Forest stand structure and dynamics at Riding Mountain National Park, Manitoba, Canada

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Abstract: We used multivariate analysis to model boreal forest stand structure and dynamics at Riding Mountain National Park, Manitoba based on data from 202 sampled stands. Eight forest stand-types were recognized based on canopy composition: black spruce on peat substrates, jack pine – black spruce, bur oak, eastern deciduous (green ash – American elm – Manitoba maple), balsam fir, trembling aspen – paper birch – mountain maple, trembling aspen – balsam poplar, and white spruce. The first four stand-types occur in edaphically distinct environments, while the four remaining boreal mixedwood stand-types occur in edaphically similar environments. We found that the composition and abundance of advance regeneration were best predicted by current canopy composition (redundancy = 54.4%); this reflects both the limited dispersal of conifer seeds and the strong vegetative reproductive capacity of hardwoods. Biotically-controlled site factors such as bareground, herb and shrub cover, ungulate browsing intensity, and stand age were also reasonably good predictors of advance regeneration (redundancy = 31.7%). Edaphic variables such as soil pH, conductivity, particle size, organic horizon depth and slope proved to be poor predictors of advance regeneration, however (redundancy = 18.1%). Size-class ordination indicated that many stand-types have relatively short successional trajectories, suggesting limited change in forest canopy composition over time. There are two exceptions: in the jack pine – black spruce stand-type, black spruce will increase over time, and in the trembling aspen – paper birch – mountain maple stand-type, eastern deciduous species (green ash, American elm, Manitoba maple, and bur oak) are forecast to become increasingly dominant. We also describe a synoptic model of mixedwood boreal forest stand dynamics for the Riding Mountain area. The model includes a number of factors that we consider to be critical determinants of forest dynamics, such as seed source availability, small and large-scale disturbances, species life-history characteristics, and environmental gradients. Our succession model is more similar those described for eastern than western Canada, which may reflect the lower frequency of catastrophic fires in the Riding Mountain area compared to boreal forests further west. Our model emphasizes that successional trajectories do not converge towards a single self-perpetuating "climax". Instead, successional vectors may diverge, converge or remain cyclical, and multiple potential pathways are possible for each stand-type. Our results also illustrate that species assemblages, and the propensity for canopy change in the absence of fire, are governed by the cumulative and synergistic effects of climate, topography, disturbance frequency, size and intensity, edaphic conditions, and the proximity of parental seed sources. Fire suppression in the southern boreal forest has resulted in a paradigm shift in disturbance regime, from large, synchronous catastrophic fires to small-scale, asynchronous gap formation. A major challenge for boreal forest ecologists is to determine the long-term consequences of this paradigm shift on the composition, structure and health of boreal forest stands and landscapes.

Abbreviations: RMNP - Riding Mountain National Park, CA - Correspondence analysis, CCA - Canonical correspondence analysis.

Nomenclature: Cody (1988).

Introduction

The boreal forest was historically a disturbance-driven biome, with fire recognized as the primary large-scale natural disturbance agent (Wein and MacLean 1983, Johnson 1992). In most regions of the boreal forest, catastrophic fires are of sufficient frequency that classical Clementsian concepts of succession are of limited relevance (Rowe 1961, Johnson 1992). Indeed, numerous studies on boreal forest succession in North America suggest that the "initial floristic composition" model (Egler 1954) is generally applicable. According to this model, changes in forest structure and composition over time simply reflect differential growth rates of tree species established contemporaneously after a catastrophic, stand initiating disturbance (Egler's "complete" model, sensu Wilson et al. 1992). In older stands that have escaped fire, the "tolerance" model of stand dynamics (Connell and Slatyer 1977) may also be relevant (Bergeron 2000, Chen and Popadiouk 2002). According to this model, subordinate

species remain in the understory in a suppressed, slow-growing state until increases in resource availability (e.g., increased light levels resulting from mortality of canopy trees) release them from suppression.

Patterns and processes of boreal stand dynamics vary regionally across the North American biome. In western regions, catastrophic fires are of sufficient frequency that most stands burn before major changes in canopy composition can occur (Zoladeski and Maycock 1990, Johnson 1992, Johnson et al. 1994, Youngblood 1995, Gutsell and Johnson 2001). As a result, young post-fire stands dominated by early succession "pioneer" tree species such as jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and paper birch (*Betula papyrifera*) are perpetuated. Studies in the boreal, boreal montane and near-boreal forests of western Canada indicate that natural fires are so prevalent that only 5-10% of the landscape is "old-growth" forest (Johnson et al. 1995, Johnson et al. 1998). In the continued absence of fire, these "old-growth" stands may undergo canopy change and become increasingly dominated by balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and/or black spruce (*Picea mariana*). In eastern regions of the boreal forest, greater precipitation results in decreased frequencies of catastrophic forest fires. This in turn increases the likelihood of young, post-fire stands becoming dominated by balsam fir, white spruce, black spruce and/or eastern white cedar (*Thuja occidentalis*) (Heinselman 1981, Bergeron and Dansereau 1993, Larocque et al. 2000). For example, boreal stands in western Quèbec become increasingly dominated by white spruce, balsam fir and/or eastern white cedar in the absence of fire (Bergeron 2000). Alternatively, older boreal stands may undergo canopy "deterioration and degeneration" (Cogbill 1985): as post-fire canopy trees die, light levels increase to favour the development of a dense tall shrub layer (e.g., mountain maple (*Acer spicatum*) or beaked hazelnut (*Corylus cornuta*)) that shades out the advanced tree regeneration., thus limiting further recruitment (Dix and Swan 1971, Carleton and Maycock 1978). The canopy transition phase of boreal forest stand dynamics is characterized by small-scale "gap" disturbances that gradually "chip away" at the continuous post-fire canopy (Frelich and Reich 1995, Kenkel et al. 1997, Kneeshaw and Bergeron 1998). Canopy gaps may be created by individual tree mortality or insect outbreaks, especially spruce budworm (Shugart et al. 1992).

The structural and compositional dynamics of later-successional boreal forest stands are ultimately determined by advanced tree regeneration (Kneeshaw and Bergeron 1998, Chen and Popadiouk 2002). Numerous

factors affect the dispersal, germination and establishment of understory tree regeneration in the boreal forest. Dispersal and germination are most influenced by the proximity of conspecific adults (i.e., seed source), primary and secondary mechanisms of seed dispersal, edaphic and seedbed conditions, stand age, competition from herbaceous and woody understory vegetation, and seed viability and predation (Johnson 1992, Kneeshaw and Burton 1997, Kneeshaw and Bergeron 1996, Lieffers et al. 1996, McLaren and Janke 1996, Galipeau et al. 1997, Morin and Laprise 1997, Cornett et al. 1998, Foré et al. 1997, Kneeshaw et al. 1998, Messier et al. 1998, Simard et al. 1998, Stewart et al. 1998). Conifer seedlings are rarely randomly distributed on the forest floor (Maguire and Forman 1983), since regeneration is commonly associated with safe microsites that vary with stand composition (deciduous or coniferous dominated, or mixedwood) and successional stage (Simard et al. 1998, Greene et al. 1999). Advance regeneration of white spruce and balsam fir, for example, is most commonly encountered on partially-decomposed logs, since elevated logs provide some protection from competing herbaceous vegetation and smothering leaf litter (Lieffers et al. 1996). The establishment and growth of advance regeneration is largely related to light and moisture availability, and damaging agents such as insect pests, fungal pathogens, and ungulate herbivory (Zasada et al. 1992). Light and moisture levels at the forest floor are largely regulated by canopy composition and heterogeneity, the presence or absence and size of canopy gaps, and interspecific competition (Zasada et al. 1992, Lieffers and Stadt 1994, Drobyshev and Nihlgård 2000).

Given the complexity of boreal forest disturbance dynamics, succession is expected to be an extremely variable process with multiple potential pathways (Zoladeski and Maycock 1990, Fastie 1995, McCune and Allen 1985a,b, Kenkel et al. 1997). Numerous synergistically-interacting factors such as disturbance type, size, frequency and intensity, seed source availability and dispersal, seedbed quality, interspecific competition, edaphic and topographic variability, ungulate herbivory, granivory, insect pests and fungal pathogens, and climatic variation have profound and long-term impacts on forest dynamics (McClanahan 1986, Johnson 1992, McInnes et al. 1992, Zasada et al. 1992, Greene and Johnson 1995, 1996, 1997, Cornett et al. 1998, Stewart et al. 1998, Morin 1994, Kneeshaw and Bergeron 1998, Bergeron 2000). The result is a complex assemblage of stands of different age, structure and composition on the landscape (Walker and Kenkel 2001).

The dynamics of boreal mixedwood forests in central Canada (Saskatchewan and Manitoba) is poorly known. Early surveys of western Manitoba boreal forest were entirely descriptive (Dickson 1909, Tunstell et al. 1922, Evans 1923, Halliday 1932, Tunstell 1940), while later studies gave only anecdotal accounts of potential successional trends (Rowe 1955, 1956, Ritchie 1957). A study in central Saskatchewan utilized the life history characteristics of boreal trees to infer stand structure and successional trends (Dix and Swan 1971). However, central Saskatchewan has a drier climate and more frequent catastrophic fires than western Manitoba (Heinselman 1978, Weir and Johnson 1998). This difference in disturbance frequency may render the dynamics of western Manitoba's boreal forests more similar to those described for eastern Canada (e.g., Bergeron 2000) than those further west (e.g., Dix and Swan 1971, Gutsell and Johnson 2001). It is clear that more detailed studies of forest dynamics in western Manitoba are needed to test the contrasting boreal mixedwood stand dynamic models developed for eastern and western Canadian boreal forests.

This study was undertaken to address the need for more detailed and comprehensive data on mixedwood boreal forest stand dynamics in central Canada (Shugart et al. 1992). Our objective is to summarize the stand dynam-ics of various mixedwood forest communities in Riding Mountain (Manitoba, Canada), and to examine the major factors driving these compositional and structural changes. We use multivariate methods to: (a) delineate eight forest stand-types and describe their composition, diversity, and vegetation-environment relationships; (b) determine the relative importance of seed source proximity, biotically-controlled site factors, and edaphic conditions in determining the composition and abundance of advance regeneration in these stand-types; and (c) infer successional trajectories for the stand-types using static size-structure analysis. Based on these results, we develop a comprehensive synoptic model of stand dynamics for the Riding Mountain region which considers environmental variation (moisture and nutrient status), seed source proximity, and disturbance. The implications of our model to the long-term sustainable management of the Riding Mountain forests are also discussed.

Study area

Location and physiography

Riding Mountain National Park (RMNP) in west-central Manitoba is approximately 3000 km^2 in size (Figure 1). It forms the extreme southeastern extension of the
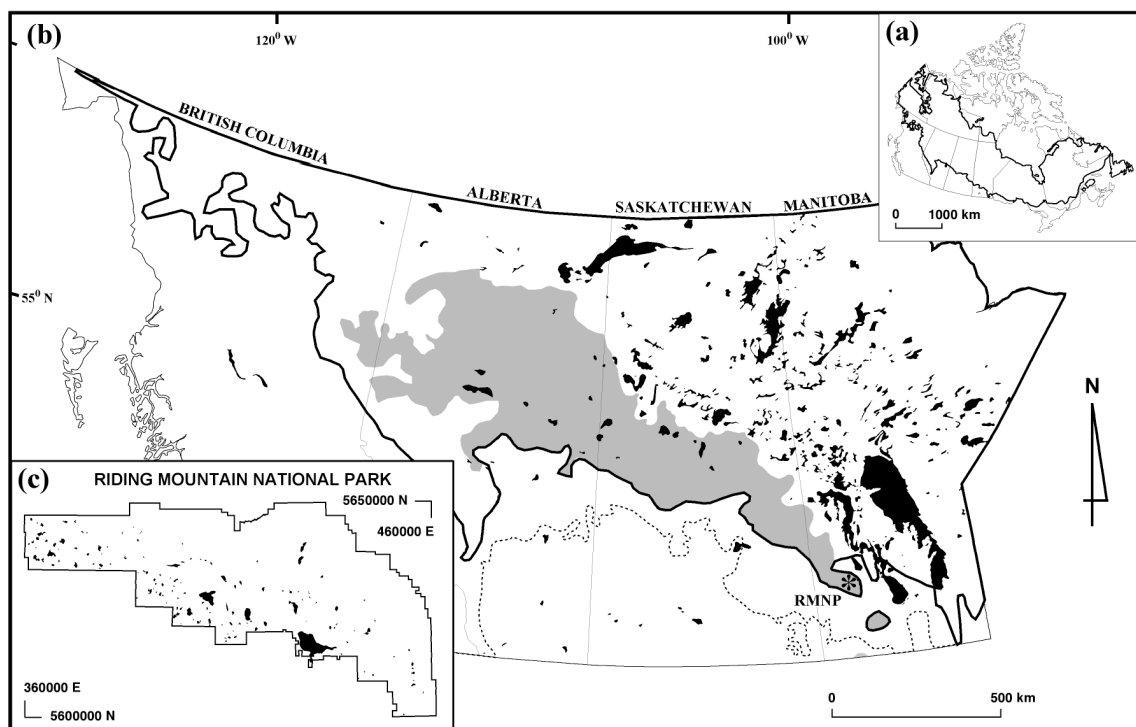

Figure 1. Study area. (**a**) Extent of the boreal forest in Canada, delineated by thick line. (**b**) Location of Riding Mountain National Park (* = RMNP) in western Canada. Shaded area is the Mixedwood Boreal Section of Rowe (1972); dotted line shows the northern limit of contiguous grasslands. (**c**) Outline of Riding Mountain National Park, Manitoba. Black areas are open water.

Mixedwood Section of the Boreal Forest Region (Rowe 1972). RMNP is bounded to the south and east by the Aspen-Oak Region, and to the west by the Aspen Region (Rowe 1972). RMNP is situated on a plateau marking the transition from the first prairie level (the Manitoba Plain) to the second prairie level (Saskatchewan Plain), an elevational rise of approximately 300 m. The Park is bounded to the east by the Manitoba Escarpment, to the north by the broad valley occupied by the Wilson and Valley rivers, and to the south by a plain that slopes gradually towards the Assiniboine valley (Lang 1974). Major river systems include the Vermillion and Wilson Rivers, which are the largest of the north-flowing rivers; the upper reaches of the Little Saskatchewan River, which drains the southeastern portion of the Park; and Birdtail Creek, which drains the western portion of the Park southward towards the Assiniboine River.

Bedrock in the region originated from silt deposits laid down in shallow Cretaceous seas between 136-165 million years ago (Lang 1974). The largest and deepest geological formation underlying the Park is the Riding Mountain formation, which covers most of southwestern Manitoba including the Porcupine Hills, Duck Mountain and Riding Mountain. This formation has a width of up to 200 km and a maximum depth of 310 m, and is composed of non-calcareous gray shale. The "upland" (Saskatchewan Plain) region of RMNP has a rolling topography, with extensive deposits of calcareous glacial till (Ritchie 1964). Conspicuous terminal moraines are rare, but hummocky disintegration moraines, till plains and local deposits of glaciofluvial gravels and alluvium are extensive. Sand and gravel beach ridges formed by glacial Lake Agassiz occur near the base of the Manitoba Escarpment.

Vegetation

Upland stands on glacial till are typically dominated by white spruce, trembling aspen, balsam poplar, paper birch and less commonly balsam fir. Black spruce is found in poorly-drained, peat-filled depressions, often in association with eastern larch (*Larix laricina*). Black spruce is also found with jack pine on well-drained sandy soils in the south-eastern portion of RMNP. A number of non-boreal tree species, including green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), Manitoba maple (*Acer negundo*), and bur oak (*Quercus macrocarpa*) also occur in RMNP, mainly on rich soils along the Manitoba Escarpment where precipitation is greater and catastrophic fires less frequent. Extensive monospecific stands of bur oak are found on excessively drained gravelly outwash plains at the base of the Manitoba Escarpment. Hybrid poplar (*P. x jackii*) occurs infrequently along the lower Escarp-

ment slopes. The dominant tall shrub of well-drained uplands is beaked hazelnut. Another tall shrub, mountain maple (*Acer spicatum*), is most commonly encountered on moist clay-textured soils and is particularly abundant on the lower slopes of the Escarpment.

Climate

RMNP lies within Köppen's Humid Microthermal Climatic zone, characterized by a rain-snow climate with cold winters and warm summers. Total summer precipitation is greatest along the Manitoba Escarpment (eastern portions of RMNP), and lowest in the west and on the Manitoba Plain to the east of the Park boundary (Caners 2001). Annual precipitation ranges from 40.6-50.8 cm, with approximately 80% falling between April and October (Bailey 1968). June is the wettest month, with a mean rainfall of 9.8 cm (Environment Canada 1993). Wasagaming (50°39'N 99°58'W; 622 m a.s.l.) has a temperature range of -19.7°C (mean January) to 16.5°C (mean July), with a mean daily temperature of 0.0°C (Environment Canada 1993). The mean annual growing season is between 160-180 days (Waldron 1966), with an average of 105 frost-free days from May 25-30 to September 10-15 (Bailey 1968).

Quaternary ecology

The last remnants of the ice sheet from the Wisconsin Ice Age retreated from the Riding Mountain area approximately 12,500 years ago (Lang 1974). An early Holocene spruce forest was present in southern Manitoba and Saskatchewan, and adjacent regions of northwestern Minnesota and the Dakotas, by 11,500 years ago. Pollen records indicate that this forest was dominated by *Picea* in association with *Artemisia*, *Shepherdia canadensis*, Cyperaceae, and to a lesser extent *Juniperus*, *Fraxinus*, *Larix*, *Populus*, *Pinus*, *Betula* and *Alnus* (Ritchie 1985). These xeric floristic elements indicate that the climate during this immigrant forest phase was comparatively dry.

By about 10,000 years ago the climate became even warmer and drier (Ritchie 1969). Spruce abundance declined sharply, and the forest was replaced by a treeless vegetation dominated by grasses, forbs and shrubs (*Salix*, *Juniperus*, *Shepherdia argentea*). This change in floristic composition was coincident with the Hypsithermal period. By about 6,500 years ago, there was an increase in the abundance of bur oak, and beaked hazelnut had appeared (Ritchie 1985). After this time, the abundance of xeric grassland species began to decline, indicating cooler and moister conditions. The regional flora changed dramatically approximately 2,500 years ago with the arrival of several boreal tree and shrub species and a further de-

cline in grasslands, the result of a "marked deterioration in regional climate" (Ritchie 1969). The forests of RMNP took their present form at this time, with increasing abundance of *Picea*, *Pinus*, *Larix*, *Alnus* and *Abies*.

Disturbance history

Fire. Fire scar records and ages of trembling aspen stands indicate that recent catastrophic fires occurred around 1822, 1853-1855, 1889-1891 and 1918-1919 (Rowe 1955). Tunstell (1940) indicated that fires were particularly common between 1885-1889, burning several hundred thousand acres. Dickson (1909) noted that two fires in close succession (about 1890) burned over 70% of the western half of RMNP. Large areas of jack pine forest in the southeastern portion of RMNP have burned repeatedly since the turn of the century (Sentar 1992, Parks Canada 1997). Recent large fires in RMNP have occurred in 1940 (21,000 ha), 1961 (9,000 ha) and 1980 (21,000 ha).

Logging. Peak logging activity in RMNP was coincident with European settlement and railway construction at the end of the 19th century (Bailey 1968). Milling operations began in Riding Mountain in the 1870s, and were concentrated close to settlement activity on the periphery of the Manitoba Escarpment (Sentar 1992). Fire frequently accompanied timber harvesting, set by loggers and settlers burning hay meadows or clearing land (Sentar 1992). White spruce was the most heavily exploited species in RMNP, but jack pine, balsam fir, trembling aspen, bur oak, green ash and black spruce were also harvested (Bailey 1968). The Riding Mountain Forest Reserve was officially established by Departmental Order on July 13, 1895. The Forest and Parks Act transferred control of this area from the Lands Branch to the Forestry Branch of the then Department of the Interior, changing its designation from Timber Reserve to Forest Reserve (Tunstell 1940). In 1906 an Order-in-Council established cutting regulations for the Reserve, although illegal timber cutting continued (Sentar 1992). Regulations were modified in 1930 when the area was given National Park status, although limited timber harvesting continued in RMNP until the mid-1960s.

Herbivores. There are no detailed accounts of ungulate population densities in RMNP prior to European settlement. Historical records document the dramatic depletion of elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) in Riding Mountain following European settlement in the late 19th century (Bird 1961, Trottier et al. 1983). The elk and moose populations declined again in the late 1940's following a series of severe winters. Subsequent elk recovery was rapid, with the population reaching an estimated 12,000 indi-

viduals by 1946. Moose were much slower to recover, with an estimated 250 individuals in 1950. In 1979, elk and moose populations were estimated at approximately 3,900 and 5,100 individuals, respectively (Trottier et al. 1983), and by 1996 at 5,000 and 4,500 individuals, respectively (Parks Canada 1997). In RMNP, ungulate herbivores selectively browse shoots of trembling aspen, balsam poplar, paper birch, green ash, Manitoba maple, American elm, bur oak and balsam fir, but largely avoid white and black spruce (personal observation). Mountain maple, beaked hazelnut and trembling aspen are important components of moose diet in southern Manitoba (Trottier et al. 1983). Hazelnut is also an important dietary component for elk, white-tailed deer and hare (Trottier 1981). Beavers (*Castor canadensis*) modify habitats through tree-felling and water impounding activities. Removal of deciduous trees (particularly trembling aspen) along watercourses favours conifer growth, while stream damming kills flooded vegetation and modifies local hydrology (Naiman et al. 1988). The history of beaver in the Riding Mountain area is similar to that of most Canadian regions. Trapping and land clearance during European settlement resulted in the near extinction of beaver (Bird 1961). Since 1976, however, the population has stabilized at approximately 3,400 colonies (1.1 colonies per km^2), with each colony consisting of 4-7 individuals (Parks Canada 1997). In 1980, the beaver density in RMNP was one of the highest measured in Canada, reflecting complete protection from trapping (Trottier 1980).

Pests and pathogens. An outbreak of eastern larch sawfly became epidemic in the Park in 1913, killing an estimated 30-40% of the larch (Evans 1923). Records indicate that spruce budworm has caused considerable damage to stands of white spruce and balsam fir in certain regions of Manitoba (Brandt 1993). Historical and recent records for RMNP indicate that budworm has not been a major disturbance agent, although occasional outbreaks have been noted (Tunstell 1940, Brandt 1993). The bronze birch borer has previously caused extensive damage to paper birch (Tunstell 1940), and Dutch elm disease has recently resulted in the widespread mortality of mature American elm (personal observation).

Methods: data collection

A total of 202 plots, each 10 x 10 m in size, were located throughout RMNP (Caners 2001). The plots were located using a stratified random approach: within each strata plots were randomly located within uniform stands, excluding areas showing evidence of past logging and other forms of human disturbance. A complete inventory of vascular and non-vascular plant species was conducted

in each plot. Cover-abundance estimates were taken for each species in each of six vertical strata: (1) canopy trees, > 15 m in height; (2) subcanopy trees, 10-15 m in height; (3) low canopy trees and tall shrubs, 2-10 m in height; (4) saplings and low shrubs, 0.5-2 m in height; (5) tree seedlings, graminoids, forbs, ferns and fern allies, typically < 0.5 m in height; (6) bryophytes and lichens, on the forest floor.

In each plot, the diameter (at 1.3 m) and height of each tree was measured, and all seedlings (< 1.3 m), saplings and mature stems were counted. An overall measure of herbivore browsing intensity was determined for each woody plant species, by estimating the ratio of the number of twigs browsed to the total number of twigs (Trottier et al. 1983). This measure was converted to an ordinal scale: (1) absent; (2) low-moderate; (3) moderate; (4) moderate-heavy; (5) heavy.

A soil pit was dug to a depth of 1 m near the centre of each plot, and a soil core from the upper 30 cm of the mineral or organic soil was collected. Depth of the A-horizon and depth to carbonates (using dilute 1:10 HCl) were recorded, and profiles were identified to the subgroup level of the Canadian System of Soil Classification (Agriculture Canada Expert Committee on Soil Survey 1987). Each soil core was analyzed for pH and conductivity (µS/cm), and particle size distribution (percent sand, silt and clay) was determined using the Bouyoucos hydrometer method (Kalra and Maynard 1991).

Percent bareground, slope, aspect and location (UTM coordinates) measures were also made at each plot. The quantity of decaying wood on the forest floor, in the form of fallen boles or large branches, was estimated using an ordinal scale: (0) absent; (1) low; (2) moderate; (3) high. Wood was considered to be "decayed" if it was spongy and could be mechanically separated by hand. Minimum stand age estimates were obtained by taking increment cores (at 1.3 m height) from 2-3 of the largest individuals of each tree species in each plot. The oldest tree provides a conservative estimate of time since the last catastrophic stand-replacing fire. Estimates are conservative since tree cores taken at 1.3 m underestimate actual tree age. Tree cores were mounted, labeled, finely sanded (with 400 grit sandpaper) and polished (with 600 grit sandpaper), and rings were counted with a dissecting microscope. Stand age estimates from tree cores were cross-referenced to published forest fire maps to verify accuracy.

Methods: data analysis

Stand classification and description

Correspondence analysis (CA), a method of "indirect gradient analysis" (Leps and Smilauer 2003), was used to produce reduced (two-dimensional) summarizations of the vegetation relationships of the sampled stands (CANOCO; ter Braak 1987). 196 plots and 247 "pseudospecies" (all non-tree species, plus tree species in each strata) were included in the initial analysis (6 regenerating plots located in the 1980 fire site were excluded). Percent cover values were square-root transformed and rare species were "downweighted" (ter Braak 1987). CA is known to highlight unique plot-species assemblages, while compressing the remaining plots in ordination space (Leps and Smilauer 2003). We used this feature of CA to our advantage to delineate characteristic forest stand-types. Specifically, we produced a series of residual CA ordinations to highlight and delineate characteristic stand-types. At each stage, a unique group of plots (a given stand-type) was removed, and the remaining plots re-ordinated. This continued until unique groups of plots could no longer be visually distinguished, indicating that the salient features of the vegetation data resolved (Caners 2001). A total of 8 floristically distinct forest stand-types were delineated in this way (Table 1).

Species diversity

Effective species richness values (Simpson's N2, Hill 1973) were determined for the tree, shrub, herb and bryophyte strata in each of the 8 forest stand-types. N2 approaches a maximum value of s (total number of species) if all species are equally abundant, and a minimum value of 1 when one of s species predominates. To allow comparisons among the 8 forest stand-types (which differed in sample size, Table 1), N2 calculations were determined from 10 randomly-selected plots of each stand-type. This randomization procedure was repeated 100 times for each stand-type – we report mean N2 values (for 10 plots) from the 100 randomizations for each vegetation strata (trees, shrubs, herbs, bryophytes).

Vegetation-environment relationships

Canonical correspondence analysis (CCA), a "direct gradient analysis" or "constrained ordination", is the canonical version of CA (ter Braak 1986, Leps and Smilauer 2003). Output describes how well the species-plot information is predicted by the environmental information. The method assumes that species abundances are unimodal functions along environmental gradients.

We used CCA (CANOCO; ter Braak 1987) to determine the relationship between 171 species in 179 stands, constrained by 6 edaphic-environmental variables (6 regeneration plots from the 1980 Rolling River burn were excluded, as were 17 plots occurring on organic substrates). The edaphic-environmental variables used in

Table 1. Sample size (*n*), dominant canopy species (>15 m), dominant advance regeneration species (>2 m), and dominant shrub species for the eight (I-VIII) defined stand types. Species are listed in order of decreasing frequency and cover.

Stand Type	n	Stand Type Name	Dominant Canopy Species	Dominant Advance Regeneration Species	Dominant Shrub Species
I	15	Black Spruce Organic	Black spruce	Black spruce	Labrador tea; Bog cranberry
II	17	Jack Pine - Black Spruce	Jack pine; White spruce	Black spruce	Prickly rose; Common snowberry
III	15	Bur Oak	Bur oak	Bur oak	Downy arrowwood; Beaked hazelnut; Choke cherry; Saskatoon
IV	16	Eastern Deciduous	Green ash; American elm; Manitoba maple	Green ash; Manitoba maple; American elm	Beaked hazelnut; Chokecherry; American bush-cranberry; Poison ivy
V	18	Balsam Fir	Balsam fir	Balsam fir	Mountain maple; Beaked hazelnut; Choke cherry; Prickly rose
VI	22	Trembling Aspen - Birch - Mountain Maple	Trembling aspen; Balsam poplar	Paper birch; green ash	Mountain maple; Beaked hazelnut; Chokecherry; Red osier-dogwood
VII	46	Trembling Aspen - Balsam Poplar	Trembling aspen; Balsam poplar	Trembling aspen	Beaked Hazelnut; Prickly rose; Chokecherry; Saskatoon
VIII	47	White Spruce	White spruce; Trembling aspen	White spruce	Beaked hazelnut; Prickly rose; Common snowberry; Saskatoon

Table 2. Mean (bold), range and standard deviation (italics) of edaphic and environmental variables measured for each of the eight (I-VIII) stand types.

Stand Type	n	Sand (%)	Silt (%)	Clay (%)	pH	Conductivity (µS/cm)	LFH Depth (cm)	Depth of A (cm)	Depth to Carb (cm)	Bareground (%)	Slope (degrees)	Browse (1-5)	Stand Age (years)
I	15	-	-	-	**6.8** (3.88 - 7.87) *0.9*	**239.6** (110 - 680) *135.9*	-	-	-	**2.3** (2.0 - 20.0) *4.9*	**0.5** (0.0 - 5.0) *1.3*	**1.7** (1.0 - 3.0) *0.7*	**123** (79-163) *34.0*
II	17	**41.3** (27.7 - 67.9) *9.0*	**28.8** (19.3 - 43.4) *7.5*	**29.9** (12.8 - 45.0) *7.5*	**6.1** (5.0 - 7.8) *0.8*	**215.5** (92.0 - 480.0) *105.2*	**5.4** (2.0 - 10.0) *1.9*	**8.7** (1.0 - 14.0) *3.7*	**24.1** (6.0 - 67.0) *18.8*	**21.1** (1.0 - 60.0) *17.4*	**3.9** (0.0 - 15.0) *3.4*	**2.5** (1.0 - 5.0) *1.1*	**102** (58-151) *29.7*
III	15	**62.7** (34.2 - 79.1) *13.6*	**19.8** (9.6 - 40.2) *8.8*	**17.5** (8.0 - 30.5) *5.8*	**6.7** (5.8 - 7.6) *0.5*	**156.5** (58.0 - 350.0) *83.2*	**4.2** (0.5 - 6.0) *1.5*	**5.2** (1.0 - 12.0) *3.4*	**20.0** (1.0 - 43.0) *11.4*	**5.7** (1.0 - 20.0) *6.3*	**2.4** (0.8 - 5.0) *1.3*	**4.5** (3.0 - 5.0) *0.6*	**152** (95-196) *26.7*
IV	16	**45.3** (8.5 - 77.5) *23.7*	**30.0** (13.5 - 64.2) *14.9*	**24.7** (9.0 - 49.8) *13.3*	**7.2** (5.9 - 7.8) *0.6*	**378.1** (170.0 - 740.0) *162.0*	**7.1** (4.0 - 11.0) *2.3*	**5.1** (0.0 - 20.0) *6.2*	**15.9** (0.0 - 66.0) *23.3*	**7.8** (1.0 - 30.0) *7.9*	**2.4** (0.7 - 5.0) *1.4*	**4.0** (3.0 - 5.0) *0.5*	**112** (76-170) *34.8*
V	18	**43.6** (24.5 - 69.5) *15.6*	**28.3** (11.2 - 40.2) *9.2*	**28.1** (17.7 - 45.0) *8.8*	**6.7** (5.1 - 8.0) *1.0*	**237.7** (75.0 - 505.0) *112.2*	**7.9** (3.0 - 18.0) *4.6*	**8.1** (0.0 - 15.0) *4.0*	**21.6** (0.0 - 49.0) *16.7*	**20.2** (1.0 - 50.0) *15.5*	**5.3** (2.0 - 15.0) *3.6*	**3.3** (2.0 - 5.0) *1.0*	**121** (66-165) *32.6*
VI	22	**38.8** (19.7 - 80.7) *17.2*	**29.3** (4.8 - 38.2) *9.2*	**32.0** (14.5 - 46.6) *9.3*	**6.6** (4.8 - 8.1) *0.7*	**243.7** (100.0 - 480.0) *96.5*	**5.9** (0.5 - 11.5) *2.5*	**14.9** (0.5 - 53.0) *14.4*	**16.1** (0.0 - 53.0) *16.1*	**18.0** (1.0 - 50.0) *14.9*	**6.6** (2.0 - 27.0) *6.9*	**3.4** (1.0 - 5.0) *1.1*	**97** (55-145) *24.0*
VII	46	**34.0** (11.7 - 74.3) *15.2*	**31.9** (8.0 - 49.8) *8.0*	**34.0** (14.8 - 67.5) *12.2*	**6.3** (5.0 - 7.7) *0.7*	**242.6** (40.0 - 520.0) *122.7*	**5.8** (1.0 - 13.0) *2.8*	**11.6** (2.0 - 40.0) *9.8*	**11.9** (0.0 - 34.0) *11.4*	**11.6** (1.0 - 70.0) *15.0*	**4.9** (1.0 - 20.0) *3.7*	**3.5** (1.0 -5.0) *1.1*	**80** (37-150) *21.3*
VIII	47	**39.9** (19.7 - 75.9) *14.5*	**29.5** (12.8 - 43.4) *7.4*	**30.7** (8.0 - 54.6) *10.5*	**6.4** (4.6 - 8.4) *0.8*	**279.6** (50.0 - 920.0) *171.6*	**6.0** (0.5 - 12.0) *3.0*	**11.3** (3.0 - 30.0) *6.6*	**10.4** (0.0 - 35.0) *9.0*	**21.0** (1.0 - 80.0) *22.2*	**6.3** (0.1 - 30.0) *6.7*	**3.3** (1.0 - 5.0) *1.0*	**92** (44-180) *25.5*

CCA were: organic depth, pH, conductivity, percent sand content, pH, conductivity, percent sand content, percent clay content, and percent slope. Species occurring in fewer than 3 plots were excluded, and rare species were downweighted. Percent cover values were square-root transformed. Percent slope was log transformed to meet the assumption of multivariate normality (ter Braak 1986, 1987).

Determinants of advance regeneration composition and abundance

We also used CCA to determine the relative importance of three variable sets (seed source proximity, biotically-controlled site factors, and edaphic conditions) in determining the composition and abundance of advance regeneration (trees <10 m in height) beneath established (post-fire) canopies. To our knowledge, CCA has not been previously used in this way: other boreal studies have used stepwise multiple regression, linear regression and/or correlation analysis to address this question (e.g., Kneeshaw and Bergeron 1996, Galipeau et al. 1997, Kneeshaw and Burton 1997). We recognize two distinct advantages of the CCA approach: it allows for the simultaneous analysis of species and environmental datasets, and it readily accommodates non-linear data (ter Braak 1987). For each of 9 tree species, we computed total basal area (of the seedlings (< 0.5 m in height), saplings (0.5-2 m) and low canopy trees (2-10 m)) to summarize the abundance of advance regeneration in each of 154 plots (some plots were excluded since they had no advance regeneration). In these analyses, we considered all seedlings, saplings and low canopy trees as "advance regeneration". However, by using basal area we gave much greater weight to larger (taller) individuals, under the assumption that such individuals have a much higher survival probability, i.e., a much greater likelihood of reaching the canopy.

Three variable sets were used to constrain the advance regeneration abundance in the 154 plots: (1) total basal area of each of 9 canopy tree species (trees >10 m in height), which quantifies reproductive source availability; (2) biotically-controlled site factors, which quantifies seedbed and early growing conditions: total cover of bareground, bryophytes, herbs, mountain maple, beaked hazelnut, other shrubs (i.e., not including beaked hazelnut and mountain maple), herbivore browsing intensity, and minimum stand age; (3) edaphic factors, which quantifies environmental conditions: soil pH, conductivity, percent sand content, percent clay content, depth of organic horizon, and percent slope. Cover values and percent slope were log transformed to meet the assumptions of multivariate normality.

Canopy dynamics

For each of the 8 forest stand-types, we determined the mean frequency of occurrence (per 10 x 10 m plot) for each of 12 tree species in each of 3 canopy height classes (upper canopy, >15 m; subcanopy, 10-15 m; lower canopy, 2-10 m). Saplings (individuals < 2 m in height) were not considered, since mortality of smaller trees may be high and thus not reflective of potential canopy change. We used CA to summarize relationships among the 8 stand-types and 3 height classes, based on differences in tree species composition. The input matrix was 24 objects (8 stand-types x 3 height classes) by 12 variables (tree species). Canopy dynamics (succession trajectories) were inferred for the 8 stand-types by connecting the 3 height classes in two-dimensional ordination space in the order upper canopy, subcanopy, and lower canopy, under the assumption that individuals in the smaller height classes represent the future composition of the upper canopy ("size-class" ordination, e.g., Carleton and Maycock 1978, Bergeron and Dubuc 1989).

Results

Stand-type characteristics

Stand-type III, and to a lesser extent stand-types IV and V, tend to occur on more coarse-textured sandy soils, while stand-types VI-VIII occur on soils of higher clay content with a deeper A-horizon (Table 2). Organic (peat) substrates are characteristic of stand-type I. The stand-types have similar values of soil pH (neutral to very slightly basic). Conductivity, a general indicator of soil nutrient status, is lowest in stand-type III and highest in stand-type IV. The depth to carbonates, a general indicator of soil drainage, is highest in types II, III and V (well-drained stands), and lowest in stand-types VII and VIII (poorly drained). Stand-types VI and VIII tend to occur on slopes.

Soils of stand-type I are organic Hydric Fibrisols. In stand-type II, Gleyed Grey Luvisols and Orthic Luvic Gleysols predominate, whereas Orthic Gray Luvisols and Gleyed Gray Luvisols are most commonly encountered in stand-types V-VIII. Orthic Eutric Brunisols, Cumulic Regosols and Orthic Regosols predominate in stand-types III and IV. The oldest forests occur in stand-type III (mean age >150 years) and in stand-types I-II and IV-V (mean ages >100 years); stand-types VI-VIII are the youngest forests (mean stand age <100 years). Ungulate herbivore browsing is heaviest in stand-type III, moderately heavy in types IV-VIII, and low in stand-types I and II.

Table 3. Effective species richness (N2) per ten 10 x 10 m plots, and standard deviation (italics), for various plant canopies for stand types I-VIII. Calculations are based on species cover.

Stand Type	n	All Species	Trees	All Understory	Shrubs	Herbs	Bryophytes
I	15	6.7	1.2	10.1	4.5	6.4	5.0
		1.0	*0.2*	*2.0*	*1.6*	*1.1*	*1.0*
II	17	7.5	3.0	5.2	6.6	13.6	2.3
		1.4	*0.6*	*1.5*	*1.2*	*2.3*	*0.2*
III	15	6.6	1.1	8.2	5.0	3.3	4.2
		0.5	*0.0*	*0.9*	*0.7*	*0.9*	*1.5*
IV	16	11.2	3.9	8.9	4.6	4.7	4.5
		1.1	*0.5*	*1.5*	*1.2*	*1.0*	*1.4*
V	18	9.2	2.5	8.5	2.2	9.2	6.2
		1.4	*0.5*	*2.9*	*0.5*	*1.2*	*1.7*
VI	22	8.0	3.2	4.9	2.6	10.5	3.3
		0.9	*0.5*	*0.9*	*0.3*	*3.2*	*0.8*
VII	46	7.3	2.2	5.7	2.5	11.3	2.4
		1.6	*0.5*	*2.3*	*0.8*	*3.9*	*0.5*
VIII	47	7.2	1.9	17.2	4.1	12.3	4.9
		1.3	*0.2*	*4.6*	*1.3*	*2.4*	*1.1*

Mean effective species richness for trees, shrubs, herbs and bryophytes varies considerably among stand-types (Table 3). Overall effective species richness is highest in stand-types IV-VI, and lowest in stand-types I and III. When only trees are considered, effective richness is highest in stand-types IV and VI (both of which have a mixed canopy composition) and lowest in stand-types I and III (monodominant stands of black spruce and bur oak, respectively). Effective richness of shrubs is highest in stand-types II and III and lowest in stand-types V-VII; the latter tend to be dominated by two aggressive tall shrubs, beaked hazelnut and mountain maple, which outcompete other species. Richness of the herb layer is greatest in stand-type II, followed by VI-VIII, and is lowest in stand-types III and IV. The high effective richness of stand-type II is largely attributable to high evenness of a comparatively species-poor flora. Bryophyte richness is greatest in stand-type V, which is attributable to high levels of downed wood debris that provides an excellent substrate for bryophytes. Lower bryophyte effective richness in stand-type II reflects dominance by a few common boreal species such as *Pleurozium schreberi* and *Hylocomium splendens*. By contrast, low bryophyte effective richness in stand-types VI and VII is attributable to the smothering effect of leaf litter in these deciduous-dominated stands.

Vegetation-environment relationships

The two-dimensional CCA ordination indicates a principal gradient (axis 1) of increasing nutrient status (higher pH and conductivity) from left to right, and a secondary gradient (axis 2) of increasing moisture status (higher soil clay content) from top to bottom (Figure 2). Stand-types II-IV form distinctive groups in the ordination space, but plots from stand-types V-VIII are intermixed. Upland stands dominated by jack pine and black spruce (stand-type II) have the lowest nutrient status, while bur oak stands (stand-type III) are characteristic of excessively drained, sandy-gravelly substrates. Plots with eastern deciduous forest species (green ash, American elm, Manitoba maple; stand-type IV) occur on nutrient-rich, basic substrates. Stand-types V-VIII occur on clay-dominated substrates of intermediate nutrient status, and are often found on slopes. Mixedwood boreal tree species (hardwoods: trembling aspen and balsam poplar; conifers: white spruce and balsam fir), and the tall shrubs beaked hazelnut and mountain maple, are characteristic of these four stand-types. The redundancy of the CCA vegetation-environment relationship (ratio of canonical to total inertia) is 0.338/4.172 = 8.1%, indicating that relatively little of the floristic variation is explained by the six measured soil-environmental variables. The unexplained variation may reflect unmeasured environmental trends, site history, and stochastic events (Borcard and Legendre 1994), as well as lack of fit of the canonical model (Okland 1999).

Determinants of advance regeneration composition and abundance

The first variable set, canopy composition (i.e., potential reproductive source), proved to be a good predictor of advance regeneration composition and abundance (Figure

3a; ratio of canonical to total inertia = 54.4%). In general, there is a strong one-to-one correspondence between the species composition of the upper canopy and that of the advance regeneration strata. This likely reflects the limited dispersability of boreal conifer seeds (white spruce, balsam fir), as well as the strong vegetative reproductive capacity of many boreal hardwoods (trembling aspen, balsam poplar, paper birch). The second variable set, biotically controlled site factors, was reasonably successful in predicting advance regeneration composition and abundance (Figure 3b; ratio of canonical to total inertia = 31.7%). Advance regeneration of trembling aspen and paper birch, which is primarily through vegetative reproduction (root or basal suckers), is associated with dense beaked hazelnut cover. White spruce and balsam fir advance regeneration is associated with high moss cover and abundant decaying wood, which offer excellent seedbed conditions for boreal conifers. In contrast, advance regen-
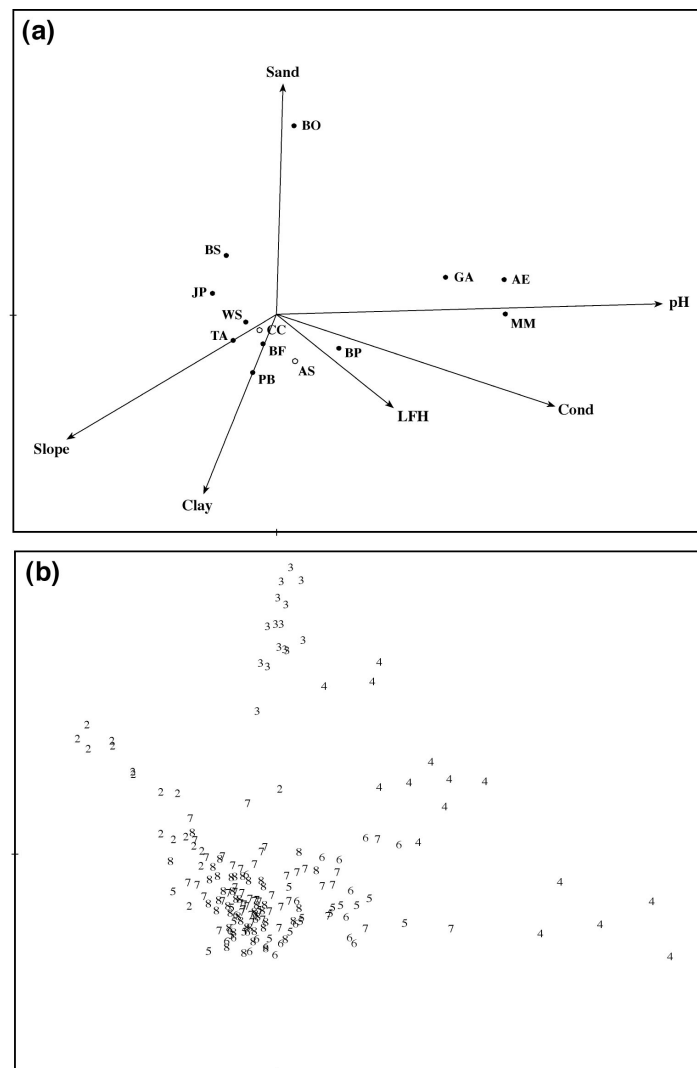

Figure 2. Canonical correspondence analysis (CCA) of 179 stands on mineral soil, utilizing 171 species and 6 environmental variables. Axis 1 (horizontal) = 39% of canonical inertia, Axis 2 (vertical) = 27% of canonical inertia. Redundancy (ratio of canonical to total inertia) = 0.338/4.172 = 8.1%. (a) Environmental variable biplot and species ordination: only the dominant trees (closed circles) and shrubs (open circles) are shown. Species codes: AE = American elm; AS = *Acer spicatum* (mountain maple); BF = balsam fir; BO = bur oak; BP = balsam poplar; BS = black spruce; CC = *Corylus cornuta* (beaked hazelnut); GA = green ash; JP = jack pine; MM = Manitoba maple; PB = paper birch; TA = trembling aspen; WS = white spruce. Environmental variable codes: Sand = percent soil sand content; pH = soil pH; Cond = soil electrical conductivity (μS/cm); LFH = depth of organic soil horizon; Clay = percent soil clay content; Slope = percent slope. (b) Stand ordination dual, wtih stands labelled by stand-type (II-VIII are labelled as 2-8). Note that stand-type I (ogranic substrates) was not included in this analysis.

eration of species of eastern deciduous forest affinity (green ash, American elm, Manitoba maple, and bur oak) are associated with sites with high herb cover and low moss cover. The third variable set, edaphic conditions, proved to be the poorest predictor of advance regeneration composition and abundance (Figure 3c; ratio of canonical to total inertia = 18.1%). Advance regeneration of eastern deciduous species is associated with more nutrient-rich, basic soils, while bur oak advance regeneration is most frequent on well-drained sandy soils. Advance regeneration of boreal mixedwood species (white spruce, balsam fir, trembling aspen, paper birch) is associated with clay soils with deep organic horizons.

Canopy dynamics

The size-class ordination of all eight stand-types (Figure 4a) reveals three strong outliers: stand-types I (Black Spruce Organic), II (Jack Pine-Black Spruce) and III (Bur Oak). The successional vector for stand-type I is circular and short, indicating that these stands are self-replacing. Stand-type II has a longer vector that converges towards dominance by black spruce. These stands will become increasingly dominated by black spruce as the jack pine naturally thin: jack pine produces serotinous cones and fails to regenerate in the absence of fire. Stand-type III also has a short successional vector, indicating that mono-dominant bur oak stands on excessively drained sites are self-replacing.

Size-class ordination was performed again after removing the outlier stand-types I-III, in order to resolve successional trends of the 5 remaining stand-types (Figure 4b). The position of paper birch near the centre of the ordination diagram suggests that this species will remain a minor component of all 5 stand-types. The successional vector for stand-type IV (Eastern Deciduous) diverges from the mixedwood species, indicating that these stands will become increasingly dominated by American elm, Manitoba maple, bur oak and green over time. Stand-type V (Balsam Fir) has a short and circular vector centered around balsam fir, indicating that these stands will become increasingly dominated by balsam fir as white spruce and paper birch are removed from the canopy.
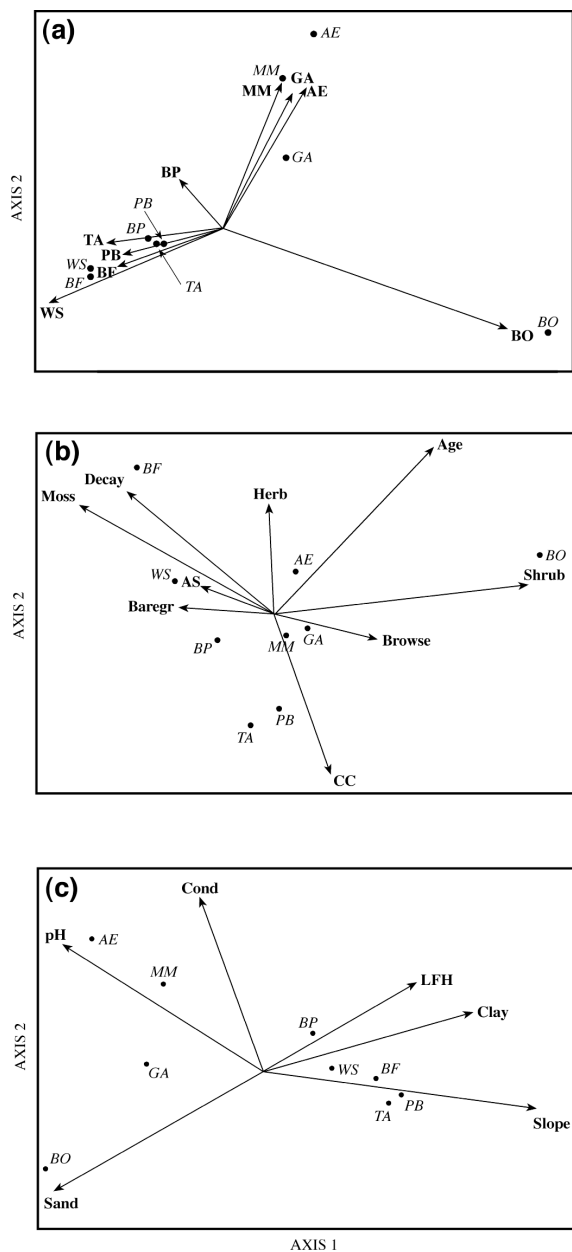
Figure 3. Canonical correspondence analysis (CCA) ordinations of three variable groups constraining the advance regeneration in 154 stands. Advance regeneration centroids are shown as filled circles with species codes in italics (codes as in Figure 2). (a) Constrained by canopy composition (arrows). Axis 1 = 33% of canonical interia, Axis 2 = 26% of canonical inertia, Redundancy (ratio of canonical to total inertia) = 2.234/4.104 = 54.5%. Canopy species codes as in Figure 2. (b) Constrained by biotically-controlled site factors (arrows). Axis 1 = 44% of canonical inertia, Axis 2 = 20% of canonical inertia, Redundancy (ratio of canonical to total inertia) = 1.299/4.104 = 31.7%. Variable codes: Moss = total moss cover; Decay = amount of decaying wood on forest floor; Herb = total herbaceous cover; Age = minimum stand age; Shrub = total shrub cover excluding beaked hazelnut and mountain maple; Browse = herbivore browsing intensity; CC = total cover of *Corylus cornuta* (beaked hazelnut); Baregr = total bareground cover; AS = total cover of *Acer spicatum* (mountain maple). (c) Constrained by edaphic factors (arrows). Axis 1 = 47% of canonical inertia, Axis 2 = 31% of canonical inertia, Redundancy (ratio of canonical to total inertia) = 0.744/4.104 = 18.1%. Variable codes: Sand = sand content of mineral soil; Clay = clay content of mineral soil; LFH = depth of organic soil horizon; Cond = soil electrical conductivity (μS/cm); pH = soil pH; Slope = percent slope.
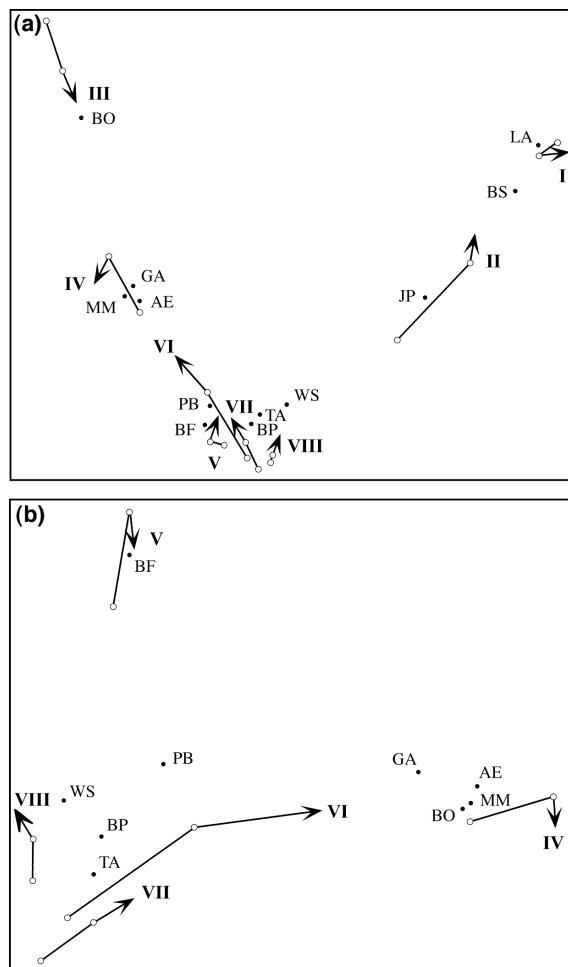
Figure 4. Correspondence analysis (CA) of tree size-classes. Species codes as in Figure 2, plus LA = larch. Each arrow connects the upper canopy, subcanopy (open circles) and lower canopy (arrow tip) of the specified stand-type. (a) CA ordination of all stand-types (I-VIII), and species ordination dual: Axis 1 (horizontal) = 27% of total inertia, Axis 2 (vertical) = 23% of total inertia. (b) CA ordination of stand-types IV-VIII and species ordination dual. Axis 1 (horizontal) = 47% of total inertia, Axis 2 (vertical) = 27% of total inertia.

Stand-type VI (Trembling Aspen-Birch-Mountain Maple) has a long directional vector, indicating a potential for strong temporal change in species composition. These stands, the canopies of which are presently dominated by trembling aspen and paper birch, are expected to become increasingly dominated by eastern deciduous species (particularly green ash) that are currently common in the lower subcanopy. This is an interesting finding, as it suggests that some deciduous boreal stands may undergo succession toward eastern deciduous dominance. Stand-type VII (Trembling Aspen-Balsam Poplar) has a fairly short vector, indicating little compositional change over time. Although individual boles of both trembling aspen and

balsam poplar are comparatively short-lived, both species are capable of prolific vegetative reproduction from root suckers, thus ensuring stand self-replacement. In addition, the high tall shrub cover characteristic of these stands strongly limits white spruce and balsam fir seedling recruitment. The succession vector for stand-type VIII (White Spruce) is short and converges toward white spruce. These stands are proceeding towards increased dominance of white spruce, possibly in association with paper birch and occasionally balsam fir. The succession vector is also directed away from trembling aspen and balsam poplar, as these species were not commonly found in lower canopies.

Discussion

Historically, fire has played a critical role in determining the distribution and development of forest stand-types in the region. The eastern uplands of Riding Mountain are cooler and have higher precipitation, resulting in fewer and less extensive fires. In addition, the dramatic relief and reticulation of stream valleys along the Manitoba Escarpment reduces fire spread (most fires are driven from the south and west by summer prevailing winds). The northeastern region of Riding Mountain has thus experienced comparatively few large, catastrophic fires; as a result, "late successional" forest stands (*sensu* Dix and Swan 1971) are much more common there. For example, mature stands of white spruce (stand-type VIII) are most frequently encountered in the east. Balsam fir (stand-type V) occurs in areas that burn infrequently - in stream valleys traversing the Manitoba Escarpment, and on the leeward side of large lakes that block the spread of fire. Stands containing eastern deciduous tree species (stand-types IV and VI) are almost exclusively found in areas that burn infrequently: stand-type IV occurs on rich soils at the base of the Manitoba Escarpment, while stand-type VI is most common on north and east-facing slopes of the Escarpment. By contrast, the western uplands of Riding Mountain are warmer and have lower precipitation, resulting in more frequent catastrophic forest fires: similar fire regimes prevail further west, in Saskatchewan (Dix and Swan 1971) and Alberta (Johnson et al. 1998). In addition, the relatively flat terrain of this region provides few barriers to the spread of fire. As a result, "early-successional" species that are adapted to recurrent catastrophic fires, such as trembling aspen, balsam poplar and beaked hazelnut (stand-type VII), are more commonly encountered in the western regions of RMNP. Balsam fir is essentially absent from the western regions, since recurrent catastrophic fires have eliminated parental seed sources of this late-successional species. Another early-successional stand-type, upland jack pine – black spruce stands (stand-

type II), occur in the south-east region of Riding Mountain on sandier soils. Historically, fires spreading from the grasslands and aspen parkland region further south regularly burned these stands.

Fire suppression, together with agricultural expansion along the periphery of protected forests, will result in decreased fire frequency and severity along the southern edge of North American boreal forest (Weir and Johnson 1998). Over time, decreased fire frequency will result in a much greater abundance of "old-growth" stands on the landscape. Small-scale canopy gap formation, rather than large-scale catastrophic fire, will become the predominant disturbance process driving canopy change in these "old-growth" forests (Frelich and Reich 1995, Kenkel et al. 1997). The size of canopy gaps may be critical: small gaps (e.g., mortality of a canopy tree) tend to favour understory vegetation and late-successional (shade-tolerant) advance regeneration (Kneeshaw and Bergeron 1998), while larger gaps (e.g., spruce budworm damage) facilitate the perpetuation of early-successional hardwoods such as trembling aspen (Kneeshaw and Bergeron 1998, Bergeron 2000). A major challenge in boreal forest ecology is to understand the consequences of this "paradigm shift" in disturbance regime – from large-scale, synchronous catastrophic fire to small-scale, asynchronous gap formation – on forest stand composition, structure, and dynamics (Kenkel et al. 1997).

Determinants of advance regeneration composition and abundance

Our results indicate that the composition and abundance of advanced tree regeneration is best explained by the composition of the existing canopy. Similar results have been obtained from both eastern hardwood forests (Abrams 1986, McClanahan 1986) and boreal forests (Kneeshaw and Bergeron 1996, Galipeau et al. 1997, Cornett et al. 1998, Kneeshaw and Burton 1997). The extant canopy provides a proximate reproductive source (seeds that can germinate in favourable microsites, and vegetative root or shoot suckers). Canopy composition also contributes directly to the growing conditions of advance regeneration (e.g., light quality and quantity, amount and type of litter, soil moisture and temperature), and indirectly determines levels of seed predation, ungulate herbivory, and understory competition (Galipeau et al. 1997, Kneeshaw and Burton 1997, Cornett et al. 1998, Messier et al. 1998, Simard et al. 1998).

We also found that biotically-controlled site factors explain a large proportion of the variation in advance regeneration composition and abundance. Similar results were obtained for boreal tree species in western Québec

(Kneeshaw and Bergeron 1996), but these authors noted that the long-term predictive value of such factors may be fairly low as they may change rapidly over time (e.g., the abundance of shrubs, herbaceous plants, bryophytes, decaying wood on the forest floor), particularly when compared to the rate of change in canopy composition and edaphic conditions. Our results demonstrate that white spruce and balsam fir regeneration (which is exclusively from seed) is severely limited in stands with a high cover of the tall shrubs beaked hazelnut and mountain maple. The inhibitory effect of a dense tall shrub canopy on advance regeneration of white spruce and balsam fir has been documented by a number of researchers (Vincent 1965, Lieffers et al. 1996, Galipeau et al. 1997, Morin and Laprise 1997, Kneeshaw and Bergeron 1996, 1998, Stewart et al. 1998). Thick herbaceous and shrub canopies in trembling aspen stands reduce photosynthetic photon flux density at the forest floor, inhibiting conifer seedling establishment and growth (Messier et al. 1998). In addition, the prolific amount of leaf litter produced by tall shrubs can smother seedlings (Lieffers et al. 1996). It is generally accepted that appropriate "microsites" (Simard et al. 1998) are necessary for the germination and successful establishment of white spruce and balsam fir: determining what constitutes a "microsite" for boreal conifer species will improve our understanding of how the coniferous component is maintained in different stand-types (Cornett et al. 1998). Although it is often stated that exposed mineral soil is a preferred germination substrate for boreal conifers (Johnson 1992, Zasada et al. 1992), advance regeneration of both white spruce and balsam fir is often found on decaying wood and mossbeds (Waldron 1966, Lieffers et al. 1996, McLaren and Janke 1996, Kneeshaw and Burton 1997, Simard et al. 1998). High canopy cover, low input of deciduous leaf litter, and north-facing aspects are particularly favourable to balsam fir regeneration (Galipeau et al. 1997, Kneeshaw and Burton 1997, Simard et al. 1998). In eastern Canada, the formation of small gaps in mixed stands promotes balsam fir regeneration, but large, slow-forming gaps in fir-dominated forests (often the result of spruce budworm infestations) are typically infilled by tall shrubs that inhibit balsam fir and white spruce regeneration (Kneeshaw and Bergeron 1996, 1998). By contrast, trembling aspen, paper birch, and balsam poplar advance regeneration (from root or basal suckers) is often abundant in younger stands in which beaked hazelnut dominates the understory. Unlike newly-germinated conifer seedlings, aspen root suckers grow very rapidly and may attain a height of 2 m or more (i.e., as high as the shrub canopy) in a single season (personal observation). Decomposition and nutrient cycling rates in deciduous-dominated boreal forests are high compared to coni-

fer-dominated stands (Kneeshaw and Bergeron 1996). This, together with the comparatively high level of light transmission through an aspen canopy (Lieffers et al. 1996), promotes the development of a dense tall shrub cover (Messier et al. 1998). These tall shrubs greatly reduce light levels at the forest floor, impeding the establishment of white spruce and balsam fir (Kneeshaw and Bergeron 1996).

Edaphic factors proved to be least effective in predicting the composition and abundance of understory advance regeneration: similar findings were reported by Kneeshaw and Bergeron (1996). These authors note that for many boreal hardwoods (e.g., trembling aspen) the presence of advance regeneration (vegetatively produced from root suckers) is simply a function of the occurrence of adult tree roots, not edaphic conditions. However, for conifer species (which reproduce from seed) edaphic conditions may be more important. Galipeau et al. (1997) found that density of the initial (post-fire) cohort of white spruce was much higher on till than clay soils. At a finer spatial scale, Kenkel et al. (2003) found that recruitment density of white spruce in post-fire aspen stands on glacial till was highest on moist, nutrient rich microsites.

Canopy dynamics

Canopy-subcanopy relationships, and size-class ordination analysis, have frequently been used to infer successional trends in boreal forest stands (e.g., Dix and Swan 1971, Carleton and Maycock 1978, Cogbill 1985, Bergeron and Dubuc 1989, Zoladeski and Maycock 1990). Such approaches have been criticized as unrealistic, since they implicitly assume that all species have similar life-history strategies, shade-tolerances, and mortality, natality and growth rates (Bergeron and Dubuc 1989, Johnson et al. 1994). Furthermore, these approaches fail to consider biotic disturbances such as ungulate herbivory, insect pest damage, and pathogen attack, that may differentially affect species mortality rates of advance regeneration. Differential species mortality of advance regeneration implies that the small saplings and seedlings present in the understory may not necessarily reflect future canopy change. To alleviate this problem, researchers typically consider only advance regeneration above a specific height (2-4 m) (Cogbill 1985, Bergeron and Dubuc 1989): this is the approach used in our study. Ideally, the analysis of canopy-subcanopy relationships should be combined with chronosequencing (Bergeron 2000, Foster and Tilman 2000), but this may be impossible since a complete sequence of stand ages is not present in most boreal landscapes.

In size-class ordination analysis, short and non-directional successional vectors are indicative of self-regenerating stands (Carleton and Maycock 1978): this is the case for stand-types I, III, IV, V, VII and VIII. Stand-type I (Black Spruce Organic) shows abundant vegetative layering by black spruce, particularly in open, nutrient-poor stands (Viereck and Johnston 1990). Self-regeneration is expected since only black spruce can survive the waterlogged, nutrient-impoverished conditions of these sites. Self-regenerating black spruce stands have been described from many regions of the Canadian boreal forest, including Alberta (Rowe 1961), Manitoba (Ritchie 1956) and northwestern Ontario (Zoladeski and Maycock 1990). Stand-type III (Bur Oak) occurs primarily on excessively-drained glacial outwash plains. While there is abundant regeneration of bur oak in these stands, few other tree species can tolerate these dry conditions. Heavy ungulate herbivory of oak saplings and shrubs in these stands may result in a more open canopy as stands develop (Lorimer et al. 1994, Ritchie et al. 1998). Stand-type IV (Eastern Deciduous) is characterized by abundant advance regeneration of American elm, Manitoba maple, green ash, and bur oak. The successional vector is directed away from trembling aspen and balsam poplar: these species are occasionally present in the canopy, but are rarely encountered as advance regeneration. In stand-type V (Balsam Fir), balsam fir is expected to replace balsam poplar, trembling aspen, white spruce and paper birch over time, since it is very shade-tolerant and does not have demanding seedbed preferences (McLaren and Janke 1996). However, paper birch, white spruce and trembling aspen may persist by regenerating in large gaps created by windblown balsam fir (Frelich and Reich 1995, Kneeshaw and Bergeron 1998, Bergeron 2000). In Alberta, mixed stands of balsam fir, white spruce and paper birch are thought to be self-replacing (Achuff and La Roi 1977). In the absence of a major disturbance, stand-type VII (Trembling Aspen-Balsam Poplar) may be self-regenerating through vegetative suckering of extant trees. However, many of these stands "degenerate" into open shrub-dominated communities as natural mortality removes trees from the canopy (Rowe 1955, MacLean 1960, Bailey 1968, Dix and Swan 1971, Carleton and Maycock 1978, Cogbill 1985, Zoladeski and Maycock 1990, personal observation). Stand-type VIII (White Spruce) will continue to be dominated by white spruce, but older stands will tend to become more open and shrub dominated (Cogbill 1985, personal observation). Ungulate herbivory is intense in shrub-dominated systems (especially those dominated by beaked hazelnut), resulting in the long-term perpetuation of dense shrub-dominated communities in the region.

Stand-types II (Jack Pine-Black Spruce) and VI (Aspen-Birch-Mountain Maple) have longer, directional vectors, indicating potential changes in canopy composition over time. Jack pine stands begin to deteriorate at an early age (60-80 years or more, Rudolph and Laidley 1990), and are typically succeeded by black spruce (Kenkel 1986, Frelich and Reich 1995). Although steady-state black spruce forests are unlikely to occur under short fire rotations (Bergeron and Dubuc 1989), even-aged post-fire jack pine stands will succeed to uneven-aged mixed stands (containing black spruce and other species) in the absence of fire (Heinselman 1973, Frelich and Reich 1995). In stand-type VI, trembling aspen and balsam poplar dominate the canopy: post-fire establishment of this canopy most likely occurred from existing rootstock (Bergeron 2000). Green ash, and more occasionally American elm, Manitoba maple and bur oak, are commonly encountered as advance regeneration in many of these stands. These eastern deciduous species are expected to gradually replace trembling aspen and balsam poplar. In some stands, paper birch dominates the advance regeneration, and is expected to gradually replace trembling aspen in the canopy.

A synoptic model of stand dynamics

The overall findings of our research are in general agreement with successional pathways established for boreal mixedwood stands in central and eastern Canada (summarized in Bergeron 2000, Chen and Popadiouk 2002). Early post-fire boreal mixedwood stands are dominated by pioneering hardwoods such as aspen, balsam poplar and paper birch (silt-clay soils), or by jack pine (sandy soils). Mid-successional stands show an increasing proportion of white spruce in the canopy, while late-successional stands are dominated by white spruce and balsam fir and are driven by gap dynamic processes. Many of the oldest stands are commonly open-canopied and dominated by tall shrubs species (mostly beaked hazelnut and mountain maple) which dramatically reduce recruitment of white spruce and balsam fir. Ungulate herbivores selectively browse trees and shrubs, impacting the long-term dynamics of these forests.

Historically, high fire frequencies in many regions of the boreal forest have resulted in forest stands dominated by early-successional species that are well adapted to recurrent catastrophic disturbance (Dix and Swan 1971, Heinselman 1973, Carleton and Maycock 1978, Zoladeski and Maycock 1990, Frelich and Reich 1995, Gutsell and Johnson 2001). However, in southern and eastern portions of the boreal forest lower fire frequencies (the result of more mesic macroclimate, or human fire suppression)

may allow directional succession to occur (Heinselman 1981, Bergeron and Dubuc 1989, Larocque et al. 2000). Directional succession involving species replacement has been described as convergence towards dominance by white spruce, black spruce and/or balsam fir (Heinselman 1973, Bergeron and Dubuc 1989, Zoladeski and Maycock 1990). In practice, stand dynamics is far more complex: at any given site, multiple or individualistic successional pathways may occur depending on disturbance history and episodic stochastic events (Fastie 1995, Bergeron 2000). Recruitment of white spruce, for example, is strongly dependent upon seed source proximity, which is in turn a function of the size, intensity and seasonality of past fires (Heinselman 1973, Grigal and Ohmann 1975, Bergeron and Dansereau 1993, Galipeau et al. 1997). Stand disturbance history (e.g. frost, drought, herbivory, pests, pathogens, fire) is undoubtedly a strong determinant of vegetation dynamics (Kenkel et al. 1997), but it is virtually impossible to quantify since it leaves "no direct, independent and measurable evidence on the site" (McCune and Allen 1985a).

A synoptic model of boreal forest stand dynamics for RMNP is presented in Figure 5. Our model represents a conceptual summarization of the ordination results. In addition, it implicitly includes factors considered to be critical determinants of forest dynamics: seed source availability, small and large-scale disturbance, species life-history characteristics (Rees et al. 2001), and gradients of soil moisture and nutrient status. The model includes only those stand-types characteristic of loam-clay mineral soils, which is the predominant substrate of the region. Thus, the model does not include stand-type I (organic peat substrates) and stand-types II and III (sand and gravelly soils), all of which are comparatively uncommon.

Post-fire stand composition is largely a function of fire size and intensity, propagule availability, and past floristic composition (Shafi and Yarranton 1973, Johnson 1992, Bergeron 2000). Post-fire mixedwood stands in RMNP are typically dominated by hardwoods – trembling aspen, balsam poplar and/or paper birch (Dickson 1909, Dix and Swan 1971) – as shown in the central box of Figure 5. Trembling aspen is more common on well-drained sites of lower nutrient status, whereas balsam poplar is more frequently encountered in mesic-hygric, nutrient-rich sites (Perala 1990, Zasada and Phipps 1990). Paper birch is most common on well-drained seepage slopes.

Seed source availability is a critical determinant of boreal stand dynamics (Fastie 1995, Kneeshaw and Bergeron 1996, Galipeau et al. 1997). In the absence of a seed source of late-successional species (e.g., white spruce,
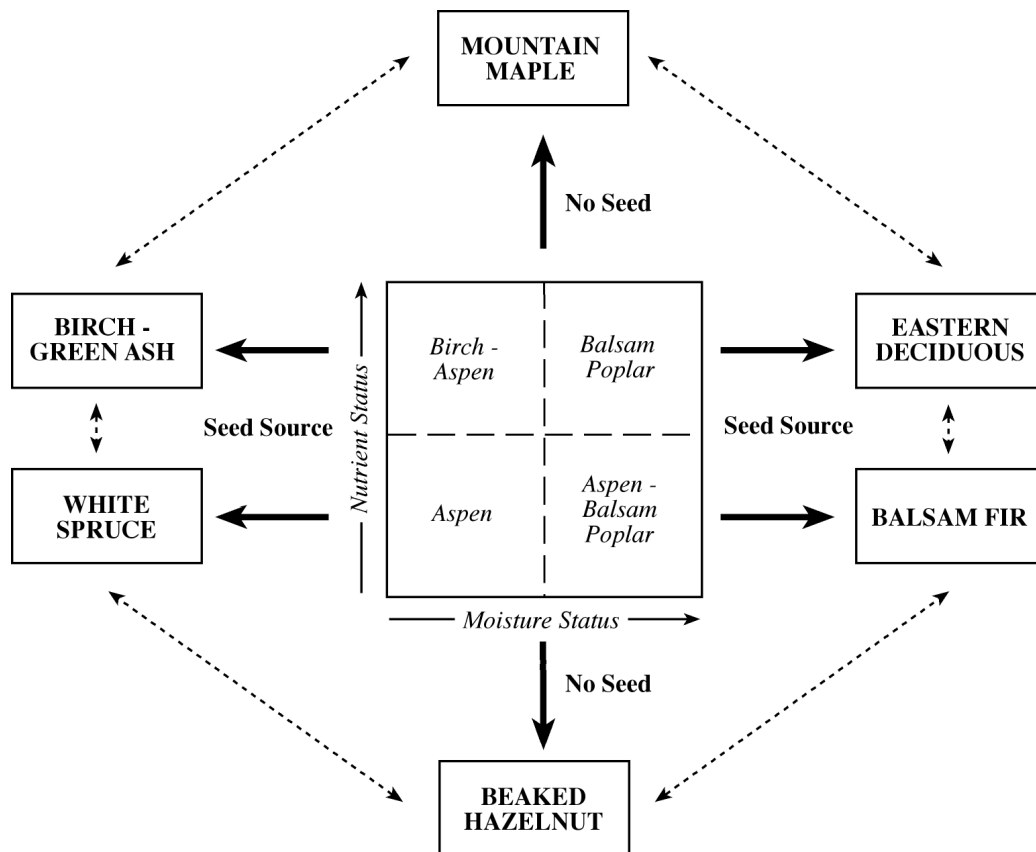
Figure 5. A synoptic forest succession model for RMNP (excluding jack pine, black spruce and bur oak stands). Post-fire stands (centre box) are generally dominated by early-succession hardwood species. In the absence of a seed source of later-successional tree species, post-fire stands will "degenerate" into open-canopied, shrub dominated systems (vertical arrows). Most stands will become dominated by beaked hazelnut, particularly under heavy ungulate browsing. Mountain maple occurs more locally in areas of higher nutrient status, especially in the east end of RMNP near the base of the Manitoba Escarpment. In these shrub-dominated stands, tree cover is highly discontinuous, and is composed of scattered senescent trembling aspen with the occasional white spruce, paper birch and/or balsam poplar. Alternative successional trajectories occur when seed sources of later-successional tree species are present (horizontal arrows). Xeric to mesic, mesotrophic habitats succeed towards paper birch (particularly on seepage slopes) or green ash. Mesic to hygric, mesotrophic sites show succession toward eastern deciduous forest stands dominated by American elm, green ash and Manitoba maple. In less nutrient-rich habitats, xeric to mesic sites succeed towards dominance of white spruce, whereas more mesic to hygric sites succeed towards mixed stands dominated by balsam fir in association with white spruce, paper birch, trembling aspen and/or balsam poplar. Double arrows indicate that transitions between forest associations may occur, and that a continuum of conditions are possible. Fire and gaps created in the forest canopy will revert stands towards earlier hardwood-dominated stages of succession (centre box).

balsam fir), post-fire hardwood stands "degenerate" into open-canopied, shrub-dominated systems (Bailey 1968, Cogbill 1985, Zoladeski and Maycock 1990) – shown as vertical arrows in Figure 5. Most stands in RMNP become dominated by beaked hazelnut, particularly under heavy ungulate browsing (Rowe 1955, Trottier 1981, personal observation). Mountain maple occurs more locally in areas of higher nutrient status (Vincent 1965, Galipeau et al. 1997), particularly along mid to lower slopes of the Manitoba Escarpment. In these "degenerate" stands, tree cover is highly discontinuous, consisting of scattered relict trembling aspen and the occasional white spruce, paper

birch and/or balsam poplar (Bailey 1968). In the absence of disturbance, trembling aspen and balsam poplar may maintain themselves in the canopy of these stands through vegetative suckering (Perala 1990, Zasada and Phipps 1990, Bergeron and Dansereau 1993). However, old stands may lose their ability to sucker (Peterson and Peterson 1992).

Alternative successional trajectories occur when seed sources of later-successional species are present – shown as horizontal arrows in Figure 5. In mesic, mesotrophic sites, succession is toward dominance by paper birch (particularly on seepage slopes) and/or green ash, while spe-

cies of eastern deciduous forest affinity (green ash, American elm, Manitoba maple, and bur oak) increasingly dominate mesic-hygric, mesotrophic sites. In less nutrient-rich habitats, mesic sites succeed toward dominance by white spruce, while mesic-hygric sites become dominated by balsam fir. Late-succession balsam fir stands will retain a mixed canopy of white spruce, paper birch, trembling aspen and/or balsam poplar (Achuff and La Roi 1977, Kneeshaw and Bergeron 1996), however, the result of gap dynamic processes (Sprugel 1976, Bergeron and Dubuc 1989, Bergeron and Dansereau 1993, Frelich and Reich 1995).

The time required to reach these late-successional stages will depend on propagule availability, intensity of ungulate herbivory, and the frequency, size and intensity of natural disturbances. Selective herbivory of hardwood species (e.g., beaver activity, ungulate herbivory of advance regeneration) may increase the rate at which conifer dominance is achieved (Naiman 1988), whereas fire, windthrow, pathogen disease and insect outbreaks may result in reversion to an earlier successional stage (Heinselman 1973, Pastor et al. 1993). The double arrows of Figure 5 indicate possible transitions between forest stand-types: for example, shrub-dominated communities may eventually be colonized by trees if seed source is available and the shrub layer is damaged by fire or other disturbances (Rowe 1961). Conversely, stands may become increasingly shrub-dominated as they naturally thin. Mature white spruce stands often have limited advance regeneration and become increasingly open, increasing light levels and promoting tall shrub growth (Rowe 1961, Dix and Swan 1971, Cogbill 1985). White spruce and balsam fir advance regeneration may occur beneath paper birch, and vice versa. Similarly, balsam fir may occasionally invade sites dominated by green ash, American elm and Manitoba maple.

In more frequently burned stands, post-fire composition is typically very similar to pre-fire canopy composition (Dix and Swan 1971, Carleton and Maycock 1978, Cogbill 1985, Bergeron and Dubuc 1989, Zoladeski and Maycock 1990). Conversely, catastrophic fire in late-successional stands generally results in reversion to an earlier, hardwood-dominated stage (Dix and Swan 1971, Shafi and Yarranton 1973, Heinselman 1973, Carleton and Maycock 1978, Bergeron and Charron 1994, Frelich and Reich 1995). Indeed, hardwood species (particularly trembling aspen) often dominate the post-fire cohort even in stands that are almost completely dominated by old-growth conifers prior to burning (Bergeron 2000). This reflects the ability of trembling aspen, balsam poplar and paper birch (Oechel and Lawrence 1985, Zasada et al.

1992), as well as beaked hazelnut and mountain maple (Heinselman 1973), to vigorously resprout after fire from established below-ground roots or rhizomes. Gap creation (from windthrow, insect damage, or pathogens) may favour the establishment of shade-intolerant hardwoods – an apparent "reversion" to an earlier successional stage (Pastor et al. 1988, Bergeron and Dubuc 1989, Bergeron and Dansereau 1993, Frelich and Reich 1995).

In conclusion, the modelling of boreal forest dynamics is a complex process, since numerous factors operating at various spatial and temporal scales can affect successional trends. Successional trajectories of stand-types in our study area clearly do not converge towards a single self-perpetuating "climax" community: instead trajectories may diverge, converge or cycle, and multiple potential pathways are possible. These results suggest that forest species assemblages, and the propensity for canopy change, are governed by the cumulative and synergistic effects of climate, topography, disturbance frequency, size and intensity, edaphic conditions and the proximity of parental seed sources. These factors have resulted in a complex mosaic of forest stands on the landscape that vary in structure, composition and seral stage (Walker and Kenkel 2001).

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