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Understanding Forest Dynamics Incorporating Both

Local and Regional Ecological Processes

by

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ABSTRACT

Classifying tree species as early-, mid-, and late-successional is often based on
their characteristics, *e.g.* age, height growth rates. Chapter Two examines the validity
of these classifications by comparing the age and height growth of upland boreal tree
species in Saskatchewan. Age classifications were examined by comparing the age of
individuals as determined by coring trees and by locating the root collar and missing
rings. Root collar ages show all species recruit within ten years after fire. Height
growth classifications were examined by comparing the mean time each species takes
to grow to each one-metre. Species classified as early-successional have relatively
higher growth rates in the first metre; however, above one metre there are few species
differences. Consequently, age and height growth rates cannot be used to classify
tree species.

Forest succession has been studied using static (*e.g.* static diameter
distribution, static age distribution, chronosequence) and dynamic methods (*e.g.*
reconstructed age distribution). Chapter Three examines the assumptions and
limitations of these methods. Results show that the assumptions of static approaches
are not met; diameter is not correlated with age, age as determined by coring a tree
does not reflect the date of recruitment, and changes in species composition and
abundance over decreasing size or age classes within a stand, or across stands, are not
the same changes one sees if the stand is followed through time. In twelve stands
sampled there is no evidence for succession, *i.e.* replacement of species over time.

Chapter Four examines the relative importance to forest dynamics of local
population processes (*i.e.* seed production, germination, recruitment, mortality, height

growth) and regional processes (*i.e.* disturbance, seed dispersal, and geomorphology). For all tree species rapid recruitment after fire is important to their regional persistence because only early recruiting species form the canopy and produce seed for the next generation. Local processes are relatively more important to the persistence of sprouting and serotinous species because local seed and sprouts are available after fire. However, regional processes are relatively more important to the persistence of wind-dispersed species because seed dispersal is required for re-colonization after fire.

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CHAPTER ONE

General Introduction

Traditionally, studies of forest succession have been interested in determining the succession of tree species over time within stands. However, because there are no records long enough to examine all of the changes in species composition and abundance within a stand over time, studies of forest succession have had to make a number of assumptions. The overall purpose of this thesis is to test these assumptions and examine their implications on our understanding of forest dynamics. Using data from the mixedwood boreal forest of central Saskatchewan, I first examine the specific assumption that is made when using age to infer patterns of succession, *i.e.* that age, as determined by coring a tree above the root collar, reflects the date of recruitment. By examining the age at root collar and height growth rates of individuals within mixed-species stands, I determine whether tree species can be classified as early-, mid- and late-successional based on their age and height growth rates. Second, I test the assumptions and limitations of static diameter distributions, static age distributions, chronosequences and reconstructed age distributions and examine the view that in forest succession there is a replacement of tree species over time. Finally, in an attempt to avoid making the assumptions of traditional approaches, I use both local population processes and regional processes to develop a regional-scale understanding of forest dynamics.

The chapters of this thesis are to be read independently; for the most part each chapter can be read without reference to other chapters. This structure has led to some

repetition among chapters. Specifically, in the Methods and Materials section of each chapter there is some repetition under the subsections: Study Area, and Field and Laboratory Methods. However, it should be noted that with each subsequent chapter there are an increasing number of stands incorporated.

Cowles (1899), studying succession on the Indiana sand dunes near Lake Michigan, was the first North American to work out a complete successional sequence. He observed that different plant associations were found on dunes that were different in age and assumed that the changes in the plant formations he saw on dunes of increasing age were equivalent to the temporal development at each site. The series of different sites of different ages came to be called a chronosequences (Jenny 1941).

Following the work of Cowles in North America and Warming (1895) in Denmark, Clements (1916), Gleason (1925), and many others (*e.g.* Shelford 1911; Cooper 1923; Oosting 1942) studied succession by simply describing the plant species present over a chronosequence of sites, typically using some measure of the relative importance of each species (*i.e.* density, frequency). It was assumed that the changes over sites of increasing age were the same changes one would see if each site was followed through time. It was believed that within each site tree species dominant in the canopy at younger sites, *i.e.* those classified as early-successional, were replaced by tree species dominant in the canopy at older sites, *i.e.* those classified as late-successional.

In an attempt to be more empirical, ecologists began to measure the size (usually diameter) of individuals (*e.g.* Hough 1936; Nelson 1964; Knowles and Grant 1983).

Static diameter distributions were constructed in order to examine patterns of the sizes of individuals within each site or stand. It was assumed that diameter was positively correlated to age and thus examining the patterns of diameters of species was similar to examining their recruitment patterns. It was believed that species in larger diameter classes, *i.e.* early-successional species, would be replaced by species in successively smaller diameter classes, *i.e.* mid- and late-successional species.

After a long period of using measures of abundance and diameter to infer the sequence of species through succession, ecologists began to measure age (*e.g.* Hett and Loucks 1968, 1971; Leak 1970; Whipple and Dix 1979; Hibbs 1979). Age was measured by coring trees at breast height and counting their annual growth rings; the number of rings counted was assumed to reflect the date of recruitment. By dividing individuals within a stand into age classes, and constructing a static age distribution, succession was inferred by assuming that changes in species composition and abundance over decreasing age classes within a stand are the same changes one would see if each stand was followed through time. The results of studies using the static age distribution often confirmed the results of studies that used a static diameter distribution. Aging trees at breast height confirmed that larger diameter individuals, *i.e.* early-successional species, were older than smaller diameter individuals, *i.e.* mid- and late-successional species.

Chapter Two examines the validity of classifying tree species as early-, mid-, and late-successional based on two characteristics: the timing of recruitment, *i.e.* age, and height growth rates. Traditionally, within mixed-species stands, tree species that appear

to be older, and have higher growth rates are often classified as early-successional, while those that appear to be younger, and have slower growth rates are often classified as mid- and late-successional. Early successional species are believed to recruit early, grow rapidly and form the initial canopy; mid- and late successional species recruit later, and grow slowly in the understorey of early-successional species. Eventually, when early-successional species begin to die, mid- and late-successional species will reach the canopy and replace early-successional species. The belief that forest succession involves such a replacement of species over time is well accepted. As a result, ecologists have become less interested in describing the patterns of succession, and have instead begun to focus on understanding the mechanisms that explain the successional sequence. Many recent studies have concluded that the characteristics used to distinguish between early-, mid-, and late-successional species (*e.g.* age and height growth rates) are the principal mechanisms that drive patterns of forest succession (*e.g.* Walker and Chapin 1986; Pickett *et al.* 1987; Veblen *et al.* 1991).

Chapter Three examines the assumptions and limitations of methods commonly used to study forest succession: chronosequences, static diameter distributions, static age distributions, and reconstructed age distributions. Chronosequences, static diameter distributions, and static age distributions share the principal assumption that changes in species composition and abundance over decreasing size or age classes within a stand, or across stands of increasing age, are the same changes one would see if each stand was followed through time. Static diameter distributions also make the assumption that

diameter and age are positively correlated, while static age distributions make the assumption that age, as determined by coring a tree, reflects the date of recruitment. While the assumption that diameter and age are positively correlated has been tested by some studies (*e.g.* Blum 1961; Gibbs 1963; Johnson and Fryer 1989; Huff 1995; Lowenstein *et al.* 2000), the other two assumptions are rarely tested with empirical data. In fact, with the widespread practise of not testing these assumptions there seems to be a general acceptance that they are valid. A few studies have attempted to overcome these assumptions by looking at changes within a stand back in time. Paleoecology, permanent plots, and reconstructed age distributions have all been used to examine changes in species composition and abundance back in time (Oliver and Stephens 1977; Henry and Swan 1974; Pickett 1983; Johnson and Fryer 1989; Jackson *et al.* 1988; Fastie 1995). What these studies have shown is that the traditional interpretations of succession, derived from chronosequences, static diameter distributions, and static age distributions, are not consistent with the patterns of abundance and composition observed back in time.

Chapter Four gives empirical evidence for forest dynamics, including both local population processes, *i.e.* tree seed production, recruitment, growth, and mortality, and regional processes, *i.e.* disturbance, seed dispersal, and moisture and nutrient gradients. By examining each of the local and regional processes it is clear that the changes in composition and abundance of species within each local population are dependent on each species having a mechanism of re-colonization that allows for their rapid recruitment after stand-replacing wildfires. Such rapid recruitment is necessary because

only those recruiting within the first few years after fire will make it into the canopy to produce seed for the next generation. Therefore, if we are to fully understand the regional scale forest dynamics, we need to better understand how the regional processes of wildfire, seed dispersal, and the regional distribution of tree species (driven by moisture and nutrient gradients) affect the ability of each tree species to rapidly recruit after fire.

Literature Cited

Bergeron, Y., and Charron, D. 1994. Post-fire stand dynamics in a southern boreal forest (Québec): A dendroecological approach. *Ecoscience* 1: 173-184.

Blum, B.M. 1961. Age-size relationships in all-aged northern hardwoods. USDA Forest Service Research Note NE-125, pp.3.

Clements, F.E. 1916. *Plant succession.* Carnegie Institute of Washington Publication 242.

Cooper, W.S. 1923. The recent ecological history of Glacier Bay, Alaska. II. The present vegetation cycle. *Ecology* 4: 223-46.

Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* 27:95-117, 167-208, 361-91.

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

Gibbs, C.B. 1963. Tree diameter a poor indicator of age in West Virginia hardwoods. USDA Forest Service Research Note NE 11, pp.4.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Club* **53**:7-26.

Henry, A., and Swan, J.M. 1974. Reconstructing forest history in a maple-beech climax. *Ecology* **55**: 772-83

Hett, H.M., and Loucks, O.L. 1968. Application of life table analysis of tree seedlings in Quetico Provincial Park, Ontario. *Forestry Chronicles* **44**: 29-32.

Hett, H.M., and Loucks, O.L. 1971. Sugar maple (*Acer saccharum* marsh.) seedling mortality. *Journal of Ecology* **59**: 507-20.

Hibbs, D.E. 1979. The age structure of a striped maple population. *Canadian Journal of Forest Research* **9**: 504-508.

Hough, A.F. 1936. A climax forest community on East Tionesta Creek in northwestern Pennsylvania. *Ecology* **17**: 9-28.

Huff, M.H. 1995. Forest age structures and development following wildfires in the western Olympic Mountains, Washington. *Ecological Applications* **5**: 471-483.

Jackson, S.L., Futyma, R.P., and Wilcox, D.A. 1988. A paleoecological test of a classical hydrosere in the Lake Michigan dunes. *Ecology* **69**:928-36.

Jenny, H. 1941. *Factors of Soil Formation*. McGraw-Hill, New York.

Johnson, E.A., and Fryer, G.I. 1989. Population dynamics in Engelmann spruce – lodgepole pine forests. *Ecology* **70**: 1335-1345.

Knowles, P., and Grant, M.C. 1983. Age and size structure analysis of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. *Ecology* **64**:

1-9.

Leak, W.B. 1970. Successional change in northern hardwoods predicted by birth and
death simulation. *Ecology* **51**: 794-801.

Linder, P., Elfving, B., and Zackrisson, O. 1997. Stand structure and successional trends
in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* **98**:
17-33.

Loewenstein, E.F., Johnson, P.S., and Garrett, H.E. 2000. Age and diameter structure of
a managed uneven-aged oak forest. *Canadian Journal of Forest Research* **30**:
1060-1070.

Nelson, T.C. 1964. Diameter distribution and growth of loblolly pine. *Forest Science* **10**:
105-115.

Oliver, C.D., and Stephens, E.P. 1977. Reconstructions of a mixed-species forest in
central New England. *Ecology* **58**:562-572.

Oosting, H.J. 1942. An ecological analysis of the plant community of Piedmont, North
Carolina. *American Midland Naturalist* **28**: 1-126.

Pickett, S.T.A. 1983. Absence of an *Andropogon* stage in old field succession at the
Hutchinson Memorial Forest. *Bulletin of the Torrey Botanical Club* **110**: 533-
535.

Shelford, V.E. 1911. Ecological succession II. Pond fishes. *Biological Bulletin* **21**: 127-
151.

Veblen, T.T. 1986. Age and size structure of a subalpine forest in the Colorado Front

Range. *Bulletin of the Torrey Botanical Society* 113: 225-240.

Warming, J.E.B. 1895. *Plantesamfund grundtak of den okologiske plantegeografe.* Copenhagen, Denmark.

Whipple, S.A., and Dix, R.L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. *American Midland Naturalist* 101: 142-157.

CHAPTER TWO

Accurately aging trees and examining their height growth rates:

implications for interpreting forest dynamics

Introduction

Clements' (1916) initial theory of plant succession involved a succession of dominant plant species in which one species took over 'the reins of social control' from another species. In practise this meant that different plant species recruited or became dominant in the canopy at different times after stand initiation. Conversely, Egler's (1954) initial floristics model argued that, in some situations at least, all species recruit simultaneously soon after stand initiation. Regardless of point of view, ecologists working in many different forest types distinguish between early-, mid- and late-successional species (also called pioneer, seral, and climax species, respectively) based on the timing of their recruitment or dominance in the canopy (*e.g.* Hofgaard 1993; Huff 1995; Kneeshaw & Burton 1997; Linder *et al.* 1997; Feller 1998; Donnegan & Rebertus 1999; Frelich & Reich 1999). Species that recruit or become dominant in the canopy immediately after stand initiation are classified as early-successional, whereas those that recruit or become dominant in the canopy some time later are classified as mid- or late-successional.

In forest trees, the empirical evidence for the timing of recruitment, supporting either Clements' relay floristics model or Egler's initial floristics model, has been

primarily the ages of individuals within a stand, where age is determined by coring each individual as close to the base as possible (typically 20-50 cm above ground level), and counting the annual growth rings. Static age distributions are then constructed in which older species are classified as early-successional, and younger individuals are classified as either mid- or late-successional, depending on the timing of their recruitment. Today, this method of aging individuals is the standard, and the static age distribution is one of the most common methods used to infer patterns of forest succession (*e.g.* Veblen *et al.* 1991; Palik & Pregitzer 1991; Desponts & Payette 1992; St-Pierre *et al.* 1992; Bergeron & Charron 1994; Huff 1995; Lieffers *et al.* 1996; Engelmark *et al.* 1998; Donnegan & Rebertus 1999; Bergeron 2000).

Using static age distributions to infer forest succession has been criticized for not meeting the critical assumption of identical age-specific recruitment and mortality rates in each age class (Johnson *et al.* 1994). Other problems with static age distributions have been raised by studies that have used dendrochronology to determine tree age. These studies have found that when tree age is measured by simply counting the annual growth rings at the base of a tree, the age may not reflect the date of recruitment (*e.g.* Schweingruber 1989; Norton & Ogden 1990; DesRochers & Gagnon 1997; Parent *et al.* 2000).

Distinctions between early-, mid- and late-successional tree species have also been based on height growth rates (Desponts & Payette 1992; Bergeron & Charron 1994, Kneeshaw & Burton 1997; Bergeron 2000). Species classified as early-successional are

believed to have higher growth rates than those classified as mid- and late-successional because from recruitment through maturity species classified as early-successional are almost always taller than those classified as mid- and late-successional. Despite this widely held belief, few studies present detailed empirical evidence, *i.e.* individual height growth curves, for a significant number of mature trees, to confirm that there are significant species differences in height growth rates (some exceptions include Palik & Pregitzer 1991; Johnson *et al.* 1994; Bergeron 2000).

Using data from eight stands in the mixedwood boreal forest of central Saskatchewan, Canada, I will examine the validity of classifying tree species as early-, mid- or late-successional based on the timing of recruitment and height growth rates. In mixed species stands I will examine whether species classified as early-successional are older, and have higher growth rates, than species classified as mid- and late-successional. I will determine the ages of all individuals within stands using the traditional method of coring a tree 30 cm above ground level and counting the annual growth rings; these age estimates will be compared to the ages of the same individuals as determined by using dendrochronology to locate the root collar and any missing annual growth rings. Then I will use stem analysis to examine the height growth rates of each individual and determine whether there are significant differences in height growth rates between species classified as early-, mid-, and late-successional. My results will demonstrate that, when tree age is determined accurately, all species, regardless of classification, recruit within the first few years after fire. Species classified as early-successional have relatively

higher height growth rates within the first one metre than those classified as mid- and late-successional. This explains why species classified as early-successional often appear older, and are taller, than those classified as mid- and late-successional.

Materials and Methods

STUDY AREA

The study area is located in Saskatchewan, Canada (53° 34' N to 54° 24' N and 105° 25' W to 107° 52' W). The topography of this area is gently rolling, ranging in elevation from approximately 525-650 metres a.s.l. The climate is characterised by long, cold winters and short, cool summers. July and August are the warmest months of the year with average maximum temperature exceeding 20°C three days out of four. The average annual precipitation ranges from 400-500 mm, of which 70% occurs as rain.

The major disturbance in this region is large, high intensity, lightning-caused wildfires that kill most of the canopy trees and understorey vegetation. These fires are controlled primarily by weather; variation in topography, substrate and microclimate has a relatively minor influence on fire intensity (Weir *et al.* 2000). The study area is part of the Boreal Mixedwood Forest (Rowe 1972), which is dominated by eight upland tree species, including: *Populus tremuloides* Michx., *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., *Pinus banksiana* Lamb., *Picea mariana* (Mill) B.S.P., *Populus balsamifera* L., *Larix laricina* (Du Roi) K. Koch., and *Betula papyrifera* Marsh. *P. tremuloides*, *P. banksiana*, and *B. papyrifera* are classified as early- successional species,

P. glauca and *P. mariana* are classified as mid- or late- successional species, and *A. balsamea* is classified as a late-successional species (Beckingham *et al.* 1996).

Moisture and nutrients are the principal environmental factors controlling the distribution of upland plant species within the area (Bridge and Johnson 2000). The gradients are controlled by surficial material (primarily glaciofluvial and glacial till) and the geomorphic processes that create hillslopes on these surfaces. The tops of glacial till hillslopes are at the middle of the moisture and nutrient gradients and are dominated by *P. tremuloides*. At mid-slope positions, *P. glauca* and *P. tremuloides* co-dominate and, as moisture and nutrients increase downslope, *P. glauca* and *A. balsamea* co-dominate. The tops of glaciofluvial hillslopes are at the dry end of the moisture gradient and low end of the nutrient gradient, and are dominated by *P. banksiana*. At mid-slope positions, *P. banksiana* co-dominates with *P. mariana*, and as moisture and nutrients increase downslope, *P. mariana* dominates.

FIELD AND LABORATORY METHODS

We sampled eight stands varying in geomorphic surface, hillslope position, species composition, and time since the last stand-replacing fire (Table 2.1). Three stands were located top-slope, mid-slope and mid-bottom-slope on glacial till hillslopes and were dominated by *P. tremuloides, P. glauca,* and *A. balsamea* (Table 2.1). One stand was located bottom-slope on glacial till overlain with glaciofluvial and was dominated by *P. glauca* and *A. balsamea*. Three stands were located mid-slope on

Table 2.1   Stand characteristics for eight upland stands from the southern mixedwood

boreal forest, Saskatchewan. Figure label indicates the stand represented

in each Figure. T-S.F is the time since the last stand replacing fire, *i.e.*

time-since-fire.

Figure label	Stand ID	Geomorphic Surface	Hillslope Position	Species Composition	N	Plot Size (m²)	Density (no./ha)	T-S-F (years)	Fire Date
a	WS4	glacial till	bottom	*P. tremuloides*	2	168	119	55	1942
				P. glauca	43		2560		
				A. balsamea	1		60		
				B. papyrifera	7		417		
b	WS2	glacial till	top-middle	*P. tremuloides*	101	320	3156	78	1919
				P. glauca	23		719		
				A. balsamea	119		3719		
				B. papyrifera	16		500		
c	TA8	glacial till	top-middle	*P. tremuloides*	88	576	1528	111	1886
				P. glauca	64		1111		
				A. balsamea	198		3438		
				B. papyrifera	68		1181		
				P. mariana	32		556		
d	WS3	till/fluvial	bottom	*P. tremuloides*	2	196	143	154	1843
				P. glauca	32		1633		
				A. balsamea	254		18143		
e	JP12	glaciofluvial	mid-bottom	*P. banksiana*	26	140	1857	59	1938
				P. mariana	80		5714		
				P. tremuloides	5		357		
				B. papyrifera	1		71		
f	JP5	glaciofluvial	middle	*P. banksiana*	22	100	2200	77	1919
				P. mariana	59		5900		
g	JP8	glaciofluvial	middle	*P. banksiana*	27	140	1286	126	1870
				P. mariana	19		1357		
h	JP11	glaciofluvial	middle	*P. banksiana*	14	200	700	153	1843
				P. mariana	87		8700		
				P. glauca	4		400		
				P. tremuloides	95		9500		
				B. papyrifera	10		1000		

glaciofluvial hillslopes and were dominated by *P. banksiana* and *P. mariana*. One stand

was located mid to bottom-slope on glaciofluvial and was also dominated by *P.*

banksiana and *P. mariana*. Time-since-last fire of these stands ranges from 55 years to

154 years. I emphasize that the stands are not intended to show different stages of

succession, *i.e.* a chronosequence. Instead, I am simply using a variety of stands on

different geomorphic surfaces and hillslope positions in which the age distribution and

height growth of individuals is examined. The selection criteria for the eight stands were

as follows: 1) stands had no evidence of anthropogenic disturbance, 2) vegetation was

rooted in mineral soil with no evidence of standing water in the top 30 cm of mineral soil,

3) each stand was visually homogenous with respect to stand age, stand structure, and

species composition, and 4) each stand contained at least two tree species. Plot size,

varying from 100–576 square metres, was established to include a minimum of 25 of the

most abundant canopy individuals (Table 2.1).

Each stand was divided into a grid at two-metre intervals, and all live seedlings

(<50 cm height), saplings (>50 cm height and <5 cm basal diameter), and trees (>5 cm

basal diameter) were labelled and mapped. Two to three workers carefully searched each

stand to ensure that all individuals (*i.e.* including newly recruited seedlings, if present)

were located. All seedlings, along with their roots, were removed from the ground.

Using hand rakes, we carefully removed all of the organic material, down to mineral soil,

from within the entire plot. Next, all sapling and tree stumps were completely removed

from the ground by first cutting each individual at the base, and then cutting all lateral

Figure 2.1   Photograph showing how all sapling and tree stumps were removed from

the ground.

roots and tap roots (Figure 2.1). Finally, a disk was cut at every metre to the top of each

sapling and tree to construct height growth curves. To remove all individuals from one

stand, including stem disks and stumps, took four people 15-30 days.

All seedlings, sapling and tree disks and stumps were brought back to the lab for

processing; no samples were processed in the field. In total, 1499 individuals were

collected and processed. Seedling ages were determined by counting bud scale scars

from the root collar to the top of each seedling. The age of most seedlings larger than

0.25 cm basal diameter was also determined by counting annual growth rings at the root

collar (Figure 2.2). To locate the root collar of each seedling, sapling and tree, each

stump was cut with a band saw into cross-sections 1-2.5 cm thick, and sanded

sequentially with coarse and fine sand papers (up to 600 grain). The root collar was

located in all samples using a 10-60X power-dissecting microscope, and noting from one

cross section to the next, the shift in the central pith, from undifferentiated parenchyma

cells in the stem, to a vascular cylinder in the root (Telewski & Lynch 1991). Also, all

tree and sapling disks were sanded and counted on two radii to construct height growth

curves.

We reconstructed the age at 30 cm above the root collar for each seedling (those

>30cm height), sapling, and tree in each stand using age at root collar and height growth

curves from the cross-dated stump sections and stem disks. Using 30 cm above the soil

surface would have more closely followed the methods of studies using the traditional

methods of aging. However, we used 30 cm above the root collar instead because we did

Figure 2.2   A schematic diagram of a three-year-old seedling recruited in 1998,

showing the location of the root collar in relation to the hypocotyl and

radicle (after Fritts 1976).

Phloem 2000
1999
1998

Pith

Hypocotyl

Xylem 2000
1999
1998

Radical
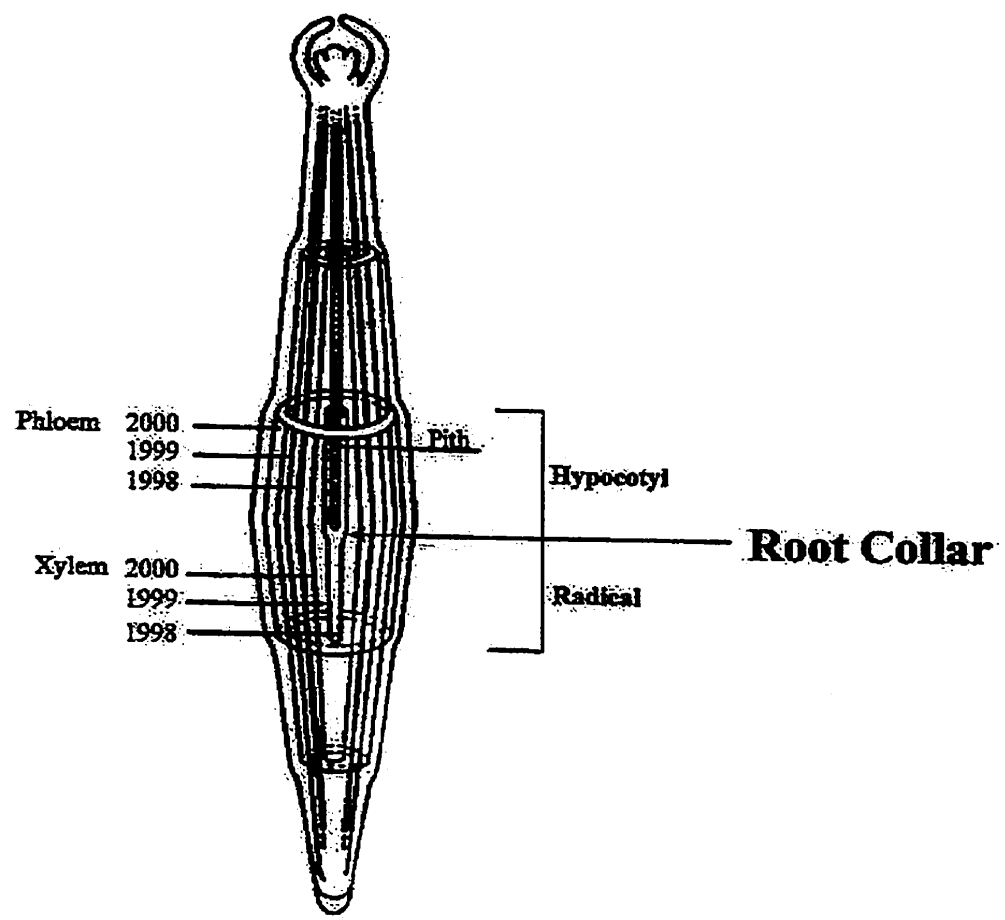
Root Collar

not mark the location of the soil surface on each individual in the field. Similarly, it was not feasible to cut a disk in the field that was 30 cm above the root collar because the location of the root collar within each individual was not known prior to analysing the stump cross sections. Mineral soil level was not a good indication of root collar level because the majority of individuals had their root collar below the mineral soil surface (S.L. Gutsell, unpublished data).

Within each seedling, sapling and tree stump section we located missing annual growth rings, *i.e.* years where an annual growth ring is not produced on all stem segments, using standard dendrochronological techniques (Schweingruber 1989; Yamaguchi 1991). For each of the stump cross-sections we constructed a skeleton plot, which is a plot of unusually narrow or wide annual rings. Each skeleton plot was first cross-dated within the stump, and then against a species-specific master skeleton plot from each stand. Missing rings were evident when marker rings in a skeleton plot were offset compared to other skeleton plots within a stump, and when compared to the master plot. For each stand, sample processing and analysis took one technician 40-60 days.

Within each stand, we compared the average time taken by each species to grow to each successive metre height increment. To do this we used the age at each metre height from the root collar to the top of each tree. Within each stand we calculated the mean and standard error of the time taken to reach each metre height for all trees of each species in each cohort. Individuals that recruited within the first ten years after fire are here referred to as the post-fire cohort, whereas individuals recruiting after that time are

referred to as the understorey cohort. All trees within a cohort were plotted with a

common starting time, despite differences in year of recruitment, in order to directly

compare height growth rates. A test of the effect of year of recruitment on height growth

rate for each cohort found no significant effect (p<0.05).

Results

RELATIONSHIP OF AGE AT 30 CM AND AGE AT ROOT COLLAR

Figures 2.3a – h show the relationship of the age at 30 cm above the root collar

and age at the root collar for each individual within each stand. Within each figure, the

diagonal line indicates a perfect correlation between the age at 30 cm and age at the root

collar. The further from the diagonal, the greater number of years underestimated at 30

cm. Notice that no points lie below the diagonal line because it is not possible for age at

30 cm to be greater than age at the root collar.

The age at 30 cm underestimates root collar age for all species, and the degree to

which it is underestimated differs both within and between species. In *P. tremuloides*, *P.*

glauca, and *A. balsamea* dominated stands (Figures 2.3a – d), the species classified as

early-successional, *P. tremuloides* and *B. papyrifera*, have the fewest number of years

underestimated at 30 cm and the smallest range, 0-8 years and 0-11 years, respectively.

Species classified as mid- and late-successional, *P. glauca* and *A. balsamea*, have the

greatest number of years underestimated at 30 cm and largest range, 0-37 years and 2-43

years respectively. In *P. banksiana*, *P. mariana* dominated stands (Figures 2.3e – h),

Figure 2.3   The relationship of the age at 30 cm above the root collar and age at the

root collar for each individual within each of eight stands. Figures a – h

indicate stands a – h, as identified in Table 2.1.

a)

Age at root collar

- ● *P. tremuloides*
- ■ *B. papyrifera*
- △ *P. glauca*
- ◇ *A. balsamea*

b)

Age at root collar

- ● *P. tremuloides*
- ■ *B. papyrifera*
- □ *P. glauca*
- ◇ *A. balsamea*

c)

Age at root collar

- ● *P. tremuloides*
- ■ *B. papyrifera*
- △ *P. glauca*
- ◇ *A. balsamea*
- □ *P. mariana*

d)

Age at root collar

- ● *P. tremuloides*
- □ *P. glauca*
- ◇ *A. balsamea*

Age at 30 cm

e)

Age at root collar

- ▲ *P. banksiana*
- ● *P. tremuloides*
- ■ *B. papyrifera*
- □ *P. mariana*

f)

Age at root collar

- ▲ *P. banksiana*
- □ *P. mariana*

g)

Age at root collar

- ▲ *P. banksiana*
- □ *P. mariana*

h)

Age at root collar

- ▲ *P. banksiana*
- ● *P. tremuloides*
- ■ *B. papyrifera*
- □ *P. mariana*
- △ *P. glauca*

Age at 30 cm

the species classified as early-successional, *P. banksiana*, has the fewest number of years

underestimated at 30 cm and the smallest range, 1-10 years, compared to

species classified as late-successional, *P. mariana*, with 3-31 years underestimated.

COMPARING HEIGHT GROWTH RATES OF TREE SPECIES

Aging an individual at 30 cm or any height above the root collar by simply

counting the annual growth rings underestimates the root collar age because the growth

rings laid down between the root collar and 30 cm above the root collar are not counted.

Figures 2.4a - h compare the means and standard errors of the time to grow from the root

collar to 1-metre height, for each species in each stand. The horizontal dotted line

indicates 30 cm above the root collar. Note that the growth trajectories of each species do

not reflect the actual growth trajectories below one metre; this would require that several

sections be cut and aged between the root collar and one metre. As we will see below,

despite the inaccurate growth trajectories below one metre, the differences between

species remain clear. Within each stand there are significant differences between species

in the time to grow from the root collar to 30 cm above the root collar (Figures 2.4a – h).

In stands dominated by *P. tremuloides*, *P. glauca*, and *A. balsamea* (Figures 2.4a – d), the

time to grow from the root collar to 30 cm above the root collar is significantly greater for

species classified as mid- and late-successional (*P. glauca* and *A. balsamea*), compared to

species classified as early-successional (*P. tremuloides* and *B. papyrifera*). Similarly, in

stands dominated by *P. banksiana* and *P. mariana* (Figures2.4e – h), the time to grow

Figure 2.4   For each species in each of eight stands, the means and standard errors of

the time to grow from the root collar to 1-metre above the root collar. The

horizontal dotted line indicates 30 cm above the root collar. Species

denoted as (uc) are from the understorey cohort.
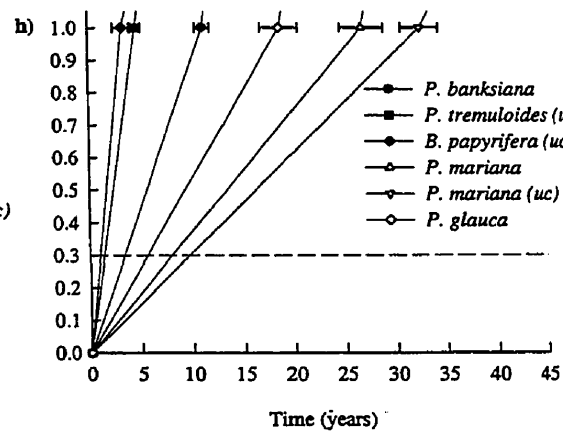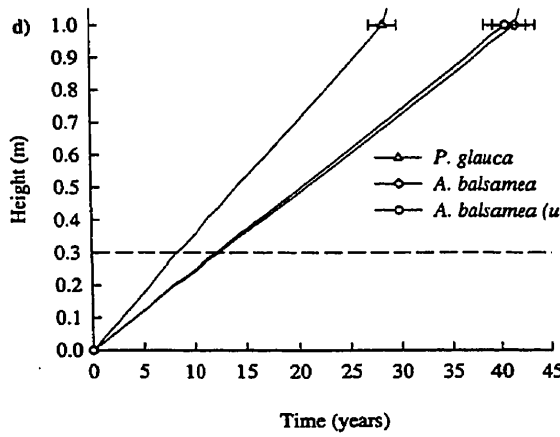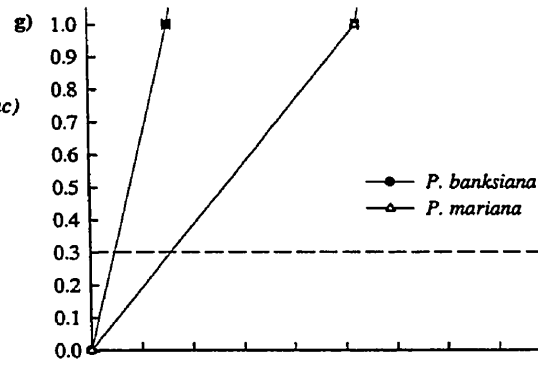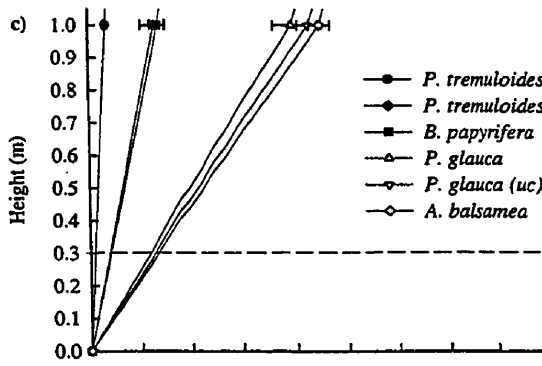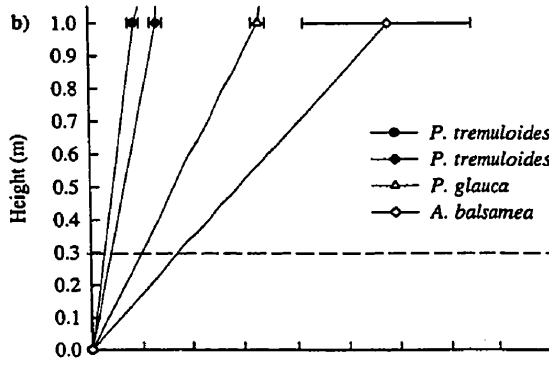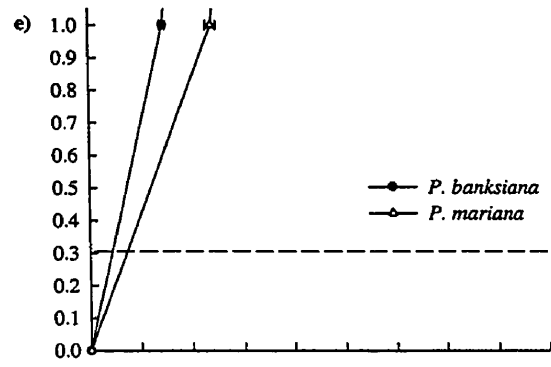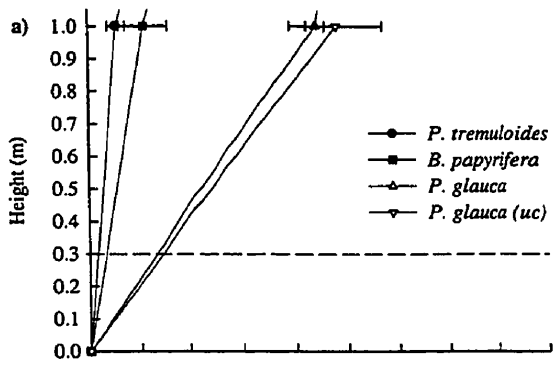
from the root collar to 30 cm above the root collar is significantly greater for the species classified as late-successional (*P. mariana*) compared to the species classified as early-successional (*P. banksiana*).

Interestingly, the differences in height growth rates between species within each stand occur only within the first one metre of growth; above one metre there appear to be few or no substantial differences in height growth rates (Figures 2.5a – h). In all stands, the species classified as mid- and late-successional attain similar, and occasionally better (Figures 2.5c, e, f), height growth rates compared to those classified as early-successional. Notice that for some species in some stands there are some decreases in time with height (Figures 2.5b – d, g – h). These decreases occur because with increasing height fewer individuals are included in the calculation of the mean and standard error, *i.e.* shorter individuals with slower growth rates are no longer included in the mean. To aid in the interpretation of these figures, we have also plotted, to the right of each figure, the actual height growth curves for the fastest and slowest individuals of each post-fire cohort.

LOCALLY MISSING ANNUAL GROWTH RINGS

Aging an individual at 30 cm above the root collar by simply counting the annual growth rings underestimates the root collar age in part because some individuals have locally missing annual growth rings, *i.e.* growth rings are not laid down each year along all stem segments. Figures 2.6a – h show for each species in each of our eight stands the

Figure 2.5   For each species in each of eight stands, the means and standard errors of

the time to grow from the root collar to each metre height. Species

denoted as (uc) are from the understorey cohort.

Time (years)
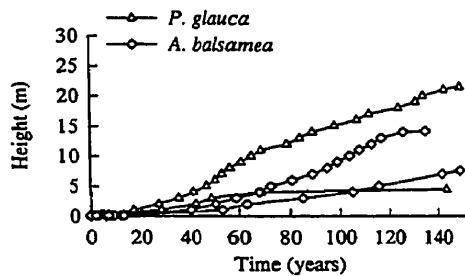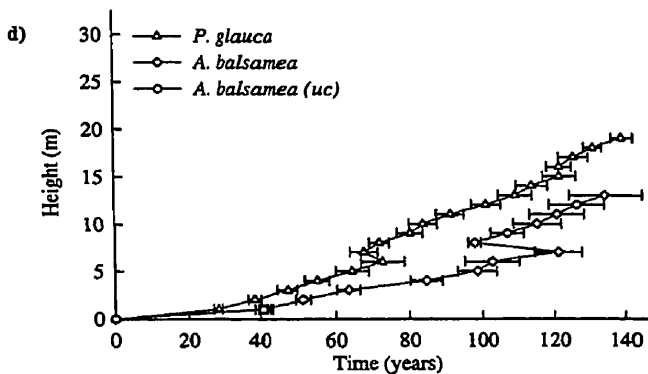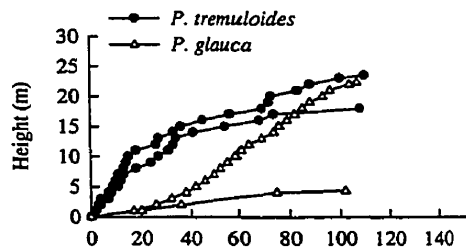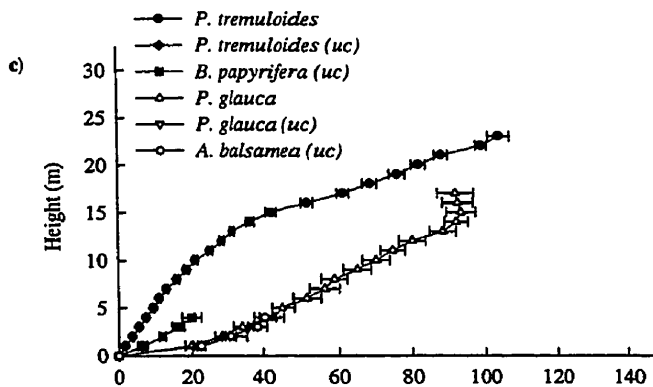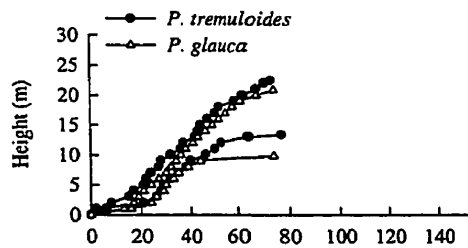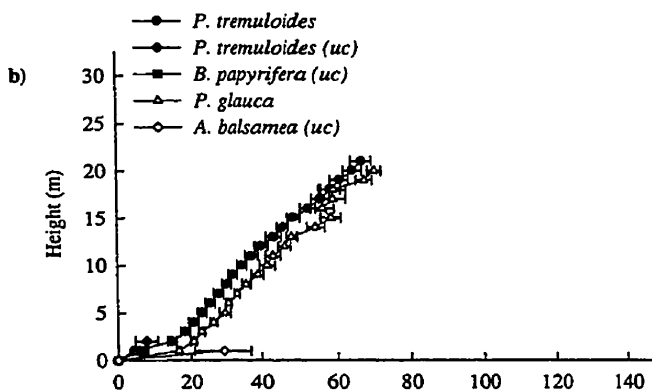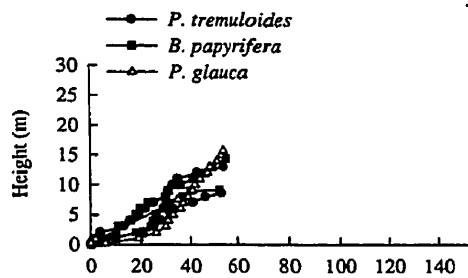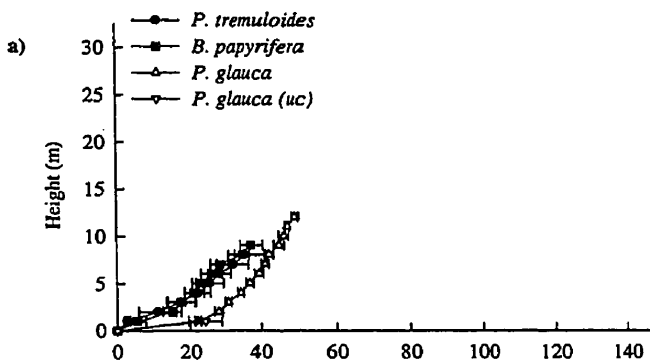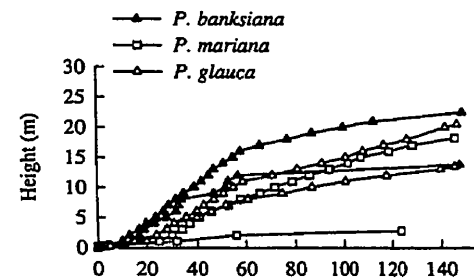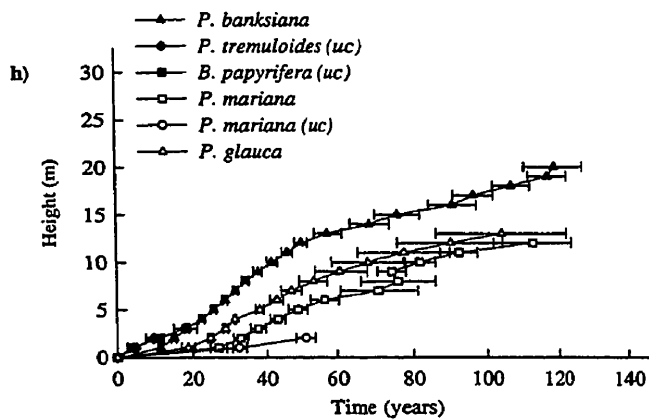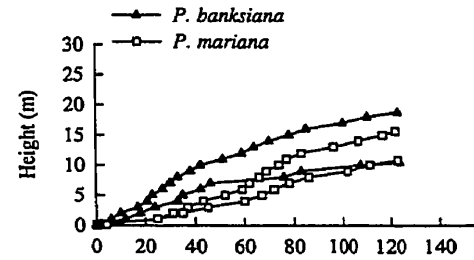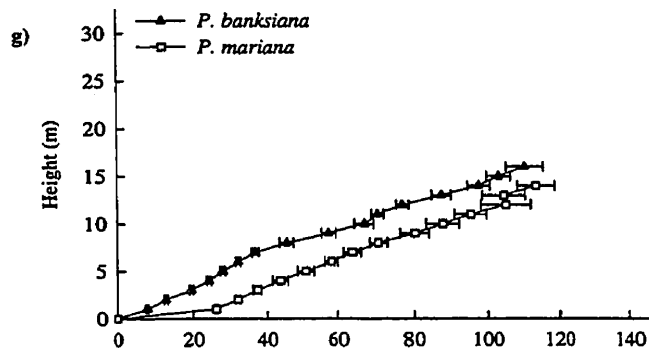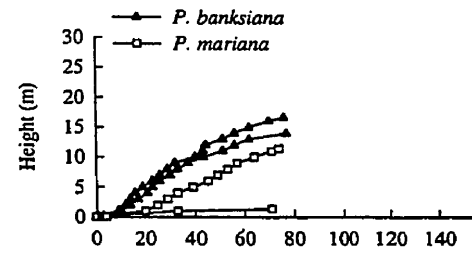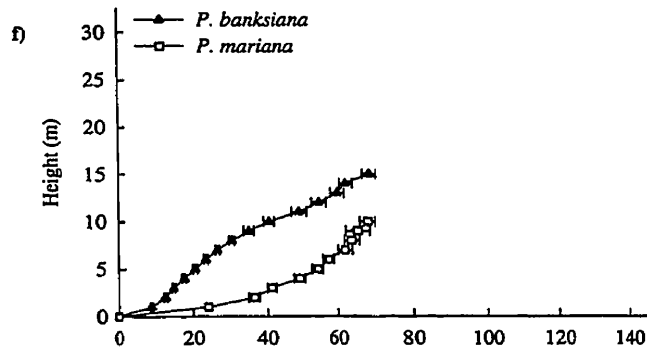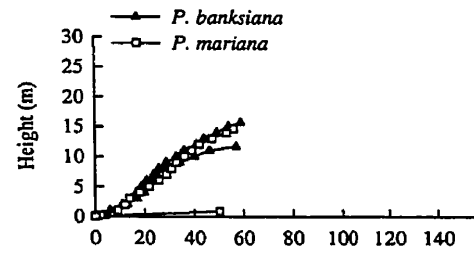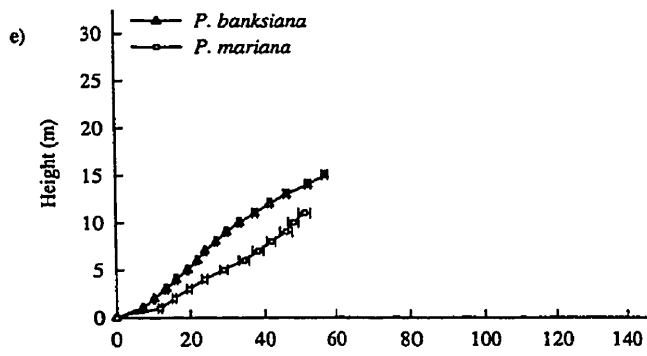
Figure 2.6   For individuals within each of eight stands, the proportion of individuals

of each species with locally missing growth rings, and number of locally

missing rings per individual.

a) *P. tremuloides* ● *B. papyrifera* ■ *P. glauca* ▲ *A. balsamea* ○

b) *P. tremuloides* ● *B. papyrifera* ■ *P. glauca* ▲ *A. balsamea* ○

c) *P. tremuloides* ● *B. papyrifera* ■ *P. glauca* ▲ *A. balsamea* ○ *P. mariana* □

d) *P. tremuloides* ● *P. glauca* ▲ *A. balsamea* ○

e) *P. banksiana* ▲ *P. tremuloides* ● *B. papyrifera* ■ *P. mariana* □

f) *P. banksiana* ▲ *P. mariana* □

g) *P. banksiana* ▲ *P. mariana* □

h) *P. banksiana* ▲ *P. tremuloides* ● *B. papyrifera* ● *P. mariana* □ *P. glauca* ▲

Number of locally missing rings

Number of locally missing rings
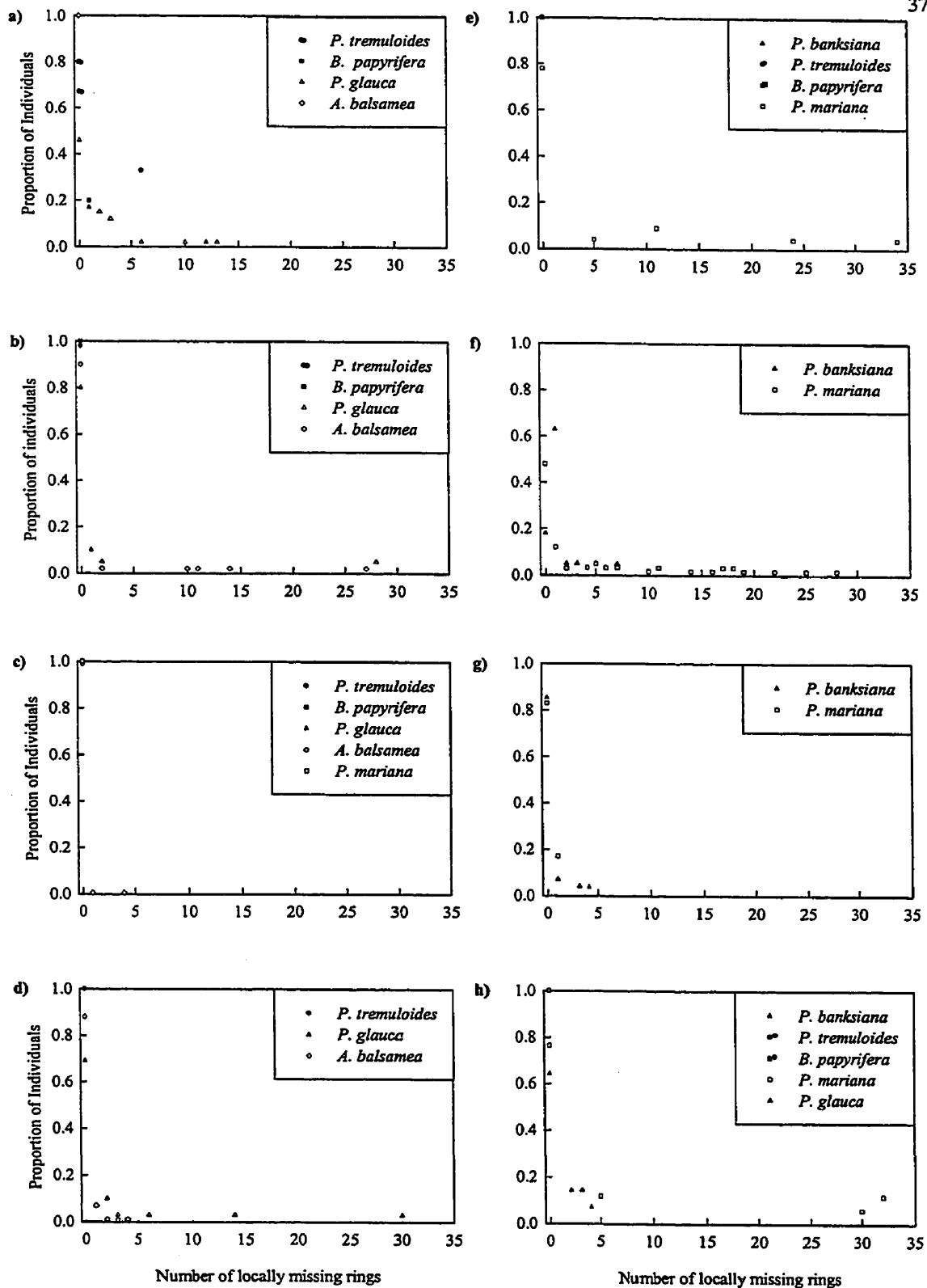
proportion of individuals with locally missing rings, and the number of missing rings per individual. Notice that in most stands species classified as mid- and late-successional have the highest proportion of individuals with missing rings and the highest number of missing rings per individual. In *P. tremuloides* and *P. glauca* dominated stands, *P. glauca* and *A. balsamea* generally have a higher proportion of individuals with locally missing rings and the highest number of locally missing rings per individual, compared to *P. tremuloides* (Figures 2.6a – d). In *P. banksiana* and *P. mariana* dominated stands, *P. mariana* has a greater proportion of individuals with missing rings and the greatest number of missing rings per individual (Figures 2.6e – h).

STATIC AGE DISTRIBUTIONS: COMPARING AGE AT 30 CM AND AGE AT ROOT COLLAR

When the age of individuals is determined by simply counting annual growth rings at 30 cm, the pattern of ages in each stand (Figures 2.7a – h: Age at 30 cm) is similar to the pattern found in nearly all other studies from the boreal forest. In stands dominated by *P. tremuloides*, *P. glauca* and *A. balsamea*, *P. tremuloides* recruits within the first 3-6 years after fire (Figures 2.7a – c: Age at 30 cm), and again 60 years and 90 years after fire. *B. papyrifera* also recruits within the first 3-6 years after fire, and again 30 years, 65 years, and 80 years after fire (Figures 2.7a – c: Age at 30 cm). *P. glauca* recruits 6-10 years after fire, with a peak in recruitment 11-14 years after fire (Figures 2.7a – d: Age at 30 cm), and low and sporadic recruitment thereafter (Figures 2.7e – h: Age at 30 cm). *A. balsamea* recruits 20 years after fire, with peaks in recruitment 25

Figure 2.7   The static age distributions of individuals within each of eight stands

where age is determined at 30 cm above the root collar by simply counting

annual growth rings (Age at 30 cm), and where age is determined using

dendrochronology to locate the root collar and locally missing annual

growth rings (Age at root collar).

a)

■	P. tremuloides
▨	B. papyrifera
■	P. glauca
■	A. balsamea

Age at 30 cm

Age at root collar

Number

Age (years)

FIRE

b)

■	P. tremuloides
▨	B. papyrifera
■	P. glauca
■	A. balsamea

Age at 30 cm

Age at root collar

Number

Age (years)

FIRE

c) Age at 30 cm / Age at root collar

Legend: P. tremuloides, B. papyrifera, P. glauca, A. balsamea, P. mariana

d) Age at 30 cm / Age at root collar

Legend: P. tremuloides, P. glauca, A. balsamea

Age (years), FIRE

e) Age at 30 cm / Age at root collar

Legend:
- P. banksiana
- P. tremuloides
- B. papyrifera
- P. mariana

f) Age at 30 cm / Age at root collar

Legend:
- P. banksiana
- P. mariana

Axis labels: Number, Age (years), FIRE

years after fire (Figures 2.7a, d: Age at 30 cm), and 50, 70, and 100 years after fire (Figures 2.7b, d: Age at 30 cm).

When the ages of the same individuals are determined by counting the rings at the root collar and cross-dating to locate missing annual growth rings, however, most individuals are in fact substantially older (Figures 2.7a – d: Age at root collar). Species classified as early-successional (*P. tremuloides* and *B. papyrifera*) and mid- and late-successional (*P. glauca* and *A. balsamea*) all recruit within the first 6 years after fire (Figures 2.7a – d: Age at root collar). *P. tremuloides* and *B. papyrifera* also recruit 60 and 80 years after fire (Figures 2.7b - c: Age at root collar), while *P. glauca* recruits 70 years after fire only in one stand (Figure 2.7c: Age at root collar). *A. balsamea* also recruits in significant numbers 50, 60, and 100 years after fire (Figures 2.7b – d: Age at root collar). Interestingly, few individuals of any species in the understorey are older than 50 years, despite wide variation in stand age.

In stands dominated by *P. banksiana* and *P. mariana*, when the age of individuals is determined by simply counting annual growth rings at 30 cm, the pattern of ages in each stand (Figures 2.7e – h: Age at 30 cm) is also similar to the pattern found in nearly all other studies from the boreal forest. *P. banksiana* recruits within the first 3-9 years after fire (Figures 2.7e – h: Age at 30 cm). *P. mariana* begins to recruit 6-9 years after fire, with a peak in recruitment 8-17 years after fire, and low and sporadic recruitment thereafter (Figures 2.7e – h: Age at 30 cm).

When the ages of the same individuals are determined by counting the rings at the

root collar, and cross-dating to locate missing rings, however, most individuals are in fact
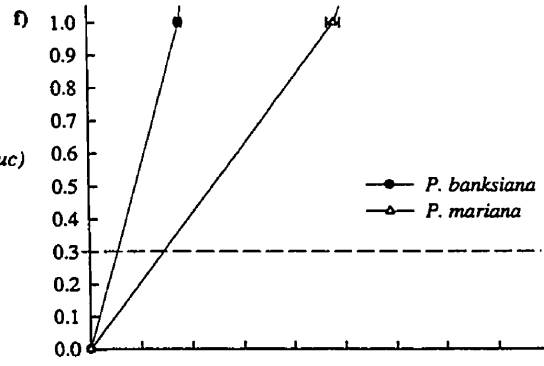
substantially older (Figures 2.7e – h: Age at root collar). Species classified as early-

successional (*P. banksiana*) and late-successional (*P. mariana*) recruit within the first

five years after fire (Figures 2.7e – h: Age at root collar). *P. mariana* recruits 30 years

and 100 years after fire (Figures 2.7e, g – h: Age at root collar). Interestingly, few

individuals in the understorey are older than 30 years, despite wide variation in stand age,

and, 71% of understorey *P. mariana* in the oldest stand is of branch layer origin from two

main *P. mariana* stems (Figure 2.7h: Age at root collar).

Discussion

In many early studies of forest succession the intention was simply to identify the

sequence of tree species through succession (*e.g.* Clements 1916; Cooper 1923; Oosting

1942). Often, this was done by subjectively classifying tree species as early-, mid- and

late-successional based on when they were dominant in the canopy. In later studies, when

tree age was determined by counting the annual growth rings at breast height or as close

to the base as possible, these successional classifications seemed to be confirmed; species

classified as early-successional always appeared to be older than those classified as mid-

and late-successional. These results have led to considerable speculation and debate as to

the cause of the delay in recruitment of species classified as mid- and late-successional, as

is evident in the vast literature generated on the subject within many different forest types

(*e.g.* Veblen *et al.* 1991; Bergeron & Charron 1994; Huff 1995; Galipeau *et al.* 1997;

Kneeshaw & Burton 1997; Feller 1998; Donnegan & Rebertus 1999; Bergeron 2000; among others). Most causes are related to the environmental and other conditions immediately after stand initiation, *e.g.* lack of nearby available seed sources, lack of suitable seedbeds, low seed crop, high seedling mortality rates in dry, open sites, *etc.* However, our results show that in the mixedwood boreal forest of central Saskatchewan when tree age is determined accurately, using dendrochronology at the root collar, there is no delay in recruitment of species classified as mid- and late-successional; all species recruit into the post-fire cohort immediately after fire. Consequently, we suggest that classifying these boreal tree species as early-, mid-, or late-successional based on the timing of their recruitment is misleading.

Our results demonstrate that counting the annual growth rings of an individual at 30 cm, or any height, above the root collar, as is done in almost all previous studies[1], underestimates the age at root collar for two reasons: growth rings laid down between the root collar and any sampling height above the root collar are not counted, and some trees do not lay down rings each year on all stem segments, *i.e.* they have locally missing growth rings. Aging trees at any height above the root collar differentially underestimates age at the root collar because there are species differences in the number of rings laid down between the root collar and any sampling height above the root collar. Species classified as early-successional (*P. tremuloides, B. papyrifera,* and *P. banksiana*) grow

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1 There appears to be a lot of confusion as to what is meant by root collar. Some studies have indicated that tree ages were determined at root collar level; however, most are unclear about what the root collar is and do not outline clearly how to find it.

relatively rapidly such that fewer rings are laid down between the root collar and sampling height, compared to species classified as mid- and late-successional (*P. glauca*, *A. balsamea*, and *P. mariana*). It should be noted that our reconstructions of age at 30 cm above root collar are likely less subject to underestimation of age at root collar than those of other studies, where age is determined by coring trees 30 cm above ground level. The distance between ground level and 30 cm is likely greater than 30 cm above the root collar because the root collar of most trees is below mineral soil (DesRochers & Gagnon 1997, Parent *et al.* 2000, S.L. Gutsell, unpublished data).

Aging tree species above the root collar also differentially underestimated root collar age because there are species differences in the occurrence of locally missing growth rings. Species classified as early-successional have relatively fewer individuals with locally missing rings, and fewer missing rings per individual, compared to those classified as mid- and late-successional. It should be noted that the number of individuals in our stands with locally missing rings is likely an underestimate because the youngest seedlings and saplings have so few growth rings that detecting locally missing rings is difficult. Also, some tree species, especially *P. glauca* and *A. balsamea*, have relatively wide rings with little variation in width, *i.e.* complacent rings. Other studies from the boreal forest of Québec have found aging to be very difficult in *A. balsamea* (Parent *et al.* 2000) and *P. mariana* (DesRochers & Gagnon 1997) due to a reverse taper phenomenon, *i.e.* a progressive loss of growth rings on the outer part of the stem on cross-sections examined from ground level towards the hypocotyl. We found few individuals of any

species with this problem. The fact that some trees do not lay down rings every year is not new; dendrochronologists have known this for many years (*e.g.* Fritts 1976; Schweingruber 1989), and have demonstrated this in a variety of tree species. What our study and other studies that have used dendrochronology to determine tree age have clearly demonstrated is that cross-dating techniques must be used in order to accurately determine the ages of all species of trees.

Despite these age corrections it is clear that some individuals, especially *A. balsamea* and *P. mariana*, do recruit in significant numbers in the understorey cohort after the initial post-fire period. Some would argue that these understorey individuals are going to replace the post-fire individuals when stands reach old age; however, their presence in the understorey is not evidence that such a replacement will occur. To determine whether such a replacement would occur is beyond the scope of this paper; however, it is interesting to note that, despite a wide range of stand ages, few individuals of *A. balsamea* are older than 50 years of age, and few individuals of *P. mariana* are older than 30 years of age. Also, in our study area, few (<5%) stands will live longer than 150 years due to the short fire cycle (Weir *et al.* 2000).

Distinctions between species classified as early-, mid- and late-successional have also been based on perceived species differences in height growth rates; species classified as early-successional are believed to have more rapid height growth rates compared to those classified as mid- and late-successional (*e.g.* Desponts & Payette 1992; Bergeron & Charron 1994; Kneeshaw & Burton 1997; Bergeron 2000). Our results show that there

are differences in height growth rates between species classified as early-, mid-, and late-successional, however, only in the early part of their growth, specifically, within the first one metre. Above one metre, the height growth rates of all species within a stand do not appear to be different. Within a stand, the mean height growth rates of *P. tremuloides*, *P. glauca*, and *A. balsamea* above one metre do not appear to be significantly different, and in some cases the mean height growth rate of *P. glauca* exceeds that of *P. tremuloides*. Similarly, within a stand, the mean height growth rates of *P. banksiana* and *P. mariana* above one metre do not appear to be different except in one stand, where the mean height growth of *P. mariana* exceeds that of *P. banksiana*. Because the height growth rate of each species changes over time, tree species cannot be characterized by a single overall growth rate. Further, because species differences in mean height growth occur only for a short period of time (relative to their life span), height growth rates cannot be used as a basis for distinguishing between boreal tree species and classifying them as early-, mid-, or late-successional.

The fact that species classified as early-successional have relatively higher growth rates between the root collar and the first one metre means that they are less severely underestimated when aged above the root collar. This explains why species classified as early-successional often appear to be older than those classified as mid- and late-successional. It also explains why species classified as early-successional are taller for most of their lifetime compared to species classified as mid- and late-successional. Because species classified as mid- and late-successional get a slow start, they remain in

the shadow of those classified as early-successional, often, until the next stand-replacing fire.

The timing of recruitment and height growth rates are only two characteristics of tree species that have been thought to be different for species classified as early-, mid-, or late-successional; other characteristics include life span, shade tolerance, and mode of seed dispersal. Many studies from a variety of forest types have concluded that these characteristics (typically called life-history characteristics) are the principal mechanisms that drive forest succession (*e.g.* Drury & Nisbet 1973; Noble & Slatyer 1980; Peet & Christensen 1980; Hibbs 1983; Walker & Chapin 1986; Pickett *et al.* 1987; Veblen *et al.* 1991; Barbour *et al.* 1999), and their role in promoting species replacement during succession has been incorporated into several successional models (*e.g.* Noble & Slatyer 1980; Huston & Smith 1987; Tilman 1988). In the mixedwood boreal forest, however, at least two of these characteristics, age and height growth rates, do not differ between tree species classified as early-, mid-, and late-successional, and consequently, these characteristics are not the mechanisms of forest succession, as is often believed.

While our conclusions may not apply to all forest types, we suggest that, before conclusions can be drawn regarding recruitment patterns and species' classifications in other areas, the age of all tree species must be determined by excavating the stump, locating the root collar, and using dendrochronology to locate any locally missing rings. If it is not possible to excavate the stumps of all individuals, as is often the case in many study areas that are on protected lands, attempts should be made to sample the stumps of

a range of sizes of each species. This may be possible in unprotected areas nearby the study area where tree species are growing under environmental conditions similar to those of the study area. Also, if species are to be classified based on height growth rates, individual height growth curves must be shown. Failing to carefully examine both age at the root collar and individual height growth rates may lead to misconceptions regarding forest dynamics.

It is clear from our results that in the mixedwood boreal forest of Saskatchewan tree species classified as early-, mid-, and late-successional recruit within the first 5-10 years after fire. Species with lower initial growth rates will, for most of their lifetime, remain relatively shorter than species with higher initial growth rates, giving the false impression that the former are younger. Some species, particularly *A. balsamea* and *P. mariana*, may recruit in large numbers in the understorey; however, there is no evidence that they will ever replace the post-fire cohorts in the canopy. Thus, we conclude that the rapid recruitment of all tree species after fire and the short fire cycle in our study area mean that, between catastrophic wildfires, any changes in the composition or abundance of species within a stand are driven primarily by the mortality rates of the post-fire canopy trees.

Literature Cited

Barbour, M.G., Burk, J.H., Pitts, W.D., Gilliam, F.S., and Schwartz, M.W. 1999. *Terrestrial Plant Ecology*. Addison Wesley Longman, Inc. Menlo Park, CA., U.S.A.

Beckingham, J.D., Nielsen, D.G., and Futoransky, V.A. 1996. *Field guide to the mid-boreal ecoregions of Saskatchewan*. Canadian Forest Service - NW Region Special Report 6.

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

Bergeron, Y. and Charron, D. 1994. Post-fire stand dynamics in southern boreal forest (Quebec): a dendroecological approach. *Ecoscience* **1**:173-184.

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

Bridge, S.R.J., and Johnson, E.A. 2000. Geomorphic principles of terrain organization and vegetation gradients. *Journal of Vegetation Science* **11**: 57-70.

Clements, F.E. 1916. *Plant Succession*. Carnegie Institute of Washington Publication 242.

Cooper, W.S. 1923. The recent ecological history of Glacier Bay, Alaska. II. The present vegetation cycle. *Ecology* **4**: 223-246.

Desponts, M., and Payette, S. 1992. Recent dynamics of jack pine at its northern distribution limit in northern Quebec. *Canadian Journal of Botany* **70**: 1157-

1167.

Desrochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of

black spruce age? *Canadian Journal of Forest Research* **27**: 1263-1267.

Donnegan, J.A., and Rebertus, A.J. 1999. Rates and mechanisms of subalpine forest

succession along an environmental gradient. *Ecology* **80**: 1370-1384.

Drury, W.H., and Nisbet, I.C.T. 1973. Succession. *Journal of the Arnold Arboretum* **54**:

331-368.

Egler, F.E. 1954. Vegetation science concepts. 1. Initial floristics composition – a factor

in old-field vegetation development. *Vegetatio* **4**: 412-417.

Engelmark, O., Hofgaard, A., and Arnborg, T. 1998. Successional trends 219 years after

fire in an old *Pinus sylvestris* stand in northern Sweden. *Journal of Vegetation

Science* **9**: 583-592.

Feller, M.C. 1998. Influence of ecological conditions on Engelmann spruce (*Picea

engelmannii*) and subalpine fir (*Abies lasiocarpa*) germinant survival and initial

seedling growth in south-central British Columbia. *Forest Ecology and

Management* **107**: 55-69.

Frelich, L.E., and Reich, P.B. 1999. Neighborhood effects, disturbance severity, and

community stability in forests. *Ecosystems* **2**: 151-166.

Fritts, H.C. 1976. *Tree Rings and Climate.* Academic Press, New York, NY.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir

colonization of a site in the southeastern boreal forest as observed 68 years after

fire. *Canadian Journal of Forest Research* **27**: 139-147.

Hibbs, D.E. 1983. Forty years of forest succession in central New England. *Ecology* **64**: 1394-1401.

Hofgaard, A. 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *Journal of Vegetation Science* **4**: 601-608.

Huff, M.H. 1995. Forest age structure and development following wildfires in the western Olympic Mountains, Washington. *Ecological Applications* **5**: 471-483.

Huston, M., and Smith, T. 1987. Plant succession: life history and competition. *American Naturalist* **130**: 168-198.

Johnson, E.A., Miyanishi, K., and Kleb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta – Picea Engelmannii* forest. *Journal of Ecology* **82**: 923-931.

Kneeshaw, D.D., and Burton, P.J. 1997. Canopy and age structures of some old sub-boreal *Picea* stands in British Columbia. *Journal of Vegetation Science* **8**: 615-626.

Lieffers, V.J., Stadt, K.J., and Navratil, S. 1996. Age structure and growth of understorey white spruce under aspen. *Canadian Journal of Forest Research* **26**: 1002-1007.

Linder, P., Elfving, B., and Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* **98**: 17-33.

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

Norton, D.A., and Ogden, J. 1990. Problems with the use of tree rings in the study of forest population dynamics. In *Methods of Dendrochronology: Applications in the Environmental Sciences*. Ed. E.R. Cook & L.A. Kairiukstis, Kluwer Academic Publications, Boston, MA.

Oosting, H.J. 1942. An ecological analysis of the plant community of Piedmont, North Carolina. *American Midland Naturalist* 28: 1-126.

Palik, 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.

Parent, S., Morin, H., and Messier, C. 2000. Effects of adventitious roots on age determination in Balsam fir (*Abies balsamea*) regeneration. *Canadian Journal of Forest Research* 30: 513-518.

Peet, R.K., and Christensen, N.L. 1980. Succession: a population process. *Vegetatio* 43: 131-140.

Pickett, S.T.A., Collins, S.L., and Armesto, J.J. 1987. Models, mechanisms and pathways of succession. *The Botanical Review* 53: 335-371.

Rowe, J.S. 1972. *Forest Regions of Canada*. Environment Canada, Canadian Forest Service, Ottawa. Publication 1300F.

Schweingruber, F.H. 1989. *Tree Rings: Basics and Application of Dendrochronology.*

Kluwer Academic Publications, Holland.

St-Pierre, H., Gagnon, R., and Bellefleur, P. 1992. Régénération après feu de l'épinette

noire (*Picea mariana*) et du pin gris (*Pinus banksiana*) dans la forêt boréale,

Québec. *Canadian Journal of Forest Research* 22: 474-481.

Telewski, F.W., and Lynch, A.M. 1991. Measuring growth and development of stems.

In: *Techniques and Approaches in Forest Tree Ecophysiology.* Ed. J.P. Lassoie

and T.M. Hinckley. CRC Press Inc., Boston, MA.

Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities.*

Princeton University Press, Princeton, N.J.

Veblen, T.T., Hadley, K.S., and Reid, M.S. 1991. Disturbance and stand development of

a Colorado subalpine forest. *Journal of Biogeography* 18: 707-716.

Walker, L.R., and Chapin, F.S. III. 1986. Physiological controls over seedling growth in

primary succession on an Alaskan floodplain. *Ecology* 67: 1508-1523.

Weir, J.M.H., Johnson, E.A., and Miyanishi, K. 2000. Fire frequency and the spatial age

mosaic of the mixedwood boreal forest in western Canada. *Ecological

Applications* 10: 1162-1177.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living

trees. *Canadian Journal of Forest Research* 21: 414-416.

CHAPTER THREE

Why methods commonly used to study forest succession

fail to accurately explain the forest dynamics

Introduction

Succession is one of the earliest concepts in ecology (Warming 1895; Cowles 1899). It is generally defined as the changes through time in community structure and function, and species abundance (Horn 1974; Crawley 1986; Veblen 1986; Barbour *et al.* 1999). Changes in species abundance lead to changes in both community structure and function, and consequently the mechanisms that drive succession are the population processes of recruitment and mortality (Peet and Christensen 1980;, Johnson and Fryer 1989; Johnson *et al.* 1994). Forest succession has been defined many ways, *e.g.* changes over time in biomass, species diversity, productivity *etc.*, (see reviews by Drury and Nisbet 1973; and Pickett 1976); however, in this chapter I will limit the definition of succession to changes over time in species composition and abundance because it appears to be one of the more commonly accepted definitions.

A clear understanding of forest succession has been limited by the long life span of trees. To get around this difficulty, ecologists have developed a number of methods that use empirical data to infer patterns of succession. These methods infer succession using one of two approaches. The first, called the static approach, uses data from a single point in time, while the second, called the dynamic approach, attempts to reconstruct data back in time.

The static approach includes at least four methods: static diameter distributions, size class associations, static age distributions, and chronosequences (*e.g.* Saldarriaga *et al.* 1988; Bergeron and Dubuc 1989; Veblen *et al.* 1991; Frelich 1992; Takahashi 1994; Frelich and Reich 1995; Huff 1995, Kubota 1995; Galipeau *et al.* 1996; Goebel and Hix 1996; Norland and Hix 1996; Goebel and Hix 1997; Linder *et al.* 1997; Kuuluvainen *et al.* 1998a,b; Bergeron 2000; DeGrandpré *et al.* 2000; Gauthier *et al.* 2000). A static diameter distribution and size class association is constructed by dividing individuals within a stand into size (usually diameter) classes. Succession is inferred by assuming that the changes in species composition and abundance observed over decreasing size classes within a stand are the same changes one would see if the stand was followed through time. A static age distribution is constructed by dividing individuals within a stand into age classes. Succession is inferred by assuming that the changes in species composition and abundance observed over decreasing age classes within a stand are the same changes one would see if the stand was followed through time. The chronosequence uses a series of spatially separate sites or stands which have been initiated at different times in the past. Data collected from within each stand is typically of species abundance, *i.e.* density (number/hectare) or basal area (m^2/ m^2). Succession is inferred by assuming that the changes in species composition and abundance observed over stands of increasing age are the same changes one would see if each stand was followed through time.

The dynamic approach includes at least three methods: permanent sample plots,

paleoecology, and reconstructed age distributions (Oliver & Stephens 1977; Pickett 1983;

Jackson et al.1988; Johnson & Fryer 1989; Johnson et al. 1994; Fastie 1995). A

permanent sample plot records the changes in composition and abundance of individuals

within a stand over a period of time, sometimes as long as 40-50 years. In paleoecology,

a sediment core is removed from a lake or pond in order to examine pollen macrofossils

deposited over time by vegetation from the surrounding area. The species present in the

area over a period of time can be reconstructed by examining the composition and relative

abundance of pollen from species within sediment layers, from the most recently

deposited upper layers, to the deepest layers deposited further back in time.

Reconstructed age distributions reconstruct the dates of recruitment and death of

individuals back in time using dendrochronology; patterns of recruitment and death can

be followed back in time within each stand.

All methods make assumptions and have limitations that prevent them from being

able to accurately determine all of the changes over time in species composition and

abundance within a stand or stands. The static diameter distribution, size class

association, static age distribution, and chronosequences share the principal assumption

that the changes in species composition and abundance observed over decreasing size or

age classes within a stand, or over stands of increasing age, are the same changes one

would see if each stand was followed through time. The static diameter distribution and

size class association also assume that diameter and age are positively correlated, while

the static age distribution also assumes that age, as determined by coring and counting

annual rings at the base of a tree, reflects the date of recruitment, *i.e.* age at the root

collar.

The assumption of the static diameter distribution and size class association, that

diameter and age are positively correlated, has been tested by some studies (*e.g.* Blum

1961; Gibbs 1963; Johnson and Fryer 1989; Huff 1995; Lowenstein *et al.* 2000). The

assumptions of the static age distribution and chronosequence have been acknowledged

by some studies, and the methods have been criticized (*e.g.* Drury and Nisbet 1973;

Pickett 1976; Johnson *et al.* 1994); however, the assumptions are rarely rigorously tested

with empirical data. In fact, with the widespread practice of not testing the assumptions

(*e.g.* Whipple & Dix 1979; Veblen 1986; Bergeron and Dubuc 1989; Veblen *et al.* 1991;

Kneeshaw & Burton 1997; Linder *et al.* 1997; Bergeron 2000; DeGrandpré *et al.* 2000),

there seems to be general acceptance that they are valid.

Permanent sample plots, paleoecology, and reconstructed age distributions

attempt to overcome the principal assumption of the static diameter distribution, size

class association, static age distribution, and chronosequences, by looking at changes

within each stand back in time. This is accomplished by recovering as much data from

the past as possible. However, these methods are limited because data from much of the

past cannot be recovered. Data collected from within long-term permanent plots are often

inappropriate for present purposes, primarily because they were often started for very

different purposes than those today. For example, often only the diameter (not age) of

individuals above a certain height (usually breast height) was recorded, leaving smaller

individuals out of the record. Data from paleoecological records is limited primarily

because there are often species differences in the ability of pollen to fossilize, and thus

there may be bias in the record. Reconstructed age distributions are limited because all

individuals that have recruited and died within a stand cannot be detected at the time of

sampling. In particular, many of the smaller individuals (*i.e.* in the seedling or sapling

stage) that die and decompose before a stand is sampled will not be included in the

reconstructions, and thus a full picture of the patterns of recruitment and mortality is not

possible.

A large number of recent studies in many different forest types have used static

diameter distributions, static age distributions, and chronosequences to infer patterns of

succession (*e.g.* Saldarriaga *et al.* 1988; Bergeron and Dubuc 1989; Veblen *et al.* 1991;

Frelich 1992; Takahashi 1994; Frelich and Reich 1995; Huff 1995; Kubota 1995;

Galipeau *et al.* 1996; Goebel and Hix 1996; Norland and Hix 1996; Goebel and Hix

1997; Linder *et al.* 1997; Kuuluvainen *et al.* 1998a,b; Bergeron 2000; DeGrandpré *et al.*

2000; Gauthier *et al.* 2000). Yet few studies have used empirical data to rigorously test

the assumptions of each method. Thus, the purpose of this chapter is to: 1) test the

assumptions of the static diameter distributions, static age distributions, and

chronosequences, and 2) compare the interpretation of succession given by static diameter

distributions, static age distributions, chronosequences, and reconstructed age

distributions. With data from the same stands, patterns of succession will be inferred

using static diameter distributions, static age distributions, and chronosequences. We will

see that the conclusions of these methods are similar to the conclusions of traditional successional studies from the boreal forest. Then, with data from the same stands as above, the assumptions of each method will be tested. Finally, patterns of succession will be interpreted using the reconstructed age distributions and compared to the patterns from the three static methods. As we will see, the interpretations given by the reconstructed age distributions are different from those of the static diameter distributions, static age distributions, and chronosequences, primarily because the assumptions of static diameter distributions, static age distributions, and chronosequences are not met.

Methods

STUDY AREA

The study area is located in central Saskatchewan, Canada (53° 45' N to 54° 45' N and 106° 0' W to 106° 57' W). The topography of this area is gently rolling, ranging in elevation from approximately 525-650 metres a.s.l. The climate is characterized by long, cold winters and short, cool summers. July and August are the warmest months of the year with average maximum temperature exceeding 20°C three days out of four. The average annual precipitation ranges from 400 to 500 mm, of which 70% occurs as rain.

The major disturbance in this region is large, high intensity, lightning-caused wildfires that kill most of the canopy trees and understorey vegetation. These fires are controlled primarily by weather; variation in topography, substrate and microclimate has a relatively minor influence on fire intensity (Weir *et al.* 2000). The fire cycle has

changed twice over the past 235 years, and is presently estimated to be 75-150 years. The study area is part of the Boreal Mixedwood Forest (Rowe 1972), which is dominated by eight upland tree species, including: *Populus tremuloides* Michx., *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., *Pinus banksiana* Lamb., *Picea mariana* (Mill) B.S.P., *Populus balsamifera* L., *Larix laricina* (Du Roi) K. Koch., and *Betula papyrifera* Marsh.

Moisture and nutrients are the principal environmental gradients controlling the distribution of upland plant species within the area (Bridge and Johnson 2000). The gradients are controlled by surficial material (primarily glacial till and glaciofluvial) and the hill slope geomorphic processes. The tops of glacial till hill slopes are at the middle of the moisture and nutrient gradient and are dominated by *P. tremuloides*. At mid-slope positions, *P. glauca* and *P. tremuloides* co-dominate, while at the bottom of slopes, where moisture and nutrients increase, *P. glauca* and *A. balsamea*, co-dominate. The tops of glaciofluvial hill slopes are at the dry end of the moisture gradient and low end of the nutrient gradient, and are dominated by *P. banksiana*. At mid-slope positions, *P. banksiana* co-dominates with *P. mariana*, while at the bottom of slopes, where moisture and nutrients increase, *P. mariana* dominates.

FIELD AND LABORATORY METHODS

We sampled 12 stands varying in geomorphic surface, hill slope position, species composition, and time since the last stand-replacing fire (Table 3.1). Stands dominated by *P. tremuloides* were located top to mid-slope on glacial till hill slopes, while stands

dominated by *P. glauca* and *A. balsamea* were located mid to bottom slope on glacial till

hill slopes. Stands dominated by *P. banksiana* and *P. mariana* were located top to mid

slope on glaciofluvial hill slopes, while stands dominated by *P. mariana* were located

bottom slope on glaciofluvial hill slopes. Stand age, reflecting time since the last stand

replacing fire, varied from 35-154 years. The time-since-fire of each stand was

determined using a high-resolution fire frequency map of the study area (Weir *et al.*

2000).

Stands varied in size from 64 to 576 square metres, to include a minimum of 25 of

the most abundant canopy individuals (Table 3.1). The selection criteria for stands were

as follows: 1) stands had no evidence of anthropogenic disturbance, 2) vegetation was

rooted in mineral soil, with no evidence of standing water in the top 30 cm of mineral

soil, and 3) each stand was visually homogenous with respect to stand age, stand

structure, and species composition.

Each stand was divided into a grid, every 2-metres, and all live and dead (standing

and downed) seedlings (<50 cm height), saplings (>50 cm height, <5 cm basal diameter),

and trees (>5 cm basal diameter) were labeled and mapped. Two or three workers

carefully searched the entire stand to ensure that all individuals (including newly

recruited seedlings, if present) were located. All seedlings, along with their roots, were

removed from the ground. Using hand rakes, we carefully removed all of the organic

Table 3.1   Stand characteristics for twelve upland stands from the southern

mixedwood boreal forest, Saskatchewan. Figure label indicates the stand

represented in each Figure. T-S.F is the time since the last stand replacing

fire, *i.e.* time-since-fire.

Figure label	Stand ID	Geomorphic Material	Hill slope Position	T-S-F	Fire Date	Tree Species	Density (no./ha)
a	TA5	Glacial till	top	55	1942	*Populus tremuloides*	3700.0
						Betula papyrifera	2200.0
b	TA1	Glacial till	top	78	1919	*Populus tremuloides*	1302.0
						Picea glauca	130
						Abies balsamea	178.0
c	TA8	Glacial till	top-mid	111	1886	*Populus tremuloides*	1860.0
						Betula papyrifera	1180.5
						Picea glauca	1111.1
						Abies balsamea	3437.5
						Picea mariana	555.6
d	WS4	Glacial till	mid-bot	55	1942	*Populus tremuloides*	178.5
						Betula papyrifera	416.7
						Picea glauca	2559.5
						Abies balsamea	59.5
e	WS2	Glacial till	middle	78	1919	*Populus tremuloides*	2720.0
						Betula papyrifera	850.0
						Picea glauca	718.8
						Abies balsamea	4030.0
f	BF2	Glacial till	mid-bot	154	1843	*Populus tremuloides*	312.5
						Betula papyrifera	60.0
						Picea glauca	562.5
						Abies balsamea	19280.0
g	BS15	Glaciofluvial	bottom	35	1964	*Picea glauca*	6388.9
						Picea mariana	16900.0
						Populus balsamifera	833.0
						Larix laricina	277.8
h	BS7	Glaciofluvial	bottom	110	1886	*Picea mariana*	8570.0
						Picea glauca	710.0
i	BS9	Glaciofluvial	bottom	153	1843	*Picea mariana*	2527.0
						Picea glauca	160.0
						Populus balsamifera	54.9
j	JP5	Glaciofluvial	middle	77	1919	*Picea mariana*	5900.0
						Pinus banksiana	2200.0
k	JP8	Glaciofluvial	middle	126	1870	*Picea mariana*	950.0
						Pinus banksiana	1285.7
l	JP11	Glaciofluvial	middle	153	1843	*Populus tremuloides*	9400.0
						Betula papyrifera	1000.0
						Picea glauca	400.0
						Picea mariana	8400.0
						Pinus banksiana	700.0

material, down to mineral soil, from within the entire plot. Organic material was removed to uncover all buried individuals, which were then labeled and mapped. Next, *all* sapling and tree stumps were completely removed from the ground by first cutting each individual at the base, and then cutting all lateral and tap roots (Figure 3.1). Total height, height to live crown base, and basal diameter were recorded for all live individuals, and total height and basal diameter were recorded for all dead (standing, downed, and buried) individuals. Finally, a disk was cut at every metre to the top of each sapling and tree for height growth analysis. To sample each stand took four workers 15-30 days.

All seedlings and sapling and tree disks and stumps were brought back to the lab for processing, *i.e.*, no samples were processed in the field. In total, the stumps and stem disks of 3902 seedlings, saplings and trees were collected and processed. Seedling ages were determined by counting bud scale scars from the root collar to the top of each seedling. The age of most seedlings greater than 0.25 cm basal diameter was also determined by counting annual growth rings at the root collar. To locate the root collar of each seedling, sapling and tree, each stump was cut with a band saw into cross-sections 1.0 - 2.5 cm thick, and sanded sequentially with coarse and fine sand papers (up to 600 grain). The root collar was located in all samples using a 10-60X power-dissecting microscope, and noting from one cross section to the next, the shift in the central pith, from undifferentiated parenchyma cells in the stem, to a vascular cylinder in the root (Telewski and Lynch 1991). All tree and sapling disks were sanded with coarse

Figure 3.1   Photograph showing how all stumps were removed from the ground.

to fine sand paper (up to 400 grain). The annual growth rings on all stem disks were counted along two radii to construct height growth curves.

To locate missing annual growth rings, *i.e.* years where an annual ring is not produced on all stem segments, within each seedling, sapling, and tree stump section we used standard dendrochronological techniques (Schweingruber 1989; Yamaguchi 1991). For each of the stump cross-sections we constructed a skeleton plot, which is a plot of unusually narrow or wide annual rings. Each skeleton plot was first cross-dated within the stump, and then against a species-specific master skeleton plot from each stand. Missing rings were evident when marker rings in a skeleton plot were offset compared to other skeleton plots from within a stump, and when compared to the master plot. Sample processing and analysis of each stand took one technician 40-60 days.

INFERRING SUCCESSION USING STATIC DIAMETER DISTRIBUTIONS, STATIC AGE DISTRIBUTIONS, CHRONOSEQUENCES and RECONSTRUCTED AGE DISTRIBUTIONS

A static diameter distribution was constructed for each stand by dividing live individuals of each species into 5 cm basal diameter classes as follows: 1) $0.1 \geq 5$ cm; 2) $5.1 \geq 10$ cm; 3) $10.1 \geq 15$ cm, etc. A static age distribution was constructed for all live individuals within each stand based on the age at 30 cm above the root collar. Age at 30 cm was reconstructed for each seedling (those >30 cm height), sapling, and tree in each stand using age at the root collar and height growth curves from the cross-dated stump sections and stem disks.

Four chronosequences were constructed for different geomorphic substrates (glacial till and glaciofluvial) and hill slope positions by plotting changes in the density (number/m^2) and basal area (m^2/m2) of live individuals of each species over stands of increasing age. Two chronosequences were constructed from stands on glacial till substrates; one was constructed with top-mid slope stands (TA5, TA1, TA8), and the other was constructed with mid-bottom slope stands (WS4, WS2, BF2). Two chronosequences were constructed from stands on glaciofluvial substrates; one was constructed with bottom-slope stands (BS15, BS7, BS9), and the other with mid-slope stands (JP5, JP8, JP11). In all chronosequences, stand age (35-154 years) was used as a surrogate for time.

Age distributions were reconstructed for each stand, every ten years back in time, using the age at root collar of each individual. Dendrochronology was used to determine the dates of recruitment and death of all live and dead individuals. Within each stand the time period reconstructed was the time period over which dead individuals were detected.

TESTING ASSUMPTIONS and EXAMINING LIMITATIONS of STATIC DIAMETER DISTRIBUTIONS, STATIC AGE DISTRIBUTIONS, CHRONOSEQUENCES, and RECONSTRUCTED AGE DISTRIBUTIONS

We tested the three assumptions of static diameter distributions, static age distributions, and chronosequences, namely: 1) diameter and age are positively correlated, 2) age at 30 cm reflects the date of recruitment, 3) changes in species composition and

abundance observed over increasing size or age classes within a stand, or over a chronosequence, are the same changes one would see if each stand was followed through time. The first assumption was tested by examining the correlation between diameter and age for all individuals within each stand. The second assumption was tested by plotting the correlation between age at 30 cm and age at the root collar for all individuals within each stand. The third assumption was tested using the reconstructed age distributions of each stand, and the height growth curves of each individual. The time-since-fire distribution for the study area was also used (Weir *et al.* 2000). It is a cumulative survivorship distribution for the landscape, and gives the probability of a stand surviving without fire over increasing ages. Finally, the limitations of the reconstructed age distributions were examined.

Results

The results are organized as follows. First, patterns of succession are inferred within each stand using static diameter distributions. The first assumption of static diameter distributions, which is that diameter and age are positively correlated, is then tested. Second, patterns of succession are inferred within each stand using static age distributions. The first assumption of static age distributions, which is that age at 30 cm reflects the date of recruitment, is then tested. Third, patterns of succession are interpreted across stands using chronosequences. The principal assumption of static diameter distributions, static age distributions, and chronosequences, which is that

changes in species composition and abundance observed over increasing size or age

classes within a stand, or over a chronosequence, are the same changes one would see if

each stand was followed through time, is then tested.

For convenience, Table 3.2 summarizes the assumptions of each of the static

methods and limitations of reconstructed age distributions. Table 3.3 summarizes the

interpretations of succession given by each of the static methods, and the interpretations

given by reconstructed age distributions, height growth curves, and the time-since-fire

distribution.

INFERRING SUCCESSION USING THE STATIC DIAMETER DISTRIBUTION

Figure 3.2 gives the diameter distributions of stands on glacial till hill slopes

(Figures 3.2a-f), and glaciofluvial hill slopes (Figures 3.2g-l). Within glacial till stands,

three general patterns of succession can be inferred: 1) *P. tremuloides* and *B. papyrifera*

(if present) recruit continuously and dominate all through succession (Figures 3.2a-b); 2)

P. tremuloides and *P. glauca* recruit and dominate in early to mid-succession, and are

replaced by *P. glauca* and *A. balsamea* in late succession (Figure 3.2c); 3) *P. glauca*

recruits continuously and dominates all through succession (Figure 3.2d).

Figures 3.2g-l gives the diameter distributions of stands on glaciofluvial

substrates. Two general patterns of succession can be inferred: 1) *P. mariana* and *P.*

glauca recruit continuously and dominate all through succession (Figures 3.2g-i), and 2)

Table 3.2   A summary of the assumptions of static methods and limitations of

reconstructed age distributions.

Method	Assumptions/Limitations
Static Diameter Distribution	1) diameter and age are positively correlated 2) the changes in species composition and abundance observed over decreasing size classes within a stand are the same changes one would see if each stand was followed through time
Static Age Distribution	1) age, as determined by coring and counting annual rings at the base of a tree, reflects the date of recruitment, *i.e.* age at the root collar 2) the changes in species composition and abundance observed over decreasing age classes within a stand are the same changes one would see if each stand was followed through time
Chronosequence	1) the changes in species composition and abundance observed over stands of increasing age are the same changes one would see if each stand was followed through time
Reconstructed Age Distribution	1) all individuals that recruit and die within a population cannot be detected at the time of sampling

Table 3.3   For each stand, a summary of the interpretations of succession given by each

static method, and interpretations using reconstructed age distributions, height

growth rates, and the time-since-fire distribution.

Static Method	Interpretations of Succession Using Static Methods	Interpretations using Reconstructed Age Distributions, Height Growth, and Time-Since-Fire
Static Diameter Distribution	Glacial Till: **Top-mid slopes** 1)*P. tremuloides* and *B. papyrifera* recruit continuously and dominate all through succession 2)*P. tremuloides* and *P. glauca* recruit and dominate in early to mid-succession, and are replaced by *P. glauca* and *A. balsamea* in late succession **Mid-bottom slopes** 3)*P. glauca* recruits continuously and dominates all through succession Glaciofluvial: **Bottom slopes** *1)P. mariana* and *P. glauca* recruit continuously and dominate all through succession **Mid-slopes** 2)*P. banksiana* recruits and dominates early in succession, and *P. mariana* recruits and co-dominates with *P. banksiana* in mid succession. *P. banksiana* is replaced by *P. mariana* in late succession	Glacial Till: **Top-mid slopes** *P. tremuloides, B. papyrifera,* and *P. glauca* recruit within five years post-fire; only low recruitment thereafter, except in the oldest stand, with high recruitment 60-110 years post-fire; all cohorts suffer low mortality, with no change in species composition over time **Mid-bottom slopes** *P. tremuloides, B. papyrifera, A. balsamea,* and *P. glauca* recruit within ten years post-fire; only low recruitment thereafter until 50 and 140 years post-fire, where high recruitment of *A. balsamea* occurs in two stands; all cohorts suffer low mortality, with no change in species composition over time; in oldest stand, two large fires killed canopy trees, allowing understorey cohorts to grow into canopy Glaciofluvial: **Bottom slopes** *P. mariana, P. glauca,* and *P. balsamifera* recruit within ten years post-fire; low recruitment of *P. mariana* continues; all cohorts suffer low mortality, with no change in species composition over time **Mid-slopes** *P. banksiana, P. mariana* and *P. glauca* recruit within ten years post-fire; only low recruitment of *P. mariana* continues, except in the oldest stand where large numbers of *P. tremuloides, B. papyrifera, P. mariana,* and *P. glauca* recruited in the past 50 years; all cohorts suffer low mortality, with no change in species composition over time

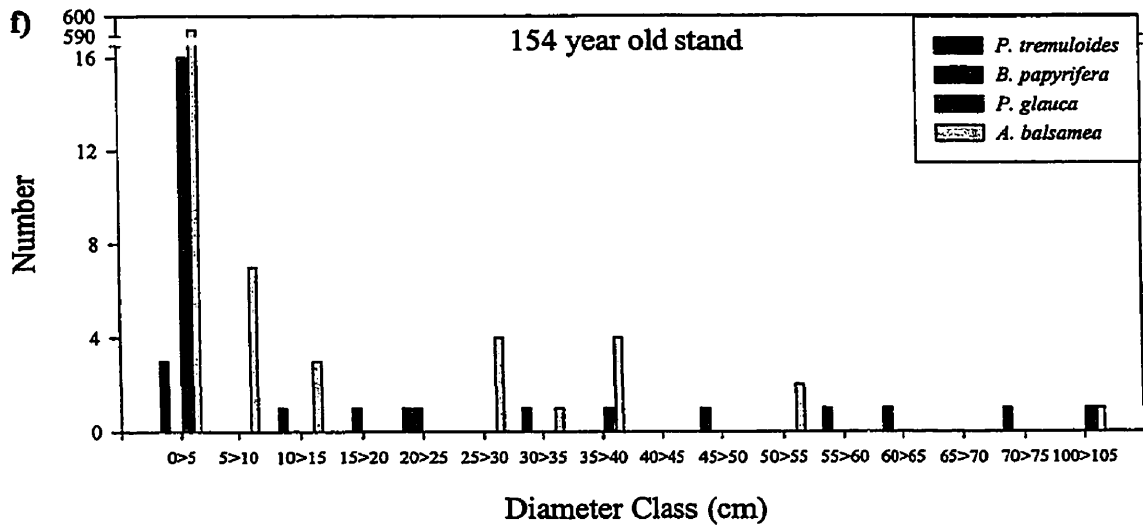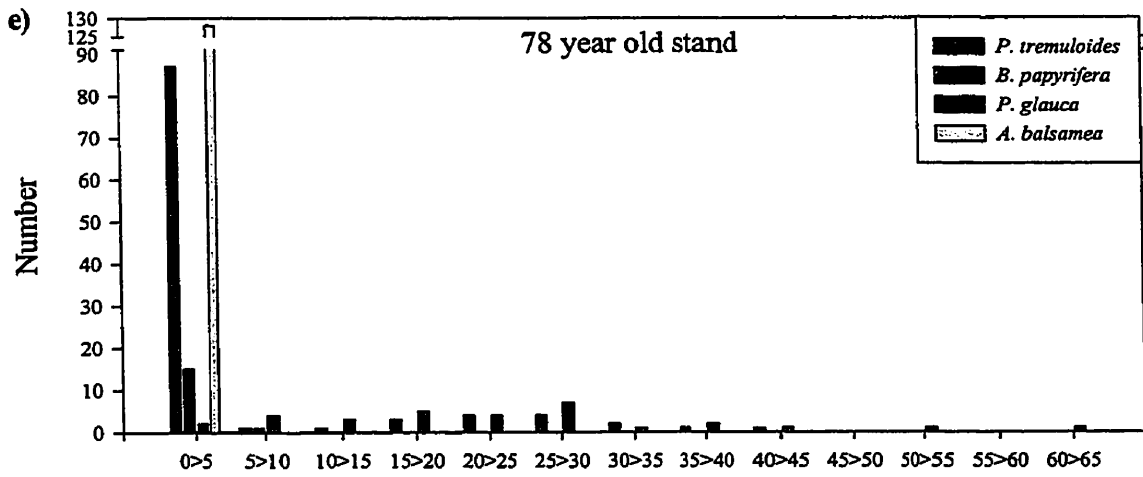| Static Method	Interpretations of Succession Using Static Methods	Interpretations using Reconstructed Age Distributions, Height Growth, and Time-Since-Fire
Static Age Distribution	Glacial Till: All slope positions 1)*P. tremuloides* and *B. papyrifera* recruit in early succession, followed after some time lag by *P. glauca*; they are replaced by *A. balsamea* in late succession	Glacial Till: Top-mid slopes *P. tremuloides*, *B. papyrifera*, and *P. glauca* recruit within five years post-fire; only low recruitment thereafter, except in the oldest stand, with high recruitment 60-110 years post-fire; all cohorts suffer low mortality, with no change in species composition over time Mid-bottom slopes *P. tremuloides*, *B. papyrifera*, *A. balsamea*, and *P. glauca* recruit within ten years post-fire; only low recruitment thereafter until 50 and 140 years post-fire, where high recruitment of *A. balsamea* occurs in two stands; all cohorts suffer low mortality, with no change in species composition over time; in oldest stand, two large fires killed canopy trees, allowing understorey cohorts to grow into canopy
	Glaciofluvial: Bottom slopes 1)*P. mariana* dominates all through succession	Glaciofluvial: Bottom slopes *P. mariana*, *P. glauca*, and *P. balsamifera* recruit within ten years post-fire; low recruitment of *P. mariana* continues; all cohorts suffer low mortality, with no change in species composition over time
	Mid-slopes 2)*P. banksiana* dominates in early succession and is replaced by *P. mariana* in late succession	Mid-slopes *P. banksiana*, *P. mariana* and *P. glauca* recruit within ten years post-fire; only low recruitment of *P. mariana* continues, except in the oldest stand where large numbers of *P. tremuloides*, *B. papyrifera*, *P. mariana*, and *P. glauca* recruited in the past 50 years; all cohorts suffer low mortality, with no change in species composition over time

Static Method	Interpretations of Succession Using Static Methods	Interpretations using Reconstructed Age Distributions, Height Growth, and Time-Since-Fire
Chronosequence	**Glacial Till:** **Top-mid slopes** *1)* In terms of density, *P. tremuloides* and *B. papyrifera* co-dominate in early succession, and *P. glauca* and *A. balsamea* co-dominate with *P. tremuloides* by late succession; in terms of basal area, *P. tremuloides* and *P. glauca* increase over time and co-dominate all through succession **Mid-bottom slopes** 2) In terms of density, *P. glauca* dominates in early succession, co-dominating with *P. tremuloides* and *A. balsamea* in mid-succession; *A. balsamea* dominates in late succession; in terms of basal area, *P. glauca* dominates in early succession, and co-dominates with *A. balsamea, B. papyrifera,* and *P. tremuloides* by late succession. **Glaciofluvial:** **Bottom slopes** 1) In terms of density, *P. mariana* and *P. glauca* co-dominate through early and mid-succession, and *P. mariana* dominates in late succession; in terms of basal area, *P. mariana* and *P. glauca* co-dominate in early succession, and *P. mariana* dominates in late succession. **Mid-slopes** 2) In terms of density, *P. banksiana* and *P. mariana* co-dominate through early and mid-succession, and *P. mariana* dominates by late succession; in terms of basal area, *P. banksiana* and *P. mariana* dominate all through succession.	**Glacial Till:** **Top-mid slopes** *P. tremuloides, B. papyrifera,* and *P. glauca* recruit within five years post-fire; only low recruitment thereafter, except in the oldest stand, with high recruitment 60-110 years post-fire; all cohorts suffer low mortality, with no change in species composition over time **Mid-bottom slopes** *P. tremuloides, B. papyrifera, A. balsamea,* and *P. glauca* recruit within ten years post-fire; only low recruitment thereafter until 50 and 140 years post-fire, where high recruitment of *A. balsamea* occurs in two stands; all cohorts suffer low mortality, with no change in species composition over time; in oldest stand, two large fires killed canopy trees, allowing understorey cohorts to grow into canopy **Glaciofluvial:** **Bottom slopes** *P. mariana, P. glauca,* and *P. balsamifera* recruit within ten years post-fire; low recruitment of *P. mariana* continues; all cohorts suffer low mortality, with no change in species composition over time **Mid-slopes** *P. banksiana, P. mariana,* and *P. glauca* recruit within ten years post-fire; only low recruitment of *P. mariana* continues, except in the oldest stand where large numbers of *P. tremuloides, B. papyrifera, P. mariana,* and *P. glauca* recruited in the past 50 years; all cohorts suffer low mortality, with no change in species composition over time

Figure 3.2   The static diameter distributions of live individuals within each of 12

stands, where individuals are divided into 5 cm basal diameter classes.

Figures a - l indicate stands a – l as identified in Table 3.1.

a) 55 year old stand
Number

Legend: *P. tremuloides*, *B. papyrifera*

Diameter classes: 0>5, 5>10, 10>15, 15>20

b) 78 year old stand
Number

Legend: *P. tremuloides*, *P. glauca*, *A. balsamifera*

Diameter classes: 0>5, 5>10, 10>15, 15>20, 20>25, 25>30, 30>35, 35>40, 40>45

c) 111 year old stand
Number

Legend: *P tremuloides*, *B. papyrifera*, *P. glauca*, *A. balsamea*, *P. mariana*

Diameter classes: 0>5, 5>10, 10>15, 15>20, 20>25, 25>30, 30>35, 35>40, 40>45, 45>50

Diameter Class (cm)

d)

55 year old stand

Legend: P. tremuloides, B. papyrifera, P. glauca, A. balsamea

e)

78 year old stand

Legend: P. tremuloides, B. papyrifera, P. glauca, A. balsamea

f)

154 year old stand

Legend: P. tremuloides, B. papyrifera, P. glauca, A. balsamea

Diameter Class (cm)

g)

35 year old stand

Legend: P. balsamifera, P. mariana, P. glauca, L. laricina

h)

110 year old stand

Legend: P. mariana, P. glauca

i)

153 year old stand

Legend: B. papyrifera, P. balsamifera, P. mariana, P. glauca

Diameter Class (cm)

j) 77 year old stand

Legend: P. banksiana, P. mariana

k) 126 year old stand

Legend: P. banksiana, P. mariana

l) 153 year old stand

Legend: P. banksiana, P. tremuloides, B. papyrifera, P. mariana, P. glauca

Diameter Class (cm)

P. banksiana recruits and dominates early in succession, and *P. mariana* recruits and co-dominates with *P. banksiana* in mid succession. *P. banksiana* is replaced by *P. mariana* in late succession (Figures 3.2j-1).

Testing the assumption that diameter and age are positively correlated

The assumption that diameter and age are positively correlated was tested by plotting the relationship of basal diameter and age at the root collar of each individual within each stand (Figures 3.3a-1). In stands where there was a range of ages for a particular species, I also fit a curve through the data to test if there was a significant positive relationship between diameter and age (Figures 3.3a, f, g, h, 1). I used age at the root collar because, as we will see below, age at root collar more accurately reflects the date of recruitment.

In general, for most species there is a very poor correlation between diameter and age (Figures 3.3a-1). Individuals that recruit within the first ten years after fire have a very wide range of diameters corresponding to a very narrow range of age. Conversely, individuals that recruit after the initial ten-year period, in the understorey, have a very wide range of ages corresponding to a relatively narrow range of diameters.

In the 55 year old stand dominated by *P. tremuloides* and *B. papyrifera* (Figure 3.3a), there is a significant relationship between diameter and age for *B. papyrifera*. However, notice that there are only eleven individuals younger than 50 years, and, of

Figure 3.3   The relationship of basal diameter and age at root collar for individuals

within each of 12 stands.

a)

b)

c)

d)

55 year old stand

Legend:
- ■ *P. tremuloides*
- ▲ *B. papyrifera*
- ▽ *P. glauca*
- △ *A. balsamea*

e)

78 year old stand

Legend:
- ■ *P. tremuloides*
- ▲ *B. papyrifera*
- ▽ *P. glauca*
- △ *A. balsamea*

f)

154 year old stand

Legend:
- ■ *P. tremuloides*
- ▲ *B. papryifera*
- ▽ *P. glauca*
- △ *A. balsamea*
- —— *A. balsamea*
  diam = 0.077e^{0.082age}, r² = 0.75

Age (years)

g)

h)

i)

j)

Diameter (cm)

- ● *P. banksiana*
- □ *P. mariana*

77 year old stand

Age values: 0 10 20 30 40 50 60 70

k)

Diameter (cm)

- ● *P. banksiana*
- □ *P. mariana*

126 year old stand

Age values: 0 10 20 30 40 50 60 70 80 90 100 110 120

l)

Diameter (cm)

- ● *P. banksiana*
- ■ *P. tremuloides*
- ▲ *B. papyrifera*
- □ *P. mariana*
- ▽ *P. glauca*
- —— *P. mariana*

$\text{diam} = -1.625 + 0.130\,\text{age}, \; r^2 = 0.86$

153 year old stand

Age (years)

Age values: 0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150

those that are 50-55 years of age, there is a wide range in diameter (6.1 – 16.8 cm). In the

154 year old stand dominated by *A. balsamea* and *P. tremuloides* (Figure 3.3f), there is a

significant relationship between diameter and age for *A. balsamea*. However, notice that

for individuals 0-22 years of age there is a narrow range of diameter (0.01 – 1.0 cm).

Also, notice that the 148 year old *A. balsamea* is well outside of the fitted curve.

In the 35 year old stand dominated by *P. mariana* and *P. glauca* (Figure 3.3g),

there is a significant relationship between diameter and age for *P. mariana*. However, for

individuals 30-35 years of age there is a relatively wide range of diameter (0.7 – 9.3 cm).

There is also a significant relationship between diameter and age for *P. glauca*; however,

for individuals 30-35 years of age there is a wide range of diameter (2.8 – 13.7 cm). In

the 110 year old stand dominated by *P. mariana* (Figure 3.3h) there is a significant

relationship between diameter and age for *P. mariana*; however, for individuals 3-47

years of age there is a narrow range of diameter (0.05 – 1.1 cm). And, for individuals

100-110 years of age there is a wide range of diameter (2.5 – 27.5 cm). Finally, in the

153 year old stand dominated by *P. banksiana* and *P. mariana* (Figure 3.3l), there is a

significant relationship between diameter and age for *P. mariana*. However, for

individuals 5-58 years there is a narrow range of diameter (0.1 – 4.7 cm)

These results show that, in nearly all stands, diameter and age are poorly

correlated, and thus diameter cannot easily be used as a correlate of age. The plots of

diameter and age reveal that there is not a continuous period of recruitment of

individuals, as inferred from the static diameter distributions. Instead, there appear to be

two distinct periods of recruitment. One period of recruitment occurs within the first ten years after fire, and another longer period of recruitment occurs within the most recent 30-50 year period.

INFERRING SUCCESSION USING THE STATIC AGE DISTRIBUTION

Figure 3.4 shows the static age distributions of all stands, where age is determined at 30 cm above the root collar. In stands on glacial till substrates (Figures 3.4a-f), the patterns of succession can be inferred as follows. *P. tremuloides* and *B. papyrifera* recruit within the first 5 years after fire, and sporadically thereafter (Figures 3.4a-d). *P. glauca* recruits 5-15 years after fire, and sporadically thereafter (Figures 3.4b-f). *A. balsamea* recruits 15-20 years after fire, and in significant numbers in late succession. In summary, within glacial till stands, *P. tremuloides* and *B. papyrifera* recruit in early succession, followed after some time lag by *P. glauca*. They are eventually replaced by *A. balsamea* in late succession.

In stands on glaciofluvial substrates (Figures 3.4g-l), the patterns of succession can be inferred as follows. *P. mariana* and *P. glauca* recruit 10-15 years after fire, and *P. mariana* recruits sporadically thereafter (Figure 3.4g-i). *P. banksiana* recruits within the first 10 years after fire, followed by *P. mariana*, which recruits 10-20 years after fire, and sporadically thereafter (Figures 3.4j-l). In summary, either *P. mariana* dominates all through succession, or *P. banksiana* dominates in early succession and is replaced by *P. mariana* in late succession.

Figure 3.4   The static age distributions for all live individuals within each of 12

stands, where age is determined at 30 cm above the root collar.

a) 55 year old stand

Legend: ■ *P. tremuloides* ■ *B. papyrifera*

Y-axis: Number

b) 78 year old stand

Legend: ■ *P. tremuloides* ■ *P. glauca* ▨ *A. balsamea*

Y-axis: Number

c) 111 year old stand

Legend: ■ *P. tremuloides* ■ *B. papyrifera* ■ *P. glauca* □ *A. balsamea* ■ *P. mariana*

Y-axis: Number

X-axis: Age at 30 cm (years)

d)

55 year old stand

Legend:
- P. tremuloides
- B. papyrifera
- P. glauca
- A. balsamea

e)

78 year old stand

Legend:
- P. tremuloides
- B. papyrifera
- P. glauca
- A. balsamea

f)

154 year old stand

Legend:
- P. tremuloides
- B. papyrifera
- P. glauca
- A. balsamea

Age at 30 cm (years)

g)

35 year old stand

Legend:
- P. balsamifera
- P. mariana
- P. glauca
- L. laricina

h)

110 year old stand

Legend:
- P. mariana
- P. glauca

i)

153 year old stand

Legend:
- P. balsamifera
- P. mariana
- P. glauca

Age at 30 cm (years)

j)

77 year old stand

P. banksiana
P. mariana

k)

126 year old stand

P. banksiana
P. mariana

l)

153 year old stand

P. banksiana
P. tremuloides
B. papyrifera
P. mariana
P. glauca

Age at 30 cm (years)

Testing the assumption that age at 30 cm reflects the date of recruitment, i.e. age at the root collar

The assumption that age at 30 cm reflects the date of recruitment, *i.e.* age at root collar, was tested by plotting the age at 30 cm above the root collar and age at the root collar of each individual within each stand (Figures 3.5a-l). Within each figure, the diagonal line indicates a perfect correlation between the age at 30 cm and age at the root collar. The further from the diagonal, the greater number of years underestimated at 30 cm. Notice that no points lie below the diagonal line because it is not possible for age at 30 cm to be greater than age at the root collar.

The age at 30 cm underestimates root collar age for all species, and the degree to which it is underestimated differs both within and between species. In stands on glacial till (Figures 3.5a – f), *P. tremuloides* and *B. papyrifera* have the fewest number of years underestimated at 30 cm and smallest range, 0-8 years and 0-11 years, respectively. Conversely, *P. glauca* and *A. balsamea* have the greatest number of years underestimated at 30 cm and largest ranges, 0-37 years and 2-43 years, respectively. In stands on glaciofluvial (Figures 3.5g - l), *P. banksiana* has the fewest number of years underestimated at 30 cm and the smallest range, 1-10 years, compared to *P. mariana*, with 3-58 years underestimated.

These results show that, for all species, age at 30 cm underestimates age at root collar and thus age at 30 cm does not accurately reflect the date of recruitment. The age at root collar reveals that there is no lag in recruitment of *P. glauca, P. mariana,* or *A.*

Figure 3.5   The relationship of age at 30 cm and age at root collar for each individual

within each of 12 stands.

a) 55 year old stand
Age at root collar
P. tremuloides
B. papyrifera

b) 78 year old stand
Age at root collar
P. tremuloides
P. glauca
A. balsamea

c) 111 year old stand
Age at rootcollar
P. tremuloides
B. papyrifera
P. glauca
A. balsamea
P.mariana

d) 55 year old stand
Age at root collar
P. tremuloides
B. papyrifera
P. glauca
A. balsamea

e) 78 year old stand
Age at rootcollar
P. tremuloides
B. papyrifera
P. glauca
A. balsamea

f) 154 year old stand
Age at root collar
p. tremuloides
B. papyrifera
P. glauca
A. balsamea

Age at 30 cm (years)

g) 35 year old stand
- ▲ B. papyrifera
- □ P. mariana
- ▽ P. glauca
- ◇ L. laricina

j) 77 year old stand
- ● P. banksiana
- □ P. mariana

h) 110 year old stand
- □ P. mariana
- ▽ P. glauca

k) 126 year old stand
- ● P. banksiana
- □ P. mariana

i) 153 year old stand
- ▼ P. balsamifera
- □ P. mariana
- ▽ P. glauca

l) 153 year old stand
- ● P. banksiana
- ■ P. tremuloides
- ▲ B. papyrifera
- □ P. mariana
- ▽ P. glauca

Age at root collar

Age at 30cm

balsamea, as inferred from the static age distributions. Instead, all species recruit within the first ten years after fire. There is another period of recruitment of some species, primarily within the most recent 30-50 year period.

INFERRING SUCCESSION USING CHRONOSEQUENCES

In this section, succession will be inferred using the chronosequences. In the next section I will test the principal assumption shared by static diameter distributions, static age distributions, and chronosequences, which is that changes over size or age classes within a stand, or across stands, are the same changes one would see within each stand if followed through time. To avoid repetition, notice that I will not re-state the interpretations of succession using static diameter distributions and static age distributions.

Figures 3.6a - d show changes in dominance of species across a chronosequence of stands, by density and basal area, on glacial till hill slopes (Figure 3.6a and b), and glaciofluvial hill slopes (Figure 3.6c and d).

The patterns of succession can be inferred as follows. On glacial till top-mid slope stands (Figure 3.6a) in terms of density, *P. tremuloides* and *B. papyrifera* co-dominate in early succession and decrease through time. *P. glauca* and *A. balsamea* increase in density over time, co-dominating with *P. tremuloides* by late succession. In terms of basal area, *P. tremuloides* and *P. glauca* increase over time and co-dominate all through succession.

Figure 3.6   Chronosequences constructed by plotting changes over density and basal

area of each species within stands on: a) top-mid slopes on glacial till, b)

mid-bottom slopes on glacial till, c) bottom-slopes on glaciofluvial, and d)

mid-slopes on glaciofluvial.

a)

b)

c)

d)
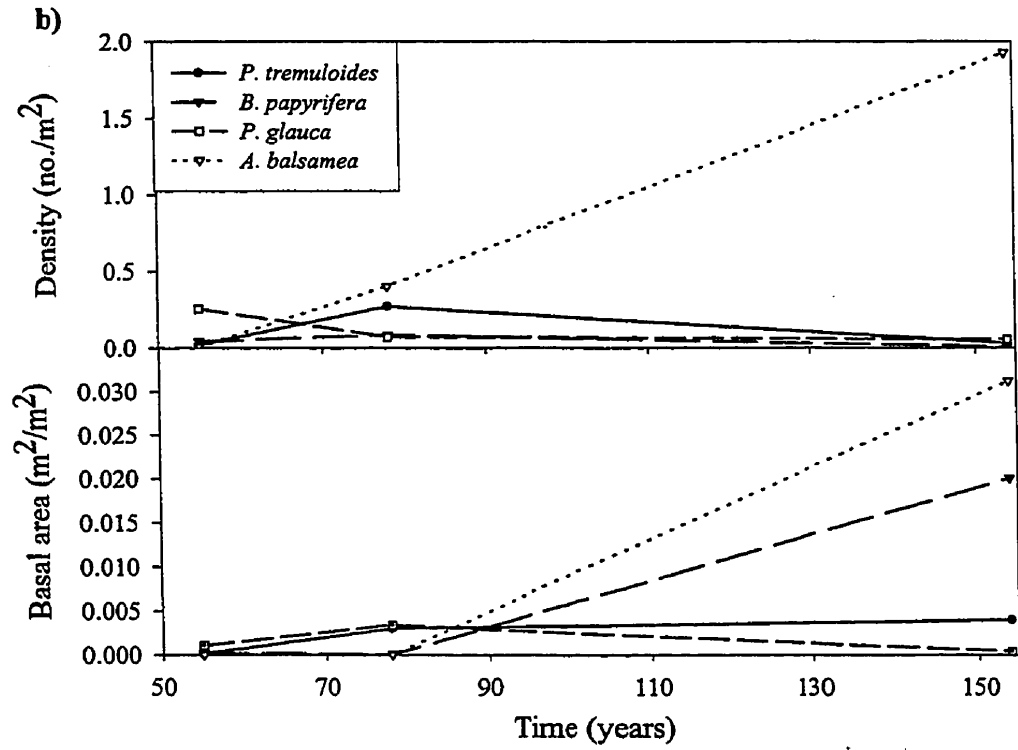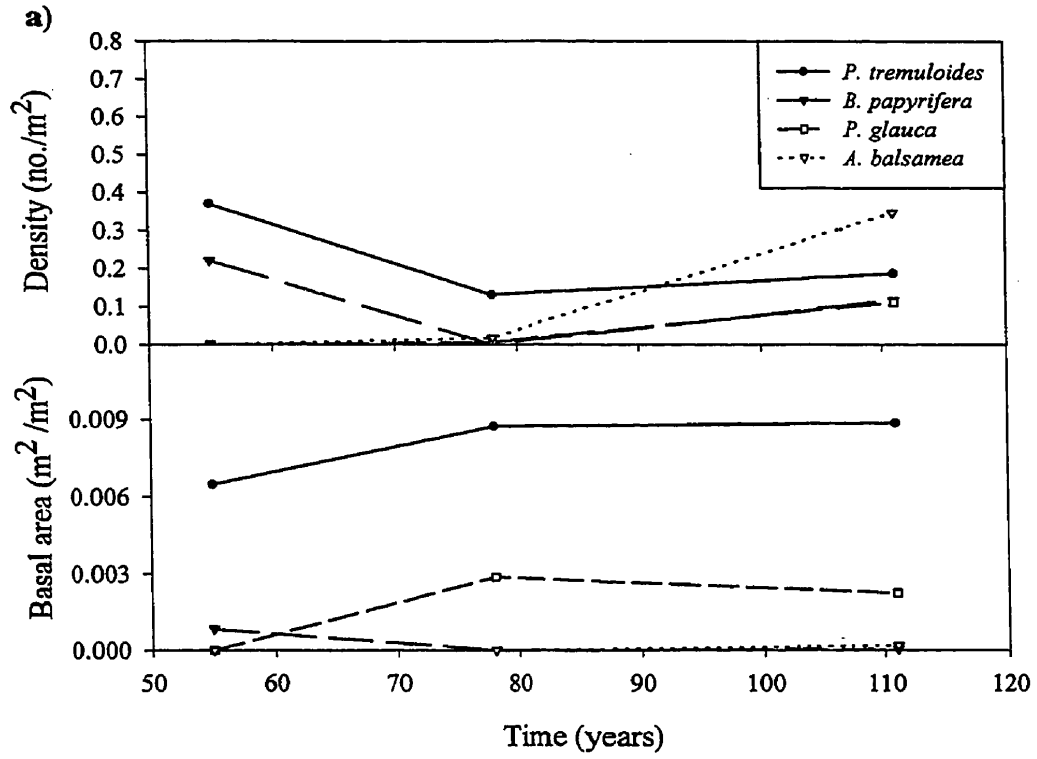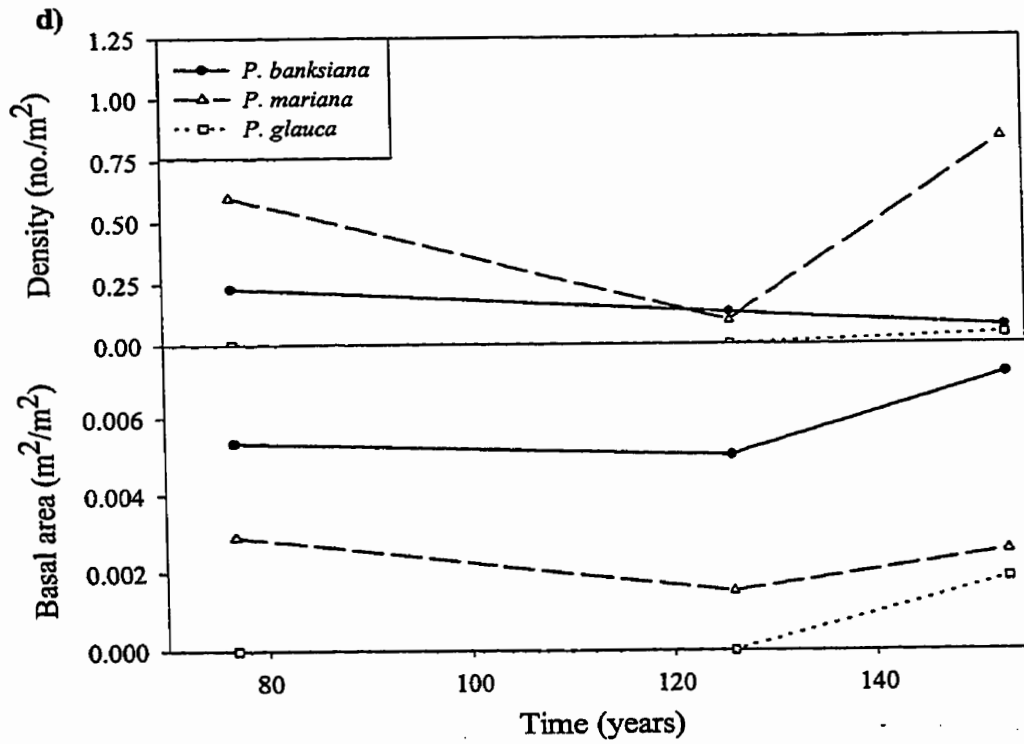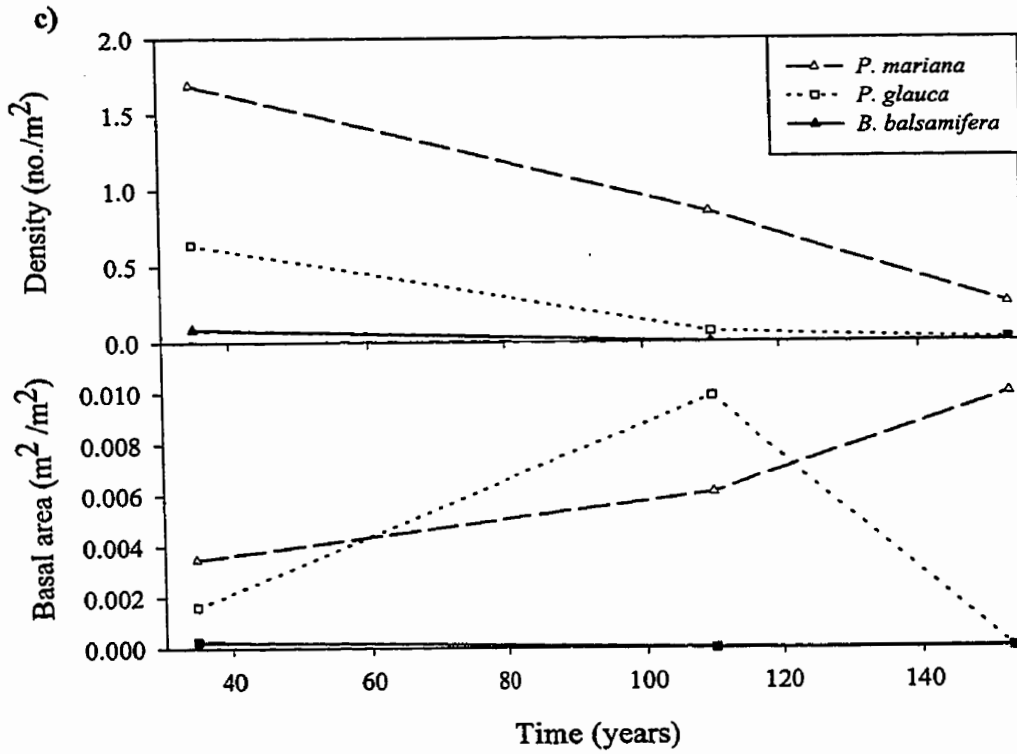
On glacial till mid-bottom slope stands (Figure 3.6b) in terms of density, *P. glauca* dominates in early succession, co-dominating with *P. tremuloides* and *A. balsamea* in mid-succession. *A. balsamea* dominates in late succession. In terms of basal area, *P. glauca* dominates in early succession , and co-dominates with *A. balsamea, B. papyrifera*, and *P. tremuloides* by late succession.

On glaciofluvial bottom slope stands (Figure 3.6c) in terms of density, *P. mariana* and *P. glauca* co-dominate through early and mid-succession, with *P. mariana* dominating in late succession. In terms of basal area, *P. mariana* and *P. glauca* co-dominate in early succession, and *P. mariana* dominates in late succession.

On glaciofluvial midslope stands (Figure 3.6d) in terms of density, *P. banksiana* and *P. mariana* co-dominate through early and mid-succession, and *P. mariana* dominates by late succession. In terms of basal area, *P. banksiana* and *P. mariana* dominate all through succession.

Testing the principal assumption of static diameter distributions, static age distributions, and chronosequences, that changes over size or age classes within a stand, or across stands, are the same changes one would see within each stand if followed through time

The principal assumption shared by static diameter distributions, static age distributions, and chronosequences will be tested by first using the reconstructed age distributions. With the reconstructed age distribution we can look back in time within

each stand to determine if there are detectable changes over time in species composition and abundance as predicted by static diameter distributions, static age distributions, and chronosequences. Then, individual height growth curves and the time-since-fire distribution will be used to further examine the probability that, within stands, there are changes over time in species composition and abundance.

Reconstructed age distributions

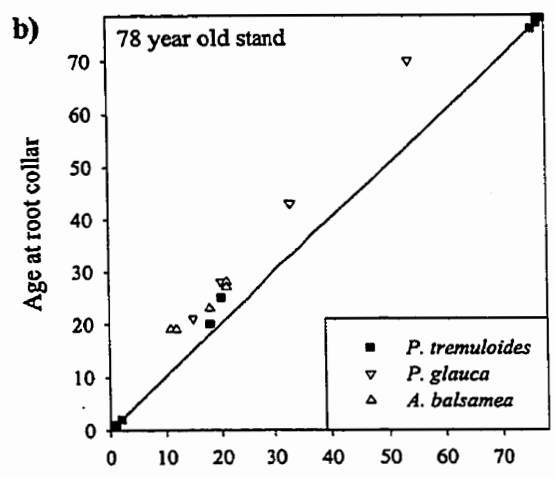Figures 3.7a - l show the reconstructed age distributions for every ten years back in time within each stand, where age is determined at the root collar. Stands were divided based on geomorphic substrate, glacial till and glaciofluvial, and based on hillslope position. Stands a-c were located top to mid slope on glacial till (Figures 3.7a - c) and stands d-f were located mid to bottom slope on glacial till (Figures 3.7d - f). Stands g-i were located bottom slope on glaciofluvial (Figures 3.7g - i), while stands j-l were located mid slope on glaciofluvial (Figures 3.7j-l).

Within top to mid slope glacial till stands, *P. tremuloides, B. papyrifera*, and *P. glauca* (if present) recruit within the first five years after fire (Figures 3.7a - c). There is very low and sporadic recruitment of *B. papyrifera* and *P. glauca* after the initial recruitment period except in the oldest stand, where large numbers of *P. tremuloides, B. papyrifera, P. glauca, P. mariana,* and *A. balsamea* recruit in the understorey 60-110 years after fire. Looking back in time within each stand shows that there has been some mortality of all species from both post-fire and understorey cohorts.

Figure 3.7   The age distributions of all 12 stands, reconstructed every 10 years

back in time to the date of the last detectable death. Age of individuals

was determined at the root collar.

a)

b)

c)

d)

e)

P. tremuloides
B. papyrifera
P. glauca
A. balsamea

1947

1957

1967

1977

1987

1997

Number

Age (years)

FIRE

h)

i)

1936

P. balsamifera
P. mariana
P. glauca

1946

1956

1966

1976

1986

1996

Number

Age (years)

FIRE

j)

Legend:
- ■ *P. banksiana*
- □ *P. mariana*

Panels (top to bottom): 1946, 1956, 1966, 1976, 1986, 1996

Y-axis: Number

X-axis: Age (years), FIRE

I)

P. banksiana
P. tremuloides
B. papyrifera
P. mariana
P. glauca

1926

1936

1946

1956

1966

1976

1986

1996

Number

Age (years)

FIRE

Within mid to bottom slope stands on glacial till, *P. tremuloides, B. papyrifera, P. glauca,* and *A. balsamea* recruit within the first ten years after fire (Figures 3.7d - f).

There is low and sporadic recruitment of most species after this period until 50 and 140 years after fire, when significant numbers of *A. balsamea* recruit in the understorey. Looking back in time within each stand shows some mortality of both post-fire and understorey cohorts. Notice in the oldest stand (Figure 3.7f) that at least two fires have burned parts of the stand within the last 154 years, one 112 years ago, and another 64 years ago. Both fires appear to have killed large numbers of individuals. The fact that fires occurred in one of our oldest stands is not surprising given the nature of the fire regime in the boreal forest. As subsequent fires over-burn each other, the amount of area originating from fires further in the past becomes increasingly smaller.

Within bottom slope glaciofluvial stands, *P. balsamifera, P. mariana,* and *P. glauca* recruit primarily within the first ten years after fire (Figures 3.7g - i). There is low and sporadic recruitment of *P. mariana* after this initial period in the two youngest stands (Figures 3.7g - h); however, notice that there are no individuals in the understorey in the oldest stand (Figure 3.7i). Looking back in time within each stand shows that there has been some mortality of both post-fire and understorey individuals.

Within mid slope glaciofluvial stands (Figures 3.7j - l), *P. banksiana, P. mariana,* and *P. glauca* (if present) recruit within the first five years after fire. There is very low recruitment of *P. mariana* after the post-fire period, except in the oldest stand (Figure 3.7l) where there is a significant number of understorey *P. tremuloides, B. papyrifera, P.*

mariana, and *P. glauca* younger than 50 years. Most (71%) of the *P. mariana*

understorey recruits are of branch layer origin, and most (96%) of the *B. papyrifera* are

sprouts growing out of the base of a single dead *B. papyrifera* canopy tree (Figure 3.71).

Looking back in time within each stand shows that there has been some mortality of both

post-fire and understorey individuals.

In stands dominated by only a single species, the interpretations of succession

from all methods are similar, that is, a single species will dominate all through

succession; however, only post-fire individuals will make it to the canopy. In stands with

more than one species, the interpretations of static diameter distributions, static age

distributions, and chronosequences differ from the interpretations of reconstructed age

distributions. The static diameter distributions, static age distributions, and

chronosequences conclude that there will be a shift in dominance, or replacement, from

those recruiting soon after fire, (*i.e.* post-fire cohorts), with those recruiting later (*i.e.*

understorey cohorts). If such a replacement is going to occur, then one should expect to

see a gradual increase in mortality of the post-fire cohorts, together with increased

recruitment and growth, and low mortality of understorey cohorts. However, the

reconstructed age distributions did not show differential increases in mortality of post-fire

cohorts; relatively few individuals of both post-fire and understorey cohorts died.

As I will discuss later (see Examining the Limitations of Reconstructed Age

Distributions, page 126), all individuals that have recruited and died within a stand cannot

be recovered. Thus, the reconstructed age distributions cannot give a complete picture of

the changes over time in the abundance and composition within stands.

Height growth and the time-since-fire distribution

Used alone, the reconstructed age distributions do not provide adequate convincing evidence that the understorey cohorts will or will not replace the post-fire cohorts when stands reach old age. In what follows, I will examine the likelihood of species replacement using the height growth curves of individuals within our oldest stands, and the time-since-fire distribution. I only examine height growth in the four oldest stands because, if species are going to be replaced over time, we should expect to begin to see evidence of such a replacement in the oldest stands. If a replacement will occur, we must assume that canopy cohorts will die and some understorey individuals will survive beyond 30 or 50 years.

We examined the height growth curves of individuals in the four oldest stands, initiated 111 years ago, 154 years ago, and 153 years ago. In the 111-year old stand (Figure 3.8a), dominated in the canopy by *P. tremuloides,* and *P. glauca,* there are a significant number of *B. papyrifera*, *A. balsamea,* and *P. mariana* in the understorey. Based on their present growth rates and the growth rates of post-fire individuals of the same species, it should take the most rapidly growing understorey individuals, on average, another 100 years to reach the canopy (Figure 3.9a). This means that the stand would have to survive without a stand replacing fire for 211 years. From the time-since-fire distribution, only 0.8% of the landscape survives without fire for 211 years (Figure

Figure 3.8   Height growth curves of individuals from the four oldest stands.

a)

111 year old stand

Legend:
- P. tremuloides
- B. papyrifera
- P. glauca
- A. balsamea
- P. mariana

Y-axis: Height (m), values 0, 5, 10, 15, 20, 25

X-axis: Year, values 1886, 1906, 1926, 1946, 1966, 1986

FIRE

b)

c)

d)
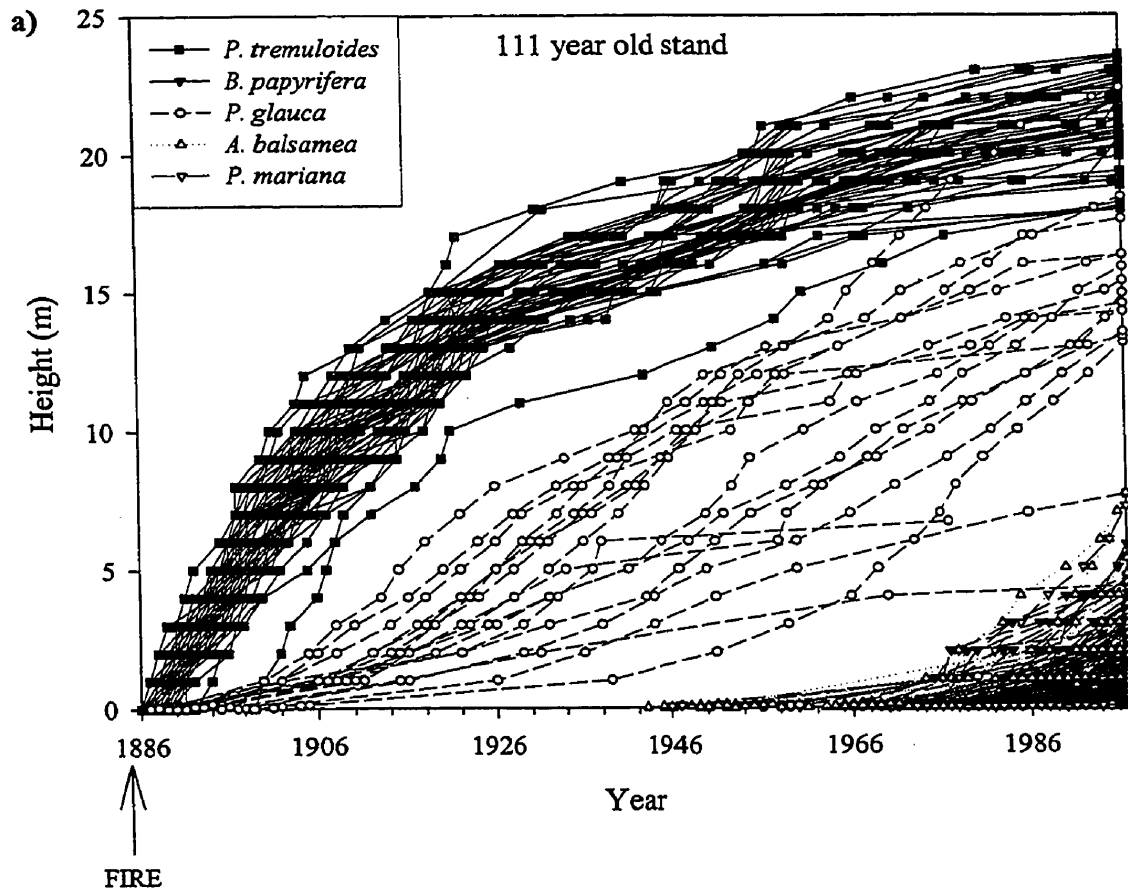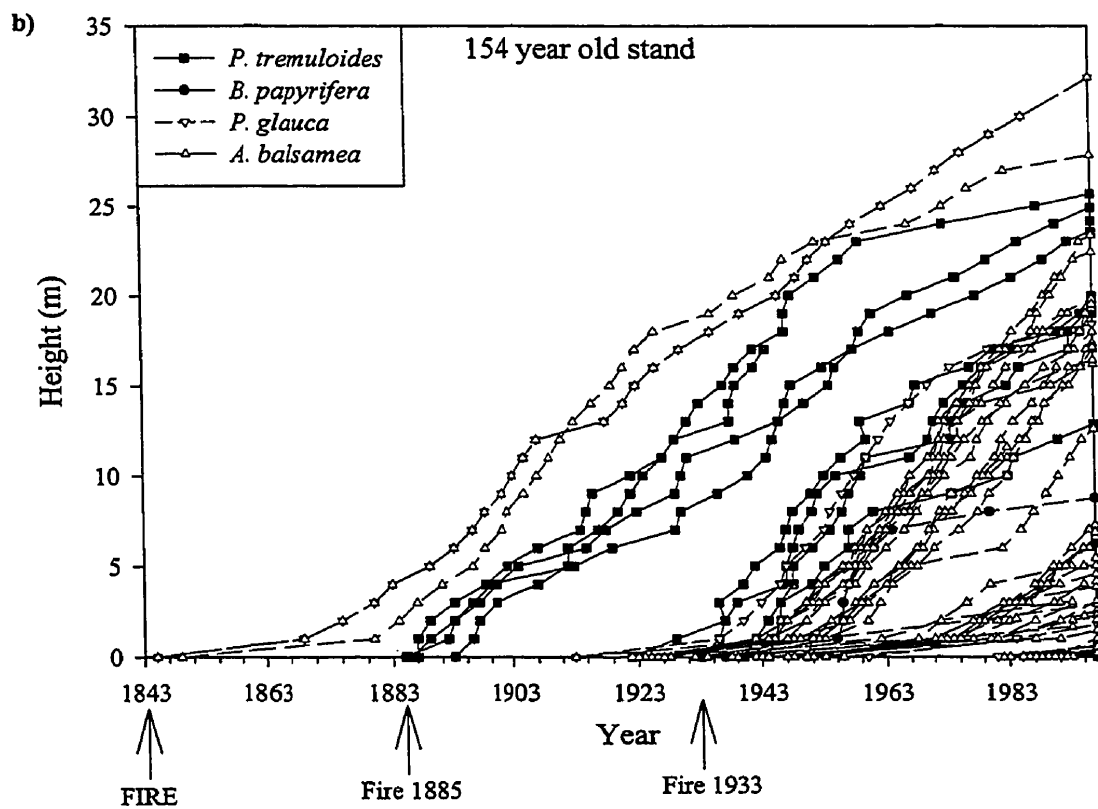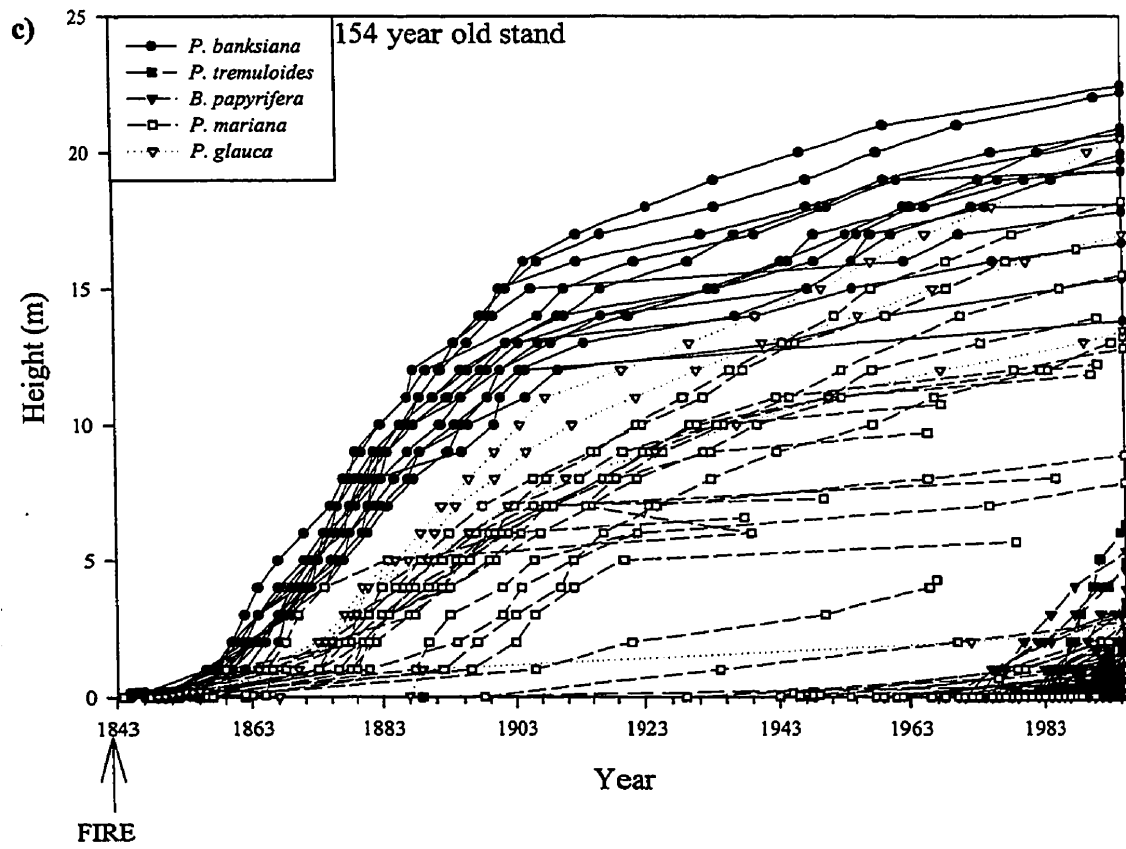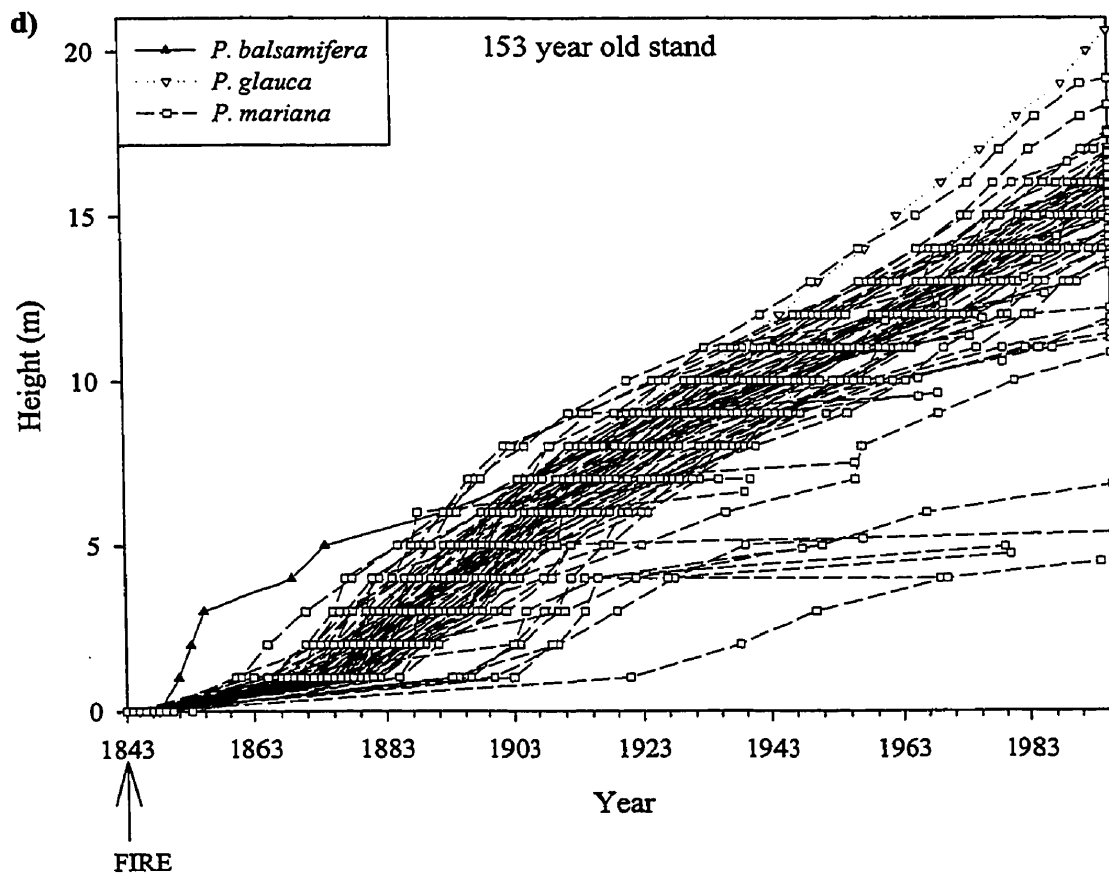
Figure 3.9   Height growth curves of individuals from three of the oldest stands, with

height growth projections used to estimate the time it would take for the

most rapidly growing understorey individuals to replace canopy cohorts.

a)

b)

Figure showing height (m) versus year for a 154 year old stand, with species P. tremuloides, B. papyrifera, P. glauca, and A. balsamea. Fire events marked at FIRE (1843), Fire 1885, and Fire 1933.

c)

Height (m) vs Year plot for a 153 year old stand, with legend:
P. banksiana
P. tremuloides
B. papyrifera
P. mariana
P. glauca

FIRE (arrow at 1843)
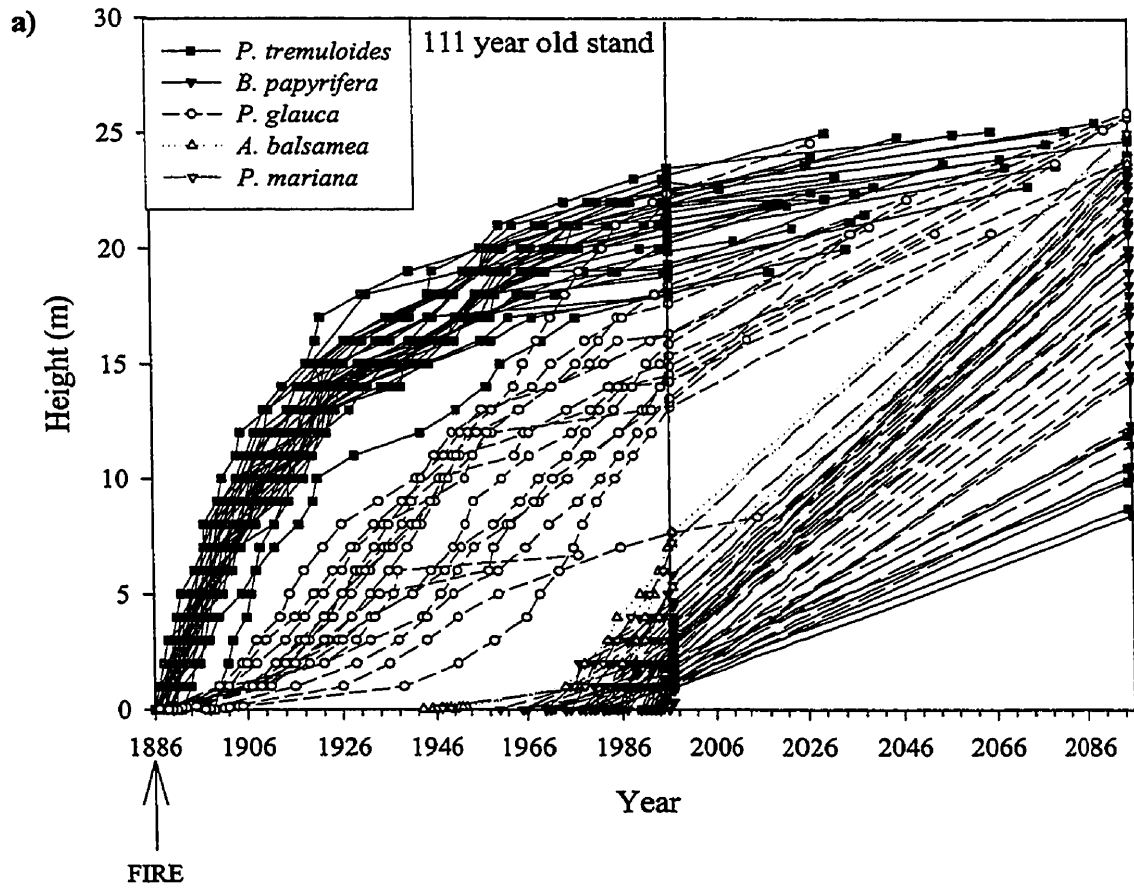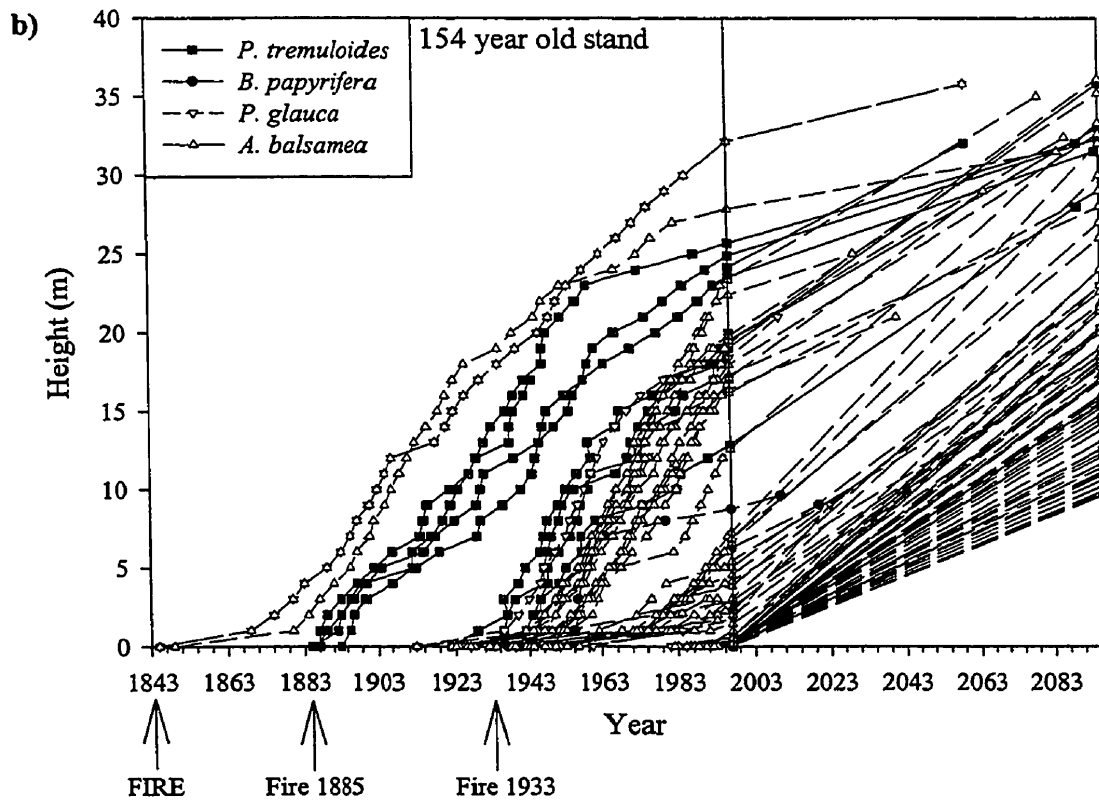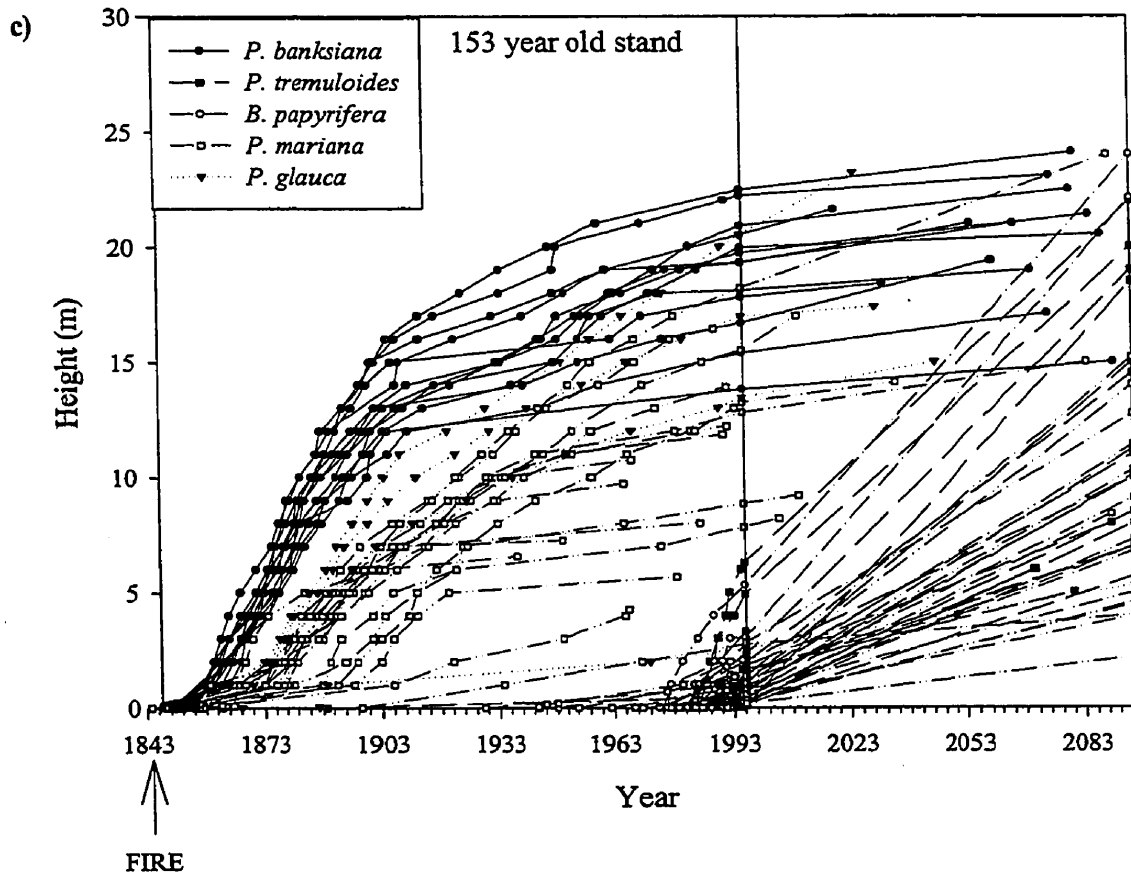
3.10).

In the 154 year old stand (Figure 3.8b), dominated in the canopy by *P. glauca, A. balsamea*, and *P. tremuloides*, there is an interesting pattern of understorey recruitment. Based on fire scars, it appears that at least two fires have burned through the stand since the stand initiating fire in 1843. One fire occurred in 1886 and was followed by the rapid recruitment and growth of *P. tremuloides*. Few individuals appear to have survived this fire, as evidenced by only two older canopy trees. Another fire occurred in 1933, and was followed by rapid recruitment of *P. tremuloides, B. papyrifera*, as well as large numbers of *A. balsamea*. Individuals recruiting after the first fire have nearly reached the canopy. Based on present growth rates and the growth rates of post-fire individuals of the same species, it should take the most rapidly growing understorey individuals, on average, another 100 years to reach the canopy (Figure 3.9b). This means that the stand would have to survive without a stand-replacing fire to 254 years. From the time-since-fire distribution, only 0.4% of the landscape survives without fire for 254 years (Figure 3.10).

In the 153 year old stand (Figure 3.8c), dominated in the canopy by *P. mariana*, it is clear that there will be no replacement of species in the canopy due to the absence of understorey individuals. Finally, in the 153 year old stand (Figure 3.8d), presently dominated in the canopy by *P. banksiana* and *P. mariana*, there are understorey cohorts of *P. tremuloides, B.papyrifera*, and *P. mariana*. *P. tremuloides* and *B. papyrifera* arose by sprouting, while 71% of *P. mariana* were of branch layer origin and 29% were

Figure 3.10   Time-since-fire distribution for the study area from Weir *et al.* (2000).

The distribution from the north region is used as no logging has occurred.
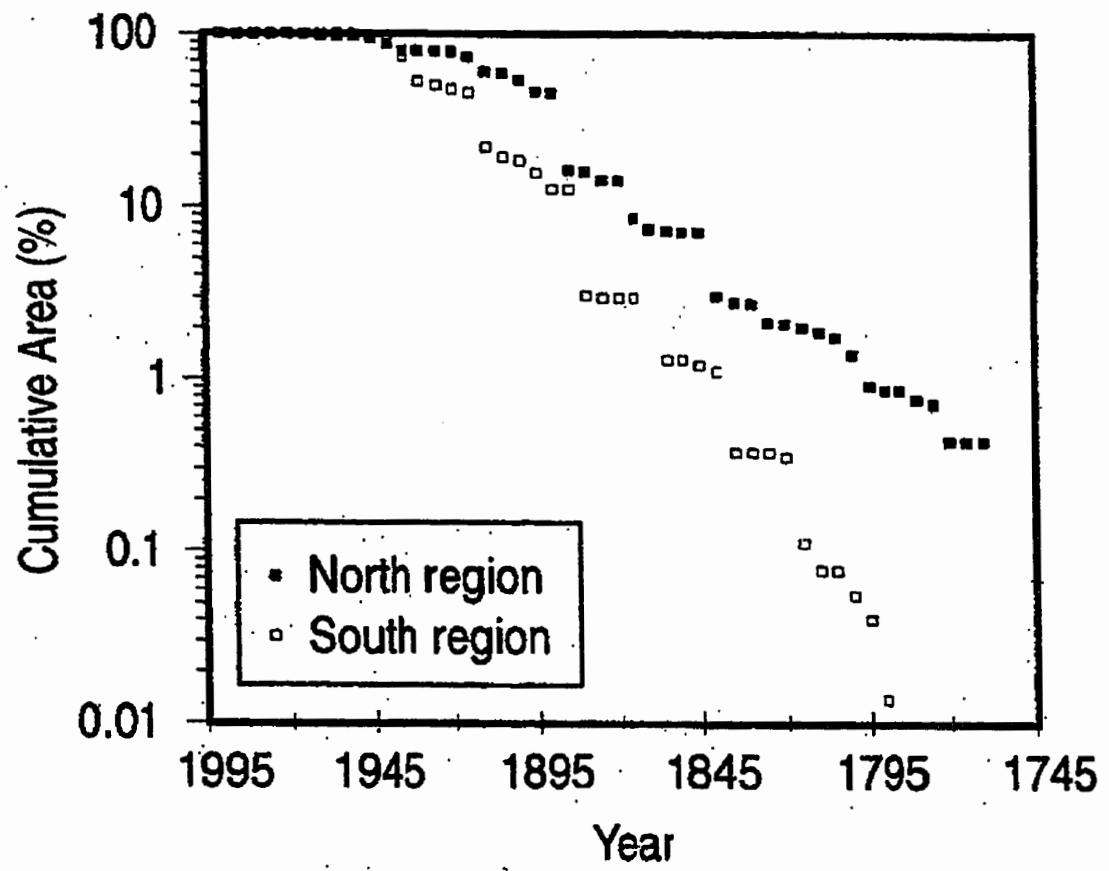
seedlings. Based on present growth rates and the growth rates of post-fire individuals of the same species, it should take the most rapidly growing understorey individuals, on average, another 100 years to reach the canopy. This means the stand would have to survive without a stand replacing fire for 253 years. From the time-since-fire distribution, only 0.4% of the landscape survives without fire to 253 years (Figure 3.10).

Thus, by examining the reconstructed age distributions, the height growth curves of individuals in post-fire and understorey cohorts, and the time-since-fire distribution, it appears that in these stands it is very unlikely that the understorey cohorts will ever replace the post-fire cohorts in the canopy.

EXAMINING THE LIMITATIONS OF RECONSTRUCTED AGE DISTRIBUTIONS

The reconstructed age distributions were used to test the principal assumption of static diameter distributions, static age distributions, and chronosequences. However, the reconstructed age distributions also have some serious limitations: they do not give a complete account of all individuals that have recruited and died within a stand from the time of stand initiation. Because all dead individuals, particularly those that are small at the time of death and/or those that have died and decomposed long before the stand is sampled, can never be accounted for, a full understanding of the patterns of changes in species composition and abundance over time is not possible. It is unclear from the reconstructions whether recruitment is continuous, from the time of the stand initiating fire until the next stand-replacing fire, or whether it is sporadic, occurring only within the

first ten years after fire, and then again after some time lag. Individuals may be recruiting sporadically or continuously in the understorey, and if so, most are dying before reaching 30 or 50 years of age. Alternatively, recruitment may only occur after some time lag, as seen in the reconstructions. Because we cannot detect all individuals, we must interpret the forest dynamics with this in mind.

Discussion

The principal assumption shared by static diameter distributions, static age distributions, and chronosequences is that the changes in species composition and abundance observed over decreasing size or age classes within a stand, or over stands of increasing age, are the same changes one would see if each stand was followed through time. One very common view of forest succession is that there is a succession of tree species over time, *i.e.* forest succession is a process of species replacement through time (*e.g.* Connell and Slatyer 1977; Huston and Smith 1987; Barbour *et al.* 1999; Bergeron and Dubuc 1989; Veblen *et al.* 1991; Bergeron 2000; DeGrandpré *et al.* 2000). Because these static methods present only a snapshot in time of the variation in diameter or age within a stand, or the variation in composition across stands, the changes over time within each stand must be inferred. When the diameters of live individuals are measured within a stand it is often assumed that smaller diameter individuals will eventually replace larger diameter individuals. When the ages of live individuals are measured within a stand it is often assumed that younger individuals will eventually replace older individuals. And

when a chronosequence of stands is used, species dominant in older stands are assumed to replace species dominant in younger stands. The view that forest succession involves a replacement of species through time is so firmly entrenched in our thinking that it is almost never questioned. Yet there has never been clear evidence presented to show that species are, in fact, replaced over time.

We used reconstructed age distributions, height growth curves, and the time-since-fire distribution to examine the possibility that replacement will occur in these boreal forest stands. In the oldest stands, where one would expect to see replacement beginning to occur, three of four stands had significant recruitment in the understorey, while the fourth stand, dominated by *P. mariana*, had no understorey recruits. In two of the stands with significant understorey recruits, one dominated by *P. tremuloides*, and the other by *P. banksiana*, the height growth curves show that the understorey are all relatively short such that their emergence into the canopy is unlikely given the time-since-fire distribution. In only one old stand, dominated by *P. glauca* and *A. balsamea*, have understorey individuals nearly made it into the canopy. It appears that this was made possible by at least two significant fires that burned through the stand and killed a large number of both canopy and understorey individuals. The near absence of canopy trees older than 112 years, and between the two recent fires, and high recruitment after the second fire indicates that both fires were of high intensity and had high duff consumption, providing adequate seed beds for germination and recruitment. Notice that the understorey species that has nearly made it into the canopy is *P. tremuloides*. Thus, even

if one did believe that this stand shows a replacement of species, the sequence of species is not the traditional sequence described in the boreal forest.

Diameter is not positively correlated with age in these boreal forest tree species. The diameter of trees does not correlate well with age for at least three reasons: 1) within any post-fire cohort, there is often large variation in the sizes of individuals, 2) within any understorey cohort there is often very small variation in the sizes of individuals, but large variation in their ages, and 3) comparing post-fire cohorts or understorey cohorts there are significant differences between species in their diameters. Individuals within the post-fire cohort of each species vary widely in their height growth rates; this leads to wide variation in their diameters, which increases over time. In contrast, individuals within the understorey cohort of each species grow very slowly for long periods such that for individuals ranging widely in age there is a very small range in their diameters. Chapter Two showed that there are significant species differences in height growth rates within the first one-metre of growth. These initial differences in growth rates lead to differences between species in the diameter of individuals, differences that are maintained throughout most of their lifetime.

Within glacial till stands, post-fire cohorts of *P. tremuloides* and *P. glauca* both show a relatively wide range in diameters for a relatively narrow range of ages. Conversely, in the understorey, *A. balsamea* has a relatively narrow range of diameters for a wide range of ages. Within glaciofluvial stands, post-fire cohorts of *P. banksiana* and *P. mariana* both show a relatively wide range of diameters for a narrow range of

ages, while in the understorey *P. mariana*, *P. tremuloides*, and *B. papyrifera* have a relatively narrow range of diameters for a wide range of ages.

The persistent differences in diameters between species have often led to the incorrect conclusion that species with a larger median diameter are, on average, older than species with a smaller median diameter. This conclusion was confirmed when ecologists began to measure the ages of individuals by coring them and counting their annual growth rings, first at breast height, and then near their base. However, as shown by our study and other studies in the boreal forest (DesRochers and Gagnon 1997, Parent *et al.* 2000), aging an individual by simply counting its annual growth rings at 30 cm, or any height, above the root collar, as done in most studies, underestimates the age at root collar for two reasons: 1) growth rings laid down between the root collar and any coring height above the root collar are not counted, and 2) some trees do not lay down rings each year on all parts of the stem, *i.e.* they have locally missing rings (see Chapter Two). Aging above the root collar is differentially inaccurate because there are species differences in the number of rings laid down between the root collar and coring height, and in the number of locally missing rings. Species that grow relatively slowly between the root collar and coring height lay down significantly more rings, and have higher numbers of individuals with locally missing rings, and higher numbers of missing rings per individual, compared to species that grow rapidly between the root collar and coring height.

Within glacial till stands, post-fire cohorts of *P. tremuloides* grow more rapidly

than *P. glauca* and *A. balsamea* in the first one metre. Thus, in stands where both species are present in post-fire cohorts, coring trees above the root collar leads to the inaccurate conclusion that *P. tremuloides* is older than *P. glauca* and *A. balsamea*. The relatively faster initial height growth of *P. tremuloides* means that fewer rings are missed when coring above the root collar. Also, *P. tremuloides* has relatively fewer individuals with missing rings and fewer missing rings per individual compared to *P. glauca* and *A. balsamea*. Similarly, within glaciofluvial stands, post-fire cohorts of *P. banksiana* grow more rapidly than *P. mariana* in the first one metre. Thus, in stands where both species are present in post-fire cohorts, coring trees above the root collar leads to the inaccurate conclusion that *P. banksiana* is older than *P. mariana*. The relatively faster initial height growth of *P. banksiana* means that fewer rings are missed when coring above the root collar. Also, *P. banksiana* has relatively fewer individuals with missing rings and fewer missing rings per individual compared to *P. mariana*.

The misinterpretations given by chronosequences reflect the problems associated with using measures of dominance (*i.e.* density, basal area) to infer patterns of succession. Measures of dominance simply reflect differences in the characteristics of species. Density (number per m^2) simply reflects the history within each stand in terms of the population processes of recruitment and mortality. The immigration of seeds determines the species available for recruitment, the extent of duff consumption determines the availability of appropriate seedbeds for seed germination, and the recruitment rates and age-specific mortality rates determine the changes in population density over time. Basal

area (m^2 per m^2) reflects species' differences in growth rates. Those that grow and become large very quickly are conspicuous and have high basal area early on, while those that have slower initial growth rates and thus take relatively longer to become large are conspicuous and have high basal area much later.

The reconstructed age distributions cannot detect all individuals that have recruited and died within a stand from the time of stand initiation. Because many of the dead individuals have already decomposed, we can never fully understand the patterns of changes in species composition and abundance over time. We do not know if there is a continuous pattern of recruitment beginning at the time the stand is initiated, or if it is more sporadic and occurs primarily after some time lag, as seen in the reconstructions. From the patterns that we can see there appear to be at least two possibilities: 1) recruitment is continuous from the time of stand initiation, but understorey cohorts that recruit after the first ten years have high mortality rates such that few individuals live beyond 30 years (*P. mariana*) or 50 years (*A. balsamea*); or, 2) recruitment is sporadic, occurring only in the first ten years after fire, and then after some time lag; the length of the time lag may be determined by the timing of an increased availability of resources, especially light (*i.e.* due to mortality of post-fire individuals). It is interesting to note that, despite a wide range in stand ages (35 to 154 years), few understorey *P. mariana* individuals are older than 30 years, and few understorey *A. balsamea* individuals are older than 50 years. This suggests that, whether recruitment is continuous or sporadic, these understorey cohorts must have high mortality rates.

Conclusions

Any method that does not enumerate every individual that has recruited from the time of stand initiation cannot give a complete understanding of the patterns of changes in species composition and abundance over time within stands. However, by testing the assumptions of static diameter distributions, static age distributions, and chronosequences, and recognizing the limitations of reconstructed age distributions, we can draw a number of conclusions regarding forest dynamics in the boreal forest of central Saskatchewan. Within the twelve boreal forest stands examined in this chapter, it appears that canopy species all recruit within the first ten years after the stand-initiating fire. The recruitment that does occur after the first ten-year period is either continuous and individuals suffer high mortality, or recruitment is sporadic and may reflect periods of increased resources (especially light). Due to the relatively slow growth rates and high mortality of understorey cohorts, and given the time-since-fire distribution in the study area, it appears that forest dynamics in the western boreal forest is not a process of species replacement over time.

Within mixed stands of *P. tremuloides, P. glauca,* and *A. balsamea* on glacial till mid slopes, all species recruit within ten years after fire. All species recruit in the understorey; however, *A. balsamea* appears to have the highest number of understorey recruits. Evidence from height growth curves in the oldest stands and the time-since-fire distribution indicate that the probability of the understorey cohorts replacing post-fire cohorts in these stands is very low.

Within mixed stands of *P. banksiana* and *P. mariana* on glaciofluvial mid slopes, both species recruit within 5 years after fire. Only *P. mariana* appears to recruit after this initial post-fire period, in the understorey. Within stands dominated by *P. mariana* on glaciofluvial bottom slopes, *P. mariana* recruits within the first ten years after fire, and then again in the understorey. Evidence from height growth curves in the oldest stands and the time-since-fire distribution indicate that the probability of the understorey cohorts replacing post-fire cohorts in these stands is very low.

Why is there not a replacement of tree species over time in these boreal forest stands? For the understorey cohorts to replace post-fire cohorts would require: 1) that the understorey cohorts recruit within about 40-50 years after fire, survive until the next stand-replacing fire, and become reproductive, and 2) that the majority of post-fire cohorts die by the time a stand reaches 100 to 150 years of age, *i.e.* old given the time-since-fire distribution. Our evidence indicates that neither occurs in these stands.

Finally, it should be emphasized that the conclusions I have drawn regarding the dynamics of stands in the southern mixedwood boreal forest of central Saskatchewan may apply only in our study area. However, I suggest that before we can be confident in conclusions based on static methods, the assumptions of static methods must be tested with empirical data. Without such rigorous testing of the assumptions the validity of conclusions based on static methods will remain unclear.

Literature Cited

Barbour, M.G., Burk, J.H., Pitts, W.D., Gilliam, F.S., and Schwartz, M.W. 1999. *Terrestrial Plant Ecology*. Addison Wesley Longman, Inc. Menlo Park, CA, U.S.A.

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

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

Bridge, S.R.J., and Johnson, E.A. 2000. Geomorphic principles of terrain organization and vegetation gradients. *Journal of Vegetation Science* 11: 57-70.

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

Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* 27: 95-117, 167-208, 361-91.

Crawley, M.J. 1986. *Plant Ecology*. Blackwell Scientific Publications. London, U.K.

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

DesRochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? *Canadian Journal of Forest Research* 27: 1263-1267.

Dix, R.L., and Swan, J.M.L. 1971. The roles of disturbance and succession in upland

forests at Candle Lake, Saskatchewan. *Canadian Journal of Botany* **49**: 647-676.

Drury, W.H., and Nisbet, I.C.T. 1973. Succession. *Journal of the Arnold Arboretum* **54**:

331-368.

Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary

succession at Glacier Bay, Alaska. *Ecology* **76**: 1899-1916.

Frelich, L.E. 1992. The relationship of natural disturbances to white pine stand

development. In: *The White Pine Symposium: History, Ecology, Policy, and

Management*. Edited by R.A. Stine and M.J. Baughman. Minnesota Extension

Service, University of Minnesota, St. Paul, U.S.A. pp. 27-37.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota

southern-boreal forest. *Ecological Monographs* **65**: 325-346.

Gauthier, S., De Grandpré, L., and Bergeron, Y. 2000. Differences in forest composition

in two boreal forest ecoregions of Quebec. *Journal of Vegetation Science* **11**:

781-790.

Goebel, P.C. and Hix, D.M. 1996. Development of mixed-oak forests in southeastern

Ohio: a comparison of second-growth and old-growth forests. *Forest Ecology

and Management* **84**:1-21.

Goebel, P.C. and Hix, D.M. 1997. Changes in the composition and structure of mixed-

oak, second-growth forest ecosystems during the understorey reinitiaion stage of

stand development. *Ecoscience* **4**: 327-339.

Horn, H.S. 1974. The ecology of secondary succession. *Annual Review of Ecology and Systematics* **5**:25-37.

Huff, M. 1995. Forest age structures and development following wildfires in the western Olympic Mountains, Washington. *Ecological Applications* **5**: 471-483.

Huston, M., and Smith, T. 1987. Plant succession: life history and competition. *American Naturalist* **130**: 168-198.

Jackson, S.L., Futyma, R.P., and Wilcox, D.A. 1988. A paleoecological test of a classical hydrosere in the Lake Michigan dunes. *Ecology* **69**: 928-36.

Johnson, E.A., and Fryer, G.I. 1989. Population dynamics in Engelmann spruce – lodgepole pine forests. *Ecology* **70**: 1335-1345.

Johnson, E.A., Miyanishi, K., and Kleb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta – Picea Engelmannii* forest. *Journal of Ecology* **82**: 923-931.

Kneeshaw, D.D., and Burton, P.J. 1997. Canopy and age structures of some old sub-boreal *Picea* stands in British Columbia. *Journal of Vegetation Science* **8**: 615-626.

Kubota, Y. 1995. Effects of disturbance and size structure on the regeneration process in a sub-boreal coniferous forest, northern Japan. *Ecological Research* **10**: 135-142.

Kuuluvainen, T., Järvinen, E., Hokkanen, T.J., Rouvinen, S., and Heikkinen, K. 1998a. Structural heterogeneity and spatial autocorrelation in a natural mature *Pinus sylvestris* dominated forest. *Ecography* **21**: 159-174.

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

Linder, P., Elfving, B., and Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* **98**: 17-33.

Norland, E.R. and Hix, D.M. 1996. Composition and structure of a chronosequence of young, mixed-species forests in southeastern Ohio, USA. *Vegetatio* **125**: 11-30.

Oliver, C.D., and Stephens, E.P. 1977. Reconstructions of a mixed-species forest in central New England. *Ecology* **58**: 562-572.

Parent, S., Morin, H., and Messier, C. 2000. Effects of adventitious roots on age determination in Balsam fir (*Abies balsamea*) regeneration. *Canadian Journal of Forest Research* **30**: 513-518.

Peet, R.K. and Christensen, N.L. 1980. Succession: a population process. *Vegetatio* **43**:131-140.

Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. *The American Naturalist* **110**: 107-119.

Pickett, S.T.A. 1983. Absence of an *Andropogon* stage in old field succession at the Hutchinson Memorial Forest. *Bulletin of the Torrey Botanical Club* **110**: 533-535.

Pickett, S.T.A. 1989. Space-For-Time Substitution as an Alternative to Long-Term Studies. In: *Long-Term Studies in Ecology: Approaches and Alternatives*. Ed.

G.E. Likens. Springer-Verlag, New York.

Rowe, J.S. 1972. *Forest Regions of Canada.* Environment Canada, Canadian Forest

Service, Ottawa. Publication 1300F.

Saldarriaga, J.G. West, D.C., Tharp, M.L. and Uhl, C. 1988. Long-term chronosequence

of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal*

of Ecology **76**:938-958.

Schweingruber, F.H. 1989. *Tree Rings: Basics and Application of Dendrochronology.*

Kluwer Academic Publications, Holland.

Takahashi, K. 1994. Effect of size structure, forest floor type and disturbance regime on

tree species composition in a coniferous forest in Japan. *Journal of Ecology* **82**:

769-773.

Telewski, F.W., and Lynch, A.M. 1991. Measuring growth and development of stems.

In: *Techniques and Approaches in Forest Tree Ecophysiology.* Ed. J.P. Lassoie

and T.M. Hinckley. CRC Press Inc., Boston, MA.

Veblen, T.T. 1986. Age and size structure of subalpine forests in the Colorado Front

Range. *Bulletin of the Torrey Botanical Club* **113**: 225-240.

Veblen, T.T., Hadley, K.S., and Reid, M.S. 1991. Disturbance and stand development of

a Colorado subalpine forest. *Journal of Biogeography* **18**: 707-716.

Warming, J.E.B. 1895. *Plantesamfund grundtak of den okologiske plantegeografe.*

Copenhagen, Denmark.

Weir, J.M.H., Johnson, E.A., and Miyanishi, K. 2000. Fire frequency and the spatial age

mosaic of the mixedwood boreal forest in western Canada. *Ecological Applications* **10**: 1162-1177.

Whipple, S.A., and Dix, R.L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. *American Midland Naturalist* **101**: 142-158.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* **21**: 414-416.

CHAPTER FOUR

Using both local and regional processes to understand forest dynamics

Introduction

Studies of stand dynamics, *i.e.* forest succession, in closed-canopied forests have

focussed on understanding the patterns of age and species composition by examining

processes operating primarily within a stand (*e.g.* Carleton and Maycock 1977; Whipple

and Dix 1979; Veblen 1986; Veblen *et al.* 1991; Hofgaard 1993; Bergeron and

Charron 1994; Huff 1995; Kneeshaw and Burton 1997; Linder *et al.* 1997; Donnegan and

Rebertus 1999; Bergeron 2000). In contrast, metapopulation studies have focussed on

understanding how larger scale processes, particularly the re-colonization of extinct local

populations by seed dispersal, affect the metapopulation dynamics, with less emphasis on

the dynamics within each local population (*e.g.* Pulliam 1988; Karieva 1990; Hanski and

Gilpin 1991; Harrison 1991; Eriksson 1996). In forests where local populations are

completely killed by catastrophic disturbances re-colonization by many tree species (*i.e.*

wind dispersed, non-sprouting, non-serotinous species) is possible only because seeds

from nearby surviving populations are dispersed there; without such dispersal local

population extinctions may occur from one generation to the next. Thus, both

disturbance and seed dispersal must be included if we are to fully understand forest

dynamics at a regional scale. In this chapter we will incorporate processes operating

locally, *i.e.* within a population, and regionally, *i.e.* across the landscape, in order to

develop a regional-scale understanding of forest dynamics. Using data from the

mixedwood boreal forest of western Canada, we will show that, in forests dominated by large-scale catastrophic disturbances, the regional scale patterns of age and species composition are driven by at least four ecological processes: 1) local population dynamics; 2) catastrophic disturbance; 3) seed dispersal, and 4) geomorphic processes.

A local population can be simply defined as a group of individuals of one species in an area circumscribed for the purposes of study (Crawley 1986). Further, it can be defined as a group of individuals relatively homogeneous with respect to their recruitment and mortality schedules (Johnson 1992; Ebert 1999). If recruitment and mortality are not homogeneous among individuals in the population, then the population is subdivided into cohorts (Ebert 1999). In forests dominated by catastrophic disturbances, where the local population is completely killed, one or more (post-fire canopy) cohorts may recruit immediately after disturbance, and other (understorey) cohorts may recruit much later. Between catastrophic disturbances, any changes within the cohorts are a function of their recruitment, growth, and age-specific mortality rates.

In the mixedwood boreal forest of western Canada, large, high intensity, lightning-caused wildfires kill most of the canopy and understorey vegetation and consume large areas of duff, i.e. litter, fermentation, and humus soil layers. These fires are controlled primarily by weather; variation in topography, substrate and microclimate has a relatively minor influence on fire intensity (Weir et al. 2000). The fire cycle of the study area has been approximately 75-150 years (Weir et al. 2000). Because fires generally occur within the life span of canopy cohorts, mortality by catastrophic wildfire

must be included as a source of mortality for all cohorts in a local population. Consequently, within each local population there is a competing risk of mortality by within-population causes (*e.g.* competition, disease) and by catastrophic wildfire.

Local populations completely killed by wildfire are re-colonized by sexually or asexually reproducing tree species. Seed from sexually reproducing tree species may come from within the local population, via aerial seed banks, or from outside the local population, by wind dispersal. Species with aerial seed banks, *i.e.* serotinous cones, deposit seed onto the burned surface after their cones are opened by heat from the passing wildfire (Beaufait 1960; Johnson and Gutsell 1993). Thus, a new generation, identical in composition to the fire-killed community, recruits on the same surface as the fire-killed populations. This replacement depends on the age of the fire-killed population, and the extent of duff consumed by fire. Seeds will be deposited from aerial seed banks within the population if the fire-killed population has reached reproductive maturity, and if the duff is consumed to the extent suitable for the successful regeneration of the population, *i.e.* thin humus or exposed mineral soil (St. Pierre *et al.* 1992; *cf.* Zasada *et al.* 1992; Fleming and Mossa 1994; Duchesne and Sirois 1995; Charron 1998). If the fire-killed population is not reproductively mature, then seed must be dispersed by wind from outside the local population. There seems to be no seed bank beyond seeds that over-winter after being shed (*cf.* Zasada *et al.* 1992).

Species that disperse via wind from outside the burned local population will deposit seed onto the burned surface if surviving reproductively mature trees are within

the dispersal range of their seeds. Thus, the successful re-colonization of wind-dispersed species in the local population depends on the locations of seed sources relative to the burned population. It also depends on the extent of duff consumed by fire, with thin humus and exposed mineral soil being the most suitable seedbed (St. Pierre *et al.* 1992; Fleming and Mossa 1994; Duchesne and Sirois 1995; *cf.* Zasada *et al.* 1992; Charron 1998).

The sprouts of asexually reproducing tree species arise from stimulated buds along the shallow lateral roots of fire-killed trees within the local population, or from the base of the stump of a fire-killed tree (Oliver and Larson 1990). The successful re-colonization by asexually reproducing species depends on the basal area of fire-killed stems (associated with the carbohydrate reserves of the parental root system (*cf.* Zasada *et al.* 1992)), and temperature of the forest floor (Perala 1990). In the absence of an adequate supply of surviving root systems, seed must be dispersed from mature live populations located outside the local population.

The local population dynamics, catastrophic wildfires, and seed dispersal processes take place on a landscape structured by geomorphic processes, *i.e.* ridgelines, stream courses, and hill slopes in between, which give rise to moisture and nutrient gradients (Bridge and Johnson 2000). The gradients are controlled by surficial material (mainly glacial till and glaciofluvial in the study area), and the shapes of hill slopes created by geomorphic processes. The distribution of local populations on the landscape is ultimately governed by the moisture and nutrient gradients because each tree species

successfully grows and reproduces within a specific range of moisture and nutrients.

The objective of this chapter is to give empirical evidence for forest dynamics using both local and regional ecological processes. We will present the results of local population processes, including seed production, seed germination rates, recruitment, mortality rates, and height growth rates, and the regional processes, including wildfire, seed dispersal and moisture and nutrient gradients. For all species whose re-colonization after fire requires seed dispersal, we will see that large-scale mortality by wildfire and subsequent dispersal of seed into fire-killed local populations couples the local populations together to form the regional population. Regional processes are relatively important because successful re-colonization of tree species after catastrophic fires depends on a regeneration mechanism that allows for rapid recruitment, *i.e.* within the first few years, following fire. Such rapid recruitment is necessary because the relatively short time between fires in the study area means that early recruiting individuals are usually the only individuals to reach the canopy, and thus the only individuals to produce seeds for the next generation.

Materials and Methods

STUDY AREA

The study area is located in Saskatchewan, Canada (53° 34' N to 54° 24' N and 105° 25' W to 107° 52' W). The topography of this area is gently rolling, ranging in elevation from approximately 525-650 metres a.s.l. The climate is characterised by long,

cold winters and short, cool summers. July and August are the warmest months of the year with average maximum temperature exceeding 20°C three days out of four. The average annual precipitation ranges from 400-500 mm, of which 70% occurs as rain.

The major disturbance in this region is large, high intensity, lightning-caused wildfires that kill most of the canopy trees and understorey vegetation (Weir *et al.* 2000). The study area is part of the Boreal Mixedwood Forest (Rowe 1972), which is dominated by eight upland tree species, including: *Pinus banksiana* Lamb., *Picea mariana* (Mill) B.S.P., *Populus tremuloides* Michx., *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., *Populus balsamifera* L., *Larix laricina* (Du Roi) K. Koch., and *Betula papyrifera* Marsh. This chapter will focus primarily on *P. banksiana*, *P. mariana*, *P. tremuloides*, and *P. glauca*.

Moisture and nutrients are the principal environmental factors controlling the distribution of upland plant species within the area (Bridge and Johnson 2000). The gradients are controlled by surficial material (primarily glaciofluvial and glacial till), and the geomorphic processes that create hill slopes on these surfaces. The tops of glacial till hill slopes are at the middle of the moisture and nutrient gradients and are dominated by *P. tremuloides*. At mid-slope positions, *P. glauca* and *P. tremuloides* co-dominate and, as moisture and nutrients increase down slope, *P. glauca* and *A. balsamea* co-dominate. The tops of glaciofluvial hill slopes are at the dry end of the moisture gradient and low end of the nutrient gradient, and are dominated by *P. banksiana*. At mid-slope positions, *P. banksiana* co-dominates with *P. mariana*, and as moisture and nutrients increase down

slope, *P. mariana* dominates.

FIELD & LABORATORY METHODS

We sampled seventeen stands varying in geomorphic substrate, hill slope position, species composition, and time since the last stand-replacing fire (Table 4.1). Eight stands were located top-slope, mid-slope and mid-bottom-slope on glacial till hill slopes and were dominated by *P. tremuloides*, *P. glauca*, and *A. balsamea* (Table 4.1). One stand was located bottom-slope on glaciofluvial overlain with glacial till and was dominated by *P. glauca* and *A. balsamea*. Five stands were located top to mid-slope on glaciofluvial hill slopes and were dominated by *P. banksiana* and *P. mariana*. Three stands were located bottom-slope on glaciofluvial and were dominated by *P. mariana*.

Time-since-last fire of these stands ranges from 8 years to 154 years. The selection criteria for stands were as follows: 1) stands had no evidence of anthropogenic disturbance, 2) vegetation was rooted in mineral soil with no evidence of standing water in the top 30 cm of mineral soil, and 3) each stand was visually homogeneous with respect to stand age, stand structure, and species composition. Plot size, varying from 64 m^2 to 576 m^2, was established to include a minimum of 25 of the most abundant canopy species (Table 4.1). Each stand was divided into a grid at two-metre intervals and all live and dead (standing, downed, and buried) seedlings (< 50 cm height), saplings (>50cm height and <5 cm basal diameter), and trees (>5 cm basal diameter) were labeled and mapped. Two to three workers carefully searched each stand to ensure that all individuals

Table 4.1   Stand characteristics for seventeen upland stands from the southern

mixedwood boreal forest, Saskatchewan. Figure label indicates the stand

represented in each Figure. T-S-F is the time since the last stand replacing

fire, *i.e.* time-since-fire.

Figure label	Stand ID	Geomorphic Material	Hill Slope Position	T-S-F	Fire Date	Tree Species	Number	Density (no./ha.)
a	TA4	Glacial till	top-mid	8	1989	P. tremuloides	208	52000
						B. papyrifera	2	200
						P. glauca	14	1400
						A. balsamea	54	5400
b	TA10	Glacial till	top-mid	35	1964	P. tremuloides	73	29200
						B. papyrifera	15	6000
						P. glauca	2	800
						A. balsamea	1	400
						P. mariana	2	800
c	TA5	Glacial till	top	55	1942	P. tremuloides	82	8200
						B. papyrifera	39	3900
d	TA1	Glacial till	top	78	1919	P. tremuloides	71	2604
						A. balsamea	6	156
						P. glauca	5	130
e	TA8	Glacial till	top-mid	111	1886	P. tremuloides	177	2463
						B. papyrifera	75	1302
						P. glauca	80	1580
						A. balsamea	204	3542
						P. mariana	32	556
f	WS4	Glacial till	mid-bot	55	1942	P. tremuloides	5	298
						B. papyrifera	15	893
						P. glauca	44	2619
						A. balsamea	2	119
g	WS2	Glacial till	top-mid	78	1919	P. tremuloides	136	4375
						B. papyrifera	16	500
						P. glauca	94	3625
						A. balsamea	119	3719
h	BF2	Glacial till	mid-bot	154	1843	P. tremuloides	34	5525
						B. papyrifera	5	125
						P. glauca	21	5425
						A. balsamea	652	237325
i	WS3	G.till-Fluvial	Bottom	154	1843	P. banksiana	3	429
						P. tremuloides	4	286
						B. papyrifera	2	214
						P. glauca	42	2194
						A. balsamea	267	19071
j	BS15	Glaciofluvial	bottom	35	1964	P. glauca	43	11944
						P. mariana	73	20278
						P. balsamifera	4	1111
						L. laricina	1	278
k	BS7	Glaciofluvial	bottom	110	1886	P. mariana	141	9931
						P. glauca	10	833
l	BS9	Glaciofluvial	bottom	153	1843	B. papyrifera	2	220
						P. mariana	87	5604
						P. glauca	3	165
						P. balsamifera	1	55
m	JP1	Glaciofluvial	middle	32	1964	P. banksiana	183	22875
						P. tremuloides	24	3000
						B. papyrifera	11	1375
						P. mariana	14	1750
						P. glauca	24	3000

n	JP12	Glacial till	mid-bot	59	1938	*P. banksiana*	75	5357
						P. mariana	86	6142
						P. tremuloides	5	357
						B. papyrifera	1	71
o	JP5	Glaciofluvial	middle	77	1919	*P. banksiana*	46	4600
						P. mariana	101	10100
p	JP9	Glaciofluvial	top	60	1936	*P. banksiana*	38	4875
						P. tremuloides	3	375
						P. mariana	225	28125
						P. glauca	31	3875
						A. balsamea	1	125
q	JP8	Glaciofluvial	middle	126	1870	*P. banksiana*	53	2952
						P. mariana	21	1500
r	JP11	Glaciofluvial	middle	153	1843	*P. banksiana*	22	1200
						P. tremuloides	112	11200
						B. papyrifera	29	2900
						P. mariana	102	10100
						P. glauca	5	500

(*i.e.* including newly recruited seedlings, if present) were located. All seedlings, along with their roots, were removed from the ground. Using hand rakes, we carefully removed all of the organic material, down to mineral soil, from within the entire plot. Next, *all* sapling and tree stumps were completely removed from the ground by first cutting each individual at the base, and then cutting all lateral roots and tap roots (Figure 4.1). Finally, a disk was cut at every metre to the top of each sapling and tree to construct height growth curves. To remove all individuals from one stand, including stem disks and stumps, took four people 15-30 days.

All seedlings and sapling and tree disks and stumps were brought back to the lab for processing; no samples were processed in the field. In total, 4022 individuals were collected and processed. Seedling ages were determined by counting bud scale scars from the root collar to the top of each seedling. The age of most seedlings larger than 0.25 cm basal diameter was also determined by counting annual growth rings at the root collar. To locate the root collar of each seedling, sapling, and tree, each stump was cut with a band saw into cross-sections 1-2.5 cm thick, and sanded sequentially with coarse and fine sand papers (up to 600 grain). The root collar was located in all samples using a 10-60X power-dissecting microscope, and noting from one cross section to the next the shift in the central pith from undifferentiated parenchyma cells in the stem to a vascular cylinder in the root (Telewski and Lynch 1991). Tree and sapling disks were sanded and counted on two radii to construct height growth curves.

Within each seedling, sapling and tree stump section we located missing annual

Figure 4.1   Photo showing how sapling and tree stumps were removed from the

ground.

growth rings, *i.e.* years where an annual growth ring is not produced on all stem

segments, using standard dendrochronological techniques (Schweingruber 1989;

Yamaguchi 1991). For each of the stump cross-sections we constructed a skeleton plot,

which is a plot of unusually narrow or wide annual rings. Each skeleton plot was first

cross-dated within the stump, and then against a species-specific master skeleton plot

from each stand. Missing rings were evident when marker rings in a skeleton plot were

offset compared to other skeleton plots within a stump, and when compared to the master

plot. For each stand, sample processing and analysis took one technician 40-60 days.

MODELS OF SEED/SPROUT PRODUCTION AND EARLY RECRUITMENT DENSITIES

Seed and sprout production models are from Greene and Johnson (1994), and

early recruitment models are from Greene and Johnson (1999, 2000). The models have

been divided into three groups based on mode of reproduction: a) aerial seed banks (*i.e.*

serotinous and semi-serotinous cones), b) asexual reproduction (*i.e.* root sprouts), and c)

wind dispersed from living sources. The models demonstrate: that both seed and sprout

production depend on tree size (pre-fire basal area density, *i.e.* area of trees per area of

ground surface, m^2/m^2) and seed size; that seed dispersal by wind depends on seed size

(which affects terminal velocity) and release height; and that germinant survivorship is

dependent on duff thickness and seed size.

Species with Aerial Seed banks

Both serotinous *P. banksiana* and semi-serotinous *P. mariana* maintain several cohorts of closed cones on their branches. Most cones abscise within three years of burning (Zasada *et al*. 1991). Greene and Johnson (1994) give seed production, Q_D (seeds/m^2), for *P. banksiana* as:

[4.1] $$Q_D = 35\ 097\ B_D^{0.86}$$

and for *P. mariana* as:

[4.2] $$Q_D = 163\ 400\ B_D^{0.95}$$

where B_D is the basal area density (m^2/m^2).

Multiplying Q_D by the initial mortality estimates for *P. banksiana* ($q = 0.0169$) and *P. mariana* ($q = 0.0049$) yields the expected regeneration density, F_D, (number per m^2) for *P. banksiana*:

[4.3] $$F_D = 593 B_D^{0.86}$$

and for *P. mariana*:

[4.4] $$F_D = 806 B_D^{0.95}$$

Asexually Reproducing Species

P. tremuloides commonly sprouts from underground stems. Greene and Johnson (1999) assumed that the initial density of sprouts produced by a clone depends on the density of roots which, in turn, depends on basal area density (B_D). They further assumed

that asexual stems begin thinning almost immediately after fire as they compete for light, and that the thinning rates are time dependent. From Greene and Johnson (1999), the recruitment density, F_D (number per m^2), is given as:

[4.5] $$F_D = 11\ 600\ B_D^{0.79}(t+1)^{-1.64}$$

where $t=0$ is the summer of the fire.

Wind-Dispersed Species

All five tree species have wind-dispersed seeds; however, only two species, *P. glauca* and *A. balsamea*, rely solely on wind dispersal for re-colonizing a fire-killed local population. The area source model of tree recruitment from wind-dispersed species comes from Greene and Johnson (1996). The area source model is the summation of the point-source recruitment curves from the basal area density (B_D) of individual trees comprising the area source with the forest edge treated as the start of the dispersal distance. Following Greene and Johnson (1999), seed production, Q_p, for *P. glauca* is given as:

[4.6] $$Q_p = 106\ 686\ B_D^{0.92}$$

and for *A. balsamea*:

[4.7] $$Q_p = 58\ 915\ B_D^{0.92}$$

Following Greene and Johnson (1989), the recruitment density, F_D, for *P. glauca* is given as:

[4.8] $$F_D = 3\ 886 B_D^{0.92}$$

and for *A. balsamea*:

[4.9] $F_D = 3\ 376B_D^{0.92}$

GERMINATION AND EARLY RECRUITMENT AND AGE-SPECIFIC MORTALITY RATES

Germination rates of *P. banksiana*, *P. mariana*, and *P. glauca* are from Charron

and Greene (submitted). Seed viability tests were first done by germinating 100 seeds of

each species on damp paper placed in petri dishes, and the results were used to correct for

percent germination in a field experiment. A field experiment was begun in early June

1997 to test for differences in germination and survival values on different seedbeds.

Equal numbers of seeds were placed on top of three different seedbeds in the field: 1)

exposed mineral soil, 2) burned humus, and 3) burned moss. Each treatment was

replicated in three 20 cm x 20 cm plots, ensuring no differences in seedbed thickness.

Germination and survival was monitored weekly for the first three months, and then

monthly during the summers (May to September) from 1998 through 2000. There was

almost no germination on burned moss seedbed so results are given only for mineral soil

and humus seedbeds. Mean and standard errors of germination rates were calculated for

each seedbed by combining the results of germination over the three summers.

Using permanent sample plots established in 1997, Charron and Greene

(submitted) measured the recruitment and age-specific mortality rates of three tree species

for the first four years following two different fires in 1995 and 1996. Four replicate

plots, each 2 m x 2 m in size, were established within each of three stands. One stand

was dominated by fire-killed *P. banksiana* and *P. mariana*, one stand was dominated by fire-killed *P. mariana*, and another stand was dominated by fire-killed *P. glauca*. The establishment and mortality of individuals was monitored monthly (May – September) over three summers. Seedbed type was noted for each germinant, with almost no germination on burned moss. Mean and standard errors of age-specific mortality rates were calculated for each species on each seedbed (mineral and humus) for the periods May to September (*i.e.* summer) and September to May (*i.e.* winter) of each year.

For this study another set of permanent plots was established in May 1999, within a fire that burned in August 1998. Within three different stands, we set up four replicate 2 m x 2 m plots. One stand was dominated by fire-killed *P. banksiana*, a second stand was dominated by fire-killed *P. mariana*, and the third stand was dominated by fire-killed *P. tremuloides* and *P. glauca*. The *P. tremuloides* dominated stand was located within 25 metres of a stand of live *P. tremuloides* and *P. glauca*. The establishment and mortality of individuals were monitored three to four times over the summers (May – September) to present (May 2001). Mean and standard errors of age-specific mortality were calculated for each species in each stand for the periods May to September (*i.e.* summer) and September to May (*i.e.* winter) of each year.

AGE-SPECIFIC MORTALITY RATES

The age-specific mortality rates were reconstructed for each cohort in each of seventeen stands using the cross-dated ages of live and dead individuals. Within each

stand the individuals of each species were subdivided into two cohorts: post-fire canopy cohort and understorey cohort. Those recruiting within ten years after fire were the post-fire canopy cohort. For individuals recruiting more than ten years after fire we tested whether differences in timing of recruitment affected the age-specific mortality rates of each cohort. There were no significant differences between individuals recruiting at different times (p<0.05) and thus all individuals of a species, recruiting 11 years or more after fire were included in the understorey cohort. Age-specific mortality rate, q_x (year^{-1}), was estimated as:

[4.10] q_x = *number of individuals dying in interval x*
                  number alive at the beginning of interval x

The time period over which q_x was calculated within each stand was the period over which the death of individuals could be detected. For each cohort q_x was calculated by starting all individuals at time zero, despite differences in the year of recruitment. It must be noted that the data in each stand are right censored, *i.e.* trees were cut down when they were still alive, and as a result, the values of q_x increase sharply in older ages. Therefore, these censored q_x values were not included in the descriptions of patterns of mortality.

HEIGHT GROWTH RATES

Height growth curves were constructed for each individual in four of our oldest stands using the age at root collar and stem disks cut at every one metre to the top of each seedling, sapling, and tree.

THE FIRE CYCLE

A five-hectare resolution, accurately dated, time-since-fire map for the large (3461 km^2) contiguous area was used to produce the landscape survivorship (*i.e.* time-since-fire) distribution in which both spatial and temporal changes in fire cycle were statistically tested (Weir *et al.* 2000). Significant changes in the fire cycle were related to climatic changes as well as land use changes in the surrounding area. The parameters of the time-since-fire distribution were estimated using the methods of Reed *et al.* (1998).

Results

The results section is divided into subsections based on the mode of reproduction of species: 1) species with aerial seed banks, 2) asexually reproducing species, and 3) wind-dispersed species. Within each of these subsections we will present the results of local processes, including seed production, seed germination rates, recruitment densities, age-specific mortality rates, and height growth rates. Then, we will present results for the importance of regional processes, including the effect of the fire cycle on extinction within a local population given the age of reproduction of each species, and the importance of seed dispersal to re-colonization after wildfire.

Species with Aerial Seed banks

LOCAL POPULATION PROCESSES

The serotinous and semi-serotinous cones of *P. banksiana* and *P. mariana*,

respectively, are opened by heat from the passing fire, providing a supply of seed within the local population. Thus, in stands where fire-killed *P. banksiana* and *P. mariana* canopy trees have reached reproductive maturity, regional processes are relatively unimportant.

Given equal basal area density, seed production is greater for the smaller seeded *P. mariana* (equation 4.2) compared to *P. banksiana* (equation 4.1). However, germination mortality rates (Figures 4.2a-b; at t=0) are lower for *P. banksiana* (mineral = 0.56 ± 0.03 year^{-1}; humus = 0.55 ± 0.01 year^{-1}) compared to *P. mariana* (mineral = 0.7 ± 0.03 year^{-1}; humus = 0.63 ± 0.02 year^{-1}). Therefore, recruitment densities are relatively higher for *P. banksiana* (equations 4.3 and 4.4). Also, in stands where both species co-dominate, the recruitment densities of *P. banksiana* are higher because they have relatively higher basal area density compared to *P. mariana*.

a) *Pinus banksiana*

Examination of the age at root collar of *P. banksiana* shows that recruitment occurs primarily within the first five years after fire (Figures 3.7j-l). For the first three years after germination (Figure 4.2a), data from Charron and Greene (submitted) show that for post-fire cohorts of *P. banksiana* age-specific mortality rates are not significantly different between mineral and humus seedbeds, except in the third summer where q_x is significantly higher on humus seedbeds. On both mineral and humus seedbeds q_x varies around 0.1 year^{-1}, ranging from 0 to 0.8 year^{-1} (Figure 4.2a: note that zero does not show

Figure 4.2   Mean and standard error of germination rates and age-specific mortality

rates, q_x, over the first three years after fire for: a) *Pinus banksiana*, and b)

Picea mariana. Note that for both species (mineral) and (humus) are

values of q_x from Charron and Greene (submitted), and *P. banksiana* pp

are data from the *P. banksiana* permanent plots.

a)

P. banksiana

q_x

Legend:
- mineral (○)
- humus (△)
- *P. banksiana* pp (●)

x-axis: Time (years)
- 0, May-Sept, Sept-May, 1, May-Sept, Sept-May, 2, May-Sept, Sept-May, 3, Sept-May

b)

P. mariana
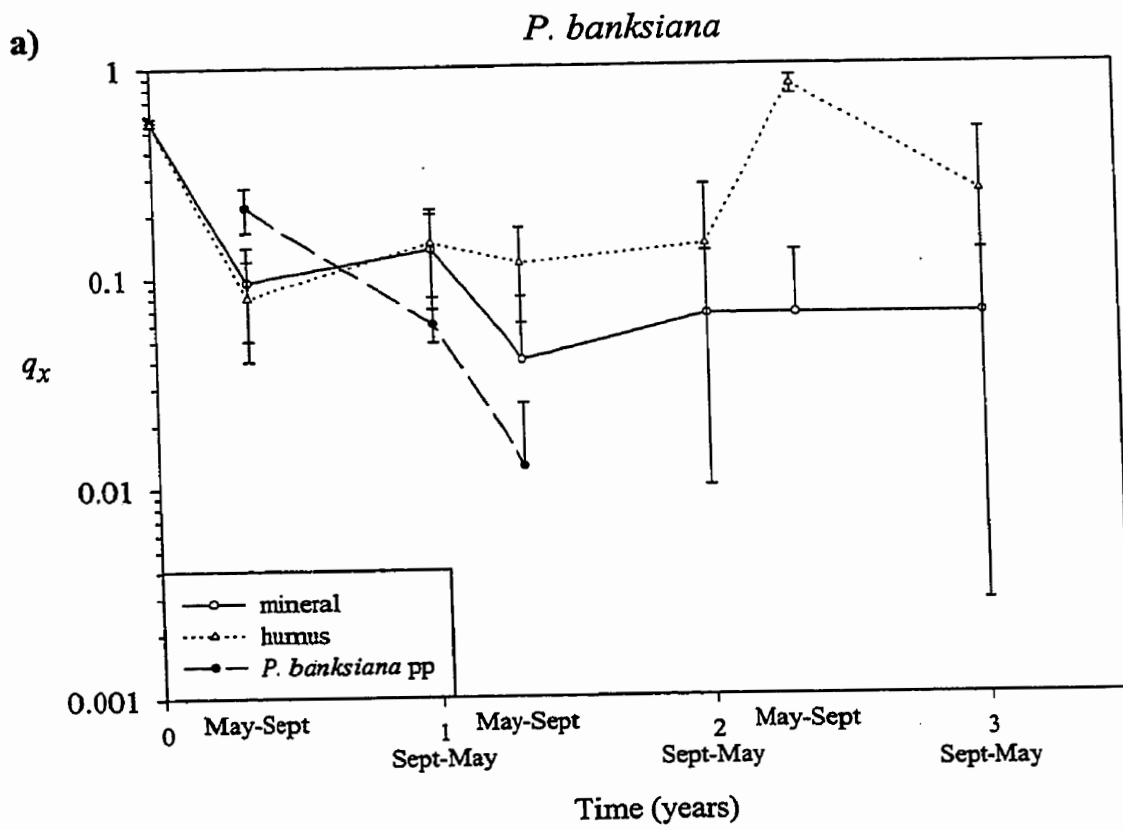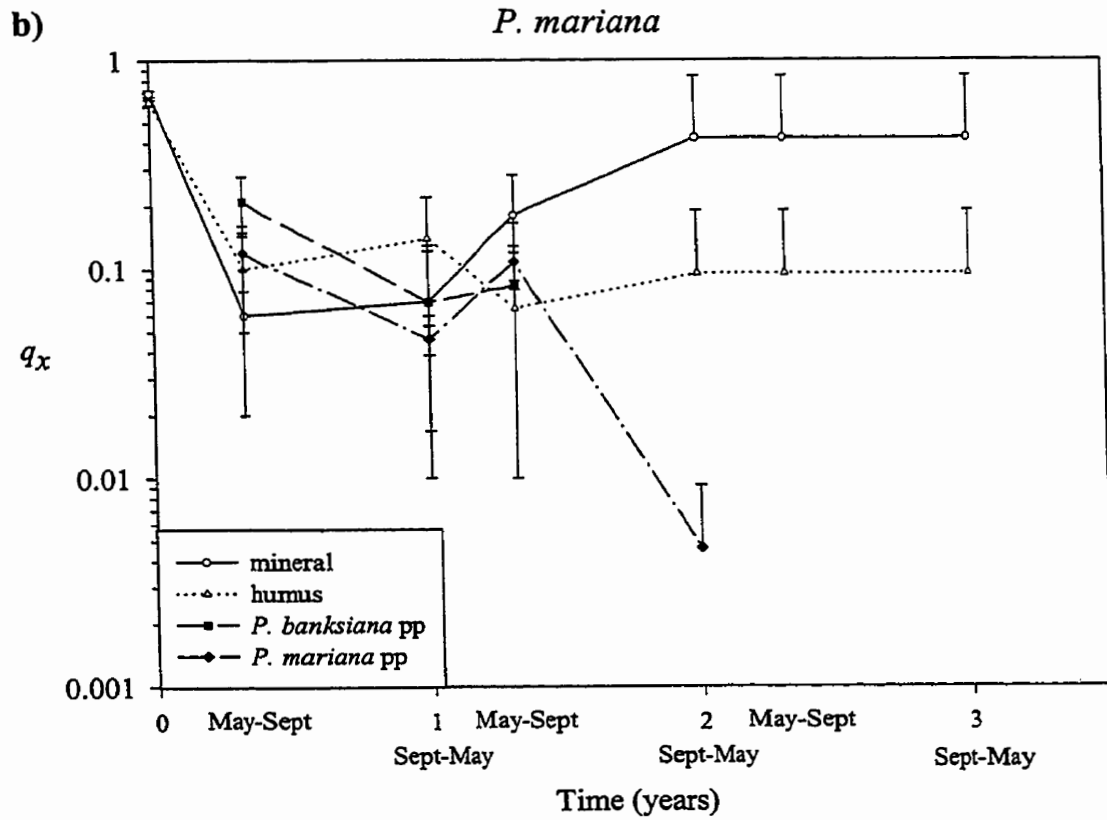
up on the logarithmic axis). From my permanent plots, q_x of *P. banksiana* is significantly higher compared to the plots of Charron and Greene only in the first summer (Figure 4.2a). After the first summer, q_x decreases to 0 year^{-1} by the end of the second winter, and is not significantly different from Charron and Greene.

Age-specific mortality rates were calculated for post-fire cohorts of *P. banksiana* in stands M-Q (Figure 4.3a). The time period over which q_x was calculated within each stand was the period over which mortality could be detected. Recall that the values of q_x where censoring begins (*i.e.* where value of q_x rises sharply in older ages) are not included in the descriptions of the patterns of mortality. The patterns of mortality for *P. banksiana* are as follows. After relatively high germination mortality rates (~0.55 year^{-1}) and lower mortality rates through the first three years (~0.1year^{-1}), mortality rates decrease to 0.00637 year^{-1} between 9 and 11 years (Figure 4.3a). Between 12 and 24 years, mortality increases, ranging from 0.0185 to 0.0769 year^{-1}. Beyond 24 years, mortality is generally lower, ranging from 0.0122 to 0.129 year^{-1}.

In stands dominated by *P. banksiana* (stands N, O, and Q), there are understorey cohorts of *P. mariana, B. papyrifera,* and *P. tremuloides* (Figure 4.3b). Notice that for all cohorts the value of q_x increases with age; this occurs primarily because fewer individuals survive to older ages and thus the denominator of equation 4.10 decreases over time. For understorey cohorts of *P. mariana,* q_x ranges from 0.2 to 0.333 year^{-1} in stand N, from 0.083 to 0.111 year^{-1} in stand O, and is 0.167 year^{-1} in stand Q. For the understorey cohort of *B. papyrifera* in stand Q, q_x ranges from 0.04 to 0.23 year^{-1}, while q_x of *P.*

Figure 4.3   Within stands M-Q and permanent plots dominated by *Pinus banksiana*,

the age-specific mortality rates, q_x, of: a) post-fire cohorts of *P. banksiana*,

and b) all understorey cohorts. Note that (mineral) and (humus) are values

of q_x from Charron and Greene (submitted). *P. banksiana* pp are data
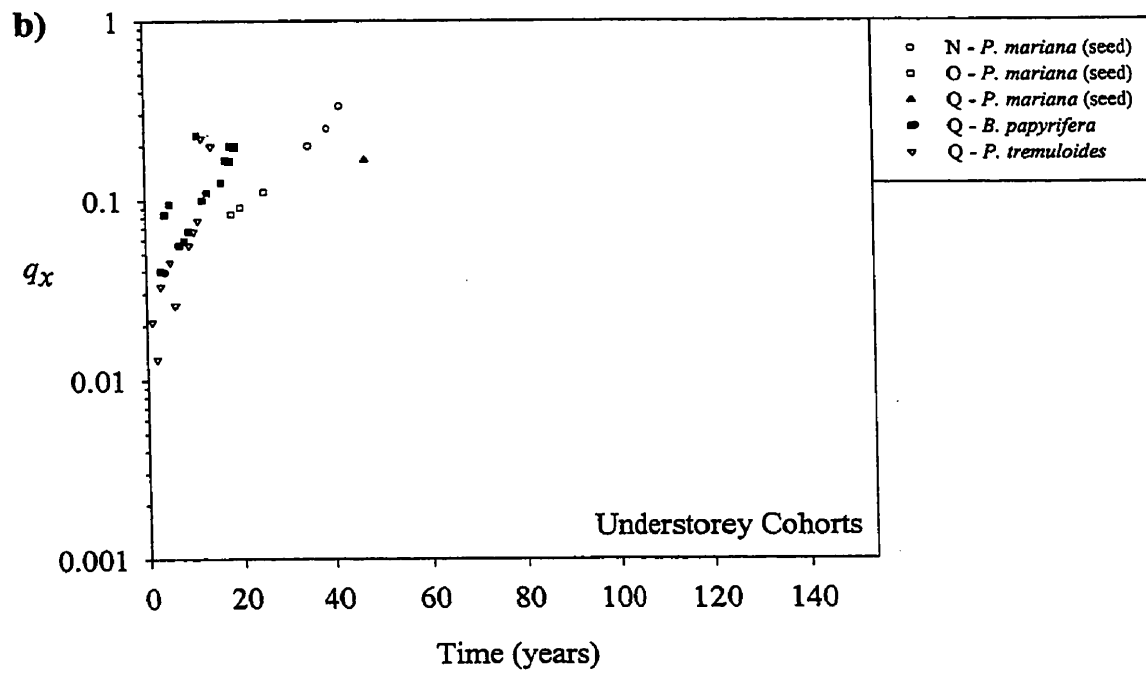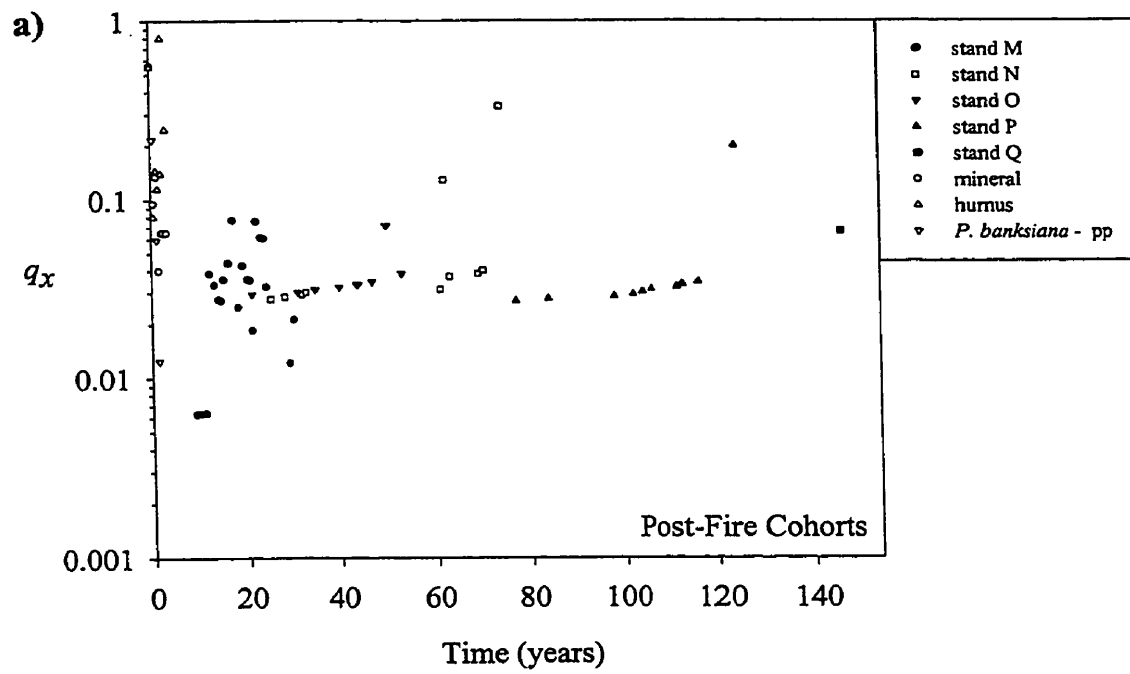
from the *P. banksiana* permanent plots, and *P. mariana* (seed) are

individuals arising from seed.

a)

b)

tremuloides in stand Q ranges from 0.013 to 0.22 year^{-1}.

Figure 4.4 gives the height growth of live and dead post-fire and understorey individuals in our oldest stand dominated by *P. banksiana* and *P. mariana*. There are large numbers of live *P. banksiana* and *P. mariana* remaining in the canopy, and large numbers of *P. tremuloides*, *B. papyrifera*, and *P. mariana* in the understorey. Notice that all understorey individuals are relatively small such that it does not appear likely that they would have made it into the canopy in the near future.

b) *Picea mariana*

For post-fire cohorts of *P. mariana* q_x calculated over the first three years after germination (Figure 4.2b) do not differ significantly between the data sets of Charron and Greene (submitted) and my permanent plots (note that some standard error bars extend to zero and thus do not show up on the figure). In all plots, q_x varies around 0.1 year^{-1}, ranging from 0 to 0.8 year^{-1}.

Only two stands dominated by *P. banksiana* (stands N and Q) had adequate numbers of post-fire *P. mariana* to calculate q_x (Figure 4.5a). Mortality in both stands appears to increase over time. Between 33 and 69 years q_x ranges from 0.0119 to 0.0429 year^{-1} (stand N). From 76 to 140 years q_x ranges from 0.05 to 0.0909 year^{-1} (stand Q). In stands dominated by *P. mariana* (stands J, K, L), the patterns of mortality of post-fire cohorts are as follows. After relatively high mortality rates from germination (~0.66 year^{-1}) through the first three years (~0.1 year^{-1}), mortality decreases, ranging from 0.0286 to

Figure 4.4   The height growth curves of all live and dead post-fire and understorey

individuals in a 153 year old stand dominated by *Pinus banksiana* and

Picea mariana (stand Q).
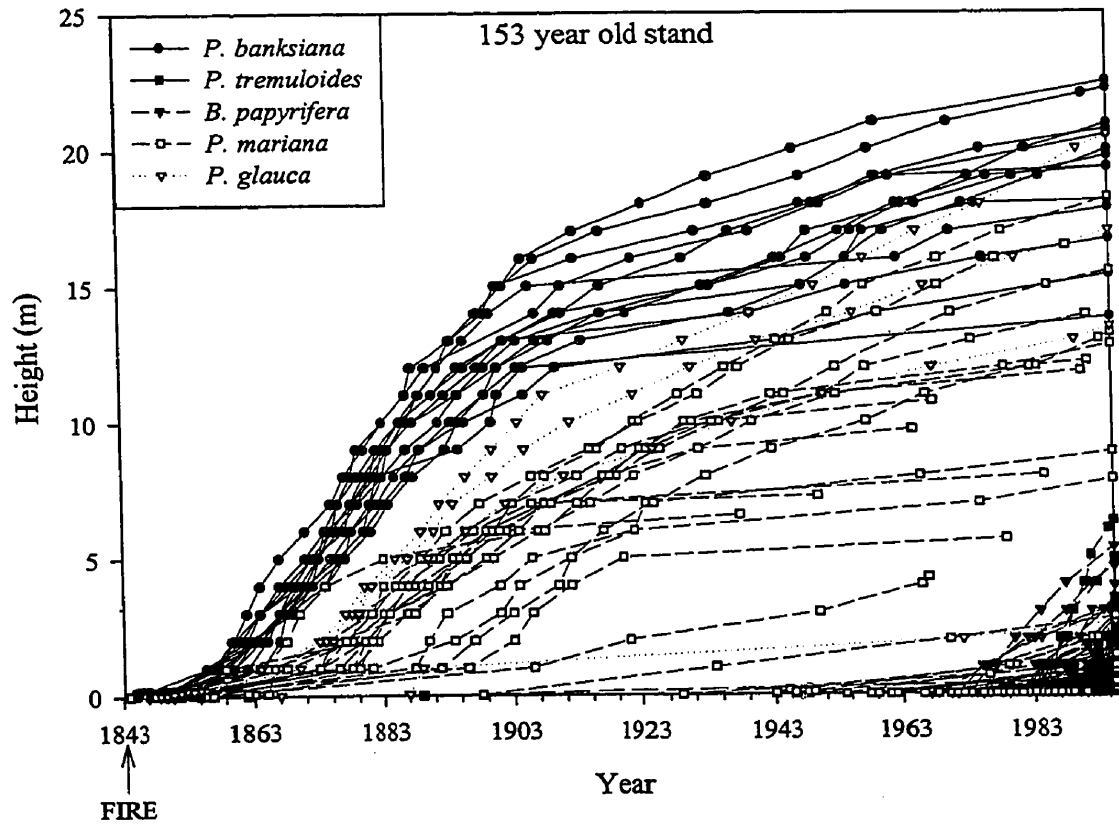
0.0323 year^{-1} between 19 and 24 years, from 0.02 to 0.0789 year^{-1} between 49 and 94 years, and from 0.0143 to 0.0577 year^{-1} between 93 and 149 years.

In two stands dominated by *P. mariana* (stands J and K) there are understorey cohorts of *P. mariana*, originating from both branch layering and seed (Figure 4.5b). In stand J, q_x of seed origin *P. mariana* between 11 and 18 years ranges from 0.667 to 0.143 year^{-1}, while branch origin *P. mariana* between 12 and 22 years ranges from 0.7692 to 0.333 year^{-1}. In stand K q_x of branch origin *P. mariana* between 25 and 32 years ranges from 0.1 to 0.22 year^{-1}. Figure 4.6 gives the height growth of live and dead post-fire and understorey individuals in our oldest stand dominated by *P. mariana*. There are large numbers of live *P. mariana* and *P. glauca* remaining in the canopy; however there are no individuals in the understorey. Thus, there will be no replacement of post-fire cohorts with understorey cohorts in this stand.

THE IMPORTANCE OF REGIONAL PROCESSES

The regional dynamics are important to species with aerial seed banks if catastrophic fire occurs prior to their age of reproduction. To examine the probability of this occurring we plotted the probability of fire given the present range of fire cycle and the time to reproduction for each species.

The age of reproduction of *P. banksiana* is approximately 30 years, while the age of reproduction of *P. mariana* is approximately 40 years (Figure 4.7). Within the range of the present fire cycle, 75-150 years, the probability of a fire occurring before the age of

Figure 4.5   Within stands J-L, N and Q, and permanent plots dominated by $P.$ *mariana* the age-specific mortality rates, q_x, of: a) post-fire cohorts of $P.$ *mariana*, and b) all understorey cohorts.

a)

Post-Fire Cohorts

Legend: stand J, stand K, stand L, mineral, humus, *P. mariana* - pp, stand N, stand Q

q_x

Time (years)

b)

Understorey Cohorts

Legend: J - *P. mariana* (seed), J - *P. mariana* (branch), K - *P. mariana* (branch)

q_x

Time (years)
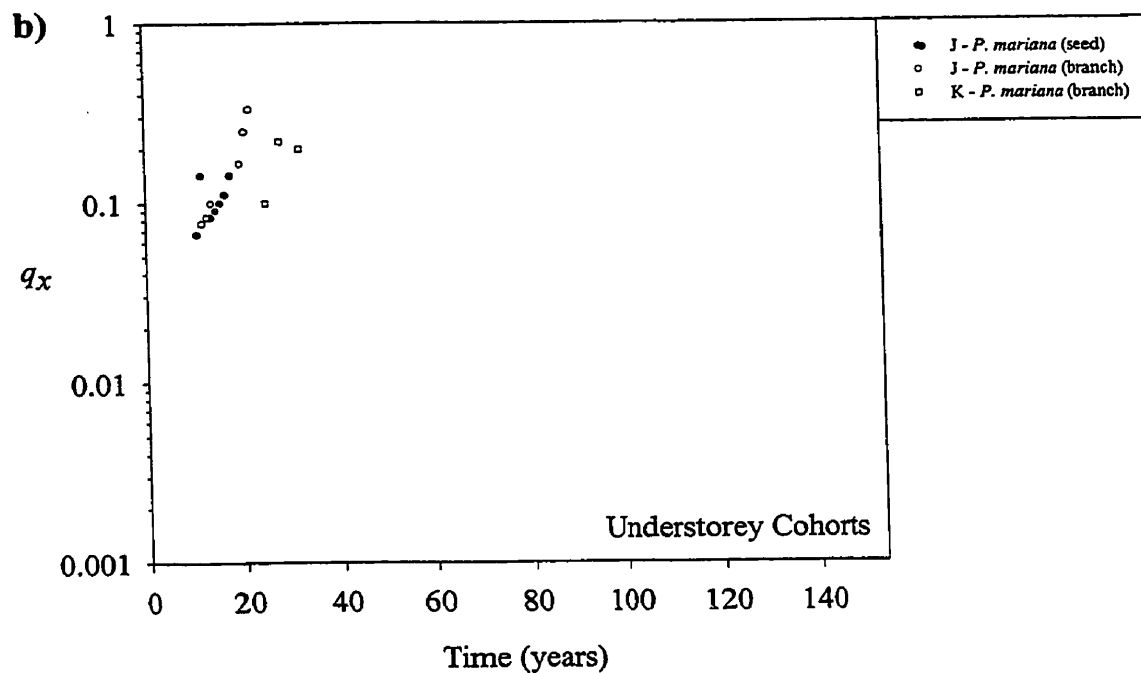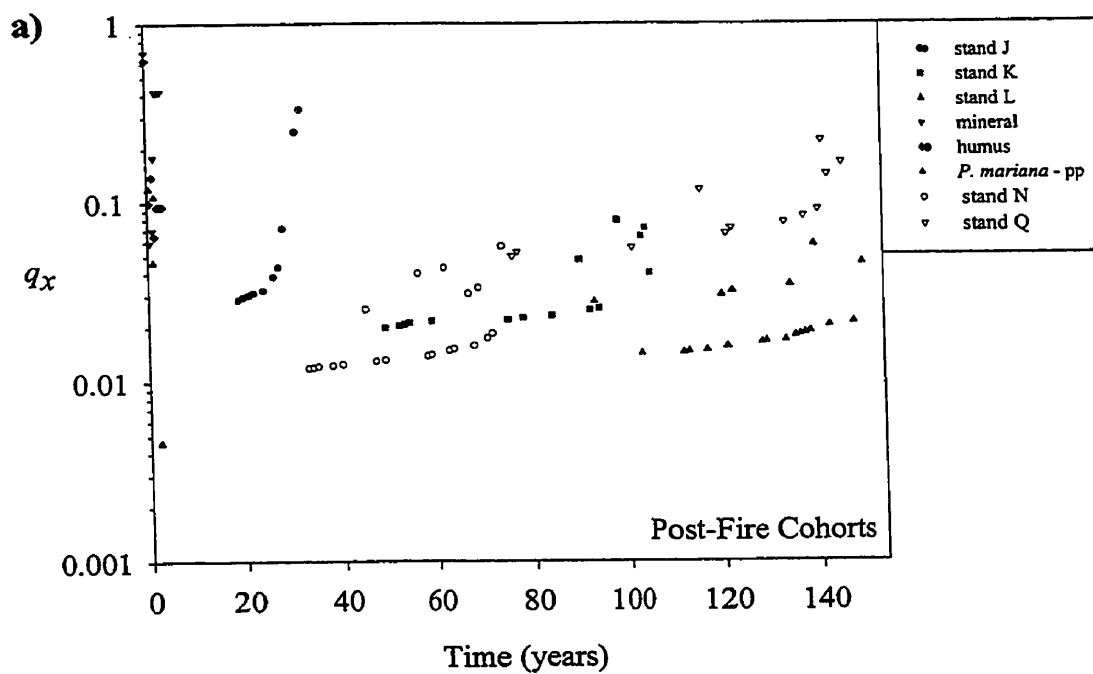
Figure 4.6   The height growth curves of all live and dead post-fire and understorey

individuals in a 153 year old stand dominated by *Picea mariana* (stand L).
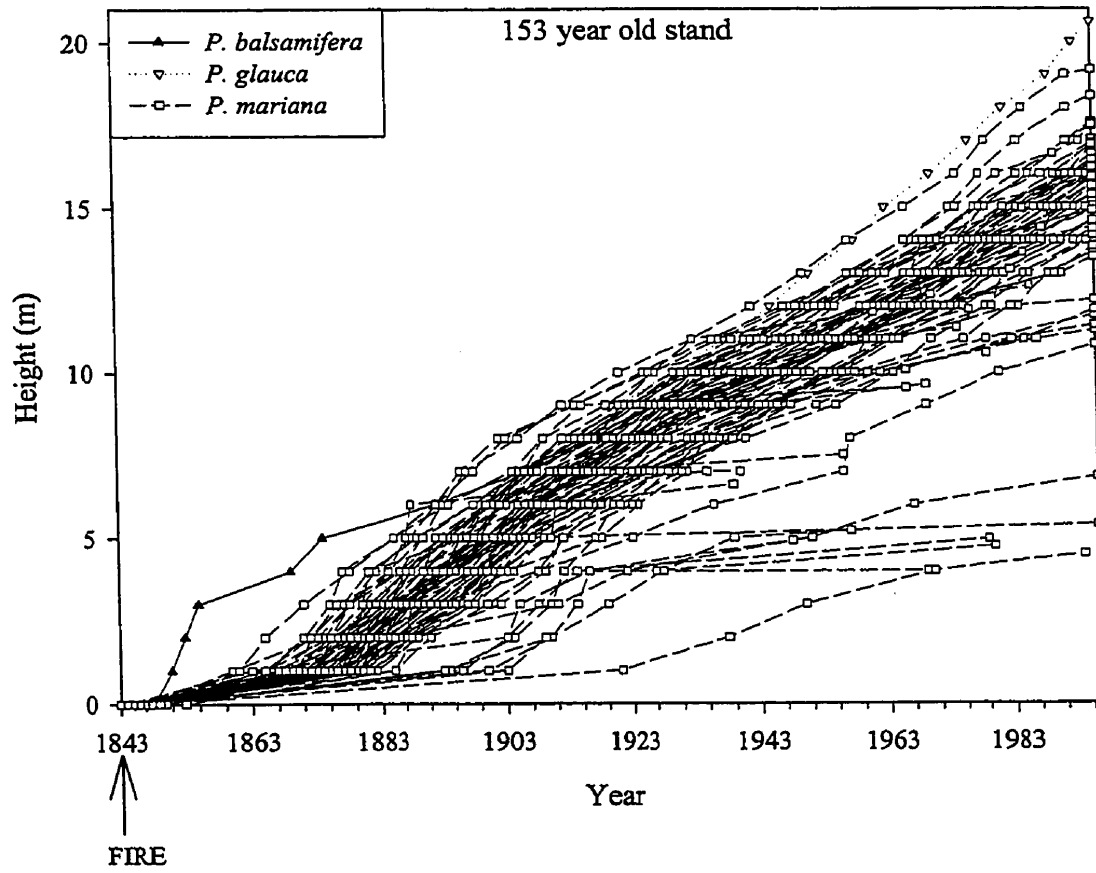
Figure 4.7   The probability of wildfire, over a range of fire cycles, prior to the age of

reproduction of *Pinus banksiana* and *Picea mariana*.
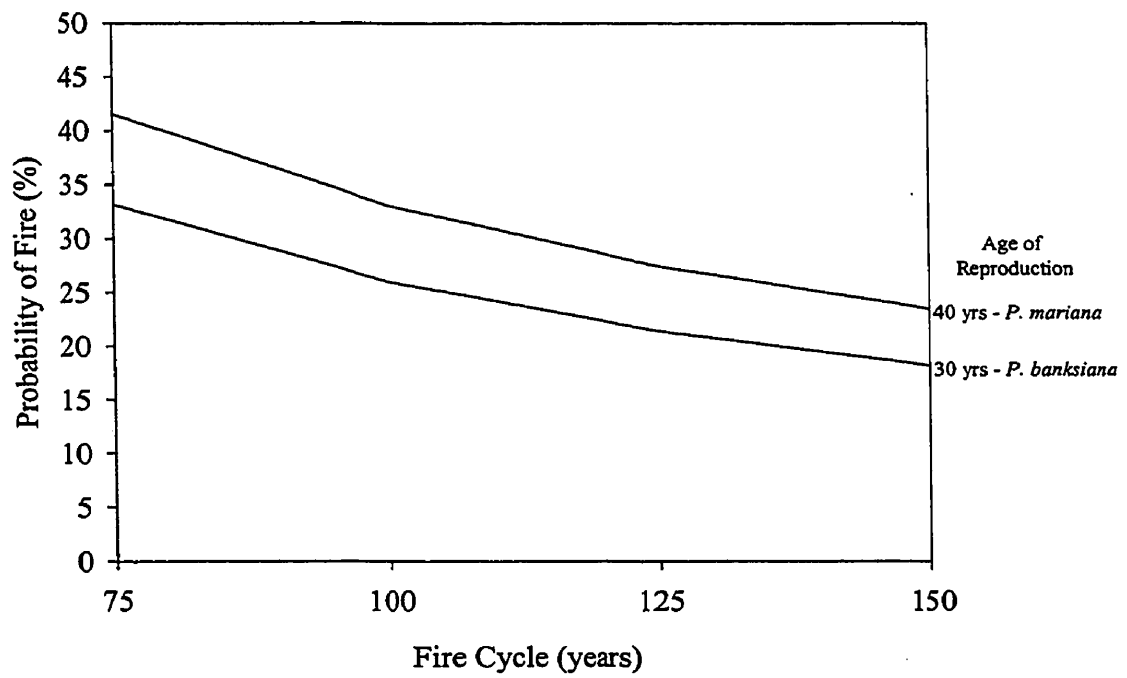
reproduction is 18-33% for *P. banksiana* and 23-42% for *P. mariana*. Thus, *P.*

banksiana is less likely to go extinct within a local population, compared to *P. mariana*.

If extinction does occur, successful re-colonization by these species requires that the seed

of both species be dispersed by wind from other, reproductively mature, fire-killed local

populations. Because the cones of *P. mariana* are semi-serotinous, *i.e.* some cones open

at maturity without fire (Johnson and Johnson 1997), seed may also be dispersed from

nearby live populations.

Asexually Reproducing Species

LOCAL POPULATION PROCESSES

Asexually reproducing *P. tremuloides* sprout primarily from underground stems.

Thus, in stands where there is a high basal area and density of fire-killed stems regional

processes are relatively unimportant.

Given equal basal areas, recruitment densities are relatively high for *P.*

tremuloides (equation 4.5) compared to *P. glauca* (equation 4.8) and *A. balsamea*

(equation 4.9) in stands where all species are present. Also, where all three species are

present, recruitment densities of *P.tremuloides* are much higher because they typically

have a much higher basal area.

The age of individuals shows that *P. tremuloides* recruits within the first ten years

after fire (Figure 3.7). For the first three years after germination (Figure 4.8), q_x of *P.*

tremuloides varies around 0.1 year^{-1}, ranging from 0.0438 to 0.4044 year^{-1}. Notice that

Figure 4.8   Mean and standard error of age-specific mortality rates, q_x, over the first

three years after fire for *Populus tremuloides*. *P. tremuloides* pp are data

from the *P. tremuloides* permanent plots.
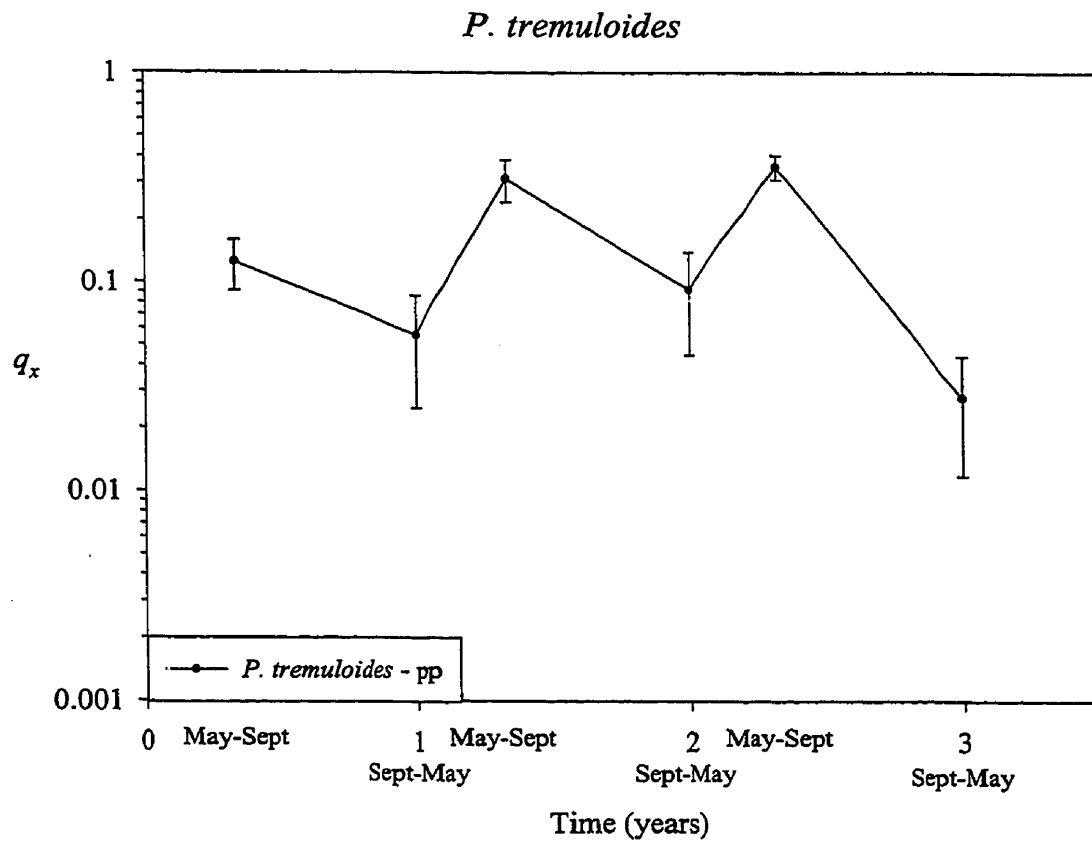
P. tremuloides

summer mortality (May to September) is significantly higher than winter mortality (September to May).

Age-specific mortality rates were calculated for post-fire cohorts of *P. tremuloides* in stands A-E and G (Figure 4.9a). The patterns of mortality for *P. tremuloides* are as follows. After mortality rates of approximately 0.1 year^{-1} for the first three years, they range from 0.0196 to 0.1288 year^{-1} between 1 and 8 years in stand A, and from 0.0156 to 0.089 year^{-1} between 8 and 33 years in stand B. Between 42 and 55 years, q_x ranges from 0.0244 to 0.0333 in stand C, and at 100 years q_x is 0.017 year^{-1} (Figure 4.9a). In stand G, dominated by *P. glauca*, q_x of *P. tremuloides* between 60 and 75 years ranges from 0.0476 to 0.0714 year^{-1}.

In stands dominated by *P. tremuloides* (stands A-E), there are understorey cohorts of *P. tremuloides*, *B. papyrifera*, *P. glauca*, and *A. balsamea* (Figure 4.9b). For understorey cohorts of *P. tremuloides*, q_x ranges from 0.333 to 0.5 year^{-1} between 12 and 24 years in stand B, is 0.5 year^{-1} at 2 years in stand D, and from 0.0132 to 0.25 year^{-1} between 1 and 20 years in stand E. For understorey cohorts of *B. papyrifera* q_x ranges from 0.111 to 0.5 year^{-1} between 8 and 17 years in stand B, from 0.0417 to 0.3 year^{-1} between 1 and 5 years in stand C, and from 0.0141 to 0.111 year^{-1} between 1 and 26 years in stand E. In stand E, for the understorey cohort of *P. glauca*, q_x ranges from 0.034 to 0.25 year^{-1} between 3 and 30 years, and for *A. balsamea* q_x ranges from 0.005 to 0.0106 year^{-1} between 8 and 16 years.

Figure 4.9   Within stands A-E and permanent plots dominated by *Populus*

tremuloides, age-specific mortality rates, q_x, of: a) post-fire cohorts of *P.*

tremuloides, and b) all understorey cohorts.

a)

qx

stand A
stand B
stand C
stand E
P. tremuloides - pp
stand G

Post-Fire Cohorts

Time (years)

b)

qx

B - *P. tremuloides*
B - *B. papyrifera*
C - *B. papyrifera*
D - *P. tremuloides*
E - *P. tremuloides*
E - *B. papyrifera*
E - *P. glauca*
E - *A. balsamea*

Understorey Cohorts

Time (years)
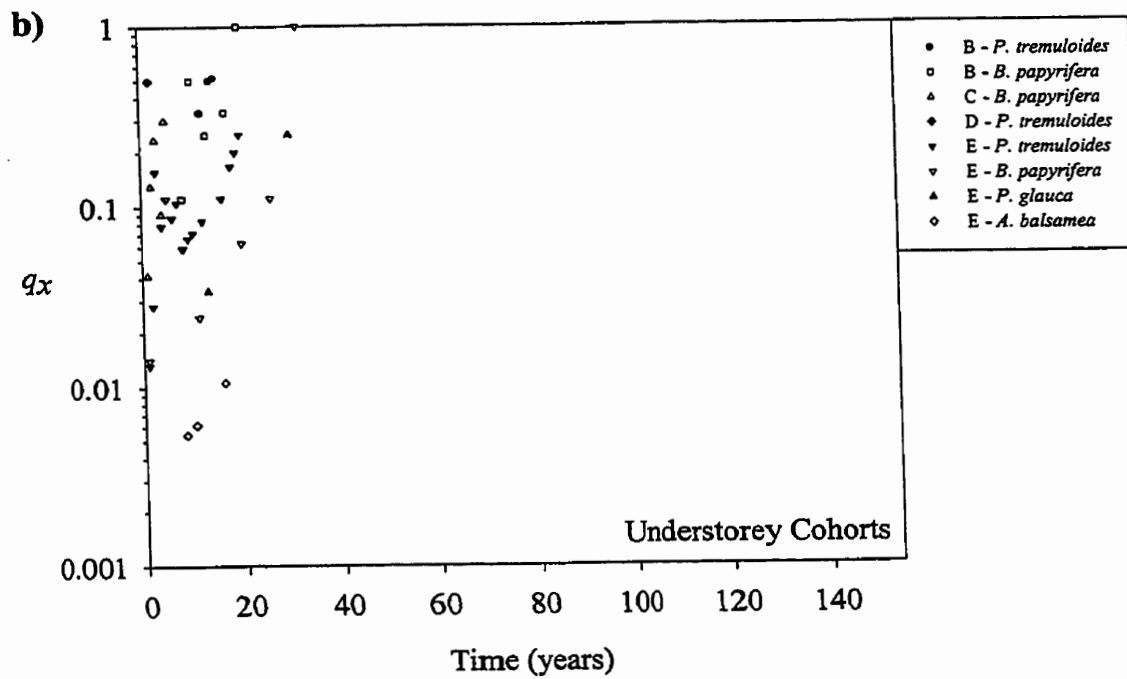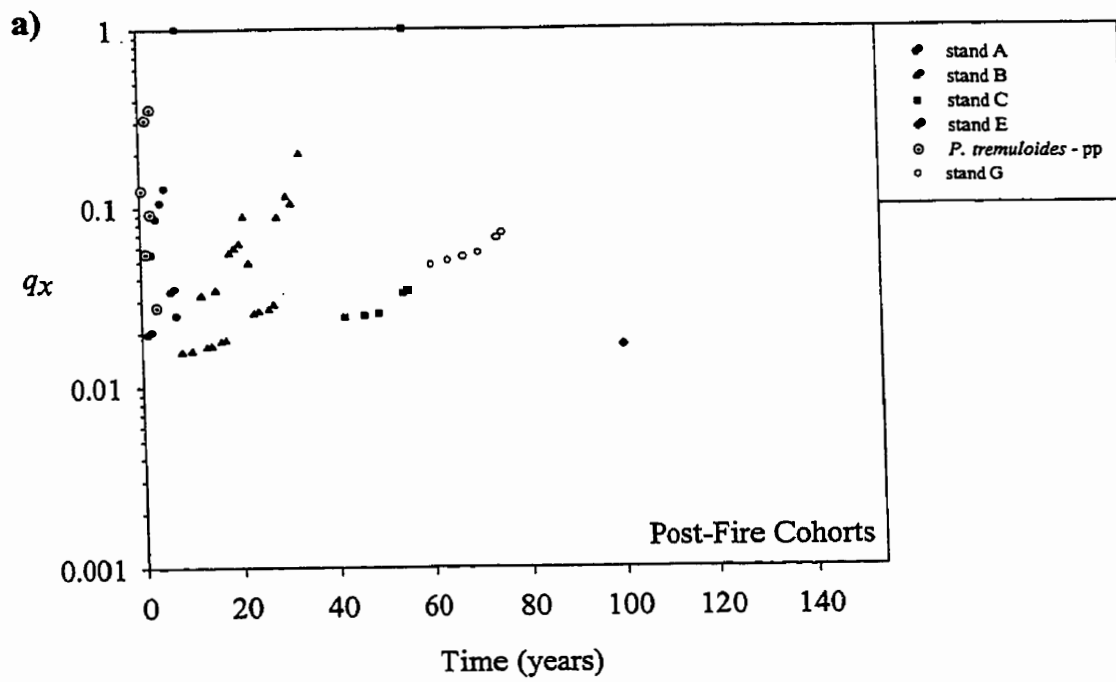
Figure 4.10 gives the height growth of live and dead post-fire and understorey individuals in our oldest stand dominated by *P. tremuloides* and *P. glauca*. There are large numbers of live *P. tremuloides* and *P. glauca* remaining in the canopy, and large numbers of *P. tremuloides*, *B. papyrifera*, *A. balsamea*, and *P. mariana* in the understorey. Notice that all understorey individuals are relatively small such that it does not appear likely that they would have made it into the canopy in the near future.

THE IMPORTANCE OF REGIONAL PROCESSES

The regional dynamics become important to asexually reproducing species if catastrophic fire occurs when the basal area of individuals within the fire-killed local population is too low to support the growth of new sprouts. In well-stocked stands in our study area this is likely to occur in stands 5 years or younger. Within the range of their present fire cycle, 75-150 years, the probability of a fire occurring before *P. tremuloides* is five years of age is 13-24% (Figure 4.11).

Wind Dispersed Species

LOCAL POPULATION PROCESSES

For wind-dispersed *P. glauca* and *A. balsamea*, seed must come from live sources on the edge of the burn, or from unburned patches within the burn. For serotinous *P. banksiana* and *P. mariana* that are killed before they are reproductive, seed must be dispersed from other, reproductively mature, fire-killed local populations. For the semi-

Figure 4.10   The height growth curves of all live and dead post-fire and understorey

individuals in a 111 year old stand dominated by *Populus tremuloides* and

Picea glauca (stand E).

Height (m) vs Year chart for a 111 year old stand showing:
- P. tremuloides
- B. papyrifera
- P. glauca
- A. balsamea
- P. mariana

FIRE (arrow at 1886)
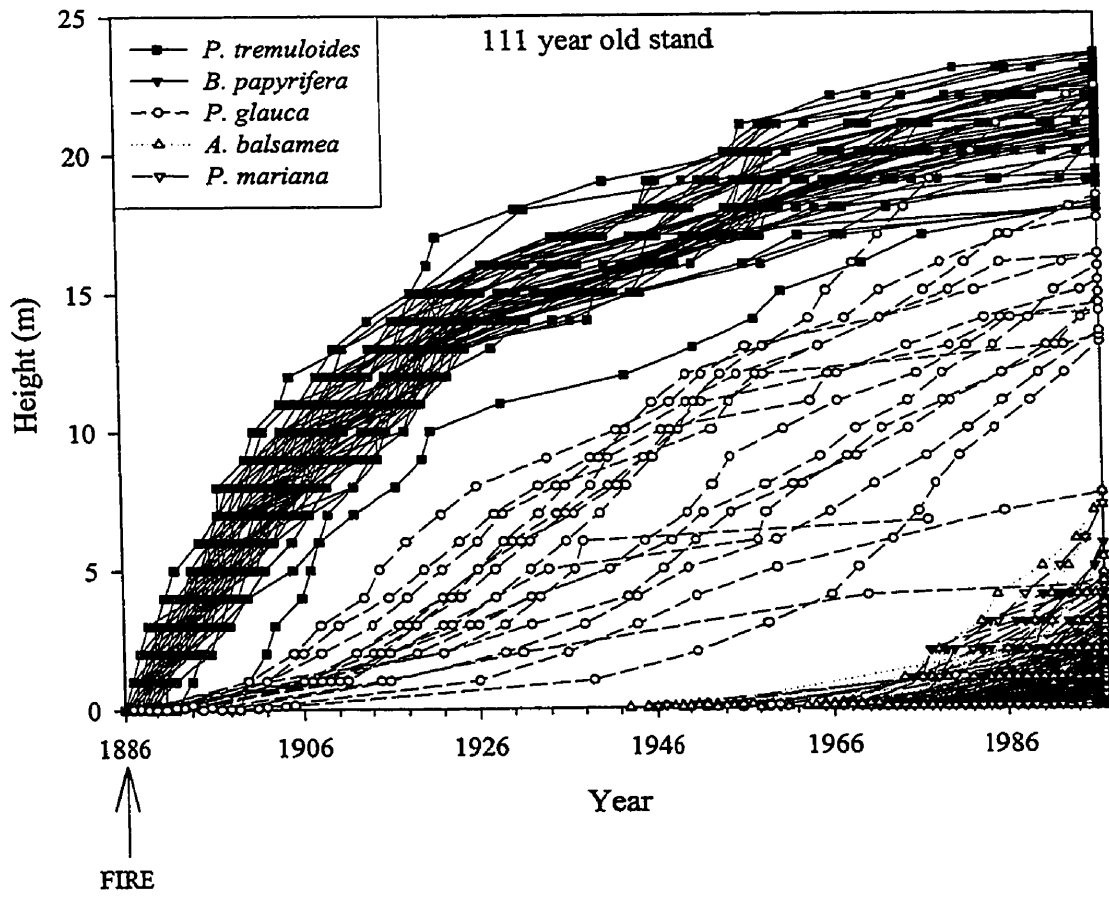
Figure 4.11   The probability of wildfire, over a range of fire cycles, prior to the

adequate stocking (*i.e.* 5 yrs) of *Populus tremuloides*.
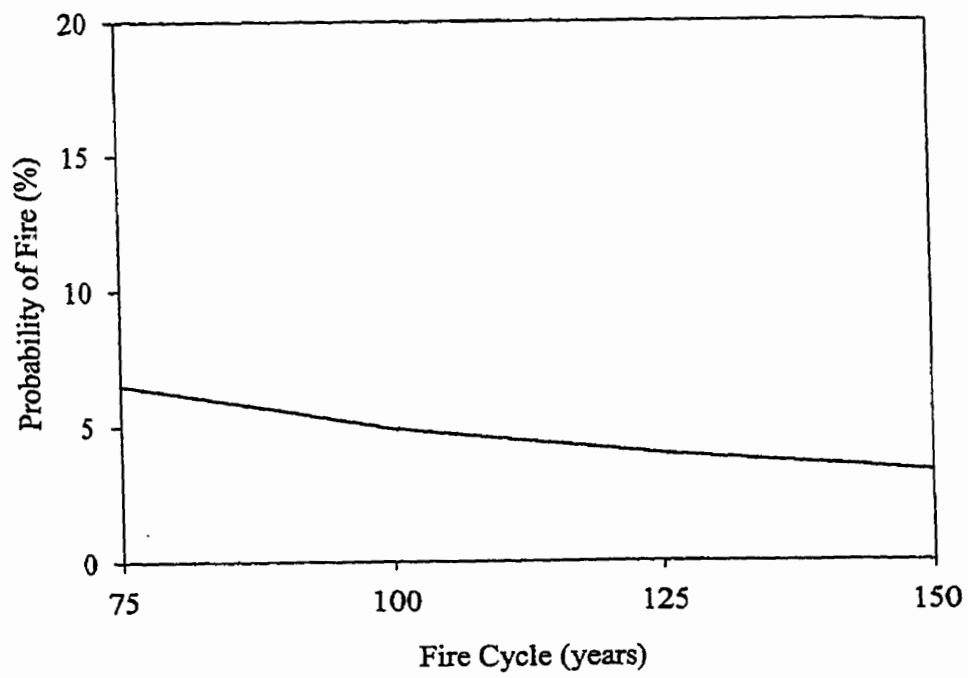
serotinous *P. mariana* seed may also be dispersed from live sources. For all species that rely on wind dispersal of their seeds for re-colonizing fire-killed local populations, the local processes are relatively more important compared to the regional processes. Seed production of *P. glauca* is relatively higher (equation 4.6) than *A. balsamea* (equation 4.7). Germination mortality rates for *P. glauca* are relatively high (mineral = 0.74 ± 0.04 year^{-1}; humus = 0.67 ± 0.02 year^{-1}) (Figure 4.12). Given equal basal areas, recruitment densities are relatively higher for *P. glauca* (equation 4.8) compared to *A. balsamea* (equation 4.9). Recruitment densities of *P. glauca* are typically higher than *A. balsamea* because their higher growth rates mean that they have a higher basal area density.

The age of individuals shows that *P. glauca* recruits within the first ten years after fire (Figure 3.7). For the first three years after germination (Figure 4.12) mortality for post-fire cohorts of *P. glauca* varies around 0.1 year^{-1}, ranging from 0 to 0.31 year^{-1} (note that standard error bars both extend to zero and thus do not show up on the figure). There are no significant differences between data sets, *i.e.* Charron and Greene (submitted) and permanent plots from this study.

Age-specific mortality rates were calculated for post-fire cohorts of *P. glauca* in stands F, G, and I (Figure 4.13a). The general pattern of mortality is as follows. After relatively high mortality rates for the first few years (~ 0.1 year^{-1}), the mortality of post-fire *P. glauca* decreases, ranging from 0.025 to 0.0769 year^{-1} between 28 and 74 years in stand G, 0.03 year^{-1} at 40 years in stand F, and 0.25 year^{-1} at 119 years. In general,

Figure 4.12   Mean and standard error of germination rates and age-specific mortality

rates, q_x, over the first three years after fire for *Picea glauca*. Note that

(mineral) and (humus) are values of q_x from Charron and Greene

(submitted) and *Populus tremuloides* pp are data for post-fire cohorts of *P.*

glauca from the *P. tremuloides* permanent plots.

P. glauca
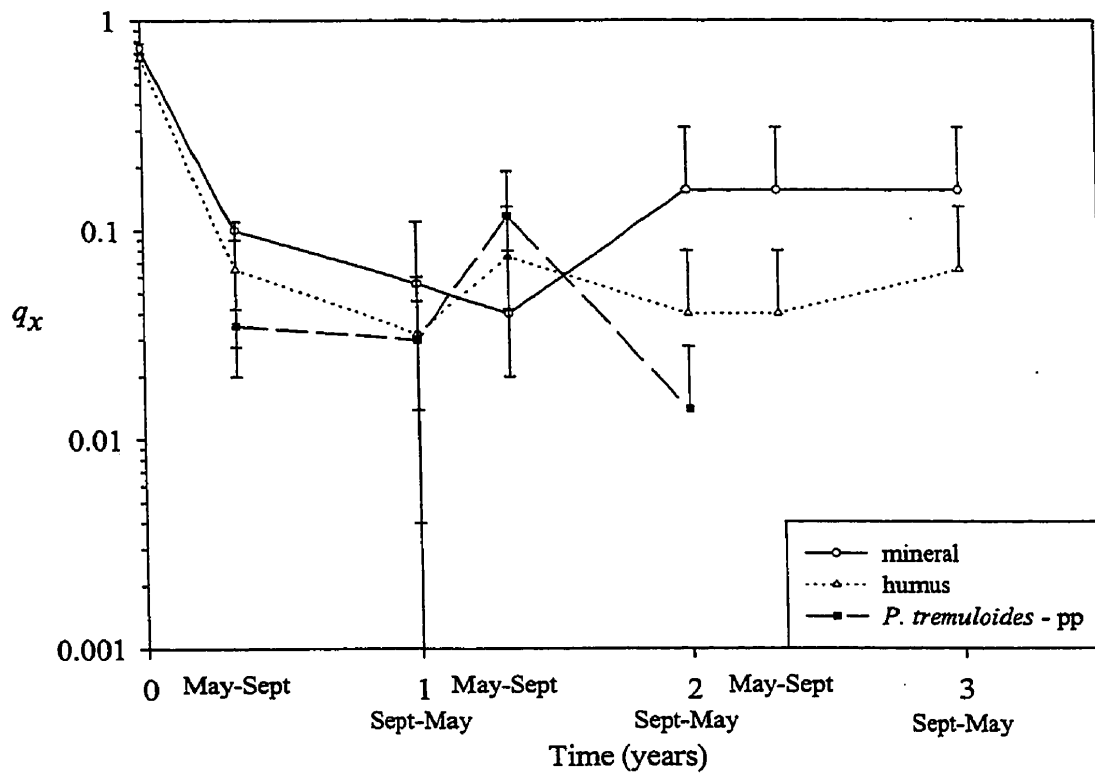
Figure 4.13   Within stands F-I and permanent plots dominated by *Picea glauca* and

Populus tremuloides, the age-specific mortality rates, q_x, of: a) post-fire

cohorts of *P. glauca,* and b) all understorey cohorts.

a)

b)
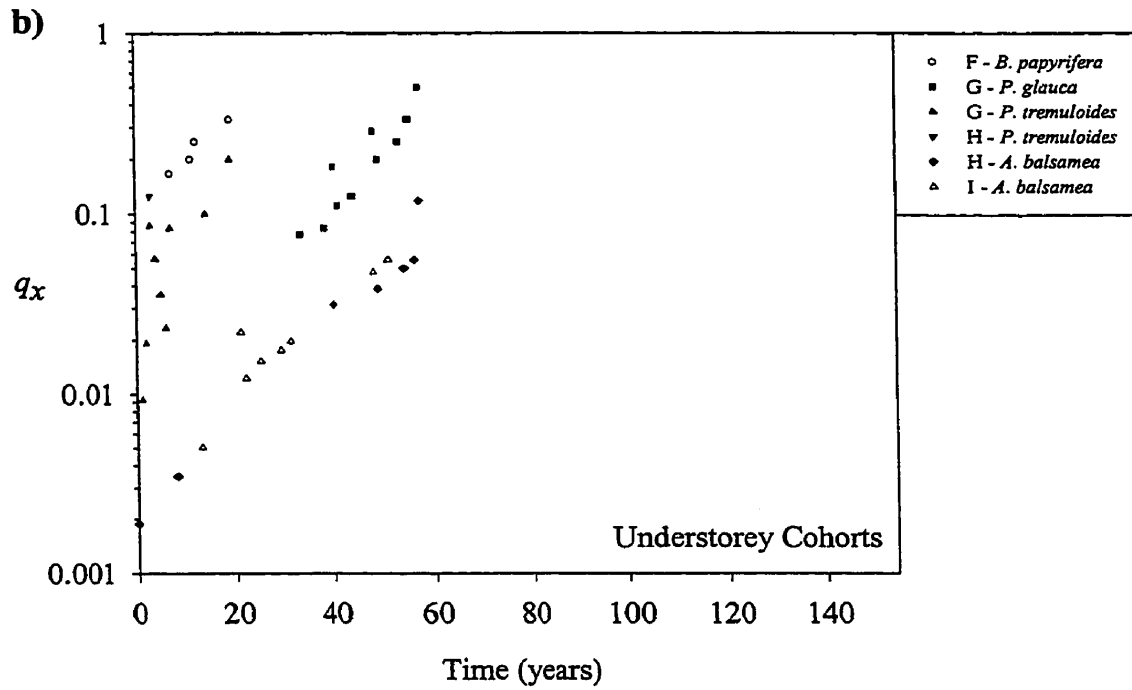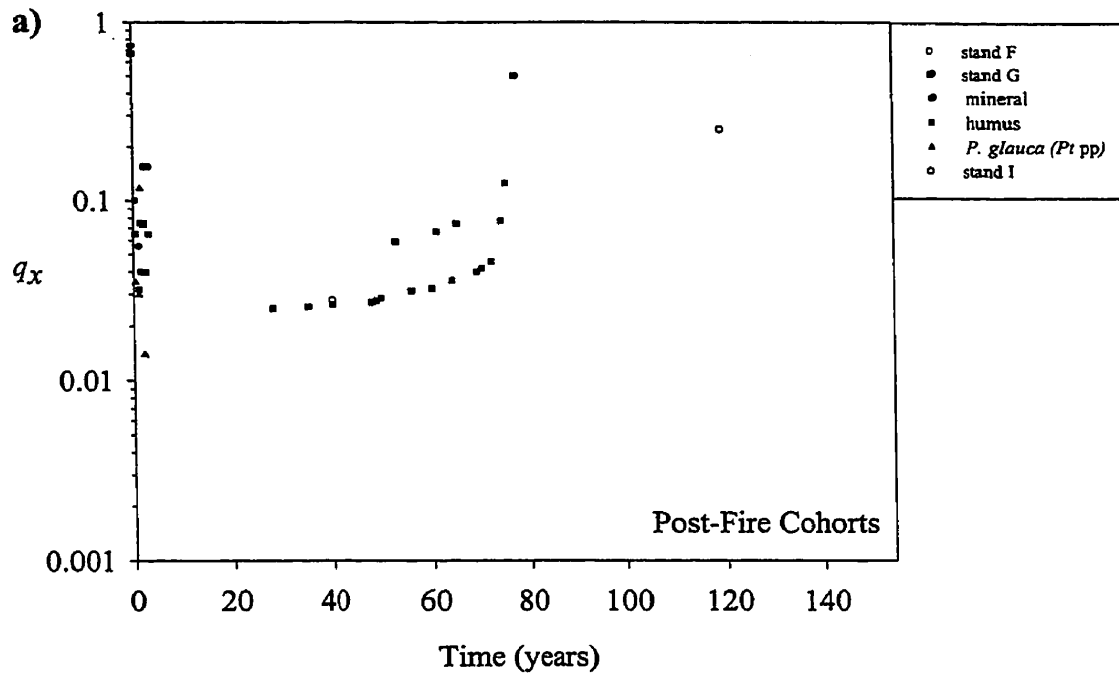
mortality appears to be relatively low beyond 80 years (Figure 4.13a).

In stands dominated by *P. glauca* (stands F-I), there are understorey cohorts of *B. papyrifera, P. glauca, P. tremuloides,* and *A. balsamea* (Figure 4.13b). Notice that for all cohorts the value of q_x increases with age. For the understorey cohort of *B. papyrifera* in stand F, q_x ranges from 0.167 to 0.333 year^{-1} between 7 and 19 years. In stand G, q_x for the understorey cohort of *P. glauca* ranges from 0.0769 to 0.5 year^{-1} between 33 and 57 years, while for *P. tremuloides* q_x ranges from 0.009-0.2 year^{-1} between 1 and 19 years. In stand H for the understorey cohort of *P. tremuloides* q_x is 0.13 year^{-1} at 3 years, while q_x of *A. balsamea* ranges from 0.002 to 0.118 year^{-1} between 0 and 57 years. In stand I, q_x of *A. balsamea* ranges from 0.005 to 0.0556 year^{-1} between 13 and 51 years.

Figure 4.14 gives the height growth of live and dead post-fire and understorey individuals in our oldest stand dominated by *P. glauca* and *A. balsamea*. There are only two large live *P. glauca* and *A. balsamea* remaining in the canopy from the original post-fire cohorts. There are a few *P. tremuloides* and *A. balsamea* in the sub-canopy and large numbers of *P. tremuloides* and *A. balsamea* in the understorey. Notice that at least two fires have burned through the stand since the stand-initiating fire. Both fires, particularly the fire 112 years ago, appear to have killed large numbers of canopy and understorey individuals.

THE IMPORTANCE OF REGIONAL PROCESSES

The regional dynamics are essential for re-colonization by the wind-dispersed

Figure 4.14   The height growth curves of post-fire and understorey individuals within a

154 year old stand dominated by *Picea glauca* and *Abies balsamea* (stand

H). Notice that two fires have burned through the stand since the time of

stand initiation.

154 year old stand
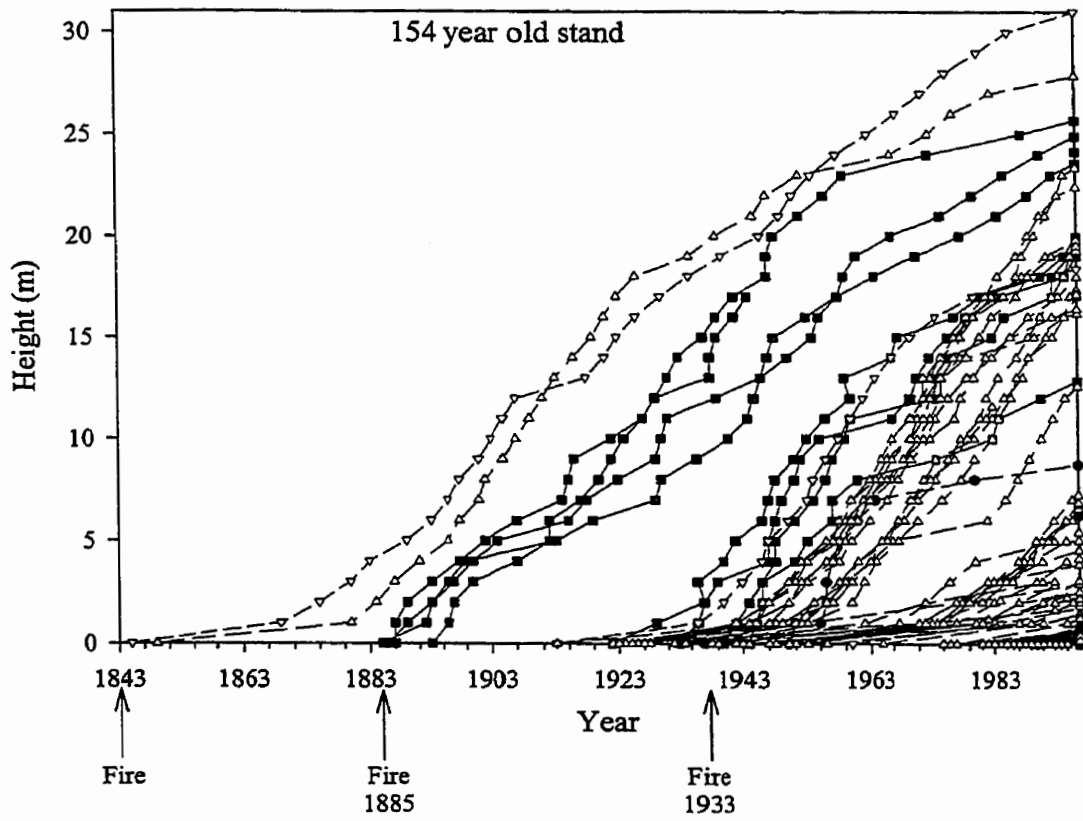
species *P. glauca* and *A. balsamea*. Reproductively mature live trees must be located within 50 metres of a fire-killed local population in order to ensure adequate re-colonization (Greene and Johnson 2000).

Within the range of the present fire cycle, 75-150 years, the probability of a fire occurring before individuals are reproductive is 28-48% for *P. glauca and* 18-33% for *A. balsamea* (Figure 4.15). Thus, *A. balsamea* is less likely to go extinct within a population, compared to *P. glauca*. This has implications for the distribution of live seed sources in the regional population.

Discussion

What have we learned about forest dynamics by examining the local processes of seed production, seed germination, recruitment, mortality, growth, and disturbance?

Traditionally forest succession has been about *stand dynamics* (Oliver and Larson 1990). Most have viewed forest succession as a process of species replacement over time, *i.e.* understorey trees replace canopy trees (*e.g.* Carleton and Maycock 1977; Carleton 1982; Foster and King 1986; Bergeron and Dubuc 1989; Bergeron 2000). This view may have come about because within stands there is often a hierarchy in the size of individuals, which is believed to represent the order of succession. The largest trees, thought to be older, are replaced in the canopy by successively smaller, *i.e.* younger, trees. The difference in age between different sized trees was confirmed by aging trees at breast height, or at the base; larger trees were older than smaller trees.

Figure 4.15   The probability of wildfire, over a range of fire cycles, prior to the age of

reproduction of *Picea glauca* and *Abies balsamea.*
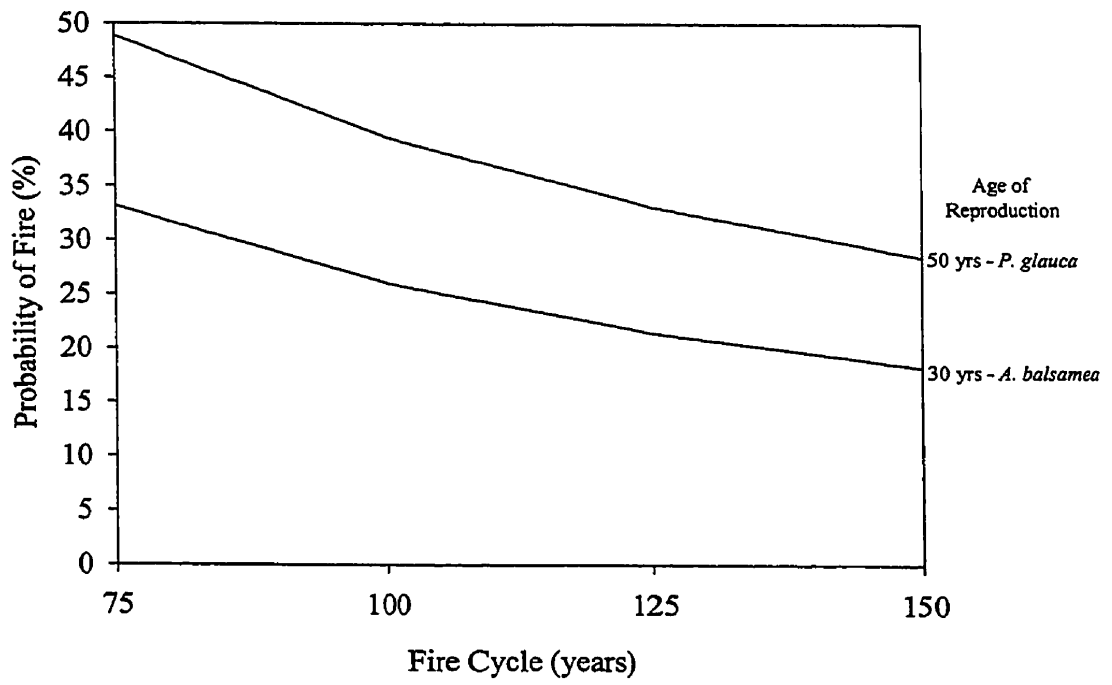
The long life span of trees has meant that the patterns of species replacement over time have always been inferred. Evidence has been almost always taken at one point in time, either using a static diameter distribution, static age distribution, or chronosequence. As shown in Chapters Two and Three, however, the methods used to infer patterns of forest succession make assumptions that are not met. Aging individuals at the root collar shows that trees different in size are often similar in age; all species recruit within the first few years after fire. Evidence from the age-specific mortality rates shows that individuals in the understorey do not replace individuals in the canopy because understorey cohorts have relatively high mortality and thus they do not live very long. Also, from the height growth curves it appears that understorey cohorts have relatively slow height growth rates such that those that do survive for longer periods will likely never make it into the canopy. Thus, in general only those recruiting within the first few years after fire make it into the canopy and produce seed for the next generation.

Under what conditions might understorey trees replace canopy trees? The replacement of species within stands, between stand-replacing disturbances, depends on the population processes of recruitment, mortality, and growth, and the time interval between disturbances. If the time between disturbances is within the lifespan of most canopy trees, enough understorey individuals may survive to replace the canopy trees if the mortality rates of understorey recruits decreased and mortality of post-fire cohorts increased. Understorey mortality rates may be decreased if the seeds of understorey species were able to germinate on seedbeds more suitable than the thick organic matter

within most stands. Logs are often proposed as providing such a suitable seedbed in the understorey of mature stands (*e.g.* Harmon and Franklin 1989; Swewczyk and Szwaggrzyk 1996). If a surface fire occurs and consumes the organic litter and fermentation layers, then the more suitable humus and mineral soil seedbeds would allow for adequate survival of understorey individuals. However, both seedbeds must be available within a few decades after the stand initiating disturbance if the surviving understorey individuals are going to make it into the canopy in the relatively short time before the next stand-replacing disturbance.

Replacement may also occur if the mortality of canopy individuals was increased significantly such that large numbers of them died within a relatively short period of time (*i.e.* 80-100 years). With significant increases in light to the understorey, growth rates of surviving understorey individuals may increase such that they are able to grow rapidly into the canopy (Berry 1982; Yang 1991; Osawa 1994). This appears to occur in some parts of the eastern boreal forest where large areas of post-fire cohorts are killed by spruce budworm outbreaks (Fye and Thomas 1963; Blais 1983; Morin *et al.* 1993; Morin 1994; Bergeron *et al.* 1995). Similarly, in other forests, windstorms frequently kill large areas of canopy trees, leaving the understorey intact (Veblen *et al.* 1989.). These situations, however, are not typically what is meant by traditional succession.

Many would argue that the reason we do not see replacement in these mixedwood stands is that the time between fires is not long enough (*e.g.* Carleton and Maycock 1977; Carleton 1982; Foster and King 1986; Bergeron and Dubuc 1989; Bergeron 2000). In

forests where the disturbance cycle is longer, the death of one or more canopy trees is believed to play an important role in promoting species replacement within local populations (Ban *et al.* 1998; Kneeshaw and Bergeron 1998). However, in the boreal forest little direct evidence of trees in the understorey growing into the canopy has ever been presented. If the death of one or more canopy trees are important in promoting species replacement, then we should expect to see death in the canopy followed by a rapid growth of individuals already present in the understorey. In one of our oldest stands, dominated in the canopy by *P. banksiana* and *P. mariana*, where there has been some mortality of post-fire canopy individuals, we did not see any change in the growth rates of understorey cohorts. In another old stand, dominated in the canopy by *P. glauca* and *A. balsamea*, some individuals have almost made it into the canopy. However, this appears to have been made possible by two fires that have burned through the stand since the stand was initiated. Notice that large numbers of canopy and understorey individuals appear to have been killed, particularly by the fire 112 years ago. Further, the species that has nearly reached the canopy, *P. tremuloides*, is not traditionally thought of as mid- or late-successional. Consequently, the sequence of species is not the traditional sequence described in the boreal forest.

Why are the regional processes of moisture and nutrient gradients, seed dispersal, and disturbance so dominant?

Within a local population the dynamics are dependent on the species available for

re-colonization within the first few years after disturbance; these are the only individuals to make it into the canopy, and thus the only individuals to produce seed for the next generation. It is these rapidly recruiting individuals that ensure the persistence of a species within the regional population. Thus, the regional distribution of local populations (determined by moisture and nutrient gradients), the size and intensity of disturbance, and the dispersal of seed between local populations play a critical role in the ability of a species to rapidly re-colonize disturbed areas.

For species that are capable of re-colonizing a disturbed area from within a local population regional processes are relatively unimportant. In the boreal forest these include species with serotinous and semi-serotinous cones, and those that can reproduce asexually by sprouting. If post-fire cohorts of fire-killed serotinous species are reproductively mature, then their seeds will simply be released within the local population after their cones are opened by fire. If the post-fire cohorts of fire-killed asexually reproducing species are of adequate basal area and have a high density of underground stems, large numbers of individuals will sprout rapidly after fire. If these conditions are not met for these species, however, their re-colonization after fire, like other species, depends on seed dispersing from outside the fire-killed local population, either from mature fire-killed local populations or, for *P. mariana*, from live sources outside of the burned area. For the serotinous species *P. banksiana* and *P. mariana*, the short time between fires means that fire may occur prior to reproduction more than is often thought, and thus dispersal from outside the local population may be more important than

traditionally believed.

The regional distributions of local populations are driven by geomorphic processes which give rise to ridgelines, stream courses, and hill slopes, which in turn give rise to moisture and nutrient gradients (Bridge and Johnson 2000). Hill slopes create the fundamental upland hydrological gradient; the downward flow of water from the ridgelines to the bottom of slopes also results in the downward flow of nutrients (Bull 1975; Anderson and Burt 1977, O'Loughlin 1981; Dawes and Short 1994). Studies that have examined the distribution of moisture along hill slopes have found that relatively dry and relatively wet parts of the hill slope are not very common; mid slope positions are the most abundant. Thus, species that dominate on these mid slope positions are the most abundant on the landscape. In the study area, the tops of glaciofluvial hill slopes are dominated by *P. banksiana*; at mid slope positions both *P. banksiana* and *P. mariana* dominate, and *P. mariana* dominates at the bottoms of hill slopes. The tops of glacial till hill slopes are dominated by *P. tremuloides*. Mid slope positions are dominated by *P.glauca* and *A. balsamea*, while *P. glauca* dominates at the bottoms of slopes. Thus, both *P. banksiana* and *P. mariana* on glaciofluvial hill slopes and *P. glauca* and *A. balsamea* on glacial till hill slopes are present over relatively large areas because they occupy the most abundant hill slope positions.

In the boreal forest the large size (10^1 to 10^3 km^2) and high intensity of wildfires means that several watersheds (0.3 to 13 km^2) and the local populations within them may be burned over in one fire. The relationship of the perimeter of burns to burn area shows

that fires tend to become narrower as they get larger. Therefore, the distance from the edge to any point in a burn will not increase greatly as fire size increases. Within a burn many unburned patches remain; the amount of area within these patches per burn area remains constant (Greene and Johnson 1998; Eberhart and Woodard 1987). Thus, despite differences in fire size, the mean dispersal distance from the burn edge or from surviving patches is not typically greater than 150 meters (Greene and Johnson 1995). Greene and Johnson (2000) suggest adequate recruitment densities within fire-killed populations of wind-dispersed species require that live seed sources be located within 50 meters of the burned local population. At distances of 150 meters seed fall density should only be about 5% of the seed fall density in the forest (Greene 1989).

So what does this mean for regional population dynamics of tree species in the boreal forest? It is clear that for species that can re-colonize from within a burned local population, either by sprouting or serotinous cones, only the regional process of local population extinction may be important. For the sprouting species, *P. tremuloides* there appear to be very few situations that would lead to its extinction within a local population. Thus, the fact that it occupies a hill slope position that is relatively uncommon on the landscape is relatively unimportant to its persistence on the landscape; it ability to re-sprout vigorously after fire means that it is still very abundant on the landscape. For the serotinous species, *P. banksiana* and *P. mariana,* their ability to re-colonize from within a local population requires that post-fire cohorts have reached reproductive maturity by the time of the next stand replacing fire. As we demonstrated,

within the present range of fire cycle, the probability of a fire occurring prior to their reproduction can be as high 33% and 42%, respectively. However, the fact that both species occupy the most abundant hill slope positions means that even when fires occur prior to their reproduction, there should be an abundant supply of seed from other, more mature, fire-killed local populations. In addition, the semi-serotinous cones of *P. mariana*, may disperse seeds from live sources at the burn edge or from unburned patches within the burn. This lack of dependence on regional dispersal, coupled with the fact that they occupy the most abundant hill slope positions, explains, at least in part, why both species have been so successful (*i.e.* persistent) in the boreal forest.

The persistence of tree species that require seed dispersal to re-colonize burned local populations has often been puzzling, given the many constraints seed dispersal poses in an area dominated by large, high intensity wildfires. However, the fact that *P. glauca* and *A. balsamea* occupy the most abundant hill slope positions may, in part, explain their persistence on the landscape. With live sources along the burn edge and in unburned patches within the burn, there may often be an adequate supply of seed to maintain the populations.

What we need to do next is develop a regional model that couples the regional processes of soil moisture and nutrient gradients, wildfire, and seed dispersal to the processes of seed production, germination, recruitment, growth and mortality within local populations. With the regional model we can potentially show the strength and influence of the four ecological processes and their effect on regional scale forest composition and

age. Because local populations are not stable the next question is whether the regional

population is stable. If so, how large or small does the regional population have to be to

ensure stability?

Literature Cited

Anderson, M.G., and Burt, T.P. 1977. Automatic monitoring of soil moisture conditions

in a hillslope spur and hollow. *Journal of Hydrology* **33**: 27-36.

Ban, Y., Xu, H., Bergeron, Y. and Kneeshaw, D.D. 1998. Gap regeneration of shade-

intolerant *Larix gmelini* in old-growth boreal forests of northeastern China.

Journal of Vegetation Science **9**: 529-536.

Beaufait, W.R. 1960. Some effects of high temperatures on the cones and seeds of

jackpine. *Forest Science* **6**: 194-199.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Québec's

southern boreal forest. *Ecology* **81**: 1500-1516.

Bergeron, Y., and Charron, D. 1994. Postfire stand dynamics in a southern boreal forest

(Québec): A dendroecological approach. *Ecoscience* **1**: 173-184.

Bergeron, Y., and Dubuc, M. 1989. Succession in the southern part of the Canadian

boreal forest. *Vegetatio* **79**: 51-63.

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**: 1375-1384.

Berry, A.B. 1982. Response of suppressed conifer seedlings to release from an aspen-pine overstorey. *Forestry Chronicles* **58**: 91-99.

Bridge, S.R.J., and Johnson, E.A. 2000. Geomorphic principles of terrain organization and vegetation gradients. *Journal of Vegetation Science* **11**: 57-70.

Bull, W.B. 1975. Allometric change of landforms. *Geological Society of America Bulletin* **86**: 1489-1498.

Carleton,T.J., and Maycock, P.F. 1977. Dynamics of the boreal forest south of James Bay. *Canadian Journal of Forest Research* **56**: 1157-1173.

Carleton, T.J. 1982. The pattern of invasion and establishment of *Picea mariana* (Mill.) BSP. into the subcanopy layers of *Pinus banksiana* Lamb. dominated stands. *Canadian Journal of Forest Research* **12**: 973-984.

Charron, I. 1998. Sexual recruitment of trees following fire in the southern mixedwood boreal forest of Canada. M.Sc. thesis, Concordia University, Montreal, Canada.

Crawley, M.J. 1986. *Plant Ecology*. Blackwell Scientific Publications. London, U.K.

Dawes, W.R., and Short, D. 1994. The significance of topology for modeling the surface hydrology of fluvial landscape. *Water Resources Research* **30**: 1045-1055.

Donnegan, J.A., and Rebertus, A.J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. *Ecology* **80**: 1370-1384.

Duchesne, S., and Sirois, L. 1995. Phase initiale de régénération après feu des populations conifériennes subarctiques. *Canadian Journal of Forest Research* **25**: 307-318.

Ebert, T.A. 1999. *Plant and Animal Populations: Methods in Demography*. Academic Press, U.S.A.

Eriksson, O. 1996. Regional dynamics of plant: a review of evidence for remnant, source-sink, and metapopulations. *Oikos* 77: 248-258.

Fleming, R.L., and Mossa, D.S. 1994. Direct seeding of black spruce in northwestern Ontario: seedbed relationships. *Forestry Chronicles* 70: 151-158.

Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press, New York, NY.

Fye, R.E., and Thomas, J.B. 1963. Regeneration of balsam fir and spruce about fifteen years following release by spruce budworm attack. *Forestry Chronicles* 39: 385-397.

Foster, D.R., and King, G.A. 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. *Journal of Ecology* 74: 465-483.

Greene, D.F. 1989. The aerodynamics and dispersal of plumed and winged seeds. PhD thesis, University of Calgary, Calgary, Canada.

Greene, D.F., and Johnson, E.A. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* 70: 339-347.

Greene, D.F., and Johnson, E.A. 1994. Estimating the mean annual seed production of trees. *Ecology* 75: 642-647.

Greene, D.F., and Johnson, E.A. 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* 77: 595-609.

Greene, D.F., and Johnson, E.A. 1999. Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. *Canadian Journal of Forest Research* **29**: 462-473.

Greene, D.F., and Johnson, E.A. 2000. Tree recruitment from burn edges. *Canadian Journal of Forest Research* **30**: 1264-1274.

Hanksi, I., and Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**: 3-16.

Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in *Picea-tsuga* forests in Oregon and Washington. *Ecology* **70**: 48-59.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* **42**: 73-88.

Hofgaard, A. 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *Journal of Vegetation Science* **4**: 601-608.

Huff, M.H. 1995. Forest age structures and development following wildfires in the western Olympic Mountains, Washington. *Ecological Applications* **5**: 471-483.

Johnson, E.A. 1992. *Fire and Vegetation Dynamics*. Cambridge University Press, Cambridge,U.K.

Johnson, E.A., and Gutsell, S.L. 1993. Heat budget and fire behaviour associated with the opening of serotinous cones in two *Pinus* species. *Journal of Vegetation Science* **4**: 745-750.

Kneeshaw, D.D.,and Bergeron, Y. 1998. Canopy gap characteristics and tree

replacement in the southeastern boreal forest. *Ecology* **79**: 783-794.

Kneeshaw, D.D., and Burton, P.J. 1997. Canopy and age structures of some old sub-
boreal *Picea* stands in British Columbia. *Journal of Vegetation Science* **8**: 615-
626.

Linder, P., Elfving, B., and Zackrisson, O. 1997. Stand structure and successional trends
in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* **98**:
17-33.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks
in the boreal zone of Quebec. *Canadian Journal of Forest Research* **24**: 730-741.

Oliver, C.D., and Larson, B.C. 1990. *Forest Stand Dynamics*. Biological Resource
Management Series. McGraw-Hill Inc. New York, NY. U.S.A.

O'Loughlin, E.M. 1981. Saturation regions in catchments and their relations to soil and
topographic properties. *Journal of Hydrology* **53**: 229-246.

Perala, D.A. 1990. *Populus tremuloides* – aspen. *In Silvics of North America. Vol. 2.
Hardwoods. Edited* by R.M. Burns and B.H. Honkala. U.S. Forest Service
Agriculture Handbook 654. pp. 555-569.

Pulliam, H.R. 1988. Source, sinks, and population regulation. *The American Naturalist*
132: 652-661.

Reed, W.J., Larsen, C.P.S., Johnson, E.A., and MacDonald, G.M. 1998. Estimation of
temporal variations in fire frequency from time-since-fire data. *Forest Science* **44**:
465-475.

Rowe, J.S. 1972. *Forest Regions of Canada.* Environment Canada, Canadian Forest

Service, Ottawa. Publication 1300F.

Schweingruber, F.H. 1989. *Tree Rings: Basics and Application of Dendrochronology.*

Kluwer Academic Publications, Holland.

Sims, R.A., Kershaw, H.M., and Wickware, G.M. 1990. The autecology of major tree

species in the north central region of Ontario. Ontario Ministry of Natural

Resources Publications 5310.

St. Pierre, H., Gagnon, R., and Bellefleur, P. 1992. Régénération après feu de l'épinette

noire (*Picea mariana*) et du pin gris (*Pinus banksiana*) dans la forêt boréale,

Québec. *Canadian Journal of Forest Research* 22: 474-481.

Szewczyk, J., and Szwagrzyk, J. 1996. Tree regeneration on rotten wood and on soil in

old-growth stands. *Vegetatio* 122:37-46.

Telewski, F.W., & Lynch, A.M. 1991. Measuring growth and development of stems. *In*

Techniques and Approaches in Forest Tree Ecophysiology. Edited by J.P. Lassoie

and T.M. Hinckley. CRC Press Inc., Boston, MA.

Veblen, T.T. 1986a. Treefalls and the coexistence of conifers in subalpine forests of the

central Rockies. *Ecology* 67: 644-649.

Veblen, T.T. 1986b. Age and size structure of a subalpine forests in the Colorado Front

Range. *Bulletin of the Torrey Botanical Society* 113: 225-240.

Veblen, T.T., Hadley, K.S., Reid, M.S. and Rebertus, A.J. 1989. Blowdown and stand

development in a Colorado subalpine forest. *Canadian Journal of Forest*

Research **19**: 1218-1225.

Veblen, T.T., Hadley, K.S., and Reid, M.S. 1991. Disturbance and stand development of a Colorado subalpine forest. *Journal of Biogeography* **18**: 707-716.

Weir, J.M.H., Johnson, E.A., and Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixedwood boreal forest in western Canada. *Ecological Applications* **10**: 1162-1177.

Whipple, S.A., and Dix, R.L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. *American Midland Naturalist* **101**: 142-157.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* **21**: 414-416.

Yang, R.C. 1991. Growth of white spruce following release from aspen competition: 35 year results. *The Forestry Chronicle* **67**: 706-711.

Zasada, J.C., Sharik, T.L., and Nygren, M. 1992. The reproductive process in boreal forest trees. *In A Systems Analysis of the Global Boreal Forest.* Edited H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge Univ. Press, Cambridge, U.K. pp. 85-126.

CHAPTER FIVE

General Conclusions

In traditional studies of forest succession there has been a long history of believing that there is a succession of species over time. This belief began with ecologists simply describing the relative importance of each species over a chronosequence of stands and finding that older stands were dominated by a different set of species than younger stands. Later studies attempted to be more empirical by measuring either the size or age of trees, and they found that within a stand some species are older than others. Despite the development of static methods all have suffered from the serious problem that the long lifespan of trees means that the dynamics cannot be observed. Consequently, succession has had to be inferred by making a number of assumptions. Although most studies acknowledge that these assumptions limit their ability to make inferences about stand dynamics, they often then proceed to make such inferences (*e.g.* Whipple and Dix 1977; Knowles and Grant 1983).

It is clear from our results that testing the assumptions of static approaches are critical to a good understanding of forest dynamics. In our stands we showed that none of the assumptions of static approaches were met, and that there is not replacement of species over time. While these results may not apply in all forest types, we suggest that before conclusions can be drawn regarding the forest dynamics the assumptions of the methods used must be rigorously tested. It is clear that failing to carefully test the assumptions leads to serious misconceptions regarding forest dynamics.

The reliance on assumptions in studies of forest succession has been puzzling;

there has been a surprising lack of interest in even trying to test or meet the assumptions. Part of the problem may have been the ease with which the diameter or age of large numbers of trees can be obtained, and the difficulty of obtaining the necessary data to test the assumptions; in many areas trees cannot be cut down as they are on protected lands.

Literature Cited

Knowles, P., and Grant, M.C. 1983. Age and size structure analysis of engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. *Ecology* **64**: 1-9.

Whipple, S.A., and Dix, R.L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. *American Midland Naturalist* **101**: 142-157.