Small-scale disturbance and vegetation dynamics in trembling aspen dominated forests in northeastern Ontario

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Abstract

The scientific understanding of boreal forest stand development and vegetation dynamics has been well documented with respect to stand-initiating disturbances; however, the role of subtler disturbance events has received less attention. Two scenarios that warrant the study of small-scale disturbance in the boreal forest of Ontario include i) forest management practices and changing climatic factors that range in spatial scale from local to global are predicted to skew age class distribution of forests towards mature, oldgrowth stages of development, and ii) during these stages of forest development, small-scale disturbance is hypothesized to be the major disturbance mechanism to influence vegetation dynamics. Many principles and methods of the research that has been conducted on vegetation dynamics and small-scale disturbance in deciduous temperate and tropical forests can be applied to the boreal forest as a study system. This thesis attempts to understand vegetation dynamics during intermediate stages of boreal forest development, with an emphasis on the role of small-scale disturbance.

The thesis is presented in four chapters that, i) develop the rationale for studying small-scale disturbances in boreal forests, ii) characterize the extent of small-scale disturbance in trembling aspen forests, and ii) quantify the effect of small-scale disturbance on understorey plant communities. Analyses varied considerably among chapters. Multivariate ordination techniques and average basal area change measurements were used to assess stand and species dynamics of 217 forests stands sampled across northeastern Ontario. Relationships between small-scale disturbance with time since stand initiation (60 – 120 years) of ten trembling aspen were assessed using linear models. Juvenile tree recruitment patterns and community changes (woody and herbaceous plant species) in gaps and understorey environments of five trembling aspen stands were assessed using general linear models and various multivariate methods.

Consistent patterns in boreal forest stand development include early dominance of shade intolerant species such as *Populus tremuloides* and *Pinus banksiana*, followed by increasing basal area of shade tolerant conifer species such as balsam fir, black spruce, and white cedar. Important declines, between 80 and 100 years since stand initiation, in the basal area of species that dominate the initial post-disturbance cohort point towards the occurrence of small-scale disturbance (i.e. mortality of mature canopy trees). The occurrence of such disturbance warrants the investigation of i) how important small-scale disturbance actually is, and ii) the effect that it has on the vegetation dynamics of understorey plant communities.

Results from chapter two clearly show that small-scale disturbances are an important and conspicuous element of forest stand development when trembling aspen are the dominant tree species. The most important factors that lead to tree mortality include infection by wood decay pathogens and wind. The increasing number of gap makers per gap, and number of gap maker decay classes per gap with time suggests that gap expansion, resulting from punctuated disturbance events is an important mechanism of gap formation. Snapped gap makers, followed by standing dead and uprooted gap makers were the most important structural attributes of gaps, and their relative importance remained similar with time.

Despite the importance of small-scale disturbance during 95-120 years since stand initiation, juvenile tree recruitment patterns and plant community response to gap environments of different sizes and ages was negligible. There was no detectable difference in stem density and growth of all important juvenile tree species (including *Abies balsamea*, *P. tremuloides*, *Picea mariana*, *Picea glauca*, and *Betula papyrifera*) when compared among gap environments and the closed canopy understorey condition. Similarly, understorey plant communities showed no difference when compared among different gap types. High across-stand variability in community composition limited the ability to detect consistent compositional trends with respect to gap size and age. However, regardless of gap type, slight increases in species richness and abundance were detected for understorey woody species of heights between 2 and 5 m.

The effect of small-scale canopy tree mortality on understorey plant communities in trembling aspen dominated forests is minimal. This is in contrast to predictions that were made based on expectations from the role of small-scale disturbance dynamics in temperate and tropical forests. Based on the results of this thesis, future studies of boreal forest development and understorey vegetation dynamics should consider i) the establishment mechanisms of shade tolerant conifer species such as *A. balsamea* during early stages of forest development, ii) minimal gap sizes that facilitate growth of shade intolerant tree species that are taller than two metres, and iii) appropriately replicate different understorey community types.

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Equally, I am indebted to Dr. Han Chen for providing support during all stages of this project. His high academic expectations foster a rigorous understanding of how to address ecological problems from a scientific perspective; he will undoubtedly be a great addition to the faculty of forestry at Lakehead University. Along with Dr. Chen, Dr. Stan Vasiliauskas provided the majority of the logistical support during the design and data collection stage of this project. Dr. Vasiliauskas' knowledge of vegetation and site history in northeastern Ontario was paramount for the success of this project. Despite his numerous commitments with the Ontario Ministry of Natural Resources (OMNR), he helped by spending many hours locating study sites and collecting data in the field.

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To all the people who have made this thesis a success - thank you.

This thesis is dedicated to the memory of my dog Skipper.

Table of Contents

Chapter 1: Stand and species dynamics of common boreal forests in northeastern Ontario

Chapter 2: Characteristics of small-scale disturbance events in trembling aspen dominated forests between 60 and 120 years since fire in northeastern Ontario

Chapter 3: Recruitment of juvenile tree species in canopy gaps and understorey environments in trembling aspen dominated forests in northeastern Ontario

Chapter 4: Plant community response to small-scale disturbances in trembling aspen dominated forests in northeastern Ontario

List of Tables

List of Figures

General Introduction

The ability to accurately predict vegetation dynamics is a major goal of plant ecology and has been an important area of research for over a century. Although accurate long-term predictions of vegetation change can be a daunting task, four important steps must be achieved to consider a model of vegetation dynamics successful, these include: i) identifying important patterns of temporal change in species composition at different spatial and temporal scales, ii) hypothesizing reasons for observed changes, iii) accepting or eliminating hypothesized reasons for change based on the results from appropriate natural or manipulated experimental designs, and iv) creation of a predictive model for vegetation dynamics using the accepted hypotheses responsible for change. The four chapters of this thesis address the first three steps of this conceptual model.

Despite the formalization of the term 'gap-phase dynamics' by Richards (1952), the paradigm emerged as an important concept in the disciplines of forestry and forest ecology during the early twentieth century. Whitmore (1995) quoted research into the role of gap creation on recruitment patterns of plants as early as the 1920s. Currently the gap dynamics concept is used in the context of soil and vegetation processes to predict forest sustainability where stand replacing disturbances are uncommon. Empirical research that corroborates the concept is limited in scope for boreal forests. However, the literature is well-established for tropical and temperate forests where studies have been conducted since the mid-1970s and 1980's respectively (Whitmore, 1974; Denslow, 1987; Runkle 1981, 1982; Brokaw, 1985, 1987; Lawton and Putz, 1988). Recent studies of gap disturbance have been expanded and tested in other forest regions including temperate coniferous forests (Lertzman and Krebs, 1991; Spies *et al.*, 1990) and subalpine spruce-fir forests (Foster and Reiners, 1986; Battles and Fahey, 2000; Bartemucci *et al.*, 2002). Only a few studies in boreal forests have attempted to address the role of gap disturbance on vegetation dynamics (Kneeshaw and Bergeron, 1998; Cumming *et al.*, 2000; Liu and Hytteborn, 1991; Kuuluvainen *et al.*, 1998; Drobyshev, 1999).

Similarity of results among studies, particularly those occurring in tropical and temperate forests, has lead to the expansion of gap-phase dynamics as an important pedagological tool for understanding processes and mechanisms that are responsible for forest stand dynamics. The ecological principles involved in the understanding of gap-phase dynamics are conceptually quite simple: the death of a dominant canopy tree or group of trees will increase the availability of otherwise limited resources (including but not limited to light, nutrients, and space) (Denslow, 1987). The release of limited resources in canopy gaps creates a different environment juxtaposed with the intact forest matrix, the former is predicted to facilitate the establishment and growth of juvenile trees.

The successful colonization of a juvenile tree species into the canopy can be generalized into three major stages: initial colonization, establishment, and growth. All stages depend on the expression of adaptive traits (e.g. niche partitioning theory) and a certain degree of chance (e.g. recruitment limitation). The colonization stage is characterized by the ability of a species to take advantage of a newly created gap environment. Juvenile trees can be present as advanced regeneration (present prior to gap creation in the understorey of the existing forest matrix, typical of shade tolerant trees), seeds, or vegetative sprouts. The major factor that limits successful colonization is dispersal of plant propagules; gap colonization will favour those species with an abundant seed-source (either in soil, or from adjacent parental trees), vegetative propagules (either in soil, or from adjacent parental trees), or advanced regeneration. After successful colonization into a gap, a juvenile tree must become established. During this stage, unfavourable microsite conditions are the major limiting factors towards movement into the growth stage. The interaction between dispersal limitation and unfavourable microsite conditions has been termed recruitment limitation and is a major antagonist of using gap dynamics theory to explain tree species coexistence, particularly in diverse tropical environments (Brokaw and Busing, 2000). Following successful colonization and establishment, juvenile stems are subjected to growth limitations. Intra- and inter-specific competition, herbivory, and fungal infection are only a few major obstacles that must be overcome to complete the stages that are involved in successful gap filling. Within the gap-phase dynamics framework, non-adaptive traits or simple bad luck will substantially impair the successful colonization of a juvenile tree into gap environment, and subsequently the forest canopy.

In the boreal forest, the gap-phase dynamics framework has been largely ignored as a method for understanding forest stand dynamics (McCarthy, 2001). One reason for this neglect is that the large-scale and frequent occurrence of fire in the boreal forest plays a major role in structuring many forest communities (Heinselman, 1981; Johnson, 1992). A review of gap dynamics (McCarthy, 2001) and conference proceedings of disturbance dynamics in the boreal forest (Bergeron *et al.*, 1998) suggest that more research into the role of small-scale disturbances such as canopy gap formation should be pursued in the boreal forest. This is paramount considering i) fire return intervals (i.e. the time between fire occurrences) is predicted to increase in northeastern Ontario (Bergeron and Archambault, 1993; Bergeron *et al.*, 2001) and ii) fire suppression since the 1950's across many regions of Ontario, including the northeast, has resulted in forests that are mature (Carleton, 2000). Both of these processes act to skew the distribution of age classes towards that of mature (over-mature or oldgrowth) forests. During this stage, small-scale disturbance is expected to become the major factor influencing vegetation dynamics (Oliver and Larson, 1990). Since the conceptual framework associated with the gap-phased dynamics is relatively simple, testable hypotheses (similar to those developed in temperate and tropical forest regions) of individual species response and community structure in gap environments can be developed.

Gap-phase dynamics are typically used to understand the stand dynamics of tropical and temperate forests because the low occurrence of stand-replacing disturbance results in forests in mature developmental stages (Oliver and Larson, 1990). There are inherent differences in the way the concept can be applied to boreal forests. In this thesis I examine the role of small-scale disturbance in forests that dominate subsequent to fire i.e. forests that are not usually considered to be oldgrowth. The thesis is broken into four chapters that explore the following research questions:

1) What are the stand and species dynamics of eight common eastern boreal forest types?
2) What are the characteristics of gap creation at the forest stand-level and individual gap level, and how are gaps created in trembling aspen dominated forests?
3) How do gaps influence the recruitment and growth of different juvenile tree species in trembling aspen dominated forests?

4) Are herbaceous and woody plant communities resistant to the effects of gap creation in trembling aspen dominated forests?

Chapter 1

Stand and species dynamics of common boreal forests in northeastern Ontario

Abstract

Forest succession has received little attention in the boreal forest compared to the study of vegetation dynamics following stand-replacing disturbance. A large-scale study of various boreal forest types was completed to gain insight into the spatial and temporal succession patterns of forest stands and common tree species. The objectives were to determine the consistency of successional patterns of forest stands when grouped by dominant canopy species, and to explain stand dynamics based on the average changes in species basal area as a function of time since fire. In northeastern Ontario 217 forest stands were randomly selected using forest resource inventory (FRI) maps. Basal area of canopy trees was estimated at two time periods using either aerial photographs or ground sampling. Aerial photographs were used to estimate basal areas (in 1946, 1947, 1949, 1961, 1963, or, 1972) and cruise transects were used to estimate current basal areas (during 2000 and 2001). Basal area sampling from aerial photographs was accomplished by delimiting a 2 ha plot around historic cruise transects. The 2000 and 2001 cruise transects were located within the 2 ha plots that were delineated on historic aerial photographs. Eight forest types were identified based on species dominance including trembling aspen, white birch, jack pine, black spruce, white cedar, hardwood dominated mixedwoods, conifer dominated mixedwoods, and pure mixedwoods. Nonmetric Multidimensional Scaling (NMS) ordination techniques were used to infer successional patterns of the forest types based on a space for time substitution approach, and a time series approach. Individual species dynamics were inferred from qualitative descriptions of the average growth function of important tree species in each forest type with respect to time since fire. The results indicated that when fire is absent for long periods of time, succession does occur in northeastern Ontario. The general successional trend is that trees that dominate after fire decline over time resulting in the formation of mixedwood forests. The two most distinct patterns of succession involved i) the replacement of trembling aspen by mixedwood forest composed of species such as balsam fir, white birch, and white cedar and ii) the replacement of jack pine by black spruce. The variable changes in other forest types can be attributed to demographic complexity in black spruce forests, facilitation of shade intolerant species via gap processes in white cedar forests, and compositional evenness in mixedwood and conifer mixedwood forests.

Introduction

Fire plays a major role in structuring vegetation patterns in Canada's boreal forest (Johnson, 1992; Heinselman, 1991; Bergeron *et al.*, 1998). Following fire, development of forest stands can be generalized by three typical successional stages: i) an initial stage dominated by shade intolerant species, ii) a mixed wood stage with equal dominance of shade intolerant (hardwood and conifer species) and shade tolerant conifer species, and iii) a final stage dominated by shade tolerant conifer species (Bergeron and Dubuc, 1989; Bergeron, 2000). The initial post-fire cohort is usually dominated by species such as jack pine (*Pinus banksiana* Ait.), trembling aspen (*Populus tremuloides*, Michx.), and white birch (*Betula papyrifera* Marsh) that have evolved fire-adaptive traits such as serotinous cones, vegetative root suckers, and vegetative basal sprouts respectively (Burns and Honkala, 1990a,b). The intermediate mixed-wood stage occurs when the initial post-fire cohort begins to decline and is characterized by a transition phase dominated by shade intolerant and shade tolerant species. The shift in dominance occurs as a result of either colonization of the shade tolerant species with the shade intolerant species following disturbance, or colonization via a mechanism of facilitation (Connell and Slatyer, 1977) under the canopy of shade intolerant species. Shade intolerant species such as trembling aspen can contribute small numbers of offspring during this stage of development if canopy gaps are large enough (Bergeron, 2000). The third stage of development is characterized by dominance of shade tolerant species such as balsam fir (*Abies balsamea* Mill.) and white cedar (*Thuja occidentalis* L.) (Bergeron and Dubuc, 1989; Bergeron, 2000). In eastern boreal forests, spruce budworm outbreaks become the major disturbance influencing vegetation dynamics when species such as balsam fir become dominant (Bergeron *et al.*, 1995).

Forest dynamics operate on time scales that are much longer than the typical three-five year long research projects or even the expected age of a life-long scientific investigator. As a result forest ecologists rarely have the time and resources to gather time-series empirical data to show actual changes in species composition over successional time. In cases where long-term studies do exist, there is very little or no replication of samples. Methods such as “space for time substitution” have been developed to accommodate the problems associated with long-term studies (Pickett, 1989). The chronosequence approach, a common “space for time” method, provides information on average trends in forest dynamics by comparing geographically adjacent spatial composition patterns of forests that have similar, but punctuated, disturbance histories (Pickett 1989). Overall the "space for time" method has been accepted by the peer-reviewed literature, as many published studies use this approach, and has been shown to be consistent with stand reconstruction data for boreal forests in northwestern Quebec (Bergeron, 2000). However, the efficacy of "space for time" substitution is rarely tested with actual time series data (but see Foster and Tilman, 2000). The accurate interpretation of long-term dynamics using "space for time" methods such as the chronosequence approach depends, among other factors, on the consistency of mechanisms that affect forest stand development and consistency of species temporal dynamics across the landscape. Therefore, the chronosequence approach will be more appropriate for inferring the long-term dynamics of forest stands that exhibit these characteristics.

Analysis of long-term survey records (forest resource inventory, FRI) and periodic aerial photographs are two approaches used to quantify canopy change in forest environments (Fensham and Fairfax, 2002). By comparing spatial patterns in tree composition at sites of different times since fire with these data, one can test the accuracy of using only spatial data to interpret successional patterns of forest communities. The main objective of this study was to use long-term surveys and aerial photographs to test the efficacy of using spatial data to predict successional trends in boreal forest stands in northeast Ontario. In this study both time-series and spatial data were used to infer the consistency of stand and species dynamics across the study region.

Methods

Site description

For this study 217 forest stands of various canopy compositions were selected in Ecozone 3E (Hills, 1959) in northeastern Ontario (Fig. 1.1). Stands were sampled randomly according to a stratified design using the factors of age class, cover type, and site condition. Only age class and cover type were considered in this study. Absences of stand-replacing disturbance such as fire and/or clear-cutting, and convenient accessibility were the main criteria by which forest stands were selected. Ecozone 3E is located within the Missinaibi-Cabonga section of the boreal forest (Rowe, 1972). Forest resource inventory (FRI) and aerial photographs are available for this region since the mid-1940s. The most common and abundant tree species include black spruce (*Picea mariana* (Mill.) BSP.), white birch, white spruce (*Picea glauca* (Moench) A. Voss), trembling aspen, jack pine, balsam fir, and white cedar (Table 1.2). Species that were less frequent and contributed small basal area included larch (*Larix laricina* (Du Roi) K. Koch), balsam poplar (*Populus balsamifera* L.), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* Ait.), red pine (*Pinus resinosa* L., and willow (*Salix* spp.) (Table 1.2).

This region has a relatively homogenous landscape. Major topographic features resulted from glacial deposits during the past ice age approximately 10000 years ago and soil orders include luvisols, podzols, and gleysols that are imperfectly to well-drained (Baldwin *et al.*, 2000). Summers are warm and short while winters are long and cold, with mean January and July temperatures –16°C and 24°C respectively (Canada Climate Normals 1961 – 2000). The average annual temperature for Timmins, Ontario is 1.2 °C and the average annual precipitation is 873 mm (Canada Climate Normals 1961 – 2000).

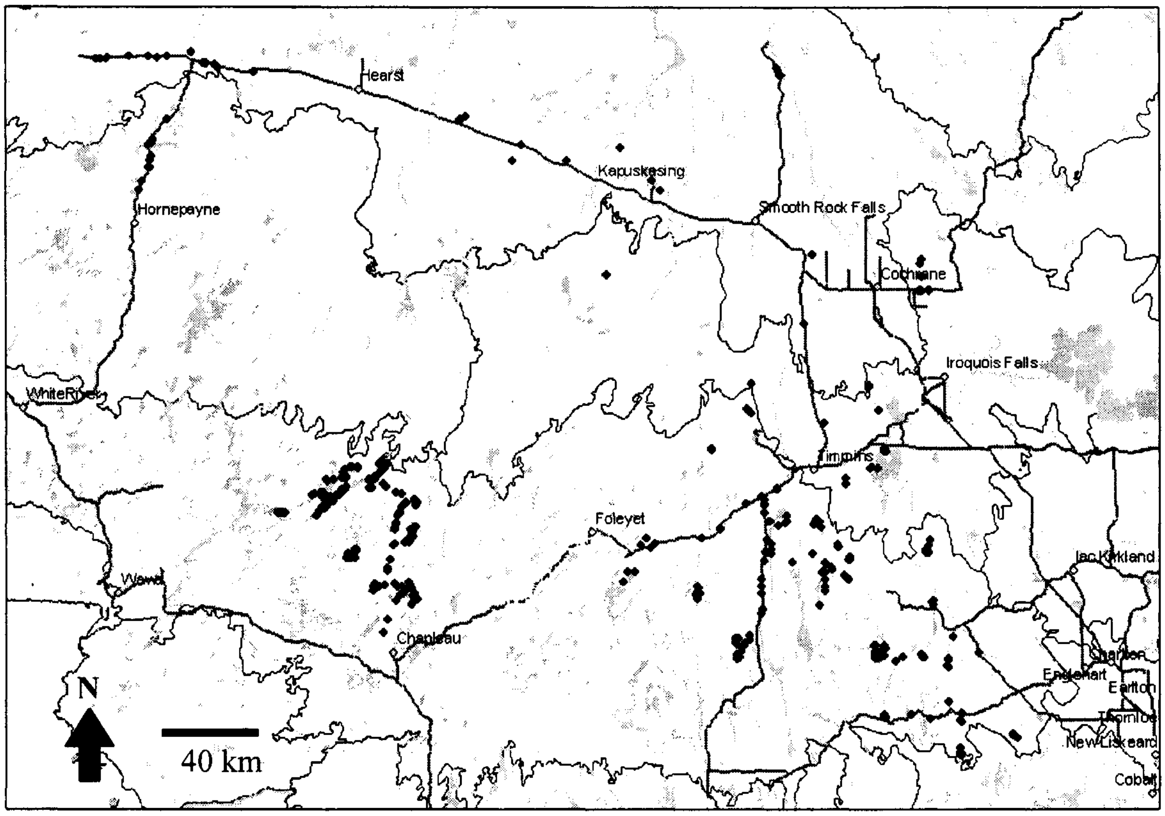

Figure 1.1 Study area with sample forest stand locations in Ecoregion 3E (47°45' – 49°30' N, 80°40' – 85°00' W), northeastern Ontario.

Data collection

Basal area of canopy trees for each forest stand was sampled twice using estimates from either aerial photographs or cruise transects. The initial samples were associated with years when FRI took place in 1946, 1947, 1949, 1961, 1963, or 1972. The same forests were then sampled a second time in 2000 or 2001 using cruise transects. For each forest stand, the same cruise line location from historic forest stand samples was used. Historic cruise lines were marked on more recent aerial photos with the corresponding data from FRI maps and were located on the ground by using their relative position to conspicuous landmarks. All stands were naturally established, presumably from wildfire and without a history of harvesting and other anthropogenic disturbances.

Sampling of forest stands using the aerial photographs (scale was 1:15,840) involved marking a 200 m x 100 m (2 ha) quadrat centred on the historic cruise transect. Species and their relative cover were estimated by eye and then basal area estimates were calculated based on site stocking (Zsilinszky, 1963; Paine, 1981). Sampling of forest stands on the ground (during 2000 and 2001) involved using cruise transects. In each sample forests, one 200 m long transect with 10 stations that were 20 m apart was used to sample the basal area (m^2/ha) of canopy trees. At each sample station along the transect a wedge prism with a basal area factor of 2 was used to estimate basal area and tree species composition (OMNR, 1978). The prism's basal area factor estimates the basal area (m^2/ha) that each tree contributes to the overall stand. For example in the present study, each tree counted in the prism sweep contributes 2 m^2 of basal area per hectare to the overall stand estimate. Trees were included only if the refracted prism image and the actual stem were not completely split.

Age of dominant tree species was used to estimate the time elapsed from the last major stand-replacing disturbance (Bergeron, 1991). In each 2 ha plot the three largest dominant canopy stems were cored at 1.3 m above. Cores were assessed in the field to ensure that age would not be obscured by the absence of pith. Trees that exhibited obvious signs (e.g. fire scars) of surviving stand-replacing disturbance were not sampled. Shade intolerant species such as jack pine, white birch, and trembling aspen were sampled even if they were not the dominant canopy species as they give better estimates of stand age (Bergeron, 1991). If any of the cored trees were affected by disease or rot, another stem was selected. Age was later determined by manually counting annual growth rings using a dissecting microscope. The estimated ages were then corrected for time to reach breast height using the methods described in Vasilauskas and Chen (2002) and then averaged for a time since fire estimate of stand age.

Inconsistencies between sampling methodology (cruise transect vs. aerial photography) could cause interpretation errors in succession dynamics. To test this, sampling methodology was compared using a subset of the data (N = 39 forest stands). For each forest stand, relative canopy composition was estimated from an aerial photograph sample and a cruise transect sample. In all cases, cruise transect samples were completed within 1 or 2 years of when the aerial photo was taken. The relative composition of each stand (using both methods) was reduced to a two-dimensional ordination space using Non-metric Multidimensional Scaling (McCune and Grace, 2002). The difference between forest stand Axes scores for each sampling technique was then compared using a confidence interval approach (Stefano, 2004). If the null hypothesis is not rejected (confidence intervals overlap zero), regardless of sampling technique, an individual forest stand will be represented in the same region of the ordination space. An acceptable level of variation was also defined by assuming that differences greater than 0.1 or less than –0.1 in the ordination space would cause misinterpretation of stand composition (therefore, confidence intervals should be within the bounds of 0.1 and –0.1). From the data subset, error between sampling techniques was not significant and was within the range of acceptable variation (Table 1.1). The mean difference and 95% confidence interval between Axes 1 and 2 scores was 0.03 ± 0.05 and –0.01± 0.06 respectively. Since the confidence intervals overlapped zero and were well within the 0.1 and –0.1 limits, estimates of forest stand composition using aerial photograph and cruise transect methods are consistent. Therefore, trajectories that are reported from the ordination space are assumed to represent succession dynamics at the forest stand scale, and not variability caused by inconsistencies with sampling methodology.

Table 1.1 Measurement error of forest stand composition using aerial photograph and cruise transect sampling techniques estimated from 39 forest stands. Values represent forest stand scores in a two-dimensional Non-metric Multidimensional Scaling ordination space. Differences between techniques that are greater than or less than 0.1 or –0.1 respectively, would likely cause error in interpreting correct stand compositions in the ordination space.

	Sampling Method						
NMS Axis	Aerial Photo (N = 39)		Cruise Transect (N = 39)		Difference	95%CI Lower	95%CI Upper
	Mean	SD	Mean	SD			
Axis 1	-0.01	0.80	0.01	0.80	0.03	-0.02	0.08
Axis 2	0.00	0.60	0.00	0.63	-0.01	-0.07	0.05

Note: SD = standard deviation

Table 1.2 Species basal area (m²/ha ± 1 standard error in brackets) of hardwood dominated and associated forests at initial sample periods (summed for all periods 1946, 1947, 1949, 1961, 1963, and 1972) and second sample periods (summed for 2000 and 2001) located in northeastern Ontario.

	Trembling aspen dominated forests (N = 41)		White birch dominated forests (N = 16)		Hardwood dominated mixedwood forests (N = 4)		Pure mixedwood forests (N = 6)	
	initial	final	initial	final	initial	final	initial	final
P. mariana	0.7 (0.3)	1.6 (0.5)	0.9 (0.4)	1.7 (0.6)	1.6 (1.0)	7.5 (4.2)	2.0 (0.4)	3.4 (2.0)
B. papyrifera	2.4 (0.5)	3.4 (0.5)	8.3 (1.5)	12.1 (1.0)	6.2 (1.9)	7.8 (0.9)	4.1 (1.2)	9.1 (2.6)
T. occidentalis	np	0.7 (0.4)	0.2 (0.1)	3.6 (0.5)	np	0.5 (0.3)	0.4 (0.3)	1.8 (0.9)
P. tremuloides	13.2 (1.1)	16.2 (1.3)	1.0 (0.3)	1.7 (0.6)	6.9 (2.1)	8.9 (2.3)	1.5 (0.5)	3.2 (1.1)
P. banksiana	1.8 (0.4)	2.7 (0.8)	0.3 (0.2)	0.6 (0.5)	0.6 (0.6)	1.1 (0.7)	0.6 (0.5)	1.0 (0.7)
A. balsamea	0.3 (0.2)	2.6 (0.4)	0.6 (0.2)	(0.8)	0.6 (0.6)	2.0 (0.4)	2.0 (1.0)	2.4 (0.9)
P. glauca	0.4 (0.2)	1.5 (0.2)	0.7 (0.3)	1.0 (0.3)	1.3 (1.3)	2.1 (0.5)	0.6 (0.4)	2.1 (0.9)
L. laricina	np	np	np	np	np	np	np	np
P. balsamifera	np	0.6 (0.3)	np	0.7 (0.5)	np	np	np	0.4 (0.4)
A. rubrum	np	np	np	0.3 (0.2)	np	np	0.3 (0.3)	0.3 (0.3)
P. strobus	np	0.01 (0.01)	np	np	np	0.1 (0.1)	np	0.2 (0.2)
P. resinosa	np	np	np	np	np	np	0.4 (0.4)	0.1 (0.1)
Salix sp.	np	np	np	0.1 (0.1)	np	np	np	np

note: np = not present

Table 1.2 cont. Species basal area (m^2/ha ± 1 standard error in brackets) of conifer dominated and associated forests at initial sample periods (summed for all periods 1946, 1947, 1949, 1961, 1963, or 1972) and final sample periods (summed for 2000 and 2001) located in northeastern Ontario.

	Jack pine dominated forests (N = 44)		Black spruce dominated forests (N = 62)		White cedar dominated forests (N = 13)		Conifer dominated mixedwood forests (N = 31)	
	initial	final	initial	final	initial	final	initial	final
P. mariana	1.7 (0.5)	5.2 (1)	18.3 (0.8)	20.3 (1.2)	3.8 (1.2)	3.1 (1.1)	5.6 (0.9)	6.6 (1.0)
B. papyrifera	0.9 (0.2)	1.4 (0.3)	0.8 (0.2)	1.2 (0.3)	1.7 (0.6)	2.8 (0.6)	2.4 (0.4)	4.1 (0.8)
T. occidentalis	np	0.01 (0.01)	0.1 (0.03)	3.0 (1.1)	19.8 (2.4)	28.4 (3.8)	2.3 (0.8)	5.5 (1.8)
P. tremuloides	2.3 (0.4)	4.7 (0.8)	0.3 (0.1)	0.6 (0.2)	np	0.1 (0.1)	1.2 (0.3)	2.1 (0.6)
P. banksiana	14.8 (0.9)	20 (1.7)	1.3 (0.3)	1.1 (0.4)	np	0.2 (0.2)	3.4 (0.8)	3.1 (0.9)
A. balsamea	np	1.4 (0.3)	0.7 (0.2)	0.7 (0.01)	1.9 (0.8)	0.4 (0.1)	2.2 (0.5)	1.2 (0.3)
P. glauca	np	0.4 (0.1)	0.1 (0.1)	0.3 (0.1)	0.4 (0.3)	0.8 (0.3)	0.6 (0.3)	1.2 (0.3)
L. laricina	np	0.1 (0.1)	0.4 (0.2)	0.7 (0.2)	0.5 (0.4)	0.2 (0.2)	0.9 (0.6)	1.1 (0.9)
P. balsamifera	np	0.01 (0.01)	np	0.1 (0.1)	np	0.03 (0.01)	np	0.04 (0.02)
A. rubrum	np	np	np	0.01 (0.01)	np	np	np	0.03 (0.02)
P. strobus	np	np	np	0.02 (0.01)	0.2 (0.2)	0.3 (0.2)	np	0.01 (0.01)
P. resinosa	np	np	np	0.003 (0.003)	0.2 (0.2)	np	np	0.04 (0.03)
Salix sp.	np	np	np	np	np	np	np	np

note: np = not present

Data analysis

Forest stands were divided into eight groups based on dominant canopy composition (Table 1.2). Stand groups that were dominated by individual species were those where the relative basal area of the dominant species was greater than or equal to 65%. The stands grouped as hardwood- or conifer-dominated mixedwoods had basal areas of the respective group that was greater than or equal to 65%. Stands were grouped as mixedwood forests if the hardwood and conifer basal area was 50% for both.

Nonmetric Multidimensional Scaling (NMS) was used to ordinate the initial basal area samples of canopy species. The results of the ordination were used i) in a chronosequence approach to infer qualitative successional trajectories based on the correlation of the major ordination axes with canopy species and time since fire (*gradient analysis of species composition*) and ii) to calibrate a model to fit the second samples. The method involves a hierarchical search for the point in the ordination space of the calibrated model that maintains the lowest possible stress for the overall ordination model (McCune and Grace, 2002). PCOrd v. 4.0 flags sample points that cause the ordination to go above an *apriori* determined stress level. Typically these points should be removed from the analysis as they potentially represent some problem with sampling error (McCune and Grace, 2002); however after determining this wasn't the case, flagged points were assumed to represent sample stands that underwent dramatic change in canopy composition or species basal area. The difference vector between initial and final sample scores in ordination space was used to determine the general direction and magnitude of change in sample forest canopy composition. To clearly show direction of forest stand change in reduced species space, the distance measures between the two sample years were standardized to a common point by subtracting the original position coordinates (initial sample of canopy species basal area) from the changed coordinates (second sample of canopy species basal area).

Fitting the second canopy composition samples to the calibrated model allowed a comparison of change in ordination space from the forest stand's original position in the initial ordination. No change in species basal area between the sample years will result no change in ordination space and therefore be directionless. On the contrary, individual species basal area changes between sample periods will be represented by changes in ordination space towards forest stands with similar canopy composition. If succession of forest stands is consistent across northeastern Ontario, then the trajectories of change predicted by the chronosequence approach and the actual time series approach will be consistent.

Analysis of individual species dynamics was exclusive to the ordination procedures and involved calculating the average growth function (stand level basal area) of important species with respect to time since fire (TSF). The procedure is described in more detail below (see *species composition patterns with time*).

Gradient analysis of species composition

NMS was used to reduce the 217 sample stands to a lower dimensional species space. McCune and Grace (2002) suggested that NMS should be the ordination of choice when analyzing community data. This method of ordination uses iterative rank differences to reduce complex multivariate data sets. The iterative randomization of sample sites in lower dimensional species space attempts to maintain the original rank of reduced distances and original distances (described by the term stress), preserving biologically important relationships among sample sites (Clarke, 1993). The "slow and thorough" autopilot algorithm was chosen in the NMS ordination selection using the PC Ord v. 4.0 software package (McCune and Mefford, 1999). This autopilot method uses the default setting of 400 maximum iterations, has an instability criterion of 1.0×10^{-5}, steps down from 6 ordination axes to 1, uses 40 real runs, and 50 randomization runs. The NMS algorithm suggested a 2 dimensional ordination solution, as stress in higher dimensions was not significantly reduced. Species samples were standardized using the arcsine square root function and all ordinations were run using Sorensen distance measures. Although NMS is a non-parametric ordination technique, standardization of sample data does impact the calculations for species distance measures (McCune and Grace, 2002).

Species composition patterns with time

Individual species change for each forest type was evaluated by calculating the average change in basal area of sample forests on a decadal scale. As each forest was sampled twice, the rate of change of individual species basal area ($m^2ha^{-1}yr^{-1}$) between the two years was used as an estimate of species change. I made the assumption that the growth function of individual species between the two sample years is linear. Therefore, if a species increased in basal area from 10 – 20 m^2/ha over a 40 year period, the estimated change in basal area for those 40 years would be 0.25 $m^2ha^{-1}yr^{-1}$. As each forest type contained numerous sample stands that overlapped in time since fire, I used the average of these values to estimate changes in species basal area. As my objective was to provide a qualitative description of species change and some species exhibited highly non-linear patterns with time since fire, I was hesitant to fit the average basal area changes with parametric functions. However, I did quantify the variability of species change by calculating the range and average standard deviation over the number of decades sampled for each species.

Some of the variability associated with both analytical techniques will be the result of sampling methodology. For example, estimates made using aerial photography are expected to be less precise than those made by sampling using cruise transects. Two important assumptions are made about the data, given the results in Table 1.1. First, it is assumed that asymmetries in sampling will be more pronounced for rare species, as it is harder to discern these species using aerial photography than cruise methods. Since changes in dominant canopy species are used to make inferences about successional dynamics and position in ordination space is not significantly different with respect to sampling method, the level of precision is less of a problem. Second, asymmetries in sampling do not result in biologically important error margins; i.e. even if one method tends to over-estimate basal area, the margin will be negligible and is not considered ecologically important.

Results

Gradient analysis of species composition

The NMS ordination algorithm produced a significant 2 dimensional ordination solution for the 217 forest stands in northeastern Ontario (Table 1.3, Fig. 1.2). Overall, both axes of the ordination maintained the structure of the original data and the chance of producing a 2 dimensional solution with lower stress was low (Table 1.3). The high stress value is predominantly the result of having many sample stands with considerably different tree species composition.

NMS results for the ordination of initial forest composition showed that time since fire (TSF) was a major factor structuring the composition of forest stands sampled in northeastern Ontario (Fig. 1.2, Table 1.4). Since TSF is positively correlated with each axis, the ordination suggests that forest composition will converge towards dominance of white cedar or black spruce over time. Axis 2 of the ordination separates three possible successional pathways (trajectories) based on initial dominance of stands by hardwood species such as trembling aspen (trajectory 1) and conifer species such as jack pine (trajectory 2) or black spruce (trajectory 3) (Fig. 1.2). Trajectory 1 shows that over time hardwood dominated stands tend to decrease in trembling aspen dominance, while becoming a hardwood mixedwood type forest with important components of white birch, balsam fir, and cedar (Fig. 1.2). Ultimately cedar becomes dominant, but white birch maintains a small importance in some of these older stands. Trajectories 2 and 3 are initially dominated by jack pine and black spruce respectively (Fig. 1.2). Jack pine dominated forests (trajectory 2) can progress towards jack pine-black spruce mixed woods, while black spruce dominated forests (trajectory 3) remain dominated by black spruce and eventually cedar increases in importance (trajectories 2 and 3, Fig. 1.2).

Table 1.3 Results of 2 dimensional Non-metric Multidimensional Scaling ordination of initial tree species composition sampled from 217 forests located in northeastern Ontario during the years of 1946, 1947, 1949, 1961, 1963, or 1972.

Final stress	Final instability	Number of iterations	% variation explained			Probability of random model with lower stress
			Axis 1	Axis 2	Total	
15.93	0.00001	84	50.9	35.1	86.0	0.0196

Table 1.4 Correlations of initial species basal areas with plot scores along Axes 1 (†) and 2 (‡) of NMS Ordination.

Species	Axis 1	Axis 2
P. tremuloides†	-0.714	0.038
B. papyrifera‡	-0.337	0.616
P. banksiana‡	-0.371	-0.709
P. mariana†	0.868	-0.146
P. glauca	-0.198	0.374
T. occidentalis‡	0.382	0.470
A. balsamea‡	0.059	0.518
L. laricina	0.320	-0.084
P. strobus	0.005	0.148
P. resinosa	0.033	0.177
A. rubrum	-0.010	0.084
TSF†‡	0.554	0.419

Note: TSF is time since fire

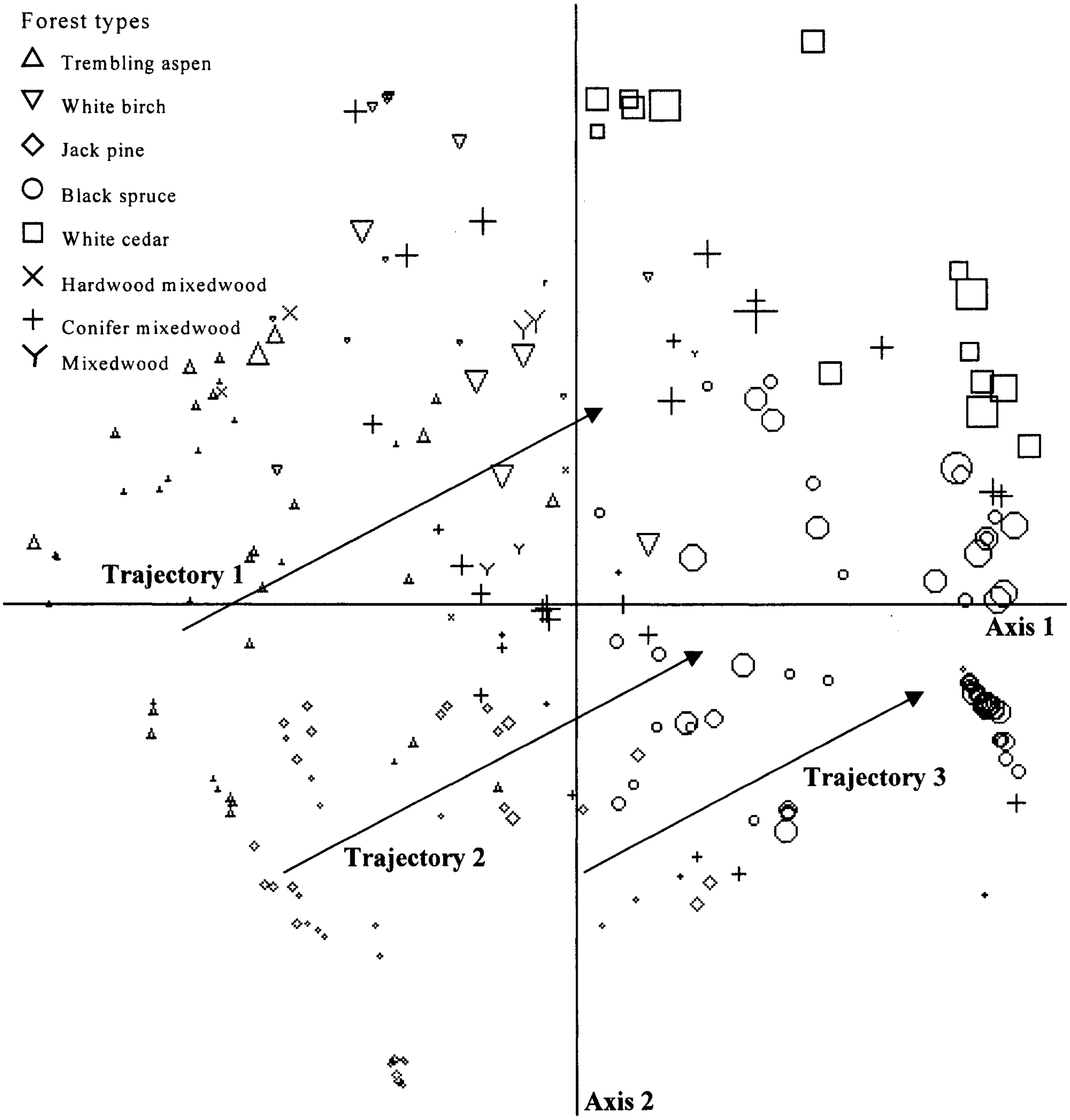

Figure 1.2 Two-dimensional solution produced by non-metric multidimensional scaling of tree species basal area for 217 forests in northeastern Ontario. Symbols represent major forest types during the years of 1946, 1947, 1949, 1961, 1963, or 1972 and are weighted by time since fire (small symbols represent young stands and large symbols represent older stands). Trajectories 1, 2, and 3 represent successional changes expected for trembling aspen, jack pine, and black spruce forests respectively.

Of the 217 forest stands, only 9 exceeded the stress limit and none exceeded the extrapolation limits defined by the calibration model created from the initial ordination (Table 1.5). Fitting the second time series data set to the calibrated NMS model shows that stands initially dominated by trembling aspen and jack pine followed the patterns of succession predicted from initial ordination (Fig. 1.2, 1.3a and 1.4a). Forest stands that were initially dominated by trembling aspen show trends towards the hardwood dominated mixedwood area of the ordination, which is associated with increases in white birch, balsam fir, and cedar (Fig. 1.3a). Forest stands initially dominated by jack pine show similar directionality as trembling aspen dominated stands however, shift in terms of composition are associated with increases in black spruce as the sites initially scored low along axis 2 (Fig. 1.2). In both cases, the differences in ordination scores for both axes were primarily positive.

Table 1.5 Summary of results from fitting the second forest samples to the original nonmetric multidimensional scaling ordination of 217 forest stands in northeastern Ontario.

			Number of sites exceeding:		
Mean stress	Standard deviation of stress	Upper stress limit	Stress limit	Lower extrapolation limit	Upper extrapolation limit
15.93	0.04	16.00	9	0	0

Forest stands initially dominated by white birch, black spruce, cedar or conifer mixedwoods were much more variable in directionality in the ordination space (Figs. 1.3b, 1.4b,c, and d). Many of the conifer dominated stands show negative differences along either axis, indicating that change was associated with shifts towards that of earlier successional forest types (i.e. either increases in “early successional” species, decreases in “late successional” species, or some combination of the two) (Figs. 1.4b,c, and d). The small sample size of hardwood dominated mixedwood forests and mixedwood forests makes it difficult to interpret possible successional changes. However, differences in hardwood dominated mixedwoods were primarily positive and mixedwoods were variable (Figs. 1.3c and d).

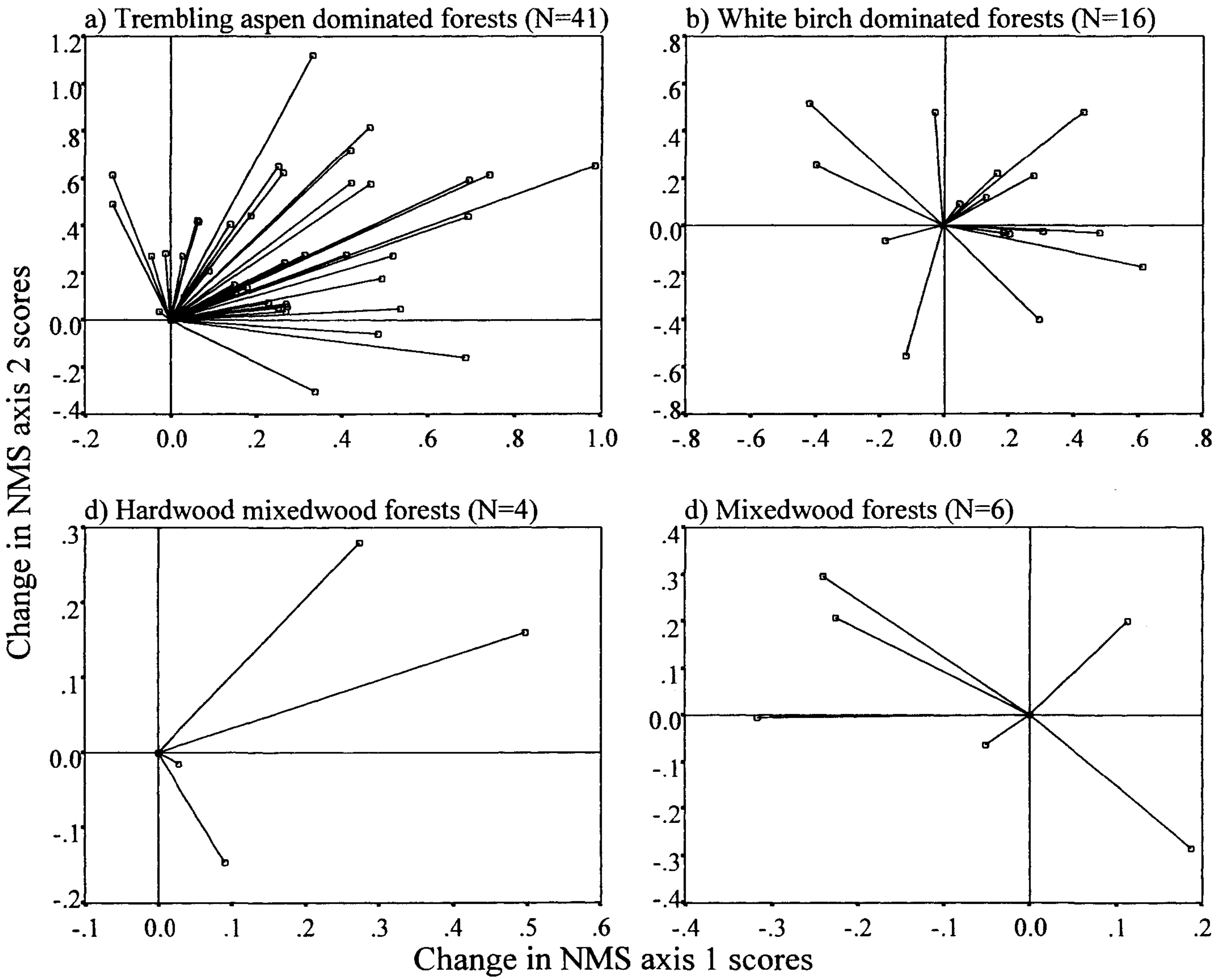

Figure 1.3 Standardized changes in NMS plot scores (represented in 2 dimensional species space) between initial sample years (1946, 1947, 1949, 1961, 1963, 1972) and final sample years (2000, 2001) for a) trembling aspen, b) white birch, c) hardwood mixedwood, and d) pure mixedwood forests in northeastern Ontario.

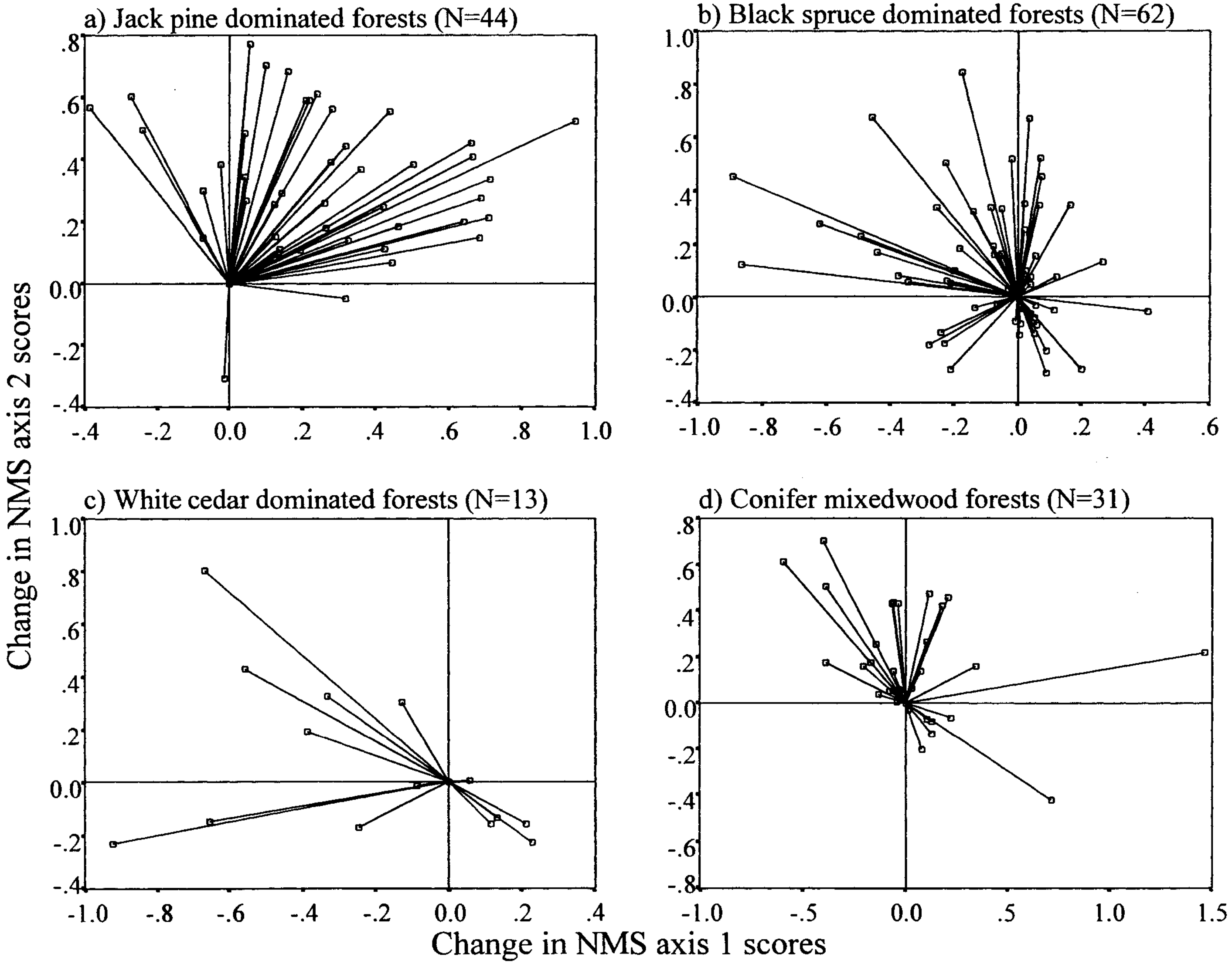

Figure 1.4 Standardized changes in NMS plot scores (represented in 2 dimensional species space) between initial sample years (1946,1947,1949, 1961, 1963, 1972) and final sample years (2000, 2001) for a) jack pine, b) black spruce, c) white cedar, d) conifer mixedwood forests in northeastern Ontario.

Species dynamics

Forests initially dominated by trembling aspen and white birch follow similar patterns for the first 100 years (Figs. 1.5a and b). Initially both forest types maintain an increase in their respective canopy dominant and at approximately 80 years this increase begins to decline. Balsam fir then replaces trembling aspen or white birch as the species showing the highest increase in basal area. Dynamics however are different following the stage of balsam fir increase. In trembling aspen dominated forests, trembling aspen maintains a steady decline in basal area, whereas in white birch dominated forests, white birch once again becomes the species showing the most important increase in basal area.

The dynamics of important species in jack pine dominated forests (Fig. 1.6a) follow a similar trend to those in hardwood-dominated forests (Fig. 1.5a,b). For the first 60 years, increases in jack pine are the most important aspect of change, but the increasing trend decelerates almost linearly with time. Between 40 and 90 years, black spruce also shows an increasing trend, but it is not as dramatic as the increase in jack pine. At approximately 60 years black spruce replaces jack pine as the species increasing the most in basal area. At approximately the same time, jack pine begins to decrease. After 80 years, the jack pine component continues to undergo decline, while other species that are present remain relatively stable (Fig. 1.6a).

Species dynamics in black spruce dominated forests, on average are simpler than other forest types as the majority of change occurring is the result of changes in black spruce (Fig. 1.6b). Black spruce increases in basal area between approximately 80 and 100 years since fire and then becomes relatively stable for the next 130 years. At about 180 years, white cedar becomes an important species affecting standing dynamics as its basal area increases (Fig. 1.6b). Other species if present tend to maintain their basal area between sample periods at all time since fire periods for this forest type (Fig. 1.6b).

In forests initially dominated by white cedar, white cedar maintains a relatively stable increase in basal area between the sample periods (Fig. 1.6c). Between approximately 140 and 190 years since fire, black spruce, white spruce, and white birch have negligible increases in basal area. Following 140 and 200 years, balsam fir and black spruce respectively show decline, whereas white birch maintains a slight yearly increase in basal area (Fig. 1.6c).

All of the mixedwood stands had variable species dynamics (Figs 1.5c, d and 1.6d). However, the average standard deviation of species in the mixedwood group of forests tended to be lower than that of forests that were dominated by one species (Table 1.6). The small sample size of mixedwood and hardwood-dominated mixedwood forests makes the generalization of species dynamics difficult. The most important dynamics in conifer-dominated mixedwoods is the increase in black spruce and jack pine prior to approximately 90 years and their subsequent decline following 90 years. After approximately 120 years white cedar becomes the most important species with increasing basal area. During this time, white birch maintains a slight increase. After 180 years, jack pine, black spruce and balsam fir show decline, where as white cedar and white birch maintain an increase in basal area (Fig. 1.6d).

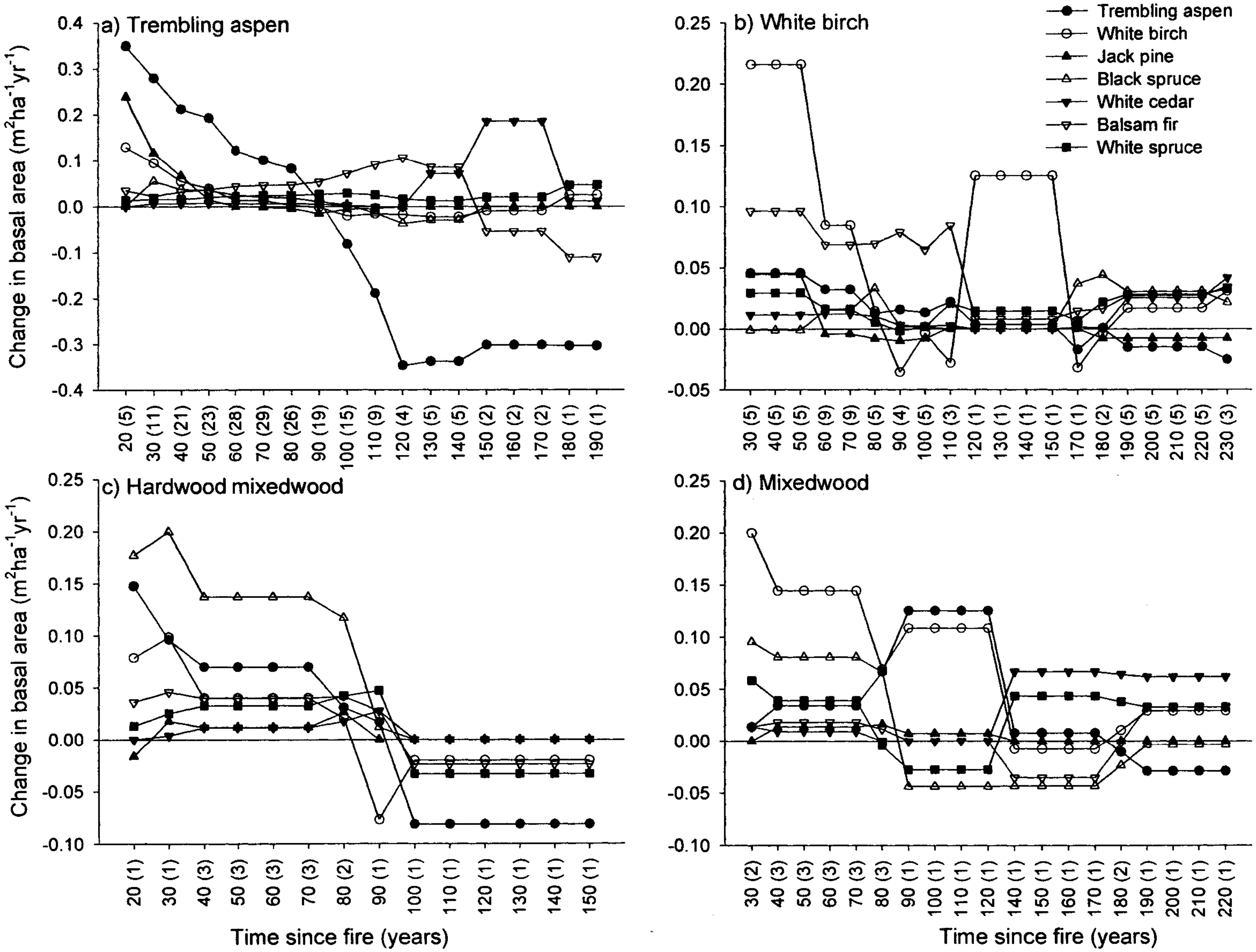

Figure 1.5 Important trends in species change (m²ha⁻¹yr⁻¹) for a) trembling aspen, b) white birch, c) hardwood mixedwood, and d) pure mixedwood forests in northeastern Ontario. Value in brackets following the time since fire is the number of sample forests used to calculated the average change in basal area for that time. Average standard deviation and range of standard deviations for each species are in Table 1.6.

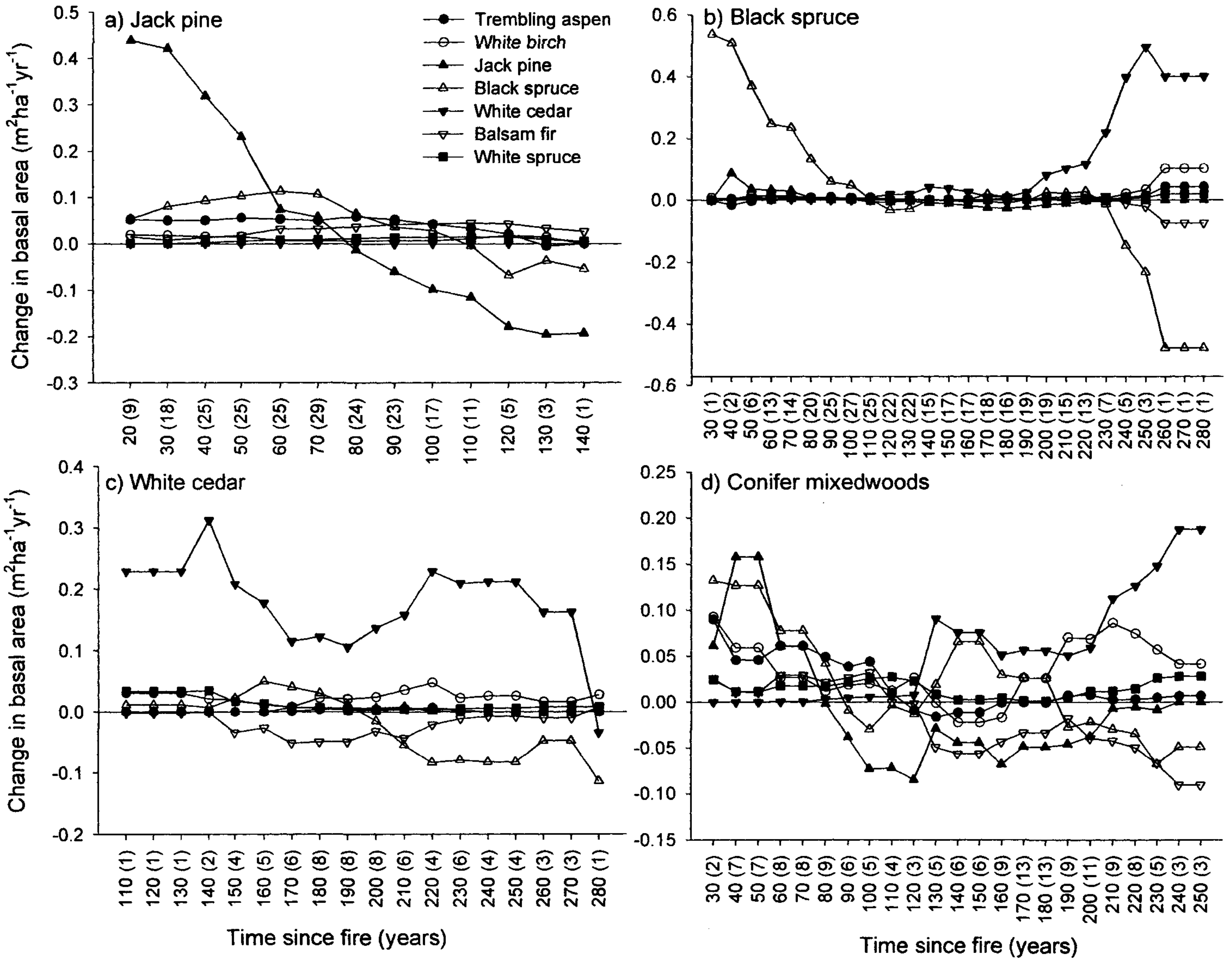

Figure 1.6 Important trends in species change ($m^2ha^{-1}yr^{-1}$) for a) jack pine, b) black spruce, c) white cedar, d) conifer mixedwood forests in northeastern Ontario. Value in brackets following the time since fire is the number of sample forests used to calculated the average change in basal area for that time. Average standard deviation and range of standard deviations for each species are in Table 1.6.

Table 1.6 Average standard deviation (SD) and range of standard deviations for the mean change in basal area ($m^2ha^{-1}yr^{-1}$) of important tree species for each forest type in northeastern Ontario.

	Forest type							
Species	Trembling aspen		White birch		Hardwood mixedwood		Mixedwood	
	SD	Range	SD	Range	SD	Range	SD	Range
Trembling aspen	0.11	0 - 0.21	0.03	0 - 0.05	0.03	0 - 0.07	0.01	0 - 0.06
White birch	0.05	0 - 0.07	0.07	0 - 0.14	0.04	0 - 0.14	0.05	0 - 0.19
Jack pine	0.06	0 - 0.32	0.02	0 - 0.10	0.02	0 - 0.05	0.01	0 - 0.02
Black spruce	0.03	0 - 0.10	0.02	0 - 0.07	0.04	0 - 0.15	0.04	0 - 0.14
White spruce	0.03	0 - 0.05	0.02	0 - 0.05	0.01	0 - 0.02	0.02	0 - 0.06
White cedar	0.07	0 - 0.25	0.02	0 - 0.07	0.01	0 - 0.01	0.005	0 - 0.02
Balsam fir	0.05	0 - 0.08	0.04	0 - 0.09	0.01	0 - 0.02	0.01	0 - 0.05

Species	Jack pine		Black spruce		White cedar		Conifer mixedwood	
	SD	Range	SD	Range	SD	Range	SD	Range
Trembling aspen	0.08	0 - 0.13	0.01	0 - 0.04	0.003	0 - 0.01	0.04	0.01 - 0.08
White birch	0.03	0 - 0.03	0.03	0 - 0.06	0.02	0 - 0.06	0.08	0.04 - 0.13
Jack pine	0.15	0 - 0.30	0.04	0 - 0.12	0.005	0 - 0.02	0.06	0 - 0.17
Black spruce	0.09	0 - 0.14	0.15	0 - 0.26	0.05	0 - 0.11	0.09	0.03 - 0.14
White spruce	0.01	0 - 0.02	0.01	0 - 0.02	0.01	0 - 0.02	0.03	0.01 - 0.05
White cedar	0.00035	0 - 0.0009	0.09	0 - 0.42	0.11	0 - 0.19	0.08	0 - 0.19
Balsam fir	0.03	0 - 0.04	0.02	0 - 0.05	0.04	0 - 0.08	0.05	0.01 - 0.08

Discussion

Efficacy of gradient analysis with time series data

The NMS ordination of the initial canopy species composition and the time series analysis using the calibrated model for determining trends in stand dynamics located in northeastern Ontario produced similar results (Fig. 1.2, 1.3, and 1.4). The NMS ordination, produced using the initial canopy composition, determined that time since fire was a major factor explaining variation among the 217 forest stands that were initially sampled (Table 1.4). However, the alternative hypothesis that site type is also an important factor influencing relationships of sites in the ordination space cannot be rejected, as it was not tested. Autecological characteristics of tree species that dominate stands on alternative ends of the axis (e.g. trembling aspen on the left and white cedar on the right) suggest that site type maybe a confounding factor and should be investigated in future analyses. Analysis of the secondary axis indicated that major differences in succession pathways exist between stands initially dominated by hardwood species (such as trembling aspen and white birch) and conifer species (such as jack pine and black spruce). The ordination produced by using only the initial forest stand samples, suggested that hardwood dominated forests will tend to increase in basal area of white birch, balsam fir, and eventually white cedar. Whereas forest stands initially dominated by jack pine and black spruce will converge to forests dominated by black spruce, and then eventually white cedar.

Fitting the re-sampled species basal area estimates from 2000 and 2001 to the initial ordination solution (Figs. 1.3a and 1.4a) showed that trembling aspen and jack pine dominated forests were consistent with the predictions from the chronosequence approach (Fig. 1.2). Low variability in the observed trajectories of forest stands initially dominated by trembling aspen and jack pine suggests that their dynamics are more predictable than stands dominated by species such as white birch, black spruce, and white cedar. The ability of the calibrated ordination to predict similar results to those observed by using the time series data suggests that patterns in succession for trembling aspen and jack pine dominated forests, when estimated by time since fire, is consistent across the region of northeastern Ontario. Although site-to-site variability may influence the rate of succession, developmental trends of trembling aspen and jack pine dominated stands are expected to be consistent across the region of northeast Ontario.

General trends in dynamics for stands dominated by white birch, black spruce, and white cedar were less consistent between the results from the calibrated ordination (Fig. 1.2) and the time series data (Figs. 1.3b and 1.4b,c). This suggests that across northeastern Ontario, site-to-site variation in species dynamics is influenced more by local variation in either disturbance dynamics or demographic complexity. Demographic variability (particularly age structure) in older forests is typically more complex than that in younger forests (Burton *et al.*, 1999). The age structure in older forests can be represented by a negative exponential curve with various cohorts present within the forest stand, as opposed to a simple single cohort forest type, typical of forests that initially dominate following fire (Oliver and Larson, 1990). As age structure was not sampled in these forests, it is not possible to make direct inferences of such impacts on species dynamics at the stand level. However, by removing or avoiding sampling in stands that underwent obvious disturbance and by making the broad assumption that disturbance dynamics are randomly distributed across the landscape (Armstrong, 1999), one can strengthen the possibility that demographic differences in stand age structure is the more probable reason for the high variability in stand dynamics of these forests (see DeGrandpre *et al.*, 2000).

The initial variability in species composition used to assign forests to one of the mixedwood type forests and the low sample size for mixedwood and hardwood dominated mixedwood forests makes accurate inference of their patterns risky. The results of the static ordination suggest that the three types of mixedwood forest represent the intermediate stages of forest development depending on the initial composition of hardwood dominance or conifer dominance. This is logical as some "intermediate" forest type must exist as species that dominate forests initially following disturbance decline in basal area and other species increase in basal area. The direction of change of hardwood dominated mixedwood forests was consistent with that of forests that were initially dominated by trembling aspen. This suggests that hardwood dominated mixedwood forests represent an intermediate stage between stands initially dominated by trembling aspen, and subsequently dominated by shade tolerant conifers. The variable direction of mixedwood forests and conifer dominated mixedwood forests were consistent with the direction of black spruce and white cedar dominated forests, however this does not aid in prediction of successional trends for these forest types based on time since fire.

Species dynamics

The dynamics of trembling aspen and jack pine dominated forests are more consistent than other forest types across the northeastern region of Ontario when analyzed using static and time series ordination techniques. The simple decelerating trend of the respective dominant species for these forest types provides some insight as to why the development of these forests is more predictable (see Figs. 1.5a and 1.6a). As trembling aspen and jack pine commonly form largely monospecific, even-aged forests following fire, their demographic and structural characteristics will be similar across the landscape. Both species are also considered shade intolerant therefore, recruitment of offspring into the understorey environment will be minimal, reducing the probability of their occurrence as important components of future forest communities (Burns and Honkala, 1990a,b). However, recruitment of trembling aspen into gap environments and subsequent formation of a secondary conspecific (same species) cohort has been documented in trembling aspen forests of western Canada (Cumming *et al.*, 2000). However, in forests of eastern Canada, Bergeron (2000) suggested that the regeneration niche responsible for the formation of a second cohort of trembling aspen can be exacerbated by increased competition from a well-developed understorey environment and competition from shade tolerant conifer saplings.

Initial dynamics of white birch, in white birch dominated forests are similar to that of respective dominant species in trembling aspen and jack pine dominated forests. However, white birch decline is short-lived; it begins to increase again shortly after 90 years. The short period of white birch decline can be explained by senescence of mature trees, without commensurate replacement. The subsequent increase could be related to the sprouting characteristics of white birch, however one must be skeptical of the increase as it is the result of only one forest sample between 120 – 170 years. White birch individuals are capable of producing basal sprouts that emanate from apical shoots located in the root collar region during tree development (Burns and Honkala, 1990b).

Although trembling aspen also produces sprouts, they are typically located on roots, not on the root collar and can be produced, among other factors, as a response to parent tree mortality or increased forest floor temperatures (Frey *et al.*, 2003). The production and development of white birch basal sprouts could potentially offer a regeneration advantage over other shade intolerant species such as trembling aspen when large-scale disturbances do not affect the forest stand; the space originally occupied by a dead parental white birch tree will be relatively free of interspecific competition from other trees or shrubs, thus ameliorating the regeneration niche of white birch sprouts. Another advantage for white birch is that production of juvenile sprouts is relatively continuous during tree development, presumably this provides a height advantage if the sprout is viable when a parent tree dies. An alternative hypothesis to shoot regeneration is the longevity of white birch as it can live for greater than 200 years (Bergeron, 2000). The suggested regeneration advantages and longevity of white birch could potentially explain the second phase of white birch increase, in white birch and other forest types.

In stands initially dominated by trembling aspen, jack pine, and white birch forests, the important increase of respective dominant species is replaced by shade tolerant species; balsam fir replaces trembling aspen and white birch, and black spruce replaces jack pine (Figs. 1.5a,b and 1.6a). Increases in the shade tolerant component of forests can be related to i) differential growth rates between shade intolerant species and shade tolerant species (Pallik and Pregitzer, 1991) or ii) establishment of shade tolerant seedlings during forest development. As forests dominated by species such as trembling aspen and jack pine typically have a stem exclusion stage (a development stage that is defined by intense intraspecific competition), one would expect that survival of other tree species will be minimal. Any shade tolerant species that recruit immediately following fire and do survive the stem exclusion stage will likely have negligible impacts on stand dynamics. Therefore, it is more probable that establishment of shade tolerant species following the stage of stem exclusion is responsible for the increase in shade tolerant species dynamics. However, if the original recruitment density of trembling aspen or jack pine stems is low (i.e. low stocking) there is an increased possibility that the transition to increases in shade tolerant species could be driven by differential growth rates.

Forests that were initially dominated by shade tolerant species showed either high variation in directions of change when the time series data was fitted to the calibrated model, or were not consistent with the expected changes predicted from the calibrated model (Figs. 1.1 and 1.3). Compositional change in black spruce dominated forests was relatively simple (Fig. 1.6b). Important increases in species that are typically considered early successional (such as trembling aspen, jack pine, or white birch) were limited, therefore the negative changes in ordination space are probably related to decreases in black spruce basal area. However, for these stands, mean change and 95% confidence intervals in black spruce basal area (-1.6 m^2/ha ± 3.7) and shade intolerant hardwood (trembling aspen and white birch) basal area (1.0 m^2/ha ± 0.7) indicate that it is a combination of decreasing black spruce basal area and increasing shade intolerant hardwood basal area resulting in succession dynamics. This is more consistent with other studies that suggest gap creation in forests dominated by shade tolerant species such as balsam fir or black spruce could facilitate the establishment of shade intolerant species, particularly those that have the ability to produce sprouts such as trembling aspen or white birch (Kneeshaw and Bergeron, 1999). The consistent increase of white cedar and the slight increase of white birch in white cedar dominated forests suggest that the phenomenon of gap exploitation by "early succession" species could potentially explain the generally negative direction of white cedar dominated forests in ordination space.

Conclusions

The results of this study show that systematically grouped (by species dominance) boreal forest types located in northeastern Ontario have considerably different stand and species dynamics. The dynamics of forest stands dominated by one or few species will be predominantly defined by changes in basal area of the respective dominant species. Species that are typically thought to function similarly with respect to shade (shade tolerant or shade intolerant) and dispersal mechanism (primarily sprout production or seed production) act very differently when sampled over different time periods, at different times during forest stand development. For example, shade intolerant species such as trembling aspen, white birch, and jack pine can all dominate a forest following fire. However, differences in sprouting ability may ultimately determine if an important component of conspecifics will be found in forests past the initial post-fire cohort. The risky dispersal and establishment life-histories of both jack pine and trembling aspen could explain their consistent declines following approximately 70-80 years since fire (Figs 1.5a and 1.6a). Jack pine typically regenerates by seeds, released from serotinous cones and trembling aspen typically regenerates by root suckers; both methods will be exacerbated by competition from tree saplings and shrubs that are already established in the understorey of these forest. However, white birch produces sprouts that primarily occur at the base of a parent tree; this potentially allows sprouts to develop directly under a convenient canopy gap created by the death of the parental clone. This mechanism has also been observed in boreal forests located in northwestern Quebec (Bergeron, 2000). The sprouting characteristics of white birch may be responsible for producing different long-term dynamics than those observed in other forests dominated by shade intolerant species.

Dynamics of older forests dominated by shade tolerant species such as black spruce and white cedar are also quite different. This study suggests that in black spruce dominated forests, canopy dynamics are the result of increases or decreases in black spruce basal area whereas in white cedar dominated forests, stand dynamics involve increases in white cedar and small increases in "early successional" species such as white birch.

The large decline of trembling aspen and jack pine that dominate the initial post-disturbance cohort suggests that the death of mature, canopy trees will result in canopy gap creation. This has important implications for long-term canopy dynamics as changes in the canopy condition could have important influence on the vegetation dynamics of the understorey environment. In the subsequent chapters I investigate the extent of small scale disturbance in trembling aspen dominated forests, and the effect that small-scale disturbance has on the vegetation dynamics of the understorey plant communities.

Chapter 2

Characteristics of canopy gaps in trembling aspen forests between 60 and 120 years since fire in northeastern Ontario

Abstract

In forests outside of the boreal zone, small-scale disturbances are important mechanisms that affect tree recruitment in the understorey. This pattern is expected to occur in regions of the boreal forest where fire disturbance has not influenced the landscape for long periods of time. However, this hypothesis has rarely been tested in the context of boreal forest development following fire. This study examined the degree to which a common post fire boreal forest type was influenced by canopy gaps (the typical result of small-scale disturbance) by describing the differences in size and structural characteristics of canopy gaps, as well as important mechanisms of gap formation during the canopy transition stage (60 –120 years following fire) in ten trembling aspen stands, in northeastern Ontario. The proportion of area occupied by expanded gaps was 13.2% in early stages of transition and 39.3% in late stages of transition. Mean gap size, area created per gap maker, and mean number of decay classes per gap all increased with stand age. Infection by pathogenic wood decay fungi was the most important factor to influence the death of gap makers and mean number of gap makers infected increased with stand age. Gap makers killed by wind were also an important factor in the gap creation process, however it showed no pattern with stand age. The results demonstrate the importance of small-scale disturbance in trembling aspen stands, even in the early stages of forest developmental. In light of this, it is clear that the impact of small-scale disturbance on understorey vegetation should be considered. This study suggests that

canopy gaps will become more complex over time, by the increasing presence of snapped, standing dead, and uprooted gap makers. Generally gap makers found in these older, structurally complex gaps will also be in more advanced stages of decay. These characteristics have the potential to influence vegetation dynamics by providing different regeneration niches for colonizing tree species, and altering the competitive interactions of plants in the understorey.

Introduction

Although numerous studies show that post-fire boreal forests undergo succession if the regional fire-return interval is sufficiently long, few expound the mechanisms involved (Bergeron, 2000; DeGrandpre *et al.*, 2000). Qualitative models such as those presented by Oliver and Larson (1990) and Peet and Christensen (1987) describe patterns of stand development that are consistent across many forest regions, including those in the boreal forest (Chen and Popadiuk, 2002). However, empirically testing qualitative predictions and developing quantitative models is much more appealing from a scientific perspective.

Important mechanisms that influence succession are present (although not always apparent) throughout the development of a forest. For perspective, these mechanisms of change may exist on a gradient that begins when seed establishment is limited by the availability of favourable microsites, and ends at the complete removal of biomass by an intense forest fire. In the boreal forest, large-scale or intense disturbances are conspicuous factors that influence plant community organization, and have received much attention (Heinselman, 1981; Johnson, 1992). Comparatively, subtle mechanisms of change are low in magnitude when they occur individually however, their summed impact can also have important implications for succession. In areas where large-scale disturbance is infrequent (particularly temperate and tropical regions) small-scale disturbance becomes the important mechanism for vegetation dynamics. In this context, a hypothesis that has been investigated to explain stand development patterns is based on the response of vegetation to canopy gaps (Runkle, 1984; Schnitzer and Carson, 2001). In boreal forests, understanding the post-disturbance development patterns of forest stands from the perspective of gap disturbance has been investigated only recently (Kneeshaw and Bergeron, 1998; Cumming *et al.*, 2000). Both of these studies, and a review by McCarthy (2001) suggest that gap disturbance can impact recruitment of tree species, resulting in important consequences for forest stand dynamics. The review by McCarthy (2001) showed that gap creation occurs in boreal forests, and that characteristics such as size, frequency, and formation are consistent with forests found in temperate and tropical regions. However, the effect that gap environments have on structuring plant communities is inconsequential without an appreciation of the stand-level prevalence of such a disturbance type. Therefore, quantifying the impact and characteristics of canopy gaps at the forest stand level is an important aspect of studying gap related processes.

If canopy gap creation influences the recruitment dynamics of juvenile tree species, then clearly a better understanding of post-fire succession in boreal forests will be achieved. I investigated the role of gap creating disturbance as a mechanism of vegetation change during the transition stage of development (60 – 120 years since fire) in trembling aspen (*Populus tremuloides* Michx.) dominated forests. In the boreal forest, trembling aspen commonly dominates an area following fire (Perala, 1990). Following the canopy break-up of the initial cohort, trembling aspen can i) remain dominant (Cumming *et al.*, 2000) or ii) be reduced, and shade tolerant conifers (e.g. balsam fir) become dominant (Bergeron, 2000). In northeastern Ontario, it has been shown that the rate of change of trembling aspen basal area undergoes a rapid decline between 60 and 100 years since fire, resulting in similar successional patterns as those observed by Bergeron (2000) (see Chapter 1, Fig. 1.5a). As trembling aspen declines, species such as balsam fir tend to increase in stand level basal area. This promotes the production of a mixedwood type forest; the mechanisms that cause this development pattern have important implications for understanding heterogeneous landscape level patterns in forest stand and species dynamics.

In post-fire boreal forests, few studies have quantified the relationship of time since fire and the prevalence and characteristics of canopy gaps during stand development. My objective was to determine the importance of canopy gaps during the development of trembling aspen dominated forests. This was achieved by quantifying the spatial and temporal characteristics, formation mechanisms, and resulting structural characteristics of canopy gaps in post-fire trembling aspen dominated boreal forests.

Methods

Study area

I conducted the study in forests around the city of Timmins (48.34N, 81.22W, 295 m altitude), in northeastern Ontario. This region of Ontario has a relatively homogenous landscape. Major topographic features are the result of deposits from the retreat of glaciers during the past ice age (approximately 10000 years ago). The study sites were located within the area defined as Hills (1959) ecoregion 3E (see Vasiliauskas and Chen, 2002). This ecoregion is approximately 486 km east-west and 228 km north-south at its widest points. The area defined by ecoregion 3E is dominated by clay soils deposited by ancient lakes Barlow and Ojibway (Baldwin *et al.* 2000) (also known as the clay belt). The study sites were selected in the southern portion of the ecoregion, which is dominated by outwash plains, predominantly composed of various loamy soils, silty-very fine sands, and fine sands (soil descriptions are defined in Taylor *et al.*, 2000). Northeastern Ontario has a moderately dry, cool climate with short summers. The average annual temperature for Timmins, Ontario is 1.2 °C and the average annual precipitation is 873 mm (Canada Climate Normals 1961 – 2000).

Forests of northeastern Ontario are typical of the boreal forest. Common associations of species include trembling aspen, white birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* (Moench) A. Voss) on upland moderately well-drained soil conditions, jack pine (*Pinus banksiana* Ait.) and black spruce (*Picea mariana* (Mill.) BSP.), on upland well-drained soils, black spruce, balsam fir (*Abies balsamea* (L.) Mill.), and eastern white cedar (*Thuja occidentalis* L.) on lowland poorly-drained soils (Taylor *et al.*, 2000). Successional relationships among species and their respective associations have been studied in adjacent areas of Quebec (Bergeron and Dubuc, 1989; Bergeron, 2000).

Stand selection

To represent the transition stage of trembling aspen forest development, ten forest sites of ages between 60 and 120 years located across the south central area of ecoregion 3E in northeast Ontario were chosen (Table 2.1). Stand age was determined based on existing fire inventory maps for the region, and a minimum of ten canopy tree cores sampled from healthy trees in each study site. A chronosequence method was used to infer temporal trends that are expected to occur with respect to canopy gap size and structural characteristics (Pickett, 1989). All forest stands were pyrogenic, dominated by trembling aspen (relative basal area per hectare 65% or greater) and were chosen based on their soil type, drainage, accessibility, and time since last fire.

Estimates of tree species basal area for each study site was evaluated systematically every 50 m along 5-9 sample transects. The individual transects were between 50 and 300 m in length and were between 1000 and 1300 m total length within a study site. Each transect was started at a point on the periphery of the forest stand, and sampling began at 50 m perpendicular to the start point. Entry points were chosen based on ease of access, for example from the side of an old logging road. Forest areas that were affected by humans or that were within 50 m from any prominent edges, including gaps that were greater than 800 m^2 were avoided. A cruise transect with prism sweep stations located every 50 m was used to determine stand basal area and species composition (OMNR, 1978).

Canopy gaps

Definition of canopy gap and expanded gap

Two main gap types were recognized: canopy and expanded (Fig 2.1). Canopy gaps were the result of single tree or multiple tree mortality that caused a break in the forest canopy greater than the interstitial distances among living trees. For time efficiency this was determined by ocular estimation (Betchtold *et al.*, 2002). Expanded gaps were defined as the area bounded by the stems of the trees adjacent to a tree fall event as has been used in other gap related studies in the boreal forest (*sensu* Kneeshaw and Bergeron, 1998; see Fig 2.1). Expanded gaps were categorized as single gap maker, multiple gap maker, and edaphic gaps. Edaphic gaps were defined by openings in the canopy that were greater than one-half a crown width where no observed tree mortality had occurred (Bartemucci *et al.*, 2002). Edaphic gaps were usually the result of topographic features such as bedrock outcrops, wet depressions, and watercourses running through the study site (*sensu* Bartemucci *et al.*, 2002).

Sampling of gaps

In each study site, canopy closure was evaluated along the same transects that were used to estimate tree species basal area. Along each transect, the canopy was evaluated as being either open or closed at each meter (*sensu* Kneeshaw and Bergeron, 1998). If the transect intersected any part of the expanded area of a canopy gap, then the gap was included as a sample. The amount of gap disturbance was quantified by measuring the percent of canopy and expanded gap distance present along the sample transects (Runkle, 1992; Kneeshaw and Bergeron, 1998).

Measurement of gap area

Only expanded gap areas were used in the analyses. The area of circular or elliptically shaped expanded gaps was estimated by substituting the length of the major axis (longest distance between living stems adjacent to the gap) and the length of minor axis (longest distance perpendicular to the major axis) into the equation for an ellipse:

$$Ga = (L \times S)/4 \times \pi \tag{1}$$

Where Ga is gap area, L is the length of the major axis, and S is the average of the minor axes measured perpendicular to the major axis. When the shape of the gap was irregular, the average of 2-4 minor axes was substituted for S.

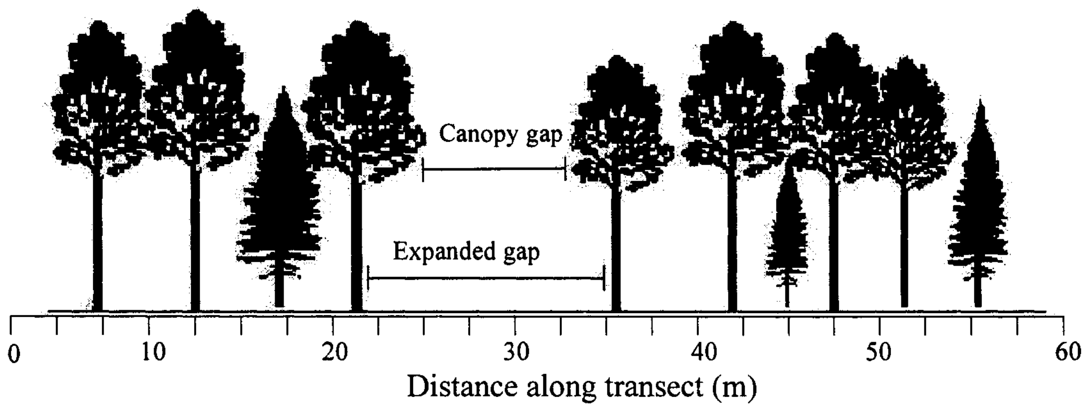

Figure 2.1 Cross-section of forest representing 60 meters of a sample transect. An example of a tree fall gap (canopy and expanded gap) is shown. At 50 meters canopy composition and basal area were sampled using a prism sweep method.

Table 2.1 Characteristics of trembling aspen dominated study sites located in northeastern Ontario, including number of sample sites for each stand age, location, number and total distance of sample transects, number of gaps sampled, and canopy composition information.

	Time since fire (years)						
	60	80	95	101	105	115	120
Number of sample sites	1	2	2	2	1	1	1
Latitude (N°)	48°10’00”	48°16’55”/ 48°21’30”	48°14’37”/ 48°32’45”	48°11’07”/ 48°17’18”	48°06’00”	48°07’20”	48°48’00”
Longitude (W°)	81°32’15”	81°17’38”/ 81°07’02”	80°58’48”/ 80°52’15”	82°15’03”/ 81°00’02”	82°17’00”	82°15’02”	82°06’09”
Number of transects	7	13	10	18	6	5	5
Transect distance (m)	1000	2205	2020	2115	1000	1025	1000
Number of gaps sampled	20	50	43	62	25	24	26
Basal area (m^2)	31.3	36.4	37.5	31.6	36.0	39.2	31.6
Other canopy species*	Bw, Bf, Sb, Sw	Sb, Pb, Sw,Bw, Pj, Bf, Ce	Bf, Sw, Pb, Bw, Sb, Pj	Sb, Bf, Bw, Pj, Pb, Sw, Pw, Pr	Bf, Sw, Sb, Bw, Ce, Pj, Pb	Bf, Sw, Pb, Bw, Ce, Sw	Bf, Sb, Bw, Sw, Pw, Ce, Pj

*note: Bw = white birch, Bf = balsam fir, Sb = black spruce, Sw = white spruce, Pb = balsam poplar, Pj, = jack pine, Ce = cedar, Pw = white pine, Pr = red pine

Gap creation

Gap maker sampling

The term gap maker defines the individual canopy tree or trees that were deemed responsible for creating a gap in the canopy of the forest after their death (Runkle, 1992). In each gap, a number of characteristics were recorded that described the condition of the gap maker, each of which is described in more detail below. The categories used to describe each gap maker were: the direct or indirect cause of death, the type of injury sustained, i.e. the structural condition that the gap maker created after its death, and the gap maker decay class.

The cause of gap maker mortality was categorized as pathogenic wood decay fungi (Fig. 2.2a), meteorological (including wind or snow-loading damage, Fig. 2.2b), insect, competition, mammal including girdling of bark and cambial layers, and other tree. If the gap maker mortality cause was questionable, it was categorized as undetermined. Wood decay was implicated as a factor in the death of a gap maker if obvious signs of wood decay fungi were present on the stem. Three major wood decaying fungi were grouped together including root rots (e.g. *Armillaria* spp.), polypores (e.g. *Phellinus* spp.), and cankers (e.g. *Hypoxylon* spp.). Armillaria root rot is a common cause of death among conifers and hardwoods in the boreal forest (Thompson, 2001). It can be easily diagnosed from the thick shoestring-like rhizomorphs (Fig 2.3c) and white mycelial mats that are produced between the bark and the cambial layer at the base of a tree (Lundquist, 2000). All the bark at the base of each gap maker was removed to assess the presence of these structures. Polypores and canker related wood decay was implicated as the factor contributing to tree death if basidiomata or stroma associated with each fungal type respectively were found on the stems of the gap maker. In some cases gap makers showed no obvious signs of wood decay fungi. However, the appearance of broken stems revealed the degree to which the heartwood and sapwood had been decayed (Fig. 2.2a). This allowed us to determine if wood decay caused the stem to snap under the influence of wind. To eliminate the possibility that wood decay was post mortem, I only inferred wood decay as a cause if there was strong evidence that the tree was still alive when the stem broke. Wind was implicated as an important factor causing mortality if a gap maker was snapped or uprooted and showed no signs of pathogenic wood decay fungi. Typically, if wind was the cause of mortality, the broken stem resembled that shown in Fig. 2.2b. Mortality caused by insects was difficult to determine in the field. The majority of stems suspected as being killed by insects were non-canopy trees, and therefore were not included in the analysis of canopy gap characteristics. Mammals were implicated in the death of gap maker if the tree was completely girdled close to the base of the stem (this was only the case for porcupine damage). Competition was assumed to have been the cause of death if dead stems showed no sign or symptoms of the above-mentioned factors and the stem diameter was sufficiently smaller than the stem diameter of dominant tree species within the stand. Again this was only the case for trees that were non-canopy trees and therefore were not included in the analyses of gap characteristics. Gap makers that were the result of fallen trees were listed as other tree. If none of these criteria could be met, the cause of death was described as undetermined. We suspect that undetermined causes of mortality were the result of either genetic inferiority, bacterial infection, viral infection, or possibly insect defoliation; all of which would be difficult to determine in the field.

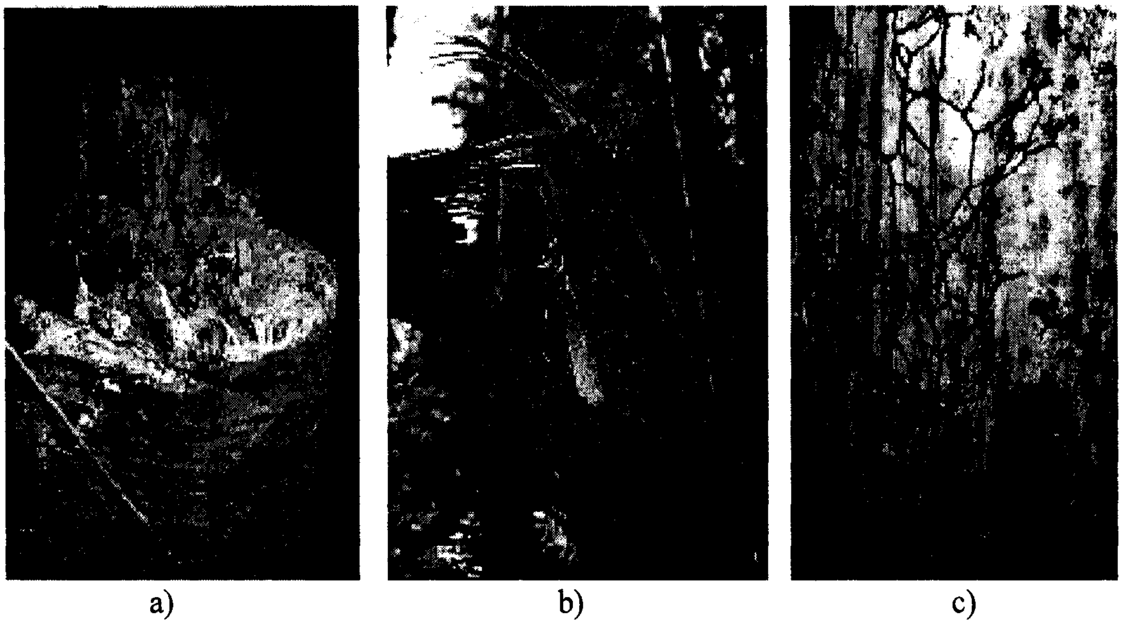

Figure 2.2 Examples of different types of damage sustained by gap makers. Photos a) and b) show trembling aspen stems that have been affected by wood decay and broken from wind respectively. Photograph c) shows a jack pine that has been infected with *Armillaria* spp., exhibiting characteristic shoestring-like rhizomorphs.

Gap maker structural condition was described as standing dead stem, broken stem, uprooted stem, damaged canopy (i.e. snapped branches, with the remaining crown still alive), or displaced tree. The latter two categories were the result of trees that were still alive.

A five-level decay class (adapted from Bartemucci *et al.*, 2002 and Ott and Juday, 2002) was used to describe the decay state of each gap maker (Table 2.2). Decay class 1 represented gap makers most recently deceased, and decay class 5 represented gap makers that were in advanced stages of decay.

Table 2.2 Decay classes used to categorize the state of gap maker decay in ten trembling aspen dominated boreal forest stands between 60 – 120 years since fire in northeastern Ontario. Decay class 1 represents living or most recently deceased gap makers and decay class 5 represents the most advanced stages of decay.

Decay Class	Branches		Bark	Wood Decomposition
	Large	Fine		
1	Intact	Intact	Intact	None
2	Mostly intact	Mostly present	Mostly intact	Little
3	Some intact	Missing	Mostly missing	Moderate
4	Missing	Missing	Very little remaining	Advanced
5	Missing	Missing	Missing	Advanced

Data analysis

A two stage stratified approach was used to sample gap characteristics at the forest stand level and the gap level. Stand level assessments included temporal trends in percent of transect occupied by expanded, canopy, single tree, multiple tree, and edaphic gap percent with linear regression. Linear regressions were also used to assess trends of gap characteristics with time since fire including, the mean gap area, number of gap makers per gap, and the number of decay classes per gap. Similarly the mean gap maker characteristics, including structural types and cause of mortality were analyzed using linear regressions to determine if significant patterns existed with time since fire. All unstandardized residuals were visually inspected to determine if the data met the assumptions of regression analysis.

Results

Gap characteristics of forest stands

The amount of gap disturbance in the study forests increased significantly with time since fire as the percent of transect occupied by both expanded and canopy gaps increased with time (Fig. 2.3a). Distance of transect occupied by expanded gaps ranged from approximately 1/8th of the distance in the youngest stand, to about 1/3rd of the distance in the older stands. Canopy gaps were approximately 1.5 to 2.5 times smaller than expanded gaps (Fig. 2.3a). Single tree gaps were less important than multiple tree gaps as the respective percent of transect was less than that of multiple tree gaps in all but the youngest forest stand (Fig. 2.3b). However, since I did not correct for sampling bias using the line intersect method, single-tree gaps may have been underestimated (Runkle, 1992). With time, multiple tree gaps covered more of the transects than the single tree gaps (Fig. 2.3b). A 2.5 times increase in transect distance occupied by multiple-tree gaps occurred between stands aged 60 and 80 years and was almost 5 times higher in the oldest stand than the youngest stand. As expected, area covered by edaphic gaps was variable and showed no significant relationship with time since fire ($R^2 = 0.026$, $p = 0.298$).

Mean expanded gap area of both multiple and single tree gaps increased significantly with time since fire (Fig. 2.3c). The expected area of multiple tree gaps was about three times larger in the oldest stand compared to the youngest stand, while the expected area of single tree gaps was about 4.5 times larger (Fig. 2.3c). Large gaps however, were not restricted to the oldest stands; gaps in excess of 400m² were present in stands as young as 80 years since fire.

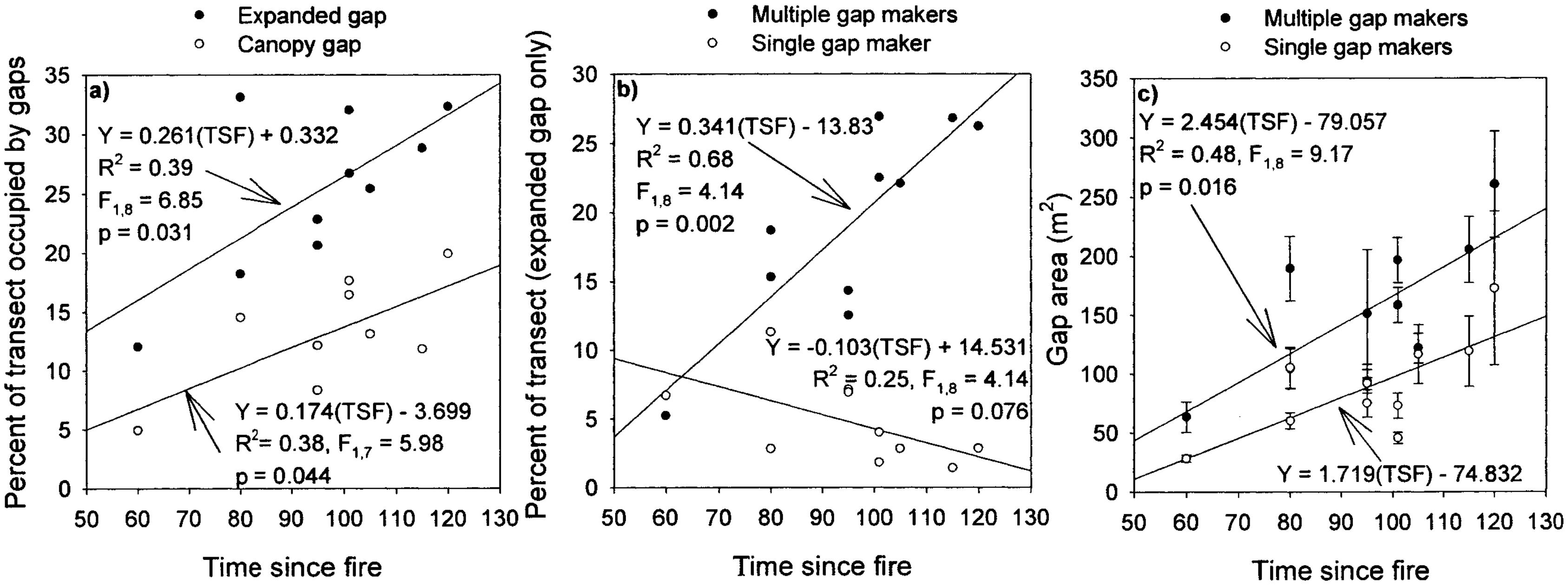

Figure 2.3 Percent of total sample transect distance occupied by gaps in ten trembling aspen dominated boreal forest stands 60-120 years since fire in northeast Ontario. a) Both the percent of transect occupied by expanded and canopy gaps increase with time since fire. b) Percent of transect occupied by multiple tree expanded gaps increase with time since fire, while that of single-tree expanded gaps tends to decrease with time since fire. c) Both single and multiple tree gaps increase in mean gap area with time since fire. The statistical information (R^2, $F_{1,8}$, and p) for estimated single gap maker gap area are the same as those for the estimated multiple gap maker gap area.

The mean number of gap makers per gap increased significantly with time; the oldest stand is shown to have about twice the number of gap makers than the youngest stand (Fig. 2.4a). The mean number of decay classes per gap showed a significant increase with time (Fig. 2.4b). The expected mean of the oldest stand is one and a half times that of expected mean number of decay classes in the youngest stand (Fig. 2.4b).

Gap maker characteristics

Structure

The three most important structural characteristics of gap makers were standing dead stems, snapped stems, and uprooted stems. Snapped gap makers were the only group to significantly increase with time since fire (Fig. 2.5). The mean number of expected snapped stems was approximately 3 times higher in the oldest stand compared to the youngest stand (Fig 2.6). Both standing dead and uprooted gap makers were important components of gap structure, however their occurrence with time was not significant ($p = 0.431$ and $p = 0.226$ respectively). Stems where the canopy had been disturbed (e.g. broken branches) and displaced stems played a minor role in gap creation ($p = 0.869$ and $p = 0.810$ respectively).

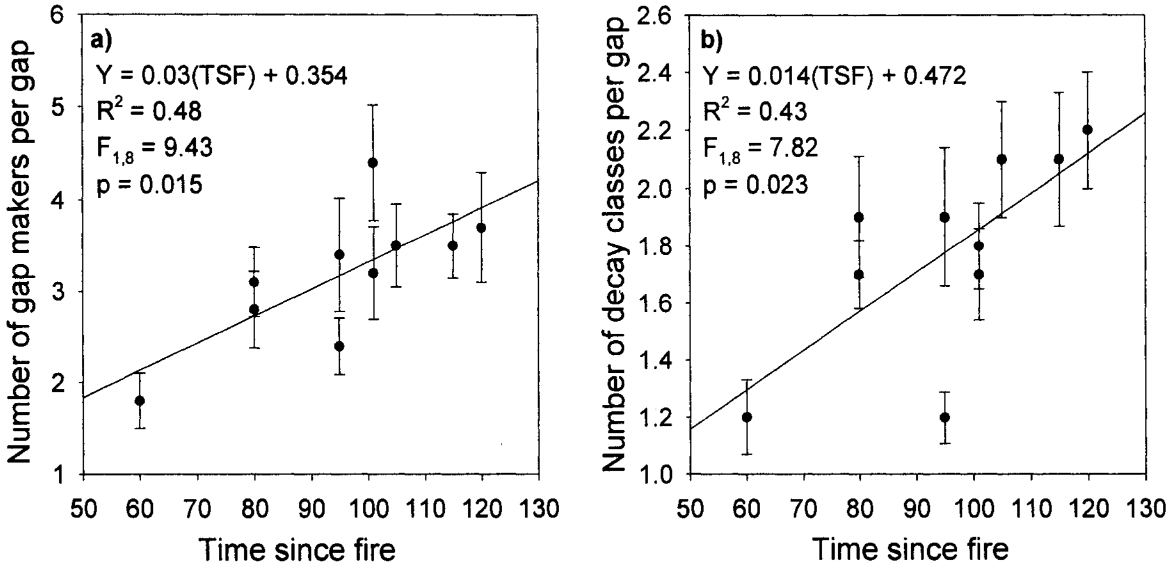

Figure 2.4 Gap characteristics of ten trembling aspen dominated boreal forest stands 60-120 years since fire in northeast Ontario. a) The mean number of gap makers per gap increases with time since fire. b) The mean number of decay classes (number of gap maker events) increases with time since fire.

Mortality

The most predominant type of mortality influencing the death of gap makers was infection by fungi that cause wood decay (Fig 2.6). Mean number of gap makers influenced by wood decay fungi significantly increased with time since disturbance (Fig. 2.6). The expected mean number of stems influenced in the oldest stand is over 1.5 times that of the youngest stand. Wind related mortality was the second most important cause of mortality, but was not significantly different over time (Fig. 2.6). The mean number of gap makers that had an undetermined cause of death increased slightly with time ($R^2 = 0.26$, $p = 0.075$), however other modes of mortality had minor occurrences and had no significant relationship with time since fire.

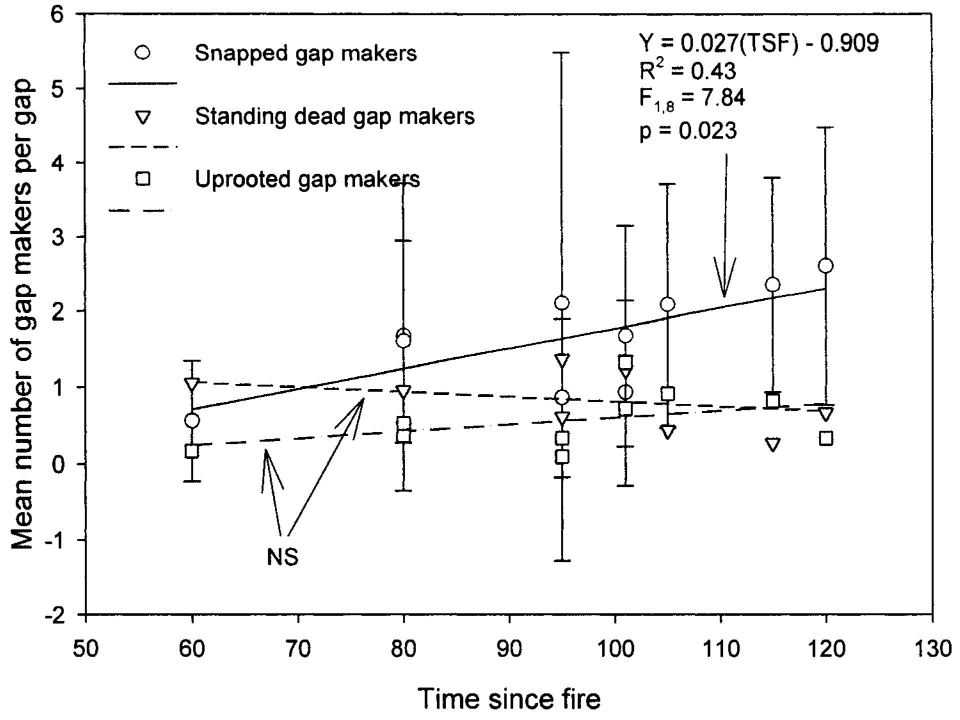

Figure 2.5 Gap maker characteristics of ten trembling aspen dominated boreal forest stands 60-120 years since fire in northeast Ontario. Only the mean number of gap makers that were snapped increased with time since fire. The other important types of gap maker structure were similar with time since fire. Standard deviation of only snapped gap makers is shown.

Gap maker decay

The frequency of gap maker decay among the five decay classes was similar for the four youngest age classes (60 –105 years since fire) and followed a strong negative distribution (Fig 2.7). Stands in the three oldest age classes each showed a more even distribution among decay classes 1 to 4. Decay class 5 gap makers were rare indicating that their role in recent gap formation is minor.

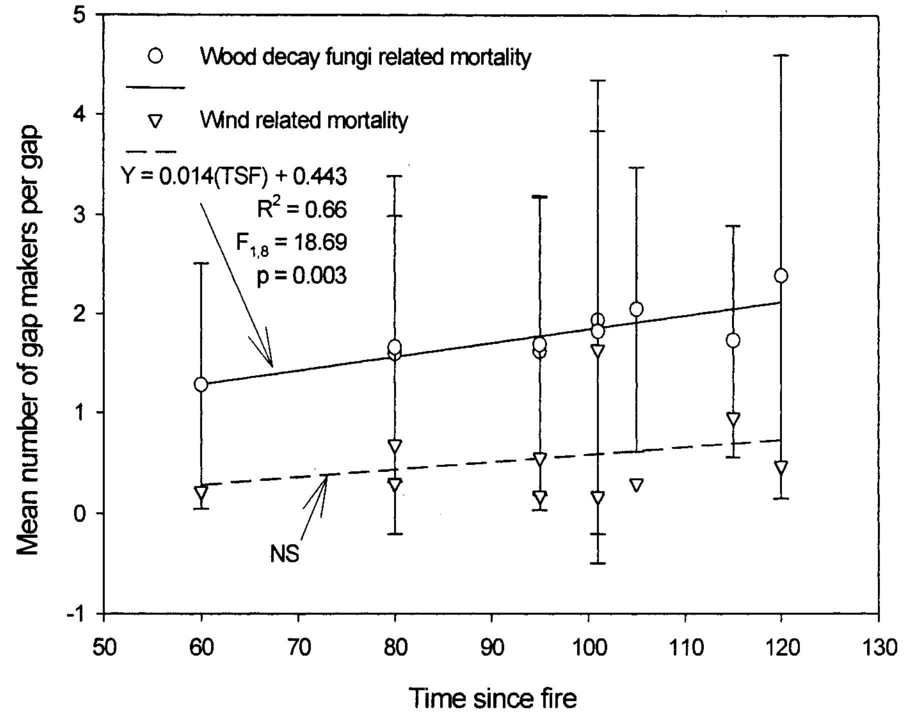

Figure 2.6 Gap maker mortality characteristics of 10 trembling aspen dominated boreal forest stands 60-120 years since fire in northeast Ontario. The mean number of gap makers influenced by wood decay fungi increases with time, whereas the mean number of stems killed by wind remains the same. Standard deviations are shown only for the mean number of gap makers influenced by wood decay fungi.

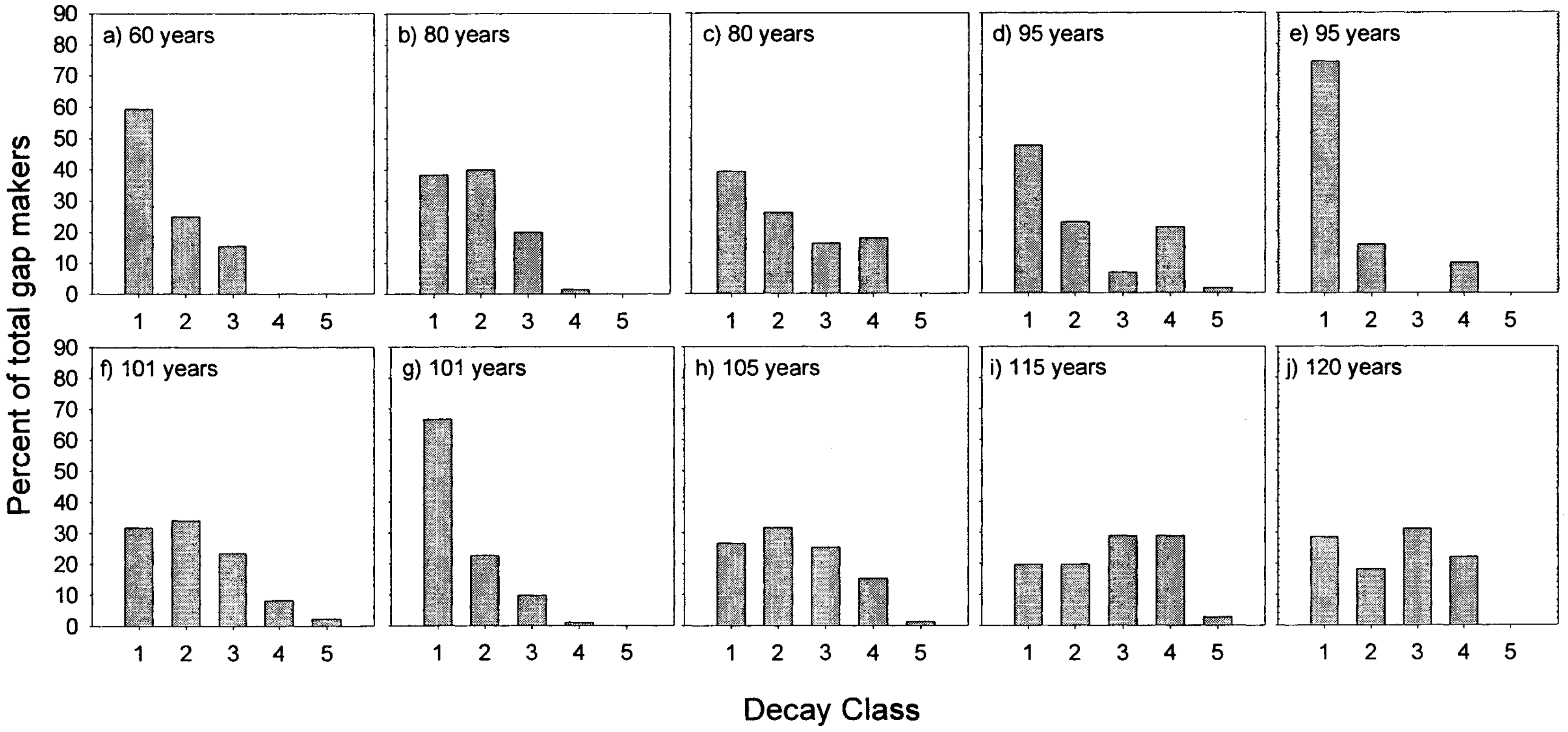

Figure 2.7 Relative frequency of gap maker decay class for ten trembling aspen dominated forests between 60 and 120 years since fire in northeastern Ontario. Stands aged 60 to 101 years tend to show a higher frequency of gap makers in decay classes 1 and 2. Stands older than 101 have a more even distribution of decay classes 1 to 4. Decay class 5 gap makers were rarely sampled.

Discussion

Gap characteristics of forest stands

Changes in gap characteristics during the transition stage of trembling aspen forests are significant. The review by McCarthy (2001) found that the average canopy gap fraction was between 6 - 36% in boreal/subalpine forests, and the average gap size was 41 – 141 m^2. When compared to the average amount of gap disturbance (gap fraction), the results of this study show that canopy gap disturbance in younger stands tend to be lower than expected. However, in older stands it becomes representative (Fig. 2.3a,c). The amount of expanded gap disturbance was representative for all forest ages (McCarthy, 2001). In McCarthy's review, the results from boreal forest study areas were dominated by coniferous species (however see Cumming *et al.* 2000 and Kneeshaw and Bergeron, 1998). Therefore, lower than expected amount of canopy gap disturbance in this study can potentially be explained by the dominance of trembling aspen. Observed expanded gap areas were within the range of canopy gap areas found in other boreal forest studies (McCarthy, 2001). The large increase in multiple gap area that occurred between 60 and 80 year old stands suggests that gap area may not have a simple linear relationship with time since fire. However, to satisfy test this relationship with confidence, more stands in the 60-80 year age class would have to be sampled. In this case, gap area is expected to increase rapidly, and then become relatively constant after 80 years (Fig. 2.3c). Increases in gap area with time since fire are attributed to the larger impact of single tree mortality (Fig. 2.3b) and expansion of existing canopy gaps (increase in mean number of gap makers) (Fig. 2.4a). The higher number of decay classes found in gaps of older stands (Fig. 2.4b) suggests that punctuated disturbance events at the gap level are an important aspect of gap creation.

Gap maker characteristics

Structure

The only significant pattern with time since fire was the increase in mean number of gap makers that had snapped (Fig. 2.5). Since stems that were initially snapped and stems that were initially standing dead and then snapped were incorporated into this group, the importance of snapped stems might be overemphasized. However, regardless of the mechanism responsible for their formation (i.e. snapped when alive, or snapped post-mortem), the resulting gap maker structure that is created is the same. The occurrence of standing dead and uprooted gap makers is similar with time since fire. However, this pattern is probably caused by different mechanisms. The formation of standing dead gap makers with time is more deterministic than the stochastic processes (such as wind) responsible for uprooting gap makers. Although, environmental factors such as soil depth will increase susceptibility to wind related mortality (Ruel and Benoit, 1999).

Mortality

The importance of wood decay fungi as a direct or indirect cause of mortality is clearly shown by the high mean number of gap makers infected by wood decay fungi compared with other causes (Fig. 2.6). As trees age, there is increased opportunity for penetration and infection by wood decay fungi (Castello *et al.*, 1995; Tainter and Baker, 1996). However, not all species of wood decay fungi are responsible for the direct death of a gap maker (e.g. *Phellinus tremulae*). Therefore in this study, the mean impact of gap maker mortality directly caused by fungal pathogens is overestimated. This clearly demonstrates a strong interaction between fungal infection and wind related mortality (although not tested statistically). Future studies should focus on the interaction between infection by wood decay fungi and wind related mortality (the majority of stems that were infected by wood decay fungi in this study had also been snapped or blown over, presumably by wind or snow loading). Wind was also an important cause of gap maker mortality, however it was not significantly different with respect to time since fire (Fig. 2.6). The lack of significance is probably the result of variability created by the stochastic nature of weather related events causing gap maker mortality. Other studies have shown that wind-related mortality increases with time since fire (Kramer *et al.*, 2001). Since wood decay fungi were implicated as the cause of mortality when gap makers were infected with wood decay fungi and were blown over, the importance of wind related mortality could be underestimated. As important interactions exist between fungal infection, wood decay, and wind-throw susceptibility, future studies of wind damage to forest environments should be fine-scale enough to detect the role of wood decay fungi and their effect on gap creation.

Conclusions

This chapter demonstrates that canopy gaps are an important and conspicuous element during the development trembling aspen forests in northeastern Ontario. The implications of these findings are important in understanding the long-term dynamics of such forests, particularly if canopy gaps influence recruitment patterns and community structure in the understorey environment. As many studies show that gap creation can influence the regeneration patterns of juvenile tree species and overall community structure, it is important to understand the degree to which this occurs in the development of boreal forests. The effect of canopy disturbance on understorey environments has rarely been studied in the boreal forest, therefore it is a much-needed area of research. Conducting this research in the boreal forest will accomplish two major objectives: i) test the principles of the gap-related paradigm that have been developed in temperate and tropical forests, and ii) determine the effect that gap disturbance has on the long-term dynamics of post-disturbance boreal forests. The next two chapters of this thesis will investigate these objectives by studying the effect that canopy disturbance has on juvenile tree recruitment patterns and vascular plant community structure.

Chapter 3

Recruitment patterns of juvenile tree species in canopy gap and understorey environments in trembling aspen dominated forests in northeastern Ontario.

Abstract

Canopy gaps are an important and conspicuous characteristic of developing trembling aspen stands in northeastern Ontario. The ability to predict recruitment patterns of juvenile tree species in the understorey offers a major step for understanding long-term patterns of stand and species dynamics in boreal forests under non-stand replacing disturbance. I investigated recruitment patterns of juvenile tree species in 20 canopy gaps in five different trembling aspen dominated forests. In each study site, four gaps and one paired understorey quadrat were used to sample the density and growth rate of all juvenile tree species. For statistical comparison, gap types and the understorey quadrats were considered discrete treatments. For each treatment combination (including the paired understorey quadrat) the density of individual juvenile trees was compared using one-way analysis of variance. Growth of three individuals from each height class was used as an estimate of growth for representative tree species, if they were present. The most common type of recruitment was balsam fir followed by trembling aspen, white spruce, black spruce, and white birch. Eastern white cedar, red maple, balsam poplar, pin cherry, and white pine were also present, but were rare. There were no significant differences in individual recruitment density among the understorey and gap environments, suggesting that establishment of juvenile trees occurs prior to gap formation, even for shade intolerant species such as trembling aspen. Trembling aspen

had the highest growth rate, followed by white birch, balsam fir, white spruce and black spruce. Growth for individual species did not differ significantly among the gap and understorey environments. As the majority of shade intolerant recruitment was from root suckers, similar growth is explained by the initial dependence of offspring on established parental root systems. Similar growth of shade intolerant advanced regeneration indicates that minimum thresholds of photosynthetically active radiation are met in the understorey and gap environments. Juvenile tree density and growth is not accurately predicted by the size and age of canopy gaps smaller than 350 m^2 in trembling aspen forests between 95 and 120 years since fire in northeastern Ontario.

Introduction

Despite low tree species richness compared to other forest biomes, forest canopy dynamics in the boreal forest is little understood (Chen and Popadiouk, 2002; Thompson, 2000). Following large-scale disturbance, forests are typically dominated by species such as trembling aspen, jack pine, black spruce and in some cases white birch. In the absence of large-scale disturbance, numerous vegetation succession pathways can occur. In northeastern Ontario, the typical pattern that has been observed is an increase in richness and abundance of shade tolerant species (Chapter 1 of this thesis); similar patterns have been observed in adjacent areas of northwestern Quebec (Bergeron and Dubuc, 1989; Bergeron, 2000).

Disturbance dynamics in the boreal forest influence spatial and temporal patterns of tree species presence and absence (Bergeron *et al.*, 1995; Johnson, 1992; Heinselman, 1981). Large-scale, stand-replacing disturbance such as fire and insect defoliation are important for initiating new stand development. The inherent spatial variability of localized environmental conditions within an area can cause considerable variation in disturbance intensity and resulting tree mortality. This is particularly true for fire disturbance (Bergeron *et al.*, 2002). Areas that are less susceptible to burning result in the survival of residual patches of forest, creating a landscape-scale mosaic of forest stands at different stages of development. In time, the residual patches that survive stand-replacing fire will be represented structurally by over-mature or old-growth patches within the even-aged matrix. Similarly, over-mature or old-growth forests can develop in regions where the mean fire return interval is greater than the typical longevity of the trees making up the post-fire cohort (Lesieur *et al.*, 2002). In both cases, regeneration dynamics of tree species switches from stand-replacing, to small-scale disturbances (Oliver and Larson, 1990).

In the past decade, several researchers have advocated the importance of further studying the role of small-scale disturbance in structuring boreal forest ecosystems (Kneeshaw and Bergeron, 1996, 1998; Bergeron *et al.*, 1998; McCarthy, 2001). Small-scale disturbances include those that cause the death of individual or small groups of trees creating a discontinuity in the canopy of a forest and altering understorey light conditions (Lieffers *et al.*, 1999). Canopy gaps are thought to be most important in their role of vegetation dynamics during old growth stages of forest development, and occur during stages of canopy transition, prior to old growth (Oliver and Larson, 1990). Regardless of when canopy gaps occur, the removal of canopy dominants can significantly alter environmental conditions in the understorey. The understorey vegetation can respond by i) the release of advanced regeneration and changes to competitive interactions among species (Suding, 2001; Suding and Goldberg, 2001) or ii) colonization and establishment of sprout or seed recruitment (Oliver and Larson, 1990). In boreal forests, few studies have addressed the role of canopy gaps and their role in vegetation dynamics (Kneeshaw and Bergeron, 1996, 1998; Cumming *et al.*, 2000). In areas where disturbance promotes secondary forest succession, development patterns are usually well described, however mechanisms of vegetation change are not well understood (Bergeron, 2000; Bergeron and Dubuc, 1989; Carelton and Maycock, 1978; Lesieur, *et al.*, 2002). The insufficient knowledge of tree recruitment dynamics during the canopy transition stage in boreal forests hinders a clear understanding of forest canopy dynamics and naturally occurring forest stand replacing processes.

In temperate and tropical forests, the formation of canopy gaps is a mechanism that promotes coexistence of tree species with different life history strategies such as shade tolerance and shade intolerance (Schnitzer and Carson, 2001). This concept of vegetation dynamics has its roots firmly set in early ecological theory that describes the differences between r-species and K-species (MacArthur and Wilson, 1967). The simple r-K selection model predicts that species of both groups will coexist if disturbance is intense and frequent enough to create favourable establishment and growing environments for r-species without destroying all of the K-species; classically described as the intermediate disturbance hypothesis (Connell, 1978). When fire is absent for long periods of time, disturbances such as wind-throw and insect defoliation can lead to disturbance patches that are large enough to promote recruitment of both shade intolerant and tolerant species (Kneeshaw and Bergeron, 1999). However, in the absence of intense, allogenic disturbance it is unclear if coexistence of shade intolerant and shade and shade tolerant boreal forest tree species will occur. When intense, allogenic disturbances are not present for long periods of time boreal forest stands should convert to forests that are dominated by shade tolerant species such as balsam fir and white cedar; a pattern observed in chronosequence studies in forests in northwestern Quebec (Bergeron and Dubuc, 1989 and Chapter 1 of this thesis). However there is some confusion regarding the mechanisms and timing of such transitions. For example, dominance of shade tolerant conifers can occur directly following an initial post disturbance forest dominated by trembling aspen, or with an intermediate second cohort of aspen (Bergeron, 2000; Cumming *et al.*, 2000).

Studying tree recruitment dynamics in canopy gaps during the canopy transition stage of a common post-disturbance boreal forest type, for example trembling aspen dominated forest, should provide insight into the possible successional pathways. Canopy gaps are a conspicuous and important structural attribute during the development of trembling aspen dominated forests in northeastern Ontario. As the effect of small-scale disturbance has rarely been studied in this region, it cannot be rejected as a possible hypothesis to explain forest dynamics when fire does not interrupt stand development. In this chapter I examine, whether in the absence of stand replacing disturbance, species belonging to shade intolerant and tolerant functional types can recruit and coexist in the resulting canopy gaps. The specific objective was to determine the effect of gap size and age on recruitment dynamics (density and growth) of tree species. Results of this study will be used to infer expected compositional changes based on those species most likely to fill the gap and thereby provide insight into future coexistence of shade intolerant and tolerant tree species.

Methods

Study sites

The study sites were located in forests around the city of Timmins (48.34N, 81.22W, 295 m altitude), in northeastern Ontario. This region of Ontario has a relatively homogenous landscape. Major topographic features are the result of deposits from the retreat of glaciers during the past ice age (approximately 10000 years ago). The study sites were located within the area defined as Hills (1959) ecoregion 3E (see Vasiliauskas and Chen, 2002). Ecoregion 3E incorporates a large area dominated by clay soils, also known as the clay belt, deposited by ancient lakes Barlow and Ojibway (Baldwin *et al.* 2000). The study sites were selected in the southern portion of the ecoregion, which is dominated by outwash plains, predominantly composed of various loamy soils, silty to very fine sands, and fine sands, for more soil descriptions see Taylor *et al.* (2000). Northeast Ontario has a moderately dry, cool climate with short summers. The average annual temperature for Timmins, Ontario is 1.2 °C and average annual precipitation is 873 mm.

Forests of Ecoregion 3E are typical of the boreal forest. Common associations include trembling aspen, white birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* (Moench) A. Voss) on upland moderately well-drained soil conditions, jack pine (*Pinus banksiana* Ait.) and black spruce (*Picea mariana* (Mill.) BSP.) on upland well-drained soils, balsam fir (*Abies balsamea* (L.) Mill.), and eastern white cedar (*Thuja occidentalis* L.) on lowland poorly-drained soils (Taylor *et al.*, 2000). Patterns in forest stand dynamics and species associations have been well documented in adjacent areas of Quebec (see Bergeron and Dubuc, 1989; Bergeron, 2000).

Stand selection

To represent the transition stage of trembling aspen forest development, I used the five forest study sites between 95 and 120 years sampled in chapter 2 of this thesis. Stand age was determined based on existing fire inventory maps for the region, and a minimum of 10 canopy tree cores sampled from healthy trees in each study site. The forest study sites were chosen based on similar canopy composition, soil type, drainage, accessibility, and time since last fire.

Estimates of tree species basal area for each study site were evaluated systematically every 50 m along 5-9 sample transects. Sample transects were between 50 and 300 m in length and were between 1000 and 1300 m total length within a study site. Each transect was started 50 m from a random entry point located on the periphery of the stand. Entry points were chosen based on ease of access, for example from the side of an old logging road. Forest areas that were affected by humans or that were within 50 m from any prominent edges, including gaps that were greater than 800 m², were avoided as I was only interested in the role of small-scale disturbance on understorey species dynamics. A prism with a basal area factor 2 was used to determine stand basal area and species composition (OMNR, 1978).

Gap and understorey environments

In each study site, four gaps with expanded gap areas less than 350 m², and one paired 400 m² understorey quadrat were sampled for this study. Gaps smaller than 350 m² were chosen since 95% of 291 gaps sampled in the study forests and similar trembling aspen dominated forests met this criterion. After sampling, the gaps were grouped based on age and size (Table 3.1). Young gaps were less than 5 years since gap maker mortality and old gaps were greater than 5 years. Gaps were then ranked by size, resulting in 5 treatment combinations (see Table 3.1). Gap age was estimated using several techniques including gap maker decay class and release of understorey vegetation (Dynesius and Jonsson, 1991). Attempts were made to determine time of death of gap maker by counting growth rings from stem cookies cut at breast height, however wood decay made dating gaps this way difficult. The expanded gap area of circular or elliptically shaped gaps was estimated by measuring the length of the major axis (longest distance between stems adjacent to the tree-fall gap) and the length of the minor axis of the expanded gap (shortest length between stems adjacent to the tree-fall gap, perpendicular to the major axis). For irregular shaped gaps, the average of numerous minor axes were used as an estimate of minor axis length and substituted into the ellipse equation. Paired understorey quadrats were 400 m^2 and were placed in the stand where canopy closure was not less than 90 % total cover (visual estimation). Canopy closure adjacent to each understorey plot was also assessed to make sure large gaps would not significantly influence vegetation in the understorey environment.

Table 3.1 Forest time since fire and areas of 20 gaps sampled in trembling aspen dominated transition forests located in northeastern Ontario.

		Gap area (m²)			
		Young (< 5 years)		Old (> 5 years)	
Stand	Time Since Fire	Small	Large	Small	Large
1	95	62.81	171.37	72.07	138.40
2	101	128.69	175.01	83.09	202.74
3	101	77.64	330.36	93.38	136.09
4	115	98.02	168.95	195.07	222.26
5	120	88.25	343.07	124.70	199.63

Data collection

Within each gap and understorey plot, the abundance of all juvenile tree species was tallied and grouped into one of three height classes 0-0.5, 0.5-2.0, and 2.0-5.0 m (stems taller than 5 m were noted, but were not included in analyses as they were relatively rare). Three individuals (if present) of each species from each height class were chosen to estimate species height growth. Growth during the past one to five years was measured to estimate yearly growth rate; only the previous year growth was used for young gaps. Individuals were chosen based on good health and lack of competition from adjacent stems. To minimize sampling error, the average of the three individuals measured was used as the respective gap estimate of growth. Growth of coniferous species such as balsam fir, black spruce, and white spruce was measured as the length between each whorl of branches. Judging from the current years growth of coniferous stems, suppression causing missing whorls was not a problem, and any stems that were questionable were not sampled. Measurement of yearly growth for shade intolerant species such as aspen and white birch was more difficult. The indeterminate growth of such species allows only the past couple of years to be measured, as bud scale scars become inconspicuous as diameter of the stem increases. However for this study, the majority of shade intolerant hardwood recruitment was two years old or younger, therefore I assumed that 2 years growth would be sufficient to represent the estimate of growth rate. Current-year growth was not included as a measurement, as differential growth of individuals over the sampling period may have resulted in higher estimates for those sampled later in the field season.

Data analysis

Since I expected differences in recruitment pattern and growth among gap and understorey environments of the juvenile tree species, I tested two hypotheses with regard to species recruitment and growth among different environment types. One-way analysis of variance was used to test the hypothesis of no difference among environments in stem density of the more abundant juvenile species. Assumptions of variance and normality were tested and met except in one case where a high trembling aspen stem density in the 0-0.5 m height class caused non-normality. When the analysis was rerun without the outlier, the conclusions were the same as presented in the results. Analysis of covariance was used to test the hypothesis of no difference between growth rates of individual species among environment types, based on their initial height. Growth measurement data were transformed using the natural logarithm function to meet statistical assumptions and trembling aspen and white birch were grouped as shade intolerant sprouting species as they had similar growth rates.

Results

Recruitment patterns of juvenile trees

Balsam fir had the highest abundance of all juvenile tree species in gap and understorey environments (Fig. 3.1). All other important juvenile trees (including trembling aspen, black spruce, white spruce, and white birch) had much lower mean recruitment densities (Fig. 3.1). Rare juveniles included white cedar, red maple, balsam poplar, pin cherry, and white pine (Fig. 3.1).

Total stem density of juvenile trees was not significantly different among gap and understorey environments (Table 3.2, Fig. 3.2). Even when species were grouped by height class, there was no significant environmental effect detected (data not shown). Large stems (2-5 m tall) tended to have lower stem density than small (0-0.5 m) and medium (0.5-2.0 m) height juveniles (Fig. 3.2). However, there was considerable variability within stands with respect to the generality of this relationship, especially for smaller juveniles.

Growth of juvenile trees

Although juvenile tree species had different growth rates, their individual growth was not significantly different among the gap and understorey environments (Table 3.3). As there was no significant gap effect, all samples were grouped to show relationship between height growth and initial height. Growth of balsam fir, black spruce and white spruce was significantly related to initial height (Fig. 3.3, Table 3.4). However, growth of trembling aspen and white birch juveniles was not significantly influenced by initial height (Fig. 3.3, Table 3.4). Shade intolerant species had greater growth rate than shade tolerant species at small heights. However, above 3 m stem height, predicted growth seems to be similar between the groups (Fig. 3.3). This pattern was most pronounced for balsam fir and black spruce.

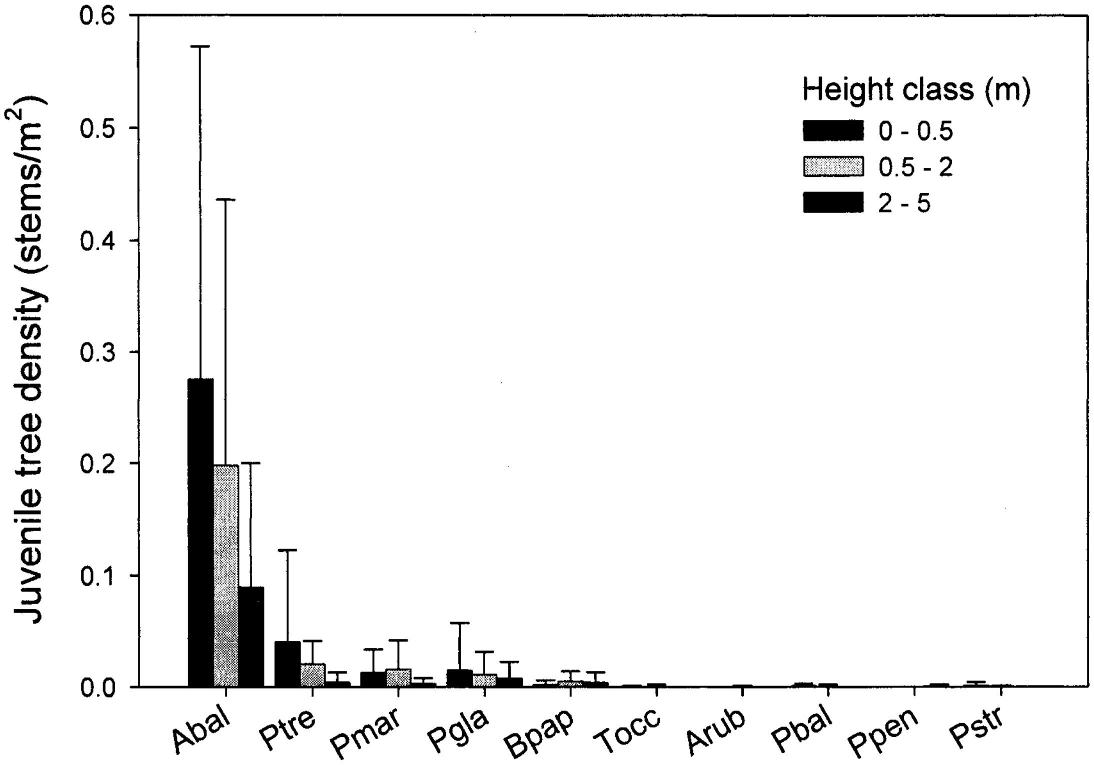

Figure 3.1 Recruitment density (stems/m^2) of juvenile tree species found in canopy gaps and understorey environments in trembling aspen forests 80-120 years since disturbance in northeast Ontario. Abal = *Abies balsamea*, Ptre = *Populus tremuloides*, Pmar = *Picea mariana*, Pgla = *Picea glauca*, Bpap = *Betula papyrifera*, Tocc = *Thuja occidentalis*, Arub = *Acer rubrum*, Pbal = *Populus balsamifera*, Ppen = *Prunus pensylvanica*, and Pstr = *Pinus strobus*.

Table 3.2 One-way ANOVA of juvenile tree density for five juvenile tree species in canopy gaps and understorey environments of trembling aspen dominated boreal forests located in northeastern Ontario.

Species	Source	df	SS	MS	F statistic	Prob. >F
Balsam fir	Environment	4	0.325	0.081	0.373	0.825
	Error	20	4.351	0.218		
	Total	24	4.676			
Black spruce	Environment	4	0.005	0.001	0.862	0.503
	Error	20	0.029	0.001		
	Total	24	0.034			
White spruce	Environment	4	0.008	0.002	0.726	0.585
	Error	20	0.053	0.003		
	Total	24	0.061			
Trembling aspen	Environment	4	0.062	0.015	2.764	0.056
	Error	20	0.111	0.006		
	Total	24	0.173			
White birch	Environment	4	0.001	1.51×10^{-4}	0.755	0.567
	Error	20	0.004	1.20×10^{-4}		
	Total	24	0.005			

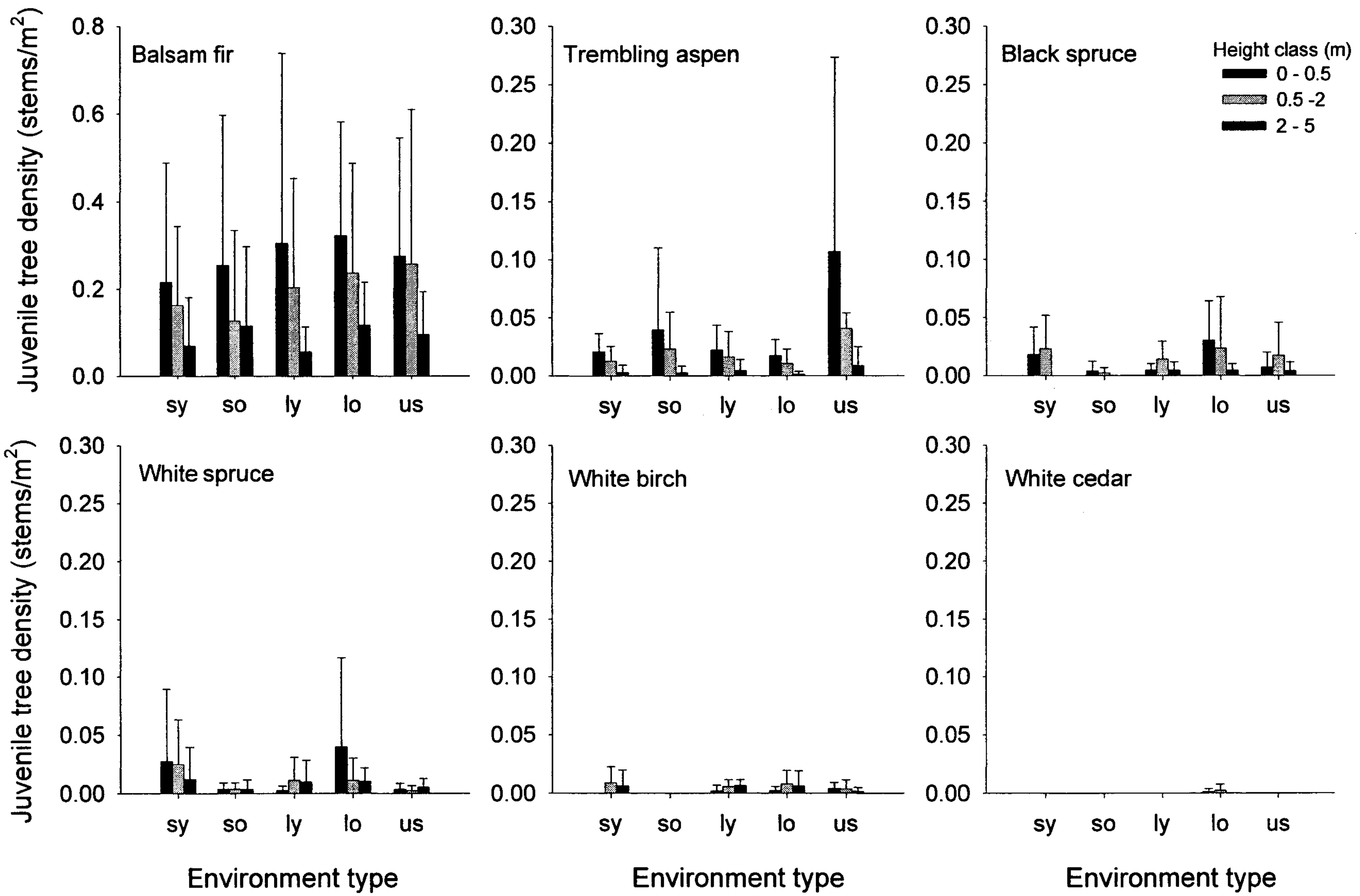

Figure 3.2 Stem density of the six most abundant juvenile tree species grouped by height class in canopy gaps and understorey environments of 5 trembling aspen dominated forests located in northeastern Ontario. Environment types are sy = small young gap, so = small old gap, ly = large young gap, lo = large old gap, and us = understorey. Also note the different scale on the ordinate axis for balsam fir.

Table 3.3 Analysis of Covariance of juvenile tree growth (ln cm/year) for the five most abundant tree species in canopy gap and understorey environments of trembling aspen dominated boreal forest stands located in northeastern Ontario. Initial height was used as a covariate to constrain the growth measurements to determine if a significant gap type x initial height interaction existed. Trembling aspen and white birch recruitment were grouped as shade intolerant to increase sample size for statistical comparison.

Species	Source	df	SS	MS	F statistic	Prob > F
Balsam Fir	Environment (E)	4	0.877	0.219	0.549	0.701
	Ln initial height (H)	1	26.814	26.814	67.129	< 0.001
	E*H	4	0.693	0.173	0.434	0.784
	Error	46	18.374	0.399		
	Corrected Total	55	51.798			
Black spruce	Environment (E)	4	0.334	0.084	0.398	0.807
	Ln initial height (H)	1	0.282	0.282	1.344	0.266
	E*H	4	0.242	0.061	0.288	0.880
	Error	14	2.938	0.210		
	Corrected Total	23	5.595			
White spruce	Environment (E)	4	1.111	0.278	0.755	0.568
	Ln initial height (H)	1	3.476	3.476	9.449	0.007
	E*H	4	1.444	0.361	0.981	0.444
	Error	17	6.254	0.368		
	Corrected Total	26	12.409			
Shade intolerant	Environment (E)	4	0.025	0.006	0.023	0.999
	Ln initial height (H)	1	0.468	0.468	1.672	0.211
	E*H	3	0.259	0.086	0.308	0.819
	Error	20	5.597	0.280		
	Corrected Total	28	7.181			

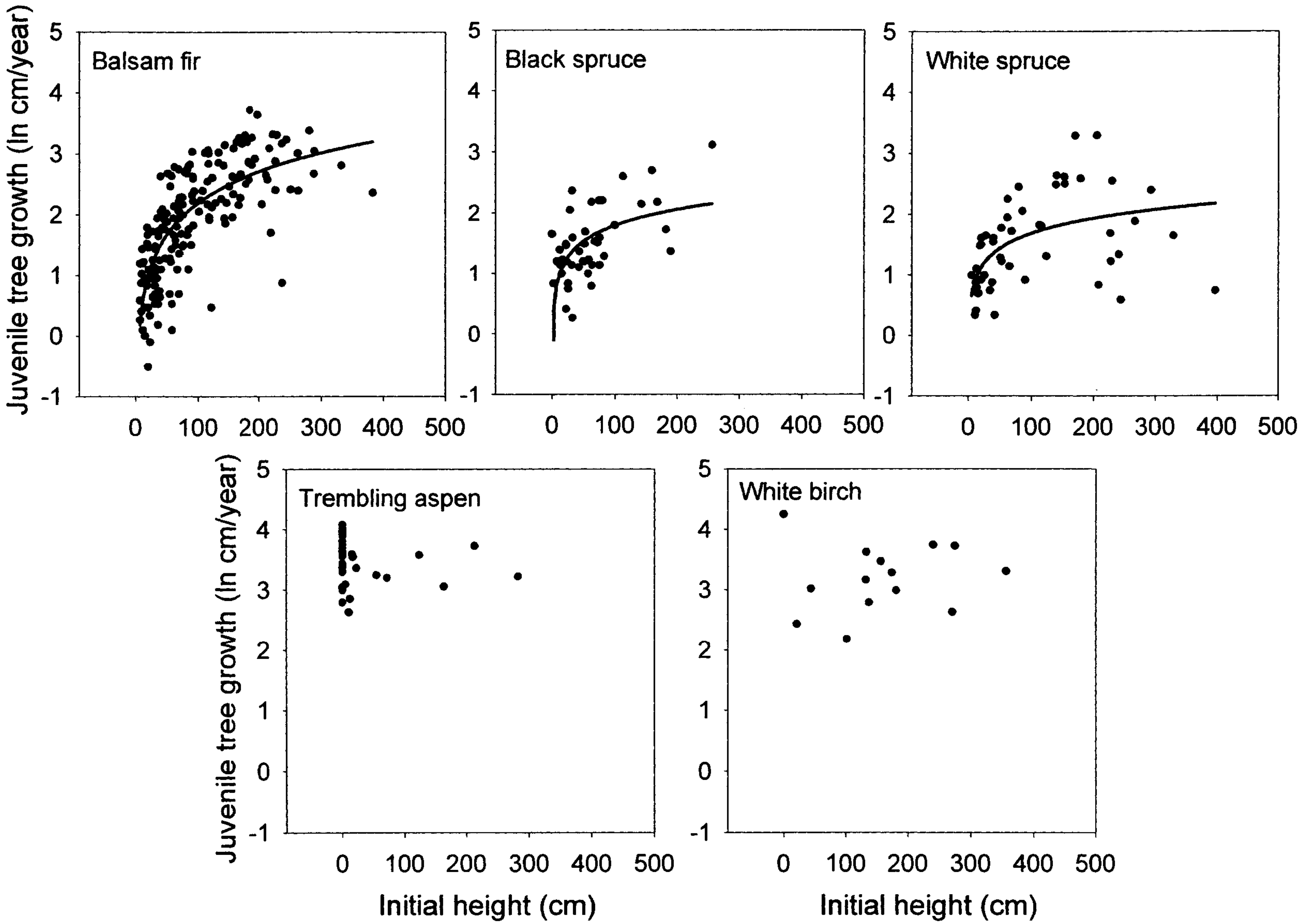

Figure 3.3. Growth rate of the five most abundant juvenile tree species as a function of initial height over 1 to 5 year periods in gap and understorey environments of trembling aspen dominated boreal forests in northeast Ontario.

Table 3.4 Relationship between growth rate (G) and initial height (H) for five juvenile tree species found in canopy and understorey environments of trembling aspen dominated boreal forests in northeast Ontario.

Species	N	Growth rate - initial height relationship	F statistic	R^2	p
Balsam fir	185	$\ln(G) = -1.28 + 0.75\ln(H)$	254.69	0.58	<0.001
Black spruce	46	$\ln(G) = 0.04 + 0.38\ln(H)$	23.33	0.33	<0.001
White spruce	50	$\ln(G) = 0.04 + 0.36\ln(H)$	19.27	0..27	<0.001
Trembling aspen	39	$\ln(G) = 3.47 - 0.001(H)$	0.54	0.0	0.465
White birch	14	$\ln(G) = 3.10 + 0.001(H)$	0.12	0.0	0.734

Discussion

Recruitment patterns of juvenile trees

The similar result of stem density of juvenile species among gap and understorey environments indicates that gap environments in this region of Ontario have little effect on the establishment of tree recruitment (Fig. 3.2). Data from this study indicate that recruitment occurs in understorey and gap environments alike. This means that juveniles of all species can be present in the understorey prior to gap formation.

Establishment of shade tolerant juvenile trees prior to gap formation commonly occurs in the understorey of boreal forests (Kneeshaw and Bergeron, 1999). However, this pattern is not likely for shade intolerant species such as trembling aspen and white birch (Burns and Honkala, 1990b). Shade intolerant species are expected to colonize following gap creation, when light levels and ground temperature increase (Frey *et al.*, 2003). Data from this study suggest that trembling aspen shoots can occur prior to gap creation; the majority of which are less than 0.5 m (Fig. 3.2). The development of trembling aspen root suckers is associated with many factors including mortality of mature aspen stems (Frey *et al.*, 2003). During the canopy transition stage, when mortality of mature aspen stems is high, this phenomenon should be common. However, as trembling aspen sucker production occurs primarily from the root system of senescing stems, it is less likely that juveniles will be found in the gap created by the dead parental stem (Homma *et al.*, 2003). Concurrent mortality of adjacent stems could create favourable conditions for further development of trembling aspen root suckers. The small proportion of stems taller than 2 m in gap and understorey environments suggests that the majority of trembling aspen juveniles die before reaching this height (Fig. 3.2); similar establishment patterns were reported for *Populus tremula* in an east Asian boreal forest in Kamchatka (Homma *et al.*, 2003). Evidence from this study suggests that as trembling aspen stems approach a height of 2 m in gaps smaller than approximately 350 m^2 physiological thresholds that limit vertical growth may be met. As shade increases, it might be the inability of trembling aspen stems taller than 2 m to maintain a positive carbon balance that limits their ability to exploit gap environments (Messier *et al.* 1999). Mortality may decrease as gaps become larger over time, as the "maximum sustainable height of surviving understorey" recruitment should increase (Messier *et al.*, 1999). If establishment of juvenile trees, even shade intolerant species is not limited by gap size, factors that negatively affect growth must be responsible for the characteristic pattern of shade tolerant dominance following the break-up of the initial post-fire cohort. Herbivory, disease, and competition are just a few antagonistic factors that can potentially limit the development of established recruitment and should receive attention in future studies concerning the North American boreal forest (Suominen *et al.*, 1999).

Herbivory and disease can be important factors that limit the presence of particular types of tree recruitment, especially trembling aspen. In a Swedish deciduous and pine mixedwood forest, moose browsing played a major role in limiting deciduous species (Suominen *et al.*, 1999). In this study, a higher number of trembling aspen stems were affected by herbivory or a fungal pathogen that causes shoot blight (suspected *Venturia macularis* (Fr.:Fr.) Mull. & Arx) (personal observation). Although the suspected herbivore was unknown, many mammals browse the succulent shoots of young hardwood species. In the future, the effect of herbivory and pathogenic fungi on gap and understorey regeneration must be investigated. This could be executed by designing a study similar to this one but including exclosure and fungicide treatments in gap and understorey environments.

The negative relationship between tree recruitment density and height class in gap and understorey environments suggests a continuous colonization of young seedlings or sprouts (Fig. 3.2). High reproductive input (high seed or sprout production) and relatively high non-random mortality associated with establishment of seedlings and sprouts on unfavourable microsites could explain the negative height class pattern. This pattern of colonization is probably associated with numerous waves of recruitment from the various parent trees in the stand and is similar to patterns that are expected during uneven-aged, oldgrowth stages of forest development (Oliver and Larson, 1990). This indicates that structural characteristics associated with old-growth forest begin to occur during the canopy transition stage for this forest type. The development of such stages is usually regarded as a process occurring in self-perpetuating conifer dominated forests. The observed pattern in height class structure of juvenile trees during the canopy transition stage shows that monospecific, even-aged stands will rapidly develop into uneven aged mixedwoods as the initial post-fire cohort of trembling aspen senesce.

Growth of juvenile trees

Among the juvenile tree species, trembling aspen and white birch have the highest initial growth rate. This suggests that when present with other juvenile species at similar height, trembling aspen should be the first to fill a canopy gap (Fig. 3.3). However the low number of individuals taller than 2 m suggests that trembling aspen juveniles either cannot grow much taller than this in the understorey and gap environments studied or they are recruited relatively recently and have not had a chance to grow to such heights (Fig. 3.2).

Differences in growth rates of individual species among gap and understorey environments indicates that light conditions had little impact on the initial growth of shade intolerant species and the continued growth of shade tolerant species (Table 3.3, Fig. 3.3). Although gaps receive more incident sunlight than understorey environments (Canham *et al.*, 1990), the minimum threshold of photosynthetically active radiation for all juvenile trees seems to be met. Root suckers of trembling aspen showed rapid growth during their initial years, possibly related to the established root system of parent trees (Frey *et al.*, 2003). It is possible that as stems reach 2 m and taller, individual leaf area becomes more important for producing photosynthate and continued growth (Messier *et al.*, 1999). If gaps are not large enough, the leaf area to biomass ratio of trembling aspen stems will remain small, and trees will soon die. The ability of asexual reproduction via root suckers by trembling aspen has presumably evolved to take advantage of canopy openings as mature stems die; this has been established as highly adaptive when large-scale disturbance occurs (Frey *et al.*, 2003). Reproduction via root suckers may not be adaptive if factors such as a well-established understorey or an abundance of advance regeneration of other tree species are not affected by the disturbance.

Data from this study suggest that even shade intolerant species will invest in understorey recruitment during the canopy transition stage of forest development. Compared with shade tolerant species, the window of opportunity for successful growth of shade intolerant individuals into the canopy is limited. Shade intolerant stems could offset the ability of suppressed growth for long periods of time by continued sprout production until favourable conditions are met. Homma *et al.* (2003) observed numerous dead root suckers of *P. tremula* at the base of newly formed sprouts. Creation of large gaps may facilitate the establishment and survivorship of shade intolerant recruitment. However, if the limiting effects of herbivory and/or fungal infection on juvenile tree outweigh the positive effects of gap creation, local extinction of shade intolerant demographic may be the norm.

Alternatively, root collar sprouting by white birch may offer a different solution to maintenance in future forests stands. White birch is typically referred to as a pioneer species, owing to its shade intolerant nature (Burns and Honkala, 1990). However, it can have an important presence in forest stands that have not undergone large-scale disturbance in over a century (Chapter 1). A possible explanation for this is that white birch tends to be longer lived than trembling aspen (Burns and Honkala, 1990). However, establishment and survivorship of root collar sprouts may provide an alternative mechanism. This sprouting strategy is different from predominantly root suckering of trembling aspen. For understanding the long-term dynamics of these two shade intolerant species, this subtlety may be very important. White birch's sprouting strategy may be more adaptive than trembling aspen when gap creation becomes the dominant type of disturbance, considering the canopy gap created by death of the parent stem will be directly overhead. Compared to trembling aspen, there is no need for coinciding mortality of adjacent canopy stems to create a favourable light environment for the establishment of birch sprouts. Also, production of sprouts by white birch occurs while the parent stem is still alive (personal observation). During the canopy transition stage, when a mature stem dies, there will be little competition for the light and space in the canopy gap from adjacent tree crowns. The combination of advanced sprout production with little lateral growth of adjacent tree crowns could facilitate the recruitment of white birch sprouts into the forest canopy.

Similar growth of balsam fir among gap and understorey environments is the result of its high shade tolerance. The light environment among the gap and understorey environments must be above the minimum PAR threshold for growth. A similar growth pattern termed "through-growth" has been observed for *Pseudotsuga menziesii* in the west coast of North America (Hunter and Barbour, 2001). During the canopy transition stage, the similar growth of balsam fir recruitment in gap and understorey environments suggests that sufficient PAR is transmitted through the trembling aspen canopy. This pattern also might be related to seasonal pattern in light attenuation in trembling apsen forests; canopy trees attenuate less light during early and late season leaf-off periods (Constabel and Lieffers, 1996). Shade tolerant conifer species can achieve an important part of their carbon budget by taking advantage of high understorey light levels during this period (Constabel and Lieffers 1996; Waring and Franklin, 1979). Therefore, growth of shade tolerant species will remain similar, regardless of canopy coverage during the summer months.

Competitive interactions between shade tolerant and intolerant recruitment prior to gap formation may play an important role in limiting shade intolerant recruitment. This is probably more important for species such as trembling aspen that regenerate via root suckers. Species that produce sprouts via the root collar (e.g. white birch) may be less affected by competition from shade tolerant advanced regeneration, as the parent stem occupies the future clone's space (Greene *et al.*, 1999). As growth rate is an increasing function of height for shade tolerant species, taller shade tolerant individuals will offer greater competition for light than smaller shade intolerant species (Fig. 3.3). Alternatively, if shade tolerant and intolerant species colonize and establish in a gap at the same time, shade intolerant species would be at an advantage as their initial growth rate is much higher. However, this does not necessarily mean that shade tolerant species will be outcompeted, it simply suggests that succession to a shade tolerant conifer dominated forest will be delayed.

Conclusions

The general pattern that emerges from this study is that canopy gaps less than 350 m^2 do not play a critical role in recruitment dynamics of juvenile tree species. Establishment is similar regardless of position in the understorey, even for shade intolerant species such as trembling aspen. This is contradictory to what is expected based on its life history as a shade intolerant species; gaps should promote increased density of shade intolerant species as a result of factors such as increased light levels. Growth of all species was also similar regardless of location in a canopy gap or in the understorey environment. Hypothetically, if shade tolerant and intolerant species recruited into canopy gaps at the same time, coexistence of these functional types would occur. However, as shade tolerant species tend to establish much earlier and attain greater heights than shade intolerant tree species, succession will be towards shade tolerant conifer dominated forests.

As canopy gaps did not influence recruitment patterns of juvenile tree species in this study it suggests that other factors should be explored. Anecdotal evidence suggests that the role of herbivory and fungal pathogens should be investigated. Also, factors that influence the early establishment of shade tolerant conifers should be examined since results of this study indicate that it is an important mechanism that allows shade tolerant conifers to compete with faster-growing shade intolerant hardwoods.

Chapter 4

Plant community response to small-scale disturbances in trembling aspen dominated boreal forests in northeastern Ontario.

Abstract

The role that canopy gap environments play in structuring plant communities that are composed of non-commercial species such as shrubs and herbs is rarely studied, particularly in the boreal forest. Knowledge of understorey plant response to canopy gaps created by small-scale disturbance is necessary for sustainable forest management. This study compares the effect of gap size and age on community structure of vascular plants found in the understorey of trembling aspen dominated forests between 95 –120 years since fire in northeast Ontario. Gap age and size were treated as separate factors to test if gaps influenced species richness and ecological distance from understorey control plots in five trembling aspen forests. Five vegetation groups were sampled including herbaceous plants and shrubs belonging to height classes 0 – 0.5, 0.5 – 2, 2 – 5, and 5 – 10 m. The most noticeable impact of canopy gaps on vegetation was for the medium sized shrubs (2 – 5 m). Gaps supported higher than average richness of these shrubs, and they were most different from the control understorey plots with respect to species abundance. Herbaceous species showed the least response to canopy gaps, however this does not mean that gaps do not have an important effect on composition.

Introduction

Gap disturbance is usually studied with respect to its effect on the establishment and growth of juvenile tree species (Kneeshaw and Bergeron, 1999; Coates *et al.*, 2002). In the preceding chapters I presented data showing that canopy gaps have a negligible effect on juvenile tree recruitment patterns, although they are a common feature of trembling aspen forests. From an ecosystem perspective, it is important to characterize the effect of gap creating disturbance on plant communities, not just individual tree species. One method for studying such effects at the community level is by determining community stability.

Stability of a plant community can indicate that species populations that make up a plant community are functioning well (Tilman *et al.*, 1996). Typically the resistance and resilience of the populations that make up a community quantify stability. Resistance describes the ability of species populations within a community to maintain their relative abundance levels when a disturbance occurs, whereas resilience describes their ability to return to pre-disturbance abundance levels (see ball and cup heuristic in Gunderson, 2000). Obviously disturbance intensity has a dramatic effect on community resistance and resilience; for example if a catastrophic disturbance occurs, plant communities would likely have little resistance, and it could take years to recuperate. Therefore, when disturbance intensity is high, quantifying community stability is better described by its resilience. On the other end of the disturbance gradient, when disturbances have a relatively low intensity, community stability should first be described in terms of its resistance (i.e. how different the post disturbance community is from a pre-disturbance reference) and if change occurs, resilience can then be described.

One objective of sustainable forest management is the maintenance of biodiversity. If silviculture prescriptions operate outside the resistance and resilience thresholds of forest communities, the natural organization of species within a community will be jeopardized and the maintenance of appropriate biodiversity may not be achieved. To mitigate the negative impacts of forest management, one recognized solution is to emulate natural disturbances. The emphasis of fire as the major factor to influence vegetation patterns in the boreal forest has resulted in clear-cutting as the predominant form of forest management in Ontario (Bergeron *et al.*, 1998). Recent research suggests that diversification of silviculture practices that emulate a variety of natural disturbances is a more favourable management practice to accommodate biodiversity concerns than clear-cutting alone (Harvey *et al.*, 2002). One suggestion is the use of partial cutting to promote mixedwood forests. As partial cutting mimics small-scale disturbances such as individual or small-group tree mortality, these types of disturbances and their impact on understorey environments under natural conditions should be studied. Such studies will provide a baseline comparison for forest harvesting practices that intend to emulate natural disturbances (Lahde *et al.*, 1999).

Similar to their woody counterparts, changes in herbaceous plants over time are thought to follow predictable successional trajectories. DeGrandpre *et al.* (1993) found that changes in understorey species dominance (using a boreal forest chronosequence) was important, but the majority of species remained similar after a stand age of 26 years. Species such as *Aster macrophyllus*, *Aralia nudicaulis*, *Acer spicatum*, and *Corylus cornuta* dominated during early stages (26-74 years following disturbance) of forest development, whereas species such as *Taxus canadensis* and *Acer spicatum* dominated during intermediate stages (120 years following disturbance). During later stages (120 – 230 years following disturbance) they observed a resurgence of early successional species followed again by the dominance of *T. canadensis*. They concluded that succession of the understorey plant community of boreal forests in the northwest region of Quebec is predictable when considering the life history characteristics of establishment ability, longevity, and shade tolerance of individual plant species.

As individual species life history characteristics differ, their respective response to disturbance should dictate community change following disturbance. The degree of change and time to recovery (resistance and resilience) of a community should reflect the overall ability of a community to handle a disturbance event. If human-induced disturbances result in little change to community structure, it suggests that ecosystem integrity has not been compromised, and the system can continue to function as it would under natural conditions. Ultimately, this should be an important objective of land management practices considering preserving biodiversity and ecosystem function are important mandates of sustainable forest management. Testing the effect of naturally occurring small-scale disturbances, such as individual or small-group tree mortality, on vegetation in understorey environments will help determine thresholds of community resistance, and variation in community response if the threshold of resistance is contravened.

The effect that small-scale disturbance creating individual and small-group tree mortality have on understorey herbaceous and woody plant species was studied in five trembling aspen dominated boreal forests of northeastern Ontario. The disturbance component was characterized as low intensity, therefore I focus on the resistance, and not the resilience, of vascular plants in understorey and gap environments. The objective was to determine how small-scale disturbances creating canopy gaps impact vascular plant communities in understorey environments of trembling aspen forests. I infer the implications of emulating such disturbance when managing a forest for commercial interest.

Methods

Stand selection

The same five trembling aspen dominated forest stands used in chapter 3 were used to collect data for the effect of canopy gaps on vegetation patterns of the herbaceous and woody plant communities in understorey environments. Stand age ranged between 95 and 120 years since fire. Other important canopy species included white birch, balsam fir, black spruce, white spruce, balsam fir, and jack pine.

Vegetation richness and abundance

The same canopy gaps and paired understorey quadrats used in chapter 3 were used in this study. In each forest stand, four gaps and one nested understorey plot were used to sample the percent cover of all species. To be consistent with the methods in the previous chapter, the expanded gap area was used to collect vegetation cover data. All the gaps were less than 350 m^2 and they were grouped based on their age (less than and greater than 5 years since creation). The paired understorey quadrats consisted of 8 adjacent quadrats that began at 1.56 m^2 and were systematically doubled until a final quadrat of 400 m^2 was created. A species-area curve was developed for the understorey condition and was subsequently compared to the richness of gap environments. To determine the vertical impacts of gap creation on species richness, vegetation was grouped into five layers based on vertical stratification. The vegetation layers were herbaceous and shrub height classes between 0-0.5, 0.5-2, 2-5, and 5-10 m.

Data analysis

Species diversity and cover

Species diversity of each environment and vegetation layer were summarized using measures of alpha, gamma, and beta diversity. Alpha diversity was calculated as the average (N = 5) of species richness in each environment, gamma diversity was calculated by the sum of species present in each environment, and beta diversity was calculated by dividing gamma diversity by alpha diversity, minus 1. Beta diversity in this case measures the variability of species present in each environment sample, where no difference in samples would yield a beta diversity of 0 (McCune and Grace, 2002). Gamma diversity measured in this study refers to a sample of what is traditionally considered gamma diversity, i.e. it is not the total community pool of woody and herbaceous species found for northeastern Ontario. Species richness and area were both log transformed (natural logarithm) to determine the linear species-area relationship of the understorey environment. This relationship was then used to calculate the expected species richness and 95% confidence interval for gap environments. Richness was considered significant if observed richness values were above or below the 95% confidence interval for individual gap areas. Total relative cover for each layer was summed and then compared using Kruskal-Wallis tests among different gap and understorey environments.

Community structure

Multiple Response Permutation Procedures (MRPP) was used to test the hypothesis of no difference in vegetation composition and abundance for each layer among understorey environment groups (Zimmerman *et al.*, 1985). Similarly the MRPP was also used to test the hypothesis of no difference among forest study areas. These tests only give general patterns in community structure as area differences in gap and the understorey environment exist.

Overall species abundances of gap and understorey environments were summarized using Nonmetric Multidimensional Scaling (NMS). This method of ordination uses iterative rank differences to reduce complex multivariate data sets. The iterative randomization of sample sites in lower dimensional species space attempts to maintain the original rank of reduced distances and original distances (described by the term stress), preserving biologically important relationships among sample sites (Clarke, 1993). The "slow and thorough" autopilot selection was chosen in the NMS ordination selection using the PC Ord v. 4.0 software package (McCune and Mefford, 1999). This autopilot selection uses the default setting of 400 maximum iterations, has an instability criterion of 1.0×10^{-5}, steps down from 6 ordination axes to 1, uses 40 real runs, and 50 randomization runs. As stress was not significantly reduced with ordination solutions that were higher than 3 dimensions, the ordination algorithm suggested that the sample forests be represented by a 3 dimensional solution. However, only the first two axes are provided since they explained most of the variation. Species samples were standardized using the arcsine squareroot function and all ordinations were run using the Sorenson distance measure. Although NMS is a non-parametric ordination technique, standardization of sample data does impact the calculations for species distance measures (McCune and Grace, 2002). The 400 m^2 understorey quadrat sample was used to represent the composition and relative abundance for all understorey environment.

City block distance measures were used to examine the effect of gap creation on differences between gap environments and paired understorey quadrats (McCune and Grace, 2002) as follows:

$$D_T = \sum_{i=1}^{N} |g_i - u_i| \qquad (1)$$

Where D_T is the ecological distance of gaps from the understorey quadrat, g_i is the cover of species *i* in a respective gap, and u_i is the cover of the same species in paired understorey quadrat. The distance measure is a simple way of quantifying similarity among gap and understorey environments. For a given plant species, if gap and understorey abundances are the same, then their difference will be zero. D_T will increase as the absolute differences in species abundances increase between gap and understorey environments. Consistently larger distances will indicate that gap environments have an effect on community structure. Distance measures for the whole plant community and only for those species that were present in both the understorey and respective gap environment were included. The latter approach was included since it removes species differences that are the result of within stand variation in species presence (beta diversity). By using this approach, it was assumed that any difference in species abundance is the result of the environmental conditions created by the canopy gap. The hypotheses of no difference in average distance index among different gap environments for each vegetation layer were tested using Kruskal-Wallis tests.

Indicator species analysis

Indicator species analysis was used to determine if any species showed significant fidelity to the different gap and understorey environments. Indicator species analysis is a simple method that combines species relative abundance and frequency within groups of interest and then compares the observed indicator values to those expected by chance (see Dufrene and Legendre, 1997).

Results

Species diversity and richness

Herbaceous species richness was consistently higher than richness in any of the shrub layers (alpha and gamma diversity were higher for the lower vegetation strata for all environments, Table 4.1). Beta diversity was relatively similar for all vegetation layers and environments, ranging from 0.8 – 2.8 (Table 4.1). Regression models reveal that all vegetation layers have significant richness and area relationships (Table 4.2, Fig. 4.1). Richness of herbaceous species and shrubs with height 5-10 m were generally less than expected from understorey environments (Table 4.3, Fig. 4.1). For herbaceous species, only small young gaps tended to have observed richness higher than the expected richness. Almost all gaps had lower or no difference in expected richness of 5-10 m high shrubs. Richness of shrubs between 0-5 m height benefited the most from canopy openings. Of gaps in this group, approximately 77% had similar or higher than expected richness. Overall, shrubs 2-5 m in both young and old small gaps and large old gaps tended to have higher than expected richness (Table 4.3). Richness of shrubs 0.5-2 m in height tended to be higher than expected in young and old large gaps (Table 4.3). Richness of shrubs between heights of 0-0.5 m tended to be higher than expected in small and large old gaps (Table 4.3).

Table 4.1. Summary of alpha, beta, and gamma diversity for species present in five vertically stratified layers of different gap and understorey environments in trembling aspen dominated forests in northeastern Ontario.

Gap type (N =5)	Diversity	Woody species height class (m)				Herbaceous species
		5-10	2-5	0.5-2	0-0.5	
Small young	alpha	1.4	3.2	6.8	8.8	16.8
	beta	1.9	1.8	1.6	1.8	1.3
	gamma	4	9	18	25	39
Small old	alpha	0.8	3.2	7.0	10.2	15.4
	beta	2.8	1.5	1.4	1.5	1.3
	gamma	3	8	17	25	36
Large young	alpha	0.6	5.0	9.4	12.0	18.2
	beta	2.3	1.4	1.1	1.2	1.0
	gamma	2	12	20	26	37
Large old	alpha	0.8	5.0	9.2	11.8	18.0
	beta	1.5	1.2	1.2	1.3	0.9
	gamma	2	11	20	27	35
Understorey	alpha	2.8	4.4	10.0	11.2	20.4
	beta	0.8	2.0	1.3	1.1	1.2
	gamma	5	13	23	23	44

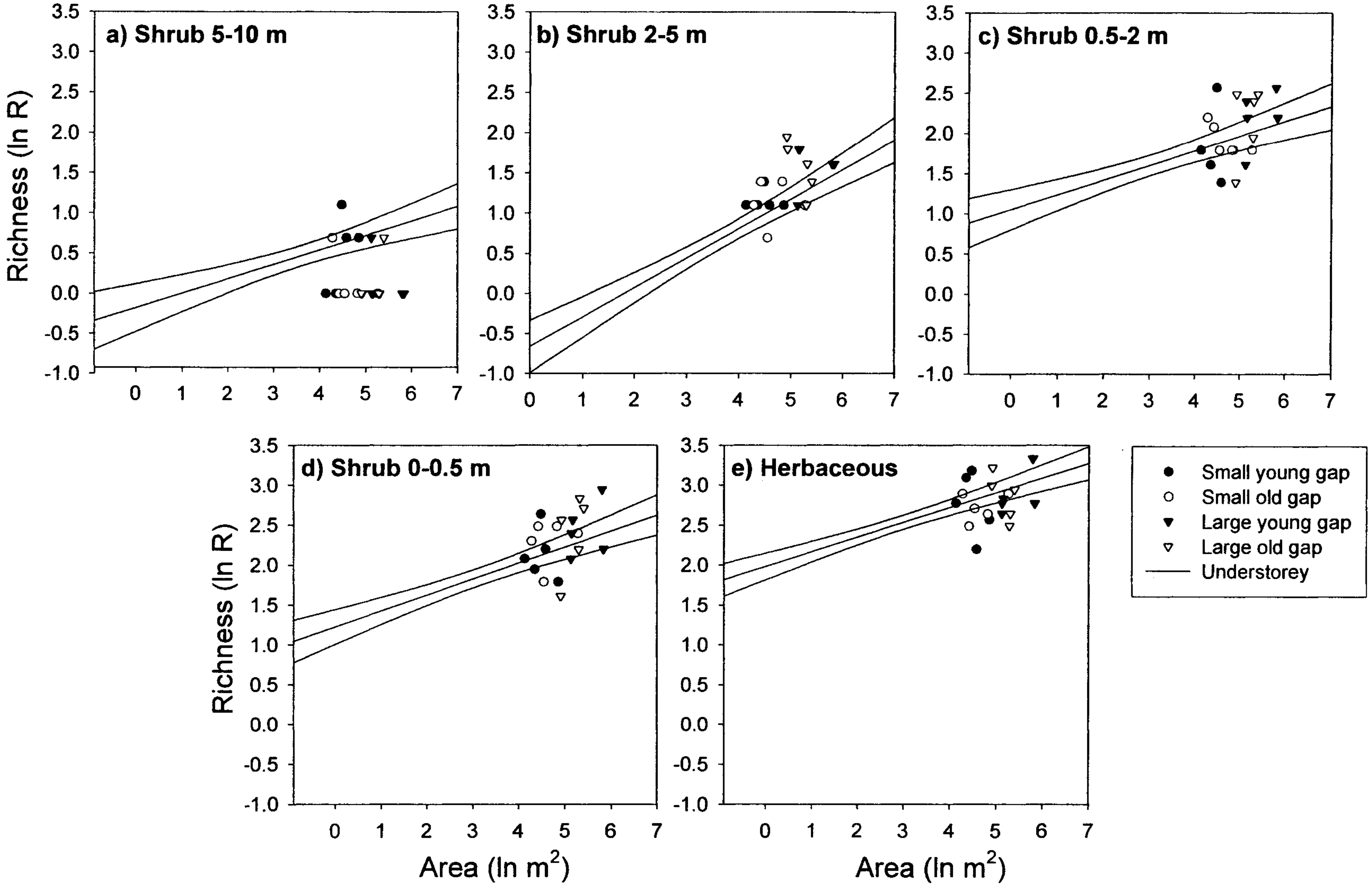

Figure 4.1 Regressions show expected richness (mean and 95% confidence interval of the five study stands) and symbols show observed richness of woody and herbaceous species data collected from canopy gaps that were sampled in trembling aspen dominated boreal forests in northeast Ontario.

Table 4.2. Species-area relationship for herbaceous and shrub layers in the understorey and gap environments of trembling aspen dominated forests in northeastern Ontario.

Layer description	N	Expected richness	R^2	F statistic	p
Herbaceous	44	$\ln(R) = 1.98 + 0.18\ln(A)$	0.59	61.20	<0.001
Shrub (0-0.5m)	48	$\ln(R) = 1.22 + 0.20\ln(A)$	0.50	45.57	<0.001
Shrub (0.5-2m)	48	$\ln(R) = 1.05 + 0.18\ln(A)$	0.39	28.94	<0.001
Shrub (2-5m)	38	$\ln(R) = -0.66 + 0.37\ln(A)$	0.70	85.76	<0.001
Shrub (5-10m)	40	$\ln(R) = -0.18 + 0.18\ln(A)$	0.38	23.49	<0.001

Note: R is expected mean species richness calculated from the measured richness from nested understorey quadrats of various areas (A) in the five study stands.

Table 4.3 Comparison of observed species richness in gap environments with expected (understorey estimates) mean and 95% confidence intervals. Expected values and confidence intervals were calculated from species richness samples in nested understorey quadrats (see Table 4.2).

Layer Description	Gap type	Mean Richness		95% Confidence intervals		
		Greater	Lower	Greater	No difference	Lower
Herbaceous	sy	3	2	2	1	2
	so	1	4	1	1	3
	ly	1	4	1	0	4
	lo	3	2	2	1	2
Shrub (0-0.5 m)	sy	3	2	1	2	2
	so	4	1	3	1	1
	ly	3	2	2	1	2
	lo	3	2	3	1	1
Shrub (0.5-2 m)	sy	1	4	1	2	2
	so	2	3	2	2	1
	ly	4	1	3	1	1
	lo	3	2	3	1	1
Shrub (2-5 m)	sy	4	1	3	2	0
	so	3	2	3	0	2
	ly	4	1	2	3	0
	lo	4	0	3	1	1
Shrub (5-10 m)	sy	2	3	1	2	2
	so	1	4	0	1	4
	ly	0	5	0	1	4
	lo	0	5	0	1	4

Table 4.4 MRPP results for congruence of understorey vegetation into i) gap type and understorey groups and ii) forest study areas.

	Observed δ	δ under null hypothesis			T	p	A
		Expected	Variance	Skewness			
Environment type	0.579	0.500	0.0078	-0.496	2.830	0.999	-0.159
Forest study area	0.272	0.500	0.0078	-0.496	-8.153	<0.001	0.456

Community Assembly

Patterns in community assembly for all layers showed no significant difference among gap and understorey environments. Results from the two MRPP analyses indicate that variance in gap types was too high to support accurate grouping. However, forest stand groups were much better predictors of species assembly (Table 4.4). The NMS ordination confirms the high among stand variation, making it difficult to group gap types by species composition (Fig. 4.2). This result justifies the distance measures used, as they represent the average within stand differences caused by gap size. The distance measures however, were not significantly different among gap environments (Kruskal Wallis tests, Table 4.5). For total species gap effect distance, herbs tended to have the highest distance index and shrubs between the heights of 5-10 m had the lowest distance (Table 4.5). However, the average distance when only species found in both gap and understorey were included shows that shrubs between 2-5 m height had the highest distance from understorey environments, and shrubs 0-0.5 m and herbaceous species had the lowest distance. This is consistent with the higher than expected observed species richness results for shrubs between 0-0.5 m.

Indicator species

Only one species was determined to be a significant indicator and two species potential indicators of gap environments (Table 4.6). White spruce between 0.5 and 2 m in height is a significant indicator of large old gaps ($p = 0.032$). Choke cherry (*Prunus virginiana*) between 2 and 5 m height is a potential indicator in small young gaps and black spruce between 5 and 10 m height is a potential indicator for understorey conditions. No herbaceous or woody species between 0.5-2 m height were found to be statistically significant indicators for the different gap and understorey environments.

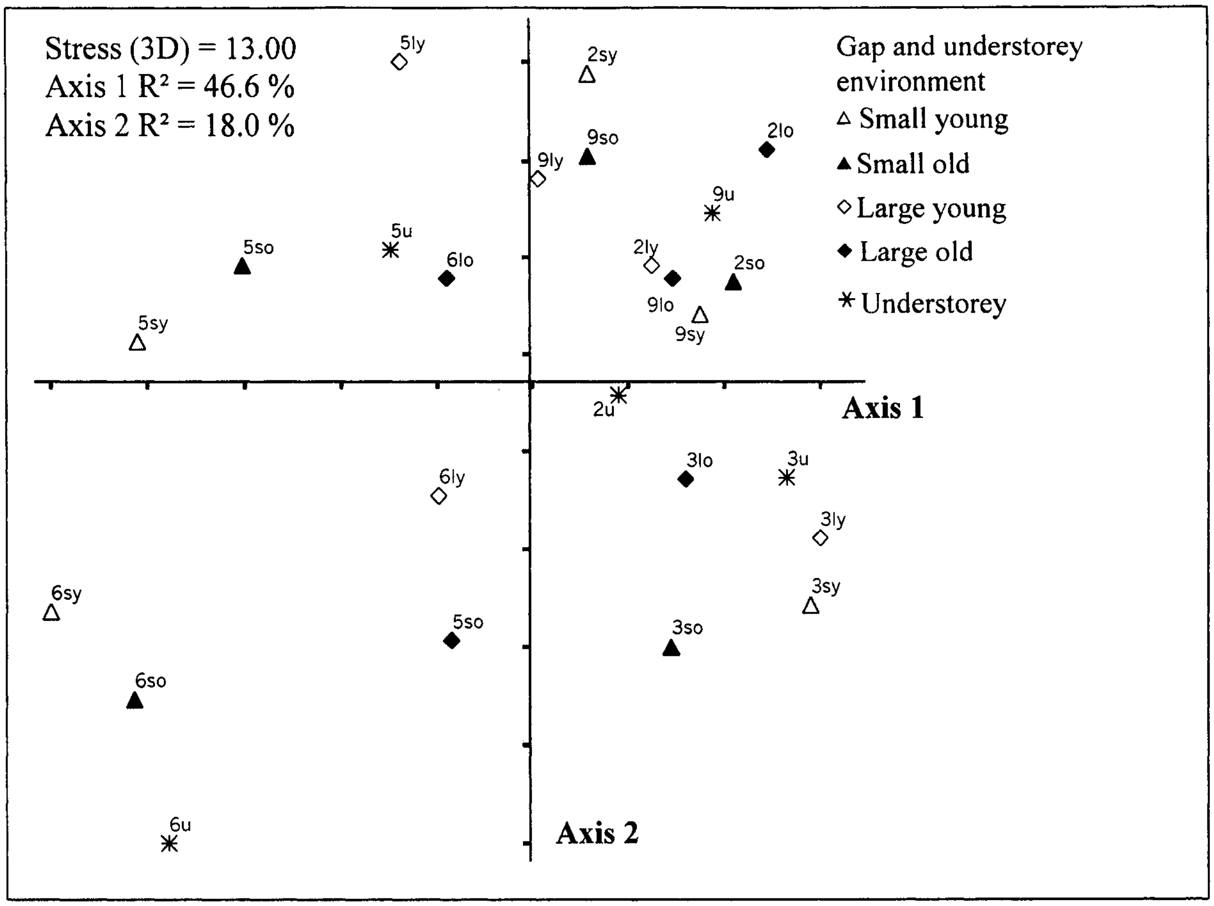

Figure 4.2 First 2 axes of 3-dimensional nonmetric multidimensional scaling of understorey species composition in all vertical layers (herbaceous to woody species 10 m tall) of gap and understorey environments in trembling aspen dominated boreal forests in northeastern Ontario.

Table 4.5 Total distance and average distance per species between gap and understorey environments when species were present in both gap and understorey environments. Values are mean (N = 5) and standard error in parentheses.

Distance Type	Gap type	Vegetation layer				
		Herbaceous	Shrub			
			0-0.5 m	0.5-2 m	2-5 m	5-10 m
Total species	sy	52.79 (21.74)	18.46 (4.61)	34.33 (6.11)	25.4 (6.21)	7.78 (3.49)
	so	42.79 (9.59)	11.85 (5.15)	36.56 (4.56)	28.19 (14.32)	0.80 (0.58)
	ly	90.79 (28.48)	14.13 (10.70)	35.32 (8.83)	27.38 (6.51)	6.40 (6.40)
	lo	78.16 (30.16)	17.26 (9.69)	36.34 (8.30)	34.59 (9.00)	4.40 (3.30)
Per species	sy	3.26 (1.70)	3.35 (1.72)	8.25 (3.42)	16.40 (13.05)	6.48 (1.32)
	so	4.03 (1.39)	1.20 (0.41)	7.49 (2.78)	9.93 (10.45)	0.85 (0.44)
	ly	5.84 (5.06)	0.44 (0.20)	3.78 (0.23)	13.75 (7.39)	8.00 (8.00)
	lo	2.12 (0.64)	3.44 (2.64)	5.60 (2.61)	15.33 (8.80)	6.75 (1.75)
Kruskal-Wallis tests	χ^2	1.606	4.166	0.349	1.050	3.681
	df	3	3	3	3	3
	p	0.658	0.249	0.951	0.789	0.298

Note: sy = small young, so = small old, ly = large young, and lo = large old.

Table 4.6 Indicator and potential indicator species for different vegetation layers and gap types in trembling aspen dominated boreal forests located in northeastern Ontario.

Layer Description	Species	Gap Type	% Relative Abundance	Relative frequency (%)	Indicator value	p
Herbaceous	none	-	-	-	-	-
Shrub (0-0.5 m)	White spruce	lo	72	80	58	0.032
Shrub (0.5-2 m)	none	-	-	-	-	-
Shrub (2-5 m)	Choke cherry	sy	83	60	50	0.060
Shrub (5-10 m)	Black spruce	u	67	60	40	0.078

Discussion

Species richness

Overall, large old gaps had the most impact on understorey species richness. In these gaps, shrub species between 0-5 m were consistently higher in richness than expected from the closed canopy understorey. Small young gaps had the least effect on understorey species richness, only shrubs between 2-5 m were higher than expected, the remaining layers tended to be no different than expected from the understorey environment. Small old and large young gaps had negative or no impact on species richness. In these gaps, only shrubs 0.5-2 m in height were higher than expected richness. Richness of herbaceous and shrubs between 2-10 m height was lower than expected and richness of shrubs between 0-0.5 and 2-5 m tended not to be impacted. These patterns suggest that the formation of canopy gaps only benefits the richness of shrub species, particularly between 0-5 m height, and this is most important in larger, older gaps. Large old gaps possibly offer more time, space, and environmental heterogeneity to allow more chance of species establishment, thus increasing the ability of species to coexist compared to similar areas in understorey environments.

The lack of any positive or negative effects of small young gaps on species richness of most layers suggests that environmental impacts are negligible in the short-term. However, there may be some long-term negative impact of increasing shrub species on herbaceous plants. The less than expected richness of woody species taller than 5 m is a more difficult pattern to explain. As plants found in this layer were all tree species, gap environments should be expected to provide a favourable environment for their establishment and growth (however see results in chapter 3). The data suggest that gaps have an overall negative impact on richness of tree species between 5-10 m height. This result could be driven by distribution bias or sampling bias. Sample areas and time may have been insufficient for detecting a gap effect on tree regeneration between 5-10 m. Using up to a 400 m^2 sample area in the understorey environment may have increased the potential for sampling tree species between 5-10 m height. Even having 1 or 2 individuals sampled in an understorey quadrat would increase the expected values calculated using the regression relationship. Therefore, the size of the gap areas sampled may simply have not been large enough to have a higher probability of encountering species of this height class. If this is the case, then one could hypothesize that gaps will have to be larger than approximately 400 m^2 to consistently have a direct impact on regeneration of tall woody species. Also, since old gaps were less than 10 years since formation, this time frame may not be sufficient for tree regeneration to reach 5-10 m height. Although this is unlikely for shade intolerant species such as trembling aspen and white birch, both of which can grow rapidly under favourable conditions. Presumably as gaps age, tree species should be able to reach such heights if environmental conditions are favourable. If trees take longer than 10 years to reach such heights, then time lags in detectable response will play an important role in empirical predictions of forest change.

Community composition

The non-significant difference of community composition and lack of significant indicator species among gap and understorey environments suggest that the death of individual and small groups of trees has little impact on the species composition of understorey environment in trembling aspen dominated forests. Although DeGrandpre and Bergeron (1997) show that canopy gaps can facilitate changes in species composition and dominance in other boreal forest types, the data from this study indicate that understorey communities are relatively resistant to the disturbance created by gaps smaller than 350 m^2. Since the dominant species in trembling aspen understorey communities tend to be shade intolerant, canopy gaps will have a minimal impact on compositional change (DeGrandpre and Bergeron, 1997). Also, the analysis used in this study focused only on species that were present in both the respective gap and paired understorey quadrat. We assumed the presence of species in one and not the other was the result of within forest stand beta diversity, however colonization or species exclusion could have occurred during the development of the gaps studied and may change the conclusions of these results. The only way to monitor these effects would involve using a time series experiment using permanent plots, which was not within the scope of this study.

The higher total distance values associated with herbaceous layer are the result of a higher number of species combinations present in gap and understorey environment. Therefore, the average species distance is a better representation of gap effects on vegetation layer. The results do suggest that gaps have different effects on taller vegetation, as shrubs of heights between 5-10 m had the highest average distance from the understorey plots, and small vegetation (herbaceous and shrubs 0-0.5 m height) had the lowest average distance (Table 4.5). This could be related to vertical light interception. Shrubs that are present in higher understorey layers will be the first to compete for light. Smaller shrubs and herbaceous species would only receive a small amount of incident light from the creation of a canopy gap; therefore, individual effects of gap creation on vegetation close to the ground will be negligible.

Conclusions

The results of this study suggest that if selective harvesting of trembling aspen is a management objective and the act of harvesting does emulate the natural occurrence of a small-scale disturbance, understorey plant communities should be relatively resistant and resilient. We suspect that applying this type of management, will not only protect the advanced regeneration of future canopy trees, but will also maintain shrub and herbaceous species that provide important habitat and food for much of the faunal communities in trembling aspen dominated boreal forests. However, since partial or selective harvesting will remove gap maker biomass, nutrient cycling in anthropogenic gaps will be different.

Impacts of canopy disturbances on boreal forest understorey plant communities are rarely studied. We show that under natural conditions, small-scale disturbance has little influence on the community structure of understorey herbaceous and woody plants in trembling aspen dominated forests. The maintenance of understorey community integrity is vital for facilitating the species diversity in oldgrowth forests. We expect that integrating low-impact, small-scale harvesting silvicultural prescriptions in boreal forest management practices, such as those offered by Harvey *et al.* (2002), will facilitate the maintenance plant species diversity and ecosystem function in boreal forests.

General Discussion

This thesis has examined stand dynamics and the role of small-scale disturbance in structuring plant communities in trembling aspen dominated boreal forests. This study provided evidence that forests in northeastern Ontario undergo canopy succession when large-scale disturbance-free intervals are long. The most consistent pattern of succession was the increase in basal area of shade tolerant conifer species following initial dominance of shade intolerant species. Chapters 2,3, and 4 examined the amount of small-scale disturbance that occurs in the study forests, patterns of juvenile tree species recruitment and growth in canopy gap environments, and overall community response to gap creation. This general discussion will reiterate the important findings for each chapter allowing a synthesis of the overall impact of small-scale disturbance as a mechanism of stand development in this region of the boreal forest.

In the absence of large-scale stand replacing disturbance boreal forest environments undergo succession or stand replacement (Lesieur *et al.*, 2002; Bergeron 2000; DeGrandpre *et al.*, 2000; Bergeron and Dubuc, 1989; Carleton and Maycock, 1978). Accepting this fact has implications for sustainable forest management in this region, as the primary forest harvesting practice is clear-cutting. Patterns of forest succession presented in chapter 1 show that forests dominated initially by trembling aspen and jack pine are replaced by shade tolerant conifer species such as balsam fir and black spruce respectively. Similar successional trajectories have been observed in Quebec's forests (Lessier et al., 2002; Bergeron, 2002; DeGrandpre *et al.*, 2000). Although numerous studies including this thesis have compelling evidence to show stand replacement actually occurs in this region of the boreal forest, there exists little information on the underlying mechanisms of this change.

Small-scale disturbance in trembling aspen dominated forests begins to have an impact on canopy structure much earlier in forest development than previously anticipated. Other studies in trembling aspen dominated forests have shown that gap formation as early as 40 years following fire can impact long-term patterns of stand dynamics (Cumming et al., 2000). In chapter 2 the importance of small-scale disturbance in trembling aspen forests in northeast Ontario is shown to increase with time during 60 – 120 years since disturbance. Over 95% of the gaps that were sampled in study forests were less than 350m². The predominant type of structure in gaps was formed by snapped, standing dead, and uprooted gap makers. Only snapped gap makers increased in abundance with time. Infection by pathogenic wood decay fungi was the most important direct or indirect cause of mortality among gap makers. Numerous factors can interact to cause the death of a tree, all of which play an important role in the gap creation process. In the boreal forest numerous studies have focused on the loss of merchantable wood to wood decay fungi, however very few study the ecological impacts of such interactions on the stand development process (McCarthy, 2001). Chapter 2 clearly shows the important influence that wood decay fungi has on tree mortality.

Recruitment patterns (establishment and growth) of juvenile tree species in trembling aspen forests are relatively simple. Balsam fir is by far the most abundant juvenile species found in understorey and gap environment of trembling aspen forests in northeast Ontario. Other important juvenile species include trembling aspen, white spruce, black spruce, and white birch. Subsequent to establishment, intolerant hardwood species such as trembling aspen and white birch tend to have higher growth rates than shade tolerant conifers. However, as stems reach approximately 3 m, growth is similar. Presumably this is the result of vegetative sprouts of hardwood species relying on established root systems of parent trees during early development, which is not the case for seed-regenerating conifer species. It is surprising however, that none of the species showed statistical differences in stem density and growth among gap and understorey environments. Two likely possibilities exist: first, the establishment of all juvenile species could be an ongoing process in the understorey environment, and gap creation is only important in that it creates space for the future canopy stems. The second possibility may be that gap creation is not an important factor that influences growth of shade tolerant conifer species or shade intolerant young hardwoods. However, the small occurrence of hardwood species taller than 2 m suggests that their photosynthetic threshold was met, and large gaps may be necessary to allow them to live. Overall the high recruitment of balsam fir corroborates its importance in canopy stand dynamics that are shown in chapter 1 and other studies (Lesieur et al., 2002, Bergeron, 2000; Bergeron and Dubuc, 1989; Carleton and Maycock, 1978). The very low occurrence and abundance of species such as white cedar suggests that their establishment occurs after 120 years since fire. Establishment of young trembling aspen and white birch suggests that they will occur in forests after the break up of the initial post-disturbance forest. However, the recruitment mechanism is probably different. The basal sprouting characteristics of white birch may be more adaptive than that of trembling aspen when small-scale disturbance becomes the driving force of succession. Trembling aspen is probably relegated to recruitment in gaps or patches that are larger than 350 m^2. It is possible that suitable microsites that are free of herbivores and disease pathogens are also important factors that can influence the establishment and growth of juvenile shade intolerant hardwood species.

There is considerable variability in the understorey community of trembling aspen dominated forests. When small-scale disturbance occurs and gaps are created the majority of change in community composition occurs in shrub species between the height of 2 and 5 m. Among the vegetation layers sampled, richness of shrub species in this layer tended to be higher and their ecological distance most dissimilar. The effect of gap size and age on herbaceous plants was minimal, however this could easily be caused by the high variation in community composition of this layer. Therefore, our statistical power to find differences in this layer is decreased (high chance of type II error). The seemingly high resistance of most vegetation layers to small-scale disturbance suggests that emulating this type of small-scale disturbance by selective harvesting in a management plan is beneficial to conserving the biodiversity of understorey plant communities.

Despite the important and conspicuous occurrence of small-scale disturbance events during the development of trembling aspen forests in northeast Ontario, they have little impact on the understorey plant community structure and dynamics. This has important implications for understanding forest development from the perspective of gap dynamics principles that have been developed in tropical and temperate forest regions. Succinctly, the results of this thesis clearly show that gap dynamics offer little insight into the understanding of long-term canopy dynamics in post-disturbance trembling aspen stands. Factors, such as site type (soil moisture, soil type, and slope), that potentially influence establishment of shade tolerant conifer species during early stages of development may offer a better understanding of conversion of trembling aspen dominated forests to mixedwoods. Also, disturbance dynamics during later stages of development, where mean gap size is expected to increase, may offer more insight into the establishment and growth of shade intolerant species such as trembling aspen and white birch. Future studies should take these suggestions into account when attempting to study the role of small-scale disturbance in boreal forest development.

References

Armstrong, G.W. 1999. A stochastic characterization of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management. Forest Ecology and Management 29: 424-433.

Baldwin, D.J.B., Desloges, J.R., and Band, L.E. 2000. Physical geography of Ontario. *In* Euler, D., Perera, A., and Thompson, I.D. (Eds) Ecology of a Managed Terrestrial Landscape: Patterns and processes of forest landscapes in Ontario. UBC Press, Vancouver, B.C.

Bartemucci, P., Coates, D.K., Harper, K.S., and Wright, E.F. 2002. Gap disturbances in northern old-growth forests of British Columbia, Canada. Journal of Vegetation Science 13: 685-696.

Battles, J.J. and Fahey, T.J. 2000. Gap dynamics following forest decline: a case study of red spruce forests. Ecological Applications 10: 760-744.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal fire regimes. Ecology 72: 1980-1992.

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

Bergeron, Y. and Archambault, S. 1993. Decreasing frequency of forest fires in the southern boreal zone of Quebec and its relation to global warming since the end of the "Little Ice Age". Holocene 3: 255-259.

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

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., and Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: Introduction. Journal of Vegetation Science 9: 464-468.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieus, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Canadian Journal of Forest Research 31: 384-391.

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

Bergeron, Y., Leduc, A., Morin, H., and Joyal, C. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Canadian Journal of Forest Research 25: 1375-1385.

Betchtold, W.A., Mielke, M.E., and Zarnoch, S.T. 2002. Comparison of field methods and models to estimate mean crown diameter. Northern Journal of Applied Forestry 19: 177-182.

Brokaw, N. and Busing, R.T. 2000. Niche versus chance and tree diversity in forest gaps. Trends in Ecology and Evolution 15: 183-188.

Brokaw, N.V.L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66: 682-687.

Brokaw, N.V.L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. Journal of Ecology 75: 9-19.

Burns, R.H. and Honkala, B.H. 1990a. Silvics of North America. Volume I. Conifers. USDA Forest Service. Washington D.C., USA.

Burns, R.H. and Honkala, B.H. 1990b. Silvics of North America. Volume II. Hardwoods. USDA Forest Service . Washington D.C., USA.

Burton, P.J., Kneeshaw, D.D., and Coates, K.D. 1999. Managing forest harvesting to maintain old growth in boreal forests. Forestry Chronicle 75: 623-631.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20: 620-631.

Carleton,T.J. 2000. Vegetation response to the managed forest landscape of central and northern Ontario. *In* Euler, D., Perera, A., and Thompson, I.D. (Eds) Ecology of a Managed Terrestrial Landscape: Patterns and processes of forest landscapes in Ontario. UBC Press, Vancouver, B.C.

Carleton, T.J. and Maycock, P.J. 1978. Dynamics of the boreal forest south of James Bay. Canadian Journal of Botany 56: 1157-1173.

Castello, J.D., Leopold, D.J., and Smallidge, P.J. 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45: 16-24.

Chen, H.Y.H. and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environmental Reviews 10: 137-166.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. Forest Ecology and Management 155: 387-398.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 1304-1310.

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

Constabel, A.J. and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Canadian Journal of Forest Research 26: 1008-1014.

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

De Grandpre, L. and Bergeron, Y. 1997. Diversity and stability of understorey communities following disturbance in the southern boreal forest. Journal of Ecology 85: 777-784.

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

De Grandpre, L., Morrissette, J., and Gauthier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. Journal of Vegetation Science 11: 791-800.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18: 431-451.

Drobyshev, I.V. 1999. Regeneration of Norway spruce in canopy gaps in *Sphagnum-Myrtillus* old-growth forests. Forest Ecology and Management 115: 71-83.

Dufrene, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Dynesius, M. and Jonsson, B.G. 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. Canadian Journal of Forest Research 21: 655-665.

Fensham, R.J. and Fairfax, R.J. 2002. Aerial photography for assessing vegetation change: a review of applications and the relevance of findings for Australia vegetation history. Australian Journal of Botany 50: 415-429.

Foster, B.L. and Tilman, D. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. Plant Ecology 146: 1-10.

Foster, J.R. and Reiners, W.A. 1986. Size distribution and expansion of canopy gaps in northern Appalachian spruce-fir forest. Vegetatio 68: 109-114.

Frey, B.R., Lieffers, V.J., Landhausser, S.M., Comeau, P.G., and Greenway, K.J. 2003. An analysis of sucker regeneration of trembling aspen. Canadian Journal of Forest Research 33: 1169-1179.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M.-J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research 29: 824-839.

Gunderson, L.H. 2000. Ecological resilience: in theory and application. Annual Review of Ecology and Sytematics 31: 425-439.

Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management 155: 369-385.

Heinselman, M.L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. *In* Fire Regimes and Ecosystem Properties. USDA Forest Service, Washington, DC. pp. 7-57.

Hills, G.A. 1959. A ready reference to the description of land of Ontario and its productivity. Preliminary report. Maple, Ontario: Ontario Department of Lands and Forests.

Homma, K., Takahashi, K., Toshihiko, H., Vetrova, V.P., Vyatkina, M.P., and Folorenzev, S. 2003. Regeneration processes of a boreal forest in Kamchatka with special reference to the contribution of sprouting to population maintenance. Plant Ecology 166: 25-35.

Hunter, J.C. and Barbour, M.G. 2001. Through-growth by *Pseudosuga menziessii*: A mechanism for change in forest composition without canopy gaps. Journal of Vegetation Science 12: 445-452.

Johnson, E.A. 1992. Fire and Vegetation Dynamics - studies from the North American boreal forest. Cambridge studies in ecology. Cambridge University Press, Cambridge, UK.

Kneeshaw, D.D. and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 81: 1500-1516.

Kneeshaw, D.D. and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Canadian Journal of Forest Research 26: 888-898.

Kneeshaw, D.D. and Bergeron, Y. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused be spruce budworm. Ecoscience 6: 214-222.

Kramer, M.G., Hansen, A.J., Taper, M.L., and Kissinger, E.J. 2001. Abiotic controls of long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology 82: 2749-2768.

Kuuluvainen, T., Syrjanen, K., and Kalliola, R. 1998. Structure of a pristine *Picea abies* forest in northeastern Europe. Journal of Vegetation Science 9: 563-574.

Lahde, E., Laiho, O., and Norokorpi, Y. 1999. Diversity-oriented silviculture in the Boreal Zone of Europe. Forest Ecology and Management 118: 223-243.

Lawton, R.O. and Putz, F.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69: 764-777.

Lertzman, K.P. and Krebs, C.J. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research 21: 1730-1741.

Lesieur, D., Gauthier, S., and Bergeron, Y. 2002. Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada. Canadian Journal of Forest Research 32: 1996-2009.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research 29: 796-811.

Liu, Q.-H. and Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. Journal of Vegetation Science 2.

Lundquist, J.E. 2000. A method of estimating direct and indirect effects of Armillaria root disease and other small-scale forest disturbances on canopy gap size. Forest Science 46: 356-362.

MacArthur, R.H. and Wilson, E.O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environmental Review 9: 1-59.

McCune, B. and Grace, J.B. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. and Mefford, M. J. 1999. PC Ord for Windows Version 4.0. Multivariate analysis of ecological data. Gleneden Beach. Oregon, USA, MjM Software.

Messier, C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C., and Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Canadian Journal of Forest Research 29: 812-823.

Oliver, C.D. and Larson, B.C. 1990. Forest Stand Dynamics. 1st edition McGraw Hill, Inc., New York, N.Y. 467 p.

Ontario Ministry of Natural Resources (OMNR) 1978. Forest inventory procedure for Ontario. Ontario Ministry of Natural Resources Publication.

Ott, R.A. and Juday, G.P. 2002. Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. Forest Ecology and Management 159: 271-291.

Paine, D.P. 1981. Aerial Photography and Image Interpretation for Resource Management. Wiley, New York, New York.

Pallik, B.J. and Pregitzer, K.S. 1991. The relative influence of establishment time and height-growth rates on species vertical stratification during secondary forest succession. Canadian Journal of Forest Research 21: 1481-1490.

Peet, R.K. and Christensen, N.L. 1987. Competition and tree death. BioScience 37: 586-594.

Perala, D.A. 1990. *Populus tremuloides. In* Silvics of North America. Volume 2. Hardwoods. USDA Forest Service. Washington, D.C., USA.

Pickett, S.T. 1989. Space-for-time substitution as an alternative to long-term studies . *In* Long-Term Studies in Ecology. Spring-Verlag, New York.

Richards, P.W. 1952. The Tropical Rainforest. Cambridge University Press, Cambridge.

Rowe, J.S. 1972. Forest Regions of Canada. Environment Canada, Ottawa, Ontario, Canada.

Ruel, J.C. and Benoit, R. 1999. Analysis of the November 7, 1994, windthrown in the regions of Carlexioz and Gaspesie (Quebec, Canada). Forestry Chronicle 75: 293-301.

Runkle, J. 1984. Development of woody vegetation in tree fall gaps in a beech-sugar maple forest. Holarctic Ecology 157-164.

Runkle, J. 1992. Guidelines and sample protocol for sampling forest gaps. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-GTR-283.

Runkle, J. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63: 1533-1546.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62: 1041-1051.

Schnitzer, S.A. and Carson, W.P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82: 913-919.

Spies, T.A., Franklin, J.F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research 20: 649-658.

Stefano, J.D. 2004. A confidence interval approach to data analysis. Forest Ecology and Management 187: 173-183.

Suding, K.N. 2001. The effects of gap creation on competitive interactions: separating changes in overall intensity from relative rankings. Oikos 94: 219-227.

Suding, K.N. and Goldberg, D. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. Ecology 82: 2133-2149.

Suominen, O., Danell, K., and Bergstrom, R. 1999. Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests. Oikos 84: 215-226.

Tainter, B. and Baker, F.A. 1996. Principles of Forest Pathology. John Wiley and Sons Inc., New York, New York.

Taylor, K.C., Arnup, R.W., Merchant, B.G., Parton, W.J., and Neippola, J. 2000. A Field Guide to Ecosystems of Northeastern Ontario. Queen's Printer for Ontario, Toronto, ON.

Thompson, I.D. 2000. Forest vegetation of Ontario: Factors influencing landscape change. *In* Euler, D., Perera, A., and Thompson, I.D. (Eds) Ecology of a Managed Terrestrial Landscape. UBC Press, West Mall, British Columbia.

Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379: 718-720.

Vasiliauskas, S. and Chen, H.Y.H. 2002. How long do trees take to reach breast height after fire in northeastern Ontario? Canadian Journal of Forest Research 32: 1889-1892.

Waring, R.H. and Franklin, J.F. 1979. The evergreen conifer forest of the Pacific Northwest. Science 204: 1380-1386.

Whitmore, T.C. 1974. Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands. State Mutual Book and Periodical Service, Ltd.

Whitmore, T.C. 1995. Perspectives in tropical rainforest research. *In* (Editors) Tropical Forests: Management and Ecology. Springer-Verlag, New York, New York.

Zimmerman, G.M., Goetz, H., and Mielke Jr., P.W. 1985. An improved statistical method for group comparisons to study effects of prairie fire. Ecology 66: 606-611.

Zsilinszky, V.G. 1963. Photographic interpretation of tree species in Ontario. Ontario Department of Lands and Forests, Timber Branch, Toronto, ON. 80p.