a maximum for each stand type, an increase in the dry weight of dead wood as first generation trees begin to deteriorate and die, an increasing abundance of understory conifers that can act as ladder fuels, increased wind-breakage and uprooting of first generation trees as they age, increased tree diseases and plant parasites with stand age cause the death of some trees and making living ones more susceptible to fire, and an increasing accumulation of litter, duff, and humus which become fuel under extreme drought conditions. In addition, certain species present in a stand can increase that stands chances of burning. For example, white birch develops loose scrolls and strips of highly flammable bark 50 to 150 years after establishment and older balsam fir stands may undergo a spruce budworm outbreak which can cause a major dieback and significantly increase fuels.

In contrast, Bessie & Johnson (1995) found that fire behavior was directly related to local weather conditions, and not fuel-type differences in upland subalpine conifer stands in the Kananaskis Valley, Alberta, and Banff and Kootenay National Parks. The authors found

that all stands, regardless of age or vegetation make-up, achieved the threshold required in their computer model to achieve crown fire development during extreme weather conditions.

Fire Cycles

Fire cycles vary across the boreal forest from both east to west and south to north. A fire cycle can be defined as the time required to burn an area equal in size to the study area (Johnson 1992). In the northern part of the boreal forest fire cycles of less than 50 years are common (Kenkel & Watson 1996), while in the south an average of 130 years has been reported (Payette 1992). Weir et al. (1999) found a pre-1890 fire cycle of 15 years in the northern portion of Prince Albert National Park, Saskatchewan, while Carcaillet et al. (1999) found a mean fire cycle of 85 years over the past 2200 years at Lake Francis, western Québec. Care must be taken when comparing fire cycles from different study areas, however, as these cycles can vary depending on the size of the study area and the time period over which the cycle is calculated (Weir et al. 1999).

Shifts in historic fire cycles coinciding with climate changes have been observed in Prince Albert National Park (Weir et al. 1999) and in the Quebec's southern boreal forest (Bergeron & Archambault 1993; Carcaillet et al. 1999).

Fire cycles have an impact on landscape vegetation patterns. Weir et al. (1999) found that shorter cycles result in a relatively young landscape with larger, more oblong polygons with irregular edges while longer fire cycles result in a relatively old landscape with smaller, circular-shaped polygons.

Fire Barriers and Forest Composition

There is a clear relationship between landscape formations, historic fire patterns, and forest communities (Heinselman 1996). Heinselman (1996) stresses that the alignment of

landforms and water bodies is important because fire weather usually comes with west, southwest, or northwest winds that push fires eastward. While even weak fire barriers can stop the north-south or westerly spread of fires, only a very large and effective barrier can stop fire spread to the east, southeast, or northeast. Heinselman makes a number of generalizations about the most effective fire barriers and fire paths in the Boundary Waters region:

- Large wide lakes, especially with few or widely-spaced islands were effective in blocking west-to-east spread.
- Streams, wetlands, valley, and troughs were effective in stopping north/south spread, but less so west-to-east movement.
- Large upland ridge complexes burned the most often, and long west-east aligned ridges can serve as fire paths for spreading fire east.
- Swamps, valleys, ravines, the lower slopes of high ridges (especially those facing east or northeast), islands, peninsulas, and the east, north, northeast, or southeast sides of large lakes or streams burned the least often.
- Most fire barriers can be jumped by spot fires under extreme burning conditions with high winds.

2.1.2c Forest Ecosystem Processes in Relation to Fire

Nutrient Cycling and Loss of Vegetation Cover

A post-fire nutrient 'pulse' results as plant nutrients, tied up in living and dead material, are redeposited on the land surface as ash. This pulse, together with increased decomposition, nitrogen fixation, and soil temperatures, favours rapid vegetative recolonisation after fire (Johnson 1992) and greatly enhances plant growth in the first 5 to 10 years following fire (Heinselman 1996). An increase in soil pH is observed following

fire, and this results in increased nutrient uptake and mineralization (MacLean et al. 1983). Fire removes litter, exposes mineral soil, and thereby promotes seed germination and seedling establishment (Johnson 1992), because all boreal tree species have optimal seed germination and seedling survival on exposed mineral substrates (Van Wagner 1983). In the north, fire may result in the reversal of the paludification process, allowing nutrients to be released (Wein 1983, Viereck 1983).

Loss of vegetation cover due to fire results in increased insolation and soil temperature, with the blackening of the substrate due to burning resulting in increased albedo (Viereck 1983). Another effect of removal of vegetation by fire is a greater fluctuation in soil temperatures on a daily, seasonal, and annual basis due to loss of the windbreak the canopy provided (Viereck 1983). Insolation-induced soil temperature increase was found to be the critical factor in the initiation of suckering in aspen (Maini & Horton 1964 in Peterson & Peterson 1992).

Effects of Fire Size and Intensity

Heinselman (1996) identifies three fire types: crown fires, surface fires, and ground fires (fires that burn in the deeper surface organic layers and in peat). All three fire types can vary in their intensity and area burned. The type of fire and its intensity affect tree mortality, nutrient release, and regeneration (Heinselman 1996). Specifically, the mortality of various vegetative components is affected (i.e. trees, shrubs, herbs, mosses, and lichens). Post-fire regeneration can be affected by fire type and intensity which can affect the opening of closed cones and seed dispersal in jack pine (Johnson & Gutsell 1993), the survival of canopy-stored seeds in the cones of jack pine and black spruce, the kill of stored seeds and vegetative reproductive structures in organic and mineral soils, and the release of nutrients and carbon from the vegetation and organic layers (Heinselman 1996).

The season of burning determines the stage of annual growth of the plants and thus affects their ability to survive or reproduce if killed (Heinselman 1996). The season of burning will also determine when the first reseedling will occur and the timing of vegetative growth.

Burn size affects regeneration from seed sources outside the burn. Bergeron et al. (1999) state that serotinous fire-adapted conifers such as jack pine and black spruce appear to be favoured by large fires, while conifers such as balsam fir and white spruce are likely favoured by smaller fires because of their need to re-invade from unburned areas. The shape and orientation of the burn with respect to landscape features such as ridges, valleys, wetlands, lakes, and streams will affect reseedling, as will unburned areas within the burn (Heinselman 1996).

Biological factors, including seed mass and tree basal area (Greene & Charron 1999), height of the seed release point, size of the seed crop, and stand characteristics (Zasada et al. 1992) will affect the distance of seed dispersal and the quantity of seed reaching various distances from the seed source. In addition, air temperature, relative humidity, wind, and atmospheric stability at the time of seed release will affect dispersal ability (Zasada et al. 1992). Secondary seed dispersal, such as over snow or along watercourses, has the potential to disperse seeds over long distances. Greene & Johnson (1997) note that secondary dispersal over snow can be important for species such as white birch that have large proportions of their seed crops abscising in winter.

The extent to which the litter and humus organic layers are burned is a vital factor influencing plant regrowth (Heinselman 1996). Exposure of mineral soil seedbeds favours the establishment success by jack pine, black and white spruce, and balsam fir. In addition,

nutrient release is proportional to the consumption of organic soil layers by fire (Viereck 1983).

Plant Strategies for Coping with Fire

Plants of the boreal forest have evolved numerous adaptations to living in a fire-prone environment. These adaptations allow them to either survive fires or reproduce even if killed. Heinselman (1996) lists five main adaptations: canopy storage of seed in persistent closed cones; wind-transported seeds and spores; seed banks in organic layers, vegetative reproduction after fire, and fire resistance strategies. These adaptations, as well as the various life history strategies (e.g. juvenile and adult growth rates, age of reproductive maturity, shade tolerance) that enable success in a fire environment, as they apply to the main tree species present in Duck Mountain, will be discussed in a later section.

The 'Patchwork Mosaic'

The term 'site history' refers to the set of cumulative disturbances, unique to each site, that have occurred since glaciation (Kenkel et al. 1997a). The hierarchical layering of these disturbances on the landscape result in a complex spatial mosaic of disturbance histories. At the local level, the patchwork mosaic, created by differences in time since fire combined with topographic variables, is reflected in abrupt changes in tree composition and/or crown height (Carleton & Maycock 1978). Within these stands, vegetation composition and heights are relatively uniform, however (Dix & Swan 1971).

2.1.2d Herbivory

The role of herbivores in boreal forest vegetation dynamics may be greater than has been traditionally acknowledged by ecologists (Kenkel et al. 1998). In a heavily browsed area, the structure, total biomass, production, and species composition of vegetation may be altered

(McInnes et al. 1992). In addition, herbivores demonstrate preferences for certain plant species and individual plants within a species (Belovsky 1981), and so can affect long term community changes.

A number of herbivore species influence vegetation dynamics in the boreal forest, including moose (*Alces alces*)(McInnes et al. 1992), elk (*Cervus elaphus*)(Pastor et al. 1988), white-tailed deer (*Odocoileus virginianus*)(McInnes et al. 1992), and beaver (*Castor canadensis*)(Pastor & Naiman 1992). Moose, for example, browse heavily on trembling aspen, white birch, red-osier dogwood, willow, beaked hazelnut, mountain maple, and balsam fir (Pastor et al. 1988, 1993; Trottier 1981; McInnes et al. 1992). Moose, elk, and white-tailed deer selectively browse balsam fir saplings and trembling aspen suckers in Riding Mountain National Park, restricting the regeneration of these species in older stands (Caners & Kenkel 1998).

McLaren & Peterson (1994) observed that balsam fir growth rates were regulated by cycles in moose density and that growth rates responded to annual changes in primary productivity only when released from herbivory by wolf predation. Beaked hazelnut undergoing heavy clipping respond with increased suckering and stem density (Trottier 1981). The resulting dense canopy limits tree seedling and sucker establishment and growth through shading and reduced soil temperatures. Incomplete tree canopy development is a possible result of the suppression of tree establishment by heavily browsed shrubs (McInnes et al. 1992).

Beaver activity can have a significant affect on vegetation dynamics at a landscape level. Beaver dams cause the flooding of low-lying areas causing stand mortality (Kenkel et al. 1998). Beavers also preferentially remove large-diameter, early-successional deciduous species from the area immediately surrounding the beaver pond (Zasada & Phipps 1990;

Pastor & Naiman 1992), resulting in the competitive release of sub-canopy conifers from shading (Pastor et al. 1993; Peterson & Peterson 1992).

Red squirrels, hares, and various bird species can also interfere with the reproduction and growth of boreal tree species (Zasada et al. 1992). After severe browsing by snowshoe hares, trembling aspen, balsam poplar, white birch, and green alder develop adventitious shoots containing large amounts of terpenes and phenolic resins (Bryant 1981). The production of these chemical defenses results in the reallocation of carbon away from growth and other processes.

2.1.2e Insect Outbreaks

Spruce budworm infestations can reverse successional trajectories by selecting against balsam fir and white spruce (Archambault & Bergeron 1992). Periodic spruce budworm infestations kill mature balsam fir forests, releasing seedlings and favouring the regeneration of less shade-tolerant species (e.g. white birch, black spruce, and white spruce)(Holling 1973; Bergeron & Dubuc 1989; Bergeron & Dansereau 1993; Frelich & Reich 1995). A larch sawfly infestation in the mid-1930's caused a large scale die-back of eastern larch across large areas of the boreal forest in North America (Johnson et al. 1995). Forest tent caterpillar outbreaks are common in trembling aspen stands in the prairie provinces, but rarely affect long-term tree health (Peterson & Peterson 1992).

2.1.2f Gap Dynamics

Disturbance in the boreal forest occurs at multiple spatial and temporal hierarchical scales (Kenkel et al. 1997a). In the absence of fire, gaps created by windthrow, snow and winter storm damage, insect pests, fungal pathogens, or parasitic plants drive boreal forest succession (Bergeron & Dubuc 1989; Frelich & Reich 1995). Boreal stand dynamics are

dependent on the timing and frequency of small-scale disturbances, as the canopy gaps created by these disturbances allow late-successional species to establish (Frelich & Reich 1995). Windthrow, for example, is a fairly common occurrence in the boreal forest, affecting shallow-rooting species such as white spruce (Kenkel et al. 1997a). The mineral soil that is exposed after a windthrow may be important to forest regeneration dynamics because many boreal tree species require a mineral seedbed to become established (Jonsson & Dynesius 1993; Galipeau et al. 1997).

2.1.2g Human Activity

Fire suppression (Furyaev et al. 1983) is actively practised in the southern boreal forest (Zoladeski & Maycock 1990). Fire shapes the boreal forest mosaic, so its suppression is expected to dramatically impact on forest composition, dynamics and structure (Bergeron & Dansereau 1993; Kenkel et al. 1997a). Under a fire suppression regime, succession may lead to perpetually self-replacing forests (Bergeron & Dubuc 1989). Reduced fire frequency may lead to increased regeneration by late-successional species such as white spruce and balsam fir, increasing the chance of spruce budworm outbreaks (Blais 1983). Under short fire cycles, ‘pioneer’ species that can endure or evade fire come to dominate, whereas ‘seed-banking’ fire-intolerant species come to dominate when fires are less frequent and/or severe (Rowe 1983, Zasada et al. 1992). In Quebec, fire cycles greater than 200 years result in a shift from deciduous to coniferous forests (Bergeron and Dansereau 1993). Heinselman (1996) refers to a “homogenizing” of the mosaic of vegetation and fuels that occurs with increasing time since the last fire. As gap dynamics become the driving disturbance across the landscape with continued fire suppression, forests of differing ages become more similar, both structurally and compositionally. Heinselman warns of the impact this loss of stand-age diversity could have on plant and animal species. As well, the loss of ‘fire-breaking’ stands containing less fuel or less fire-prone vegetation

could result in larger-than-natural burns occurring across the landscape. It must be noted, however, that the perception of successional dynamics is scale-dependent (Kenkel et al. 1997a). While adjacent stands may become more similar to each other, each stand is becoming more complex within as gap dynamics works to “chip-away” the uniform, even-aged canopy.

Kenkel et al. (1997a) refer to a paradigm shift in the disturbance regime of boreal forest stands as a result of fire suppression. Under fire suppression, broad-scale, frequent, and synchronous catastrophic disturbances are replaced with small-scale, asynchronous disturbances. Most boreal species have life-history characteristics that are adapted to recurring catastrophic fires, and these attributes “will prove mal-adaptive under a fire suppression scenario” (Kenkel et al. 1997a). Few boreal tree species act as ‘secondary’ colonizers able to establish and grow in small canopy gaps or under an established canopy (Rowe 1961). Balsam fir has these ‘secondary’ successional features, but is generally limited to mesic, mesotrophic environments which experience fewer catastrophic fires (Kenkel et al. 1997a). Peterson & Peterson (1992) state that in certain areas a lack of fire threatens the survival of local aspen populations.

In addition to fire suppression, permanent conversion of forested land to agriculture and the control of herbivore and carnivore populations by hunting and trapping affect the structure and dynamics of boreal forests (Caners & Kenkel 1998).

2.1.3 Succession and Vegetation Dynamics

2.1.3a Introduction

The prediction of forest succession trajectories has been a major focus of ecological research (Frelich & Reich 1995). Through most of the 140 years since theorists first began describing and modeling succession it has been a controversial issue. As such, numerous alterations and developments in both the theory and its application have arisen.

2.1.3b Succession Theory

Johnson (1979) divides the development of successional theory into four distinct periods (Johnson 1979). Between 1859 and 1900, many of the underlying tenets of the theory were laid out. The first fully described sequence of forest succession was completed during this time (Cowles 1899). Johnson identifies a 'developmental and elaborative' or 'classical' period following this initial period, and persisting until 1930. Clementsian theory arose at this time (Clements 1916, 1928, 1936), dominating successional theory for years to come. Clements thought succession to involve the "growth and development of a complex organism", or superorganism (McCook 1994), with the eventual outcome of this development being regional or climatic climax (Cook 1996). Under this model of succession, dominant plant species were thought to alter their environment over time, allowing later successional species to establish and rendering the environment unsuitable for themselves. Gleason, a contemporary of Clements, held a different view of plant succession. Species assemblages were seen as no more than fortuitous assemblages of species populations (Gleason 1926). In both Clement's and Gleason's succession models, disturbance is viewed as uncommon and nonessential (Cook 1996). A third period in the development of successional theory occurred between 1930 and 1947. This 'scholastic

period' (Johnson 1979) involved a general rejection of Clementsian theory in favour of Gleason's reductionist approach (Kenkel et al. 1998).

A "confused period" (Johnson 1979) occurred after 1947, persisting to this day. Conventional views of successional theory were largely discounted, with no clear replacement arising. Watt (1947) described community vegetation dynamics at the patch level (Cook 1996), in which these patches interact and together make up the community. Cyclical, not seral, succession occur in these patches (Kenkel et al. 1998). Stochasticity, plant life-histories, and biotic interactions were all considered by Watt to be important in determining community structure and dynamics. Watt is generally acknowledged as the first to include disturbance as an implicit part of a vegetation dynamics model (Kenkel et al. 1998). The "initial floristic composition" model proposed by Egler (1954) considers succession as proceeding from (and being limited by) the propagules available at a site following disturbance.

Drury & Nisbit (1973) further challenged Clementsian views by arguing that succession was better explained at the autoecological or physiological level than the community level (Cook 1996). Pickett (1976) presented the first successional theory based on plant evolutionary strategies best suited to "environmental conditions along a successional continuum" (Cook 1996). In addition, this theory considered disturbance as common and integral to succession, depredation as potentially very influential, and biotic pressures such as herbivory as important (Cook 1996). Pickett saw the landscape as consisting of patches of different successional environments, with patches continually changing in relative size, position, and geography due to given disturbance regimes (Kenkel et al. 1998).

Three successional models were suggested by Connell & Slayter (1977); facilitation, tolerance, and inhibition. Disturbance was considered to be of "critical importance to the

course of succession". The facilitation model is considered to be "essentially, the classical, relay floristic pathway" (Noble & Slatyer 1980) with the presence of early colonizing species enhancing the conditions for invasion and growth by later successional species. The tolerance pathway suggests that life history characteristics mediate changes in succession, along with relative resource-use efficiency (Cook 1996). Under this model, early successional species will suppress the establishment and growth of later successional species. The inhibition model states that initial colonizers prevent the establishment of all other species (Cook 1996) until these colonizers are damaged or die. The inhibition model deviates most from the classic Clementsian view because the initial species assemblage is superior, and succession can be arrested or multi-directional (Cook 1996).

Species vital attributes were used by Noble & Slatyer (1980) to model vegetation dynamics in communities subject to repeated disturbance. Under this model, a species' vital attributes, or life-history characteristics, are key to that species success or lack of success at various points in a disturbance-driven successional sequence. The vital attributes of a species are considered by Noble and Slatyer to be those "which are vital to its role in a vegetation replacement sequence". Vital attributes determine the method by which a species arrives and persists at a disturbed site, its ability to establish and mature in the post-disturbance community, and the time needed to reach critical stages in life history. Certain species attributes are beneficial under some types of disturbance regimes, but detrimental under others. Species with high rates of dispersal will be at an advantage following catastrophic disturbance, and hence usually make up the early pioneer species community in a succession sequence. Multiple successional pathways can exist under this model (Cook 1996).

In the two decades since Johnson identified the post-1947 era as the "confused period" much forest succession research has been conducted. However, the concept remains in a

“state of definition”, and traditional (pre-1947) theories have been rejected, at least in their original form (Cook 1996). No single theory of succession is widely accepted at present (Caners & Kenkel 1998). There is, however, an emerging common consensus on a number of points (Kenkel et al. 1998):

- Disturbances are frequent and ubiquitous and operate at various temporal and spatial scales.
- Clementsian ‘climax communities’ are rarely reached. Multiple successional pathways, retrogression, and arrested succession can all occur.
- Stochasticity may significantly affect vegetation dynamics. Cumulative stochastic events are likely.
- Species vital attributes, and their evolution, are important.
- Mechanisms driving succession vary spatially and temporally, and numerous mechanisms may operate simultaneously.

2.1.3c Boreal Forest Succession

Early studies of the boreal forest were largely descriptive, examining phytosociological associations and speculating on vegetation dynamics (e.g. Rowe 1956; Ritchie 1956; Rowe 1961; Swan & Dix 1966; La Roi 1967; Newsome & Dix 1968; Achuff & La Roi 1977; Rowe 1983). These studies facilitated later studies of vegetation-environment relationships (Bergeron & Bouchard 1983; Kenkel 1986, 1987) and vegetation dynamics (Dix & Swan 1971; Shafi & Yarranton 1973; Carleton & Maycock 1978, 1980; Bergeron & Debuc 1989; Zoladeski & Maycock 1990; Bergeron & Charron 1994; Bergeron & Dansereau 1993).

Distinct community composition in different regions of the boreal forest may imply dissimilarities in interregional vegetation dynamics. The high floristic diversity of the Great Lakes region is attributable to a combination of boreal and deciduous elements. However, as one moves north and west the number of species markedly declines, as many species reach their range limits at Minnesota, western Ontario and eastern Manitoba (Swan & Dix 1966). Rowe (1956) comments on the "remarkable floristic similarity" that exists in Manitoba, Saskatchewan and Alberta. Care must be taken, therefore, in applying findings from one region of the boreal forest to another.

A Review of Major Studies of Boreal Forest Succession

Rowe (1956, 1961) challenged the application of Clementsian successional theory to the boreal forest (Bonan & Shugart 1989), where he suggested multi-directional successional trajectories were likely (Rowe 1961). In addition, Rowe (1961) characterized the boreal forest as being disturbance-driven, and recognized that recurrent catastrophic fires promote heterogeneity at the landscape-level and maintain the health of stands. Rowe recognised the importance of site history, edaphic conditions, species life-history attributes, and stochasticism as being important factors affecting stand dynamics and composition.

Dix and Swan (1971) used size-class and age-class distributions to study the dynamics of upland boreal mixed-wood tree species at Candle Lake, Saskatchewan. Trembling aspen, balsam poplar, white birch, and jack pine were classed as pioneer species unable to reproduce in an established stand. White and black spruce were both found to establish in stands immediately following disturbance, and to have the ability to continually establish for up to 20 years thereafter. Little evidence was observed of an ability to invade after 20 years, however. Balsam fir is the only species at Candle Lake with a continual ability to invade established stands, although it does not seed in immediately following disturbance. Abundant balsam fir regeneration below an established canopy was observed in only 9 of

the 89 stands enumerated, indicating that succession is relatively unimportant at this location.

Achuff and La Roi (1977) studied the stand structure, composition, and community-environmental relationships of white spruce-balsam fir forests in the highlands of northern Alberta. Two broad plant communities were delineated. The first group, termed 'cool-oligotrophic', had the highest cover values for balsam fir, *Pinus contorta*, Labrador tea, *Rubus pedatus*, *Vaccinium membranaceum*, *Ptilium crista-castrensis*, *Pleurozium schreberi*, and total bryoid; had higher stand age, and were associated with higher altitude, higher precipitation, cooler summer temperatures, and lower soil nutrient availability. The second group, termed 'warm-mesotrophic' had the highest cover values of white spruce, trembling aspen, total tree, high-bush cranberry, prickly rose, total shrub, *Rubus pubescens*, twinflower, and *Hylocomium splendens*, and is associated with lower altitudes, lower precipitation, warmer summer temperatures, and higher soil nutrient levels. The authors note that the climax population age structure of balsam fir is quite different from that of white spruce. Balsam fir seedling establishment rates are greater than those of white spruce, but sapling mortality is also much higher. These differences, combined with balsam fir's much shorter lifespan and smaller size at maturity, lead to the continued presence of both species in most climax stands.

Carleton and Maycock (1978) used size-class analysis to study the population dynamics of tree species in the boreal forest south of James Bay, Ontario. Stand successional trajectories were generally found to be short, circular, and somewhat divergent. This divergence suggests that communities do not show a successional tendency to progress to a single climax stand type. The circular nature of the vectors corresponds to the fact that species are adapted to establishment in burned areas, while the shortness of the vectors indicates that interspecies associations are weak and not subject to major change during

succession. In contrast to the vectors of other tree species, balsam fir exhibited a linear trajectory. This suggests that balsam fir does not form self-replacing climax stands. The authors note that balsam fir does not show an affinity for any one tree species in young stands, but associates (essentially) with white spruce, balsam poplar, white birch, and trembling aspen in older stands. Young- to medium-aged stands of jack pine often exhibited invasion by black spruce and/or balsam fir, while older stands tended to have little black spruce or balsam fir regeneration and often became open and "savanna-like". Black spruce and balsam fir regeneration was also observed under trembling aspen canopies. Few upland stands appeared to be dominated by these species, however. Carleton & Maycock demonstrate that fire is a vital component of boreal forest ecosystems, that self-regenerating climax stands are absent in these forests, and that stand composition and dynamics are influenced by fire-adaptive species life-history and biological attributes. Vegetative reproduction after fire, serotinous and semi-serotinous cones, and the increased flammability of species on fire-prone sites are given as examples of species attributes that can affect forest composition and dynamics.

Zoladeski and Maycock (1990) used age-class analysis to investigate trends in forest dynamics in northwestern Ontario. Regeneration patterns tended to indicate a perpetuation of the initial tree composition, supporting Carleton & Maycock's (1978) findings and Egler's (1954) initial floristic composition model. The authors note that the sites dominated by rapid colonizers such as trembling aspen and jack pine are fire-prone. Stand-initiating fires are frequent enough in these locations that little compositional change occurs. In contrast to Carleton & Maycock (1978), mature balsam fir stands were found to be self-perpetuating. These stands were found in areas on the landscape that were the least prone to burning. Continuous recruitment of balsam fir into most stands was observed. Vegetative layering in black spruce lowlands and bogs results in the perpetuation of the current species composition, making these the most stable forest type. Conversely, upland black spruce

stands are dense and likely to burn before canopy break-up begins. Zoladeski & Maycock hypothesized that succession in both trembling aspen and jack pine stands moves toward a mixed black spruce-balsam fir forest, but that frequent fires normally prevent this outcome.

Shafi and Yarranton (1973) sampled stands burned at a range of 0 to 57 years before present in the Clay Belt of northern Ontario. Stages of succession and lengths of these stages were examined. Four stages were identified. The initial heterogeneous phase persists for a year and is attributable to spatial variation in the intensity of burning and heterogeneity in the prefire vegetation. The early stage is less heterogeneous because of rapidly-spreading plants which come to dominate the site with its low levels of competition and in the absence of a canopy. A heterogeneous phase follows, attributed by Shafi & Yarranton to an increase in competition and its interaction with environmental heterogeneity. The late phase begins when canopy development occurs and ephemeral species disappear. The timing of the onset of this last phase is a function of the times of colonization and the growth rates of the major tree species present. This study found that the first three successional stages converged on one of two late phases, depending on local physiographic conditions: black spruce on poorly drained peaty areas, and jack pine on overdrained sandy areas. It is also noted that on some upland clay sites, not included in this study, trembling aspen may come to dominate. Evidence is shown that shifts from one successional phase to the next are spatially heterogeneous because some sites mature faster than others. It is also noted that the evolutionary pressures exerted on species of the boreal forest likely differ greatly from those on species in more stable environments. The inherent instability of the region favours late phase species adapted for rapid growth and reproduction (before the next fire) and effective regeneration following fire.

Cogbill (1985) examined stand establishment and development patterns of forests of the Laurentian Highlands in east-central Québec. Using age-class distributions and

chronosequencing, he found that 71% of tree establishment occurred in the first 30 years following stand initiation. Cogbill concludes that the changes observed in canopy composition are not species replacement, but simply a reflection of the differing growth rates of individuals that established simultaneously. Jack pine stands became co-dominated by black spruce about 100 years post-fire, attributed by the author to the mortality of older jack pine individuals and the slow growth of black spruce. The conifer content of trembling aspen and white birch stands increases with age, leading to (in theory) forest dominated by black spruce and/or balsam fir. However, Cogbill notes that the oldest upland stands exhibit limited regeneration and suffer from severe deterioration. Spruce budworm outbreaks and windthrow regularly disturb balsam fir stands in the region. The accumulation of humus and feathermoss in the understory tends to interfere with seedling establishment, delaying canopy replacement. The dense shrub cover that establishes in many sites tends to preserve pioneer communities by preventing the establishment and growth of secondary tree species.

Bergeron and Dubuc (1989) used size-class analysis to examine boreal forest succession in west-central Québec. The authors found that all tree species were present in a stand in within the first 50 years following stand initiation. Stand composition was also found to be similar to that before the burn. The authors found that all communities, regardless of initial canopy composition, tend to converge toward balsam fir and eastern white cedar on mesic and hydric substrates, and eastern white cedar and black spruce on xeric substrates. Despite finding this evidence of successional convergence, Bergeron & Dubuc state that true self-replacement (i.e. Clementsian climax communities) does not occur in the boreal ecosystem. Patch dynamics (as a result of windthrow, spruce budworm outbreaks, etc.) and periodic fires will alter or 're-set' these successional trajectories. In addition, when seed sources for late-successional species were not present or abundant, non-converging patterns of succession were observed. Based on their observations, the authors conclude that both

Egler's (1954) 'initial floristic composition' and Connell and Slatyer's (1977) 'tolerance' models of succession are applicable to boreal forest stand dynamics.

Bergeron and Dansereau (1993) used elapsed time since fire to reconstruct post-fire successional trajectories for Clay Belt forests south of Lake Abitibi, Québec. A shift from deciduous-dominated young post-fire stands to mid-successional mixed deciduous stands to mixed coniferous and coniferous-dominated stands was observed. This pattern of succession has also been noted for other areas of the southern boreal forest: Candle Lake, Saskatchewan (Dix & Swan 1971); Boundary Waters Region, Minnesota (Heinselman 1981); Laurentian Highlands, Québec (Cogbill 1985); Lake Duparquet, Québec (Bergeron & Dubuc 1989). In general, shade-intolerant species such as trembling aspen and white birch are replaced by more shade-tolerant species such as balsam fir and white spruce. In forests with fire cycles > 200 years spruce budworm outbreaks may periodically open up the canopy. Deciduous species can re-establish in these gaps, and the long-term persistence of mixed coniferous-deciduous forests on the landscape results. The authors observed large variations in species replacement patterns and attributed this to a number of factors, including differing substrate types and availability of seed source. The authors found jack pine-dominated stands to be rare on the landscape, and attributed this to past fire regimes that may have excluded the species from the area. As jack pine does not have the ability to easily re-seed from a distance into a burned area, regeneration is reliant on the opening of serotinous cones present on trees located within a burn. As inter-fire recruitment is very low under shaded conditions (Gauthier et al. 1993), the authors note that long intervals between fires may result in the local extinction of jack pine. Considering these facts, Bergeron & Dansereau warn that using the time-since-fire method will only be successful for predicting jack pine abundance in a succession if that species was present before the stand-initiating fire.

Bergeron and Charron (1994) used tree-ring analysis in conjunction with life-history characteristics (e.g. growth rates) to examine stand dynamics over a 230 year period at Lake Duparquet, Québec. Eastern white cedar and balsam fir dominated the pre-fire forest composition, but trembling aspen dominated immediately post-fire due to vegetative reproduction. Shade-tolerant conifers dominated the understory of these aspen stands, suggesting a future shift in canopy composition.

De Grandpré et al. (1993) used chronosequencing to study changes in understory vegetation during succession at Lake Duparquet, Québec. The shifts observed were correlated with thickness of the organic layers, stand age, and canopy composition. The most significant shifts in understory vegetation were observed early in the succession, with most of the species that were present 26 years after fire persisting throughout the later stages. In some older stands, an increase in the diversity and abundance of certain pioneer species was observed. The authors attribute this partly to openings in the canopy arising due to a major spruce budworm outbreak in sites dominated by balsam fir. The authors note that at least 70% of the understory species present may have the ability to survive fire and resprout afterwards or have germinated from the seed bank. Furthermore, many of these species can persist throughout the succession through clonal growth. Without further disturbances such as spruce budworm outbreaks and windthrow, however, a net decrease in species diversity and abundance will occur. Herb and shrub succession was related to Egler's (1954) initial floristic composition model, due in large part to the vegetative reproduction strategies of many of these species. Mosses were observed to have higher richness on old sites, but not greater abundance, partly fitting Connell and Slatyer's (1977) facilitation model.

Heinselman (1973) found that fire and other disturbances maintain an ever-changing mosaic of differing stand types and age-classes in the Boundary Waters region of northern

Minnesota. However, the fire suppression techniques that have been practised in the region since ca. 1900 have resulted in successional changes across the landscape. Heinselman found that succession in jack pine communities results in a shift towards fir-spruce-birch or black spruce-feathermoss communities. However, he states that these climax communities would not be stable due to non-fire disturbances such as spruce budworm outbreak, and wind breakage and uprooting.

Frelich and Reich (1995) examined the relationships between spatial patchiness, spatial scale, and canopy succession in the boreal forest of Minnesota. They found that prior to fire suppression, high fire frequencies maintained even-aged stands of jack pine and trembling aspen on the landscape. Under fire suppression, over time pure stands of jack pine or trembling aspen shift to uneven-aged mixtures of black spruce, balsam fir, white birch, and eastern white cedar. In the absence of fire, gap dynamics become a major force driving succession in these older stands. At the regional scale (1-16 ha), gap dynamic-driven succession leads to a convergence to stands of mixed composition, while at the smaller scale (0.01-0.1 ha) succession is divergent as monodominant stands develop.

Caners and Kenkel (1998) summarized the vegetation dynamics and vegetation-environment relationships for forests at Riding Mountain National Park, Manitoba. A combination of size-class and age-class analyses and species vital attributes were used to infer successional trends of the major stand types present in the region. Balsam fir stands, as well as black spruce stands growing on organic soil, were found to have very short, circular successional vectors indicating that these stands are self-replacing. The vector of jack pine-black spruce stands was longer and converged toward an increased abundance of black spruce. A strong shift toward green ash and white birch was predicted by the long directional vector of trembling aspen-birch-mountain maple stands. The authors state that although the short vector of trembling aspen-balsam poplar stands indicates little

compositional change, succession towards a white spruce dominated canopy will occur in some of these stands. The vector for white spruce was found to be short, suggesting self-replacing stands. Caners and Kenkel note that the abundance of trembling aspen and balsam poplar will decrease in white spruce stands over time.

Kenkel et al. (1998) developed a synoptic model of forest succession in the boreal ecoregion of northwestern Ontario. Size-class analysis, combined with the use of species vital attributes and the enumeration of stands at different post-fire ages was used to infer successional trends. White spruce-balsam fir mixedwood, trembling aspen, birch-tall shrub mixedwood, and balsam poplar stands were found to be converging toward mixed coniferous-deciduous stands dominated by balsam fir, white spruce, white birch, and black spruce in the canopy with a species-rich, herb-shrub understory. Conversely, jack pine-black spruce feathermoss, black spruce feathermoss, and birch-trembling aspen mixedwoods were found to be converging on stands dominated by black spruce in the canopy with an ericaceous shrub-feathermoss understory. The authors indicate that these two self-perpetuating stand types are found on different substrates. The black spruce type is found primarily in nutrient-deficient areas, while the mixed-wood type occurs on less nutrient-limited sites. Changing edaphic conditions and/or disturbance regimes can initiate transitions between the two self-perpetuating forest canopy types, and within their subtypes.

Using both stand-reconstruction and chronosequencing, Bergeron (2000) found that simple processes occurring at the stand level explain changes in forest composition observed while sampling areas of a landscape originating from different fires. Mesic sites located adjacent to Lac Duparquet in the mixed woods of Quebec's southern boreal forest, sampled in eight differing fire areas, were observed to converge towards dominance by shade-tolerant conifers. Bergeron notes that this convergence pattern appears to eclipse effects of differing pre-fire composition and fire behaviour. As such, succession processes

can be adequately explained by species life-history traits such as longevity, type of regeneration, growth rate, and shade tolerance. Stands exhibited change with time-since-fire from hardwood-dominated (trembling aspen and white birch) to mixed with a significant white spruce component to coniferous (balsam fir and white cedar). Trembling aspen was found to persist in most stands, suckering from roots to fill canopy gaps.

2.1.3d Methods for Studying Boreal Forest Succession

The long-lived nature of boreal tree species has meant that following individuals through time to study patterns of succession is very impractical. As a result, ecologists have had to infer succession using a number of techniques (e.g. chronosequencing, canopy-subcanopy relationships (size-class ordinations), static age distributions, static diameter distributions). Another approach, termed stand reconstruction, has also been used recently to study past succession patterns. These methods vary in the number and type of assumptions they make, and in their practical application to studying boreal forest succession.

Static-Age Distributions and Chronosequencing

Using static-age distributions to predict patterns of succession involves coring all live trees in a stand (either at breast height or at the base), and then making a frequency histogram of all the species present divided into age classes (Gutsell & Johnson 1999). It is assumed that the older individuals in the stand represent the early stages of succession, while the younger individuals represent the future stand composition. A chronosequence is simply a series of static-age distributions for a number of stands in an area (Gutsell & Johnson 1999). Here it is assumed that, between stands, younger stands represent earlier stages of succession. It must also be assumed that the sites being compared differ only in their age, and not in any of substrate, climate, disturbance history, or propagule availability (Finnegan 1984). This assumption must be questioned, however, especially when the

acknowledged importance of initial floristic composition to boreal forest dynamics is considered (Kenkel et al. 1998). Other criticisms of the chronosequencing approach to determining successional trends in the boreal forest include the fact that in fire prone areas, in particular, older stands are often poorly represented (Heinselman 1973). Comparing the relative ages of trees cored at breast height or at the base (typically 30 cm from the ground surface) can also be problematic. Slow growing trees (e.g. black spruce, white spruce) may take 20 years to reach coring height, and so will appear to be recruiting into stands later than their faster-growing cohorts (Gutsell & Johnson 1999). However, if careful attention is paid to differences in species' life-history traits, possible misinterpretations of static age structures can be avoided.

Negative effects of chronosequencing assumptions can be ameliorated through large sample sizes and sufficient replication of stands in each age class present on the landscape (Kenkel et al. 1998). A number of studies of boreal forest dynamics have employed chronosequencing (e.g. Shafi & Yarranton 1973; Taylor et al. 1987; Bergeron & Dansereau 1993; De Grandpré et al. 1993; Frelich & Reich 1995; Kelly et al. 1999).

Static-Diameter Distributions and Size-Class Ordination

When static-diameter distributions are employed to study succession, the diameter of each live individual in a stand is measured (at breast height or at the base)(Gutsell & Johnson 1999). Individuals are divided into size-classes, and a frequency histogram is produced from which the pattern of succession present in the stand is inferred based on examination of which species dominate which size class. A size-class ordination involves using a series of stands (Gutsell & Johnson 1999). Stands are ordinated based on the relative proportion of each species present within each diameter class. When the ordination diagram is produced, lines are drawn linking the largest size classes with the smallest, from the same stand. Both of these methods make the same major assumption; that the largest

individuals in a stand represent earlier stages of succession, and that the smallest individuals represent future successional stages (Gutsell & Johnson 1999). Size-class ordinations are used in a similar way to age-class ordinations. Size-class ordinations have been used to infer boreal forest canopy successional trajectories (Carleton & Maycock 1978, 1980, Bergeron & Dubuc 1989).

Canopy-Subcanopy Relationships

Often size- and age-class ordinations are used in conjunction to examine canopy-subcanopy relationships, and infer successional processes. The canopy-subcanopy approach to studying succession assumes that mortality, natality and growth rates, and life-history strategies are similar between species (Kenkel et al. 1998). Under certain circumstances, however, these assumptions may be questionable (Bergeron & Dubuc 1989). For example, if preferential ungulate browsing of balsam fir and trembling aspen saplings is not considered then the importance of these species in later successional stages may be overestimated (Kenkel et al. 1998). To help ameliorate the problems associated with differential mortality of young individuals, Bergeron & Dubuc (1989) excluded from their analysis all stems < 5 cm in diameter. Life-history and vital attributes vary greatly among boreal tree species, and will be examined in detail in Section 2.3. Canopy-subcanopy relationships have been widely used, usually in conjunction with chronosequencing, to infer patterns of boreal forest succession (e.g. Dix & Swan 1971, Cogbill 1985, Zoladeski & Maycock 1990, Caners & Kenkel 1998, Kenkel et al. 1998).

Stand Reconstruction

Stand reconstruction (Johnson & Fryer 1989, Johnson et al. 1994 in Gutsell & Johnson 1999) involves reconstructing the history of births and deaths of individual trees within each of a series of stands (Gutsell & Johnson 1999). In this method, all live and dead (including standing, fallen, and buried individuals) are aged at the root collar level. In such a way the

past successional processes within the stand is observed rather than inferred. Aging trees at the root collar allows a very accurate estimate of the sampled tree's age, especially when missing rings are located using dendrochronology (Gutsell & Johnson 1999). The stand reconstruction method of studying boreal forest succession is, unfortunately, very time consuming and impractical when studying a variety of stands spread over a large area. In addition, predictions of future successional trajectories assume, as do predictions made with other methods, that future stand conditions will be the same as they have been in the past.

2.2 Duck Mountain Provincial Park and Forest

2.2.1 Introduction

Duck Mountain Provincial Park and Forest extents over 3760 km² in south-west Manitoba. It occupies a large portion of the southeastern extension of Rowe's (1972) Mixedwood Section (B18a) of the Boreal Forest Region. The boreal mixedwood extends from western Manitoba into central Saskatchewan and Alberta. In Manitoba, the boreal mixedwood forest occurs along the Manitoba Escarpment. Duck Mountain occupies the central position of the three large uplands found in western Manitoba, being flanked by the Porcupine Hills to the north and Riding Mountain to the south. These wooded uplands are separated by broad valleys that support intensive agriculture.

2.2.2 Climate

Duck Mountain lies within the humid microthermal climatic region, and is characterized by a humid continental climate with warm summers (Canada Department of Mines and Technical Surveys 1957). Annual precipitation in the region averages 43 cm and has ranged between 25 and 66 cm. The wettest month is June with 5-8 cm and the driest months are

February and December with 2 cm of precipitation per month. While no weather stations are situated within Duck Mountain, data from Riding Mountain indicate that total summer precipitation decreases from higher to lower elevations on the Escarpment, likely due to a “precipitation-shadow” affecting the lower escarpment slopes (Ritchie 1964; Parks Canada 1977). Three distinct air masses influence the climate of Duck Mountain: cold, dry continental polar air in the winter; occasional winter intrusions of cool, moist Pacific air; and common intrusions of warm, moist air from the Gulf of Mexico in the summer.

2.2.3 Landscape and Landform

The current topography of Duck Mountain is largely a result of Late Wisconsin glacial activity prior to the ice-sheet recession 11 000 to 12 000 BP (Neilsen 1988). Glacial meltwater fed glacial lake Agassiz, of which Duck Mountain made up part of the western shore. The Swan River Valley, however, remained ice-free for only a short time before the glacier re-advanced onto the Swan River and Westlake Plains (Davy 1995). This Swan River sublobe melted to form glacial Lake Swan, merging with Lake Agassiz by 10 800 years BP (Teller & Thorleifson 1983 *in* Davy 1995). Two large beachlines, the Upper and Lower Campbell, are prominent on the escarpment slopes. These formed about 9900 and 9500 years BP, respectively (Neilson et al. 1984). The large scale ‘dewatering’ of the Manitoba escarpment that occurred both in the Emerson (beginning 9 900 years BP) and Nipigon (beginning 9 300 years BP) phases of Lake Agassiz caused extensive landslides in parts of Duck Mountain (Neilson 1988). Lake Agassiz disappeared from the area by 8 300 years BP (Ringrose 1975 *in* Davy 1995).

Most of Duck Mountain Provincial Park and Forest lies within the Saskatchewan Plains physiographic region, with a small part at the base of the Escarpment on the Manitoba Plain (called the Westlake Plain west of Lake Winnipegosis)(Klassen 1979). The bulk of the

study area is within the Duck Mountain upland, a physiographic division of the Saskatchewan Plain. To north of the upland is the Swan River Plain (Swan River Valley), to the south is the Valley River Plain (Grandview Valley), and to the south west is the Assiniboine River Plain. The Manitoba Escarpment rises 170-370 m above the Manitoba plain, which it divides from the Saskatchewan Plain. Baldy Mountain, near the edge of the Escarpment in the southeastern portion of the upland, is the highest point in Manitoba at 831 m above sea level.

Underlying bedrock in the region is largely marine shale of the Upper Cretaceous Riding Mountain Formation (Klassen 1979). Glacial till overlies this bedrock, ranging in thickness from 150 to 300 m. Doe (1975) states that due to the great drift thickness on the Duck Mountain upland, broad topographic elements of the underlying bedrock are not expressed at the surface as they are at Riding Mountain. A hummocky moraine complex covers most of the Duck Mountain upland, although other glacial features such as till plains, outwash and lacustrine complexes, end moraines, eskers, kames, moraine plateaus, meltwater channels, and buried valleys are expressed in the region (Klassen 1979).

Drainage in the region is almost exclusively towards the northeast (Neilsen 1988). The Roaring, Ruby, East and West Favel, and Sinclair Rivers drain the north side of Duck Mountain and the southern part of the Swan River Valley. The Point, Garland, Pine, South Duck, Sclater, North Duck, Drake, and Pelican Rivers drain the east side of Duck Mountain and parts of the Westlake Plain. A major exception to the northeast drainage in the region is the Shell River, which drains the southwest portion of the upland southward into the Assiniboine River.

2.2.4 Quaternary Ecology: Post Glacial Development of Flora

Ritchie (1976) suggests that an early, spruce-dominated version of the boreal forest expanded northward as Wisconsin glaciers receded, being replaced on its southern margin by grasslands or deciduous forest. Xeric floristic elements of this early *Picea-Artemisia* forest suggest that the climate during this immigrant forest phase was comparatively dry (Ritchie 1985). The shift from spruce-dominated forest to grassland appears to have occurred south of the Duck Mountain region about 10 500 BP (Ritchie 1964, 1969). By 9 000 to 10 000 BP a 50-100 km belt of birch-dominated deciduous forest separated the open grassland south of Duck Mountain from the spruce-dominated boreal forest just to the north of Duck Mountain (Ritchie 1976). Bison remains found along glacial Lake Agassiz beachlines in the Swan River Valley and dating from between 10 300 and 9 400 BP support Ritchie's (1964, 1969, 1976) pollen evidence that the early spruce dominated forest had moved north of the Duck Mountain region by 9 000 to 10 000 BP. Bison are believed to have been more numerous on grasslands and in deciduous forests than in coniferous forests (Neilsen et al. 1984).

Ritchie & Yarranton (1978) found for two sites in the southern boreal mixed-wood forest of Saskatchewan that the early spruce forest phase was replaced 9 000–10 000 BP by grassland or parkland vegetation from the south. This grassland/parkland period, which lasted until 3 000 BP, corresponds to the warm 'hypsihermal' period, which reached its peak in Manitoba between 6 000 and 4 000 BP (Löve 1959). The modern mixedwood boreal forest stands of Ritchie & Yarranton's (1978) study must have developed, therefore, during the past 3 000 years from non-forest and non-coniferous parkland vegetation, being invaded from the north and west by pine, spruce, and tree birch. Ritchie (1969) found an increase in the abundance of oak and the appearance of hazelnut about 6 500 BP in Riding Mountain. Cooler and moister conditions brought about a reduction in the abundance of

xeric grassland species after this time, with a further decline occurring about 2 500 BP as boreal trees and shrubs immigrated into the Riding Mountain area. Jack pine reached Riding Mountain about 2 500 BP (Ritchie 1969), likely from a western refugium (Ritchie & Yarranton 1978).

2.2.5 Current and Historical Disturbance Regimes in Duck Mountain Provincial Park and Forest

2.2.5a Settlement/Permanent Clearing For Agriculture

Settlement patterns generally followed expansion of railroad lines into the Duck Mountain region (Goldrup 1992). The south side of Duck Mountain was settled beginning in 1885, with the east side being settled a few years later. In 1899 the Winnipeg Great Northern Railway Company built a rail line from Sifton to Swan River, with extensive settlement of the north side of Duck Mountain beginning soon after.

In 1906, in response to concerns over 'misuse' and possible overclearing, the Duck Mountain Forest Reserve was created by the Dominion Government (Goldrup 1992). Roads were cut along the reserve boundaries, intended to act as identifiers of the reserve and as fire breaks.

2.2.5b Logging

Records indicate the first large-scale logging operations in Duck Mountain began in the early 1880's, with the industry becoming 'well-established' in the region by 1912 (Goldrup 1992). The southern slopes of Duck Mountain supported most early logging, as this area was settled first. Most timber berths allotted during the main settlement period were intended for the building and fuelwood needs of individual settlers. The 1883 Dominion

Lands Act required that all merchantable trees with outside-bark diameters > 25 cm at their stump be harvested (Weir & Johnson 1998). In Duck Mountain, white spruce was the principle tree species harvested (Goldrup 1992), meaning that most other species and white spruce smaller than 25 cm in diameter would have been left uncut.

The clearcutting of softwoods (primarily black spruce) for pulp and paper has occurred since the mid-1900's. Large-scale harvesting of trembling aspen and balsam poplar for oriented-strand board has occurred since the mid-1990's.

2.2.5c Fire

Fire records have been kept for the Duck Mountain area since 1912. There are reports, however, of a number of large fires occurring in the 1880's (Goldrup 1992). A particularly large fire is reported to have burned the northern portion of the area in 1885, sweeping "through from Saskatchewan to Cowan". Fire control began in the early 1900's, with the first fire tower being built at Baldy Mountain in 1912 (Goldrup 1992). The construction of a central fire-fighting access trail through the region began in 1916.

Fires appear to have repeatedly burned the southern margins of Duck Mountain prior to 1940 (this report). Two large fires occurred in 1937; the Dead Horse Fire started along the Valley River and burned to Angling Lake while a second fire burned from Elk Lake to Singuish Lake. In 1961, 20 720 ha. were burned by large fire that occurred in the central uplands north of the Blue Lakes (Palidwor 1990 in Goldrup 1992). Timber salvage operations are often arranged to harvest burnt areas (Goldrup 1992).

The numerous forest-margin forests observed occurring at the turn of the century may be related to settlement and the subsequent clearing of land. Major fires in close succession

can result in the dominance of vegetatively-reproducing species such as trembling aspen, and the elimination of conifers (Heinselman 1973). Weir and Johnson (1998) found that the combination of short-interval, clearance-caused fires and the selective logging of white spruce resulted in a significant reduction in the abundance of sexually reproducing trees (e.g. white spruce) and an increase in vegetatively reproducing trees (e.g. trembling aspen) and trees with serotinous cones (e.g. jack pine) in mixedwood forests at Prince Albert, Saskatchewan.

2.2.5d Herbivory, Granivory, and Insect Pests

Duck Mountain ungulate populations have been estimated at 1500 moose (1987) and 1200-1400 elk (1985-86) (Manitoba Natural Resources 1988). A large population of white-tailed deer also exists in the area. In Riding Mountain, ungulate herbivores have been found to selectively browse shrubs and the saplings and seedlings of trembling aspen, balsam poplar, white birch, and balsam fir (Caners & Kenkel 1998). Mountain maple, beaked hazelnut, and trembling aspen comprise an important fraction of the diet of moose in southern Manitoba (Trottier 1981).

Hares may feed on the buds and small-diameter twigs of white spruce in winter, occasionally killing white spruce up to 1 m in height through repeated browsing (Rowe 1955). When high vole populations coincide with medium or poor white spruce seed years, amounts of overwintering seed can be greatly reduced (Rowe 1955). Except during heavy seed years, most white spruce cones and seeds are taken by red squirrels (Rowe 1955; Nienstaedt & Zasada 1990).

A spruce budworm outbreak has been active in the area to the northwest of Child's Lake since 1991 (Knowles & Matwee 1996). The infected area has increased from 200 ha. in

1991 to 5946 ha. in 1994. A decline to 1816 ha. in 1995 was observed, followed by a substantial increase to 20 390 ha. in 1996. In 1997 the outbreak declined to 5585 ha (Knowles & Matwee 1997).

2.3 Regeneration Dynamics of Major Tree Species in Duck Mountain Provincial Park and Forest

A summary of major ecological and autoecological factors affecting regeneration dynamics is presented for each of the seven major boreal tree species in Duck Mountain: black spruce (*Picea mariana* (Mill.) B.S.P.); balsam fir (*Abies balsamea* (L.) Mill.); jack pine (*Pinus banksiana* Lamb.); white spruce (*Picea glauca* (Moench) Voss); white birch (*Betula papyrifera* Marsh.); trembling aspen (*Populus tremuloides* Michx.); and balsam poplar (*Populus balsamifera* L.). Five major life history stages are recognised: production of seeds and asexual buds; dispersal of seeds and asexual stems; germination and early survivorship; advance regeneration; and maturity and senescence.

2.3.1 Production of Seeds and Asexual Buds

Greene et al. (1999) state that in situ regeneration post-disturbance can confer a huge advantage. Trembling aspen, balsam poplar, and white birch sucker from root collar/buds, while jack pine and black spruce regenerate in situ from aerial seed banks.

Black spruce cones remain partially closed, releasing seeds over several years (Viereck & Johnston 1990). Seed abundance and viability decline rapidly as cones age, but some viable seeds may remain in the cones for up to 25 years. When heated by fire, cone opening and seed dispersal occurs more rapidly (Zasada et al. 1992). Seeds mature in late August or

early September, 3 months after pollination (Viereck & Johnston 1990). Heavy seed years occur at intervals of 2 to 6 years, with peak crops every 4 years over most of the range.

Regular seed production of balsam fir usually begins after 20 to 30 years, but cone development has been reported for trees 15 years of age and younger and only 2 m tall. Seed production peaks every 2 to 4 years, with some production occurring in intervening years.

Cone production by jack pine trees begins at a younger age than in most other pine species. Female flowering has been induced as early as 12 months from seed sowing (Rudolph 1979). Under natural conditions, cones are produced at 10-15 years of age, giving jack pine an advantage in areas with short fire cycles (Rowe 1956; Heinselman 1973). Cone production is fairly regular, with production increasing until crown competition begins to interfere (Rudolph & Laidly 1990). Year to year variability in seed production is common, but at least some seed production occurs every year. Over much of its range, jack pine cones are predominantly serotinous, but nonserotinous cones occur in the southern part of its range. Seed viability inside cones may be significantly reduced after 5 to 10 years.

White spruce seed production in large quantities begins at 30 years or older in most natural white spruce stands. Seed production is prolific, with good seed crops every 2 to 6 years and lighter crops in between (Sutton 1969). Rowe (1955) reports heavy crops every 3 to 4 years in white spruce-trembling aspen stands in the Duck Mountain and Porcupine Hills of Manitoba, with seed production not beginning until individuals are 45 to 60 years of age. Heavy seed crops average 7 years apart in Alberta (Dix & Swan 1971). The interval between years of good seed and cone crops varies due to differences in site conditions and geographic location (Nienstaedt & Zasada 1990). Hot, dry summers at the time of bud differentiation may result in excellent seed years (Nienstaedt 1981). These are always

followed by years with a poor seed crop however, due to carbohydrate and nutrient deficiencies or a lack of sites in the crown that have the ability to produce reproductive buds (Neinstaedt & Teich 1972). Years with no seed production do occur (Waldron 1965).

White birch seed production begins at about 15 years of age, with optimal seed production occurring between 40 and 70 years under normal conditions (Safford et al. 1990). On average, good seed years occur at two year intervals.

Abundant trembling aspen seed production occurs every 4 to 5 years after age 10-20, with lighter crops in the years between (Perala & Russell 1983 in Peterson & Peterson 1992). Seed dispersal may last from 3 to 5 weeks, and peaks during July (Perala 1990). Seeds are light and have long silky hairs, resulting in dispersal over many kilometers by wind or water. Seed viability is normally short-lived, lasting only 2 to 4 weeks after maturity. Vegetative reproduction through suckering is an important adaptation to disturbance. Aspen clones (an aggregation of stems, or ramets, produced asexually from a single sexually produced individual, or genet) are formed from the surviving root system of a genet following destruction of all or most of the aboveground stems. Suckering ability is not affected by stand age, unless the stand is in decline due to decay (Stenecker 1976). Carbohydrate reserves are the energy source for suckers until they elongate enough to reach the soil surface and conduct photosynthesis (Perala 1990). Repeated grazing, and insect defoliation can exhaust these carbohydrate reserves.

As with trembling aspen, vegetative reproduction is an important aspect of balsam poplar's life history. New stems can originate from intact or broken roots, preformed or adventitious buds at tree bases or on stumps, or buried stems or branches (Zasada et al. 1987). Balsam poplar generally suckers less prolifically after disturbance than trembling aspen does (Zasada & Phipps 1990). Sucker density was found to be greatest in sites where

disturbance of the organic layer had occurred (Zasada et al. 1981). The insulating effect of organic soil layers may limit vegetative sprouting by lowering soil temperature. Sucker production may be important in the invasion and establishment of disturbed areas (Zasada & Phipps 1990), and may be especially important on dry sites where seedling establishment is low. Asexual and sexual reproduction are seen in burned and cutover areas, but only sexual reproduction is important on intensively burned sites (Zasada & Phipps 1990).

2.3.2 Dispersal of Seeds and Asexual Stems

Black spruce seeds are dispersed throughout the year, with dispersal highest in the spring and lowest in the fall (Viereck & Johnston 1990). Dispersal occurs primarily by wind and is effective only up to 79 m from the windward edge of a mature stand. Vegetative reproduction through layering is an important black spruce regeneration strategy, especially on lowland sites where rapidly growing mosses cover the lower branches of slower growing seedlings and saplings. Layering is most common in open stands, occurring less frequently in dense, productive stands which commonly lack live lower branches. Layering is commonly seen in black spruce/speckled alder communities on organic soil, but is rare in well-stocked black spruce/Labrador tea stands. Black spruce is a common postfire pioneer of both uplands and peatlands, with fire usually resulting in its immediate reestablishment as long as seed source is available.

The seedfall period for balsam fir is long, beginning in late August, peaking in September and October, and continuing into November (Frank 1990). Some seeds continue to fall throughout winter and into early spring. Seed dispersal distances vary, with most being spread by wind - sometimes to great distances over frozen snow, and some by rodents. Effective seed dispersal distances are from 25 m to 60 m, although seeds may disseminate up to 160 m. Wind dispersal of balsam fir is less than that of white spruce due

to their larger seeds (Galipeau et al. 1997). Secondary dispersal of balsam fir and white spruce on snow can be extensive for balsam fir and white spruce (Greene et al. 1999). Vegetative reproduction of balsam fir by layering is not an important means of regeneration, but will occur in open swamps and deep mossy areas and under jack pine overstories (Frank 1990). Trees of any age will apparently layer.

Effective seed dissemination from partially serotinous and nonserotinous jack pine cones is approximately two tree heights, being low beyond one tree height. Dispersal of this type can occur at any time of year. Some jack pine cones will open in dry weather when the temperature exceeds 27° C, but most remain closed until exposed to either fire or high temperatures near the ground after branch wind breakage or logging. Rudolf (1965) reports that cones may also open during very cold winters, when the temperature reaches -46° C or colder.

Initiation and pattern of white spruce seed dispersal both depend on weather conditions (Nienstaedt & Zasada 1990). Cool, wet, or snowy weather delays dispersal onset and can also cause cone closure after dispersal has begun. Cones will then reopen during dry weather. Most seeds fall in September, with a small number being dispersed in August. Small amounts of seed have been found in cones remaining on trees into the summer following their production (Rowe 1955). This phenomenon may explain the establishment of white spruce seedlings after severe spring or summer fires have destroyed the humus layer and the seeds contained within. Seeds are primarily wind-dispersed, with effective dispersal dropping rapidly at distances greater than 100 m from the seed source. Seed may occasionally travel a great deal further, however, due to convection currents, turbulence, and the skidding of seed on top of a snow crust (Rowe 1955; Waldron 1965; Ritchie & MacDonald 1986).

Most white birch dispersal occurs from September to November, although Zasada (1981; *in* Safford et al. 1990) found at least some dispersal year round in Alaska. Seeds falling in late fall and winter have higher germination rates than those falling earlier (Safford et al. 1990). The majority of seedfall remains in the stand that produced it, with dispersal rates into openings dropping precipitously with distance from the stand edge. Due to their winged structure and light weight, however, a minority of white birch seeds can travel great distances by wind, particularly across the surface of snow.

Trembling aspen seed production peaks every 4 or 5 years; crops are lighter in intervening years (Perala 1990). Exposed mineral soils are the best substrate for trembling aspen germination and growth, while litter is the poorest. Aspen suckering from the roots occurs under established canopies, as well after large disturbances such as fire or logging. The majority of trembling aspen and balsam poplar suckers appear to arise within 5 m of their parent tree, but occasionally up to 21 m away (Greene et al. 1999). East of the Rocky Mountains, clones typically have ramets spread over an area up to a few tenths of a hectare in size (Perala 1990). Kemperman and Barnes (1976) state that differences in clone sizes are a result of differential clone age, number of seedlings initially established, and the frequency and degree of disturbance since seedling establishment.

Balsam poplar seed dispersal normally begins in May or June, and continues for at least two weeks. Rapid dispersal occurs during relatively warm, dry weather. Seeds have no endosperm at maturity, are light, and have an attached tuft of long, silky hair, allowing for long distance dispersal via wind and convection currents. Long distance dispersal by water can occur when stands are located on flood-plain sites. Seeds remain viable for only a few weeks, with viability being lost by 4 to 5 weeks of age. The duration of viability is extended under cooler, drier conditions.

2.3.3 Germination and Early Survivorship

Black spruce seeds remain viable on the forest floor for at least 10 months, losing viability completely by 16 months (Viereck & Johnston 1990). Greene et al. (1999) note that most experimental and descriptive work on the relationship between survivorship and seedbed conditions post-fire points to mineral soil, humus, and well-rotted logs as the substrates having the highest initial black spruce survivorship. Feathermosses can provide a suitably moist seedbed during moist years, but are unreliable and commonly dry out before seedling root penetration occurs (Viereck & Johnston 1990). Fires that remove the surface organic soil horizon usually create a seedbed conducive to black spruce establishment. Forest floor accumulation affects layering (Greene et al. 1999); in the western boreal forest layering is more common in lowland sites where moss overgrows lower branches (Viereck & Johnston 1990).

Moisture is more important than light for balsam fir germination, with light intensities of 10% of full sunlight resulting in success (Frank 1990). High moisture retention capacity makes mosses and rotting wood preferred substrates for establishment (McLaren & Janke 1996). Seeds lose viability rapidly on the forest floor, usually within 1 year (Frank 1990). In cold swamps, however, viability may be retained for 2 to 3 years. Mineral soil that is neither too sandy nor too clayey is best for germination, but if enough moisture is available almost any seedbed type is satisfactory. A duff layer exceeding 8 cm is not favourable to balsam fir growth, but is even less favourable to black and white spruce growth. McLaren & Janke (1996) report that high mortality may occur during the first year, especially under a deciduous canopy or dense cover. Due to their susceptibility to frost damage, balsam fir seedling survival may be limited until a partial canopy develops (Frank 1990). Seedlings can be crushed or buried by litter, ice, snow, and hardwood leaves.

Jack pine germination usually occurs within 15 to 60 days under favourable conditions (Rudolph & Laidly 1990). Some seeds, however, require greater than 100 days to germinate. Optimal establishment and seedling growth conditions include exposed mineral substrates and burned seed beds (where interspecific competition is less severe), a high water table, and enough shade to reduce surface temperatures and evapotranspiration. Due to a poor moisture regime, germination on litter and humus is usually poor. Most seedlings will die if the organic matter left on the soil is 1.3 cm thick or more. On clay soils in Manitoba and Saskatchewan, competition from trembling aspen and beaked hazelnut results in poor jack pine seedling survival (Rudolph & Laidly 1990). During its first 20 years of life jack pine is the fastest growing conifer other than eastern larch (Rudolf 1965).

White spruce reproduction at a particular site depends on seed-bed quality, favourable climatic and biotic factors, and on seed production and distribution (Rowe 1955). Seedling establishment occurs on a variety of seedbeds, and frequently on decaying logs (Nienstaedt & Zasada 1990). La Roi and Stringer (1976) found that in mature white spruce stands the most common seedbed type is feather mosses and associated organic layers. When the L- and F- soil layers exceed 5 to 8 cm regeneration is restricted (Nienstaedt & Zasada 1990). In mature stands where windthrow and floods have resulted in areas of exposed mineral soil, these areas were found to be best for regeneration. Growth rates on mineral soil are much greater than on decayed wood (Rowe 1955). Kneeshaw and Bergeron (1996) comment on the importance of parent tree composition and how the established canopy influences seedbed conditions. At Lac Duparquet in Quebec, balsam fir and white spruce advance regeneration abundance was greatest in stands with a mixed coniferous-deciduous overstory. Canopy gaps in the overstory of these stands tended to be smaller than those in deciduous or coniferous stands and often not large enough to become dominated by shrub species that could outcompete conifer regeneration.

The small size and weight of white birch seeds results in newly germinated seedlings that can be easily damaged by a variety of environmental conditions (Safford et al. 1990). Moisture, temperature, light, and seedbed condition can all negatively affect seedling survival if not optimum. Germination rates are highest on mineral soil, intermediate on organic soil, and lowest on undisturbed litter. In a partially wind-thrown conifer forest in Minnesota, most established white birch seedlings were found growing on decomposing logs, stumps and tree boles (Webb 1988). Germination is approximately twice as great in shaded sites than in full-sun sites (Safford et al. 1990). Vegetative reproduction can be considerable in white birch stands. Following cutting or fire regeneration from sprouts will occur. Sprouting may also occur from the base of live trees when exposure increases due to the removal of neighbouring trees.

The most critical factor affecting trembling aspen suckering is insolation-induced soil temperature increase (Peterson & Peterson 1992). Initiation and development is optimal at approximately 23° C. The depth of the forest floor thus potentially influences aspen suckering through its influence on soil temperature in the aspen root zone (Greene et al. 1999). Severe drought and excess soil moisture limit vegetative reproduction (Peterson & Peterson 1992). Aspen suckering under an established canopy does not appear to be related to light conditions. Kneeshaw and Bergeron (1996) observed that while gaps resulting from spruce budworm outbreaks had a positive influence on the density of most conifer species seedlings, hardwood seedling abundance did not respond to these gaps. Few sexually-reproduced trembling aspen seedlings naturally survive due to a short period of seed viability, unfavourable moisture during seed dispersal, high soil surface temperatures, fungi, adverse diurnal temperature fluctuations during initial seedling growth, and an unfavourable chemical balance in some seedbeds (Perala 1990).

Moist mineral soil surfaces make the best seedbeds for balsam poplar, although some germination will occur on moist organic seedbeds (Zasada & Phipps 1990). Seedling growth appears to be controlled by nitrogen availability at certain stages of succession, and by light, water, and nutrient availability at other stages. Zasada & Phipps (1990) report greater greenhouse-grown seedling biomass on soil from alder stands than on soils from earlier successional stages, suggesting a benefit to balsam poplar from nitrogen fixation.

2.3.4 Advance Regeneration

As defined by Greene et al. (1999);

"advance regeneration consists of seedlings and vegetative reproduction present in a mature forest and potentially able to replace the overstory following natural or human disturbance"

Growth rates, competition from tree and shrub species, and type and severity of disturbance are important factors influencing the canopy replacement potential of advance regeneration.

Black spruce generally exhibits slow growth rates, often requiring 15 to 20 years to attain 1.5 m of height (Zasada et al. 1992). Black spruce is shade-tolerant, but less so than balsam fir (Viereck & Johnston 1990). Seedlings, and apparently layerings, will develop under conditions with as little as 10% of full light intensity. Survival and growth are, however, much better under more open conditions. Black spruce grows slower than many of the trees and shrubs with which it is associated. Intense competitive pressure on black spruce can result in a mixed stand, therefore, particularly if the other species present reproduce from suckers or sprouts rather than from seed. Black spruce can, however, endure many years of suppression and still respond to competitive release (Frank 1990).

Balsam fir successfully establishes and grows under the shade of larger trees (Frank 1990). It is very shade tolerant, and is more tolerant than either black or white spruce. In sapling and small pole-size stands of pure balsam fir intraspecific competition is evident. Competition is severe in dense fir thickets, with growth rates of individual trees being greatly reduced. Balsam fir can survive many years of suppression and still respond to competitive release. Regeneration patterns of balsam fir are closely related to gap disturbance, as seedlings aggressively colonize windfall gaps (McLaren & Janke 1996). Kneeshaw et al. (1999) found balsam fir density and height were reduced in canopy gaps when mountain maple is abundant.

Jack pine is a pioneer species of burns and other exposed areas, and as such is not an important component of advance regeneration.

White spruce will regenerate in mature stands of spruce and early successional tree species, but establishment is highly variable and densities are low (Walker et al. 1986). Its shade tolerance is equal to or less than that of black spruce and balsam fir, while it is more tolerant than aspen and white birch (Nienstaedt & Zasada 1990). Following disturbance, large numbers of seedlings may establish and eventually form even-aged stands. White spruce will form even-aged pure stands, multi-aged pure stands, or can be a component in multi-aged, late successional stands. In multi-age stands, white spruce age distributions are not continuous, but rather consist of several groups of ages separated by periods when no establishment occurred.

White birch is considered shade intolerant (Safford et al. 1990). Hutnik and Cunningham (1965 *in* Safford et al. 1990) report that white birch usually only lasts one generation in a stand before it is replaced by more tolerant species. When growing in mixture with spruce or spruce-fir, however, it usually persists in the stand (Reiners & Lang

1979). Kneeshaw and Bergeron (1996) found that the density of balsam fir, white spruce and white birch advance regeneration was negatively correlated with competing shrub abundance.

Trembling aspen growth is rapid for the first 20 years after germination, then slows. Suckers, however, grow faster than seedlings. Trembling aspen is considered to be very intolerant of shade at all life stages (Perala 1990). It is an aggressive pioneer species, invading grasslands if fire is excluded and soil moisture is adequate. It is generally considered a non-climax species that is able to dominate a site until less fire resistant but more shade-tolerant conifers replace it. The rate of replacement by conifers can vary greatly, however, taking a single aspen generation or up to 1000 years of fire exclusion (Perala 1990). The uneven age distribution within some trembling aspen stands in western North America suggests that aspen stands can be self-perpetuating in the absence of major disturbance.

Balsam poplar exhibits many typical characteristics of an early successional species: low shade tolerance, rapid juvenile growth, high rates of seed production, relatively short life-span, a 'good' self-pruning regime, and replacement in the canopy by more tolerant species (Zasada & Phipps 1990). It is classified as very shade intolerant. Asexual suckers will be produced under stand conditions, but they will be short-lived (Zasada & Phipps 1990).

Messier et al. (1999) state that in a deeply shaded environment fast vertical growth is not favourable to long-term survival of advance regeneration because there is no corresponding increase in light levels with increasing height. The increased carbon required to maintain this increased tree size is not available, and mortality results. Differing morphological and developmental plasticity among species leads Messier et al. to hypothesize that large, infrequent gaps and small but frequent gaps will favour advanced regeneration of species

that are shade intolerant and have fast height growth (jack pine, trembling aspen, and white birch), whereas small, infrequent gaps will favour shade tolerant species which have slow height growth but greater proportionate leaf area (balsam fir, black spruce, white spruce).

Both white spruce and balsam fir are considered shade-tolerant conifers. Messier et al. (1999) note that it is the ability to undergo morphological change and plasticity that confers this ability on these species. Specifically, in shaded conditions lateral branch growth is favoured over increase in height, a decrease in whorl and interwhorl branches occurs, live crown fraction decreases, and the horizontal display of branches/needles increases. In contrast, white birch and trembling aspen, considered shade intolerant, display little change in apical dominance and height morphological plasticity in relation to light.

2.3.5 Maturity and Senescence

Under natural, unmanaged conditions, black spruce at maturity average 12 to 20 m in height and approximately 23 cm in diameter at breast height (D.B.H.) on good sites, and 8 to 12 m in height and approximately 13 cm in D.B.H. on poor sites (Viereck & Johnston 1990). Average maximum age is about 200 years, although ages up to 280 years have been reported. Rowe (1956) notes that stunted trees growing in lowlands may reach ages of over 200 years, and that rapidly growing trees growing in upland sites may mature at 100 years of age, and die soon after.

Balsam fir heights, at maturity, range from 12 to 18 m, with D.B.H.s from 30 to 46 cm. Maximum age is about 200 years, with an ordinary lifespan of 150 years (Heinselman 1996). Root systems are generally confined to the upper 60 to 75 cm of soil, making balsam fir prone to windthrow.

Mature jack pine average 17 to 20 m tall, with D.B.H. measuring 20 to 25 cm (Rudolph & Laidly 1990). Stand degeneration begins after 80 years on good sites and after 60 years on poor sites. In Manitoba and Saskatchewan, Rowe (1956) found that jack pine matured after 60 to 80 years on dry sandy soils, and may not mature until 100 years of age on clay loams. While the ordinary lifespan of jack pine is 150-200 years, it can persist as a remnant in the overstory for up to 250 years (Heinselman 1996). Except on shallow soils (e.g. rock outcrops), windthrow is not common in jack pine stands (Rudolph & Laidly 1990). Stem breakage due to wind, ice, and snow is a more regular occurrence (Benzie 1977).

At maturity, white spruce can be 25 m tall with D.B.H.s of approximately 60 cm (Farrar 1995). Ordinary white spruce lifespan is 200-250 years (Heinselman 1996). White spruce grows slower than its early successional associates, and may remain in the understory for 50 to 70 years. Growth is reduced during this suppressional period, but will increase after release in trees up to 200 or more years old (Neinstaedt & Zasada 1990).

Young white birch grow rapidly, but growth rates decline with age and eventually become nearly negligible (Safford et al. 1990). In mature stands, D.B.H.s average 25 to 30 cm and 21 m in height. White birch is considered a short-lived species, reaching maturity between 60 and 70 years of age and rarely living beyond 140 to 200 years. Vegetatively reproduced white birch trees tend to mature earlier (at 50 to 60 years of age) and begin to deteriorate sooner (at 70 to 90 years of age) than those of seedling origin.

Typical mature trembling aspen stems range from 20 to 25 m in height, and obtain an average D.B.H. of 18 to 30 cm (Perala 1990). Ordinary trembling aspen lifespan is 120-160 years (Heinselman 1996). Trembling aspen canopy deterioration is thought to be related to summer temperatures, and begins when crowns can no longer grow quickly

enough to fill the gaps left by dying trees (Perala 1990). Canopy deterioration is a slower process in the western range of aspen than in the east due to replacement by conifers.

Mature balsam poplar are up to 25 m tall with a D.B.H. of 50 cm, but are occasionally much larger (Farrar 1995). Ordinary lifespan is 130-150 years (Heinselman 1996). While trembling aspen has little flooding tolerance, balsam poplar commonly occurs in areas subject to flooding (Peterson & Peterson 1992). At maturity, balsam poplar can withstand light forest fires (Zasada & Phipps 1990).

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Area

The 376,000 ha Duck Mountain Provincial Forest in west-central Manitoba is characterized by a complex interdigitation of small lakes, wetlands, and forested uplands. The Duck Mountains form part of the Manitoba Escarpment, which includes Riding Mountain and the Pembina Hills to the south and the Porcupine and Pasquia Hills to the north. The Escarpment is a distinctive physiographic feature that strongly influences the vegetation, soils, groundwater hydrology, mesoclimate, and natural disturbance regime of the region. The eastern Escarpment slopes are moderately steep, punctuated by large valleys and ravines, and occasionally overlain by ancient beach ridges. In contrast, the southern, northern and western sides of Duck Mountain are more gently sloped and characterized by a gently rolling topography. The upland regions of the Duck Mountains are characterized by a landscape physiography consisting of numerous lakes interspersed with ridges and hills.

In 1996, the province of Manitoba awarded Louisiana-Pacific Canada Ltd. an Environmental License to sustainably manage the boreal mixedwood forests of the Duck Mountains. In addition to the hardwood volume harvested by Louisiana-Pacific, a number of smaller operators harvest softwoods in the region. The Duck Mountains are also an important recreation/tourism area. The region is a critical habitat resource for maintaining the biological and landscape diversity of western Manitoba, and is part of a landscape corridor connecting the continuous boreal forest of northern Manitoba to Riding Mountain National Park to the south. Wetlands in the Duck Mountains store vast quantities of water,

making the Escarpment the principal watershed for the extensive agrarian lands to the east, north and south.

3.2 Stand Selection

A total of 70 stands (3 plots per stand, for a total of 210 plots) were sampled over two field seasons. Sampling was conducted from June 23 to August 27 in 1998, and from June 2 to August 31 in 1999. A number of stands were revisited in October of 1999 and August 2001 to obtain additional data on the size and age of canopy and advance regeneration trees.

Sampling was necessarily limited to forest stands that were reasonably accessible by road or trail. Stands showing any evidence of logging (including selective cutting) were avoided. As a result, most stands were located only after walking a considerable distance from the nearest access road. Stands were selected using the following criteria: (a) no evidence of human disturbance; (b) uniform post-fire age; (c) uniform environmental conditions, such as slope, aspect, and edaphic conditions.

Initial reconnaissance of the study area indicated considerable spatial variation in forest composition and structure within environmentally uniform stands (most stands were approximately 1 ha in size). Each stand was therefore sampled using three randomly located 10 x 10 m plots (a cluster sampling approach) in order to sufficiently characterize within-site variation. Plots were randomly located within each stand. However, the three plots were at least 25 m apart to minimize spatial autocorrelation.

3.3 Data Collection

3.3.1 Tree Sizes

Data on the identity, bole size (D.B.H.), and height of all living trees was recorded in each 10 x 10 m plot. In addition, the bole size and identity of all standing dead ('snags') and identifiable fallen trees that had once occupied the canopy was recorded. Most stands were characterized by a clear overstory cohort comprised of one dominant species, or two co-dominant species, of similar height and D.B.H.

3.3.2 Tree Ages

Within each 10 x 10 m plot, individual trees of each species in each of five height classes were aged. The height classes are: (1) upper canopy or initial cohort, > 15 m in height; (2) lower canopy, 10-15 m; (3) subcanopy, 2-10 m; (4) saplings, 0.5-2 m; (5) seedlings, < 0.5 m. Within each plot, 3-5 individuals of the dominant initial cohort species were randomly selected for aging. When present, all individuals of less abundant species in the upper canopy were also aged. These canopy cohort data were used to determine minimum stand age, and to confirm that all canopy trees were of similar age (i.e. that they form the initial post-fire cohort). In most plots, all individuals in the lower canopy, subcanopy and sapling height classes were aged. However, if a large number of similar-sized individuals of a given species were present, only a random subset of trees were aged. Most upper and lower canopy trees were cored at 30 cm from the base, but some had rotten bases and had to be cored at 1.2 m. A number of trees were cored at both 1.2 m and 30 cm to quantify discrepancies in age estimates. Many upper and lower canopy trees (particularly trembling aspen and balsam poplar) had heart-rot and could not be accurately aged. These cores were not considered in subsequent analyses. Over 800 useable increment cores were obtained from upper and lower canopy trees. Smaller trees (< 10 m in height) were cut at their base

(as close to the root collar as was possible) using a chainsaw or handsaw. In total, over 1000 trees were aged in this way.

Basal disks and cores were prepared by sanding with coarse (100 grit) sandpaper and finishing with fine (400 grit) sandpaper. 600 grit sandpaper was used when further resolution was required. Tree rings were counted with the aid of a dissecting microscope.

3.3.3 Understory

Percent cover of each shrub species was estimated in each 10 x 10 m plot. Cover estimates for understory graminoids, forbs, ferns (and fern-allies), bryophytes and lichens were obtained from four 1 x 1 m plots randomly located within each 10 x 10 m plot.

3.3.4 Soils

A soil pit was dug in each stand, and a representative soil core collected. Soils were classified, soil horizons measured, and depth to carbonates recorded. Soils were analyzed for pH and conductivity, and particle-size (percentage sand, silt and clay)(Kalra & Maynard 1991).

3.3.5 Physiography and Landscape

Distance to seed source was estimated for late-successional species such as balsam fir and white spruce. Landscape structural features (slope, aspect, drainage, landform, local proportion of lakes) were also recorded for each stand.

3.3.6 Natural Disturbance

Herbivory (spruce budworm, ungulates, beaver activity) and browsing intensity were estimated for tree saplings and shrubs in each plot, and general tree health (e.g. evidence of spruce budworm infestation) was noted.

3.4 Characterization of Stands

3.4.1 Determination of Stand Ages

Post-fire stand age was determined from aged canopy trees in each stand, together with available forest fire maps. While fires in the Duck Mountains have been recorded since 1912, questionable recording in remote areas prior to 1940 limited the applicability of fire maps. A map of recorded 20th century fires in Duck Mountain is presented in **Fig. 3.1**. Major fires occurred from the 1910's to the early 1960's, with only minor fires (too small to map) since that time. In most stands canopy trees were aged at 100-115 years, however, which corresponds to historical records of a large catastrophic fire in the Duck Mountains in 1885 (Harrison 1934). The most reliable stand age estimates were obtained from individuals of jack pine, since this species only establishes immediately post-fire. Where stands contained one or two fire-surviving individuals (determined through fire scars and/or lack of evidence of a recently-fallen contemporary cohort), post-fire individuals were used to determine stand age. To account for differences in tree core heights (1.2 m and 30 cm), all individuals aged within 20 years of the maximum estimated stand age were considered part of the initial cohort.

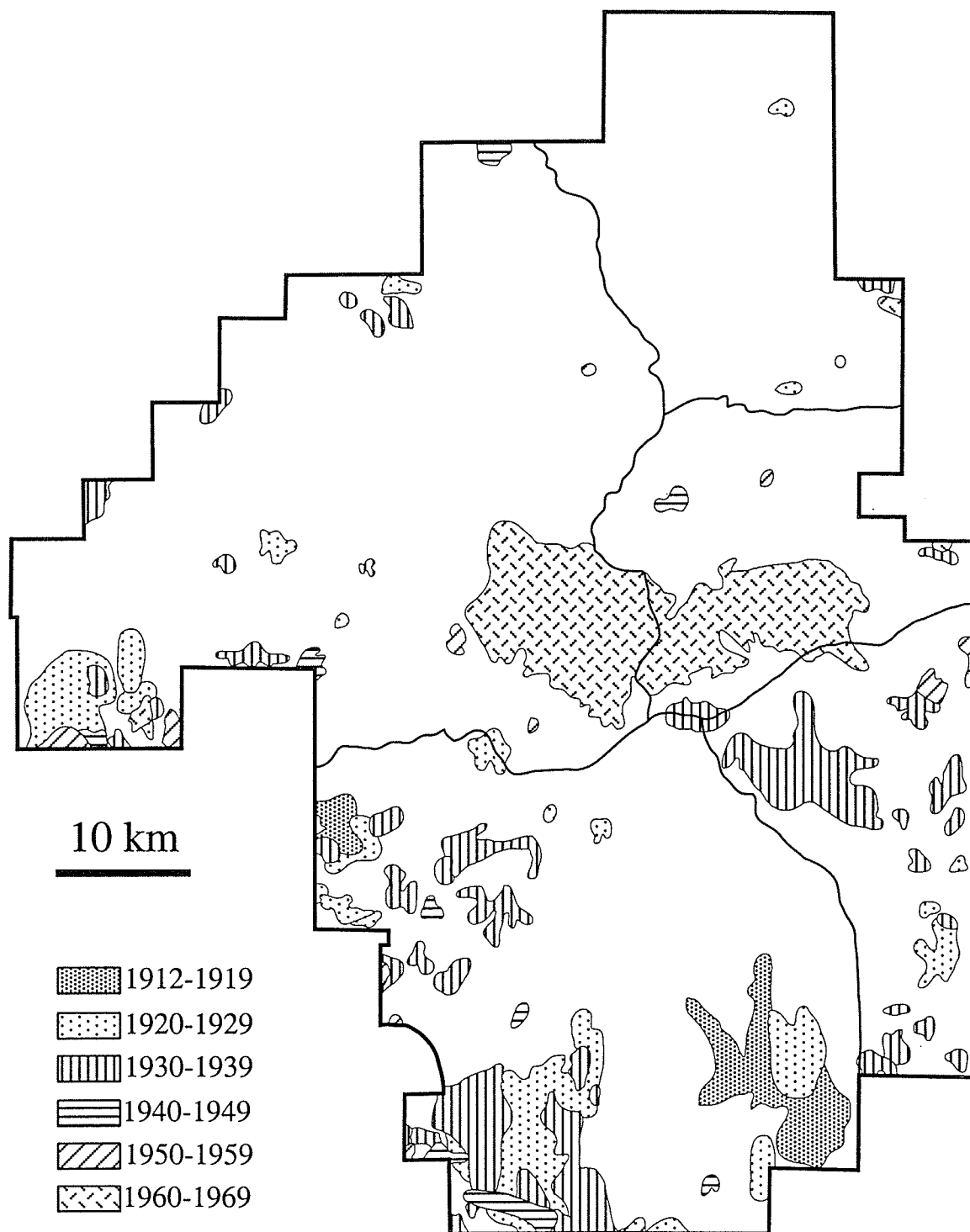


Figure 3.1. Forest fire history for Duck Mountain Provincial Park and Forest, 1912-present. Spot fires are not included (compiled from data collected by the Manitoba Department of Conservation).

3.4.2 Delineation of Post-fire Stand Types

The oldest living canopy trees were assumed to form the initial post-fire cohort. When present, recently fallen and standing dead trees were also used to reconstruct the initial canopy cohort. The known autecology of major tree species was also considered (see section 2.3 for a more detailed review of species autecology):

- Jack Pine: This species produces serotinous cones that result in immediate establishment following crown-killing fire. Jack pine is very shade intolerant and therefore fails to establish beneath an existing canopy. Jack pine stands undergo extensive self-thinning starting at age 40-50 (Kenkel et al. 1997b).
- Trembling Aspen and Balsam Poplar: These species produce sucker shoots from the root system immediately following crown-killing fire or other disturbance. Less commonly, they may establish from seed. Stands undergo extensive self-thinning at an early age, particularly in dense stands (Peterson & Peterson 1992). Both species are shade-intolerant, but may undergo secondary suckering (advance regeneration) following canopy breakup if light conditions are favourable.
- Black Spruce: This species produces semi-serotinous cones, resulting in immediate establishment following a crown-killing fire. Unlike jack pine, black spruce is quite shade-tolerant and can seed into older stands. It also has the ability to produce new individuals through layering of lower branches, though this is only common in open stands growing on organic peat substrates.

- White Spruce: Provided a proximate seed source is present, this species can establish immediately following a crown-killing fire. Later recruitment into established stands, which is more common, is episodic and highly variable (Lieffers et al. 1996).

- Balsam Fir: This is considered a later-successional species. Our results indicate that balsam fir in the Duck Mountains rarely establishes immediately following a crown-killing fire. Balsam fir requires moist organic seedbeds, such as well-rotted logs in moderately dense forests, for successful germination and establishment. This species is shade tolerant, but grows very slowly under a closed canopy. Once established, growth is most rapid in canopy gaps. It is generally considered to be drought-intolerant (Galipeau et al. 1997).

- White Birch: This species may establish immediately following a crown-killing fire from seeds or sucker shoots emanating from the root collar. White birch may also invade established stands, with most seedlings establishing on well-rotted logs. The species is considered moderately shade-tolerant.

For each stand, the initial post-fire abundance of each tree species was estimated using the following relative rankings:

- 0 = absent at stand initiation.
- 0.1 = single tree present at stand initiation.
- 1 = low abundance at stand initiation (2-5 trees per stand).
- 2 = species codominant at stand initiation.
- 3 = species dominant at stand initiation.

Using this method, the floristic composition of the initial canopy cohort was estimated for each of the 70 stands. The resulting data set was subjected to cluster analysis in order to

delineate five post-fire stand types: Trembling Aspen ($n = 16$), Balsam Poplar ($n = 11$), White Spruce ($n = 17$), Jack Pine ($n = 18$), and Black Spruce ($n = 8$).

3.4.3 Summarization of Stands

The 70 forest stands sampled in this study are summarized in **Table 3.1**. For the purpose of developing a forest succession model, the 70 stands were classified into five groups:

1. Stands 1-48

These stands occur on mineral soil, and range in age from 80 to 130 years (mean age = 110 years). Most of these stands developed following the catastrophic 1885 fire. In all these stands, tree aging revealed that the vast majority of individuals in the upper canopy (> 15 m in height) represent the initial post-fire cohort. These 48 stands therefore formed the data set for examining forest successional trends, based on size- and age-class analysis of trees in the canopy (initial cohort) and advance regeneration height classes. Temporal patterns of recruitment, and the degree of canopy recruitment by non-contemporaneous trees, were also examined using these stands. The number of stands in each stand type are: Trembling Aspen, $n = 12$; Balsam Poplar, $n = 10$; White Spruce, $n = 10$; Jack Pine, $n = 13$; Black Spruce, $n = 3$.

2. Stands 49-56

These eight stands range in age from 55-75 years. Advance regeneration in these stands was often absent or very limited, and if present was not well developed (i.e., individuals were < 2 m in height). These stands could therefore not be used for size- and age-class analysis of successional trends. Instead, they were used to validate information on the timing of advance regeneration recruitment obtained from stands 1-48.

Analyses	Stand	Stand Age	Class	Dominant I.R.	Dominant A.R.	Soil Order
1-6	1	80	TA	TA	TA	Brun isolic
1-6	2	85	TA	TA	TA	Brun isolic
1-6	3	80	TA	TA	TA	Brun isolic
1-6	4	85	TA	TA	TA	Brun isolic
1-6	5	90	TA	TA	TA	Luvi solic
1-6	6	115	TA	TA, WB, WS	TA	Luvi solic
1-6	7	115	TA	TA	(TA, BP)	Brun isolic
1-6	8	100	TA	TA	TA	Brun isolic
1-6	9	90	TA	TA	WS, TA	Brun isolic
1-6	10	115	TA	TA	WS	Brun isolic
1-6	11	115	TA	TA	WS	Brun isolic
1-6	12	115	TA	TA, WB, WS	WS	Luvi solic
1-6	13	100	BP	BP	(BP, TA)	Brun isolic
1-6	14	115	BP	TA, BP	WS	Brun isolic
1-6	15	110	BP	BP	WS	Gleysolic
1-6	16	80	BP	BP	WS	Gleysolic
1-6	17	85	BP	TA, BP	WS	Brun isolic
1-6	18	105	BP	BP	WS	Gleysolic
1-6	19	115	BP	BP	TA	Gleysolic
1-6	20	95	BP	TA, BP	TA, WB, BS	Brun isolic
1-6	21	130	BP	BP	BF	Gleysolic
1-6	22	90	BP	WB, BP	BF	Brun isolic
1-6	23	130	WS	TA, WS	BF	Brun isolic
1-6	24	130	WS	TA, WB, WS	BF	Luvi solic
1-6	25	105	WS	WS, TA, WS	BF	Luvi solic
1-6	26	130	WS	WS, TA	BF	Brun isolic
1-6	27	115	WS	WS	BF	Luvi solic
1-6	28	100	WS	TA, BP, WS	BF, WS	Brun isolic
1-6	29	80	WS	TA, WS	WS	Brun isolic
1-6	30	110	WS	WB, WS	BF, TA	Brun isolic
1-6	31	80	WS	TA, WB, WS	WB, BF, WS, TA	Brun isolic
1-6	32	90	WS	WS, TA, BP	TA, BF, WS	Luvi solic
1-6	33	105	JP	BS, TA, JP	TA	Brun isolic
1-6	34	105	JP	JP, BS, TA	(TA, BS)	Luvi solic
1-6	35	110	JP	TA, JP	WB, TA	Brun isolic
1-6	36	110	JP	TA, JP	WB	Brun isolic
1-6	37	105	JP	JP, TA	WB	Brun isolic
1-6	38	115	JP	JP, BS	(WB, TA)	Brun isolic
1-6	39	105	JP	TA, JP	WB	Brun isolic
1-6	40	95	JP	JP	WB	Brun isolic
1-6	41	105	JP	JP	BF, WS, BS	Brun isolic
1-6	42	110	JP	JP	BF, BS	Brun isolic
1-6	43	110	JP	JP	BF	Feg osol
1-6	44	110	JP	TA, WS, JP	BF	Brun isolic
1-6	45	120	JP	TA, WS, JP, BS	BF	Brun isolic
1-6	46	110	BS	BS, JP	(BS)	Luvi solic
1-6	47	110	BS	BS, JP	(BS)	Brun isolic
1-6	48	105	BS	BS	(BS)	Brun isolic
1, 2	49	55	TA			Brun isolic
1, 2	50	60	TA			Brun isolic
1, 2	51	60	TA			Brun isolic
1, 2	52	65	TA			Brun isolic
1, 2	53	60	BP			Gleysolic
1, 2	54	60	WS			Feg osolic
1, 2	55	70	WS			Brun isolic
1, 2	56	75	WS			Luvi solic
1, 2	57	150	WS			Luvi solic
1, 2	58	170	WS			Brun isolic
1, 2	59	220	WS			Luvi solic
1, 2	60	155	BS			Brun isolic
1, 2	61	155	BS			Brun isolic
1	62	38	WS			Brun isolic
1	63	37	JP			Brun isolic
1	64	37	JP			Brun isolic
1	65	37	JP			Brun isolic
1	66	38	JP			Brun isolic
1	67	38	JP			Brun isolic
1	68	37	BS			Organic
1, 4	69	110	BS			Organic
1, 4	70	165	BS			Organic

¹ Data Analyses Conducted: 1. Cluster analysis of initial composition, 2. Canonical correspondence analysis (CCA) of extant vegetation, 3. CCA of advance regeneration constrained by initial cohort, 4. Analyses of temporal patterns of recruitment, 5. Examination of the height class structure of initial and subsequent cohorts, 6. Analyses of factors affecting presence and abundance of non-contemporaneous recruitment.

Table 3.1. Data analyses conducted¹, stand age, initial cohort class, dominant post-fire (initial) regeneration (I.R.), dominant advance regeneration (A.R.) and soil order for 70 sampled stands. Species codes: BF = balsam fir, BP = balsam poplar, BS = black spruce, JP = jack pine, TA = trembling aspen, WB = white birch, WS = white spruce. Species codes in brackets when A.R. is minimal.

3. Stands 57-61

These five stands are at least 150 years old. In all cases, the upper canopy of these stands consisted of a few 'remnant' individuals of the initial canopy cohort (often very old white spruce or white birch) and a predominance of much younger trees recruited as advance regeneration (often balsam fir). These stands were therefore used to validate the successional trends obtained from the age and size-class analyses of stands 1-48.

4. Stands 62-68

These 37-38 year old stands all occur within the large 1961 fire. Data from these stands were used to validate the initial cohort reconstructions of stands 1-48, and to confirm information on the timing of advance regeneration recruitment.

5. Stands 69-70

These two stands occurred on organic peat substrates, and were dominated by black spruce. Advance regeneration was almost exclusively from black spruce layers. Since substrate conditions, vegetation, and stand development in these stands are unique, they are not considered in most subsequent analyses.

3.5 Data Analysis

3.5.1 Vegetation-environment Relationships

Canonical correspondence analysis (CCA) of stands 1-61 was undertaken to summarize the relationship between forest stand composition (percent cover of trees and shrubs) and the following 14 environment-landscape variables:

CLAY - Percent clay content of soil.
SAND - Percent sand content of soil.
PH - Soil pH.
COND - Soil conductivity.
ORG - Depth of litter (LFH) layer.
CARB - Depth to carbonates.
LITT - Percent cover of deciduous litter.
WOOD - Percent cover of coarse woody debris.
MOSS - Percent cover of moss.
HERB - Percent cover of herbaceous plants.
SLOPE - Percent slope of landscape.
ELEV - Elevation of stand.
AGRIC - Distance to agricultural land.
AGE - Stand age.

3.5.2 Cohort Classification: Initial Cohort, Advance Regeneration and Recent Regeneration

Each living tree in stands 1-48 was assigned to one of three age-cohort classes:

1. Initial Cohort – trees that established within the first 20 years following fire. These trees almost invariably formed the upper canopy (> 15 m in height). The only exception were heavily shaded, suppressed individuals of white or black spruce that were occasionally

encountered in very dense stands. These trees were easily recognizable in the field and were considered part of the initial cohort, even though they occurred in the subcanopy.

2. Advance Regeneration – trees that established at least 20 years following stand initiation (i.e. at least 20 years younger than individuals forming the initial cohort), but greater than 20 years old. The majority of the advance regeneration in this study was at least 40 years younger than the initial cohort class.

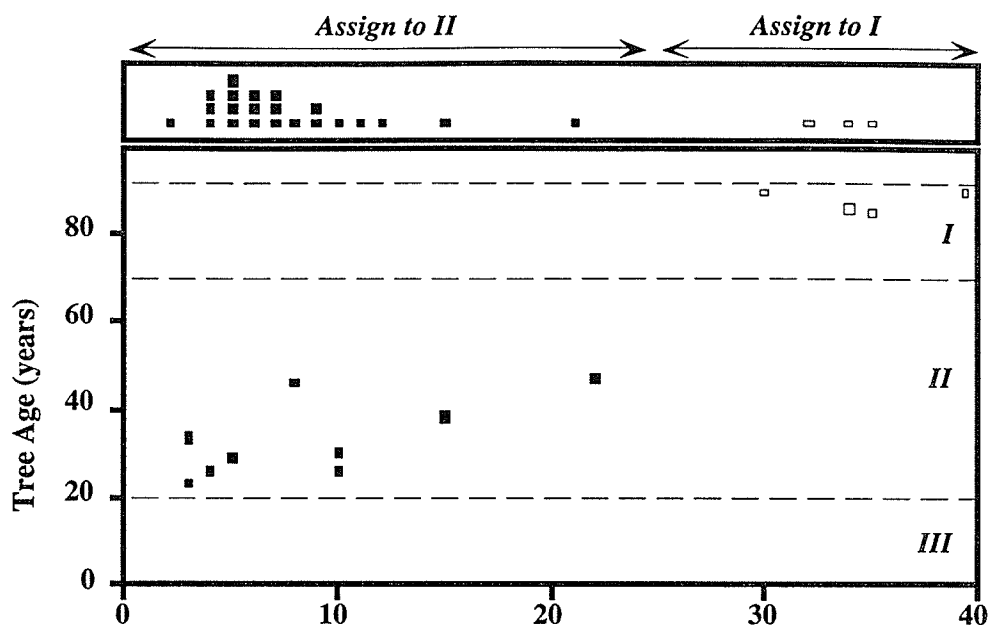
3. Recent Regeneration – saplings and seedlings 20 years of age or younger.

Aged trees were assigned to one of these three classes without difficulty. For unaged individuals in a given stand, likelihood-based assignments were made based on measured stem diameters; an example of the method, using stand 5 as illustration, is presented in **Fig. 3.2**. Using this approach, mean per-species densities (per 10x10 m plot) of the initial cohort, advance regeneration and recent regeneration classes were determined for each of the 48 stands.

3.5.3 Multivariate Modeling of Stand Dynamics

Stand dynamic modeling was undertaken for stands 1-48, which ranged in age from 80-130 years and occurred on mineral substrates. The majority of these stands established following the 1885 fire, i.e. they are approximately 110-115 years old. This is an ideal stand age ‘window’ to examine boreal forest dynamics, since trees of the initial post-fire cohort are reaching their maximum age: while senescence (stand breakup) has started to occur, the initial post-fire cohort still dominates the upper canopy. Furthermore, a well-developed advance regeneration cohort is present in most stands. By sampling such stands, it is possible to obtain data on both the initial post-fire cohort (which forms the upper canopy)

(a) TREMBLING ASPEN



(b) WHITE SPRUCE

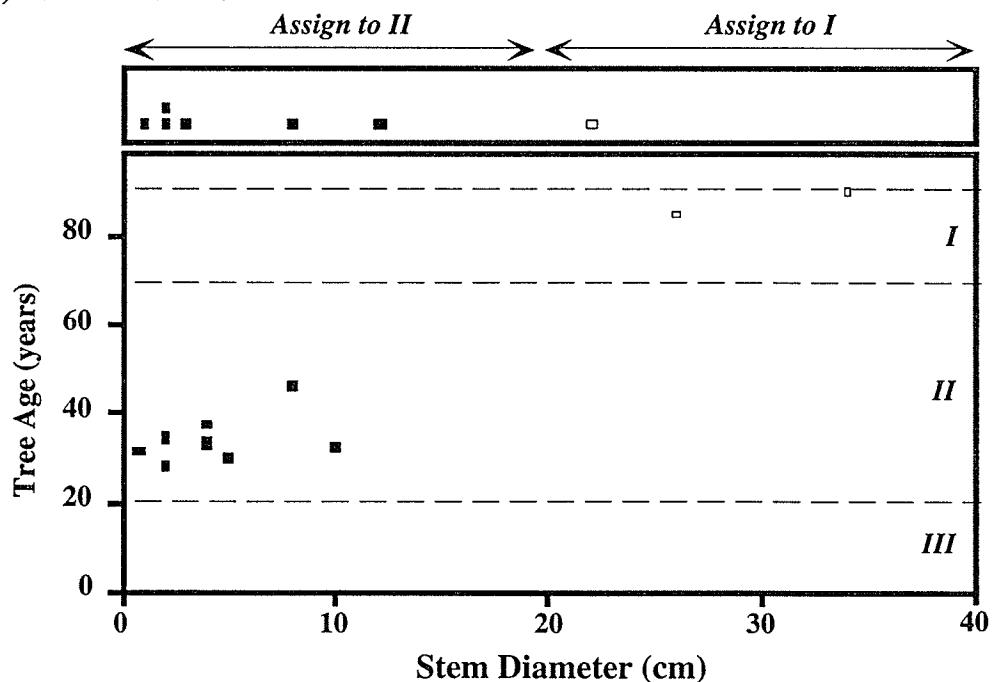


Figure 3.2. The relationship between stem diameter and age for aged (a) trembling aspen and (b) white spruce individuals in stand 5. Aged individuals were assigned to one of three age classes: initial cohort (□= established in first 20 years following disturbance), advanced regeneration (■= established at least 20 years following disturbance, but are greater than 20 years old), and recent regeneration (20 years of age or younger; not shown). Frequency histograms of the stem diameters of unaged individuals are presented above each scatterplot. Unaged individuals were assigned to one of the establishment classes through comparison with the size distribution and establishment class of aged trees of the same species, on a stand by stand basis.

and the advance regeneration (generally present in the lower canopy, subcanopy and sapling layers). Quantification of the age and size structures of such stands therefore provides a 'snapshot' of stand dynamics at a critical time in stand development, i.e. when the initial canopy has begun to break up and advance regeneration trees (the successive canopy cohort) are well established. For the purposes of stand dynamic modeling, the initial cohort and advance regeneration were defined as follows:

A. Initial Cohort – as stated previously, the initial cohort includes trees that established within the first 20 years following fire. For the purpose of modeling stand dynamics, standing dead and recently fallen trees were also included in the initial cohort class.

B. Advance Regeneration – as stated previously, advance regeneration trees are those that established at least 20 years following stand initiation, but are greater than 20 years old.

However, for the purpose of modeling stand dynamics we used a more restrictive definition of advance regeneration: non-contemporaneous individuals that have achieved a height greater than species-specific critical mortality pressures, i.e. individuals considered to have a high likelihood of survival and continued growth and that are therefore likely to contribute to long-term stand canopy dynamics. Since mortality rates of smaller saplings are high (competition, ungulate browsing), they should not be considered in modeling stand dynamics. Therefore only hardwood saplings ≥ 4 m in height were considered as advance regeneration. Softwood saplings are more shade-tolerant than hardwoods, and were therefore considered as advance regeneration provided they were at least 2 m in height. As a justification for this approach, consider heavily browsed balsam fir saplings: such trees are invariably < 2 m in height, but are often quite old. These individuals should not be considered as advance regeneration, since the likelihood of their ever reaching the canopy is very low.

Canonical correspondence analysis (CCA) was used as a multivariate ordination model to examine the relationship between the initial canopy cohort composition and advance regeneration composition. Specifically, the advance regeneration data were canonically constrained by the initial cohort data. Such a model is appropriate since tree regeneration (seed dispersal and vegetative propagation, including suckering and trunk sprouting) and establishment (microenvironmental conditions created by the extant canopy) are necessarily constrained by the composition of the initial stand cohort. This model therefore allowed us to examine the relationship between the initial canopy cohort and subsequent advance regeneration. The following set of analyses were undertaken:

1. Overall Analysis: CCA was performed on all 48 stands to examine general trends in the relationship between initial canopy cohort composition and subsequent advance regeneration. Environmental trends were also summarized, by rotating the CCA axes to environmental congruence using canonical correlation analysis (CANCOR).
2. Stand Type Analyses: Individual CCA ordinations were undertaken for the Trembling Aspen ($n = 12$), Balsam Poplar ($n = 10$), White Spruce ($n = 10$), and Jack Pine ($n = 13$) stand types. The three stands forming the Black Spruce stand type were not examined in this manner, since these stands had very little advance regeneration.

3.5.4 Age-height Relationships

This analysis was undertaken using data from stands 1-48. Within each of the five stand types, vertical canopy stratification was examined using a contingency table approach. Specifically, each tree was classified by cohort class (initial cohort, advance (intermediately established) regeneration, and recent regeneration, as defined above) and vertical canopy (height) class. The following height classes were used:

1. Upper Canopy: > 15 m
2. Lower Canopy: 10-15 m
3. Subcanopy: 2-10 m
4. Sapling: 0.5-2 m
5. Seedling: < 0.5 m

The vertical distribution of cohort classes in each stand type was summarized by computing means (and standard errors) of density values for major species in each height-cohort class combination. This approach is particularly useful in determining whether advance regeneration remains in a highly suppressed state, or reaches the canopy/subcanopy to form a secondary canopy cohort.

3.5.5 Temporal Recruitment Patterns of Advance Regeneration

This analysis was undertaken using data from stands 1-48. The age structure of advance regeneration trees was examined to determine temporal recruitment patterns of dominant species in each stand type. As before, advance regeneration trees were defined as those establishing at least 20 years after stand initiation but more than 20 years old. Only trees aged at the root collar were included in this analysis, and hardwoods < 4 m in height and softwoods < 2 m in height were not considered. Age profiles, presented as age since stand establishment, were summarized in histogram form.

3.5.6 Species Richness of the Initial and Advance Regeneration Cohorts

Using density data at the stand level, average species richness and average effective species richness were calculated for the initial and advance regeneration cohorts within each of four stand types. Small sample size precluded the calculation of species richness in the Black Spruce stand type. One hundred iterations of a random draw of 8 stands within each stand type was taken, with replacement, and richness and effective richness (Simpson's) calculated for each iteration. The average and standard deviation of these calculated values were tabulated.

CHAPTER 4

RESULTS AND DISCUSSION

4.1 Post-Fire Stand Types

4.1.1 Trembling Aspen

These stands are characterized by an initial cohort of trembling aspen, sometimes in mixture with small amounts of balsam poplar, white spruce and/or white birch. Trembling aspen stands in the Duck Mountains are relatively young (mean stand age is 90 years). Cover of tall shrubs (beaked hazelnut, mountain maple and/or green alder) in these stands is moderate to high. Other common shrubs include prickly rose, willows, saskatoon, and chokecherry. Pincherry and speckled alder are occasionally encountered at high cover. The herb layer is poorly developed under dense tall shrub cover, but is well developed otherwise. Major herb species include wild strawberry, fringed aster, wild lily-of-the-valley, wild sarsaparilla, Canada violet, palmate-leaved coltsfoot, tall bluebells, dewberry and mountain rice grass. Canada goldenrod and bishop's cap occasionally having significant cover. Moss cover is low: species of *Brachythecium* and *Mnium* occur on rotting logs at low cover. **Appendix A** contains detailed information on the frequency, standard deviation, and average cover of major shrub, herb, and non-vascular plants within the five post-fire stand types.

Trembling aspen stands are most commonly found on the well-drained north, south, and west slopes of the Duck Mountains, and along the upper slopes of major valleys. Locations of stands within the Duck Mountain Provincial Forest are presented in **Fig. 4.1**. North-facing slopes are often dominated by trembling aspen, with some white birch and balsam poplar but few conifers. Mountain maple or green alder are often the dominant shrubs in

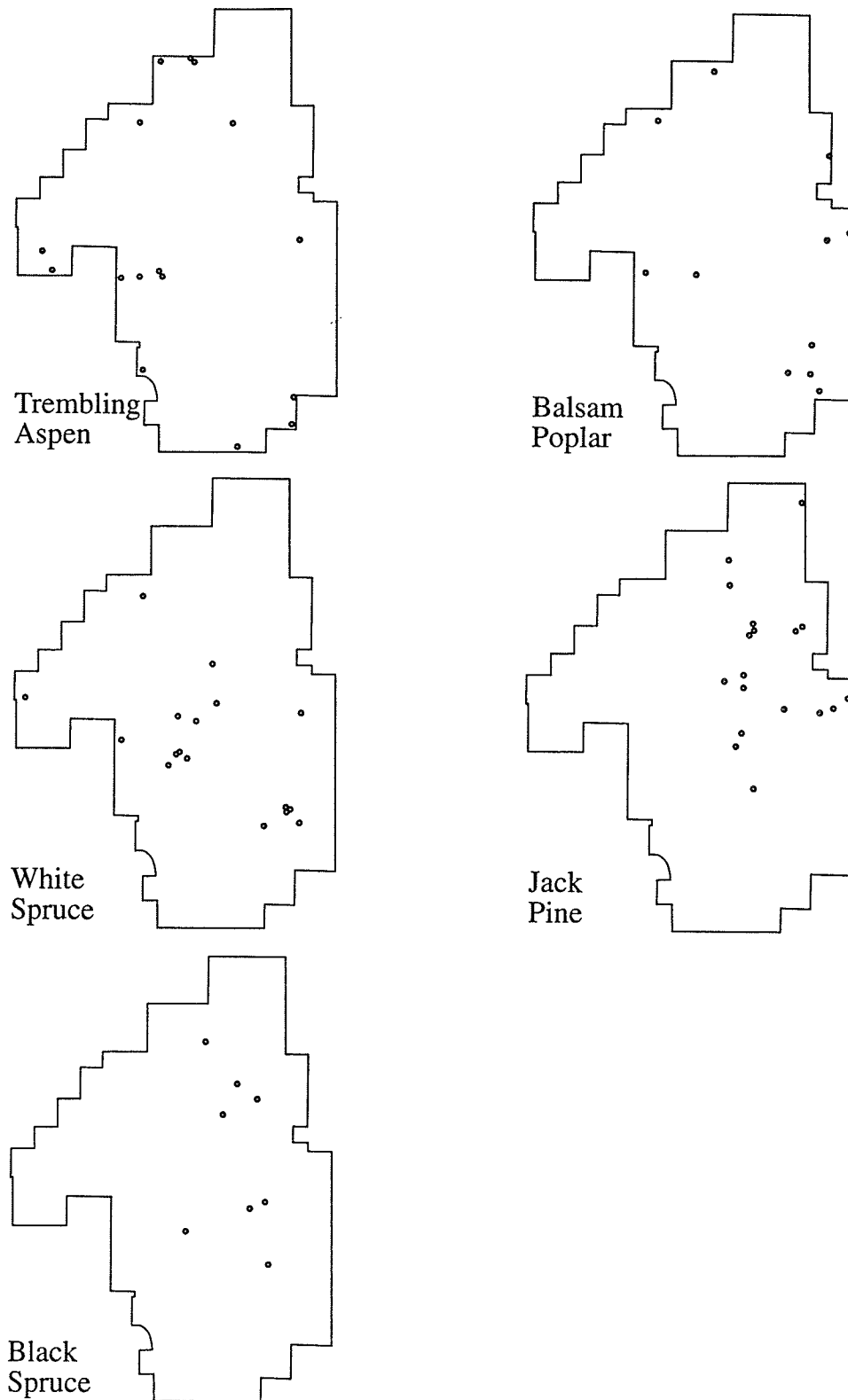


Figure 4.1. Location of the 70 stands sampled in Duck Mountain Provincial Park and Forest, by post-fire stand type.

these nutrient-rich, cool stands. Aspen stands in the Duck Mountain uplands often contain one or more contemporaneously-established white spruce. By contrast, stands more proximate to agricultural land are less likely to include a softwood component. Historically high fire cycles, repeated settlement-era fires, and selective logging of white spruce at the turn of the century are thought to have contributed to the development of extensive monodominant aspen stands adjacent to agricultural land (cf. Weir & Johnson 1998).

4.1.2 Balsam Poplar

The initial cohort of these stands is dominated by balsam poplar, often in mixture with trembling aspen. Mean stand age is 100 years. Balsam poplar is the dominant species of floodplains and in imperfectly-drained, nutrient-rich stands. By contrast, mixed stands of balsam poplar and trembling aspen occur in better-drained sites. Contemporaneously-established white spruce is present in many stands, albeit at low densities. Tall shrub cover ranges from low to high. Beaked hazelnut is often the dominant tall shrub, but occasionally mountain maple or green alder dominate. Other shrub species present include prickly rose, red-osier dogwood, saskatoon, speckled alder, pincherry and wild red raspberry. Common species in the herb layer include wild sarsaparilla, dewberry, bishop's cap, Canada violet, fringed aster, tall bluebells, sedges and rice grass. Moss cover is low: as in the Trembling Aspen stand type, species of *Brachythecium* and *Mnium* occur on rotting logs at low cover. Common horsetail is occasionally abundant, as are feathermosses.

Balsam poplar typically occurs in moderately drained low-lying areas and on seepage slopes, generally where nutrient status is moderate to high. Groundwater flow is critical: black spruce is favoured over balsam poplar in oligotrophic, poorly drained anoxic sites. Stands of balsam poplar are often associated with trembling aspen stands, occupying local depressions and flats within a larger background 'matrix' of trembling aspen forest.

4.1.3 White Spruce

These stands are characterized by an initial cohort of white spruce, almost invariably in mixture with trembling aspen. White birch and/or balsam poplar may also be present, and very rarely contemporaneous balsam fir are present. Pure post-fire stands of white spruce are uncommon in the Duck Mountains. The cover of tall shrubs is generally low to moderate, and dominated by beaked hazelnut, green alder and/or mountain maple. Other common shrubs include prickly rose, wild red currant, twinflower, wild red raspberry, common snowberry and low-bush cranberry. Common species in the herb layer include wild sarsparilla, tall bluebells, dewberry, wild lily-of-the-valley, bunchberry, palmate-leaved coltsfoot, bishop's cap and wild strawberry. Moss cover tends to increase with increasing conifer abundance in the canopy. Feathermosses and species of *Mnium* and *Brachythecium* are most frequent. Stiff club-moss is occasionally present at high cover.

While pure trembling aspen stands are generally found along the lower slopes of the Duck Mountains adjacent to agricultural land, mixed white spruce–trembling aspen stands are more often encountered in more complex upland hummocky terrain in the central, higher elevational regions. This upland landscape is punctuated by numerous small lakes and hills. These are older stands, with a mean age of 115 years.

4.1.4 Jack Pine

Jack pine rarely forms extensive pure stands in the Duck Mountains. Instead, the species most often occurs in a patchy mixture with trembling aspen. White birch and/or white spruce may also establish contemporaneously, but at low density. In well-drained sites, jack pine may occur in mixture with black spruce. Shrub cover is low in most stands, but beaked hazelnut may be common in stands with high cover of aspen. Green alder occasionally occurs in sites where the water table is within 2 m of the surface. Other shrub species in

these stands include prickly rose, low-bush cranberry, twinflower, wild red raspberry, saskatoon, red-osier dogwood, chokecherry and bush honeysuckle. Herbaceous cover is variable, and feathermosses are favoured in stands with a significant component of black spruce. Common herbs include wild sarsparilla, bunchberry, dewberry, wild strawberry, palmate-leaved coltsfoot, tall bluebells, and bishop's cap. Feathermosses are common and occasionally present at high cover.

Jack pine stands are commonly found on well-drained substrates in uplands near Wellman Lake, in the region north of Baldy Mountain and south of Highway 366, and on sandy ancient beach ridges along the northeast side of Duck Mountain. The occasional presence of jack pine on clay soils proximate to lakes is likely a reflection of the frequency of historical fires. Most jack pine stands originated following the catastrophic burn of 1885. Mean stand age is 110 years.

4.1.5 Black Spruce

Black spruce usually forms a dense initial cohort on mineral substrates, often in mixture with some jack pine. Trembling aspen and white birch are occasional at low density. Shrub and herb cover is low. Twinflower, prickly rose, bog cranberry, Labrador tea, palmate-leaved coltsfoot, bunchberry, lesser rattlesnake-plantain, bishop's cap and stiff club-moss are the most frequently encountered understory species. Speckled alder is occasionally abundant in canopy openings. Most stands are characterized by a continuous cover of feathermosses. Black spruce stands are common in the central uplands of the Duck Mountains, in areas of impeded drainage and low nutrient status. Extensive stands are found in the area north and east of Wellman Lake, and on the extensive flats around Singuish Lake. Average stand age is 115 years.

Post-fire black spruce stands also occur on organic peat substrates, occasionally with small amounts of tamarack. Organic substrates vary in drainage and depth to water table: if the water table is close to the surface, black spruce are stunted. Labrador tea, speckled alder, cloudberry and bog cranberry are the most common shrub species of organic substrates. Moss cover is continuous and dominated by feathermosses, *Tomenthypnum nitens*, and *Sphagnum* species. Black spruce stands on organic substrates occur in hummocky upland and on extensive flats in the Wellman Lake area, usually grading into adjacent black spruce stands on mineral substrates.

4.2 Vegetation – Environment Relationships

Canonical correspondence analysis (CCA) was used to examine the relationship between the woody vegetation (trees and shrubs) and 14 environment-landscape variables in stands 1-61 (Fig. 4.2). Stands are coded by initial stand type. The first CCA axis reflects a gradient from hardwood-dominated to softwood-dominated stands. The second CCA axis separates the softwood stands, from white spruce stands on clayey substrates to jack pine and black spruce stands on well-drained sandy soils. Hardwood stands (trembling aspen, balsam poplar) are associated with the richer soils (higher pH and conductivity) on the lower slopes of the Duck Mountains adjacent to agricultural land. These stands have the highest herb cover and greatest accumulation of deciduous litter. Conversely, softwood stands occur further from agricultural lands at higher elevations in the central Duck Mountains. These stands also tend to be older, and have higher moss cover, greater accumulation of coarse woody debris, and a deeper organic (LFH) layer. Jack pine and black spruce stands are associated with well-drained (sandier) soils compared to white spruce stands.

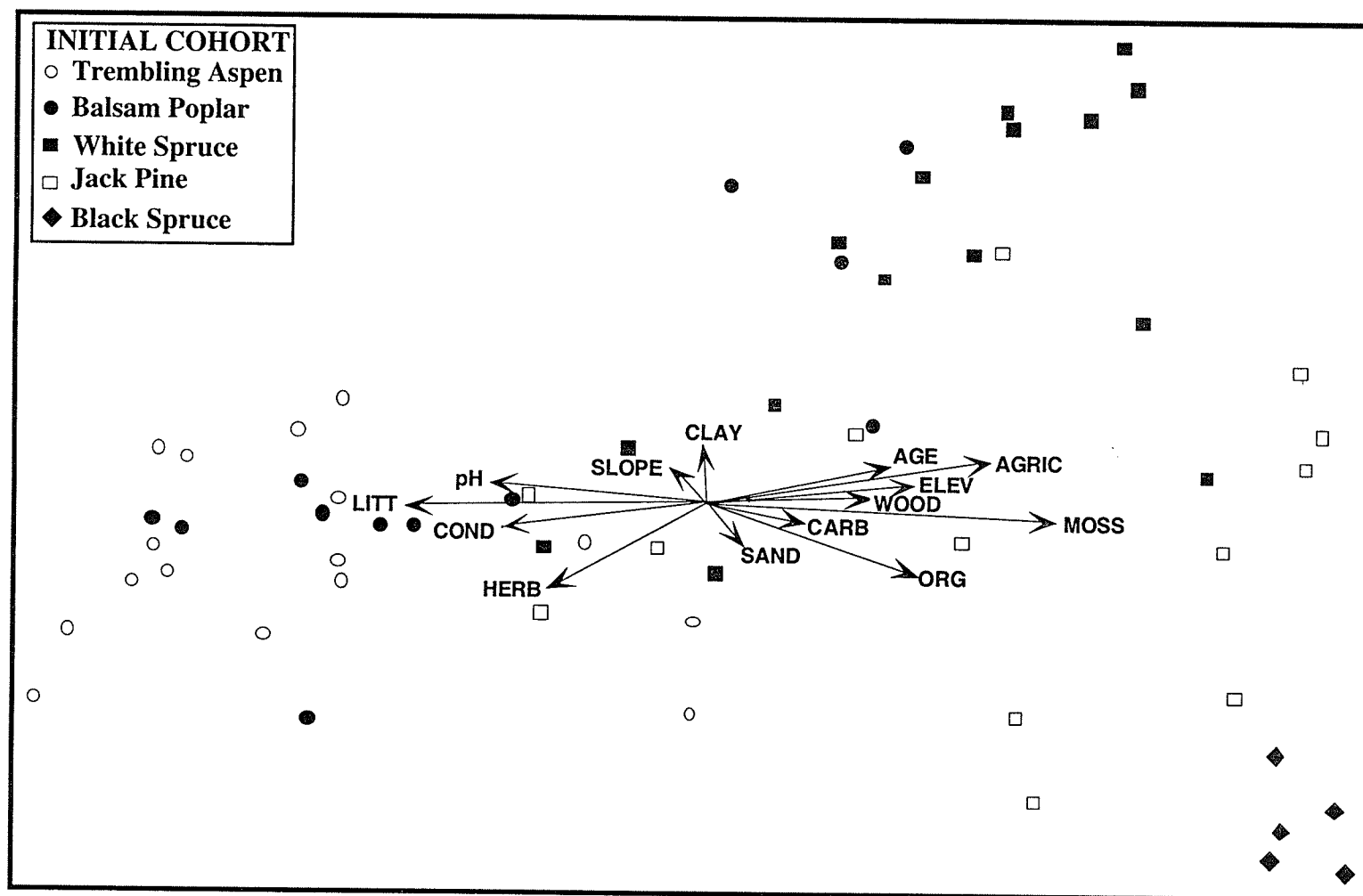


Figure 4.2. Canonical correspondence analysis ordination biplot of woody vegetation cover in stands 1-61 and 14 environment-landscape variables. Stands are coded by initial stand-type. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.900$, $R_2^2 = 0.763$. The redundancy (ratio of the canonical inertia to total inertia) = $0.690/1.610 = 42.85\%$. Environment-landscape codes are given in the Methods section.

The CCA species biplot indicates that trembling aspen, balsam poplar, white spruce and white birch are ordinated near the centre of the diagram (**Fig. 4.3**). Jack pine and black spruce are ordinated at the lower right, indicating their occurrence on well-drained, nutrient-impooverished substrates in the north-central region of the Duck Mountains. Balsam fir occurs at the upper right, indicating its association with older white spruce stands in the central Duck Mountains. Shrub species associated with hardwood stands include poison ivy, wild rose, chokecherry, snowberry, beaked hazelnut, and mountain maple. Ericaceous and evergreen shrubs such as twinflower, Labrador tea, bog cranberry and blueberry are associated with jack pine and black spruce stands.

4.3 Multivariate Modeling of Stand Dynamics

The CCA of advance regeneration composition constrained by initial cohort composition is presented in **Fig. 4.4**. The 48 stands are coded by initial stand type. To aid in the CCA interpretation, relative abundances of the initial cohort species of each stand are given in **Fig. 4.5** (the CCA input data for both the initial and advance regeneration cohort is presented in **Appendix B**). Three major trends in the relationship between initial cohort and advance regeneration are apparent: (1) advance regeneration of balsam fir is associated with stands containing white spruce and white birch in the initial cohort; (2) advance regeneration of trembling aspen, balsam poplar and white spruce are associated with stands in which trembling aspen and balsam poplar dominate the initial cohort; (3) advance regeneration of white birch and black spruce are associated with stands in which black spruce or jack pine dominate the initial cohort.

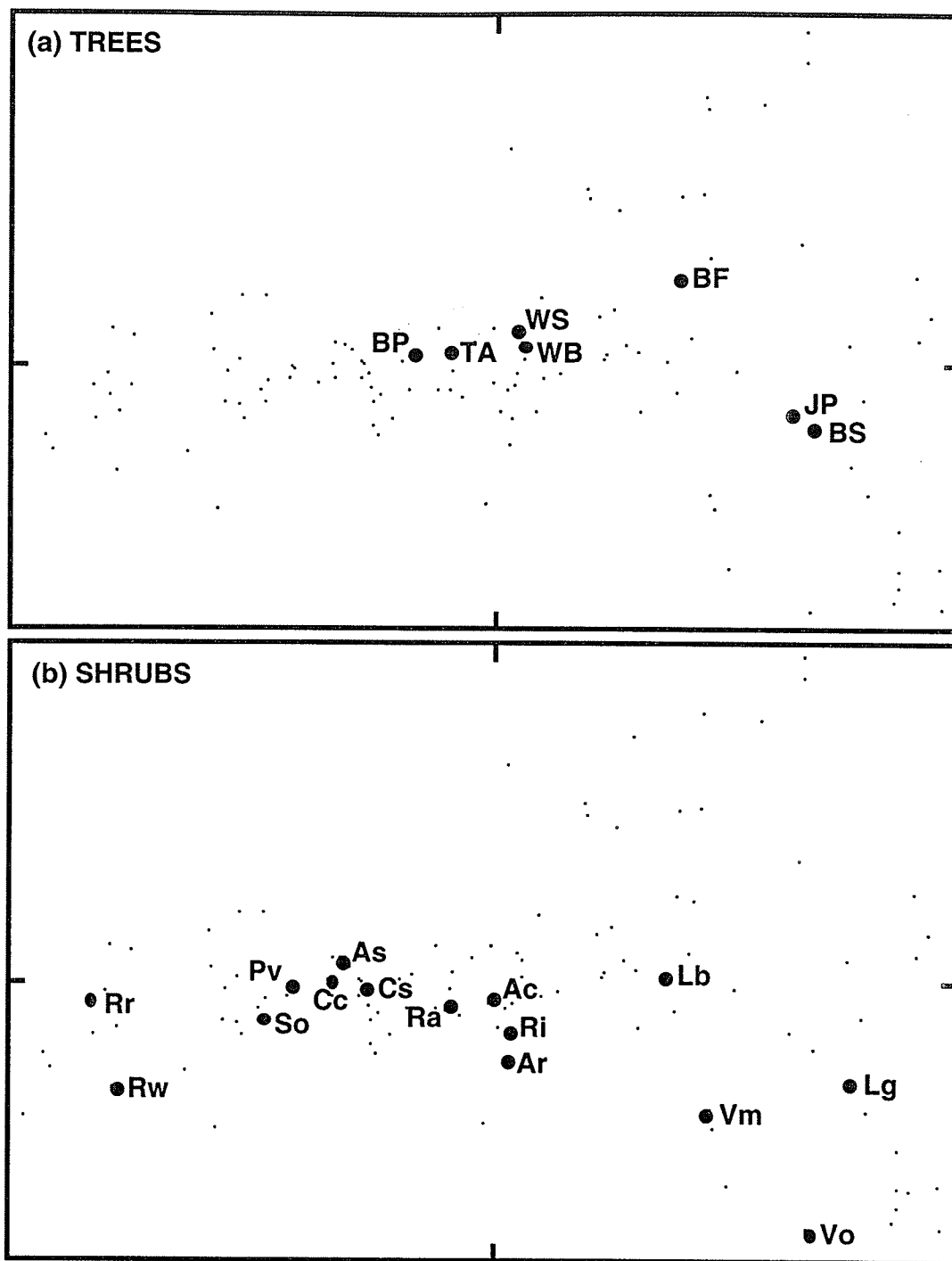


Figure 4.3. Canonical correspondence analysis ordination biplot of the woody vegetation cover in stands 1-61, showing major tree (a) and species (b) species. The corresponding species-environment biplot is presented in Figure 2. Species codes: BF = balsam fir, BP = balsam poplar, BS = black spruce, JP = jack pine, TA = trembling aspen, WB = white birch, WS = white spruce, Rr = poison ivy, Rw = common wild rose, Pv = chokecherry, So = western snowberry, Cc = beaked hazelnut, As = mountain maple, Cs = red-osier dogwood, Ra = alder-leaved buckthorn, Ac = green alder, Ri = wild raspberry, Ar = speckled alder, Lb = twinflower, Vm = blueberry, Lg = Labrador tea, Vo = bog cranberry.

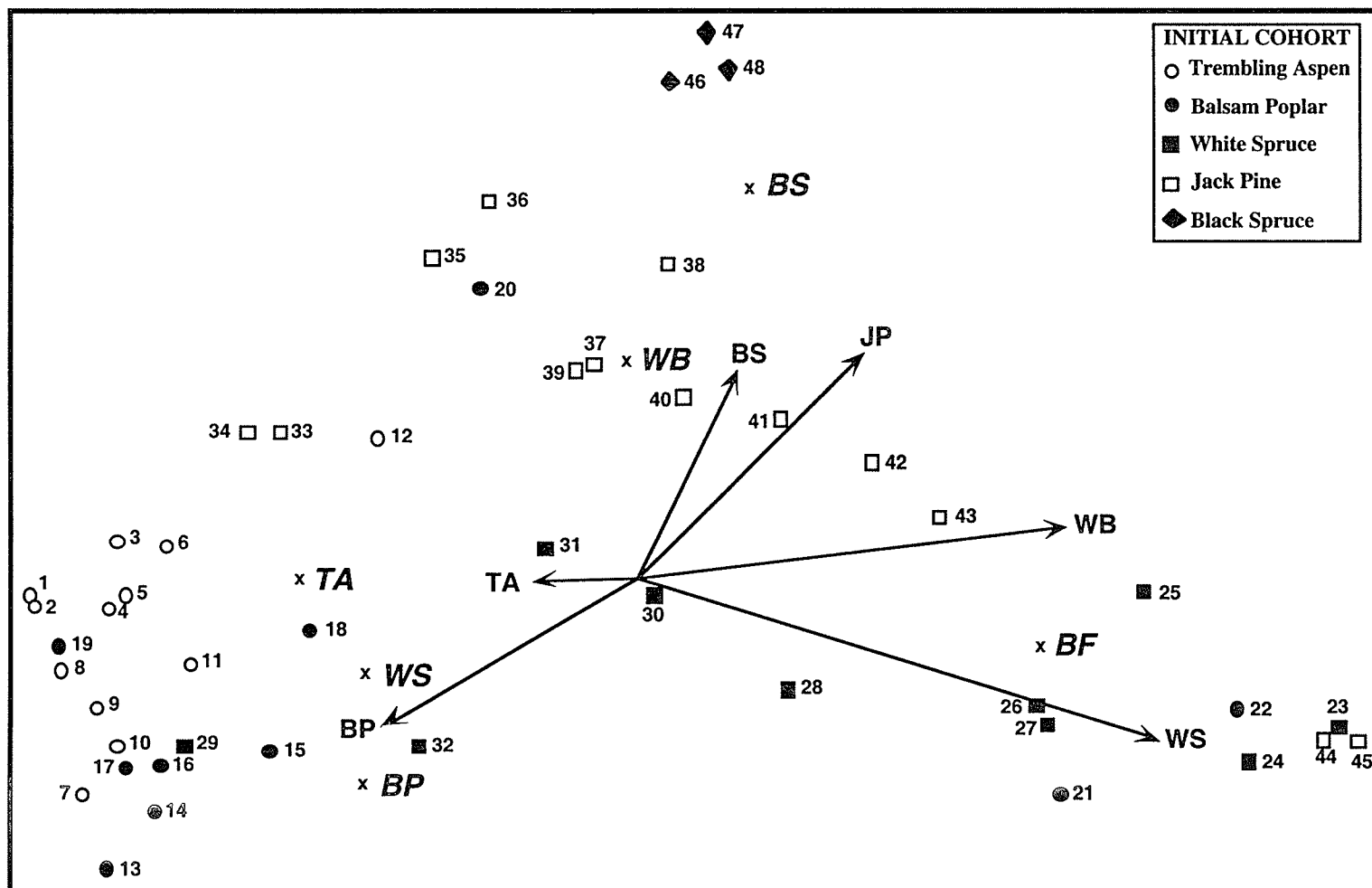


Figure 4.4. Canonical correspondence analysis ordination biplot of the advanced regeneration density in stands 1-48 constrained by initially-established cohort composition (vectors). Stands are coded by initial stand type. Centroids of species advance regeneration are indicated by x. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.731$, $R_2^2 = 0.735$. The redundancy (ratio of the canonical inertia to total inertia = $0.586/1.680 = 34.88\%$). Species codes: BF = balsam fir, BP = balsam poplar, BS = black spruce, JP = jack pine, TA = trembling aspen, WB = white birch, WS = white spruce.

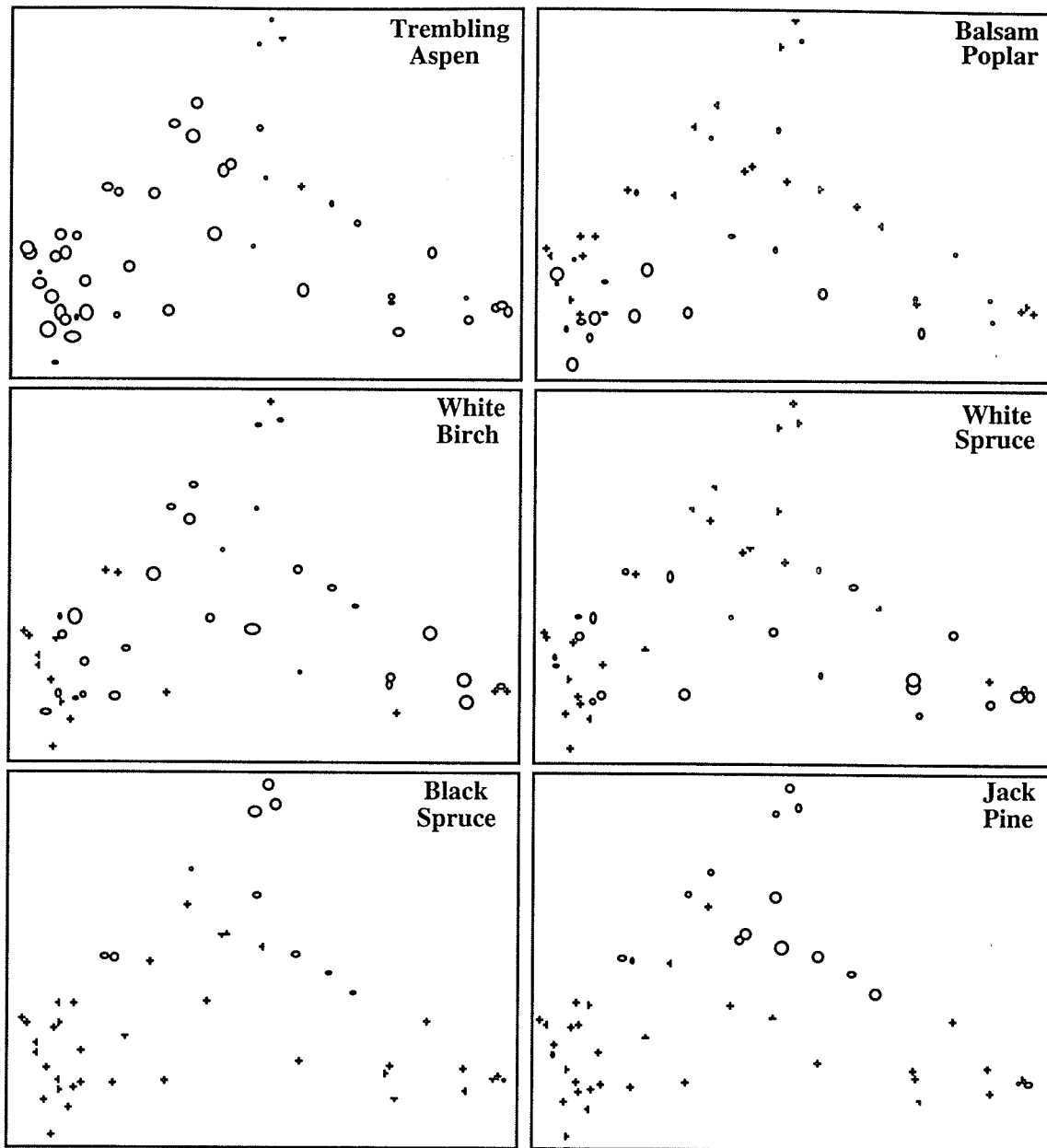


Figure 4.5 Relative abundance of initial cohort tree species in the 48 stands ordinated using canonical correspondence analysis and presented in Figure 4. Open circles are proportional to relative species abundance at stand initiation; crosses indicate species absence at stand initiation.

The majority of stands belonging to the trembling aspen and balsam poplar initial stand types are characterized by advance regeneration of trembling aspen, balsam poplar and/or white spruce. Two stands belonging to the White Spruce stand type (stands 29 and 32) show a similar pattern of advance regeneration. Two stands belonging to the balsam poplar initial stand type (stands 21 and 22), and two belonging to the Jack Pine stand type (stands 44 and 45) are strongly associated with balsam fir advance regeneration. However, the majority of stands showing strong advance regeneration of balsam fir belong to the White Spruce stand type. Stands belonging to the Jack Pine stand type are most often characterized by black spruce and/or white birch advance regeneration, but balsam fir may also be present. Stands in the black spruce initial stand type are self-perpetuating, i.e. associated with black spruce advance regeneration.

A canonical rigid rotation of the two-dimensional CCA ordination to environmental congruence is shown in **Fig. 4.6**. The trembling aspen and balsam poplar initial cohort stand types, which are characterized by advance regeneration of trembling aspen, balsam poplar and/or white spruce, are characterized by higher soil nutrient status (pH and conductivity), as well as higher shrub cover and deciduous litter accumulation. Softwood initial cohort stand types (white spruce, jack pine and black spruce) occur at higher elevations far from agricultural land, and are characterized by higher moss cover and greater accumulation of coarse woody debris. Stands showing strong advance regeneration of balsam fir are associated with finer-textured soils, whereas advance regeneration of black spruce and white birch (jack pine and black spruce initial stand types) are associated with coarser-textured, nutrient-poor substrates.

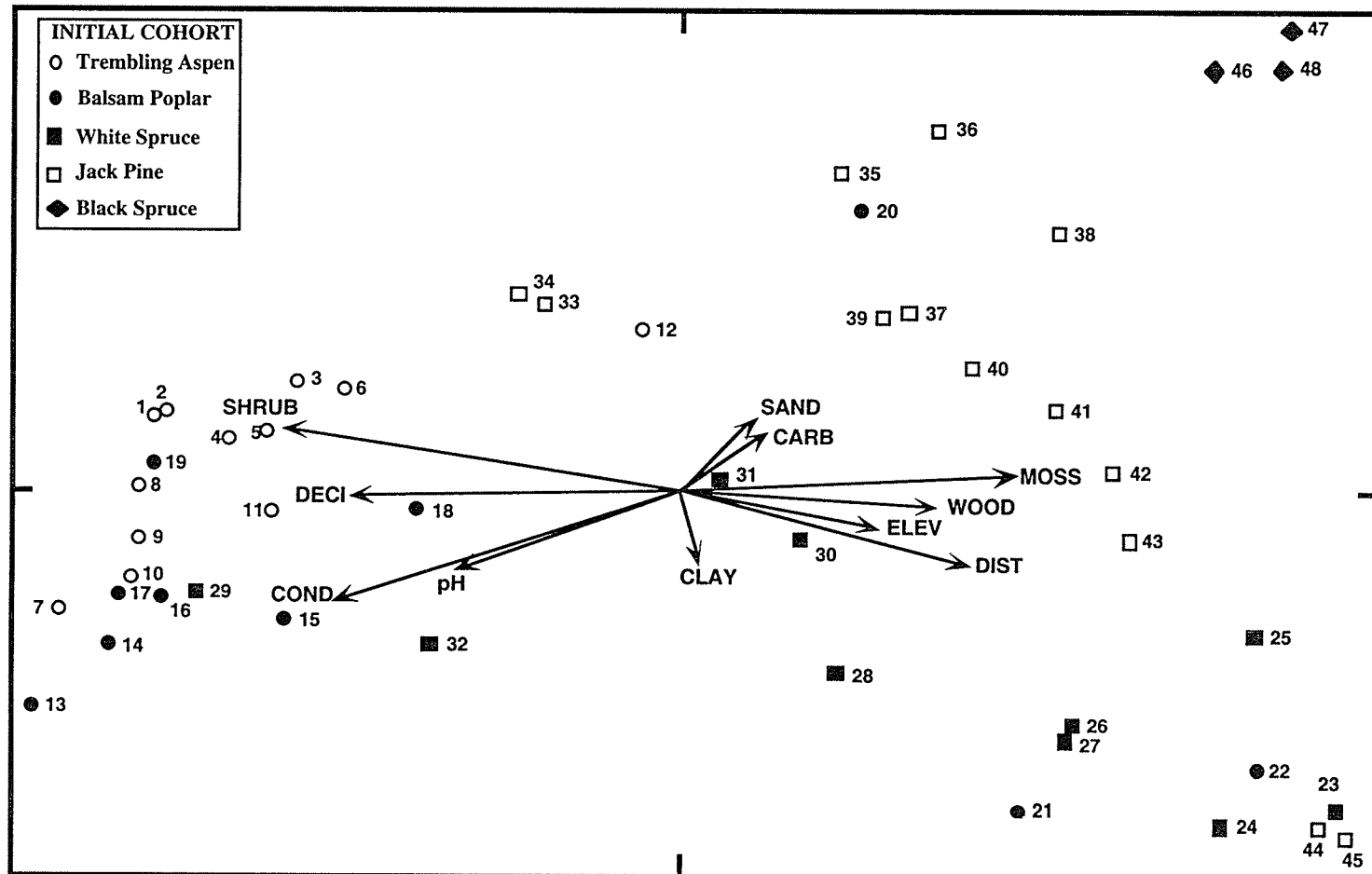


Figure 4.6. Rotation of canonical correspondence analysis (CCA) ordination (Figure 5) to environmental congruence using canonical correlation analysis, based on 11 'environmental' variables. The 48 stands are coded by initial stand type. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.860$, $R_2^2 = 0.728$. The canonical relationship is highly significant ($\chi^2 = 83.96$, $P < 0.001$), redundancy of CCA ordination = 63.88%. Environment codes: SHRUB = percent tall shrub cover; DECI = percent hardwood canopy cover; COND = soil conductivity; pH = soil pH; SAND = percent soil sand content; CLAY = percent soil clay content; CARB = depth to carbonates; MOSS = percent moss cover; WOOD = percent coarse woody debris cover; ELEV = elevation above sea level; DIST = distance (km) to agricultural land.

4.3.1 Trembling Aspen Stand Type (n = 12)

The CCA of advance regeneration constrained by initial cohort composition for the aspen stand type indicates two broad regeneration patterns (**Fig. 4.7**). Stands 1-8 are characterized by secondary aspen suckering. Balsam poplar, white spruce and white birch advance regeneration may also occur in these stands at low densities. These are nearly pure hardwood stands. Stands 1, 2 and 7 lack a proximate white spruce seed source. By contrast, stands 9-12 are dominated by trembling aspen but contain one or more contemporaneously-established white spruce that serve as a proximate seed source. Advance regeneration in these stands is dominated by white spruce, with some secondary recruitment from aspen root suckers and white birch basal trunk suckers.

Advance regeneration suckers of trembling aspen have already reached the upper and lower canopies of some stands (**Table 4.1**), suggesting that aspen stands may be self-perpetuating in the absence of a proximate softwood seed source. Some white spruce advance regeneration has also recruited into the upper and lower canopies, but most individuals are between 2-10 m in height.

Successful advance regeneration suckers of trembling aspen do not appear until at least 50 years post-fire (**Fig. 4.8**), which probably coincides with the first stages of canopy self-thinning. White spruce advance recruitment into these stands peaks about 60 years post-fire. This recruitment delay in white spruce may reflect improved environmental and seedbed conditions as aspen stands self-thin. Self-thinning results in increased light levels at the forest floor (Peterson & Peterson 1992), as well as an abundance of reliably moist decomposing logs that are elevated above the smothering effects of deciduous leaf litter (Waldron 1966; Koroleff 1954). These conditions may be conducive to white spruce establishment (Lieffers et al. 1996).

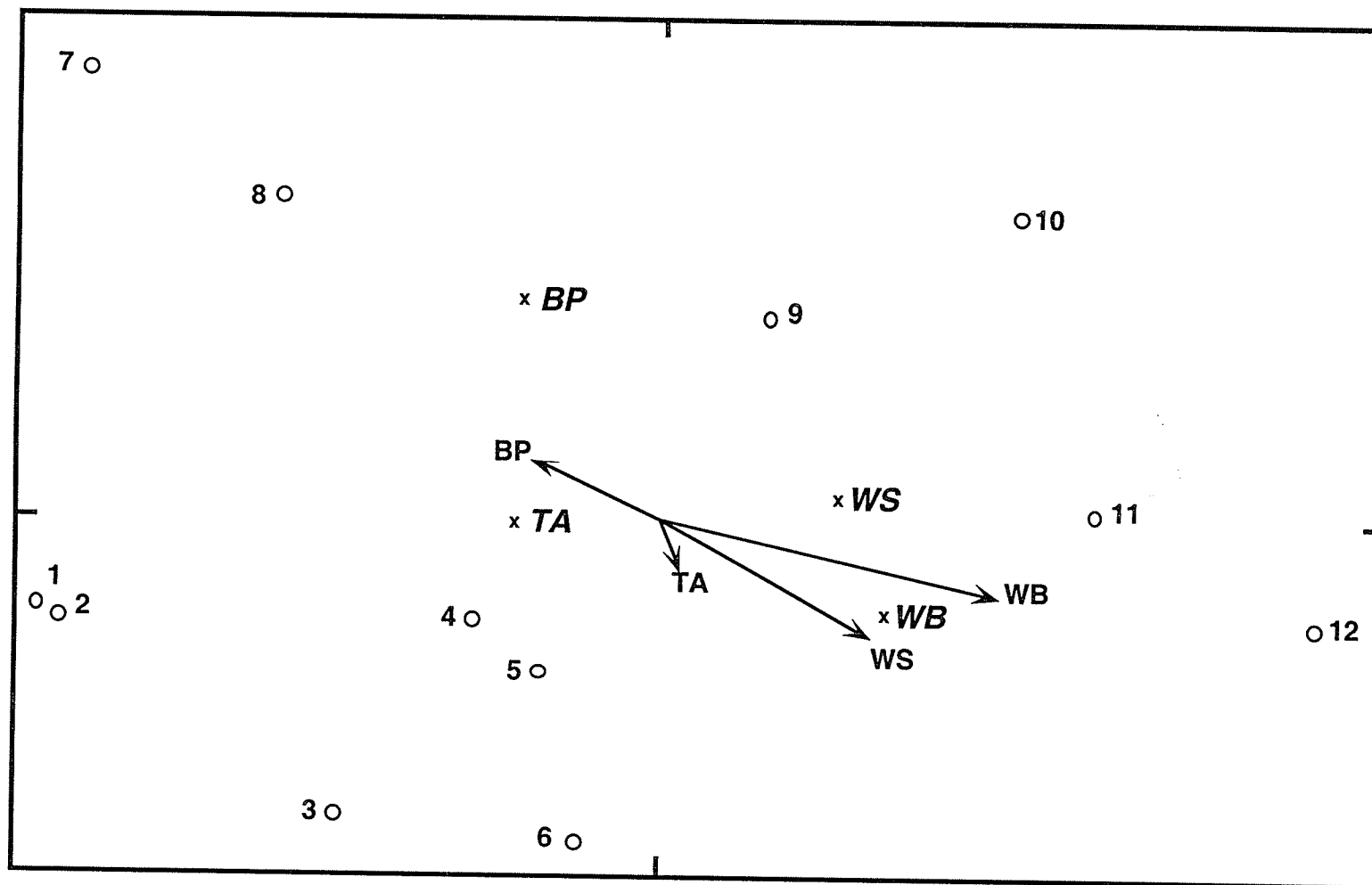


Figure 4.7. Canonical correspondence analysis ordination biplot of the advanced regeneration density (x) constrained by the initially-established cohort composition (vectors) of 12 trembling aspen stands. Centroids of species advance regeneration are indicated. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.773$, $R_2^2 = 0.794$. The redundancy (ratio of the canonical inertia to total inertia) = $0.319/0.559 = 57.1\%$. Species codes: BP = balsam poplar, TA = trembling aspen, WB = white birch, WS = white spruce.

WHITE SPRUCE				TREMBLING ASPEN			
	<i>C</i>	<i>I</i>	<i>R</i>		<i>C</i>	<i>I</i>	<i>R</i>
1	0.70 (0.19)	0.57 (0.25)		1	4.53 (0.70)	0.83 (0.46)	
2	0.13 (0.08)	0.30 (0.15)		2	0.17 (0.14)	1.50 (0.56)	
3	0.03 (0.03)	1.77 (0.46)		3		0.87 (0.29)	3.10 (1.14)
4		0.10 (0.06)	0.27 (0.10)	4			2.80 (2.23)
5			0.47 (0.13)	5			2.10 (0.40)
	5/12	7/12	8/12		12/12	7/12	8/12

Table 4.1. Average density/100 m² (standard error) of three age classes and five height classes for trembling aspen and white spruce in 12 trembling aspen stands. Age classes are coded: C = contemporaneously established, I = intermediately established (advance regeneration), R = recently established. Height classes: 1 = >15 m, 2 = 10-15 m, 3 = 2-10 m, 4 = 0.5-2 m, 5 = < 0.5 m. The fraction of stands containing representative individuals are indicated below the corresponding age-class columns.

The presence of white spruce advance recruitment in trembling aspen stands is strongly dependent on seed source proximity (**Table 4.2**). Observed differences in the abundance of white spruce regeneration in stands having a proximate seed source may be a function of competition from tall shrubs, as well as abiotic factors related to surface moisture and seedbed requirements (Kneeshaw & Bergeron 1996).

Aspen advance regeneration success is a function of light conditions. A multiple regression analysis incorporating percent tall shrub cover (beaked hazelnut and mountain maple) and basal area of aspen and white spruce explained 54.2% of the variation observed

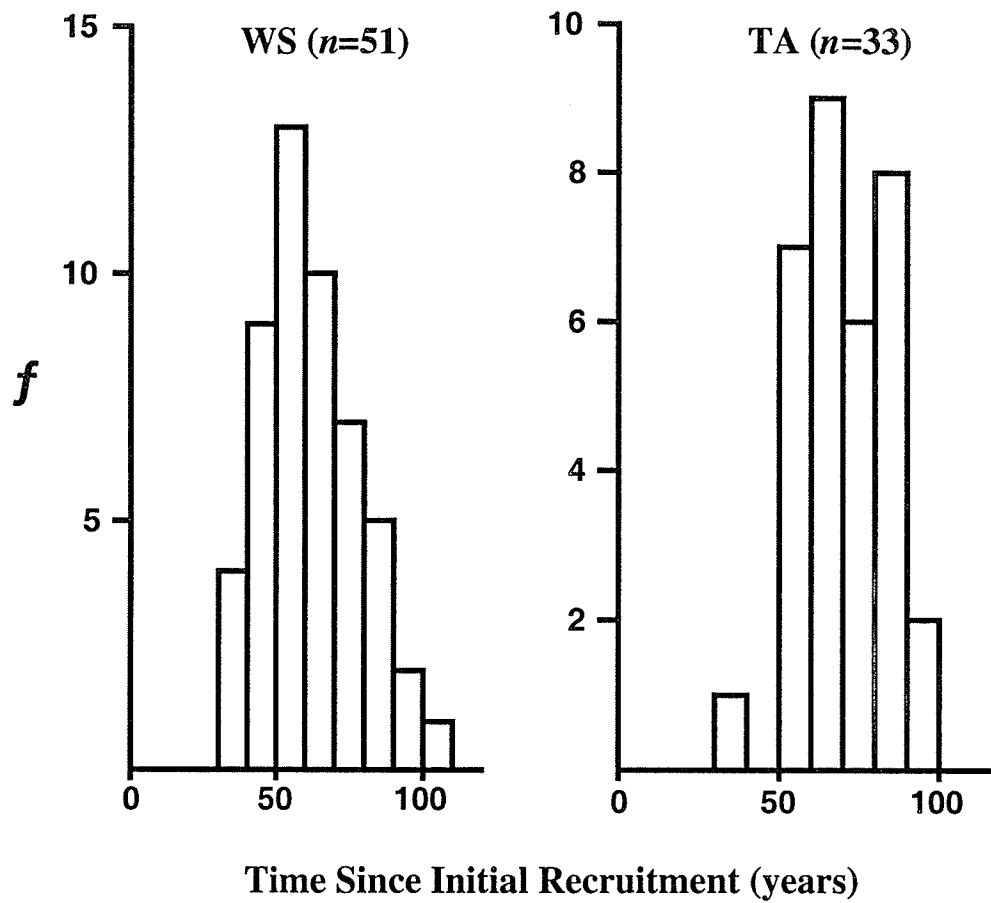


Figure 4.8. Age-class histograms of time since initial recruitment for white spruce and trembling aspen advance regeneration in the trembling aspen stand-type.

in aspen sucker density ($n = 21$, $F = 4.73$, $P < 0.001$). Highest aspen suckering success occurred in stands where tall shrub cover and canopy basal area were low, indicating higher light conditions.

Average effective species richness is greater in the advanced regeneration cohort (2.29) than in the initial cohort (1.75) (Table 4.3). Among the four stand types for which it was calculated, effective species richness was lowest in trembling aspen stands for both the initial and advanced regeneration cohorts.

Table 4.2. Density of white spruce advance regeneration (A.R.) per 100 m² for 12 Trembling Aspen stands with a near (within stand) or far (greater than 500 m away) white spruce seed source.

Distance to Seed Source	Site Code	White spruce A.R. Density
Near	9	8.00
	12	8.00
	11	7.00
	10	5.00
	5	3.00
	4	1.50
	6	0.67
	8	0.67
	3	0.33
Far	7	0
	2	0
	1	0

Table 4.3 Average species richness and average effective species richness (Simpson's) of the initial and advance regeneration cohorts of four stand types (standard deviation in parentheses).

Stand Type	Initial Cohort		Advance Regeneration Cohort	
	Eff. Richness	Richness	Eff. Richness	Richness
Trembling Aspen	1.75	4.48	2.29	4.28
	(0.27)	(0.52)	(0.39)	(0.59)
Balsam Poplar	2.40	3.99	3.22	5.84
	(0.29)	(0.10)	(0.70)	(0.37)
White Spruce	3.21	4.55	2.47	5.49
	(0.22)	(0.50)	(0.60)	(0.50)
Jack Pine	3.31	5.74	3.45	5.43
	(0.45)	(0.44)	(0.63)	(0.52)

4.3.1a Trembling Aspen stand dynamics

In the absence of a proximate white spruce seed source, trembling aspen stands may be self-perpetuating. Advance regeneration aspen suckers are already an important canopy component in many stands, and continued canopy recruitment is evident. However, older aspen stands are multi-aged and of lower density, and in some cases take on a 'decadent' appearance (cf. Cogbill 1985). A dense tall shrub layer (beaked hazelnut and/or mountain maple) develops in many older stands, and this can negatively impact secondary aspen suckering. Ungulates (particularly elk and moose) can do considerable damage to secondary aspen suckers and so limit successful recruitment (see **Appendix C** for average indexed browsing levels on major tree and shrub species). These factors may lead to the development of decadent aspen shrublands as seen along Highway 10 in Riding Mountain National Park (Caners & Kenkel 1998).

White spruce abundance will increase in stands with a proximate seed source. Typically, white spruce recruitment densities are low, and growth of established seedlings is compromised by heavy shading from the tree canopy and shrub layer. These stands will continue to be dominated by aspen for some time, but white spruce will slowly increase in abundance. Ungulate herbivory of aspen suckers may result in these stands reverting to a 'white spruce parkland', characterized by a broken canopy dominated by white spruce, with some balsam poplar and white birch and high tall shrub cover (chiefly beaked hazelnut). In some stands a stronger shift to white spruce is possible, but aspen suckering and white birch resprouting will maintain a secondary deciduous component. Aspen stands on south-facing slopes with sandy substrates may have a proximate white spruce seed source but little or no advanced recruitment. Rapid drainage and excessive temperatures in these stands will likely preclude white spruce from becoming a significant canopy component. White spruce recruitment is also limited on north- and east-facing slopes dominated by mountain maple.

4.3.2 Balsam Poplar Stand Type (n = 10)

The CCA of advance regeneration constrained by initial cohort composition for the Balsam Poplar stand type indicates four regeneration trends (Fig. 4.9). Stand 13 is a floodplain site that exhibits very low recruitment of balsam poplar and trembling aspen, and no softwood advance regeneration. By contrast, advance regeneration in stands 14-18 is dominated by white spruce, although trembling aspen, birch, balsam fir, balsam poplar and/or black spruce may also occur at low abundance. The canopy of stands 13-18 is dominated by balsam poplar, with aspen present as a secondary component. By contrast, trembling aspen and balsam poplar codominate the initial cohort of stands 19 and 20, which are characterized by advance regeneration of aspen. Heavy advance regeneration of balsam fir characterizes stands 21 and 22. The initial cohort of these stands, which occur on

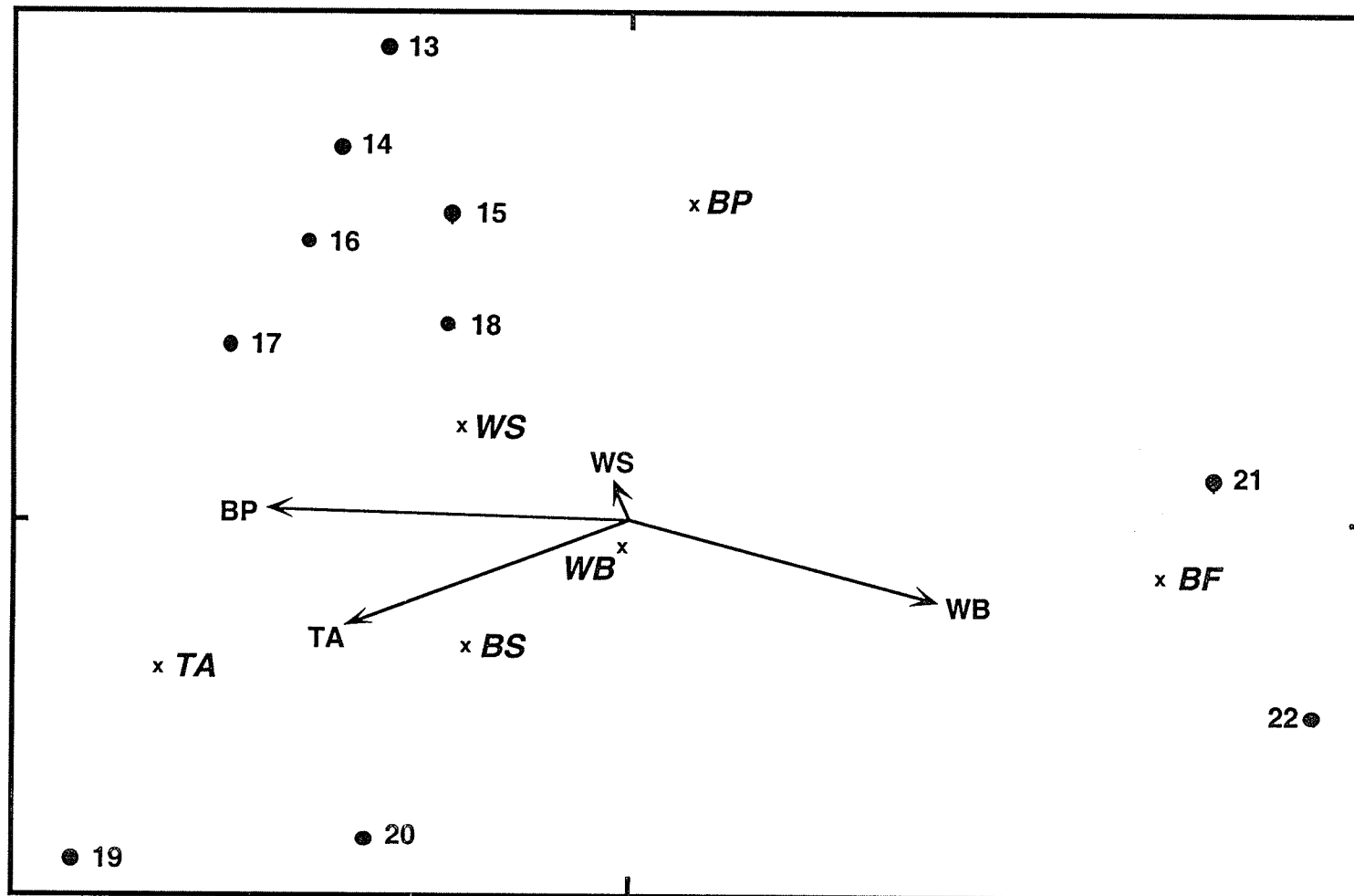


Figure 4.9. Canonical correspondence analysis ordination biplot of the advanced regeneration density (x) constrained by the initially-established cohort composition (vectors) of 10 balsam poplar stands. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.924$, $R_2^2 = 0.841$. The redundancy (ratio of the canonical inertia to total inertia) = $1.007/1.733 = 58.1\%$. Species codes: BF = balsam fir, BP = balsam poplar, BS = black spruce, TA = trembling aspen, WB = white birch, WS = white spruce.

nutrient-rich seepage slopes, consists of balsam poplar in mixture with lesser amounts of white birch.

Interestingly, balsam poplar advance regeneration is minimal in these stands. Advance regeneration aspen suckers occasionally reach the upper or lower canopies, but most are between 2-10 m in height (**Table 4.4**). White birch secondary suckers are occasional, and some have reached as high as the lower canopy. Non-contemporaneous white spruce are common in some stands, and many of these trees have already reached the upper or lower canopies. Balsam fir advance regeneration was found in half the stands, and occurs at extremely high densities in stands 21 and 22. Many of these trees have already reached the lower canopy.

Continuous white spruce recruitment begins 30 years following stand establishment (**Fig. 4.10**). Balsam fir recruitment is also continuous, and begins only 20 years post-fire. White birch advance regeneration peaks 50 years after stand establishment, mostly as root collar suckers. Trembling aspen suckering peaks at 80 years, generally occurring in canopy gaps.

Light availability is the most important factor determining aspen suckering success. Advance regeneration of aspen is positively associated with a poplar–aspen canopy, and negatively associated with the deep shade of balsam fir and white spruce advance regeneration (**Fig. 4.9**). When advance regeneration of aspen is observed in stands with a high conifer component, it invariably occurs in canopy ‘gaps’. Advance regeneration of white spruce is negatively associated with balsam fir advance regeneration. High balsam fir regeneration densities (stands 21 and 22) create deeply shaded conditions that restrict white spruce regeneration. Balsam fir advance regeneration is strongly influenced by distance to seed source: stands 21 and 22 are adjacent to mature balsam fir stands. White birch

TREMBLING ASPEN				WHITE BIRCH				BALSAM POPLAR			
	C	I	R		C	I	R		C	I	R
1	1.36 (0.42)	0.36 (0.15)		0.84 (0.46)				3.40 (3.33)	0.04 (0.20)		
2		0.32 (0.18)		0.08 (0.05)	0.24 (0.12)			0.04 (0.20)	0.32 (0.80)		
3		0.88 (0.39)	0.20 (0.20)			0.52 (0.40)	0.16 (0.16)			0.12 (0.44)	
4			0.36 (0.20)				0.12 (0.09)				0.32 (0.69)
5											
	6/10	8/10	4/10	3/10	4/10	2/10		9/10	6/10	3/10	

WHITE SPRUCE				BALSAM FIR			
	C	I	R		C	I	R
1	0.24 (0.10)	0.28 (0.18)				0.40 (0.20)	
2		1.88 (0.87)				2.20 (0.94)	
3	0.04 (0.04)	1.40 (0.44)				2.52 (1.16)	
4		0.80 (0.41)	0.08 (0.06)			0.96 (0.88)	
5			0.80 (0.32)				23.04 (9.88)
	4/10	8/10	4/10	0/10	5/10	4/10	

Table 4.4. Average density/100 m² of three age classes and five height classes for trembling aspen, white birch, balsam poplar, white spruce and balsam fir in 10 balsam poplar stands. Age classes are coded: C = contemporaneously established, I = intermediately established (advance regeneration), R = recently established. Height classes: 1 = >15 m, 2 = 10-15 m, 3 = 2-10 m, 4 = 0.5-2 m, 5 = < 0.5 m. The fraction of stands containing representative individuals are indicated below the corresponding age-class columns.

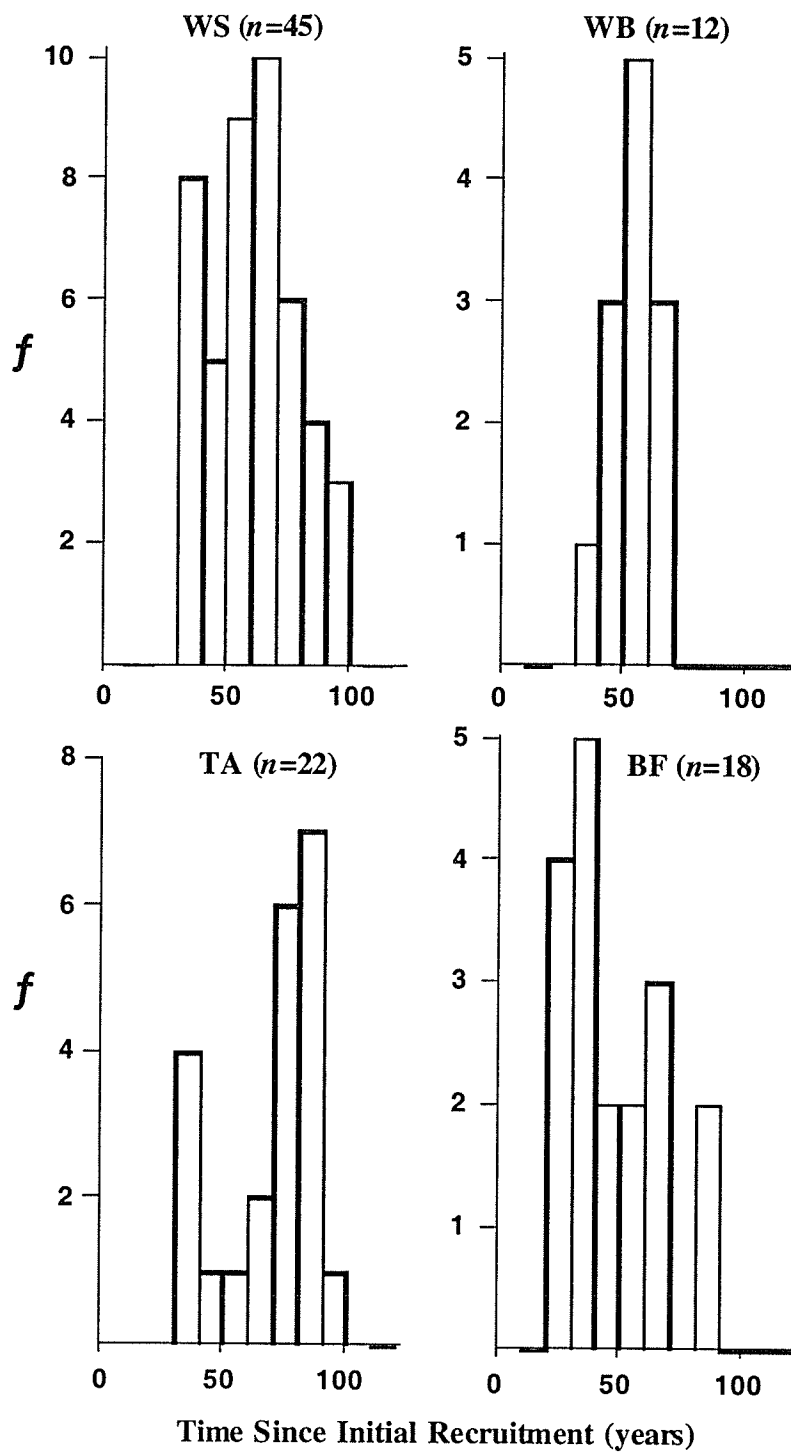


Figure 4.10. Age-class histograms of time since initial recruitment for white spruce, trembling aspen, balsam fir and white birch advance regeneration in balsam poplar stands.

regeneration in these stands is limited to root collar suckers from the bases of initial cohort trees.

The average effective species richness of the advanced regeneration cohort (3.22) is greater than that of the initial cohort (2.40) (**Table 4.3**).

4.3.2a Balsam Poplar stand dynamics

Most balsam poplar stands in the Duck Mountains are invaded by white spruce. The moist, nutrient-rich substrate of these stands appears to be highly conducive to white spruce establishment. Significant trembling aspen, white birch, balsam fir, balsam poplar and/or black spruce advance regeneration may also occur, indicating complex multiple successional pathways and reflected in the high average effective species richness of the advance regeneration cohort. If a balsam fir seed source is proximate, succession proceeds quickly to balsam fir dominance. These shorter-statured trees initially form a continuous subcanopy beneath the hardwood canopy, becoming dominant upon breakup of the initial canopy cohort. Floodplains are not invaded by conifers, however.

4.3.3 White Spruce Stand Type (n = 10)

The CCA of advance regeneration constrained by initial cohort composition for the White Spruce stand type indicates three regeneration trends (**Fig. 4.11**). Advance regeneration in stands 23-27 is dominated by balsam fir, with lesser amounts of trembling aspen, white spruce and/or white birch. The initial cohort of these stands is dominated by white spruce and white birch, with little balsam poplar or trembling aspen. Advance regeneration of white spruce is characteristic of stands 28 and 29, which have a higher proportion of trembling aspen and balsam poplar in the initial cohort. Stand 29 was the only

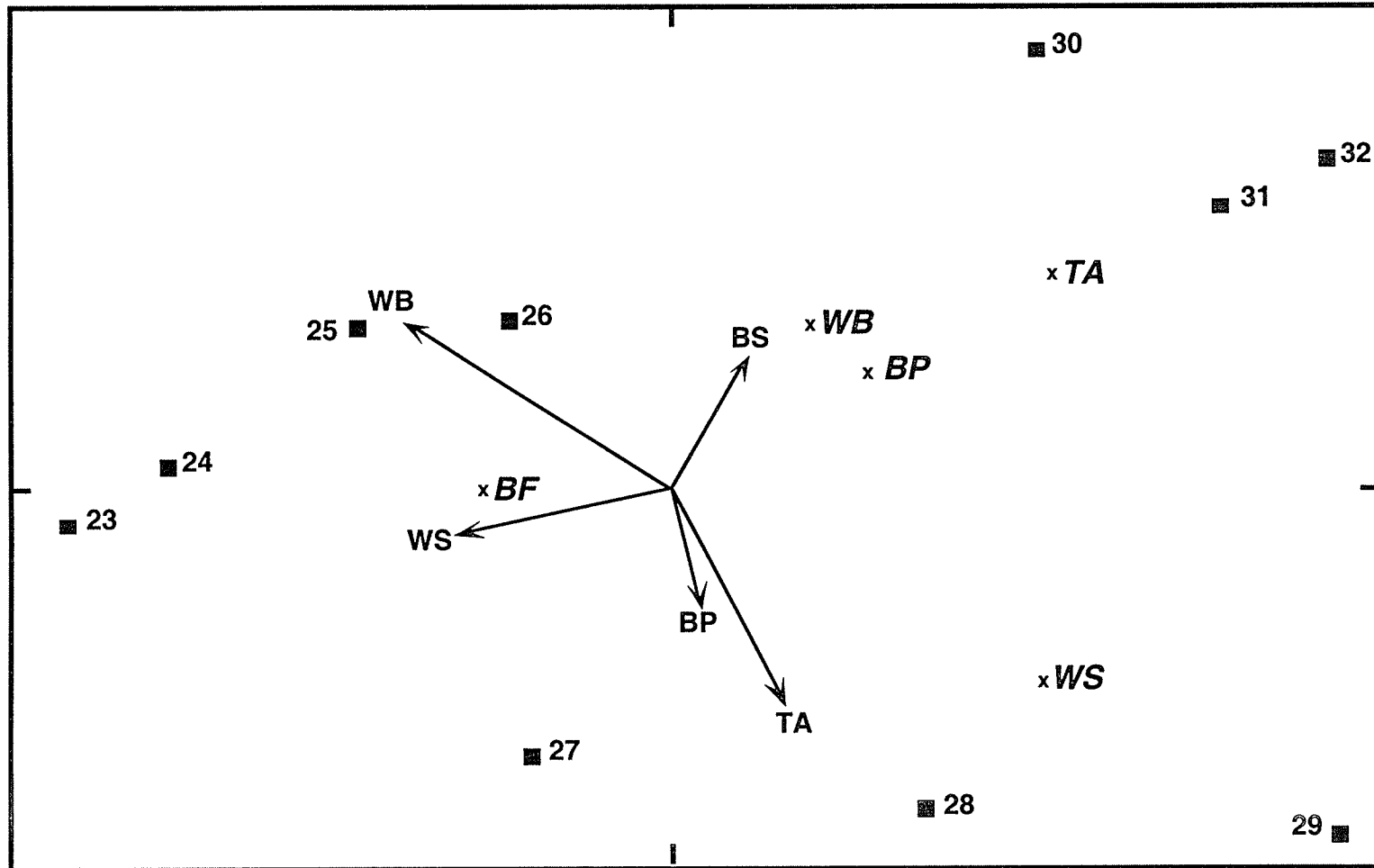


Figure 4.11. Canonical correspondence analysis ordination biplot of the advanced regeneration density (x) constrained by the initially-established cohort composition (vectors) of 10 white spruce stands. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.925$, $R_2^2 = 0.917$. The redundancy (ratio of the canonical inertia to total inertia) = $0.475/0.695 = 68.3\%$. Species codes: BF = balsam fir, BP = balsam poplar, BS = black spruce, TA = trembling aspen, WB = white birch, WS = white spruce.

white spruce stand in which no balsam fir advance regeneration was observed: there was no proximate seed source. The third regeneration trend (stands 30-32) is more complex. The advance regeneration is mixed, including trembling aspen, balsam poplar, balsam fir, white spruce and/or white birch. These stands have the lowest density of white spruce in the initial cohort.

Advance regeneration of white spruce occurs at low to moderate density, and most trees are under 10 m in height (**Table 4.5**). Balsam fir invasion has occurred in 9 of 10 stands, and in most stands a proportion of these trees have reached the upper or lower canopy. Advance regeneration aspen suckers have also reached the upper or lower canopy of many stands, at low to moderate density. White birch advance regeneration (root collar suckers) occurs at low density, and occasionally reaches the upper or lower canopy.

White spruce and balsam fir show continuous recruitment into these stands, with little or no apparent temporal delay (**Fig. 4.12**). This may be attributable to less amounts of deciduous litter, lower shrub cover, and the proximity of softwood seed sources. An initial cohort dominated by conifers may also create site micro-conditions conducive to advance conifer regeneration, by providing protection from the desiccating effects of winter winds and spring insolation while the ground is still frozen. Appreciable advance regeneration of trembling aspen does not occur until about 40 years post-fire, which coincides with the first stages of hardwood canopy self-thinning and improved light conditions. Advance regeneration of aspen is restricted to canopy 'gaps'. White birch suckering from the root collar begins about 30 years post-fire. Advance regeneration of white birch and white spruce declines sharply after 70 years post-fire, which corresponds to the increasingly shaded conditions created by a dense balsam fir canopy.

WHITE SPRUCE				BALSAM FIR			
	C	I	R	C	I	R	
1	2.00 (0.52)	0.50 (0.33)			2.54 (0.88)		
2	0.29 (0.20)	0.25 (0.15)			1.39 (0.63)		
3	0.29 (0.25)	0.71 (0.27)			6.54 (2.69)		
4		0.64 (0.57)	0.39 (0.16)		0.50 (0.20)	1.43 (0.80)	
5			0.54 (0.17)			66.50 (15.37)	
	9/10	6/10	6/10	0/10	9/10	9/10	

TREMBLING ASPEN				WHITE BIRCH			
	C	I	R	C	I	R	
1	1.50 (0.45)	0.25 (0.13)		0.21 (0.12)	0.21 (0.11)		
2		0.86 (0.37)		0.57 (0.46)	0.50 (0.16)		
3		0.50 (0.29)	0.07 (0.07)		0.32 (0.16)	0.04 (0.04)	
4			1.36 (0.56)			0.36 (0.17)	
5			3.96 (1.00)			1.71 (0.62)	
	7/10	7/10	7/10	5/10	8/10	7/10	

Table 4.5. Average density/100 m² of three age classes and five height classes for white spruce, balsam fir, trembling aspen and white birch in 12 white spruce stands. Age classes are coded: C = contemporaneously established, I = intermediately established (advance regeneration), R = recently established. Height classes: 1 = >15 m, 2 = 10-15 m, 3 = 2-10 m, 4 = 0.5-2 m, 5 = < 0.5 m. The fraction of stands containing representative individuals are indicated below the corresponding age-class columns.

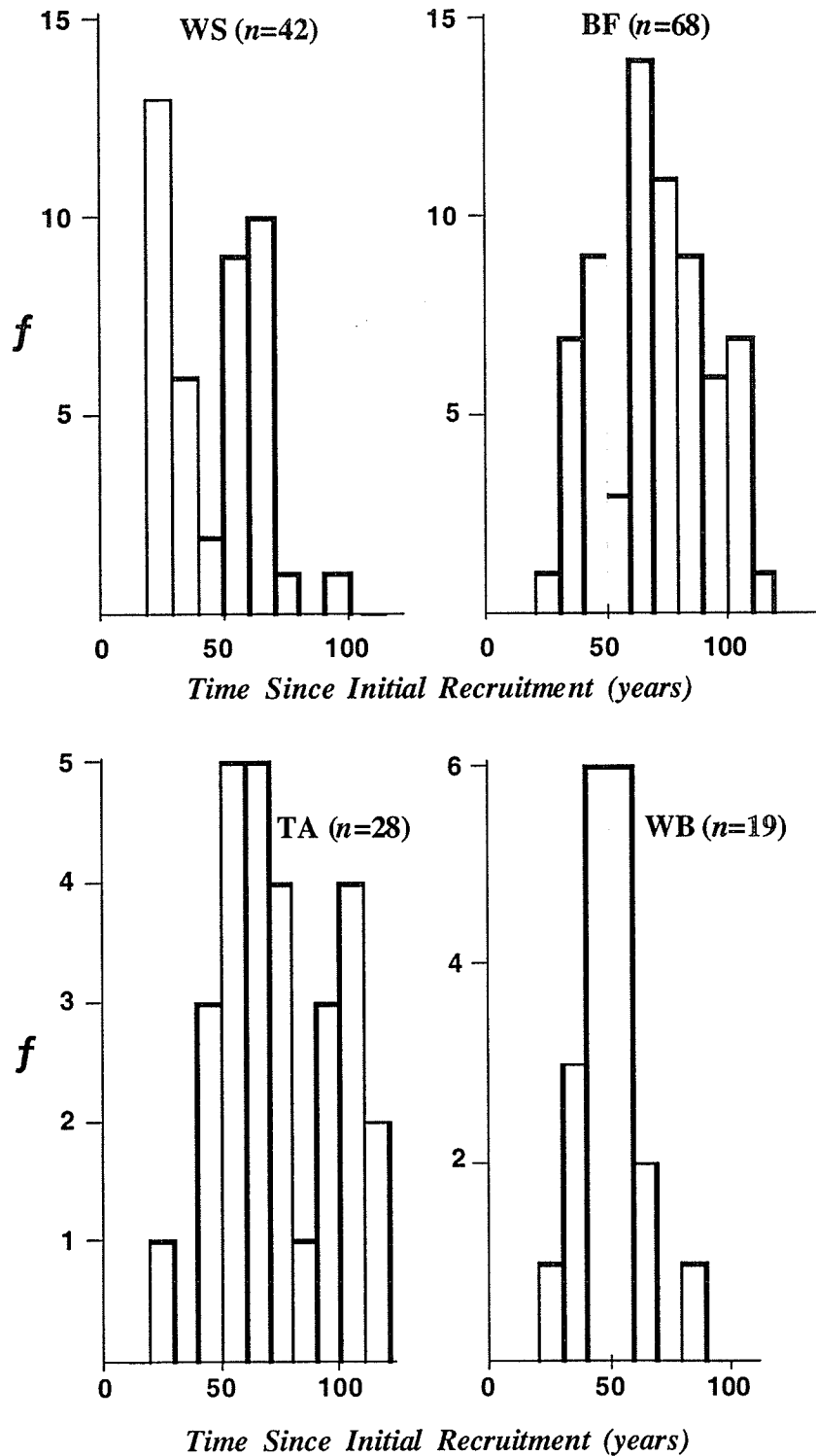


Figure 4.12. Age-class histograms of time since initial recruitment for white spruce, trembling aspen, balsam fir and white birch advance regeneration in white spruce stands.

As in other stand types, light availability is the critical factor controlling aspen advance regeneration. Aspen regeneration is negatively associated with both higher conifer abundance in the initial cohort and higher regeneration of balsam fir (**Fig. 4.11**). Balsam fir advance regeneration occurs in all but one stand, and is highest in stands where initially-established white spruce densities are greatest. Balsam fir regeneration appears to deter white spruce recruitment: the two species are negatively associated, and white spruce advance regeneration is limited to stands with a higher hardwood abundance (**Fig. 4.11**). White birch root collar suckering occurs in 8 of the 9 stands that had initial birch establishment.

The average effective species richness of the advanced regeneration cohort (2.47) is less than that of the initial cohort (3.21) (**Table 4.3**). Of the four stand types for which effective species richness was calculated, this is the only stand type in which this occurred.

4.3.3a White Spruce stand dynamics

The initial cohort of these stands is typically a codominant mixture of white spruce and trembling aspen, with white birch occasionally present as well. These stands are generally adjacent to unburned areas that serve as a proximate seed source for rapid post-fire establishment of white spruce. This stand type is therefore most commonly encountered in the uplands of the Duck Mountains where numerous lakes and wetlands, and a hummocky physiography, result in natural fire barriers (Heinselman 1996). Balsam fir advance regeneration in these stands is often very high, and many of these trees have already reached the lower canopy. Balsam fir often forms a dense impenetrable subcanopy, minimizing ungulate herbivory and creating deeply shaded conditions that greatly reduce shrub cover and advance regeneration of other species. Trembling aspen sucker prolifically in these stands, but mortality is high. However, suckers occurring in 'gaps' grow rapidly and will

perpetuate trembling aspen in these stands, albeit at low density. The deeply shaded conditions of these stands (created by a dense balsam fir subcanopy) greatly limits white spruce advance regeneration. The exception is stands with a higher initial density of trembling aspen, which generally have less balsam fir regeneration and higher white spruce regeneration.

Late-successional forests of this stand type are typically characterized by a balsam fir canopy punctuated by occasional trembling aspen (from suckers) and white birch (from root collar sprouts), with an open 'super-canopy' of very old white spruce and white birch (e.g. stand 57, which occurs on Baldy Mountain). When a balsam fir seed source is distant (e.g. stand 29), regeneration is dominated by trembling aspen suckering and white spruce advance recruitment. Older forests of this type have a complex, multi-aged mixed softwood–hardwood canopy. Long-lived white spruce are present in the canopy along with secondarily recruited aspen, white spruce, balsam fir (initially at low density) and white birch.

4.3.4 Jack Pine Stand Type (n = 13)

The CCA of advance regeneration constrained by initial cohort composition for the Jack Pine stand type indicates four major regeneration trends (**Fig. 4.13**). Stands 33 and 34 have an initial cohort of jack pine and black spruce that forms a very dense closed canopy. Advanced recruitment consists of minor amounts of white spruce, black spruce, white birch and aspen. Stands 35-40 have an initial mixed cohort of jack pine and trembling aspen. Advance regeneration of white birch (from seed) characterizes these stands, with lesser amounts of trembling aspen. Conifer recruitment is limited, but may include balsam fir, black spruce, and/or white spruce. Stands 41-43 have a moderately dense initial cohort of jack pine, often in mixture with black spruce. Advance regeneration is primarily to balsam

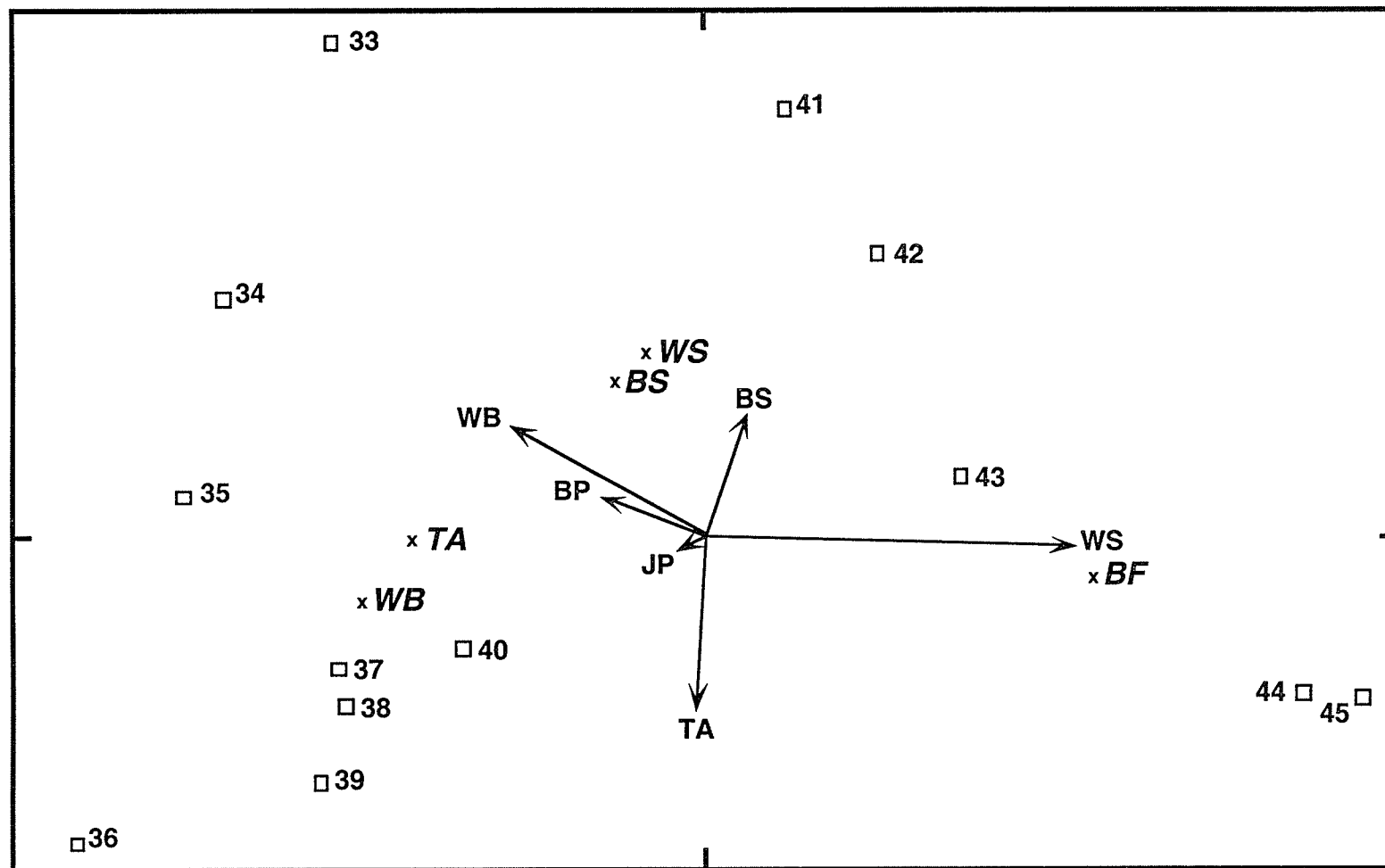


Figure 4.13. Canonical correspondence analysis ordination biplot of the advanced regeneration density (x) constrained by the initially-established cohort composition (vectors) of 13 jack pine stands. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.957$, $R_2^2 = 0.841$. The redundancy (ratio of the canonical inertia to total inertia) = $0.684/0.926 = 73.9\%$. Species codes: BF = balsam fir, BP = balsam poplar, BS = black spruce, TA = trembling aspen, WB = white birch, WS = white spruce.

fir, but black and white spruce may also occur. The initial cohort in stands 44 and 45 is codominated by jack pine and white spruce. Dense balsam fir advance regeneration is characteristic of these stands.

Advance regeneration of white birch, generally from seed, occurs in 9 of 13 stands and often reaches the lower canopy (**Table 4.6**). Balsam fir has recruited at moderate density in many stands, but most of these trees are < 10 m in height. Advance regeneration of black spruce and white spruce occurs at low density, and most trees are < 10 m in height. Aspen suckering is common in most stands, and many individuals have already reached the lower canopy.

Advance regeneration of aspen peaks at approximately 60 years post-fire (**Fig. 4.14**). Significant white birch recruitment is delayed by about 40 years, which coincides with jack pine self-thinning and thus increased availability of rotting log seedbeds. Black spruce recruitment is generally delayed until 60 years post-fire, while balsam fir advance regeneration is delayed by about 50 years. By contrast, white spruce exhibits continuous and immediate recruitment, albeit at very low densities.

Jack pine stands on north and east-facing slopes were found to have abundant white birch advance regeneration from seed: the cooler microclimate of these sites may be conducive to white birch establishment. Balsam fir advance regeneration in jack pine stands is highest along lakeshores, particularly if a proximate seed source is present. The moister conditions near watercourses, wetlands and lakes may promote balsam fir recruitment in jack pine stands. White spruce advance recruitment is low in most jack pine stands, and appears to be unrelated to seed source proximity. Substrate conditions (coarse-textured acidic soils of lower nutrient status) may limit white spruce recruitment into these stands. Edaphic factors may also influence black spruce regeneration: recruitment is much higher in

WHITE BIRCH				BALSAM FIR				BLACK SPRUCE			
	C	I	R		C	I	R		C	I	R
1	0.25 (0.13)	0.11 (0.07)			0.28 (0.20)				0.69 (0.21)		
2	0.19 (0.09)	2.36 (0.76)			1.33 (0.55)				1.14 (0.44)	0.33 (0.14)	
3		3.03 (0.81)	0.53 (0.23)		9.39 (2.88)				0.64 (0.42)	0.81 (0.39)	
4			0.42 (0.36)		1.78 (0.65)	0.53 (0.27)				0.33 (0.28)	0.11 (0.07)
5			0.75 (0.31)		0.53 (0.38)	37.81 (14.97)					0.92 (0.32)
	7/13	9/13	8/13		0/13	9/13	10/13		8/13	6/13	5/13

WHITE SPRUCE				TREMBLING ASPEN			
	C	I	R		C	I	R
1	0.47 (0.23)				2.11 (0.45)	0.72 (0.22)	
2	0.47 (0.22)	0.17 (0.07)			1.83 (0.60)		
3	0.14 (0.08)	0.58 (0.20)			0.69 (0.19)	0.17 (0.08)	
4		0.03 (0.03)	0.25 (0.18)				0.53 (0.21)
5			0.67 (0.21)				2.33 (0.55)
	5/13	7/13	6/13		10/13	12/13	12/13

Table 4.6. Average density/100 m² of three age classes and five height classes for white birch, balsam fir, black spruce, white spruce and trembling in 13 jack pine stands. Age classes are coded: C = contemporaneously established, I = intermediately established (advance regeneration), R = recently established. Height classes: 1 = >15 m, 2 = 10-15 m, 3 = 2-10 m, 4 = 0.5-2 m, 5 = < 0.5 m. The fraction of stands containing representative individuals are indicated below the corresponding age-class columns.

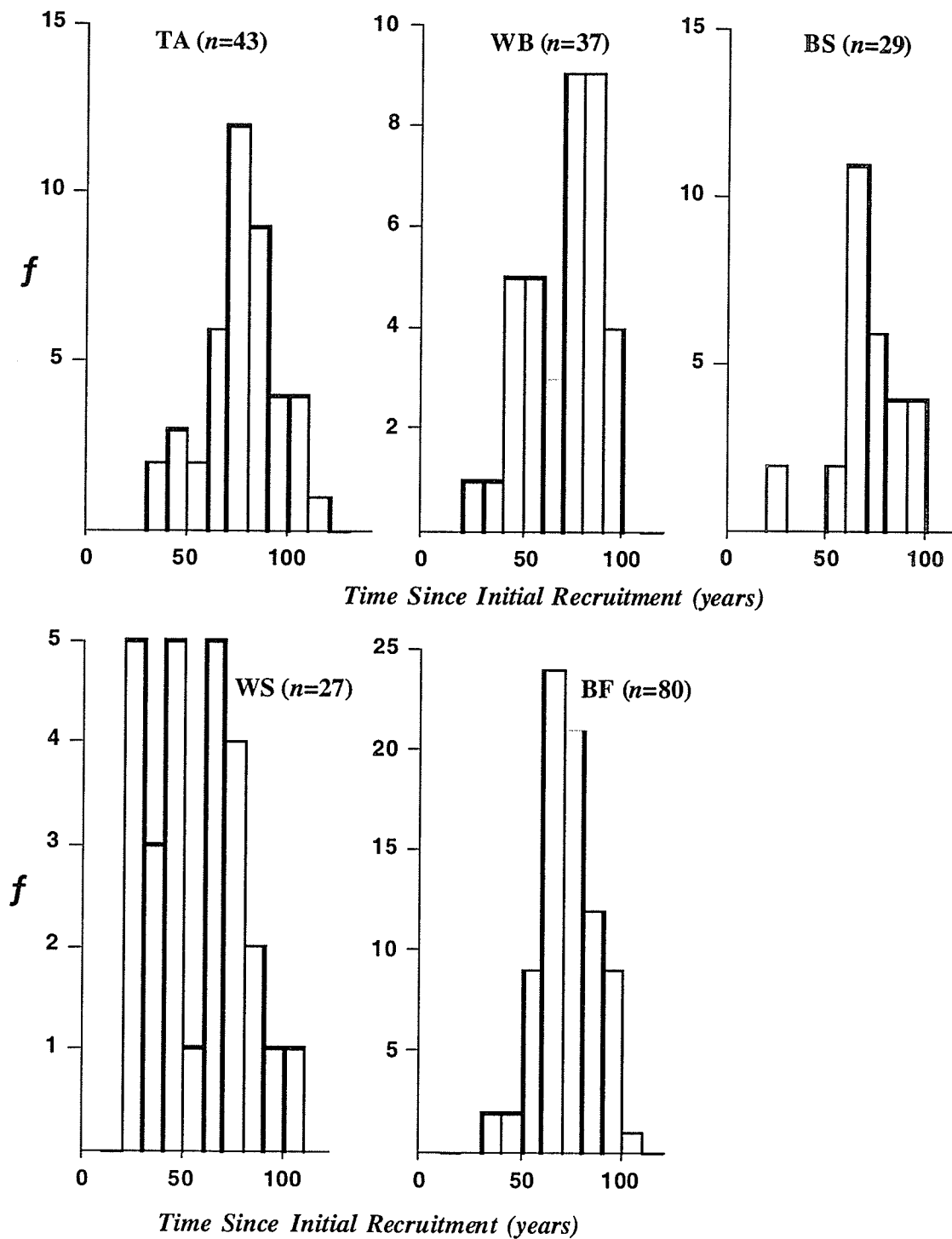


Figure 4.14. Age-class histograms of time since initial recruitment for white spruce, trembling aspen, balsam fir, white birch and black spruce advance regeneration in jack pine stands.

stands with soil pH < 6.0. Previous studies have found that black spruce recruitment is higher on 'poorer' sites, which may reflect decreasing levels of interspecific competition (Kneeshaw & Bergeron 1996). As in the previous stand types, light conditions determine aspen suckering success: suckering is limited in dense, conifer-dominated stands, but prolific under less dense mixed hardwood-softwood canopies and in canopy 'gaps'.

Average effective species richness of the advance regeneration cohort (3.45) is only slightly higher than that of the initial cohort (3.31) (**Table 4.3**). Among the four stand types for which it was calculated, effective species richness was highest in jack pine stands for both the initial and advanced regeneration cohorts.

4.3.4a Jack Pine stand dynamics

Most commonly, trembling aspen or black spruce codominate with jack pine in the initial cohort of these stands. Advance regeneration is highly variable and appears to reflect differences in seed source proximity, physiography, edaphic factors, and initial post-fire stand composition. Site conditions appear to be particularly important in determining recruitment patterns and stand dynamics. For example, advance regeneration of balsam fir, white spruce, and black spruce is lowest on rapidly-drained sandy soils. Balsam fir advance regeneration occurs in most jack pine stands, but is a significant component only in moist sites along lakeshores where white spruce is present in the initial cohort. These stands will develop into balsam fir forest with a secondary white spruce component. Stands with significant amounts of black spruce in the initial cohort are typically very dense, and become increasingly dominated by black spruce as shorter-lived jack pine individuals senesce. Advance regeneration in these dense stands is virtually non-existent. Stands occurring on northern and eastern slopes will become increasingly dominated by white birch as the initial jack pine cohort senesces, but low levels of advance regeneration by conifers (particularly

black spruce and balsam fir) will ensure a diverse mixed deciduous–coniferous canopy at later successional stages. In stands initially dominated by jack pine and trembling aspen, low levels of advance regeneration through aspen suckering and softwood recruitment (balsam fir, black spruce and white spruce) will result in a complex, multi-aged canopy as succession proceeds.

4.3.5 Black Spruce Stand Type ($n = 5$)

Black spruce stands on mineral soils are very dense and have no or limited amounts of advance regeneration. These stands ($n = 3$) are characterized by a dense canopy dominated by black spruce, often with some jack pine also present. Trembling aspen or white birch may also be present, but generally as only one or two individuals per stand. When present, advance regeneration is limited to very occasional black spruce that remain in an extremely suppressed state (**Table 4.7**). Most of these individuals established at least 80 years following stand establishment, typically in small canopy ‘gaps’.

Two black spruce stands on organic peat substrates were also sampled. These stands are characterized by open, short statured canopies dominated by black spruce. Tamarack may also be encountered. Advance regeneration is primarily continuous black spruce layering, but saplings of tamarack and balsam fir may also be present at low abundance. Balsam fir grows very slowly under these conditions and does not reach the canopy.

BLACK SPRUCE

	<i>C</i>	<i>I</i>	<i>R</i>
1	16.77 (6.26)		
2	6.11 (3.02)		
3	1.78 (2.52)	1.56 (0.69)	
4		0.22 (0.38)	
5			0.67 (0.58)
	3/3	3/3	2/3

Table 4.7. Average density/100 m² of three age classes and five height classes for black spruce in 3 black spruce stands on mineral soil. Age classes are coded: C = contemporaneously established, I = intermediately established (advance regeneration), R = recently established. Height classes: 1 = >15 m, 2 = 10-15 m, 3 = 2-10 m, 4 = 0.5-2 m, 5 = < 0.5 m. The fraction of stands containing representative individuals are indicated below the corresponding age-class columns.

4.3.5a Black Spruce stand dynamics

Dense black spruce stands are characteristic of poorly-drained, flat lowlands of low nutrient status. Two sub-types are recognized:

1. Mineral Substrates: These stands generally occur on flat, poorly-drained lowlands. Black spruce and jack pine establish at very high densities, but jack pine rapidly thins and is a minor component by age 80-100. A dense feathermoss mat is characteristic of the understory, but in very dense stands even feathermosses are shaded out. Advance regeneration is very limited, and these stands will continue to be dominated by the long-lived black spruce into the foreseeable future.

2. Organic Substrates: These stands occur on organic peat substrates that may be 1 m or more in depth. The water table is usually within 50 cm of surface. Black spruce is the dominant post-fire species, with tamarack occurring at low abundance in poor fens. The understory is dominated by feathermosses, peatmosses, and ericaceous shrubs. Stand density is much lower than on mineral substrates, resulting in lower branch retention and active vegetative layering. Layering will help perpetuate black spruce over the long term. Advance recruitment of tamarack may occur in older stands. As organic peat accumulates, the surface becomes drier and balsam fir may establish. These trees grow very slowly, however, and their root systems remain close to the surface. Black spruce forms an edaphic climax in these sites, with tamarack as a minor secondary component.

4.4 Stand Dynamics – Role of the Advance Regeneration Cohort

Using static stand structures and chronosequencing to infer forest succession trends has been criticized by a number of researchers. Johnson et al. (1994) note that “forest succession cannot be viewed as simply a sequence of species replacements based on shade tolerance ... canopy replacement can only occur if the dynamics (recruitment and mortality rates) of the understory cohorts are such that they have a significant probability of reaching the canopy”. In studying boreal forest succession it is therefore critical to establish whether, and if so to what extent, the understory cohort (advance regeneration) reaches the canopy. In our study, we specifically examined this by summarizing the vertical (height) distribution of advance regeneration trees of various species in the five initial stand types (Tables 4.1, 4.4-4.7). Our results reveal that individual trees of the advance regeneration cohort are often found in the upper and lower canopies (> 10 m in height), indicating that successful recruitment of understory cohorts into the canopy does occur. The extent of advance regeneration recruitment into the canopy varies by species and across stands. Advance

regeneration in black spruce and mixed jack pine–black spruce stands is virtually non-existent. These stands are very dense, and deeply shaded, severely limiting advance regeneration recruitment. These stands are most similar to the mixed lodgepole pine–Engelmann spruce stands studied by Johnson et al. (1994). Most other stands in our study showed evidence of successful advance regeneration recruitment into the canopy, in agreement with studies of mixedwood stands in Québec (Bergeron 2000). Trembling aspen advance regeneration (from secondary root suckers) is occurring in many stands, and is particularly prolific in canopy ‘gaps’. While aspen sucker mortality is high (attributable to both light competition and ungulate herbivory), our results indicate that many advance regeneration suckers have reached the canopy to perpetuate the species in these stands (c.f. Bergeron 2000). White birch advance regeneration (from root collar suckers) shows a similar trend, but balsam poplar advance recruitment is very limited. Our results also suggest continuous recruitment of white spruce into many stands. While some of the white spruce advance regeneration remains in a highly suppressed state, many of these trees have already reached the canopy (e.g. **Tables 4.1 and 4.4**). Successful secondary recruitment of balsam fir has also occurred in many stands, particularly in the White Spruce and Jack Pine stand types (**Tables 4.5 and 4.6**).

4.5 Mixedwood Stand Dynamic Model

A synoptic model of forest dynamics in Duck Mountain boreal mixedwood stands is presented in **Fig. 4.15**. The model incorporates the Trembling Aspen, Balsam Poplar and White Spruce stand types, as well as mixed initial cohort jack pine–trembling aspen stands within the Jack Pine stand type. Mixed jack pine–black spruce stands, and stands within the Black Spruce stand type, are not included. Our model incorporates both disturbance (light vs. catastrophic fire, timber harvesting, and gap dynamics) and conifer seed source proximity in explaining the long-term dynamics of mixedwood forests at the ecosite scale.

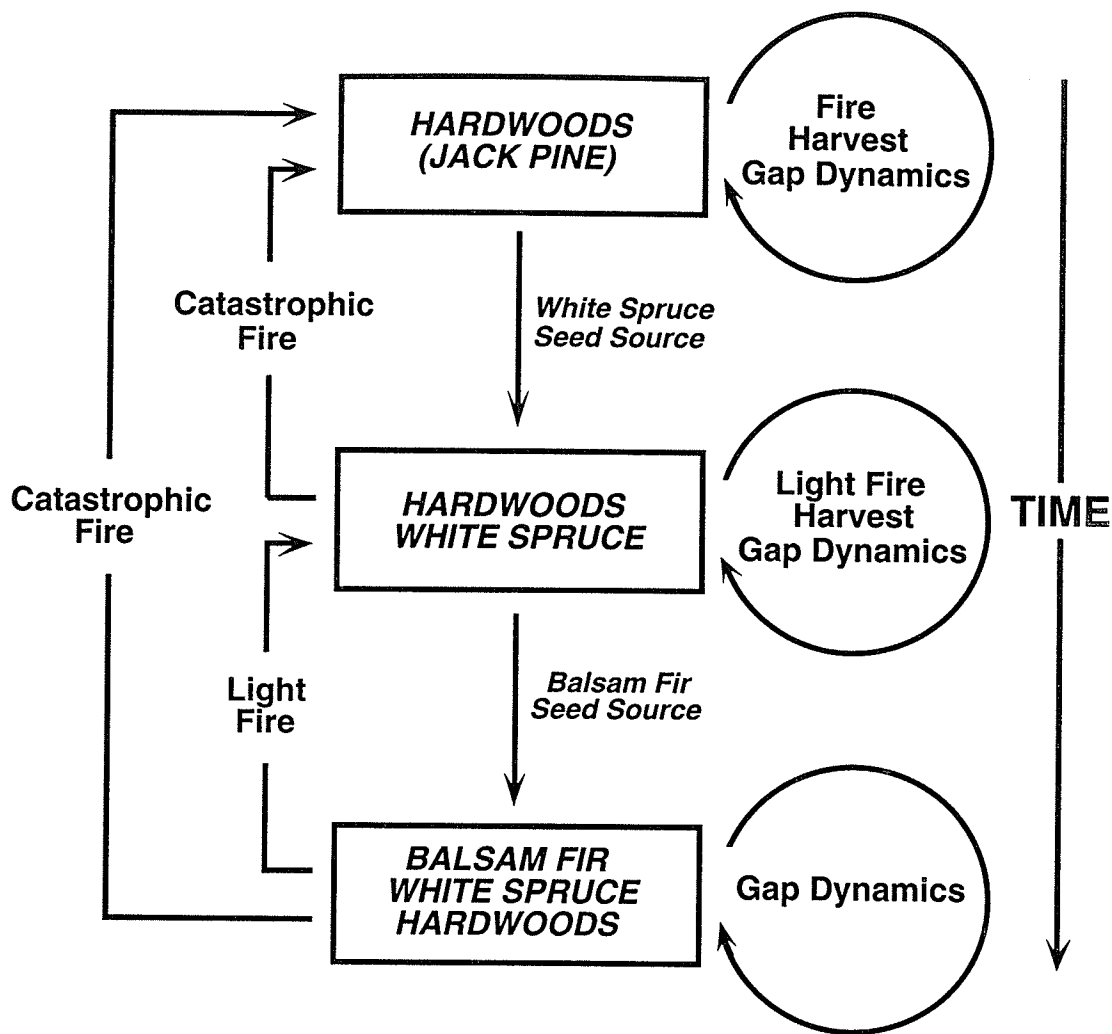


Figure 4.15. A synoptic forest succession model for boreal mixedwood stands in the Duck Mountains, Manitoba. Following catastrophic fire, stands are generally dominated by vegetative hardwood regeneration (trembling aspen, balsam poplar, and/or white birch). These stands are self-replacing under recurrent light or catastrophic fire, clear-cut harvesting, and canopy gap dynamics. Jack pine may also occur with trembling aspen following catastrophic fire, but the species is not self-perpetuating. Both hardwood-dominated and jack pine stands can develop into mixed hardwood - white spruce stands given a proximate white spruce seed source. Hardwood - white spruce stands can reestablish after light fires that expose mineral soil but preserve a proximate white spruce seed source. Selective white spruce harvest and gap dynamics will also result in the perpetuation of these stands, but catastrophic fire that eliminates proximate seed sources will result in reversion to hardwood dominance. Hardwood - white spruce stands can develop a canopy component of balsam fir, given a proximate balsam fir seed source. A mixed balsam fir - white spruce - hardwood canopy is maintained through gap dynamics. Balsam fir rarely establishes immediately post-fire in Duck Mountain, and light fire will result in reversion to a hardwood - white spruce forest. Catastrophic fires that eliminate proximate white spruce seed sources will result in reversion to hardwood dominance.

Following a catastrophic fire, mixedwood stands are dominated by hardwoods (trembling aspen, balsam poplar, and white birch), sometimes in mixture with jack pine. In the absence of a white spruce seed source, the hardwood component of these stands is maintained through timber harvesting or gap dynamic processes. Recurrent fire will also perpetuate these stands: if catastrophic fires are regular, jack pine may also occur.

Recruitment of white spruce into hardwood stands will occur provided there is a proximate seed source. Our results indicate that recruitment patterns of white spruce into hardwood stands are variable and sporadic, which is in general agreement with studies from central Alberta (e.g. Lieffers et al. 1996). Contemporaneous, heavy post-fire recruitment is characteristic of sites with exposed mineral soil substrates and a proximate seed source. Such stands have a short period of white spruce recruitment, however, since the dense initial canopy cohort casts a deep shade that limits white spruce advance regeneration. By contrast, sites having poor post-fire seedbed conditions and a distant seed source have continuous but delayed and sporadic recruitment, resulting in a multi-aged advance regeneration cohort. In the absence of a proximate balsam fir seed source, mixed hardwood–white spruce stands are maintained by smaller, lighter fires (i.e. exposing mineral soil, but sparing some seed trees), timber harvesting, and gap dynamic processes. A catastrophic wildfire will result in these stands reverting to hardwood dominance (possibly in mixture with jack pine).

Balsam fir recruitment into mixed hardwood–white spruce stands will occur provided there is a proximate seed source. Our results indicate that recruitment patterns of balsam fir are quite variable. Very heavy recruitment is associated with high canopy cover of white spruce, mesic site conditions, and a nearby seed source. Recruitment is lighter and more sporadic when hardwoods dominate the canopy, in xeric sites, and when the seed source is more distant. Mixed balsam fir–white spruce–hardwood stands are maintained through gap dynamic processes, particularly recurrent spruce budworm outbreaks. Although hardwood

abundance in these stands declines over time, small-scale gap dynamic processes will maintain the hardwood component for many years. Smaller, lighter fires will result in these stands reverting to mixed hardwood–white spruce forest, while a catastrophic wildfire will result in reversion to hardwood dominance (possibly in mixture with jack pine).

Our model is in broad agreement with long-term stand dynamic processes described for the Lake Duparquet region of boreal Québec (Bergeron 2000). Mixedwood stands in this region pass through three successive waves: initial dominance of hardwoods (primarily trembling aspen and white birch), followed by mixed hardwood–white spruce stands, and ending with coniferous stands dominated by balsam fir and white cedar. Post-fire recruitment of white spruce and balsam fir is continuous, but very often large increases in abundance are not seen until the early-colonizing individuals mature and produce seed (Bergeron & Charron 1994). At each stage, there is a decrease in the hardwood component and a concomitant increase in conifers (Bergeron 2000). However, the patchy distribution of conifer regeneration and limitations on the ability of conifers to rapidly fill canopy gaps ensures hardwood occurrence even in late-successional forest stages. The oldest stands are driven by gap dynamic processes, particularly recurrent outbreaks of spruce budworm whose primary host is balsam fir. Achuff and La Roi (1977) note that, compared to white spruce, balsam fir has a shorter lifespan, establishes at a higher rate, and has a much higher sapling mortality. These differences in life-history attributes serve to maintain the presence of both species in late-successional forest in the northern Alberta highlands.

Our model recognizes the importance of conifer seed source proximity in driving boreal forest stand dynamics. Bergeron and Dubuc (1989) noted that stands tend to converge towards shade-tolerant and late-successional species such as balsam fir, eastern white cedar and/or black spruce (depending on site moisture conditions), but such convergence does not

occur if seed sources for shade-tolerant species are not present or abundant (see also Bergeron & Charron 1994; Bergeron & Dansereau 1993).

4.6 Disturbance and Stand Dynamics

Our results reveal that landscape-scale succession in the Duck Mountains does not result in convergence to a single self-perpetuating 'climax' forest community. Advance regeneration, and hence stand dynamics, is variable and appears to reflect differences in initial post-fire stand composition, seed source proximity, physiography, edaphic factors, and other site conditions. Even among stands with similar post-fire stand composition, successional trajectories can vary depending on site conditions and subtle differences in initial composition. Historically, many stands likely burned with sufficient frequency that canopy succession did not occur, resulting in long-term reestablishment of pre-fire canopy composition. In the absence of a catastrophic fire, the initial post-fire cohort composition may be retained through gap dynamic processes. More often, however, recruitment of other species along with regeneration of the initial cohort species results in increased canopy diversity and complexity over time. Occasionally the initial cohort may be completely replaced by late-successional species. All three of the theoretical succession models proposed by Connell and Slatyer (1977) are relevant to forest succession in the Duck Mountains. The 'inhibition' model holds for dense black spruce stands: advance regeneration is inhibited by the dense, dark canopy characteristic of these stands (c.f. Johnson et al. 1994). The 'tolerance' model is appropriate for most mixedwood stands: for example, white spruce often recruits beneath aspen canopies but remains in a somewhat suppressed state until canopy breakup (Lieffers et al. 1996; Bergeron 2000). The 'facilitation' model may hold for balsam fir recruitment into mixedwood stands: our results indicate that balsam fir recruitment is strongly correlated with the presence and abundance of white spruce in the canopy.

Historical fire frequency plays a critical role in determining boreal forest stand structure and composition. Throughout much of the western boreal forest the fire cycle is less than 100 years, which is well within the lifespan of pioneer tree species. This short fire cycle tends to “stabilize forest composition so that the pre-fire forest will predominate after fire” (Dix & Swan 1971). Fire-adapted species such as trembling aspen, balsam poplar, white birch, jack pine and black spruce tend to dominate such landscapes, while later-successional species such as white spruce and especially balsam fir are far less common. Regular wildfire disturbance normally precludes the development of self-replacing climax communities (Bergeron & Dubuc 1989). Recurrent fires also favour species with vital attributes and life-history characteristics that are best adapted to recurrent, large-scale disturbance. These include cone serotiny, vegetative or clonal growth, rapid growth following disturbance, high density at establishment (followed by extensive self-thinning), a short lifespan and shade-intolerance.

In regions of lower fire frequency, and in areas where active fire suppression is practiced, gap dynamic processes caused by insect pests (particularly spruce budworm), fungal pathogens, and windthrow become increasingly important factors in boreal stand dynamics (Bergeron 2000). Thus, there is a shift from large, frequent synchronous disturbance regimes (recurrent catastrophic wildfires within the normal lifespan of pioneer tree species) to small, infrequent and asynchronous disturbances. In the absence of fire, boreal forest succession results in increasing conifer abundance (Bergeron & Bouchard 1993). Even in the absence of fire, however, the creation of forest gaps perpetuate mixed conifer–hardwood stands for a considerable period (Bergeron & Charron 1994; Bergeron & Dansereau 1993).

In northern Minnesota boreal forest, fire suppression since 1900 has resulted in “widespread successional changes” (Hienselman 1973). Prior to 1900, high fire

frequencies maintained a landscape dominated by extensive, even-aged stands of jack pine and trembling aspen. Since the advent of fire suppression, these even-aged stands of pioneer species have developed into old-growth, uneven-aged mixed stands of black spruce, balsam fir, white birch and eastern white cedar. This 'climax' vegetation is not stable, however, since frequent small-scale disturbances (e.g. spruce budworm outbreaks, wind breakage and uprooting) serve to continually alter forest dynamics. These small canopy openings (10-30 m across) influence the direction of succession in older stands (Frelich & Reich 1995). At the regional or 'ecosite' scale (1-16 ha), gap-dynamic succession results in convergence toward stands of mixed composition, but at the smaller 'plot' scale (0.01-0.1 ha) succession diverges toward monodominant stands of different species. The result is a landscape consisting of different patches that are continually changing in terms of their relative size, position and geography in response to disturbance regimes (Pickett 1976; Kenkel et al. 1997a). Vegetation development at the landscape level is driven by disturbance history and episodic stochastic events, with the result that successional dynamics are attributable to the "vagaries of seed production, weather, insects and disease" (McCune & Allen 1985).

The current canopy composition observed in Duck Mountain, and the potential for canopy change, is a reflection of local physiography and site disturbance history. For example, the complex hummocky terrain characteristic of the Duck Mountain uplands acts as a barrier to wildfire spread, such that even the most catastrophic fires will skip small stands (e.g. leeward slopes and areas adjacent to wetlands and lakes, see Heinselman 1973). In addition, mesoclimatic conditions in the eastern uplands of Duck Mountain are likely similar to those in the eastern upland of Riding Mountain, where higher precipitation and cooler conditions likely act as impediments to the rapid spread of wildfires from the warmer and drier mesoclimatic regions to the west and south (Caners & Kenkel 1998). Later-successional conifers such as balsam fir and white spruce are favoured under such conditions, since they must re-invade early-successional stands from adjacent unburned

areas (Bergeron et al. 1999). Pure hardwood stands, on the other hand, are located mainly on the moderately well-drained, low-relief slopes of Duck Mountain where fire barriers are absent. White spruce and balsam fir seed sources are often distant, and this is reflected in relatively low densities of recruitment of these species into many aspen stands. Changes in fire return frequency and/or severity resulting from fire suppression or climate change will result in a corresponding change in the structure and composition of forest stands.

Recurrent, large wildfires that swept relatively unimpeded across the lower slopes of the Duck Mountains likely played an important role in perpetuating the Trembling Aspen stand type. Regular and recurrent wildfires promoted post-fire suckering while largely eliminating refugia of late-successional conifers such as white spruce and balsam fir. The combination of settlement-era fires and widespread selective logging of white spruce have also contributed to the monodominant nature of trembling aspen stands in areas adjacent to agricultural land (cf. Weir & Johnson 1998).

Most balsam poplar stands are located within the matrix of trembling aspen stands on the north, west, and south slopes of Duck Mountain. The richer soils and moister conditions in these stands promote rapid invasion by white spruce and/or balsam fir, so these areas tend to become 'islands' of conifer in a landscape largely dominated by nearly-pure deciduous stands. As such, unburned balsam poplar stands likely act as an important seed source for later-successional conifers into nearby aspen burns or clearcuts.

Balsam fir abundance is increasing in most white spruce stands. An continued increase in balsam fir abundance over large portions of the Duck Mountain uplands is likely given increased fire cycles. A corresponding increase in the abundance and or severity of spruce budworm outbreaks may result. Complete replacement by balsam fir is not expected to occur in most stands since gap dynamics (including spruce budworm), the long-lived nature

of white spruce, and vegetative regeneration by hardwoods will promote the perpetuation of mixed-species ecosites (Achuff & La Roi 1977; Bergeron 2000).

Most jack pine ecosites in the Duck Mountains are patchy mixtures of jack pine and trembling aspen, with high density phases of jack pine alternating with dense groves of trembling aspen. In general, these stands are becoming increasingly diverse as jack pine senesces and is removed from the canopy. A dramatic decline in jack pine abundance in the Wellman Lake area is expected in the absence of fire. Most stands originated following the 1885 fire, and these trees are nearing the end of their life-span (while individual jack pine trees can live for 150 years or more, in competition with other species most trees senesce by 100-120 years of age). The jack pine seed source in this area will therefore disappear within the next 40 years unless another fire occurs (cf. Heinselman 1996). Trembling aspen would likely dominate in the absence of jack pine. Jack pine stands are common at the eastern end of the 1961 burn north of the Blue Lakes. Early successional jack pine communities will therefore be represented in the Duck Mountains for some time.

Black spruce is a slow-growing but comparatively long-lived species that generally establishes at very high densities in moist, poorly drained lowlands on mineral and organic peat substrates. Few other species can survive these fire-prone, nutrient-impooverished, anoxic and often water-logged substrates. In the absence of a dramatic decrease in the fire cycle of the region, black spruce stands will continue to dominate the poorly drained lowlands and flats of Duck Mountain.

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APPENDICES

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APPENDIX A

Table A1. Frequency, average cover, and standard deviation of common shrub species in 16 Trembling Aspen stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Rosa acicularis</i>	1.00	5.27	5.88
<i>Corylus cornuta</i>	0.88	31.95	26.96
<i>Salix spp.</i>	0.81	2.76	2.86
<i>Amelanchier alnifolia</i>	0.81	2.11	2.53
<i>Prunus virginiana</i>	0.75	2.98	3.14
<i>Cornus stolonifera</i>	0.69	1.34	2.35
<i>Symphoricarpos albus</i>	0.69	1.22	1.52
<i>Rubus idaeus</i>	0.63	1.54	3.49
<i>Viburnum edule</i>	0.56	0.58	0.79
<i>Prunus pennsylvanica</i>	0.50	3.15	8.00
<i>Linnaea borealis</i>	0.50	0.20	0.36
<i>Lonicera dioica</i>	0.44	0.25	0.37
<i>Ribes triste</i>	0.44	0.18	0.25
<i>Lonicera spp.</i>	0.38	0.13	0.24
<i>Ribes oxyacanthoides</i>	0.38	0.07	0.11
<i>Alnus rugosa</i>	0.25	1.25	2.96
<i>Shepherdia canadensis</i>	0.25	0.15	0.34
<i>Acer spicatum</i>	0.19	13.98	30.36
<i>Alnus crispa</i>	0.19	9.80	21.34
<i>Viburnum opulus</i>	0.19	0.31	1.12
<i>Symphoricarpos occidentalis</i>	0.19	0.27	0.67
<i>Rhamnus alnifolia</i>	0.19	0.05	0.13
<i>Ribes lacustre</i>	0.19	0.03	0.07
<i>Diervilla lonicera</i>	0.13	0.97	3.87
<i>Craetegus chrysocarpa</i>	0.13	0.04	0.13

Table A2. Frequency, average cover, and standard deviation of common herb and graminoid species in 13 Trembling Aspen stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Fragaria virginiana</i>	1.00	2.05	2.39
<i>Aster ciliolatus</i>	1.00	1.14	0.77
<i>Maianthemum canadense</i>	1.00	1.11	0.35
<i>Galium boreale</i>	1.00	0.39	0.23
<i>Galium triflorum</i>	1.00	0.31	0.18
<i>Aralia nudicaulis</i>	0.91	7.06	8.48
<i>Viola canadensis</i>	0.91	5.62	6.05
<i>Petasites palmatus</i>	0.91	1.07	0.75
<i>Pyrola asarifolia</i>	0.91	0.58	0.78
<i>Mertensia paniculata</i>	0.82	3.86	4.62
<i>Rubus pubescens</i>	0.82	2.36	1.68
<i>Disporum trachycaulum</i>	0.82	0.39	0.40
<i>Actaea rubra</i>	0.82	0.31	0.31
<i>Vicia americana</i>	0.82	0.25	0.37
<i>Cornus canadensis</i>	0.73	0.67	0.70
<i>Lathyrus venosus</i>	0.64	0.64	0.81
<i>Lathyrus ochroleucus</i>	0.64	0.21	0.37
<i>Apocynum androecium</i>	0.64	0.18	0.36
<i>Taraxacum officinale</i>	0.64	0.08	0.07
<i>Solidago canadensis</i>	0.55	1.24	2.03
<i>Mitella nuda</i>	0.55	0.92	1.88
<i>Pyrola secunda</i>	0.55	0.09	0.11
<i>Sanicula marilandica</i>	0.45	0.50	0.80
<i>Thalictrum venulosum</i>	0.45	0.48	0.81
<i>Epilobium angustifolium</i>	0.45	0.27	0.40
<i>Smilacina stellata</i>	0.36	0.39	0.71
<i>Erysimum cheiranthoides</i>	0.36	0.03	0.04
<i>Anemone canadensis</i>	0.27	0.11	0.28
<i>Osmorhiza longistylis</i>	0.27	0.10	0.25
<i>Lilium philadelphicum</i>	0.27	0.03	0.06
<i>Viola renifolia</i>	0.27	0.03	0.06
<i>Achillea millefolium</i>	0.27	0.02	0.04
<i>Thalictrum dasycarpum</i>	0.18	0.43	1.38
<i>Fragaria vesca</i>	0.18	0.33	1.03
<i>Solidago spp.</i>	0.18	0.17	0.53
<i>Trientalis borealis</i>	0.18	0.05	0.13
<i>Anemone quinquefolia</i>	0.18	0.04	0.10
<i>Viola adunca</i>	0.18	0.04	0.09
<i>Aster umbellatus</i>	0.18	0.02	0.05
<i>Heracleum lanatum</i>	0.18	0.02	0.05
<i>Solidago spathulata</i>	0.18	0.02	0.05
<i>Petasites vitifolia</i>	0.18	0.02	0.03
<i>Oryzopsis asperifolia</i>	1.00	1.62	2.41
<i>Grass spp.</i>	0.91	0.26	0.22
<i>Carex spp.</i>	0.82	0.32	0.32
<i>Cinna latifolia</i>	0.36	0.05	0.07
<i>Elymus canadensis</i>	0.27	0.04	0.07
<i>Poa spp</i>	0.27	0.03	0.06
<i>Bromus spp.</i>	0.18	0.05	0.11

Table A3 Frequency, average cover, and standard deviation of common moss, lichen and fern species in 13 Trembling Aspen stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Brachythecium spp.</i>	0.91	1.30	0.94
<i>Mnium spp.</i>	0.91	0.42	0.34
<i>Peltigera spp.</i>	0.64	0.09	0.09
<i>Equisetum arvense</i>	0.55	0.11	0.17
<i>Cladonia spp.</i>	0.45	0.06	0.08
<i>Haplocladium spp.</i>	0.45	0.05	0.07
<i>Botrychium virginianum</i>	0.18	0.03	0.08
<i>Drepanocladus spp.</i>	0.18	0.02	0.05
<i>Eurhynchium spp.</i>	0.18	0.02	0.05
<i>Ptilium crista-castrensis</i>	0.18	0.02	0.03

Table A4 Frequency, average cover and standard deviation of common shrub species in 11 Balsam Poplar stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Rosa acicularis</i>	0.91	1.68	1.54
<i>Corylus cornuta</i>	0.82	16.10	21.63
<i>Cornus stolonifera</i>	0.73	1.82	2.48
<i>Symphoricarpos albus</i>	0.64	0.71	0.97
<i>Amelanchier alnifolia</i>	0.55	2.53	7.47
<i>Alnus rugosa</i>	0.55	2.18	4.11
<i>Prunus pennsylvanica</i>	0.55	1.72	2.00
<i>Prunus virginiana</i>	0.55	0.94	1.30
<i>Rubus idaeus</i>	0.45	1.47	4.11
<i>Salix spp.</i>	0.45	0.64	0.77
<i>Viburnum edule</i>	0.45	0.57	1.31
<i>Rhamnus alnifolia</i>	0.45	0.48	0.77
<i>Ribes oxycanthoides</i>	0.45	0.27	0.35
<i>Ribes triste</i>	0.45	0.24	0.34
<i>Acer spicatum</i>	0.36	5.48	17.64
<i>Linnaea borealis</i>	0.36	0.52	0.94
<i>Ribes glandulosum</i>	0.36	0.26	0.54
<i>Alnus crispa</i>	0.27	2.23	5.30
<i>Sorbus decora</i>	0.27	0.56	1.49
<i>Lonicera dioica</i>	0.27	0.16	0.29
<i>Ribes spp.</i>	0.27	0.15	0.30
<i>Symphoricarpos occidentalis</i>	0.18	0.17	0.37

Table A5 Frequency, average cover, and standard deviation of common herb and graminoid species in 6 Balsam Poplar stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Aralia nudicaulis</i>	1.00	4.57	4.10
<i>Rubus pubescens</i>	1.00	2.35	1.38
<i>Mitella nuda</i>	1.00	1.81	2.58
<i>Viola canadensis</i>	1.00	1.74	2.01
<i>Aster ciliolatus</i>	1.00	0.82	0.50
<i>Maianthemum canadense</i>	1.00	0.53	0.41
<i>Petasites palmatus</i>	1.00	0.40	0.16
<i>Galium boreale</i>	1.00	0.29	0.20
<i>Galium triflorum</i>	1.00	0.25	0.14
<i>Carex spp.</i>	0.83	2.68	3.81
<i>Mertensia paniculata</i>	0.83	2.15	2.44
<i>Fragaria virginiana</i>	0.83	0.82	1.15
<i>Oryzopsis asperifolia</i>	0.67	1.01	1.66
<i>Cornus canadensis</i>	0.67	0.82	1.02
<i>Disporum trachycaulum</i>	0.67	0.14	0.16
<i>Actaea rubra</i>	0.67	0.11	0.10
<i>Smilacina stellata</i>	0.50	0.33	0.47
<i>Pyrola asarifolia</i>	0.50	0.21	0.32
<i>Grass spp.</i>	0.50	0.18	0.29
<i>Heracleum lanatum</i>	0.50	0.17	0.33
<i>Sanicula marilandica</i>	0.50	0.14	0.20
<i>Pyrola secunda</i>	0.50	0.11	0.19
<i>Circaea alpina</i>	0.50	0.10	0.16
<i>Lathyrus ochroleucus</i>	0.50	0.06	0.07
<i>Solidago spp.</i>	0.33	0.86	2.07
<i>Fragaria vesca</i>	0.33	0.17	0.26
<i>Solidago canadensis</i>	0.33	0.15	0.34
<i>Viola renifolia</i>	0.33	0.13	0.21
<i>Anemone canadensis</i>	0.33	0.10	0.20
<i>Trientalis borealis</i>	0.33	0.08	0.17
<i>Vicia americana</i>	0.33	0.06	0.10
<i>Cinna latifolia</i>	0.33	0.04	0.07
<i>Caltha palustris</i>	0.33	0.03	0.04

Table A6 Frequency, average cover, and standard deviation of common moss, lichen and fern species in 6 Balsam Poplar stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Brachythecium spp.</i>	1.00	1.21	0.87
<i>Mnium spp.</i>	0.83	0.40	0.28
<i>Equisetum arvense</i>	0.67	4.65	11.19
<i>Cladonia spp.</i>	0.67	0.17	0.17
<i>Equisetum pratense</i>	0.50	0.07	0.08
<i>Hylocomium splendens</i>	0.33	2.44	5.91
<i>Pleurozium shreberii</i>	0.33	1.78	3.78
<i>Peltigera spp.</i>	0.33	0.08	0.14
<i>Eurhynchium spp.</i>	0.33	0.08	0.17
<i>Dicranum spp.</i>	0.33	0.07	0.13
<i>Drepanocladus spp.</i>	0.33	0.03	0.04

Table A7 Frequency, average cover and standard deviation of common shrub species in 16 White Spruce stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Rosa acicularis</i>	0.88	2.10	3.01
<i>Ribes triste</i>	0.88	0.72	1.34
<i>Linnaea borealis</i>	0.81	2.03	3.90
<i>Rubus idaeus</i>	0.81	2.46	5.11
<i>Symphoricarpos albus</i>	0.75	1.53	1.99
<i>Viburnum edule</i>	0.75	1.16	2.18
<i>Amelanchier alnifolia</i>	0.69	0.60	1.12
<i>Corylus cornuta</i>	0.63	3.75	7.69
<i>Ribes lacustre</i>	0.56	0.20	0.25
<i>Ribes oxycanthoides</i>	0.50	0.16	0.27
<i>Cornus stolonifera</i>	0.50	0.11	0.21
<i>Prunus virginiana</i>	0.44	0.14	0.23
<i>Rhamnus alnifolia</i>	0.38	0.22	0.39
<i>Lonicera spp.</i>	0.38	0.07	0.12
<i>Ribes spp.</i>	0.38	0.05	0.07
<i>Sorbus decora</i>	0.31	0.19	0.46
<i>Alnus crispa</i>	0.25	2.64	8.07
<i>Acer spicatum</i>	0.25	1.61	4.22
<i>Lonicera dioica</i>	0.25	0.08	0.19
<i>Shepherdia canadensis</i>	0.25	0.05	0.11
<i>Ribes glandulosum</i>	0.19	0.03	0.07
<i>Alnus rugosa</i>	0.13	0.77	2.29
<i>Prunus pennsylvanica</i>	0.13	0.67	2.56
<i>Salix spp.</i>	0.13	0.09	0.33

Table A8 Frequency, average cover, and standard deviation of common herb and graminoid species in 14 White Spruce Stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Aralia nudicaulis</i>	1.00	7.36	9.69
<i>Mertensia paniculata</i>	1.00	2.91	3.63
<i>Rubus pubescens</i>	1.00	2.72	2.16
<i>Maianthemum canadense</i>	1.00	0.85	0.66
<i>Cornus canadensis</i>	0.93	2.35	1.89
<i>Petasites palmatus</i>	0.93	1.11	1.19
<i>Aster ciliolatus</i>	0.93	0.71	0.77
<i>Carex</i> spp.	0.93	0.42	0.74
<i>Galium boreale</i>	0.93	0.32	0.24
<i>Actaea rubra</i>	0.93	0.27	0.27
<i>Mitella nuda</i>	0.86	2.96	5.48
<i>Fragaria virginiana</i>	0.86	1.29	1.89
<i>Grass</i> spp.	0.86	0.39	0.45
<i>Pyrola asarifolia</i>	0.79	0.52	0.46
<i>Galium triflorum</i>	0.79	0.27	0.40
<i>Pyrola secunda</i>	0.71	0.20	0.18
<i>Disporum trachycaulum</i>	0.64	0.42	0.57
<i>Viola renifolia</i>	0.64	0.39	0.85
<i>Epilobium angustifolium</i>	0.64	0.14	0.20
<i>Viola canadensis</i>	0.57	1.35	2.37
<i>Oryzopsis asperifolia</i>	0.57	0.65	1.39
<i>Vicia americana</i>	0.57	0.09	0.15
<i>Lathyrus venosus</i>	0.50	0.09	0.12
<i>Lathyrus ochroleucus</i>	0.43	0.07	0.09
<i>Taraxacum officinale</i>	0.36	0.04	0.05
<i>Thalictrum venulosum</i>	0.29	0.12	0.26
<i>Fragaria vesca</i>	0.29	0.09	0.24
<i>Petasites vitifolius</i>	0.29	0.07	0.14
<i>Osmorhiza depauperata</i>	0.29	0.04	0.08
<i>Cinna latifolia</i>	0.29	0.04	0.09
<i>Erysimum cheiranthoides</i>	0.29	0.04	0.06
<i>Circaea alpina</i>	0.21	0.83	3.00
<i>Solidago canadensis</i>	0.21	0.02	0.05
<i>Achillea millefolium</i>	0.21	0.02	0.04
<i>Sanicula marilandicum</i>	0.21	0.02	0.04
<i>Heracleum lanatum</i>	0.14	0.10	0.26
<i>Calamagrostis canadensis</i>	0.14	0.05	0.18
<i>Solidago spathulata</i>	0.14	0.02	0.07
<i>Osmorhiza longistylus</i>	0.14	0.02	0.05
<i>Smilacina stellata</i>	0.14	0.02	0.05
<i>Solidago</i> spp.	0.14	0.02	0.05
<i>Trientalis borealis</i>	0.14	0.02	0.05
<i>Apocynum androsaemifolium</i>	0.14	0.01	0.03
<i>Corallorhiza maculata</i>	0.14	0.01	0.03
<i>Monotropa uniflora</i>	0.14	0.01	0.03

Table A9 Frequency, average cover, and standard deviation of common moss, lichen and fern species in 14 White Spruce stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Hylocomium splendens</i>	0.86	4.59	6.07
<i>Pleurozium shreberii</i>	0.79	3.98	7.06
<i>Mnium spp.</i>	0.79	1.70	3.55
<i>Brachythecium spp.</i>	0.79	1.18	1.03
<i>Dicranum spp.</i>	0.71	0.14	0.12
<i>Ptilium crista-castrensis</i>	0.64	0.58	1.21
<i>Drepanocladus spp.</i>	0.64	0.52	0.91
<i>Cladonia spp.</i>	0.57	0.12	0.18
<i>Peltigera spp.</i>	0.50	0.07	0.10
<i>Lycopodium annotinum</i>	0.43	1.77	4.87
<i>Equisetum arvense</i>	0.43	0.08	0.11
<i>Thuidium spp.</i>	0.36	0.13	0.35
<i>Eurhynchium spp.</i>	0.29	0.08	0.18
<i>Equisetum sylvaticum</i>	0.29	0.06	0.11
<i>Equisetum pratense</i>	0.29	0.03	0.05
<i>Botrychium virginianum</i>	0.14	0.08	0.27
<i>Polytrichum spp.</i>	0.14	0.02	0.05
<i>Pohlia spp.</i>	0.14	0.01	0.03

Table A10 Frequency, average cover, and standard deviation of common shrub species in 13 Jack Pine stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Rosa acicularis</i>	0.92	4.17	3.38
<i>Viburnum edule</i>	0.85	2.92	3.88
<i>Linnaea borealis</i>	0.85	2.74	2.55
<i>Corylus cornuta</i>	0.77	11.26	22.98
<i>Symphoricarpos albus</i>	0.77	0.56	0.67
<i>Rubus idaeus</i>	0.69	1.96	2.71
<i>Ribes triste</i>	0.69	0.92	2.26
<i>Amelanchier alnifolia</i>	0.54	1.34	4.14
<i>Cornus stolonifera</i>	0.54	1.26	1.79
<i>Alnus crispa</i>	0.46	6.14	12.81
<i>Prunus virginiana</i>	0.46	1.10	1.92
<i>Sorbus decora</i>	0.46	0.17	0.31
<i>Lonicera spp.</i>	0.46	0.17	0.21
<i>Salix spp.</i>	0.38	0.66	1.63
<i>Rhamnus alnifolia</i>	0.38	0.21	0.30
<i>Lonicera dioica</i>	0.38	0.08	0.16
<i>Acer spicatum</i>	0.31	0.46	1.06
<i>Vaccinium myrtilloides</i>	0.31	0.30	1.01
<i>Prunus pennsylvanica</i>	0.31	0.20	0.34
<i>Diervilla lonicera</i>	0.23	1.34	4.39
<i>Ledum groenlandicum</i>	0.23	0.51	1.45
<i>Ribes lacustre</i>	0.23	0.06	0.12
<i>Ribes glandulosum</i>	0.23	0.03	0.05
<i>Ribes oxyacanthoides</i>	0.23	0.02	0.04
<i>Vaccinium vitis-idaea</i>	0.15	0.03	0.08
<i>Ribes spp.</i>	0.15	0.01	0.03

Table A11 Frequency, average cover, and standard deviation of common herb and graminoid species in 11 Jack Pine stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Aralia nudicaulis</i>	1.00	8.92	8.46
<i>Cornus canadensis</i>	1.00	3.92	2.58
<i>Rubus pubescens</i>	1.00	3.48	2.07
<i>Maianthemum canadense</i>	1.00	0.68	0.55
<i>Galium boreale</i>	1.00	0.36	0.30
<i>Actaea rubra</i>	1.00	0.19	0.18
<i>Fragaria virginiana</i>	0.91	1.36	1.77
<i>Petasites palmatus</i>	0.91	1.13	1.19
<i>Aster ciliolatus</i>	0.91	0.64	0.48
<i>Oryzopsis asperifolia</i>	0.91	0.42	0.64
<i>Galium triflorum</i>	0.91	0.16	0.09
<i>Mertensia paniculata</i>	0.82	1.67	1.74
<i>Grass spp.</i>	0.82	1.12	2.45
<i>Disporum trachycaulum</i>	0.82	0.42	0.55
<i>Mitella nuda</i>	0.73	1.57	1.71
<i>Epilobium angustifolium</i>	0.73	0.68	1.09
<i>Viola renifolia</i>	0.73	0.29	0.32
<i>Trientalis borealis</i>	0.73	0.21	0.27
<i>Viola canadensis</i>	0.64	0.79	1.21
<i>Lathyrus venosus</i>	0.64	0.23	0.43
<i>Pyrola secunda</i>	0.64	0.17	0.17
<i>Fragaria vesca</i>	0.55	0.23	0.33
<i>Lathyrus ochroleucus</i>	0.55	0.16	0.23
<i>Goodyera repens</i>	0.55	0.07	0.08
<i>Carex spp.</i>	0.55	0.30	0.74
<i>Pyrola asarifolia</i>	0.45	0.35	0.56
<i>Thalictrum venulosum</i>	0.36	0.04	0.06
<i>Sanicula marilandicum</i>	0.36	0.04	0.06
<i>Apocynum androsaemifolium</i>	0.27	0.14	0.29
<i>Pyrola elliptica</i>	0.18	0.13	0.40
<i>Aquilegia brevistyla</i>	0.18	0.05	0.15
<i>Erysimum cheiranthoides</i>	0.18	0.02	0.03
<i>Petasites vitifolia</i>	0.18	0.02	0.03
<i>Taraxacum officinale</i>	0.18	0.02	0.03
<i>Cinna latifolia</i>	0.18	0.02	0.03

Table A12 Frequency, average cover, and standard deviation of common moss, lichen and fern species in 11 Jack Pine stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Hylocomium splendens</i>	0.91	4.47	10.64
<i>Pleurozium shreberii</i>	0.82	3.30	7.37
<i>Lycopodium annotinum</i>	0.73	1.36	1.64
<i>Ptilium crista-castrensis</i>	0.73	0.73	1.57
<i>Brachythecium spp.</i>	0.64	0.76	0.82
<i>Mnium spp.</i>	0.64	0.63	1.15
<i>Cladonia spp.</i>	0.55	0.23	0.27
<i>Dicranum spp.</i>	0.55	0.13	0.24
<i>Drepanocladus spp.</i>	0.45	0.39	0.58
<i>Lycopodium complanatum</i>	0.36	0.34	0.71
<i>Equisetum arvense</i>	0.36	0.05	0.07
<i>Peltigera spp.</i>	0.27	0.03	0.06
<i>Eurhynchium spp.</i>	0.18	0.32	0.80
<i>Rhytidiadelphus triquetrus</i>	0.18	0.05	0.13
<i>Equisetum pratense</i>	0.18	0.03	0.08

Table A13 Frequency, average cover and standard deviation of common shrub species in 5 Black Spruce (mineral substrate) stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Linnaea borealis</i>	1.00	2.48	2.69
<i>Rosa acicularis</i>	1.00	1.52	0.97
<i>Vaccinium vitis-idaea</i>	1.00	0.90	1.47
<i>Ledum groenlandicum</i>	0.80	1.10	0.98
<i>Alnus rugosa</i>	0.60	6.93	9.92
<i>Rubus idaeus</i>	0.60	1.25	2.43
<i>Viburnum edule</i>	0.60	0.47	0.78
<i>Ribes triste</i>	0.60	0.12	0.13
<i>Vaccinium myrtilloides</i>	0.40	0.37	0.65
<i>Salix spp.</i>	0.40	0.27	0.55
<i>Sorbus decora</i>	0.40	0.08	0.14
<i>Arctostaphylos uva-ursi</i>	0.40	0.05	0.07
<i>Ribes lacustre</i>	0.40	0.03	0.05

Table A14 Frequency, average cover, and standard deviation of common herb and graminoid species in 5 Black Spruce (mineral substrate) stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Petasites palmatus</i>	1.00	2.28	3.19
<i>Cornus canadensis</i>	1.00	1.65	1.03
<i>Goodyera repens</i>	1.00	0.13	0.11
<i>Mitella nuda</i>	0.80	1.93	2.61
<i>Maianthemum canadense</i>	0.80	0.40	0.48
<i>Mertensia paniculata</i>	0.80	0.40	0.58
<i>Grass spp.</i>	0.80	0.30	0.44
<i>Rubus pubescens</i>	0.60	1.37	2.17
<i>Aster ciliolatus</i>	0.60	0.35	0.65
<i>Carex spp.</i>	0.60	0.30	0.40
<i>Viola renifolia</i>	0.60	0.20	0.24
<i>Galium boreale</i>	0.60	0.12	0.17
<i>Fragaria vesca</i>	0.60	0.05	0.05
<i>Aralia nudicaulis</i>	0.40	1.60	3.35
<i>Pyrola asarifolia</i>	0.40	0.47	0.66
<i>Epilobium angustifolium</i>	0.40	0.07	0.09
<i>Galium triflorum</i>	0.40	0.07	0.11
<i>Corallorhiza maculata</i>	0.40	0.03	0.05
<i>Pyrola secunda</i>	0.40	0.03	0.05

Table A15 Frequency, average cover, and standard deviation of common moss, lichen and fern species in 5 Black Spruce (mineral substrate) stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Hylocomium splendens</i>	1.00	46.62	16.45
<i>Pleurozium shreberii</i>	1.00	16.70	13.58
<i>Ptilium crista-castrensis</i>	1.00	6.22	6.91
<i>Dicranum spp.</i>	0.80	0.53	0.67
<i>Equisetum arvense</i>	0.60	0.35	0.69
<i>Equisetum pratense</i>	0.60	0.17	0.17
<i>Equisetum scirpoides</i>	0.60	0.12	0.14
<i>Cladonia spp.</i>	0.60	0.10	0.14
<i>Lycopodium annotinum</i>	0.40	2.70	5.94
<i>Drepanocladus spp.</i>	0.40	0.45	0.92
<i>Mnium spp.</i>	0.40	0.12	0.22
<i>Peltigera spp.</i>	0.40	0.03	0.05

Table A16 Frequency, average cover and standard deviation of common shrub species in 2 Black Spruce (organic substrate) stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Ledum groenlandicum</i>	1.00	22.79	7.95
<i>Alnus rugosa</i>	1.00	15.79	17.50
<i>Rubus chamaemorus</i>	1.00	3.58	3.65
<i>Vaccinium vitis-idaea</i>	1.00	2.17	0.24
<i>Linnaea borealis</i>	1.00	0.46	0.06
<i>Vaccinium oxyacanthoides</i>	1.00	0.25	0.12
<i>Salix spp.</i>	1.00	0.21	0.18
<i>Ribes glandulosum</i>	0.50	0.29	0.41
<i>Gaultheria hispidula</i>	0.50	0.25	0.35
<i>Andromeda glaucophylla</i>	0.50	0.08	0.12
<i>Corylus cornuta</i>	0.50	0.04	0.06
<i>Lonicera spp.</i>	0.50	0.04	0.06
<i>Shepherdia canadensis</i>	0.50	0.04	0.06

Table A17 Frequency, average cover, and standard deviation of common herb and graminoid species in 2 Black Spruce (organic substrate) stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Carex spp.</i>	1.00	3.83	4.01
<i>Mitella nuda</i>	1.00	1.21	1.59
<i>Rubus acaulis</i>	1.00	0.17	0.12
<i>Cornus canadensis</i>	1.00	0.08	0.00
<i>Epilobium angustifolium</i>	0.50	0.17	0.24
<i>Habenaria obtusata</i>	0.50	0.13	0.18
<i>Pyrola elliptica</i>	0.50	0.13	0.18
<i>Caltha palustris</i>	0.50	0.08	0.12
<i>Rubus pubescens</i>	0.50	0.08	0.12
<i>Grass spp.</i>	0.50	0.08	0.12
<i>Fragaria virginiana</i>	0.50	0.04	0.06
<i>Goodyera repens</i>	0.50	0.04	0.06
<i>Pyrola asarifolia</i>	0.50	0.04	0.06
<i>Pyrola secunda</i>	0.50	0.04	0.06
<i>Viola renifolia</i>	0.50	0.04	0.06

Table A18 Frequency, average cover, and standard deviation of common moss, lichen and fern species in 2 Black Spruce (organic substrate) stands.

Species	Frequency	Average Cover	Standard Deviation
<i>Pleurozium shreberi</i>	1.00	50.33	23.22
<i>Hylocomium splendens</i>	1.00	22.54	6.42
<i>Tomenthypnum spp.</i>	1.00	3.67	5.07
<i>Sphagnum spp.</i>	1.00	3.29	1.00
<i>Ptilium crista-castrensis</i>	1.00	1.67	0.94
<i>Equisetum pratense</i>	1.00	0.71	0.77
<i>Equisetum scirpoides</i>	1.00	0.46	0.18
<i>Mnium spp.</i>	1.00	0.46	0.53
<i>Drepanocladus spp.</i>	1.00	0.46	0.53
<i>Polytrichum spp.</i>	1.00	0.33	0.00
<i>Peltigera spp.</i>	1.00	0.29	0.29
<i>Dicranum spp.</i>	1.00	0.25	0.12
<i>Equisetum sylvaticum</i>	1.00	0.21	0.18
<i>Haplocladium spp.</i>	0.50	0.17	0.24
<i>Aulacomnium spp.</i>	0.50	0.04	0.06
<i>Cladonia spp.</i>	0.50	0.04	0.06

APPENDIX B

Table B1. The initial post-fire cohort of the 48 stands used in modelling stand dynamics, expressed proportionally.

Stand	Stand Type	Trembling Aspen	Balsam Poplar	White Birch	White Spruce	Black Spruce	Jack Pine
1	Trembling Aspen	0.95	0.05	0.00	0.00	0.00	0.00
2		1.00	0.00	0.00	0.00	0.00	0.00
3		0.87	0.00	0.06	0.06	0.00	0.00
4		0.93	0.07	0.00	0.00	0.00	0.00
5		0.56	0.00	0.13	0.31	0.00	0.00
6		0.34	0.00	0.34	0.31	0.00	0.00
7		0.81	0.06	0.13	0.00	0.00	0.00
8		0.62	0.19	0.00	0.13	0.00	0.06
9		1.00	0.00	0.00	0.00	0.00	0.00
10		0.88	0.00	0.13	0.00	0.00	0.00
11		0.79	0.05	0.16	0.00	0.00	0.00
12		0.44	0.00	0.32	0.24	0.00	0.00
13	Balsam Poplar	0.03	0.97	0.00	0.00	0.00	0.00
14		0.67	0.33	0.00	0.00	0.00	0.00
15		0.15	0.70	0.10	0.05	0.00	0.00
16		0.12	0.72	0.04	0.12	0.00	0.00
17		0.57	0.43	0.00	0.00	0.00	0.00
19		0.23	0.69	0.00	0.08	0.00	0.00
20		0.71	0.18	0.12	0.00	0.00	0.00
18		0.26	0.61	0.13	0.00	0.00	0.00
21		0.29	0.50	0.00	0.21	0.00	0.00
22		0.19	0.19	0.61	0.00	0.00	0.00
23	White Spruce	0.46	0.00	0.23	0.31	0.00	0.00
24		0.37	0.14	0.26	0.23	0.00	0.00
25		0.29	0.16	0.29	0.26	0.00	0.00
26		0.31	0.06	0.16	0.47	0.00	0.00
27		0.13	0.00	0.13	0.74	0.00	0.00
28		0.62	0.23	0.08	0.08	0.00	0.00
29		0.61	0.03	0.06	0.30	0.00	0.00
30		0.17	0.03	0.55	0.21	0.03	0.00
31		0.70	0.04	0.22	0.04	0.00	0.00
32		0.33	0.28	0.00	0.39	0.00	0.00
33	Jack Pine	0.36	0.07	0.00	0.00	0.43	0.14
34		0.29	0.00	0.00	0.03	0.36	0.32
35		0.42	0.00	0.19	0.00	0.08	0.31
36		0.47	0.00	0.12	0.00	0.02	0.39
37		0.44	0.00	0.04	0.00	0.00	0.52
38		0.08	0.05	0.01	0.00	0.34	0.52
39		0.54	0.00	0.08	0.00	0.00	0.38
40		0.12	0.00	0.02	0.00	0.00	0.86
41		0.00	0.00	0.19	0.09	0.25	0.47
42		0.17	0.00	0.17	0.21	0.14	0.31
43		0.09	0.00	0.05	0.00	0.04	0.82
44		0.53	0.00	0.00	0.34	0.00	0.13
45		0.29	0.00	0.00	0.27	0.20	0.24
46	Black Spruce	0.14	0.00	0.01	0.00	0.51	0.33
47		0.05	0.00	0.00	0.00	0.59	0.36
48		0.00	0.02	0.08	0.00	0.61	0.29

Table B2. The advance regeneration cohort of the 48 stands used in modelling stand dynamics, expressed as density/100 m².

Stand	Stand Type	Trembling Aspen	Balsam Poplar	White Birch	White Spruce	Balsam Fir	Black Spruce
1	Trembling Aspen	7.30	0.00	0.00	0.00	0.00	0.00
2		8.00	0.00	0.00	0.00	0.00	0.00
3		4.00	0.00	0.67	0.33	0.00	0.00
4		4.50	0.00	0.50	1.50	0.00	0.00
5		8.00	0.00	1.33	3.00	0.00	0.00
6		2.30	0.00	0.67	0.67	0.00	0.00
7		1.00	0.67	0.00	0.00	0.00	0.00
8		3.30	0.33	0.00	0.67	0.00	0.00
9		7.00	0.00	0.00	8.00	0.00	0.00
10		2.00	0.00	0.00	5.00	0.00	0.00
11		2.50	0.00	1.50	7.00	0.00	0.00
12		0.50	0.00	2.50	8.00	0.00	3.00
13	Balsam Poplar	1.00	1.33	0.00	0.00	0.00	0.00
14		0.00	0.00	0.00	9.00	0.00	0.00
15		0.00	0.00	0.00	6.00	0.50	0.33
16		0.67	0.00	0.33	6.33	0.00	0.00
17		1.67	0.00	0.00	6.00	0.00	0.00
19		0.67	0.33	1.67	4.00	0.33	0.00
20		10.00	0.00	0.00	3.00	0.00	0.00
18		4.50	0.00	4.00	2.00	1.00	3.50
21		0.00	1.67	0.00	1.67	10.00	0.00
22		0.33	0.33	0.67	0.00	10.00	0.00
23	White Spruce	0.00	0.00	0.33	0.00	13.67	0.00
24		0.33	1.33	0.00	0.00	17.00	0.00
25		0.00	0.00	2.33	0.33	7.33	0.00
26		3.67	0.00	0.33	1.00	14.67	0.00
27		0.00	0.00	0.67	2.67	8.33	0.00
28		0.00	0.00	1.00	7.00	8.00	0.67
29		0.67	0.67	0.67	5.00	0.00	0.00
30		2.00	0.33	1.33	0.33	2.33	0.00
31		2.67	0.00	3.00	2.67	2.67	0.00
32		3.00	1.00	0.00	1.67	2.00	0.00
33	Jack Pine	3.00	0.33	0.00	1.33	0.00	1.67
34		1.33	0.00	0.33	0.33	0.00	0.33
35		6.67	0.00	7.67	1.00	0.33	3.00
36		3.33	0.00	12.00	0.00	0.00	0.00
37		1.50	0.00	5.00	1.00	1.50	0.00
38		0.67	0.00	2.00	0.00	0.67	0.33
39		1.67	0.00	2.67	0.00	1.00	0.00
40		1.67	0.00	8.33	2.00	4.00	0.00
41		0.00	0.00	1.50	3.00	3.50	2.50
42		0.50	0.00	1.50	2.50	5.50	2.50
43		6.67	0.00	0.67	0.00	16.00	4.67
44		0.33	0.00	0.00	0.00	15.00	0.00
45		0.00	0.00	0.00	0.00	16.00	0.00
46	Black Spruce	0.33	0.00	0.33	0.00	0.00	1.33
47		0.33	0.00	0.00	0.00	0.00	1.67
48		0.00	0.00	1.67	0.00	0.00	1.67

APPENDIX C

Mean and standard deviation of browsing intensity recorded for major tree and shrub species. All tree and shrub species having % cover > 5% were assigned a rank between 1 (no apparent browsing) and 5 (severe browsing).

Species	Mean Browse	Standard Deviation
Trees		
Balsam Poplar	2.58	1.28
Balsam Fir	2.42	1.26
Trembling Aspen	2.36	1.10
White Birch	1.90	1.01
White Spruce	1.16	0.44
Black Spruce	1.05	0.23
Shrubs		
<i>Amelanchier alnifolia</i>	3.13	1.18
<i>Cornus stolonifera</i>	2.94	1.00
<i>Prunus virginiana</i>	2.47	1.45
<i>Viburnum edule</i>	2.29	1.04
<i>Salix</i> spp.	2.27	1.33
<i>Rosa acicularis</i>	2.26	0.84
<i>Corylus cornuta</i>	2.23	1.03
<i>Prunus pennsylvanica</i>	2.21	1.81
<i>Acer spicatum</i>	1.78	0.67
<i>Rubus idaeus</i>	1.56	0.97
<i>Sorbus decora</i>	1.50	1.00
<i>Symphoricarpos albus</i>	1.20	0.66
<i>Ribes triste</i>	1.18	0.40
<i>Alnus rugosa</i>	1.11	0.33
<i>Rhamnus alnifolia</i>	1.09	0.30
<i>Alnus crispa</i>	1.00	0.00

APPENDIX D

Biodiversity Analysis

Using cover data at the plot (10x10 m) level, biodiversity and species richness were calculated for tree and understory species within each of the five stand types. One hundred iterations of a random draw of 15 plots within each stand type was taken, with replacement, and richness and effective species richness (Simpson's) was calculated for each iteration. The average of these, and their standard deviation, was tabulated.

Stand type	Trees Only		Understory	
	Eff. Richness	Richness	Eff. Richness	Richness
TA	1.63	4.36	8.11	95.97
STDEV	0.20	0.50	1.97	7.19
BP	3.83	5.00	11.24	81.68
STDEV	0.48	0.00	3.65	4.88
WS	3.83	5.91	21.33	88.85
STDEV	0.30	0.29	2.85	4.57
JP	4.44	7.00	16.59	81.63
STDEV	0.50	0.00	3.75	4.39
BS MIN	1.82	6.66	5.84	69.15
STDEV	0.19	0.65	1.09	5.55

The species richness of the tree component of a given stand appears to be reflected in understory species richness. Trembling Aspen and Black Spruce stands have the lowest effective tree species richness, as well as the lowest effective understory species richness. Aspen stands tend to be dominated by deep-shade casting shrubs, typically beaked hazelnut. Jack Pine stands have high tree diversity in both the initial and advanced regeneration cohorts. As the jack pine component senesces, balsam fir moves into these stands and so tree diversity remains high. The understory of Jack Pine stands reflects the diversity in the tree component and the likely influence of these trees on the microclimate and microhabitat below the canopy. Understory richness is very high in White Spruce stands as well, due to a diversity of microhabitats at the stand level. The tree component of these stands tends to be characterized by alternating groves of coniferous and deciduous species. Under groves of conifer conditions are cool and shaded, and understory species with a boreal affinity dominate. In deciduous tree-dominated parts of the stand, however, conditions are more open and drier. Deciduous shrubs and species typical of aspen parkland tend to dominate these areas. While the Balsam Poplar stand type has high effective tree richness, its effective understory richness is only moderate. The dense conifer regeneration in these stands, typically white spruce and sometimes balsam fir, casts deep shade and limits the establishment of understory species.

APPENDIX E

List of species encountered in enumerated stands at Duck Mountain.

Trees

Abies balsamea

Acer negundo

Betula papyrifera

Larix laricina

Picea glauca

Picea mariana

Pinus banksiana

Populus balsamifera

Populus tremuloides

Quercus macrocarpa

Shrubs

Acer spicatum

Alnus crispa

Alnus rugosa

Amelanchier alnifolia

Andromeda glaucophylla

Arctostaphylos uva-ursi

Betula pumila

Cornus stolonifera

Corylus cornuta

Craetegus chrysocarpa

Diervilla lonicera

Gaultheria hispidula

Juniperus horizontalis

Kalmia polifolia

Ledum groenlandicum

Linnaea borealis

Lonicera dioica

Lonicera spp.

Lonicera villosa

Prunus pennsylvanica

Prunus virginiana

Rhamnus alnifolia

Rhus radicans

Ribes glandulosum

Ribes hudsonianum

Ribes lacustre

Ribes oxycanthoides

Ribes spp.

Ribes triste

Rosa acicularis

Rosa woodsii

Rubus chamaemorus

Rubus idaeus

Salix spp.

Shepherdia canadensis

Sorbus decora

Spiraea alba

Symphoricarpos albus

Symphoricarpos occidentalis

Vaccinium angustifolium

Vaccinium caespitosum

Vaccinium myrtilloides

Vaccinium oxycoccus

Vaccinium vitis-idaea

Viburnum edule

Viburnum lentago

Viburnum opulus

Herbs

<i>Achillea millefolium</i>	<i>Halenia deflexa</i>
<i>Achillea sibirica</i>	<i>Heracleum lanatum</i>
<i>Actaea rubra</i>	<i>Hieracium umbellatum</i>
<i>Anemone canadensis</i>	<i>Humulus lupulus</i>
<i>Anemone quinquefolia</i>	<i>Lathyrus ochroleucus</i>
<i>Anemone riparia</i>	<i>Lathyrus venosus</i>
<i>Antennaria</i> spp.	<i>Lilium philadelphicum</i>
<i>Apocynum androsaemifolium</i>	<i>Lysimachia ciliolatus</i>
<i>Aquilegia brevistyla</i>	<i>Maianthemum canadense</i>
<i>Aralia nudicaulis</i>	<i>Mentha arvensis</i>
<i>Arenaria lateriflora</i>	<i>Mertensia paniculata</i>
<i>Aster canadensis</i>	<i>Mitella nuda</i>
<i>Aster ciliolatus</i>	<i>Monarda fistulosa</i>
<i>Aster laevis</i>	<i>Moneses uniflora</i>
<i>Aster umbellata</i>	<i>Monotropa uniflora</i>
<i>Caltha palustris</i>	<i>Osmorhiza depauperata</i>
<i>Campanula rotundifolia</i>	<i>Osmorhiza longistylis</i>
<i>Circaea alpina</i>	<i>Oxytropis</i> spp.
<i>Cirsium arvense</i>	<i>Petasites palmatus</i>
<i>Coptis trifolia</i>	<i>Petasites sagittatus</i>
<i>Corallorhiza maculata</i>	<i>Petasites vitifolia</i>
<i>Corallorhiza striata</i>	<i>Pyrola asarifolia</i>
<i>Corallorhiza trifida</i>	<i>Pyrola chlorantha</i>
<i>Cornus canadensis</i>	<i>Pyrola elliptica</i>
<i>Disporum trachycaulum</i>	<i>Pyrola secunda</i>
<i>Epilobium angustifolium</i>	<i>Rubus acaulis</i>
<i>Erigeron philadelphicum</i>	<i>Rubus chaemorus</i>
<i>Erysimum cheiranthoides</i>	<i>Rubus pubescens</i>
<i>Fragaria vesca</i>	<i>Sanicula marilandica</i>
<i>Fragaria virginiana</i>	<i>Smilacina stellata</i>
<i>Galium boreale</i>	<i>Smilacina trifolia</i>
<i>Galium triflorum</i>	<i>Smilax herbacea</i>
<i>Goodyera repens</i>	<i>Solidago canadensis</i>
<i>Habenaria obtusata</i>	<i>Solidago spathulata</i>
<i>Habenaria orbiculata</i>	<i>Solidago</i> spp.

Herbs Continued...

Sonchus arvensis
Spiranthes romanzoffiana
Taraxacum officinale
Thalictrum dasycarpum
Thalictrum venulosum
Trientalis borealis

Urtica dioica
Vicia americana
Viola adunca
Viola canadensis
Viola renifolia

Graminoids

Bromus spp.
Calamagrostis inexpansa
Calamagrostis canadensis
Carex spp.
Cinna latifolia
Elymus canadensis

Elymus innovatus
Grass spp.
Luzula pilosa
Oryzopsis asperifolia
Poa spp.
Schizachne purpurascens

Ferns and Fern-allies

Botrychium virginianum
Dryopteris spinulosa
Equisetum arvense
Equisetum fluviatile
Equisetum pratense
Equisetum scirpoides

Equisetum sylvaticum
Gymnocarpium dryopteris
Lycopodium annotinum
Lycopodium complanatum
Lycopodium obscurum
Matteuccia struthiopteris

Mosses and Lichens

Aulacomnium spp.
Brachythecium spp.
Cladina spp.
Cladonia spp.
Dicranum spp.
Drepanocladus spp.
Eurhynchium spp.
Haplcladium spp.
Hylocomium splendens
Lophozia spp.
Mnium spp.

Oncophorus wahlenbergii
Parmelaria spp.
Peltigera spp.
Pleurozium shreberi
Pohlia spp.
Polytrichum spp.
Ptilium crista-castrensis
Rhytidiadelphus triquetrus
Sphagnum spp.
Thuidium spp.
Tomenthypnum spp.