PROJECT REPORT 2001-4

FINAL PROJECT REPORT

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Structure and Dynamics of Boreal Forest Stands in the Duck Mountains, Manitoba

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Cary Hamel and Norm Kenkel

For copies of this or other SFM publications contact:

Sustainable Forest Management Network
G208 Biological Sciences Building
University of Alberta
Edmonton, Alberta, T6G 2E9
Ph: (780) 492 6659
Fax: (780) 492 8160
http://www.ualberta.ca/sfm

ISBN 1-55261-112-4

Structure and Dynamics of Boreal Forest Stands in the Duck Mountains, Manitoba

Forest succession and post-logging regeneration dynamics in the Duck Mountain ecoregion, west-central Manitoba

Cary Hamel and Norm Kenkel
Department of Botany
University of Manitoba

March 2001

EXECUTIVE SUMMARY

Knowledge of natural forest successional processes is critical to the long-term sustainable management and environmental stewardship of Canada s boreal forests. 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. A synoptic succesional model that explains the long-term dynamics of mixedwood forests at the ecosite scale was produced, incorporating both disturbance (light vs. catastrophic fire, timber harvesting, and gap dynamics) and conifer seed source proximity. Successional trajectories for major stand types were determined and important biological and non-biological processes driving stand composition, structure and dynamics were identified.

Detailed tree size and age data were obtained from each of 70 sampled stands (3 plots per stand, for a total of 210 plots) located throughout the study area. All individuals were assigned to one of three age cohorts: initially established, intermediately established (including advance regeneration), and recently established. Our approach involved reconstructing the initial post-fire composition of all 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, such as canopy mortality and the vertical distribution of advance regeneration, 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. Repeated catastrophic burns encourage the development of hardwood-dominated stands, sometimes in combination with jack pine. 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. Lack of catastrophic fire and the proximity of a late successional conifer seed source results in the development of a canopy increasingly dominated by conifers, usually white spruce. In areas where a complex landscape physiography has historically limited fires to small extent and low severity, balsam fir often becomes a significant canopy component. Hardwoods maintain a presence in most stands, however, as they undergo successful vegetative regeneration in gaps. The elimination of late-successional seed source refugia by catastrophic fire can result in a reversion to hardwood-dominated stands.

Current harvesting practices are largely sustainable, provided the maintenance of current canopy diversity and its potential for change are promoted. An ecosite-based management approach that seeks to mimic local disturbance history, preserves proximate late successional seed sources, recognises interactions among canopy trees and subsequent recruitment, and incorporates competitive interactions and local site edaphic features can be used to promote natural post-disturbance successional trajectories. Management efforts should focus on maintaining representative examples of all seral stages of all stand-types, so as to preserve species and landscape diversity.

ACKNOWLEDGEMENTS

This research was funded by the Sustainable Management Network (National Centres of Excellence) and the Province of Manitoba Centres of Excellence Fund. Thanks to Margaret Donnelly, Ken Broughton, Vern Baumann, Brad Epp and others at Louisiana Pacific Canada (Swan River) for technical expertise and in-kind support. Manitoba Natural Resources provided camping facilities, fire history maps, and expertise. Thanks as well to Dana Neuman, Richard Caners, Bethany Gowryluk, Samantha Murray, Scott Hamel and Janet Skavinski for providing valuable field assistance, and to David Walker and Rod Lastra for technical and computer assistance in the lab.

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 and 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 and 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 Qu bec 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 and 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 (Dix and Swan 1971; Carleton and Maycock 1978; Cogbill 1985; Bergeron and Dubuc 1989; Bergeron and Dansereau 1993; Bergeron 2000; Zoladeski and Maycock 1990). 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-succesional stands often develop toward mixed black spruce and balsam fir stands, but hypothesized that fire would normally halt such a trend (see also Dix and 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 succesional pathways. Boreal hardwood stands may become increasingly dominated by late-successional softwoods, but this trend is periodically interrupted by outbreaks of spruce budworm (Bergeron and 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 and Maycock 1978; Cogbill 1985; Zoladeski and Maycock 1990; Fastie 1995; 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; DeGrandpr 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 and Maycock 1990; Caners and 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 and Slatyer 1980; Huston and 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 and 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 and 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 and Swan 1971; Carleton and Maycock 1978; Cogbill 1985; Bergeron and Dubuc 1989; Zoladeski and Maycock 1990).

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. In addition, mature (80-130 year old) forest stands were compared to stands from the large 1961 burn in order to validate post-fire recruitment patterns. 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.

METHODS

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 the Turtle and Riding Mountains to the south and the Porcupine and Pasqia 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.

Stand Selection

A total of 70 stands (3 plots per stand, for a total of 210 plots) were enumerated over two field seasons. Stands were sampled 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 randomly located 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 enumerated 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.

Data Collection

Tree sizes

Data on the identity, bole size (diameter at breast height), and height of living trees were 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 were recorded. Most stands were characterized by a clear overstory cohort comprised of one dominant species, or two co-dominant species, of similar height and DBH.

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 (< 10m 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 compound microscope.

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 x1 m plots randomly located within a 10 x 10 m plot.

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).

Physiography and landscape

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

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.

Characterization of Stands

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 **Figure 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.

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 (snags) were also used to reconstruct the initial canopy cohort. The known autecology of major tree species was also considered:

1. 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. 1997a).

2. 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 and Peterson 1992). Both species are shade-intolerant, but may undergo secondary suckering (advance regeneration) following canopy breakup if light conditions are favourable.

3. 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.

4. 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).

5. 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

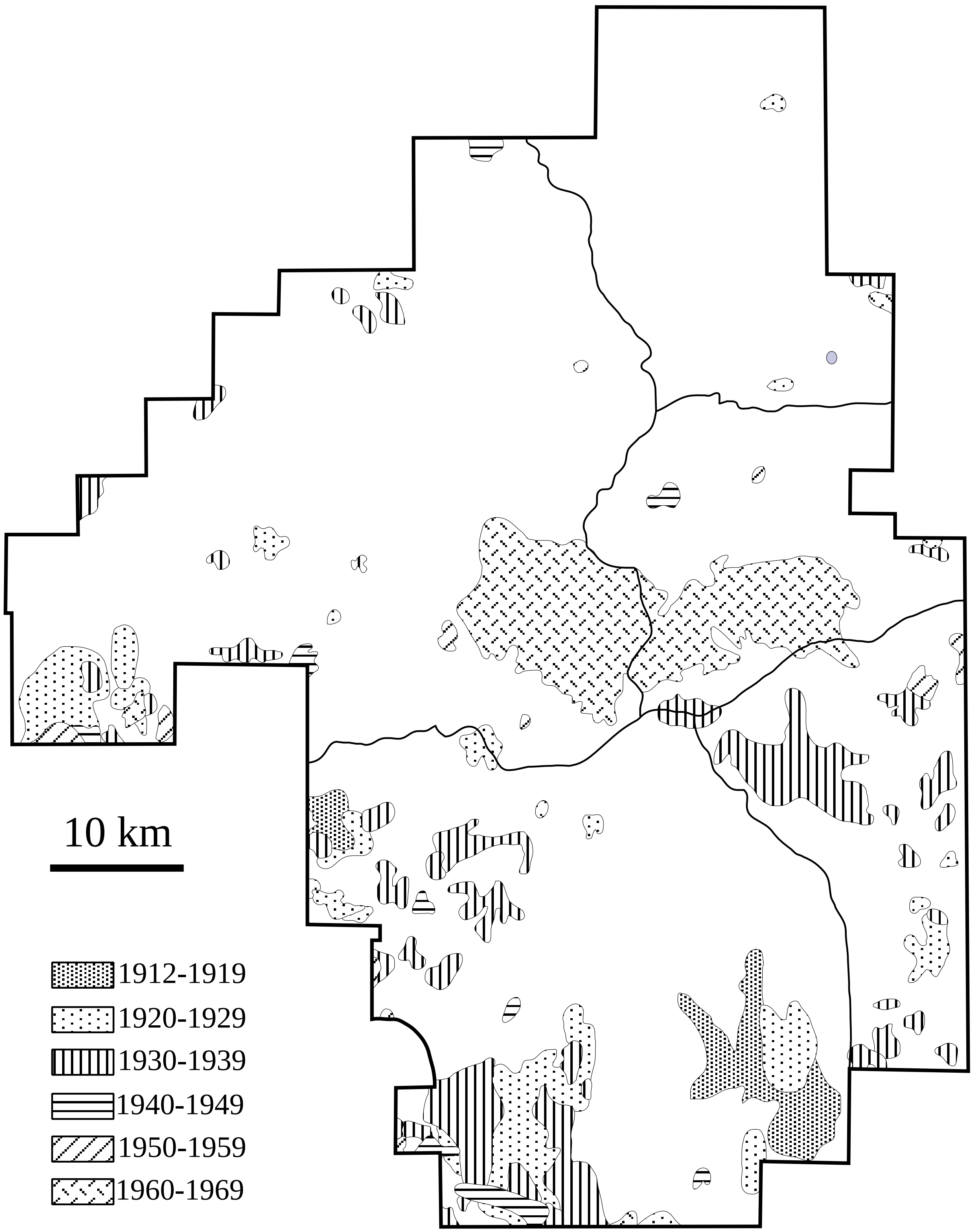

Figure 1. Forest fire history for Duck Mountain, 1912-present. Spot fires are not included.

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).

6. 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).

Summarization of stands

The 70 forest stands enumerated in this study are summarized in **Table 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 8 stands range in age from 55-70 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.

Table 1. Data analyses conducted[1], 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.

Analyses	Stand	Stand Age	Class	Dominant I.R.	Dominant A.R.	Soil Order
1 - 6	1	65	TA	TA	TA	Brunisolic
1 - 6	2	85	TA	TA	TA	Brunisolic
1 - 6	3	75	TA	TA	TA	Brunisolic
1 - 6	4	85	TA	TA	TA	Brunisolic
1 - 6	5	90	TA	TA	TA	Luvisolic
1 - 6	6	115	TA	TA,WB,WS	TA	Luvisolic
1 - 6	7	115	TA	TA	(TA,BP)	Brunisolic
1 - 6	8	100	TA	TA	TA	Brunisolic
1 - 6	9	90	TA	TA	WS,TA	Brunisolic
1 - 6	10	115	TA	TA	WS	Brunisolic
1 - 6	11	115	TA	TA	WS	Brunisolic
1 - 6	12	115	TA	TA,WB,WS	WS	Luvisolic
1 - 6	13	100	BP	BP	(BP,TA)	Brunisolic
1 - 6	14	115	BP	TA,BP	WS	Brunisolic
1 - 6	15	110	BP	BP	WS	Gleysolic
1 - 6	16	80	BP	BP	WS	Gleysolic
1 - 6	17	85	BP	TA,BP	WS	Brunisolic
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	Brunisolic
1 - 6	21	130	BP	BP	BF	Gleysolic
1 - 6	22	90	BP	WB,BP	BF	Brunisolic
1 - 6	23	150	WS	TA,WS	BF	Brunisolic
1 - 6	24	150	WS	TA,WB,WS	BF	Luvisolic
1 - 6	25	105	WS	WS,TA,WS	BF	Luvisolic
1 - 6	26	145	WS	WS ,TA	BF	Brunisolic
1 - 6	27	115	WS	WS	BF	Luvisolic
1 - 6	28	100	WS	TA,BP,WS	BF,WS	Brunisolic
1 - 6	29	75	WS	TA,WS	WS	Brunisolic
1 - 6	30	110	WS	WB,WS	BF,TA	Brunisolic
1 - 6	31	80	WS	TA,WB,WS	WB,BF,WS,TA	Brunisolic
1 - 6	32	90	WS	WS,TA,BP	TA,BF,WS	Luvisolic
1 - 6	33	105	JP	BS,TA,JP	TA	Brunisolic
1 - 6	34	105	JP	JP,BS,TA	(TA,BS)	Luvisolic
1 - 6	35	110	JP	TA,JP	WB,TA	Brunisolic
1 - 6	36	110	JP	TA,JP	WB	Brunisolic
1 - 6	37	105	JP	JP,TA	WB	Brunisolic
1 - 6	38	115	JP	JP,BS	(WB,TA)	Brunisolic
1 - 6	39	105	JP	TA,JP	WB	Brunisolic
1 - 6	40	95	JP	JP	WB	Brunisolic
1 - 6	41	105	JP	JP	BF,WS,BS	Brunisolic
1 - 6	42	110	JP	JP	BF,BS	Brunisolic
1 - 6	43	110	JP	JP	BF	Regosol
1 - 6	44	110	JP	TA,WS,JP	BF	Brunisolic
1 - 6	45	120	JP	TA,WS,JP,BS	BF	Brunisolic
1 - 6	46	110	BS	BS,JP	(BS)	Luvisolic
1 - 6	47	110	BS	BS,JP	(BS)	Brunisolic
1 - 6	48	105	BS	BS	(BS)	Brunisolic
1, 2	49	55	TA			Brunisolic
1, 2	50	60	TA			Brunisolic
1, 2	51	60	TA			Brunisolic
1, 2	52	65	TA			Brunisolic
1, 2	53	60	BP			Gleysolic
1, 2	54	60	WS			Regosolic
1, 2	55	70	WS			Brunisolic
1, 2	56	75	WS			Luvisolic
1, 2	57	150	WS			Luvisolic
1, 2	58	170	WS			Brunisolic
1, 2	59	220	WS			Luvisolic
1, 2	60	155	BS			Brunisolic
1, 2	61	110	BS			Brunisolic
1	62	38	WS			Brunisolic
1	63	37	JP			Brunisolic
1	64	37	JP			Brunisolic
1	65	37	JP			Brunisolic
1	66	38	JP			Brunisolic
1	67	38	JP			Brunisolic
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 corresponence 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.

3. Stands 57-61

These 5 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.

Data Analysis

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.

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:

A. 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.

B. 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.

C. 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 present in **Fig. 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.

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) 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 (snags) and recently fallen trees were also included in the initial cohort class.

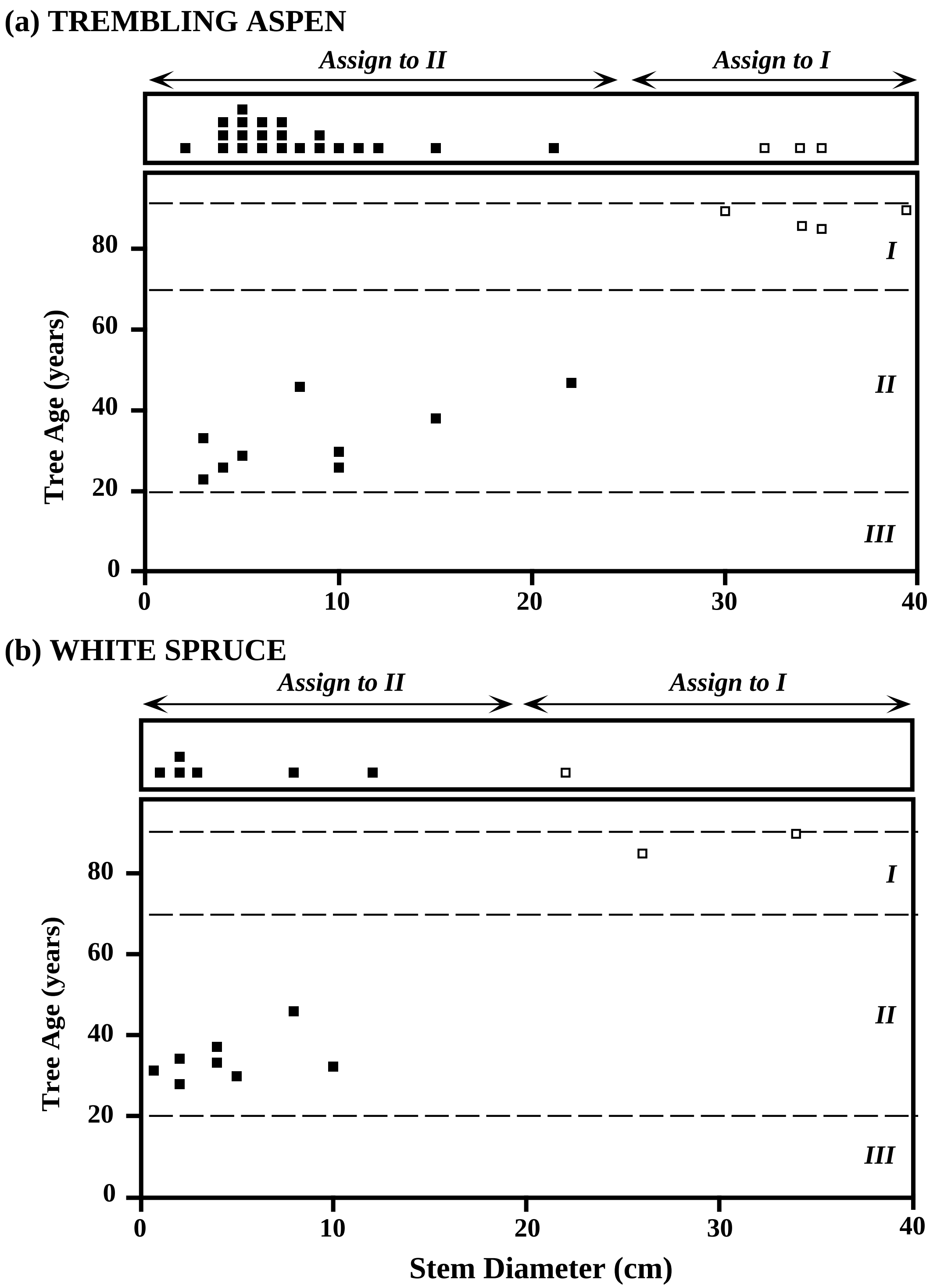

Figure 2. The relationship between stem diameter and age for aged (a) trembling aspen and (b) white spruce individuals in stand 5. Aged individuals were assigned to one of three age classes: initial cohort (□= established in first 20 years following disturbance), advanced regeneration (■= established 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.

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 way, since these stands had very little advance regeneration.

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 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.

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 < 2m in height were not considered. Age profiles (presented as age since stand establishment) were summarized in histogram form.

RESULTS

I. Post-Fire Stand Types

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.

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. 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 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 and Johnson 1998).

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.

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.

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 —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. 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, bishop s cap and stiff club-moss.

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. The jack pine stands enumerated in this study averaged 110 years.

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, *Tomenthhypnum niten*s, 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.

II. 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 (**Figure 3**). 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.

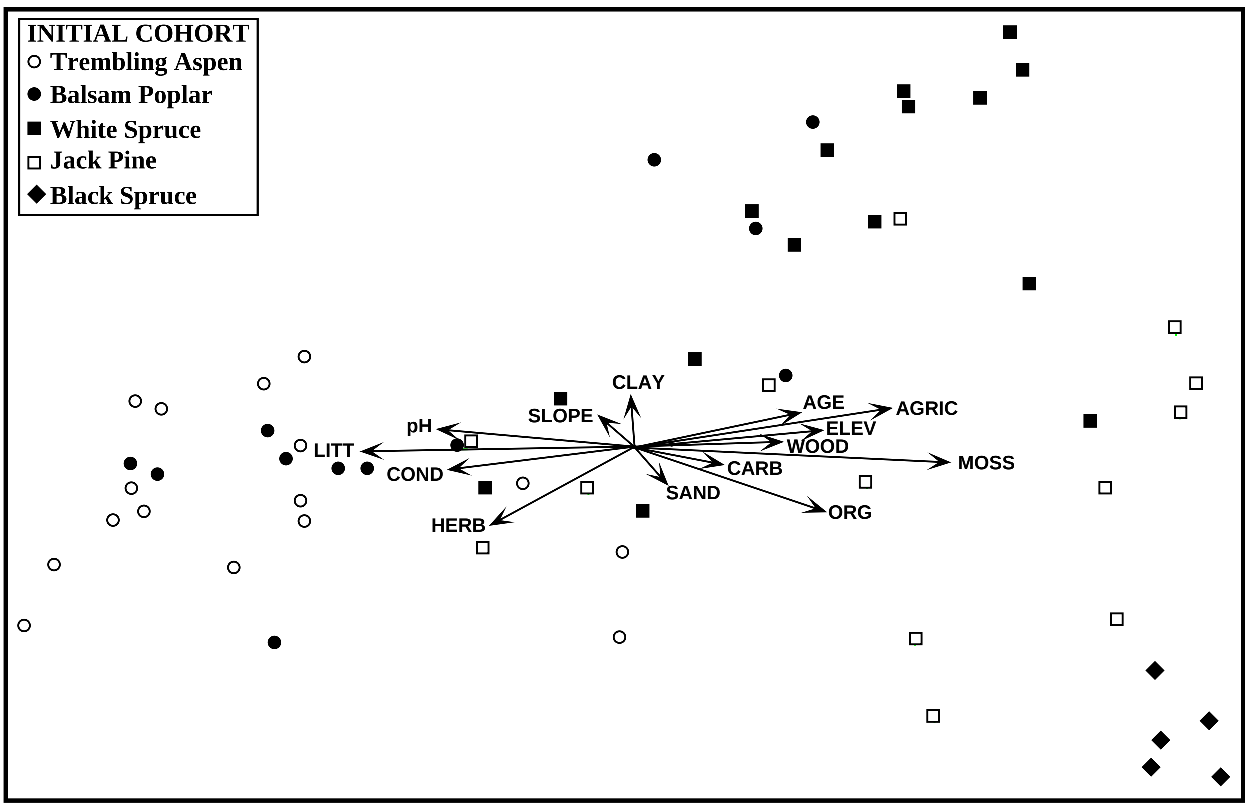

Figure 3. Canonical correspondence analysis ordination biplot of woody vegetation cover in stands 1-61 and 14 environment-landscape variables. Stands are coded by initial stand-type. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.900$, $R_2^2 = 0.763$. The redundancy (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 (**Figure 4**). Jack pine and black spruce

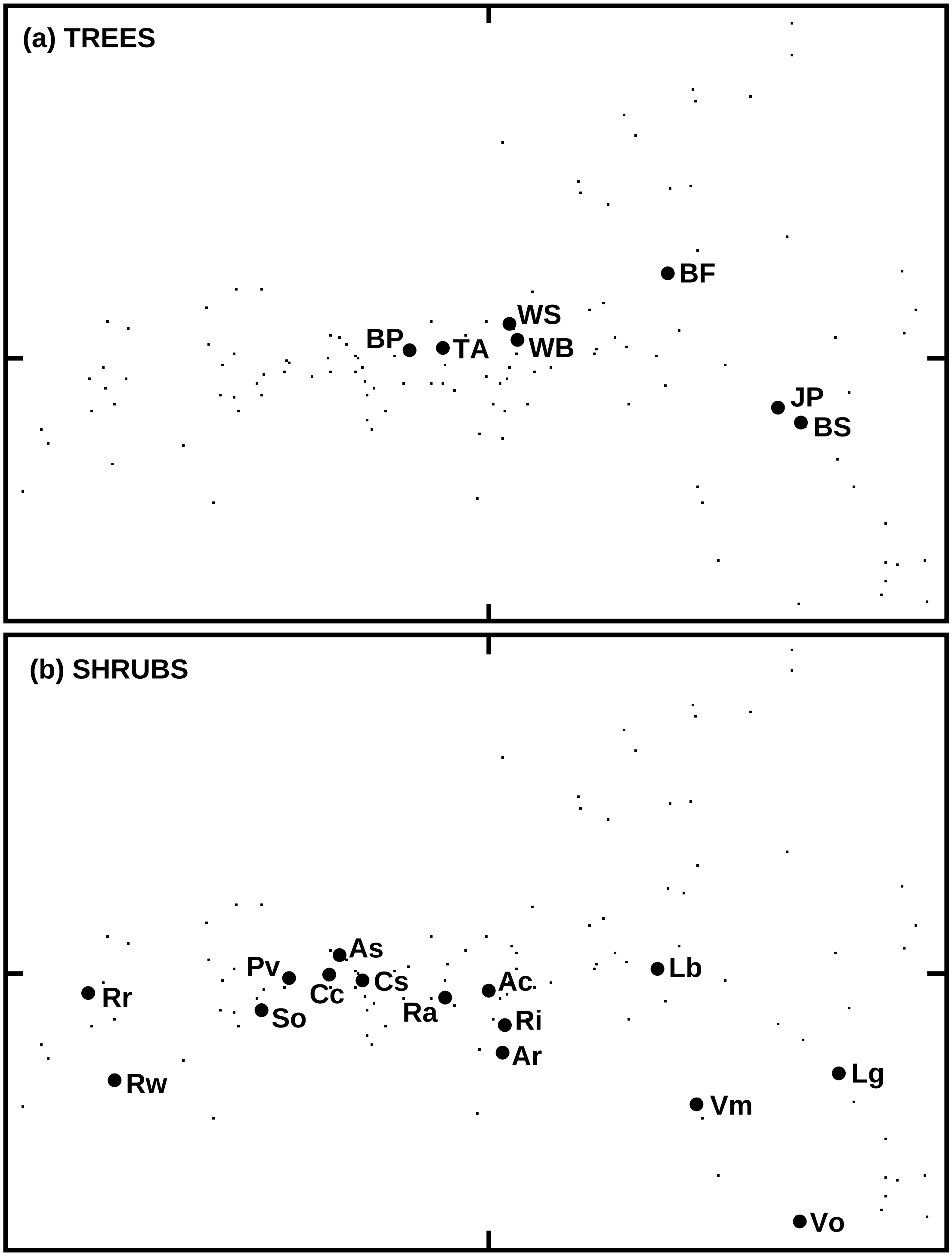

Figure 4. Canonical correspondence analysis ordination biplot of the woody vegetation cover in stands 1-61, showing major tree (a) and shrub (b) species. The corresponding species-environment biplot is presented in Figure 3. Species codes: BF = balsam fir, BP = balsam poplar, BS = black spruce, JP = 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 rapsberry, Ar = speckled alder, Lb = twinflower, Vm = blueberry, Lg = Labrador tea, Vo = bog cranberry.

are ordinated at the lower right, indicating their occurrence on well-drained, nutrient-impoverished 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.

III. Multivariate Modeling of Stand Dynamics

The CCA of advance regeneration composition constrained by initial cohort composition is presented in **Figure 5**. 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 **Figure 6**. 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.

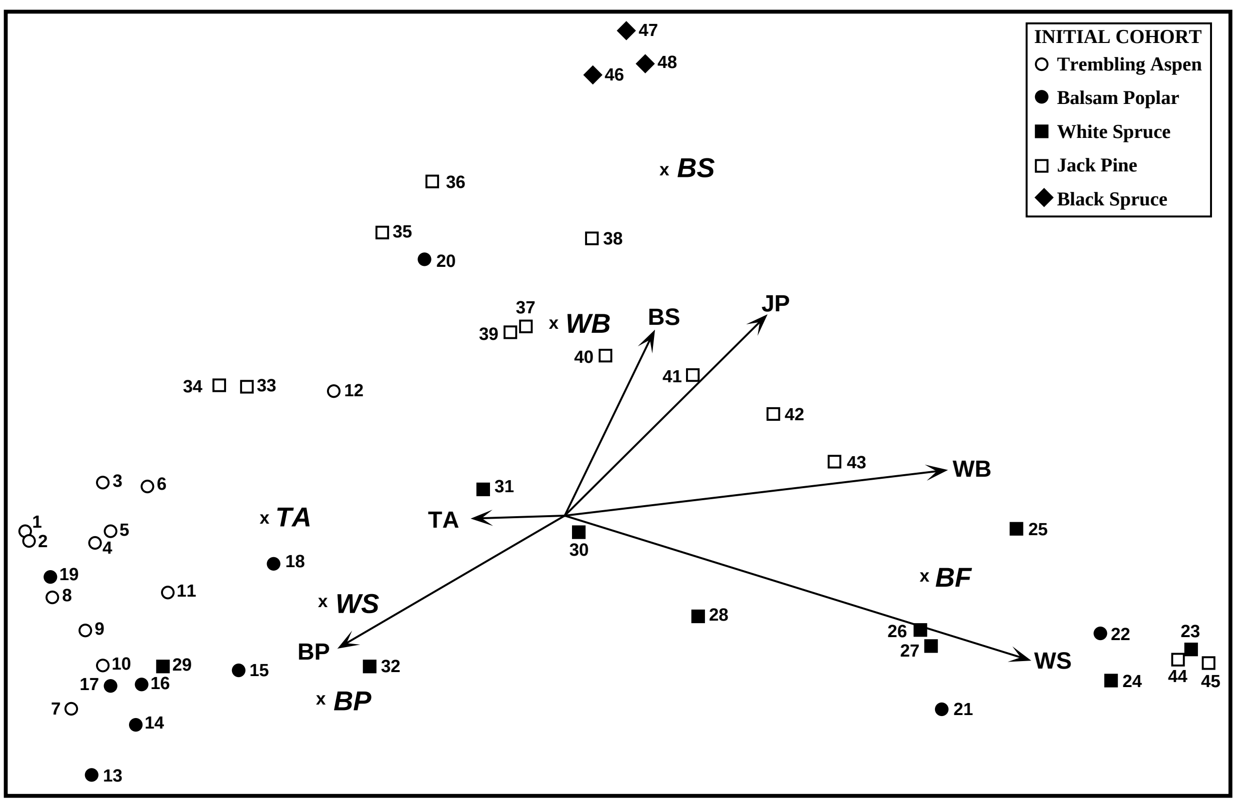

Figure 5. Canonical correspondence analysis ordination biplot of the advanced regeneration density in stands 1-48 constrained by initially-established cohort composition (vectors). Stands are coded by initial stand type. Centroids of species advance regeneration are indicated by x. Horizontal axis is 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.

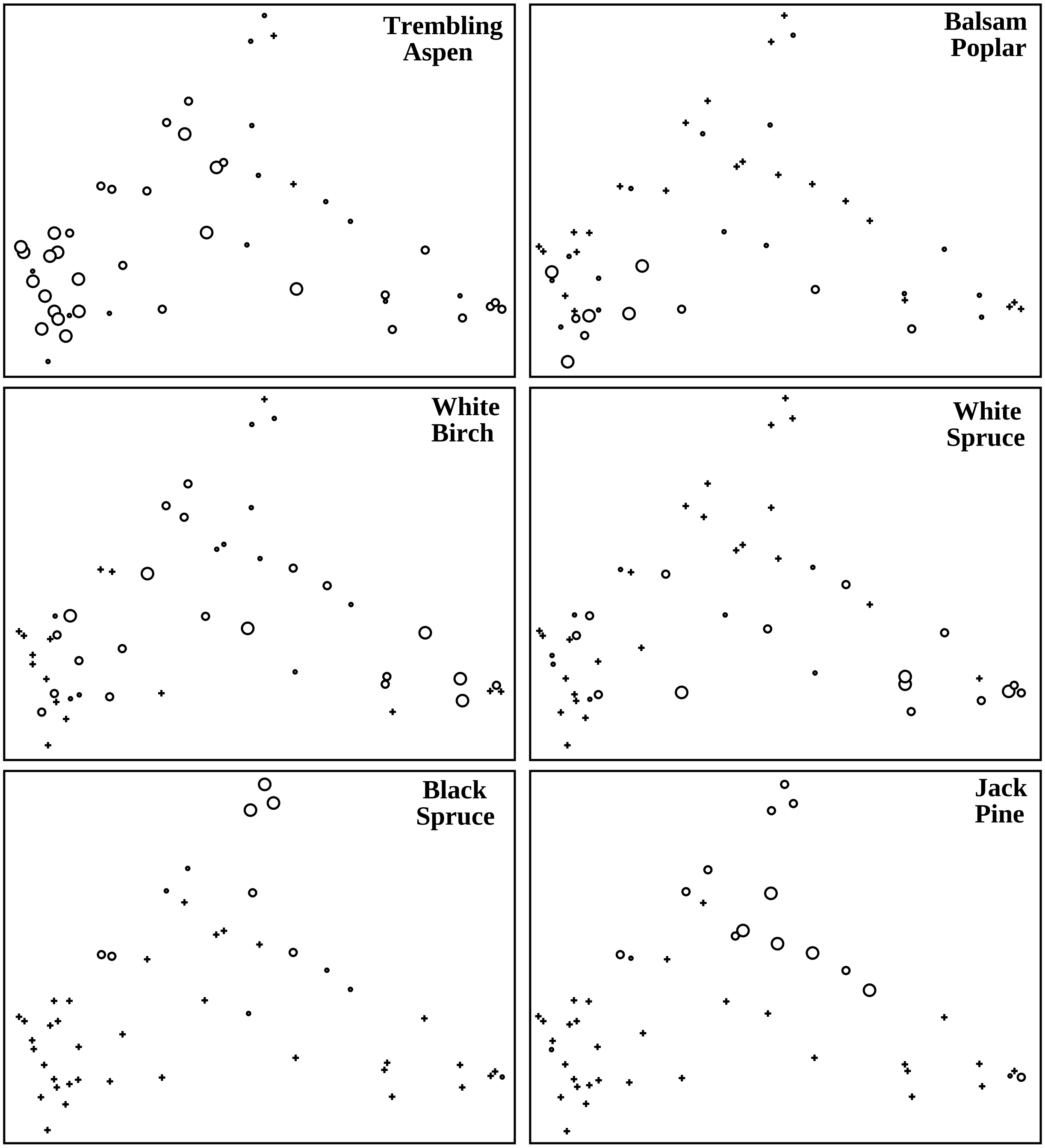

Figure 6. Relative abundance of initial cohort tree species in the 48 stands ordinated using canonical correspondence analysis and presented in Figure 5. Open circles are proportional to relative species abundance at stand initiation; crosses indicate species absence at stand initiation.

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 **Figure 7**. 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.

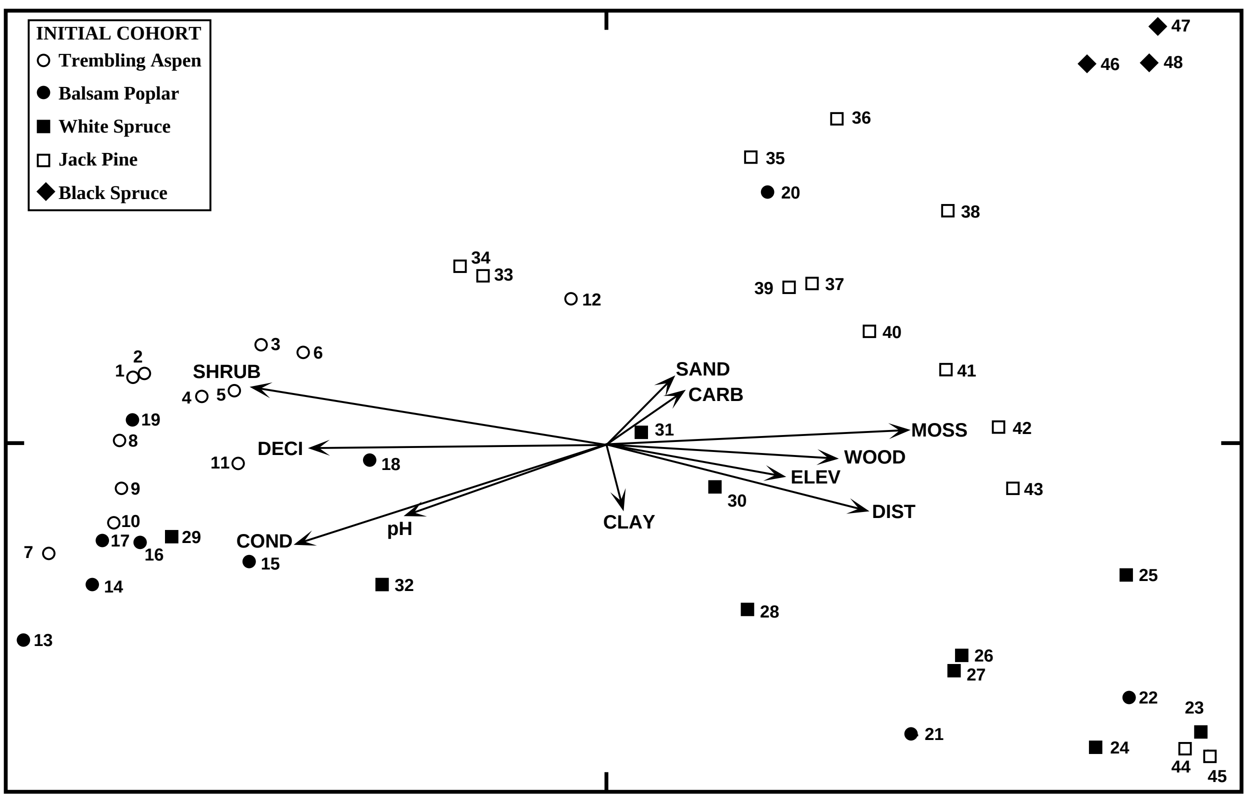

Figure 7. Rotation of canonical correspondence analysis (CCA) ordination (Figure 5) to environmental conguence using canonical correlation analysis, based on 11 'environmental' variables. The 48 stands are coded by initial stand type. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.860$, $R_2^2 = 0.728$. 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.

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 (**Figure 8**). 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.

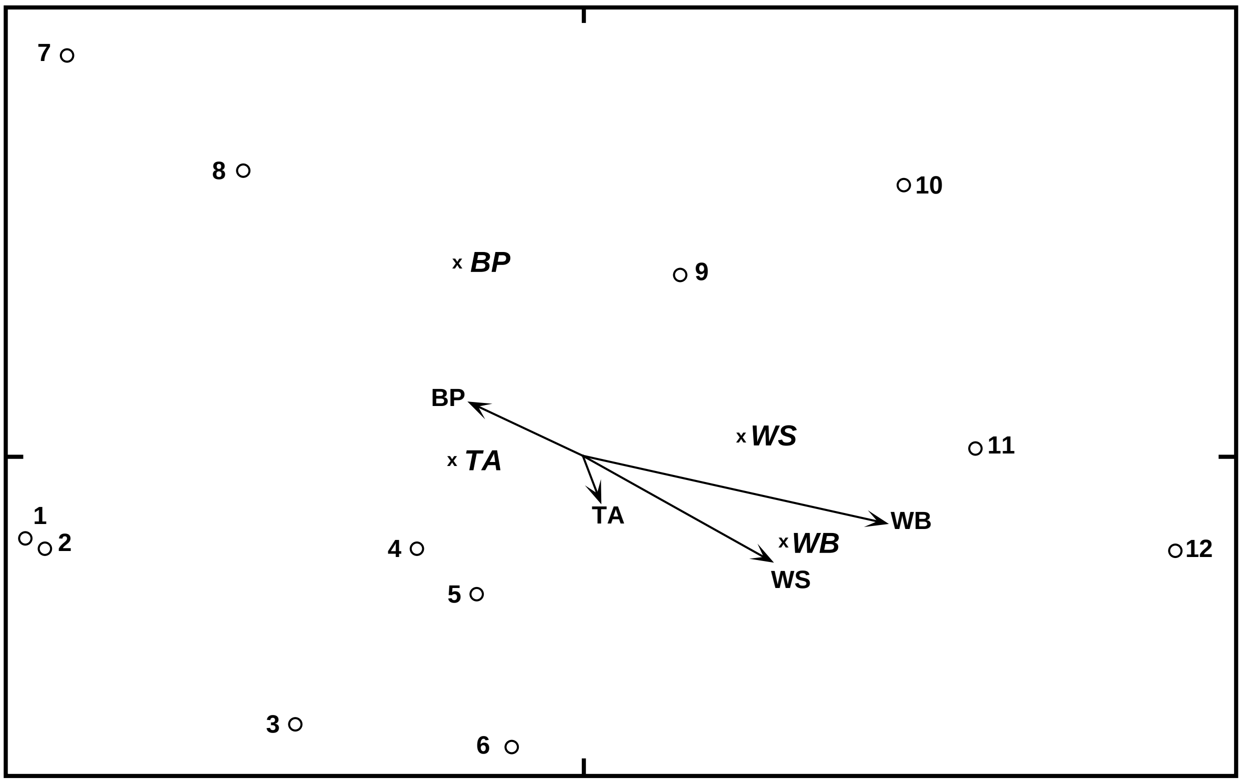

Figure 8. Canonical correspondence analysis ordination biplot of advance regeneration density (x) constrained by the initially-established cohort composition (vectors) of 12 trembling aspen stands. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.773$, $R_2^2 = 0.794$. 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.

Advance regeneration suckers of trembling aspen have already reached the upper and lower canopies of some stands (**Table 2**), 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.

Table 2. Average density/100 m^2 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.

WHITE SPRUCE

	C	*I*	*R*
1	**0.70 (0.19)**	**0.57 (0.25)**	
2	**0.13 (0.08)**	**0.30 (0.15)**	
3	**0.03 (0.03)**	**1.77 (0.46)**	
4		**0.10 (0.06)**	**0.27 (0.10)**
5			**0.47 (0.13)**
	5/12	**7/12**	**8/12**

TREMBLING ASPEN

	C	*I*	*R*
1	**4.53 (0.70)**	**0.83 (0.46)**	
2	**0.17 (0.14)**	**1.50 (0.56)**	
3		**0.87 (0.29)**	**3.10 (1.14)**
4			**2.80 (2.23)**
5			**2.10 (0.40)**
	12/12	**7/12**	**8/12**

Successful advance regeneration suckers of trembling aspen do not appear until at least 50 years post-fire (**Figure 9**), 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 and 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).

The presence of white spruce advance recruitment in trembling aspen stands is strongly dependent on seed source proximity (**Table 3**). 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 and Bergeron 1996).

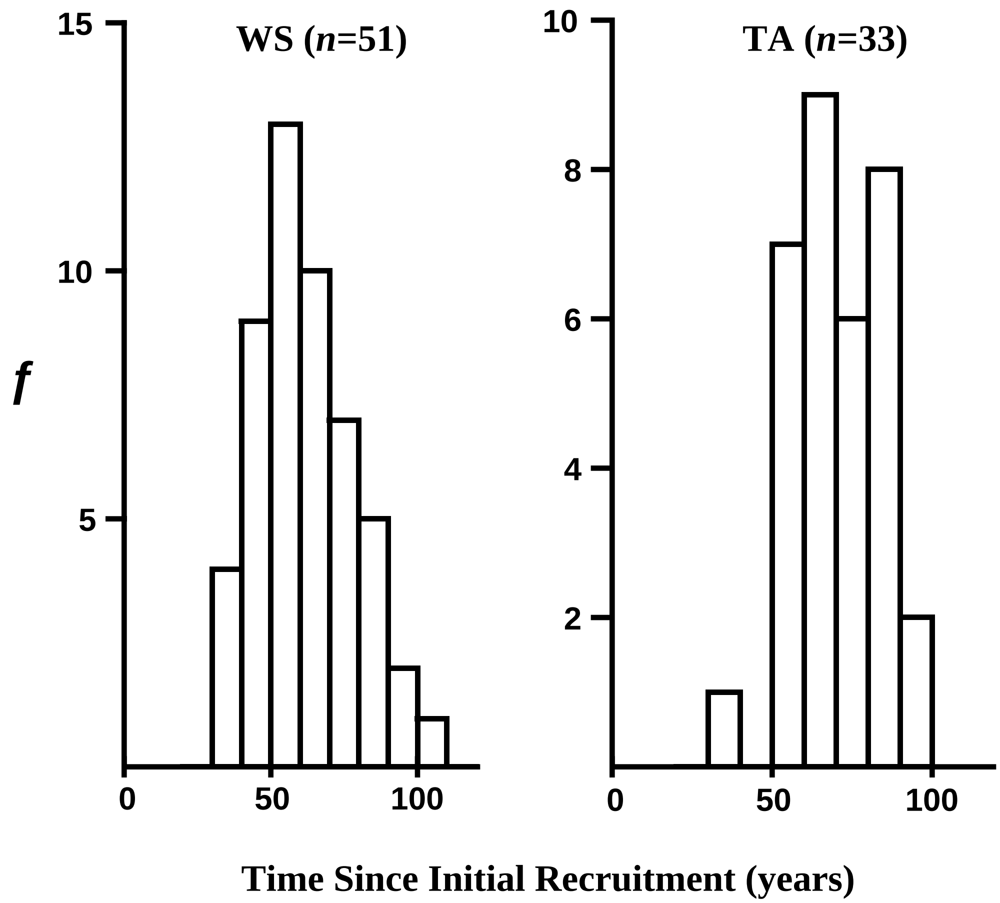

Figure 9. Age-class histograms of time since initial recruitment for white spruce and trembling aspen advance regeneration in the trembling aspen stand-type.

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 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.

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. These factors may lead to the development of decadent aspen shrublands as seen along Highway 10 in Riding Mountain National Park (Caners and Kenkel 1998).

Table 3. Density of white spruce advance regeneration (A.R.) per 100 m^2 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	Ecosite 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

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.

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 (**Figure 10**). 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 nutrient-rich seepage slopes, consists of balsam poplar in mixture with lesser amounts of white birch.

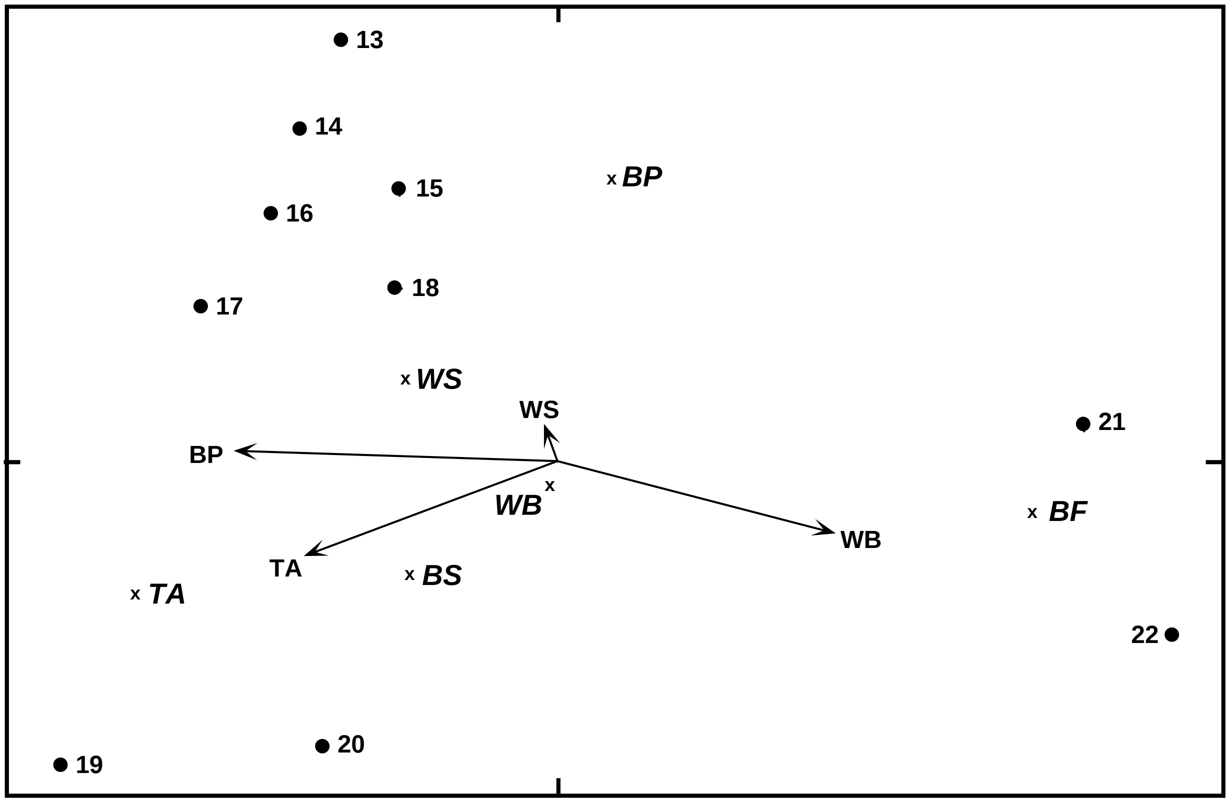

Figure 10. Canonical correspondence analysis ordination biplot of advance regeneration density (x) constrained by the initially-established cohort composition (vectors) of 10 balsam poplar stands. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.924$, $R_2^2 = 0.841$. 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.

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**). 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 (**Figure 11**). 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 (**Figure 10**). 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

Table 4. Average density/100 m^2 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.

TREMBLING ASPEN

	C	I	R
1	1.36 (0.42)	0.36 (0.15)	
2		0.32 (0.18)	
3		0.88 (0.39)	0.20 (0.20)
4			0.36 (0.20)
5			
	6/10	8/10	4/10

WHITE BIRCH

	C	I	R
1	0.84 (0.46)		
2	0.08 (0.05)	0.24 (0.12)	
3		0.52 (0.40)	0.16 (0.16)
4			0.12 (0.09)
5			
	3/10	4/10	2/10

BALSAM POPLAR

	C	I	R
1	3.40 (3.33)	0.04 (0.20)	
2	0.04 (0.20)	0.32 (0.80)	
3		0.12 (0.44)	
4			0.32 (0.69)
5			
	9/10	6/10	3/10

WHITE SPRUCE

	C	I	R
1	0.24 (0.10)	0.28 (0.18)	
2		1.88 (0.87)	
3	0.04 (0.04)	1.40 (0.44)	
4		0.80 (0.41)	0.08 (0.06)
5			0.80 (0.32)
	4/10	8/10	4/10

BALSAM FIR

	C	I	R
1		0.40 (0.20)	
2		2.20 (0.94)	
3		2.52 (1.16)	
4		0.96 (0.88)	
5			23.04 (9.88)
	0/10	5/10	4/10

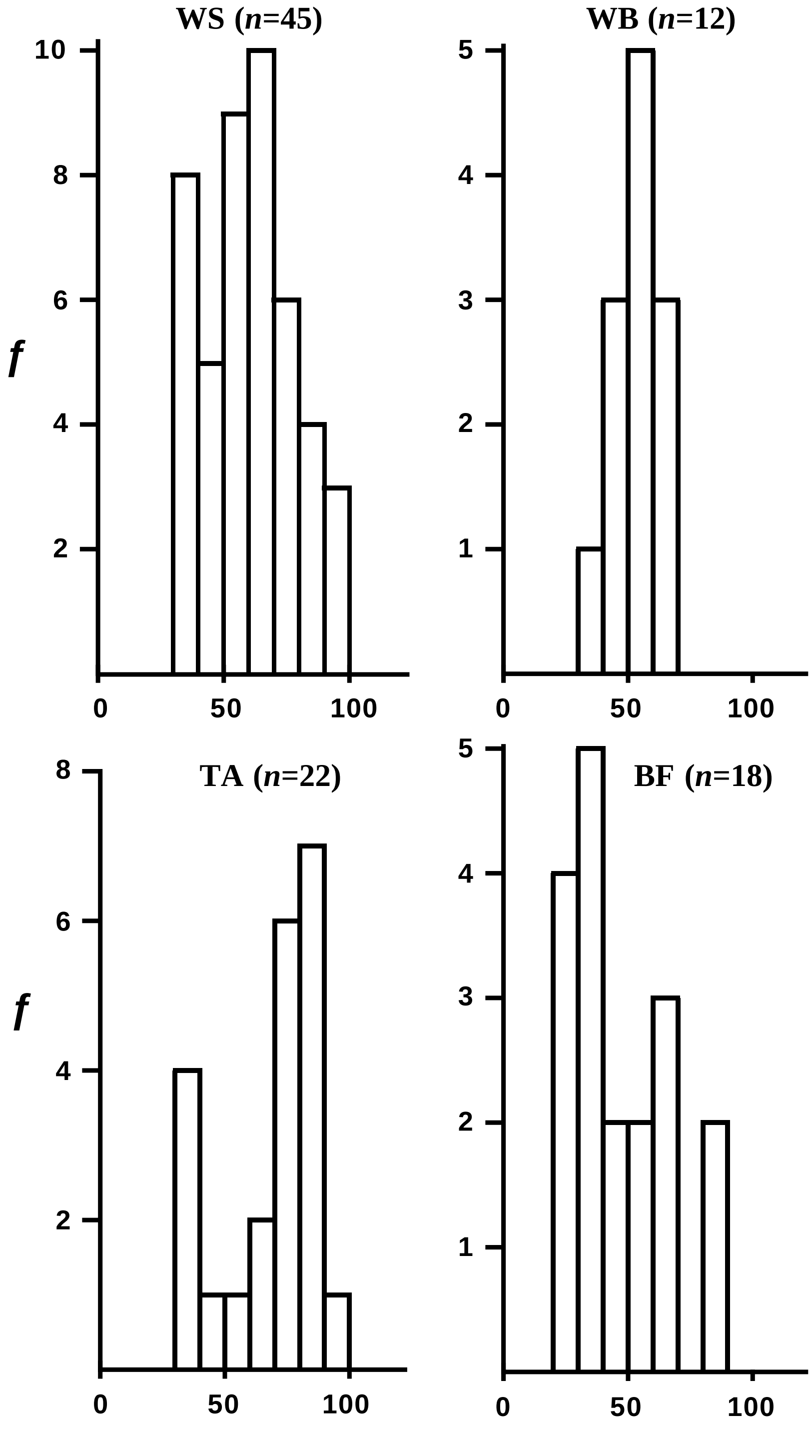

Figure 11. Age-class histograms of time since initial recruitment for white spruce, trembling aspen, balsam fir and white birch advance regeneration in balsam poplar stands.

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

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. 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.

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 (**Figure 12**). 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 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 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 (**Figure 13**). 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

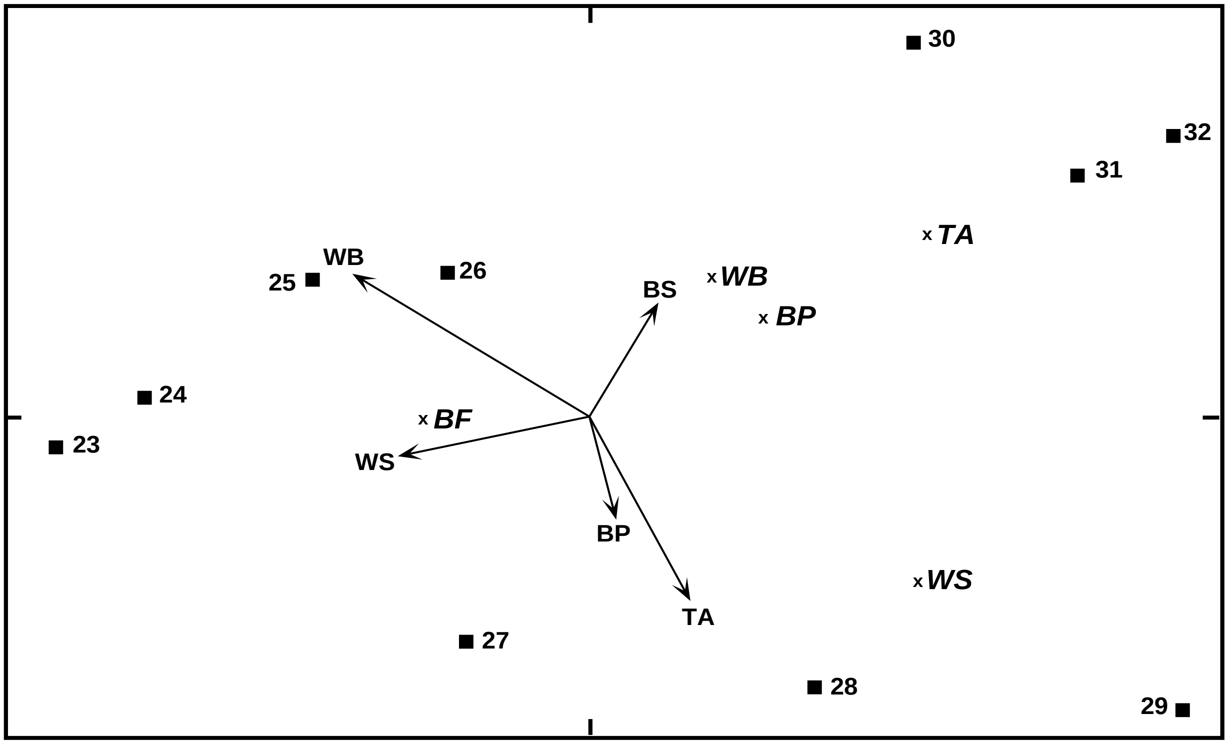

Figure 12. Canonical correspondence analysis ordination biplot of advance regeneration density (x) constrained by the initially-established cohort composition (vectors) of 10 white spruce stands. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1{}^2 = 0.925$, $R_2{}^2 = 0.917$. 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.

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.

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 (**Figure 12**). Balsam fir advance regeneration occurs in all but one stand, and is highest in stands where 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 (**Figure 12**). White birch root collar suckering occurs in 8 of the 9 stands that had initial birch establishment.

<u>White Spruce stand dynamics</u>

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

Table 5. Average density/100 m^2 of three age classes and five height classes for white spruce, balsam fir, trembling aspen and white birch in 10 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.

WHITE SPRUCE

	C	*I*	*R*
1	2.00 (0.52)	0.50 (0.33)	
2	0.29 (0.20)	0.25 (0.15)	
3	0.29 (0.25)	0.71 (0.27)	
4		0.64 (0.57)	0.39 (0.16)
5			0.54 (0.17)
	9/10	6/10	6/10

BALSAM FIR

	C	*I*	*R*
1		2.54 (0.88)	
2		1.39 (0.63)	
3		6.54 (2.69)	
4		0.50 (0.20)	1.43 (0.80)
5			66.50 (15.37)
	0/10	9/10	9/10

TREMBLING ASPEN

	C	*I*	*R*
1	1.50 (0.45)	0.25 (0.13)	
2		0.86 (0.37)	
3		0.50 (0.29)	0.07 (0.07)
4			1.36 (0.56)
5			3.96 (1.00)
	7/10	7/10	7/10

WHITE BIRCH

	C	*I*	*R*
1	0.21 (0.12)	0.21 (0.11)	
2	0.57 (0.46)	0.50 (0.16)	
3		0.32 (0.16)	0.04 (0.04)
4			0.36 (0.17)
5			1.71 (0.62)
	5/10	8/10	7/10

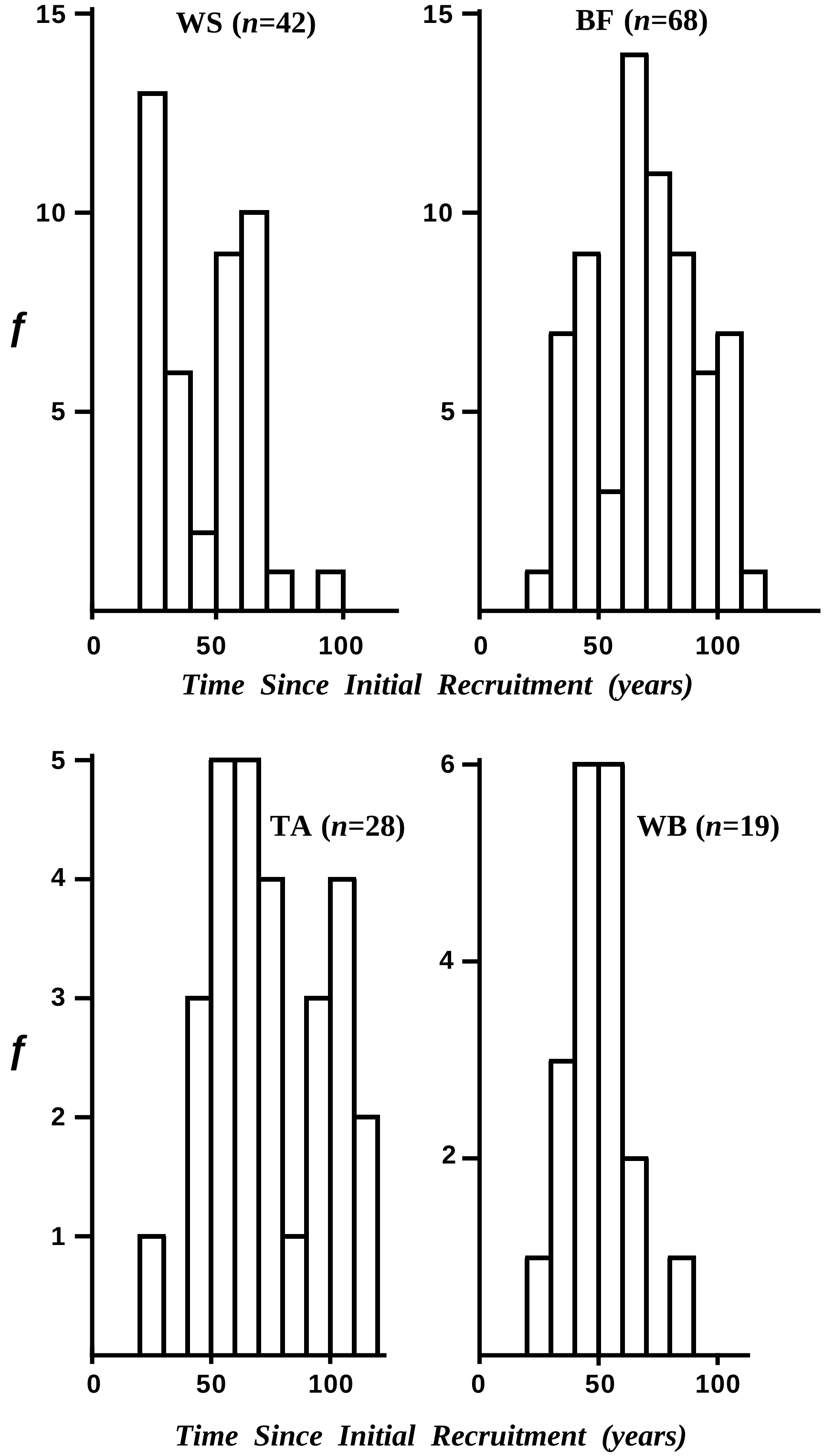

Figure 13. Age-class histograms of time since initial recruitment for white spruce, trembling aspen, balsam fir and white birch advance regeneration in white spruce stands.

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.

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 (**Figure 14**). 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 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 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 (**Figure 15**). 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

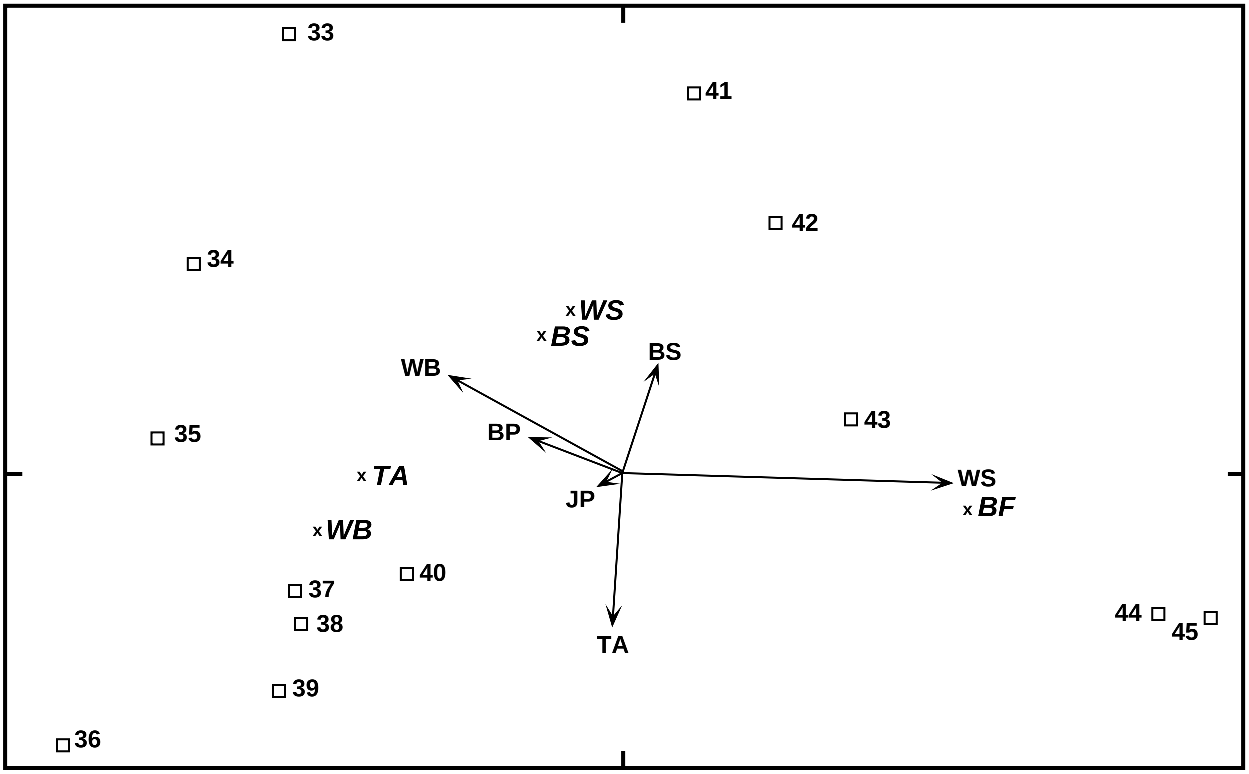

Figure 14. Canonical correspondence analysis ordination biplot of advance regeneration density (x) constrained by the initially-established cohort composition (vectors) of 13 jack pine stands. Horizontal axis is axis 1, vertical axis is axis 2. Canonical correlations: $R_1^2 = 0.957$, $R_2^2 = 0.841$. 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.

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. Black spruce recruitment is strongly dependent on seed source. Substrate conditions are also important, as recruitment is much higher in 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 and 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 .

Table 6. Average density/100 m^2 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.

WHITE BIRCH

	C	I	R
1	0.25 (0.13)	0.11 (0.07)	
2	0.19 (0.09)	2.36 (0.76)	
3		3.03 (0.81)	0.53 (0.23)
4			0.42 (0.36)
5			0.75 (0.31)
	7/13	9/13	8/13

BALSAM FIR

	C	I	R
1		0.28 (0.20)	
2		1.33 (0.55)	
3		9.39 (2.88)	
4		1.78 (0.65)	0.53 (0.27)
5		0.53 (0.38)	37.81 (14.97)
	0/13	9/13	10/13

BLACK SPRUCE

	C	I	R
1	0.69 (0.21)		
2	1.14 (0.44)	0.33 (0.14)	
3	0.64 (0.42)	0.81 (0.39)	
4		0.33 (0.28)	0.11 (0.07)
5			0.92 (0.32)
	8/13	6/13	5/13

WHITE SPRUCE

	C	I	R
1	0.47 (0.23)		
2	0.47 (0.22)	0.17 (0.07)	
3	0.14 (0.08)	0.58 (0.20)	
4		0.03 (0.03)	0.25 (0.18)
5			0.67 (0.21)
	5/13	7/13	6/13

TREMBLING ASPEN

	C	I	R
1	2.11 (0.45)	0.72 (0.22)	
2		1.83 (0.60)	
3		0.69 (0.19)	0.17 (0.08)
4			0.53 (0.21)
5			2.33 (0.55)
	10/13	12/13	12/13

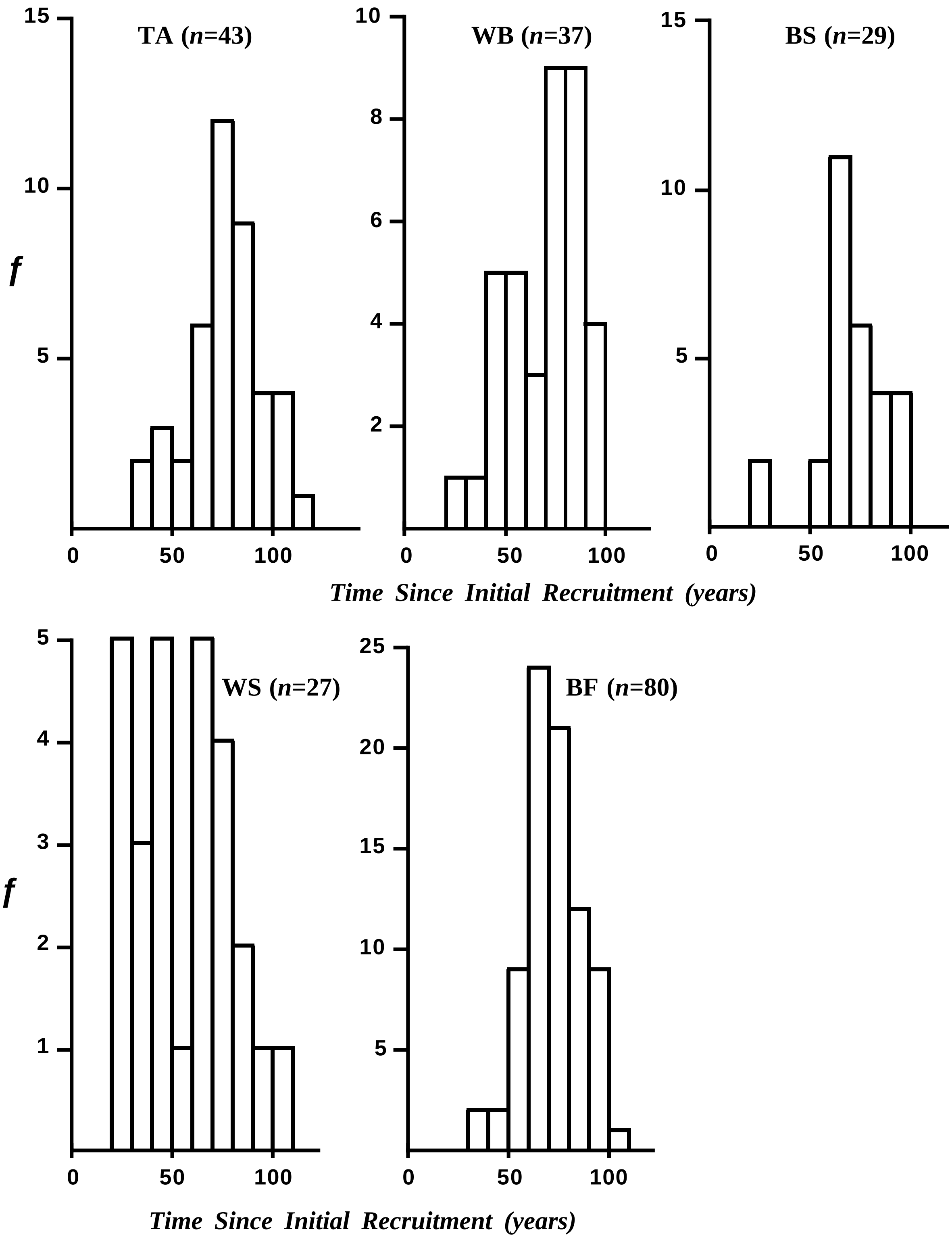

Figure 15. Age-class histograms of time since initial recruitment for white spruce, trembling aspen, balsam fir, white birch and black spruce advance regeneration in jack pine stands.

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.

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 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 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,

Table 7. Average density/100 m^2 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.

BLACK SPRUCE

	C	*I*	*R*
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**

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.

DISCUSSION

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 2, 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 Qu bec (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 2 and 4**). Successful secondary recruitment of balsam fir has also occurred in many stands, particularly in the white spruce and jack pine stand-types (**Tables 5 and 6**).

Mixedwood Stand Dynamic Model

A synoptic model of forest dynamics in Duck Mountain boreal mixedwood stands is presented in **Figure 16**. 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.

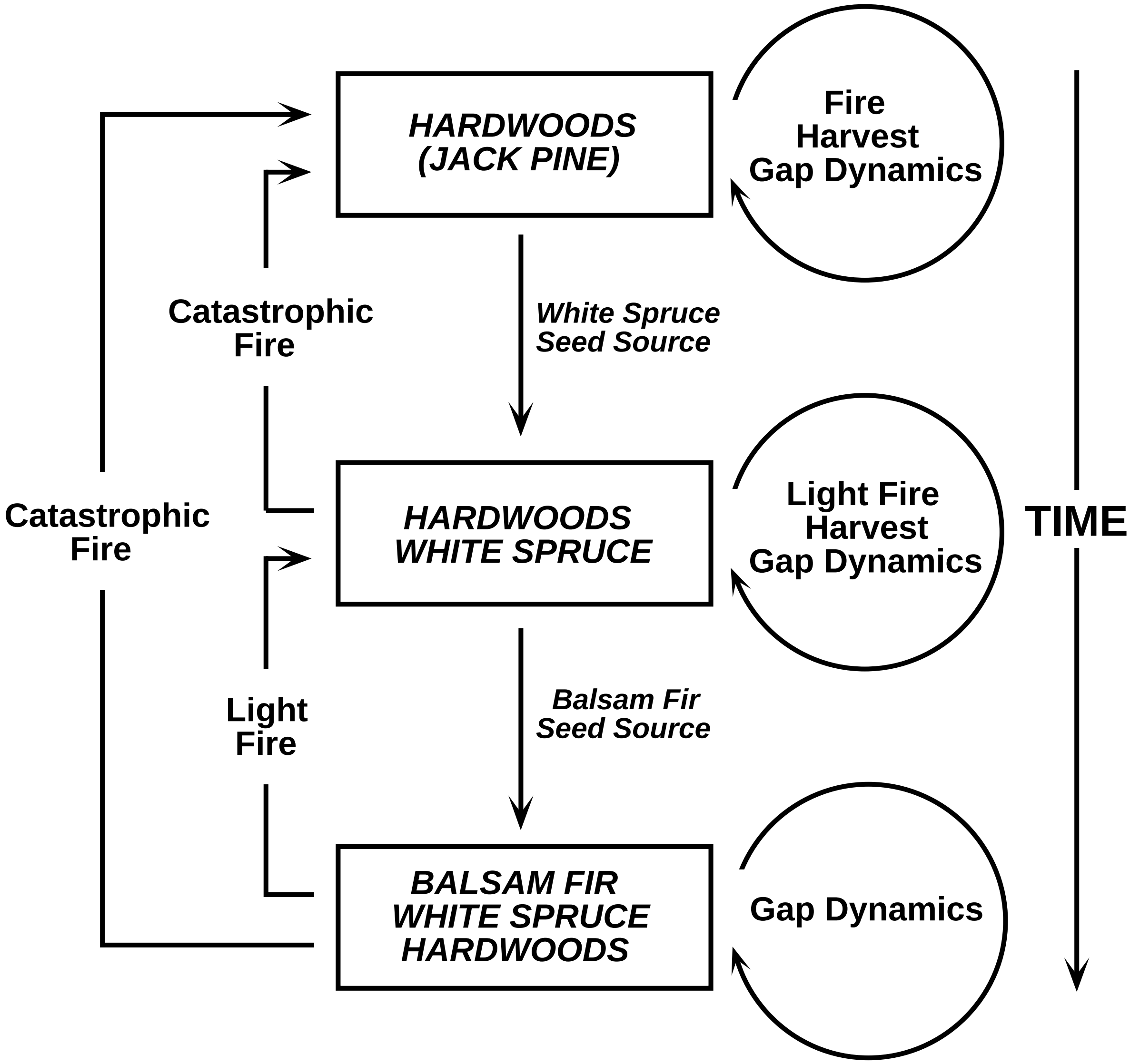

Figure 16. A synoptic forest succession model for boreal mixedwood stands in the Duck Mountains, Manitoba. Following catastrophic fire, stands are generally dominated by vegetative hardwood regeneration (trembling aspen, balsam poplar, and/or white birch). These stands are self-replacing under recurrent 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 Qu bec (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 endingwith 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 and 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 and Charron 1994; Bergeron and Dansereau 1993).

Disturbance and Stand Dynamics

The Alberta highlands are characterized by moist and short summers, resulting in less frequent and extensive wildfires when compared to much of the western (prairie) boreal region (Achuff and La Roi 1977). As a consequence, late-succesional conifers generally dominate seral and climax forests in this region. Similar mesoclimatic conditions hold for the eastern uplands of the Duck Mountains and Riding Mountain, where precipitation amounts are higher and cooler conditions prevail (Caners and Kenkel 1998). In addition, physiographic features of the Duck Mountain uplands (e.g. numerous lakes and wetlands, and a hilly terrain) act as impediments to the rapid spread of wildfires from the warmer and drier mesoclimatic regions to the west and south. As a result, mature stands of white spruce and balsam fir are much more common in the higher elevation regions of the Duck Mountains. By contrast, historically higher wildfire frequencies along the lower slopes of the Manitoba Escarpment have resulted in greater dominance of trembling aspen and other early-successional or pioneer species.

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 and 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 and 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 and Bouchard 1993). Even in the absence of fire, however, the creation of forest gaps perpetuate mixed conifer-hardwood stands for a considerable period (Bergeron and Charron 1994; Bergeron and 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, paper 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 and 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. 1997b). Vegetation development at the landscape level is driven by disturbance history and episodic stochastic events, with the result that succesional dynamics are attributable to the vagaries of seed production, weather, insects and disease (McCune and Allen 1985).

Our results suggest that similar conditions hold for the Duck Mountains. Current canopy composition, 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). 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.

In the Duck Mountains, changes in fire return frequency and/or severity resulting from fire suppression will result in a corresponding change in the structure and composition of forest stands. In particular, later-succesional species such as white spruce and balsam fir will increase in abundance. This trend could be mitigated through the clear-cut harvesting of aspen and selective harvesting of white spruce, since such harvesting emulates well natural disturbance.

In summary, 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 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 & 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.

MANAGEMENT APPLICATIONS

The Duck Mountain ecoregion is currently an island of mixedwood boreal forest surrounded by cleared agricultural land. Present-day forest stands are adapted to, and are a reflection of, the regional cumulative disturbance history as well as physiographic and edaphic features. The landscape consists of a patchwork mosaic of forest stands that vary in age, structure and composition. The Duck Mountain forests are a storehouse of biological diversity, performing ecosystem functions and providing habitat to unique assemblages of wildlife. Changes in historical disturbance regimes will likely be reflected in shifts in the size, spatial pattern, age, and dominance of various forest stand-types. Management efforts should therefore focus on maintaining representative examples of all seral stages of all stand-types, so as to preserve species and landscape diversity.

The following is a summary of recommended sustainable harvesting and management strategies for each of the five initial stand-types identified in this study.

(a) Trembling Aspen

Upland aspen stands are slowly invaded by white spruce, provided there is a reliable and proximate seed source. In most stands, aspen naturally regenerates from secondary suckers and will therefore maintain canopy dominance. Recurrent, large wildfires that swept relatively unimpeded across the lower slopes of the Duck Mountains likely played an important role in perpetuating this 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 and Johnson 1998). Trembling aspen recovers quickly from wildfire by suckering (Bergeron 2000), and responds in the same manner following clear-cut harvesting.

Logging emulates well natural fire disturbance. Efforts should be made to ensure that rotations are such that various age and size structures of aspen stands are maintained in the landscape. Careful logging, particularly the protection of softwood advance regeneration (primarily white spruce) during harvesting, is to be promoted as a method for retaining pre-harvest biodiversity. On-site slash retention is recommended, as this promotes nutrient cycling and provides substrata for germination of other species such as white spruce and white birch.

(b) Balsam Poplar

The largely deciduous canopy of young balsam poplar stands is rapidly succeeded by a mixed deciduous-coniferous canopy, with balsam poplar remaining as only a minor component in stands greater than 120 years old. If a balsam fir seed source is proximate, these stands are rapidly dominated by balsam fir. Most commonly, however, a mixed canopy of white spruce, trembling aspen, white birch, balsam poplar and black spruce develops. An exception is seasonally flooded areas, where softwoods cannot colonize.

The harvesting of balsam poplar stands is unattractive, since balsam poplar fibre is of low quality and such stands are of limited spatial extent. As white spruce abundance increases, selective logging may become feasible. Sustainable harvesting of white spruce is promoted by removing only the largest trees.

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. Maintenance of these habitat islands will promote habitat biodiversity, and ensure a seed source for later-succesional conifers into nearby clearcuts.

(c) White Spruce

Balsam fir abundance is increasing in most white spruce stands. However, complete stand replacement by balsam fir is not expected 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 and La Roi 1977; Bergeron 2000). In the absence of major balsam fir recruitment, the canopy of white spruce stands retains its mixed nature through the recruitment of aspen, balsam fir, and white spruce in gaps, and the resprouting of birch from the root collar of initially established trees.

Following fire, white spruce establishes on exposed mineral soil from proximate seed sources, while aspen vegetatively suckers. Clearcutting of these stands will generally promote trembling aspen suckering, expect where balsam fir is abundant. Extensive balsam fir cover would likely limit light and keep soil temperatures cool enough that suckering would be compromised. White spruce does not naturally re-establish to any appreciable extent on the organic soils that remain post-logging. If such stands are logged and emulation of post-fire succession is desired, the entire overstory, including balsam fir, should be removed and pockets of advanced white spruce regeneration left unharvested. Limited selective logging of large white spruce may be sustainable in stands lacking a heavy balsam fir component, but care should be taken to protect white spruce advance regeneration.

An 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. Balsam fir saplings are a favoured winter forage for large ungulates such as moose and elk, so that increased balsam fir sapling abundance may help sustain higher ungulate populations.

(d) Jack Pine

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. The fine-scale rolling topography of the region creates complex and variable drainage conditions that preclude the formation of extensive, monodominant jack pine stands. Patterns of advance regeneration recruitment into these stands are variable and diverse, reflecting inter-stand differences in depth to water table, edaphic factors, site drainage and aspect, seed source proximity, initial cohort composition and seedbed conditions. In general, these stands are becoming increasingly diverse as jack pine senesces and is removed from the canopy. A diverse mixture of balsam fir, white spruce, black spruce, trembling aspen and/or white birch characterizes many stands. Recruitment densities of most species is low, with the result that advance regeneration is usually not dominated by any one species.

The mixed nature of these stands makes them less desirable for logging. Larger patches of trembling aspen and jack pine could be harvested, and selective logging of white spruce is also possible. Neither would do great harm to these stands, as they retain a very mixed canopy as they age. Management of jack pine stands must recognise their diverse canopy composition and variable successional pathways, and attempt to preserve this diversity.

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, which is already codominant in most stands, 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.

(e) Black Spruce

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-impoverished, anoxic and often water-logged substrates. Layering will perpetuate black spruce on organic substrates. There is currently little if any advance regeneration in black spruce stands on mineral substrates. Such stands are very dense and thin slowly, remaining very dark in the understory even after codominant jack pine senesces. A deeply shaded understory and poor seedbed conditions (a combination of a very thick feathermoss layer and cold soils) characterize these stands. Dense upland black spruce stands often fringe open wetlands, forming a natural buffer to the boreal mixedwood stands further upslope. These fringe forests may be the result of past activity by beaver, which consolidated the abundance of black spruce by felling aspen trees adjacent to the wetlands.

Clear-cut harvesting of upland black spruce, if undertaken, should be followed by replanting and active suppression of potential competitors (herbaceous vegetation and tall shrubs). Clear-cutting of black spruce stands occurring on organic substrates should be undertaken in winter to ensure minimal damage to the substrate and established layers (advance regeneration).

REFERENCES

Achuff, P.L., and La Roi, G.H. 1977. *Picea-Abies* forests in the highlands of northern Alberta. Vegetatio 33:127-146.

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

Bergeron, Y., and Bouchard, A.. 1993. Use of ecological groups in analysis and classification of plant communities in a section of western Queb c. Vegetatio 56:45-63.

Bergeron, Y., and Charron, D. 1994. Postfire stand dynamics in a southern boreal forest (Qu bec): A dendrological approach. coscience 1:173-184.

Bergeron, Y., and Dansereau, P. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. J. Veg. Sci. 4:827-832.

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

Bergeron, Y, Gauthier, S., Carcaillet, C., Flannigan, M., Prairie, Y., and Richard, P.J.H. 1999. Variability in fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. In Proceedings of the Sustainable Forest Management Network Conference: Science and Practice: Sustaining the Boreal

Forest., 14-17 Feb. 1999, Edmonton, AB. Edited by T.S. Veeman, D.W. Smith, B.G. Purdy, F.J. Salkie, and G.A. Larkin. Sustainable Forest Management Network, Edmonton, AB. pp. 74-80.

Bonan, G.B., and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst. 20:1-28.

Caners, R.T., and Kenkel, N.C. 1998. Modelling landscape-level vegetation dynamics in Riding Mountain National Park. Department of Botany, University of Manitoba, Winnipeg. 156 pages.

Carleton, T.J., and Maycock, P.F. 1978. Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56:1157-1173.

Cogbill, C.V. 1985. Dynamics of the boreal forests of the Laurentian Highlands, Canada. Can. J. For. Res. 15:252-261.

Connell, J.H., and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-1144.

De Grandpre, L., Gagnon, D., and Bergeron Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. Jo. Veg. Sci. 4:803-810.

Dix, R.L., and Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. 49:657-676.

Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412-417.

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

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecological Monographs 65:325-346.

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

Harrison, J.D.P. 1934. The Forests of Manitoba. Department of the Interior, Forest Service, Ottawa. Forest Service Bulletin No. 85.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329-362.

Heinselman, M.L. 1996. The Boundary Waters Wilderness Ecosystem. University of Minnesota Press, Minneapolis, MN. 336 pages.

Huston, M., and Smith, T. 1987. Plant succession: life history and competition. Am. Nat. 130:168-198.

Johnson, E.A., Miyanishi, K., and Kelb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta-Picea engelmannii* forest. J. Ecol. 82:923-931.

Kenkel, N.C., Hendrie, M.L., and Bella, I.E. 1997a. A long-term study of *Pinus banksiana* population dynamics. J. Veg. Sci. 8:241-254.

Kenkel, N.C., Walker, D.J., Watson, P.R., Caners, R.T., and Lastra, R.A. 1997b. Vegetation dynamics in boreal forest ecosystems. Coenoses 12:97-108.

Kenkel, N.C., Watson, P.R., and Uhlig, P. 1998. Modelling landscape-level vegetation dynamics in the boreal forests of northwestern Ontario. Ontario Ministry of Natural Resources, Sault Ste. Marie. 151 pages.

Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. 26:888-898.

Koroleff, A. 1954. Leaf litter as a killer. J. For. 52:178-182.

Larsen, J.A. 1980. The boreal ecosystem. Academic Press, New York. 482 pages.

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

McCune, B. and Allen, T.F.H. 1985. Will similar forests develop on similar sites? Can. J. Bot. 63:367-376.

Noble, I.R. and Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. Vegetatio 43:5-21.

Peterson, E.B., and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. Spec. Rep. 1. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. 252 pages.

Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. Am. Nat. 110:107-119.

Rowe, J.S. 1956. Vegetation of the southern boreal forest in Saskatchewan and Manitoba. PhD Thesis. University of Manitoba, Winnipeg. 305 pages.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. Can. J. Bot. 39:1007-1017.

Waldron, R.M. 1966. Factors affecting natural white spruce regeneration on prepared seedbeds at the Riding Mountain Forest Experimental Area. Can. Dep. For. Rural Dev. For. Branch Tech. Note 74.

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

Wilson, J.B, Gitay, H., Roxburgh, S.H., King, W.M., and Tangney, R.S. 1992. Egler s concept of initial floristic composition in succession - ecologists citing it don t agree what it means. Oikos 64:591-593.

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