

**White Spruce Regeneration Thirty-nine Years Post-fire in the Boreal  
Mixedwoods of Duck Mountain, Manitoba**

By Cathy Foster

A thesis presented to the University of Manitoba in partial fulfillment  
of the requirements for the degree Master of Science in the Faculty of Graduate Studies

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BOREAL MIXEDWOODS OF DUCK MOUNTAIN, MANITOBA**

**BY**

**Cathy Foster**

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University  
of Manitoba in partial fulfillment of the requirements of the degree  
of**

**MASTER OF SCIENCE**

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## ACKNOWLEDGMENTS

This research was funded by the Sustainable Forest Management Network (Canada's Network of Centres of Excellence Program), Natural Sciences and Engineering Research Council of Canada, Manitoba Centres of Excellence Fund and Manitoba Careerstart grants to Dr. N.C. Kenkel. Camping passes and hospitality were provided by Manitoba Conservation. Field assistants and help in the lab were provided by Dave Walker, Boyan Tracz, Jeff Anderson, Richard Caners and Rod Lastra. I am also thankful for the time and help provided by my Advisor, Dr. Norm Kenkel, and the time and feedback given by my committee members, Dr. Sylvie Renault and Dr. Rene Van Acker. Special thanks also go to Jeff Anderson, my parents, family and friends for listening and for their support, encouragement and patience.



## ABSTRACT

The effects of distance to seed source, biotic (vegetation cover) and abiotic (moisture and nutrients) factors on temporal and spatial patterns of white spruce dispersal, establishment and growth were examined at two sites, 39 years post-fire. Partial Mantel tests and partial regressions were used to determine factors affecting recruitment. A growth model, based on empirical results was developed to study growth suppression. A total of 2 042 white spruce trees were aged at the base, 938 of which were also aged at 1.25 m (breast height). The first cohorts to establish (ages 25-39) were affected very little by seed source proximity. Biotic factors such as birch, *Corylus cornuta* and moss cover were better able to predict abundance of earlier establishing white spruce. The second cohorts to establish (ages 5-24) were most affected by seed source proximity. Abiotic factors such as topographic complexity were also able to predict abundance of later establishing white spruce, in addition to biotic factors. Based on site comparisons it was concluded that *Corylus cornuta* and other deciduous vegetation limit white spruce recruitment through competition and shedding of broadleaf litter, and may suppress growth, especially of later establishing white spruce. Intraspecific competition between white spruce on these sites often leads to density-dependent mortality, in addition to growth suppression.

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# CHAPTER 1

## BACKGROUND AND OBJECTIVES

### 1.1 The Boreal Forest

#### 1.1.1 Introduction

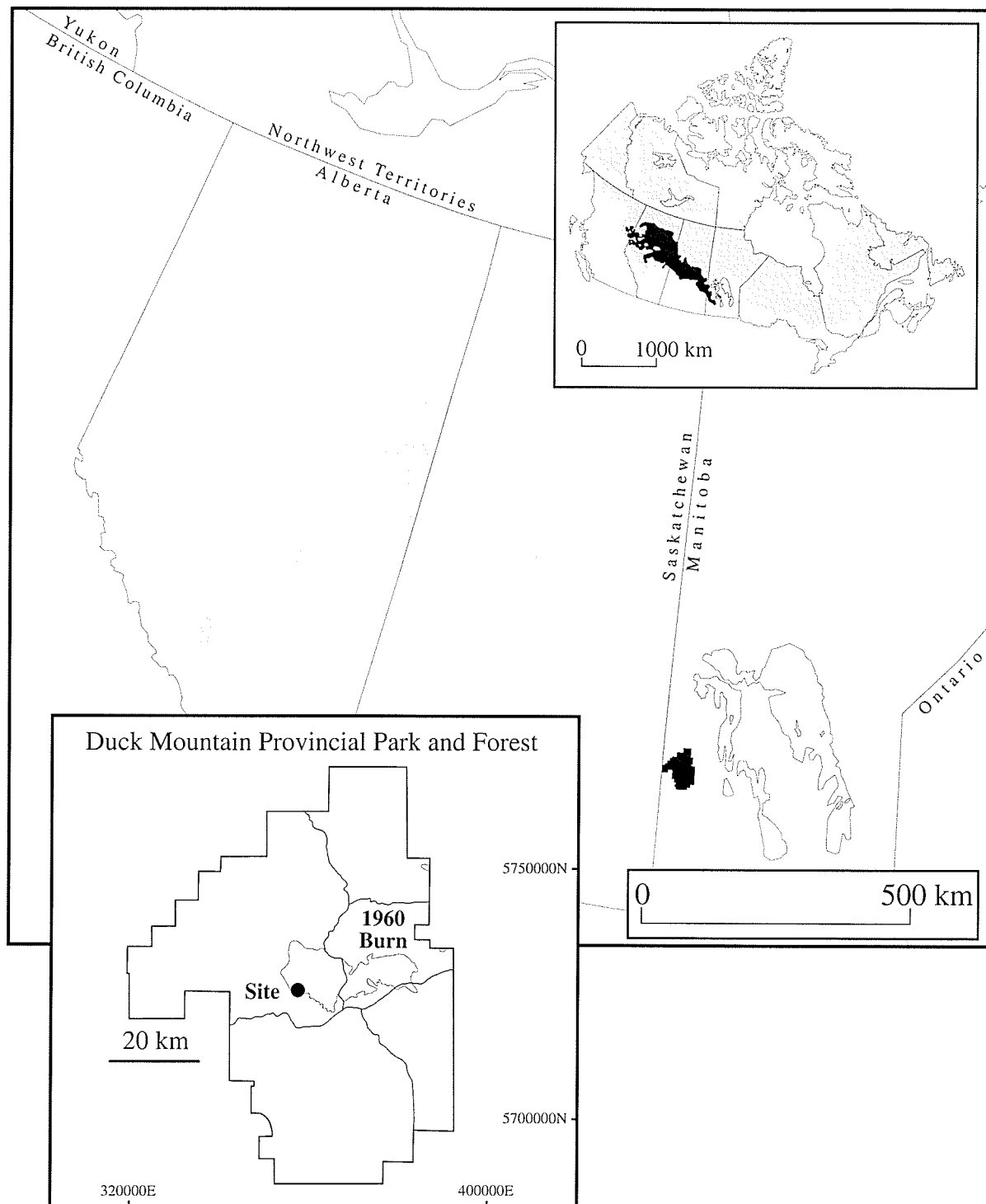
The boreal forest occupies a belt encircling the globe. Boreal ecosystems constitute approximately 11% of the earth's terrestrial surface (Bonan and Shuggart 1989) and 80% of Canada's forests (Larsen 1980). The Canadian boreal forest spans approximately 800 km from its northern limit at the tree line to its southern limit, which grades into aspen parkland in central Canada (Swan and Dix 1966) (Fig. 1.1).

Globally, the boreal forest has a characteristic appearance with conifers being the dominant species. Only nine tree species dominate the Canadian boreal forest along with mosses, herbs and low shrubs that are adapted to extreme environmental conditions (Payette 1992). Dominant coniferous species in the Canadian boreal forest are *Picea glauca* (white spruce), *Picea mariana* (black spruce), *Pinus banksiana* (jack pine) *Abies balsamea* (balsam fir), *Thuja occidentalis* (white cedar) and *Larix laricina* (tamarack), which is also deciduous. Common deciduous species include *Populus balsamifera* (balsam poplar), *Populus tremuloides* (trembling aspen), *Betula papyrifera* (white birch).

In general, species diversity of the boreal forest is relatively low, although species composition varies across Canada, with differences in climate and physiography (Larsen 1980). Across Canada this is illustrated by the greater abundance of white cedar and balsam fir to the east and white spruce to the west. From north to south, black spruce

dominates at higher latitudes, while deciduous species become much more prolific at lower latitudes.

The central Canadian boreal forest is geologically young only developing over the last 10 000 years following glacial retreat (Ritchie and Yarranton 1978). The revegetation of this region following the disappearance of glaciers that covered Canada was dependent on tolerance limits and reproductive capabilities of species (Oechel and Lawrence 1985). Species well-adapted to extreme conditions and capable of dispersing great distances were able to outcompete less robust species. Pollen and macrofossil evidence suggests that the early boreal forest was dominated by white spruce (Ritchie and Yarranton 1978).



**Figure 1.1.** Duck Mountain Provincial Park and Forest (lower left inset), Manitoba, Canada. The study area is situated within the Mixedwood Section (B18a, Rowe 1972) of the Boreal Forest Region (shaded area) a southern extension of the boreal forest in western Canada (upper right, modified from Johnson 1994).

### 1.1.2 Climate

The boreal forest climate consists of long, cold winters and short moderately warm summers. Temperatures and precipitation become lower towards central and northern Canada. In central and northern Manitoba mean monthly surface air temperatures range from  $-22$  to  $-30$  °C in January and  $12$  to  $18$  °C in July. The mean data of the spring thaw ranges between April 1 and April 15, while the mean data of the autumn freeze up ranges between October 10 and November 1 (Larsen 1980). Incursions of warm air masses from the south result in distinct seasonality in south-central Canada (Smith 1989). As one moves northward there is a decrease in deciduous species, with conifer canopies becoming shorter and more open in the extreme north (Rowe and Scotter 1973).

Precipitation and temperature are important in determining the southern boundary of the boreal forest in the prairie provinces. The southern limit coincides with the isoline above which precipitation is greater than evapotranspiration. Central and Northern Manitoba is relati

### 1.1.3 Physiography and Soils

The parent materials and topography of a region influence its insolation and drainage patterns, which in turn influence soil characteristics and species assemblages. In eastern Canada the Canadian Shield, composed of granitic bedrock and shallow acidic soils, spans from Quebec to northern Saskatchewan. Paleozoic limestone, dolomite, sandstone and shale separate the Precambrian shield from Cretaceous shales and siltstones further west in Manitoba and Saskatchewan, which are overlain by glacial till and form relatively basic soils. Differential erosion of resistant and weak Cretaceous bedrock is responsible for the formation of the Manitoba escarpment, which lies between the Precambrian shield and the Rocky Mountains (Klassen 1989).

Soil characteristics are highly dependent on climate, parent material, topography and vegetation. The cold temperatures of the boreal forest slow decomposition rates and nutrient cycling, while precipitation, which is greater than evapotranspiration, causes massive leaching (Larsen 1980). The high content of lignified acidic conifer needles increases acidity and decreases decomposition rates. Thus the lower soil horizons accumulate increasing amounts of minerals and nutrients, while the overlying forest floor becomes increasingly nutrient poor. Further south and west, in the southern interior of the boreal forest, soils have more clay and are more calcareous, as deciduous trees become more common (Larsen 1980).



#### 1.1.4 Disturbance

The boreal forest is a disturbance-driven ecosystem. Fire is the most common form of natural disturbance, whereas spruce budworm outbreaks are also important in wetter regions of eastern Canada (Kneeshaw and Bergeron 1998). Fires release nutrients from organic materials and increase soil temperatures and pH, which in turn increase decomposition and nutrient uptake. Furthermore, fire also removes litter and exposes mineral soil promoting seed germination and establishment (Johnson 1992). Thus fires are responsible for the renewal of forest growth and vigour. Fire cycles of the southern boreal forest average 130 years, although cycles vary and are often shorter in the north (Payette 1992). Following fire, early successional species such as aspen and jack pine commonly reforest a site. Later successional species such as white spruce and balsam fir replace the less shade tolerant species as they begin to senesce. Conversely, spruce budworm outbreaks attack spruce and balsam fir forests in the east, reverting them to earlier stages of succession (Bergeron and Dansereau 1993).

On a smaller scale, wind throw and senescence of individual trees create canopy gaps and expose mineral soil, promoting further species replacements (Rowe 1961). Selective herbivory by ungulates and hares, granivory by birds and squirrels, and removal of trees and flooding by beavers also influence stand characteristics by changing species composition (Pastor et al. 1993; Zasada et al. 1992; Naiman 1988). The combination of large and small scale disturbances over different time intervals result in the regeneration of forests along different successional paths. Consequently, heterogeneity between stands and homogeneity within stands produces a “patchwork quilt” effect (Dix and Swan 1971).

### 1.1.5 Succession Theory

Succession was originally viewed as being unidirectional, eventually reaching a self-perpetuating climax (Clements 1916, 1928, 1936). Later, the Gleasonian reductionist theory of succession considered plant communities to be more unique with floristic composition and chance events dictating vegetational change (McCook 1994). Watt (1947) introduced the concept of cyclic succession, wherein patches of vegetation change with chance events, plant life-histories and biotic interactions to produce an inter-related mosaic of patches. Egler (1954) developed the initial floristics model of succession in which all species in a community are present shortly following disturbance with changes in species composition being a function of seed availability, which in turn is a function of site history. Connell and Slater (1977), after reviewing previous notions of succession, suggested that species replacement may be facilitated or inhibited by other species or that a species may tolerate sub-optimal conditions until competition is reduced and more resources become available. They noted that succession may take many different paths and usually does not end in a stable climax community. They, along with McCune and Allen (1985), also stressed the importance of disturbance. Several authors have maintained that life-history traits, based on dispersal, establishment and growth characteristics, confer advantages and disadvantages to species depending on the level of disturbance experienced (Noble and Slatyer 1980; Grime 1977; Pickett 1976; Drury and Nisbit 1973).

Presently, there are still many different views on succession. However, there is general agreement that many factors influence succession over different spatial and temporal scales including disturbance, life-history traits and chance events.

Consequently, succession may be convergent, divergent, cyclic, suppressed, reversed or arrested. Many systems, especially those in the boreal forest, may not reach a stable climax community (Cook 1996).

#### **1.1.6 Succession in the Boreal Forest**

In the boreal forest there are many different paths that succession may follow depending on site history and adaptive abilities of different species. Frequent fires in the western boreal forests of Alberta and Saskatchewan disrupt succession towards climax communities of white spruce and balsam fir populations. Thus forest composition following fire will be very similar to that of the pre-fire forest (Dix and Swan 1971). However, when fire cycles are longer and climax communities do occur the different life-attributes of white spruce and balsam fir allow both to persist in these older stands (Achuff and La Roi 1977).

Further east in Ontario, frequent fires favour rapidly recruiting, monospecific stands of jack pine and aspen. Without fire black spruce, and later balsam fir, may become established in these stands. Jack pine stands may also become open and savanna like (Carleton and Maycock 1978). In moister areas spruce budworm may attack balsam fir and spruce, reverting stands back to earlier stages of succession. In boggy lowlands black spruce persists through vegetative layering (Zoladeski and Maycock 1990).

Further east, in Quebec, less frequent fires result in eastern white cedar and balsam fir on moist sites and eastern white cedar and black spruce on dry sites. Succession towards conifers may be attributed to differential shade tolerance and longevity (Bergeron 2000). However, altered stand dynamics from fire, spruce budworm

and wind throw may prevent self-replacing climax communities from persisting (Bergeron and Dubuc 1989).

Succession in the boreal forest is often slowed as shrubs, herbs and mosses interfere with the germination of boreal tree species (Cogbill 1985). Also, the creation of gaps by spruce budworm, wind throw and senescence may slow the transition to coniferous species, leading to persistent mixed deciduous-coniferous stands (Bergeron and Dansereau 1993). Regardless of the variability in regeneration patterns across Canada following fire, there is a general tendency towards conifer dominance (Bergeron 2000; Larsen and Mac Donald 1998). The shift from hardwood to conifer dominance ultimately depends on proximity of seed source and seedbed suitability.

#### **1.1.7 Mixedwood Boreal Forest Dynamics**

Duck Mountain Provincial Park, Manitoba is situated in Rowe's (1972) Mixedwood Section of the Boreal Forest Region (Fig. 1.1). The boreal mixedwood forest extends from the Manitoba Escarpment in western Manitoba into central Saskatchewan and Alberta. The southern boreal forest grades into aspen parkland, which grades into grasslands further the south (Swan and Dix 1966).

Typical early successional species of the mixedwood region include trembling aspen (*Populus tremuloides*), which is an aggressive invader, exhibits rapid growth and is shade intolerant (Perala 1990) and balsam poplar (*Populus balsamifera*) on moist yet well-drained sites. Paper birch (*Betula papyrifera*) is also considered an early successional species although it may tolerate shade and recruit into older stands (Safford et al. 1990). While the latter species often invades by vegetative suckering, jack pine

(*Pinus banksiana*), an early successional species characteristic of drier sites, regenerates by seed. In the presence of frequent fires the hardwood species tend to persist, while regular catastrophic fires tend to promote jack pine (Hamel 2001).

White spruce (*Picea glauca*) may recruit into hardwood stands immediately post-fire or continuously for an extended period and remains as a late successional species barring severe fires (Hamel 2001). Balsam fir (*Abies balsamea*) is considered a late successional species establishing under shade and moist conditions. Black spruce (*Picea mariana*) and tamarak (*Larix Laricina*) are more common on wetter lowland sites, although black spruce may also occur on dry sites following fire.

## 1.2 Purpose of study

Knowledge of regeneration dynamics of white spruce is becoming increasingly important as silvicultural systems turn towards mixedwood management strategies and natural regeneration (Leiffers and Beck 1994; Wang et al. 1995). Such awareness will promote adequate yields of economically important species, while conserving biodiversity and ecological integrity (Messier et al. 1999).

However, natural regeneration of white spruce has been consistently problematic, often as a result of competition from aspen, shrubs, herbs and grasses or mechanical injury during harvesting (Leiffers and Beck 1994; Harvey and Bergeron 1989). Successful recruitment of white spruce depends on seed availability and seedbed conditions (Youngblood 1995; Lieffers et al. 1996; Kneeshaw and Bergeron 1996; MacDonald et al. 2001). Through managing seed sources, seedbeds and optimizing density to promote unrestricted growth, white spruce regeneration may be improved (Wang et al. 1995; Leiffers and Beck 1994; Man and Lieffers 1999; MacPherson et al. 2001). For example, delayed spruce recruitment from an outside seed source has been observed to contribute more to stocking than advanced regeneration, which is present before harvesting (Hughes and Bechtel 1997). Natural regeneration of white spruce has also been found to be more successful in cutover areas where seedbeds have been prepared by burning (Densmore et al. 1999). Thus investigations into seed source and seedbed effects are needed to further our understanding and promote success of natural regeneration of white spruce.

Problems encountered in attempting to regenerate white spruce may also be mitigated through the promotion of mixedwood management, as mixedwood systems are

generally more productive than monocultures (Wang et al. 1995; Man and Lieffers 1999; MacPherson et al. 2001). Regeneration of white spruce under deciduous or mixed canopies is important where fire remains the most common stand initiating disturbance or where logging practices protect and promote natural regeneration of softwoods under mixed and hardwood stands. Recruitment of conifers under early successional stands is particularly complex, reflecting the variable conditions created by the relative abundance of hardwoods versus softwoods. As hardwood stands ultimately succeed towards conifer dominance, recruitment patterns are influenced by changes in seed source availability and seedbed conditions (Lieffers et al. 1996; Galipeau et al. 1997; Simard et al. 1998; Stewart et al. 1998). Furthermore, recruitment into the canopy is much different in hardwood stands than softwood stands due to differences in light availability and competition from understory vegetation (Messier et al. 1999; Kneeshaw and Bergeron 1996). By studying white spruce regeneration patterns after fire, through the development of natural mixedwood stands, the time at which various factors become most important can be elucidated. Baskerville (1986) suggests that natural regeneration is one of the hardest things to predict in forest management and as such, indicators involving site, original stand and disturbance conditions should be forest specific. Thus, this study will complement others that have investigated white spruce regeneration by furthering our understanding of the conditions required for successful natural regeneration of white spruce.

### 1.3 Objectives

This study explores the factors influencing regeneration dynamics of white spruce into two aspen stands over a 39 year period following fire. Seed source availability, seedbed suitability and growing conditions are evaluated in relation to cohorts that established at different times since fire. Specifically the goals of this study are to:

- 1) Examine the temporal patterns of white spruce recruitment. Age distributions are produced to determine the timing of white spruce dispersal and establishment.
- 2) Examine the spatial patterns of white spruce recruitment. The effects of distance from seed source, biotic and abiotic factors on the abundance of white spruce, dispersing and establishing during different periods of time since fire, are determined.
- 3) Examine growth and mortality of regenerating white spruce. Age-size relationships of white spruce, growth rates between base and breast height (1.25m) and the degree of suppression occurring in these stands are determined. Mortality is determined as a function of white spruce density.



## **CHAPTER 2**

### **WHITE SPRUCE REGENERATION**

#### **2.1 Introduction**

Recent reviews have addressed issues related to advance regeneration dynamics in boreal forests (Greene et al. 1999; Messier et al. 1999; Lieffers et al. 1999). This review focuses on the recruitment dynamics of white spruce into post fire stands from dispersal, through establishment, and growth into the canopy. More specifically, the relative importance of seed source, seedbed quality and competition for light will be evaluated and related to their influence on recruitment patterns. Although this review is primarily concerned with white spruce, studies of other species of spruce that occur in other regions of the global boreal forest will also be referred to.

#### **2.2 White Spruce Biology and Ecology**

White spruce (*Picea glauca* (Moench) Voss) is distributed across Canada and extends from the treeline south to the United States. It grows from sea level up to 1520 m (5 000 ft) above sea level (Nienstaedt and Zasada 1990). The climate over this range is temperate to subarctic, and the growing season may be as short as 20 days to as long as 180 days. White spruce may occur on clays, sands and organic soils of pH 4-7 (Nienstaedt and Zasada 1990). It prefers well drained sites but tolerates more extreme conditions than trembling aspen (Rowe 1956).

The normal lifespan of white spruce is 250-300 years (Sutton 1969). Under good conditions heights may exceed 30 m and DBH (diameter at breast height) may exceed 90 cm (Nienstaedt and Zasada 1990).

White spruce is dependent on dispersal of seed for its reproduction and germinates best on moist sites (Waldron 1966). It establishes on burned sites with the period of recruitment greatly influenced by seedbed conditions. Although it often establishes on mineral soil immediately following fire, it is also considered a later successional species as it is relatively shade tolerant. White spruce typically does not form monodominant stands, but is more often found growing at relatively low densities in mixed stands (Greene et al. 1999).

### **2.3 Trembling Aspen Biology and Ecology**

White spruce regeneration commonly occurs under aspen canopies. Trembling aspen (*Populus tremuloides* Michx.) is more widely distributed than any other tree species in North America, although its distribution is limited where evapotranspiration is greater than annual precipitation (Perala 1990). Although found on a wide range of soil types, growth is sub-optimal on dry sandy sites, poorly aerated heavy clays and very acidic sites, with organic soils generally being avoided (Rowe 1956).

Trembling aspen has a relatively short lifespan and is fast growing. It rarely lives longer than 150 years although may live up to 200 years (Rowe 1956). Typical height at maturity is about 35m with trunk diameter at breast height reaching approximately 140 cm (Perala 1990).

Aspen may reproduce sexually by seed. However, vegetative propagation by suckering is faster and has better survival rates barring excess moisture or shade (Rowe 1956). This method of reproduction is commonly observed on post-fire sites, such as those in the present study. Aspen rapidly colonizes burned sites until out shaded by competitors, such as spruce, as trembling aspen is very shade intolerant (Perala 1990).

## **2.4 White Spruce Dispersal**

### **2.4.1 Seed Production**

#### Reproductive Maturity

Recruitment of white spruce into deciduous stands requires a nearby source of mature individuals capable of producing seed. The rate at which trees become sexually mature influences recruitment rates in the long term. Once the first cohort to establish begins to produce seed, it may contribute to the further recruitment of subsequent cohorts (Galipeau et al. 1997; Stewart et al. 1998).

Although sexual maturity has often been related to age, it is more a function of stem size (Greene et al. 1999). More specifically stem size, relative to its nearest neighbors, is a measure of the carbohydrate pool available for reproduction. Because the tallest individuals in the canopy receive more light, they are more able to acquire the energy needed for reproduction. Thus faster growing species will dominate the canopy and reach sexual maturity earlier.

Stem size is often correlated with age in mature trees that are not suppressed by the overstory. Regular seed production of white spruce is reported to begin at approximately 30 years of age, although it may start producing seed as early as 15 years

or younger, depending on site conditions; four year old white spruce has been observed to produce seed (Nienstaedt and Zasada 1990).

Thus the age of sexual maturity for white spruce is highly variable. Some of this variability results from extreme growing conditions in which size is not an accurate reflection of age. Older trees growing under suppressed conditions may not reach maturity as early as expected, if at all. Even the size of sexual maturity may vary widely depending on light availability and competition for limiting resources.

#### Timing of Seed Production

White spruce is a masting species. Recruitment of white spruce into deciduous stands is less influenced by the timing of mast years than is recruitment into recently burned sites. The amount of time that passes between a stand-initiating fire and a mast year of seed production will influence germination success, as seedbed quality decreases and abundance of competitive species increases (MacDonald et al. 2001). Good seed crops are reported to occur at two to six year intervals, up to ten to twelve year intervals, for white spruce depending on site conditions and geographic location (Nienstaedt and Zasada 1990).

Mast years are most often associated with climate (Runions et al. 1995). Hot, dry weather at the time of bud differentiation is thought to trigger masting the following year at which time wet weather is thought to encourage fertilization. Moderately light rains may promote fertilization by aggregating pollen at the micropyle, although heavy rain may be detrimental (Runions and Owens 1996). When mast years are particularly productive, resulting from wet weather, germinants will further benefit from moist

seedbed conditions. The relationship between climate and timing of seed production becomes especially important when fire is responsible for stand initiation. Because fires occur more frequently during years of persistent drought, and mast seeding often follows such years, there is a high likelihood that a good seed crop will be available from the remnant unburned patches for the revegetation of burned sites.

Timing of seed fall during mast years is also affected by weather. White spruce seed dissemination increases from August through to September and October (Dobbs 1976; Nienstaedt and Zasada 1990). Seed abscission may be triggered by low relative humidity and high wind speeds (Greene and Johnson 1989), while cool, wet, snowy weather inhibits dissemination by causing cones to close (Nienstaedt and Zasada 1990).

#### Quantity of Seed Produced

The amount of seed produced by a source plays a major role in determining the abundance of conifer regeneration within deciduous stands, providing suitable substrates are available for germination (Galipeau et al. 1997). The amount of seed produced by a source depends on its size, the density of reproducing trees and the seed production of individual trees.

As with reproductive maturity, the quantity of seed produced by a tree is also related to its size and the availability of carbon. In general, larger trees produce more seed (Greene and Johnson 1994). However, very large trees produce less seed than expected as they begin to senesce (Greene et al. 1999). Seed production is also related to seed size, with small-seeded species producing more seed than large-seeded species (Greene and Johnson 1994). Thus white spruce has the potential to be a prolific seed

producer as its seeds are relatively small (1.1-3.2 mg) and its height at maturity is usually quite tall (Nienstaedt and Zasada 1990). However, white spruce often tends to grow at relatively low densities, which decreases its combined reproductive output (Greene et al. 1999).

### Seed Mass

Seed mass greatly influences seed dispersal potential. Thus the small seeds of white spruce have relatively high capacities for dispersal. Seed mass also influences germination success as it is proportional to hypocotyl length (Grime and Jeffrey 1965). Thus, white spruce has a limited ability to penetrate less favourable substrates and access moisture. In addition, the higher surface to volume ratio of white spruce seeds increases its risk of dessication (Greene et al. 1999). Thus seed mass may play a role in explaining the consistent observations of low seedling abundances of spruce (Galipeau et al. 1997; Hughes and Bechtel 1997; Knapp and Smith 1982).

### Seed Viability and Mortality

White spruce seeds typically do not remain viable past one year (Greene et al. 1999). Thus there is no persistent seed bank within the forest floor. Viability is related to timing of dissemination and dispersal distance. Seed quality of white spruce is greatest during the peak period of dissemination (Dobbs 1976). Seeds falling during this period mostly come from the well-developed central cone scales, while those falling earlier or later often come from less well developed basal or apical cone scales. Seed viability of white spruce seeds is greatest within 100 m of the seed source because viable seeds are

heavier than empty, non-viable seeds (Dobbs 1976). Even though many seeds may fall at great distances from the source, a high proportion of them may not be capable of germinating. Thus patterns of seed dispersal may provide only rough approximations of the likelihood of germination success.

Viability may also be related to the type and timing of disturbance events. For example, logging subsequent to seed dissemination will leave viable seeds on the forest floor, while severe fires may kill viable seeds. However, seeds of white spruce have been found to remain viable following ground fires that kill parent trees, when the fire occurs following embryo maturation (Greene et al. 1999).

Seed viability may be compromised in species commonly found at low densities, such as white spruce, due to decreased chances of cross pollination. Also, in regions where spruce budworm occurs seed production may be limited in white spruce (Greene et al. 1999).

## **2.4.2 Seed Source**

### Pattern of Survivors

The size, shape and number of seed sources available for the dispersal of white spruce into deciduous stands depends on the nature of the stand-initiating fire. The large size and intensity of fires typical of the boreal forest result in large tracts of land being burned so that remnant patches of unburned stands may be somewhat rare (Bergeron 1991). However, fires occurring in landscapes with variable topography, vegetation, and moisture regimes may leave small pockets of unburned forest behind (Larsen 1997). In lake landscapes, lakes may act as highly successful fire breaks often leaving large tracts

of land unburned (Bergeron 1991). Where fires are less severe, residual seed sources may also include individual or small groups of survivors. These survivors, dotted throughout the burn, have the potential to initiate conifer regeneration at great distances from major seed sources. Without these smaller patches within the burn, white spruce recruitment into more remote sites would take much longer. Where survivors are distributed at low densities, the abundance of advance regeneration will reflect the basal area of survivors (Greene et al. 1999).

Seed source strength is also dependent on the presence of seed bearing trees. Thus the interval between disturbance events must be long enough to allow white spruce to reach reproductive maturity. As this period of time increases, dispersal capacity will increase as trees grow above the surrounding canopy and produce greater quantities of seed (Stewart et al. 1998).

#### Distance from Seed Source

Dispersal distance from a seed source depends on both the species and the environment through which the seed must travel (Stewart et al. 1998). This distance, in turn, influences the degree of expansion that is possible by subsequent cohorts (Galipeau et al. 1997).

The distances traveled by white spruce seeds are highly variable ranging from an average of 33 m (Zasada and Lovig 1983) to a maximum of 300 m (Sims et al. 1990). The majority of studies have found that most white spruce seeds fall within a few tens of metres of the parent tree (Dobbs 1976). Further seed fall decreases rapidly to



approximately 100 m, although adequate dispersal for natural regeneration has been observed up to 300 m (Dobbs 1976).

White spruce regeneration has been reported to occur as far as 2000 m from an unburned seed source (Galipeau et al. 1997). The presence of these seedlings is likely a result of dispersal across snow, by small mammals, or from isolated trees having survived the fire. However, long distance dispersal on snow does not occur to any significant degree within intact forests (Greene and Johnson 1997). If masting occurs before early successional species revegetate a site, long distance dispersal will be much more likely.

#### Wind and Barriers to Dispersal

The distances traveled by dispersing seeds is often greatly influenced by weather conditions, as well as the structure of surrounding forest. Seed abscission may be triggered by high winds, thereby maximizing the distances traveled (Greene and Johnson 1989). Wind direction and speed may highly modify seed dispersal. For example, greater establishment of white spruce occurs downwind than upwind (Stewart et al. 1998) and 16% of white spruce seeds have been observed to be caught in updrafts (Zasada and Lovig 1983). This upward travel increases the potential for long distance dispersal and dispersal above canopies. Conversely, downdrafts may be responsible for depositing seeds immediately beneath the parent tree.

A combination of high wind speeds and frequent updrafts will lead to greater dispersal distances. Even greater distances will be observed for seeds falling on snow within clearings (Greene and Johnson 1997). Indeed it has been reported that up to 30 -

50% of white spruce seeds may abscise on snow (Greene et al. 1999) and that, within clearings, winter dispersal distances tend to be greater than in the fall (Dobbs 1976).

Dispersal distances are lower within canopies as a result of lower wind speeds and inconsistent wind direction. This has been observed for white spruce dispersing into aspen canopies (Stewart et al 1998). Dispersal within deciduous canopies will also vary seasonally. Distances traveled during the fall, after leaves are shed, will be greater and much less variable in terms of direction (Stewart et al. 1998). Variable topography may also influence wind patterns, thereby affecting dispersal.

Within intact forests, or where topography is variable, seeds are much more likely to become trapped on the forest floor. It is imperative for seeds to remain stationary long enough to imbibe water and begin the process of germination (Johnson and Fryer 1992). When mast years are associated with wet weather, seeds will be more likely to remain stationary long enough to germinate. Also, rough surfaces, such as moss or decaying wood, may assist in trapping seeds (Cornett et al. 1997).

An issue that may be particularly problematic for white spruce is the possible conflict between seed dispersal behaviour and seedbed preference. White spruce seeds may be more easily trapped in depressions, while elevated microsites are favoured substrates for white spruce germinants (DeLong et al. 1997). Both white and red spruce show evidence for and against seed-seedling conflicts (Dobbs 1976; Hughes and Bechtel 1997).

## 2.5 White Spruce Establishment

### 2.5.1 Germination Requirements

#### Moisture and Temperature

Moisture availability will greatly influence germination success. White spruce seedlings are very prone to dessication (Neinstaedt and Zasada 1990). Moist soil strength has been reported as the most important variable in determining establishment success of white spruce across several sites and seedbed types (DeLong et al. 1997). Seedbeds that promote moisture availability include mineral soil, humus and rotten logs (Greene et al. 1999). Dry seedbeds present greater resistance to developing roots (DeLong et al. 1997). Thus white spruce may be prone to moisture stress as a result of its higher surface to volume ratio and small hypocotyl.

In cooler regions, or during the spring when temperatures are low, warmer soil temperatures decrease moisture stress, resulting in higher growth rates (Brand and Janas 1988). Low temperatures may lead to frost mortality, especially for seedlings growing in depressions (Cornett et al. 1997). Where moisture availability is high, sunny conditions will promote germination, whereas shady conditions may be needed where moisture is limiting. Suitable conditions for germination are also seasonally dictated. For example, *Picea engelmannii* (Engelmann spruce) is able to germinate quickly and under relatively cool conditions allowing it to avoid moisture stress by establishing earlier in the season (Knapp and Smith 1982).

## Light and Vegetation Cover

Solar radiation may be more important to early establishment through its influence on moisture availability, while light availability per se may play a more direct role in seedling growth. Vegetation cover dictates the degree of interspecific competition for water and nutrients (Comeau et al. 1993). White spruce may survive long periods under aspen canopies, while shrub and herbaceous cover are much more detrimental (Xiaohong et al. 2001). Much lower regeneration of white spruce has been found on sites with dense cover of *Calamagrostis Canadensis* (bluejoint), *Alnus crispa* (green alder), *Corylus cornuta* (beaked hazelnut), *Epilobium angustifolium* (fireweed) and low shrubs (Stewart et al. 1998; Lieffers and Stadt 1994). Maguire and Forman (1983) found negative correlations between seedling densities and herb cover, while no correlations were found between seedling densities and environmental factors in a hemlock-hardwood forest. Beach and Halpern (2001) report that most regenerating *Picea stichensis* (sitka spruce) occurs where shrub and herbaceous cover is less than 10%. Thick herbaceous layers are often associated with rich sites which may, in part, explain lower abundances of advance regeneration on richer sites (Harvey and Bergeron 1989). Xiaohong et al. (2001) report increased mortality on richer sites due to increased competition and note that smaller trees are especially vulnerable.

Shrubs may sprout immediately following disturbance, while white spruce must seed in from outside sources. Shrubs with faster initial growth rates have the ability to inhibit establishment of white spruce (Post 1970). Furthermore, the adverse affects of competition may be cumulative (Comeau et al. 1993). Reductions in photosynthetic

tissue, due to competition, will further limit growth in future years, therefore limiting the ability to out compete neighbors.

### Litter

The abundance of white spruce seedlings under deciduous canopies may be limited by leaf litter. Broadleaf litter inhibits root penetration and leads to mortality through smothering of seedlings (DeLong et al. 1997; Simard et al. 1998). Advance regeneration abundance is lower in hardwood stands than conifer or mixed stands partly as a result of smothering by leaf litter (Kneeshaw and Bergeron 1996). In addition to litter from the canopy, the herbaceous layer may also contribute litter, further inhibiting seedling establishment and survival.

### Soil and Depth of Organic Layer

Exposed mineral soil is one of the best seedbeds for the establishment of white spruce (DeLong et al. 1997). One of the benefits of stand initiation by high intensity fires is that it burns the organic layer and exposes mineral soil. Exposed mineral soil provides a stable moisture supply and permits rapid root development, which is especially important for white spruce (DeLong et al. 1997). Potential competitors and shaders are also removed.

Thick organic layers may be less favourable for white spruce germination as its smaller and slower growing tap root is less able to penetrate through a thick organic layer than other species such as balsam fir (Frank 1990). Thus establishment of white spruce is more restricted in deciduous stands, where leaf litter contributes to a thick organic layer. However, mineral soil may be exposed and elevated in these stands by blow downs and

animal burrowing (DeLong et al. 1997). The benefits of mineral soil exposure are further increased when elevated on mounds. Mounds have lower soil strength, warmer temperatures and better water relations, less leaf litter, and less vegetation cover (DeLong et al. 1997). Furthermore, uprooting may affect nutrient cycling by mixing soil and bringing nutrients to the surface (Schaetzl et al. 1989).

Soil type also influences establishment. Galipeau et al. (1997) report greater densities of white spruce seedlings on sandy and loamy textured soils derived from till, versus clay soils. Although sandy soils may be less fertile, they have better aeration and drainage, whereas clay soils may become saturated when wet and produce a hardpan when dry, thus inhibiting root penetration. Conversely, Kneeshaw and Bergeron (1996) report greater abundances of white spruce on fine-textured soils, such as clay and silt, versus sandy soils, possibly resulting from higher fertility of clay soils. Harvey and Bergeron (1989), however, suggest that lower abundances of advance regeneration are associated with richer sites, where thick herbaceous layers interfere with establishment. Thus there appears to be a tradeoff between fertility and competition in some instances. White spruce germinating on less fertile sites may escape competition from more demanding species, while white spruce may also escape competition on rich sites that are too shady for shade intolerant competitors.

### Moss Cover and Decaying Logs

In established stands, rotting logs are more common substrates than exposed mineral soil. In the absence of disturbance, white spruce seedlings are frequently observed growing on decaying logs (DeLong et al. 1997; Lieffers et al. 1996). Rotten

logs retain moisture and attain higher temperatures, improving water relations (Cornett et al. 1997; McLaren and Janke 1996). Decaying wood may also provide higher abundances of bacterially fixed nitrogen and mycorrhizae, thus improving nutritional status (Cornett et al. 1997; DeLong et al. 1997). Rotten logs are particularly favoured by white spruce, as the low soil strength and soft porous structure of rotting logs allows for rapid growth of white spruce roots, even under drier conditions. Lieffers et al. (1996) report 32% of white spruce recruitment on rotten logs, which only covered 5% of the study area. Other benefits of establishment on decaying logs are related to the increase in micro-elevation of seedlings. These benefits include warmer temperatures, less smothering from leaf litter, less shading from the herbaceous layer, and less competition from vegetation cover (DeLong et al. 1997).

Germination success on logs is dependent on the stage of decay. There are conflicting opinions regarding the best stages of decay for seedling establishment and survival. White spruce germinants prefer undecomposed logs and are restricted to logs with shorter moss communities, while taller seedlings are more commonly found on decomposed, moss covered logs (Simard et al. 1998). Freshly fallen logs may provide a better substrate for germination than the forest floor or older logs that have accumulated high abundances of mosses and other vegetation (Harmon and Franklin (1989). However, low densities of moss on freshly fallen logs may promote seedling establishment by increasing water retention capacity and by capturing dispersing seeds, although organic seedbeds may retain more moisture than moss (Wright et al. 1998a).

Older logs that have already begun to break apart may support seedlings. However, seedlings that are already established when bole fragmentation occurs are

likely to die. Germination of *Picea abies* (Norway spruce) in Sweden only occurs on logs older than 50 years (Hofgaard 1993a) and continues for approximately 150 years (Hofgaard 1993b).

Preference for a specific seedbed, such as decaying logs, does not necessarily continue throughout subsequent developmental stages. Although rotten logs appear to be beneficial for the germination of spruce and fir, subsequent growth may not benefit to the same degree. Lieffers et al. (1996) report similar growth in height for white spruce established on rotten logs and the forest floor. In fact, although most seedlings established on rotten logs, those establishing on the forest floor had greater ground level diameters. Ball and Walker (1995) also report poorer development of white spruce growing on decaying wood. Lower seedling densities on the forest floor, versus logs, may confer an advantage to seedlings by lowering competition (Cornett et al. 1997).

### **2.5.2 Timing of Establishment**

#### Recruitment Patterns and Dispersal

The timing of white spruce establishment under deciduous canopies may vary widely and is partly dependent on seed source strength and proximity. White spruce recruitment may be delayed for 20 years or more when seed sources contain low densities of parent trees or are located at great distances, whereas immediate recruitment occurs close to adequately stocked seed sources (Lieffers et al. 1996).

Galipeau et al. (1997) describe bimodal recruitment of white spruce. The initial cohort density of white spruce is the most important factor determining the abundance of the second cohort invading a burned area. The highest white spruce recruitment was



observed within the first 25 years, in conjunction with early pioneer species. After a ten year period of lower recruitment, a second wave of white spruce recruitment was observed. The period of low recruitment is thought to be a result of either low seed production, due to a spruce budworm outbreak, or competition from increasing densities of shrubs and herbs. The subsequent increase in recruitment is partly attributed to higher seed production associated with the sexual maturation of the first cohort.

Youngblood (1995) describes unimodal patterns of white spruce recruitment in Alaska. Recruitment following fire occurred immediately, along with aspen, as a single cohort. Some sites showed rapid establishment, while in others, establishment continued sporadically for longer periods. Recruitment of white spruce individuals destined to make it to the canopy did not continue beyond 30 years.

Lieffers et al. (1996) also observed variable lengths of recruitment periods for white spruce establishing in aspen stands. In addition to recruitment occurring immediately following stand initiation they observed delayed recruitment following time lags of 20 years and greater. They attribute the differences in recruitment patterns to variable seed source strength as well as seedbed quality. Good seedbeds, in close proximity to a seed source, lead to earlier colonization. Contrary to Youngblood (1995), recruitment continued well past 30 years in most stands. Recruitment persisting for longer periods was more likely to approach bimodal distributions similar to those observed by Galipeau et al. (1997).

### Modifications of the Seedbed Over Time

White spruce recruitment patterns are linked not only to dispersal ability, but also to the seedbed. While white spruce has a preference for specific seedbed characteristics, such favourable conditions are not consistently present throughout all stages of stand development. Modifications of the seedbed are closely related to the changing composition and structure of the canopy along a successional gradient. Not only does the availability of preferred substrates change over time, but the availability of light, water and nutrients changes as stands develop (Messier et al. 1999).

Early successional deciduous stands tend to be more open than older stands with a coniferous component, and therefore transmit sufficient light for the rapid proliferation of shade intolerant understory species (Cornett et al. 1998; Messier et al. 1998). This leads to extremely low light levels on the forest floor, inhibiting subsequent establishment of later dispersing species. The high cover of herbaceous layers and shrub cover also increases litter production and competition for resources (Simard et al. 1998; DeGrandpre et al. 1993). Older deciduous stands may produce very thick layers of decomposing litter, further limiting conifer regeneration (Barras and Kellman 1998). A further detriment to white spruce in the younger stands is the low abundance of nurse logs, which are preferred substrates for establishment in the absence of exposed mineral soil.

Where white spruce has shown bimodal recruitment patterns, the establishment of the second cohort is likely to be more difficult as the thickness of the organic layer and litter cover increase. First year survivorship of white spruce should decline with stand age as vegetation cover increases and light availability decreases (Greene et al. 1999). Of the white spruce that do establish after a lag of more than 20 years, height and diameter

growth have been shown to be lower than those that establish immediately following disturbance, as a result of increasing competition and shading (Lieffers et al. 1996). Diameter growth of seedlings recruiting more than 40 years following disturbance was less than half of that for those recruiting within 10 years. Conversely, seed production and dispersal should increase as seed sources are enlarged by younger cohorts. Thus the lower success rates of germination later in stand development may be partly buffered by a higher abundance of dispersing seeds.

During mid-successional stages of stand development, Kneeshaw and Bergeron (1996) found white spruce seedling abundance to be at its highest. White spruce was more abundant in mixed stands. They suggest that these mixed stands transmit less light than deciduous stands, thereby reducing understory competition. Meanwhile, the development of small gaps from senescing early successional trees transmit enough light for the recruitment of shade tolerant conifer species, but insufficient light for potential shrubby competitors. Mixed stands, characteristic of mid-successional stages of development (120 yrs), have also been found to support the highest abundance of rotten logs well suited to the establishment of white spruce (Simard et al. 1998). They also produce less broadleaf litter with the reduction of understory vegetation and the decreasing proportion of hardwoods (Simard et al. 1998). Continued recruitment of white spruce may therefore be promoted in these stands (Lieffers et al. 1996; Kneeshaw and Bergeron 1998).

In older stands (234 yrs), the advanced stages of decomposition of nurse logs may support less regeneration of white spruce (Simard et al. 1998). A low abundance of conifer seedlings under conifer parent trees may be attributed to the presence of larger

gaps, which provide enough light for the invasion of shrubby competitors (Kneeshaw and Bergeron 1996). White spruce may be perpetuated in large spruce budworm created gaps of these older forests only if competition is limited. The effects that gaps have on seedlings will vary with developmental stage. For example, the increase in light availability may benefit the growth of well established seedlings, while causing dessication of younger, more sensitive germinants.

## **2.6 White Spruce Growth and Survival**

### **2.6.1 Shade Tolerance**

#### Growth Form

While seedlings may be fully capable of establishing under full canopies, their ability to grow, survive and reach the canopy may be compromised by the light conditions experienced, and their tolerance to shade. White spruce is considered to be a relatively shade tolerant species (Messier et al. 1999). The degree of shade tolerance demonstrated determines the ability of its seedlings to survive underneath an existing canopy, as well as their ability to take advantage of opportunities created by canopy openings.

There is an increasing light requirement as plants grow and the proportion of non-photosynthetic tissue increases, which in turn increases respiratory costs and energy required (Messier et al. 1999). In order to decrease this light requirement, shade tolerant species increase carbon allocation to photosynthetic leaves and decrease allocation to non-photosynthetic branches and stems. However, carbon allocation to roots may also increase, allowing for better competition for water and nutrients. As a result of this

increasing light requirement, height growth may be detrimental if not met by higher light levels. Thus, understory survival is negatively correlated with growth (Messier et al. 1999).

Shade tolerant conifers are able to take advantage of the low light levels underneath full canopies through numerous morphological, anatomical and physiological adaptations. With decreasing light levels, lateral branch growth is greater than height growth, the number of branches decreases, live crown ratio decreases, and needles and branches are held horizontally (Messier et al. 1999). Architectural adaptations of the crown greatly influence the amount of light received by an individual and its nearby neighbors by intercepting and transmitting variable amounts of light. Thus crown modifications influence growth of the tree itself, as well as its competitors.

Although shade tolerant, spruce is limited in its ability to survive long periods under persistent shade as a result of its inability to increase radial growth under such conditions without risking mortality (Kobe and Coates 1997). Thus spruce is often found growing in larger gaps with higher light levels. Its conservative growth strategy is consistent with its long lifespan. Thus spruce is viewed as being favoured by less frequent disturbances (Messier et al. 1999.)

#### Turnover versus Stagnation

Considering the increasing light requirement with growth, smaller seedlings are often much more abundant under dense upper canopies than taller seedlings or saplings (Messier et al. 1999). Taller seedlings tend to be aggregated within gaps, where increasing light interception with height makes growth advantageous. Under the shade of

closed canopies white spruce appears to exhibit a lack of growth. Thus one strategy that may be used to cope with low light levels is growth stagnation, whereby seedlings wait for a sufficient amount of light needed to realize full growth potentials (Kneeshaw and Burton 1997). Veblen (1986) observed stagnation of *Picea engelmannii*. Approximately half of the individuals studied were released at least once and 15% were released at least twice. Alternatively, this apparent lack of growth may be explained by seedling turnover, whereby seedlings continuously die off to be replaced by younger individuals until conditions improve (Morin and Laprise 1997). Both stagnation and turnover may occur simultaneously, with stagnation being more pronounced during stressful periods i.e. spruce budworm outbreaks, and turnover being more likely during periods of high seed production. Stagnation may also be periodic, with suppression and release depending on growing conditions. Likewise, the predominance of stagnation versus turnover may depend on site conditions. That is, seedlings growing under relatively moderate conditions may be more fit to wait for better conditions, while those subject to poor conditions will be more likely to die off and be replaced by others.

## **2.6.2 Recruitment into the Canopy**

### Light Interception

Light availability beneath the canopy is influenced by the composition and structure of both the overstory and understory. The nature of the overstory determines the amount of sunlight reaching the understory, which further modifies the amount of light reaching the forest floor. The thinner crowns of shade intolerant, deciduous species let more light through the canopy than shade tolerant conifers (Messier et al. 1998; Lieffers

et al. 1999). Thus the light captured by deciduous stands promotes understory growth which further reduces light received at the forest floor. The leaf area of the understory in these stands may in fact be greater than that of the overstory (Constabel and Lieffers 1996). Furthermore, light availability under deciduous stands will increase seasonally as leaves are shed (Constabel and Lieffers 1996; Ross et al. 1986). The taller structure of aspen canopies will also increase light transmittance, especially at higher latitudes where sun angle is low (Kneeshaw and Bergeron 1998). Light transmission through aspen canopies may also increase as leaf area declines with age (Constabel and Lieffers 1996). Thus older aspen stands may support higher understory cover than younger aspen stands. This will work in favour of seedlings that are able to establish early, while understory cover is low, and overtop the surrounding vegetation by the time the understory becomes very dense.

Light reaching the forest floor is similar among different stand types, but the amount of light transmitted through the canopy layer versus the understory layer varies (Constabel and Lieffers 1996). Most of the light in conifer stands is intercepted at the canopy, while under deciduous stands, more light is intercepted by shrubs and herbs. Thus seedling versus sapling success may vary with stand type. Seedlings will be subjected to less competition from understory vegetation within conifer stands, while sapling growth should benefit once above the understory layer within deciduous stands. This may explain observations of seedlings in the understory of older conifer stands with no indication of any reaching the canopy (Youngblood 1995).

### Growth Under Canopies

Light availability and shade tolerance become increasingly important following germination, as seedlings grow and are forced to compete with one another, and with other species, for limiting resources. Whether or not a seedling becomes a reproductively mature individual that is able to perpetuate its population, is dependent on surrounding vegetation and recruitment into the canopy above. While species composition as a seed source, as well as its influence on the seedbed, is important at the establishment stage, its influence on light availability greatly influences the likelihood of saplings being recruited into the canopy.

Seedlings under deciduous canopies must first compete with and overtop the herbaceous and shrub layer in order to capture enough light to survive and grow. Furthermore, there must be sufficient light below the canopy to supply the larger sapling with its greater light requirement (Lieffers et al. 1999). Growth rates of white spruce increase once above the understory of aspen stands. In fact, growth under aspen canopies is comparable to that on clearcut sites (Lieffers et al. 1996) as height growth of white spruce under 40% sunlight is equivalent to that under full sunlight (Lieffers and Stadt 1994). Thus increasing light availability further does not increase competitive status. Aspen canopies transmit sufficient light for recruitment of white spruce, until the regenerating white spruce becomes well developed, at which time further recruitment under the developing spruce will be limited (Lieffers et al. 1996).



## Growth in Gaps

The type of canopy best suited for recruitment of advance regeneration not only depends on species composition, but on the number and sizes of gaps in the canopy. When gaps are created, the resulting increase in light availability allows seedlings “waiting” in the understory to be recruited into the canopy. Gaps caused by storms are the primary agent for the recruitment of *Picea abies* in Swedish montane forests (Hytteborn et al. 1987). However, similar to aspen understories, large gaps are invaded by dense herb and shrub layers that compete with seedlings. Therefore, smaller gaps that let less light through to the forest floor convey a competitive advantage to shade tolerant seedlings (Messier et al. 1999). Kneeshaw and Burton (1997) suggest that the second cohort of *Picea engelmannii* is initiated by gap creation.

More abundant advance regeneration is observed within small gaps of mixed stands, which are not subject to heavy shrub competition (Kneeshaw and Bergeron 1996) and conifer recruitment is highest within small gaps of young aspen stands (Kneeshaw and Bergeron 1998). Thus moderate shade, characteristic of relatively small gaps, may allow shade tolerant seedlings and saplings to out compete intolerant species.

While younger stands tend to produce smaller gaps, more suddenly, through the senescence of individual or small groups of trees, older stands dominated by spruce often produce larger gaps, more gradually, often as a result of spruce budworm outbreaks. White spruce regeneration does not decrease with gap size, but is positively correlated with gap size in mixed and coniferous forests (Kneeshaw and Bergeron 1998). This is in keeping with the findings of Lieffers et al. (1996) that white spruce, although a shade tolerant species characteristic of later stages of succession, may have similar

establishment patterns to those of early successional shade intolerant species, provided competition from shrubs is low.

## **2.7 Conclusions**

The importance of seedsource availability must be stressed when managing for natural white spruce regeneration. Although protection of advance regeneration is important, further recruitment from outside sources may be needed due to mortality of advance growth from cutting (Ruel 1995). Later recruitment may actually contribute more to stocking than advance regeneration (Hughes and Bechtel 1997).

Conflicting results concerning the timing of white spruce recruitment remain unresolved (MacDonald et al. 2001; Youngblood 1995). Regional differences are likely contributing to the differences observed in white spruce recruitment dynamics. Climatic variation across regions will not only influence disturbance regimes, but will also affect such variables as masting behaviour and seedbed characteristics. Wright et al. (1998b) also found shade tolerance of saplings to differ across climatic regions. Thus further research focusing on such regional differences is required.

## CHAPTER 3

### STUDY AREA

#### 3.1 Landscape

The study area is located in Duck Mountain Provincial Park, Manitoba, which belongs to the physiographic subdivision of the Saskatchewan Plain in south-west Manitoba (Fig. 1.1) (Fraser 1982). The Duck Mountain uplands make up part of the Manitoba escarpment, which also includes Riding Mountain National Park to the south and Porcupine Hills to the north. The park and forest reserve are approximately 3770 km<sup>2</sup> (Hamel 2001). The landscape is characterized by undulating to hummocky till plain underlain by loamy, moderately calcareous glacial till formed from a dominant bedrock of Cretaceous marine shale from the Riding Mountain Formation (Fraser 1982). Dolomite from the Interlake area and igneous cobbles and boulders from the Precambrian Shield remain as more resistant deposits within the glacial till. This heterogeneity in parent materials derived from various means of glacial deposition modify the soils at relatively small spatial scales. The soils of these landscapes also reflect the high degree of topographic variability, which in turn influences the local hydrology. Clayey glaciolacustrine veneers and blankets, sandy and gravely glaciofluvial deposits and organic peat contribute to the heterogeneity of the landscape. The irregular morainal topography gives rise to well drained slopes, dominated by Gray Luvisols. Very poorly drained Rego and Rego Humic Gleysols are found adjacent to lakes and depressions (Fraser 1982). The complex physiography of the region gives rise to many different types of forest communities interspersed with lakes and wetlands (Hamel 2001).

### 3.2 Climate

Duck Mountain belongs to the Cold Cryoboreal climatic region, in which the climate of the uplands is cold humid continental (Fraser 1982). Weather stations in the nearby surrounding lowlands report a mean annual air temperature of 1.4 degrees C at Swan River and 1.7 degrees C at Dauphin. Based on these weather stations January is the coldest month with a daily mean temperature of -18 to -19 degrees C and July is the warmest month with a daily mean temperature of about 18 degrees C. Swan River and Dauphin weather stations report February as being the driest period with 16 to 18 mm of snow. June and July are the wettest months with 78 to 80 mm of rain (Environment Canada 1984). The annual precipitation of this region is approximately 500 mm, two thirds of which falls as rain and one third as snow.

The uplands of the Duck Mountains have higher precipitation, lower temperatures and a shorter growing season than the surrounding lower lying areas (Fraser 1982). This may be attributable to air movement over the Manitoba escarpment in addition to the many lakes and wetlands. These conditions are similar to those found in Riding Mountain National Park, where precipitation is greater than in the surrounding areas (Caners 2001; Wolfe 2001).

The mean annual air temperature of the Duck Mountain uplands ranges between -1 and -0.5 degrees C. Summers are short and warm with a frost-free period of less than 100 days and a growing season less than 1300 days, occurring between May 1 and September 30. The mean annual soil temperature is 2 degrees C (Fraser 1982).

### **3.3 Vegetation**

As part of the Manitoba Escarpment, Duck Mountain belongs to the Mid-Boreal Upland Ecoregion (Acton et al. 1998). The vegetation on the uplands forms a forest mosaic of open and treed fens and bogs with mixedwood and conifer stands dominating the interior. Mixedwood stands are composed of trembling aspen, balsam poplar, jack pine, white birch, white spruce (Sauchyn and Hadwen 2001) and balsam fir. Trembling aspen stands populate the lower elevations around the periphery of the park and are relatively young with a mean stand age of 90 years (Hamel 2001). Balsam poplar intrusions occur in these stands in lower lying areas where nutrient status is high. Pure conifer stands are less common than mixed. Stands dominated by white spruce, jack pine, or black spruce averaging 110 – 115 years are more common at higher elevations (Hamel 2001). Black spruce is also found in association with tamarack surrounding wetlands. White spruce in the understory (advance regeneration) may remain in a suppressed state for lengthy periods. However, recruitment of white spruce advance regeneration into aspen canopies is commonly observed (Hamel 2001).

### **3.4 Disturbance History**

Logging in the Duck Mountains began in the early 1800's, followed by settlement and clearing for agriculture beginning in 1885 and the creation of a forest reserve in 1906 (Goldrup 1992). Large fires have been a persistent disturbance throughout the Duck Mountains since the 1800's (Goldrup 1992). In 1885 there was a large fire that burned much of the Duck Mountain area (Harrison 1934). Since the 1960's fires have been less extensive (Hamel 2001). Selective logging of white spruce, in addition to frequent

clearance caused fires, may increase vegetatively reproducing and fire adapted species, such as aspen and pine (Weir and Johnson 1998). These rapid colonizers out compete white spruce, which is classified as a fire avoider (Ehnes and Shay 1995) as it depends on a proximate seed source for regeneration.

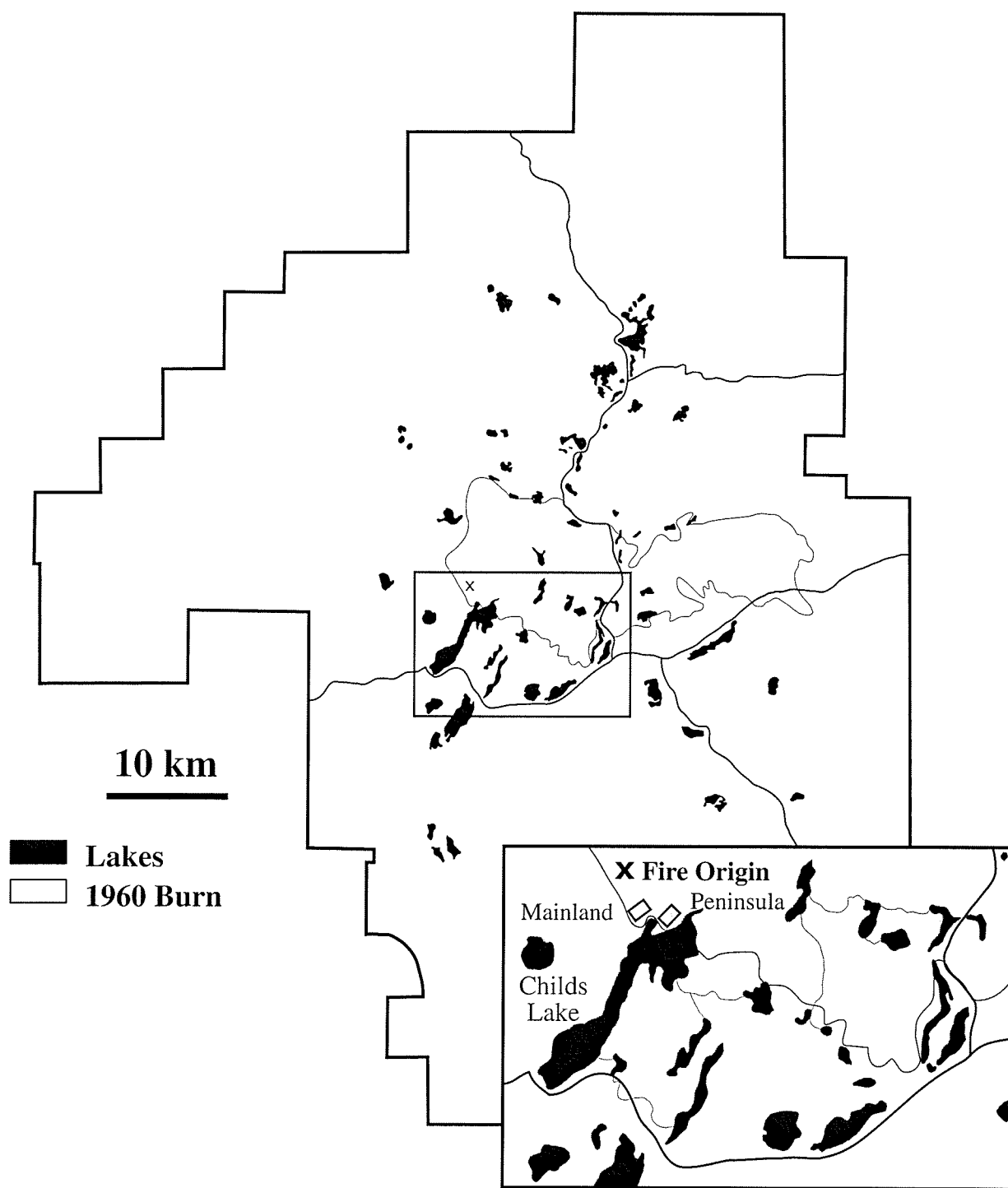
Spruce budworm outbreaks have been reported to occur since 1991 northwest of Child's Lake (Knowles and Matwee 1996). However, there was no evidence of spruce budworm at the study sites and very little balsam fir, which is the primary carrier of spruce budworm.

Browsing of shrubs by ungulates is a common occurrence within the study area, which indirectly affects white spruce regeneration. Considering the preference for balsam fir over white spruce, browsing of fir may increase the proportion of spruce in regenerating stands (McInnes et al. 1992). In addition to altering community composition directly, the removal of potential deciduous litter, through browsing will decrease nutrient cycling, thereby decreasing productivity (Pastor et al. 1993). Thus those species better able to compete for limiting nutrients will benefit. Considering the propensity for shrubs to proliferate on richer sites, decreased nutrient cycling may actually decrease shrub competition and favour spruce regeneration. The relative success of conifer regeneration versus shrubs will also be highly influenced by light availability, which is also affected by browsing of shrubs.

Hares may kill white spruce in the winter by browsing on buds and small twigs. Voles and red squirrels may drastically reduce the abundance of white spruce seed (Rowe 1955). Beaver activity was also observed in the study area, which may affect white spruce regeneration through flooding and hardwood removal.

### 3.5 Location of Study Sites

Research was carried out at two sites just north of Childs Lake in the Duck Mountain Uplands (Fig. 3.1). The MAINLAND site is centered around UTM coordinates with an easting of 356859 and a northing of 5722205. The center of the PENINSULA site has an easting of 357318 and a northing of 5721941. Both sites are quite variable topographically with ridges, hills and depressions forming irregular, hummocky terrain with fens dotted throughout. The sites are located within a large burn that took place in 1961. Unburned old growth forest remains to the south of each site (Fig. 3.1). A fireguard that separates the old growth forest from the burn was constructed by bulldozers and is still present adjacent to the MAINLAND study site. There was evidence of post-fire salvage logging in this area, although very limited. Cut stumps were observed along trails only. No evidence of logging was found within any of the plots.



**Figure 3.1.** Locations of the MAINLAND and PENINSULA sites in Duck Mountain Provincial Park. The extent of the 1961 forest fire is indicated in grey.



### **3.6 The 1961 Forest Fire**

The fire that burned the two study sites was detected on August 16, 1961 and burned until October 22, 1961, at which time the fire was still burning in the ground. The fire originated on grass and scrub about a half mile northwest of Childs Lake by an unextinguished campfire (Fig. 3.1). It was spread by west and southwest winds of up to 35 mph. A total area of 52 000 acres was burned. The amount of wood lost is equivalent to a 250 mile long train (Dept. of Mines. 1961).

Average rainfall from 1958-1960 was below normal and snowfall during the winter proceeding the fire was less than 1.5 feet (Dept. of Mines 1961). From June 1960 to September 1961 almost no rainfall was recorded. Indeed 1961 was the driest year of the past 169 years (Sauchyn and Hadwen 2001).

#### **3.6.1 Fire Behaviour and Burn Severity**

Fire is responsible for initiating secondary succession through tree mortality and seedbed preparation (Bradley et al. 1992). The pattern of forest regeneration following fire is strongly dependent on fire intensity, which is in turn dependent on weather, topography and fuel moisture content. High intensity fires occur following extended dry periods that lower fuel moisture content (Heinselman 1973). Such conditions were experienced in the years preceding the 1961 burn in Duck Mountain. However, wind-driven fires, such as the 1961 burn, may spread quickly consuming relatively small amounts of fuel (Johnson and Miyanishi 1995). Furthermore high wind fires are much more likely to jump fire barriers such as lakes, wetlands, peninsulas and ridges

(Heinselman 1996). Thus within wind-driven burns small patches may remain unburned or less severely burned.

The study sites are characterized by variable topography interspersed with wetlands and the old growth adjacent to the burn on the MAINLAND site had relatively high densities of aspen. These conditions are conducive to low intensity fires (Larsen 1997; Dansereau and Bergeron 1993). White spruce with fire scars on the lower trunks and with higher branches left living were observed between the two study sites. In addition, ridges are reported to burn most often (Heinselman 1996), whereas unburned white spruce remained on the ridge system surrounding the MAINLAND site. Furthermore, the wind was strongly blowing away from the study sites at the time of the burn. Considering the close proximity of the point of origin of the fire it is possible that its full intensity had not yet been reached when it burned the study area.

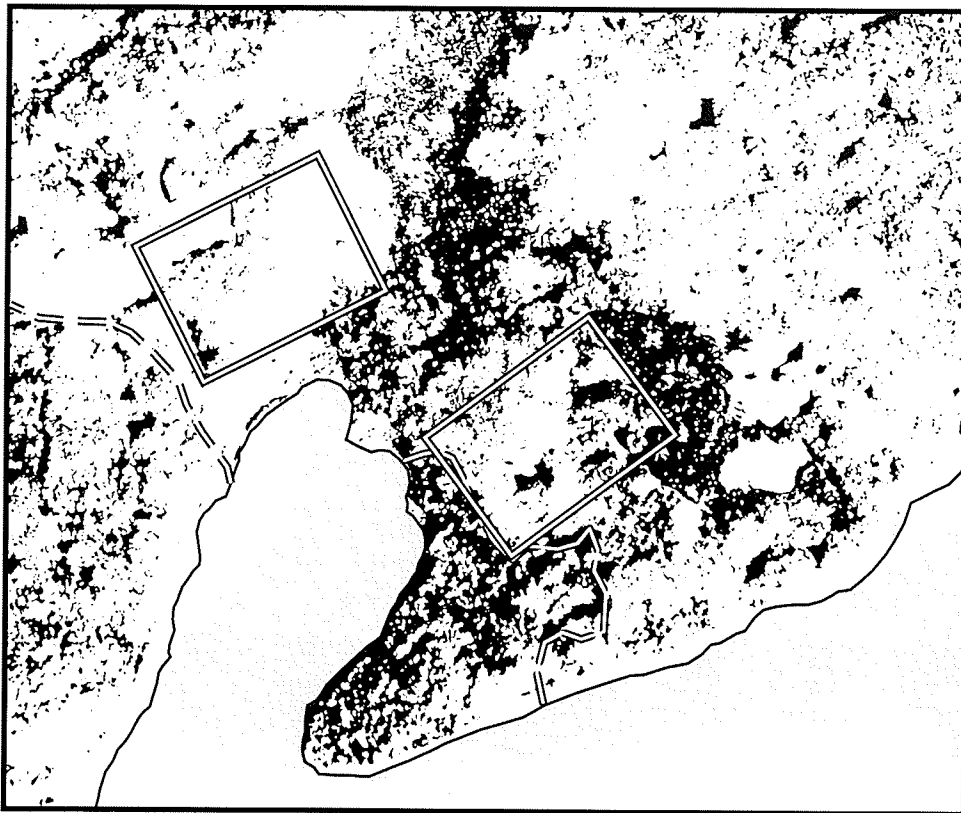
It is also possible that the location and orientation of firebreaks within the study area decreased the severity of the fire in some areas. East and northeast facing ridges act as effective fire breaks (Heinselman 1996). Thus the ridges separating the fire's point of origin from the MAINLAND site may have protected this area from more severe burning. Indeed, small stands may be protected by the hummocky terrain of the Duck Mountains from the most catastrophic fires (Hamel 2001). Lakes are also effective in ameliorating the spread of fire from west to east, with northeast perimeters of lakes acting as effective fire breaks (Heinselman 1996). This explains the greater densities of remnant white spruce within the burn on the PENINSULA site on the northeast side of Childs Lake.

The presence of recently dead fallen, remnant white spruce, also suggest that the burn may have skipped some areas of the study sites, particularly around wetlands. Two

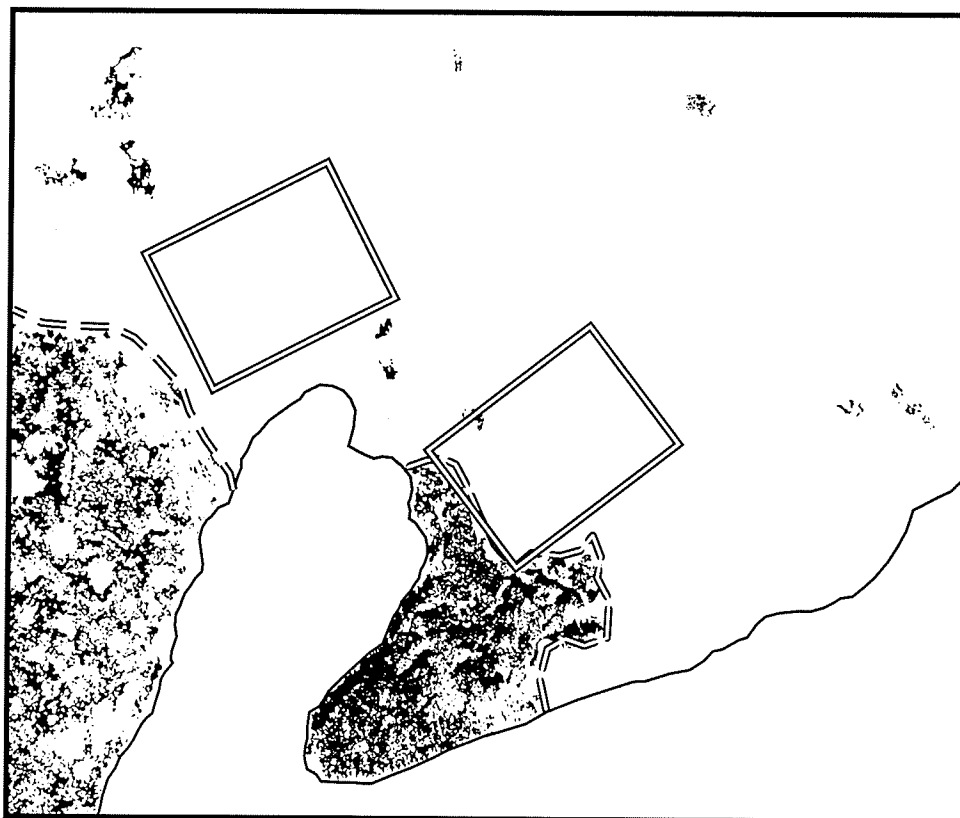
men died fighting this fire as a consequence of the fire jumping across a road. With this type of fire behaviour surviving seed trees may have been able to avoid the fire and contribute to white spruce regeneration.

Aerial photos from before (1946) and after (1963) the 1961 burn were digitized and density sliced to show the contrast between areas of dense conifer cover and areas with no conifer cover (Fig. 3.2). Before the burn, conifer cover was slightly higher at the PENINSULA study site. However, both sites were mixedwood with a large deciduous component. Both before and after the fire the seed source area on the peninsula had denser conifer cover than the old growth adjacent to the MAINLAND site. After the burn, dense remnant white spruce cover was more common on the peninsula. Smaller, less dense conifer cover is not visible as a result of the black and white density slice. The greater distance to seed source, in combination with the lower conifer component within and beside the MAINLAND site likely would have made recruitment of white spruce onto this site slower and less abundant than on the PENINSULA site.

a



b



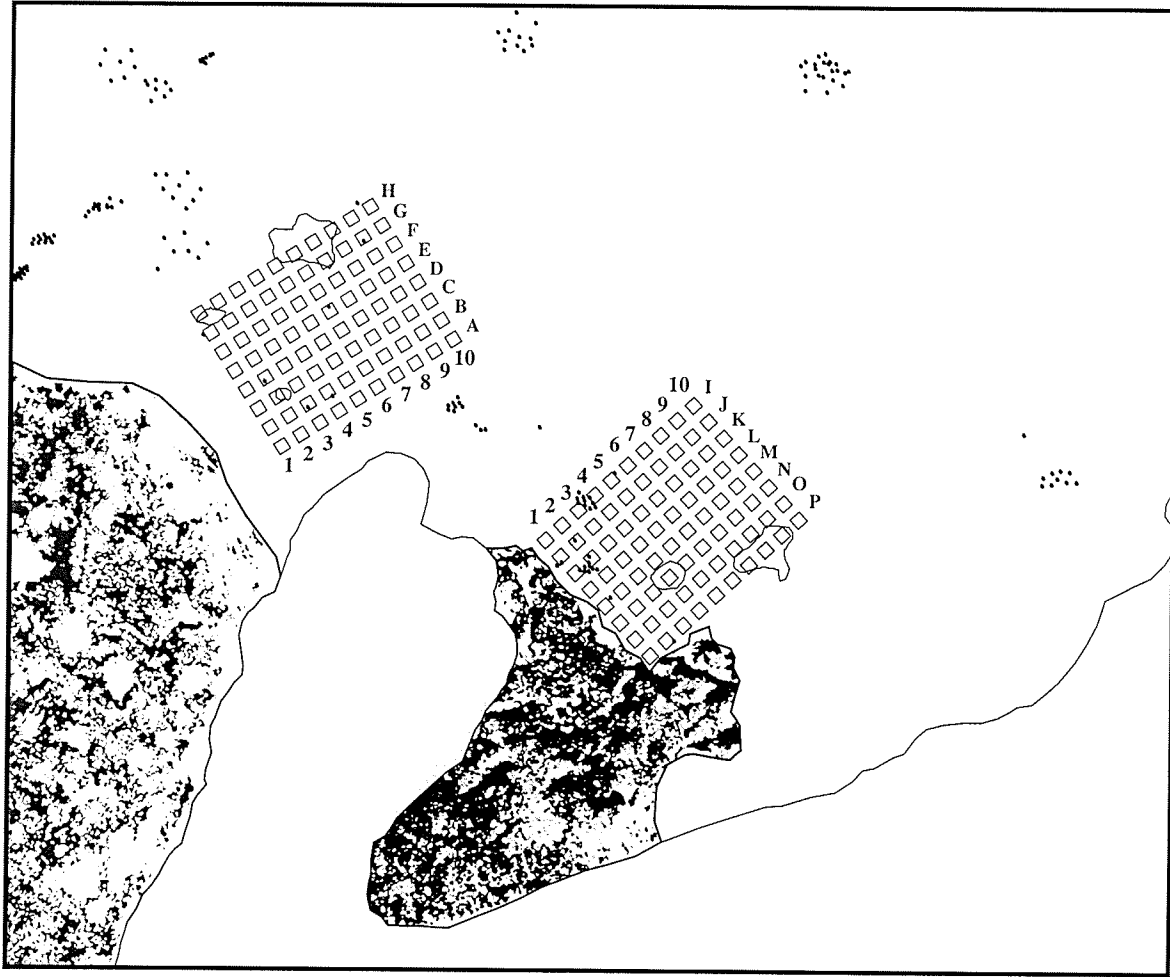
**Figure 3.2:** Time series comparison between digitized aerial photos of the two study sites, a) 1940's; b) 1963 following the 1961 burn. The location of conifer dominated areas is indicated in black. The area unburned in 1961 and some scattered remnant seedsources are shown (b).

## CHAPTER 4

### METHODS

#### 4.1 Sampling Design

Data were collected for 80 plots on each of the two sites (Fig. 3.3). The plots were arranged as 10 by 8 plot grids, oriented lengthwise away from the old growth forest edge, with plots spaced 30 m apart. The MAINLAND plots were 10x10m and the PENINSULA plots were 5x5m as the spruce density on the PENINSULA site was very high. On the MAINLAND site, four randomly placed 1x1m quadrats were set up within each 10x10 plot to collect seedbed data. Two randomly placed 1x1m quadrats were set up within each 5x5m plot on the PENINSULA site to collect the seedbed data. The distance of the old growth forest to the edge of the MAINLAND site averaged approximately 40 m, while the old growth on the peninsula occurred immediately adjacent to the study site. Relative distance, rather than absolute distance, was used for data analyses. The total number of plots used in the data analyses was 169 as 4 plots on the MAINLAND site and 4 on the PENINSULA site occurred in wetlands (Fig 3.3) and three (L10, M9 and M10) on the PENINSULA site occurred in bogs.



**Figure 4.1.** Plot design for the two sites sampled in the study. A series of transects, identified by letter (MAINLAND site: A-H, PENINSULA site : I-P) were laid out every 30 m perpendicular to the edge of the 1961 burn. Along each transect, 10 quadrats were place every 30 m and the locations of all seed trees (dots), and other topographical features such as waterbodies (grey) were mapped. Location of conifers in the unburned forest are indicated as black.

## **4.2 Data Collection**

### **4.2.1 Description of the Old Growth Forest Adjacent to the Study Sites**

The density of the old growth forest was determined using the point-centered quarter method, in which the closest four trees to a point are enumerated (Barbour et al. 1980). Twenty points (80 trees) were used to estimate old growth density in the unburned forest adjacent to each study site. The DBH (diameter at breast height) of each tree was measured to calculate basal areas of each species. Percent cover of shrubs, herbs and mosses was estimated within quadrats located at each point.

### **4.2.2 Plot Data**

Within each plot, all live and dead trees were identified and mapped, and heights and DBH's were measured. Fallen logs were also mapped and the decay class of each was recorded. Percent cover was estimated for tree and tall shrub species. One soil pit was dug in each plot to gather organic matter and sample the first 30 cm of mineral soil. The mineral soil was taken for determination of soil moisture, texture, pH and conductivity. The depth of the organic matter was also recorded.

White spruce cross sections were taken from the base and at 1.25m for age determination. Height, diameter at the base and diameter at breast height (1.25m) were recorded. The total number of rings were counted on each cut face of each cross section, using a dissecting microscope. For consistency, the greatest number of rings counted on each cross section was used for the age data. A total of 2 042 spruce trees were aged at the base, 938 of which were aged at breast height. Records were kept of spruce germinating on logs, along with associated moss species.

#### **4.2.3 Quadrat Data**

Within each 1x1m quadrat the percent cover of herbaceous species, low shrub species and moss species was recorded. The seedbed characteristics were also recorded within each 1x1m quadrat as percent cover of moss, exposed mineral soil, broadleaf litter and needle litter, decaying deadwood and undecayed wood.

#### **4.2.4 Topographic Survey**

A topographic survey was carried out for each site using a digital laser total station (Sokkia set 4110 series). The angle accuracy was 2 seconds and the distance accuracy was 2 mm up to 1 km. Elevations were recorded at 10m intervals for each grid, including a 10m buffer zone. Elevations were corrected to absolute elevation by using Childs Lake as a reference point. Digital elevation models (DEM's) were produced and slope was calculated in Idrisi 32 using the "topographic variables" option in the "surface analysis" module.

### **4.3 Data Analysis**

#### **4.3.1 Description and Summary of Study Sites and Adjacent Old Growth Forest**

##### Old Growth

Density, basal area and percent cover of tree species in the old growth forest adjacent to each site were calculated from the point centered quarter data (Barbour et al. 1980). Common shrubs, herbs and mosses were tabulated.



## Biotic Data

For the biotic data, live and dead tree densities were calculated and mean percent cover values were given for spruce, deciduous, shrub and herb canopies, along with standard errors. The seedbed was characterized by percent cover values of broadleaf litter, decayed wood, undecayed wood and moss. Dominant species of low shrubs, herbs and mosses on each site were also reported. T-tests were performed on the tree density data. A two group discriminant analysis (Morrison 1990), which is an extension of the T-test for multivariate data, was performed on the low shrub, herb and moss cover data to determine if the two sites were significantly different in species composition.

Since the biotic variables follow similar trends and tend to be correlated with one another, principal component analyses (PCA's) (Morrison 1990) were performed to reduce the biotic variables into one variable, or PCA axis, for each site. The objective of this type of analysis is to reduce the trended variables into one variable that encompasses as much of the trended variation as possible. A correlation matrix, measuring the association between each variable, was computed from the raw data, so as to standardize variables measured in different units, and used for the PCA analysis. The first PCA axis passes through the point swarm in multidimensional space such that the variation along the axis is maximized. The eight variables used in the biotic PCA analyses were:

deciduous canopy cover (%)

shrubs cover (%)

basal area of live aspen and poplar ( $\text{cm}^2$ )

basal area of dead aspen and polar ( $\text{cm}^2$ )

basal area of live birch ( $\text{cm}^2$ )

basal area of dead birch (cm<sup>2</sup>)

moss cover (%)

herbaceous cover (%)

Plots occurring in wetlands were excluded from the analyses and all biotic data was log-transformed.

### Abiotic data

The mean values of the abiotic variables were calculated for each site. The abiotic variables used were elevation, slope, soil moisture, percent sand, silt and clay, organic matter depth, pH and conductivity. A two group discriminant analysis was performed on the abiotic data to determine if the two sites were significantly different in terms of the abiotic variables. As with the biotic data, much of the abiotic data followed similar trends. Thus PCA analyses were carried out for the abiotic data to produce one composite abiotic variable for each site. The thirteen variables used in the abiotic PCA analyses were:

elevation (m)

slope (%)

soil water content (%) (gravimetric method)

depth of organic matter (cm)

percent sand in soil (%) (hydrometer method)

percent silt in soil (%) (hydrometer method)

percent clay in soil (%) (hydrometer method)

soil pH (pH) (pH/conductivity meter)

soil conductivity (uS/cm) (pH/conductivity meter)

decayed deadwood cover (%)

undecayed deadwood cover (%)

moss cover (%)

broadleaf litter cover (%)

All abiotic variables were log transformed and plots occurring in wetlands were excluded from the analyses.

#### Spruce Data

Density per hectare of live and dead spruce was calculated for each site. Mean height, DBH and age at base and breast height (1.25 m) were calculated with standard errors.

#### **4.3.2 Age Distributions of White Spruce**

Growth ring counts from the base of each tree were used to construct age distributions for live white spruce and to calculate coefficients of variation in age at each site. Based on these age distributions, white spruce trees were separated into three cohort classes at each site: cohort 1 = initial white spruce to establish (ages 25-39), cohort 2 = intermediate white spruce (ages 5-24), and cohort 3 = most recently established white spruce seedlings (ages 3 and 4). No seedlings under 3 years old were observed. Further analyses were carried out on separate cohorts to determine how dispersal, establishment and growth of white spruce were affected by different factors over time. Cumulative age

distributions of white spruce on each of the two sites were also compared to show differences between sites in the rate of white spruce recruitment over time.

### **4.3.3 White Spruce Establishment**

#### Spatial Autocorrelation

Three variables are of interest for the purpose of predicting white spruce recruitment in this study: distance to seed source, biotic factors (biotic PCA axis 1) and abiotic factors (abiotic PCA axis 1). Since a relatively close seed tree is required for white spruce recruitment, distance to seed source, a spatial variable, must be considered. The nature of the environmental data is also spatially dependent, which lends them to spatial autocorrelation (Wise et al. 2001; Zhang and Griffith 2000). For example abiotic variables, such as soil moisture content, are typically more similar between short distances and less similar between long distances. The same is generally true for biotic variables such as species abundance.

Before carrying out any analyses aimed at determining which variables best predict white spruce establishment (abundance), the degree of spatial autocorrelation within each variable must be determined, as some modeling methods are inappropriate for spatially autocorrelated data and require alternative methods of data analysis (Khaemba and Stein 2000; Kitron et al. 1996; Preisler et al. 1997; Kessel 1996; Fotheringham and Rogerson, 1993). A variable is spatially autocorrelated when its values are correlated with values at nearby geographic locations. Thus if white spruce abundance is high for plots close to each other, then white spruce abundance is positively spatially autocorrelated. Simple Mantel tests were performed to determine the degree of

spatial autocorrelation within each variable. Variables tested were white spruce abundance in each cohort (log-transformed), the biotic PCA axis and the abiotic PCA axis. Distance is inherently spatially autocorrelated.

Mantel's test calculates the correlation between two association matrices (Manly 1991). Each matrix contains measures of difference between data points. One matrix represents the variable of interest, i.e. differences in spruce abundance between plots, while the other contains the geographic distances among plots. The matrix of ecological associations is then compared with the distance matrix to give the correlation of the ecological variable with space, or spatial autocorrelation. This correlation is the Mantel statistic ( $r_M$ ), which is calculated as the sum of cross products in the two matrices.

Since only relatively close plots are likely to have similar values, the reciprocals of geographic distances are used to emphasize plots that are close to each other (Mantel 1967). Thus a negative correlation between an ecological association matrix and a reciprocal distance matrix indicates that close plots have similar values and therefore are positively spatially autocorrelated.

Significance of the Mantel test is determined by a randomization test, in which one of the matrices is randomized a number of times (999 in the present study) and the Mantel statistic is recomputed (Manly 1993). If the recomputed Mantel statistics are significantly different from the Mantel statistic for the observed data, then the test is considered significant.

### Correlations Among Variables After Removing Spatial Effects

Because most of the variables were significantly spatially autocorrelated, partial Mantel tests were performed to determine the correlations between the variation of spruce and the environmental variables after removal of spatial effects. A positive correlation between the variation of two variables, after accounting for geographic location, suggests that the two variables are associated for reasons other than confounding spatial effects (Legendre and Legendre 1998).

The partial Mantel test is performed by extending the simple Mantel test to include three, rather than two, matrices. Two matrices contain the associations of the variables of interest e.g. spruce abundance and abiotic, while a third contains the geographic distances between the plots. The partial Mantel statistic is computed in the same manner as a partial correlation coefficient (Legendre and Legendre 1998) except that standardized Mantel statistics are used rather than Pearson correlations. Likewise, the partial Mantel statistic only gives the correlation between the variations in the association matrices of the two variables of interest. It does not determine if one variable is capable of predicting the other, as regression analyses do. Furthermore, the partial Mantel test only considers two variables at a time, after accounting for space. It does not consider any additive or confounding effects of additional variables. Thus the combined effects of both the biotic and the abiotic on white spruce abundance is not assessed with the partial Mantel test.

White spruce abundance (log-transformed) in each cohort was entered into partial mantel tests with the biotic and abiotic PCA axes. Inverse Euclidean distance was used to emphasize associations between close plots.

### Factors Affecting Establishment

Regression analysis is commonly used to predict a dependent variable (i.e. white spruce) from one or more independent variables (i.e. distance from seed source, biotic and abiotic). When spatial autocorrelation is present within the data, standard regression modelling may be inadequate, as standard errors of regression coefficients and tests of significance are often unreliable for autocorrelated data (Kessel 1996; Wise et al. 2001; Zhang and Griffith 2000; Lowell 1991). One method used to deal with this problem is to include spatial location as a predictor variable in a multiple regression analysis (Preisler et al. 1997). This was the method opted for in the present study.

#### Multiple regressions

A multiple regression analysis was performed to determine the effects of the biotic PCA axis scores, the abiotic PCA axis scores and the x (distance between transects) and y (distance to old growth) grid coordinates of each plot on white spruce abundance in each cohort for each site. The multiple regression coefficients indicate the unique contribution of each variable in predicting white spruce abundance (Legendre and Legendre 1998).

#### Partial regressions

Partial regressions were performed to determine the amount of variation in white spruce abundance attributable to one set of variables after the effects of the other set have been removed (Legendre and Legendre 1998). The effects of the spatial variables (x and y coordinates) were determined, after removing the effects of the environmental

variables. Similarly, the effects of the environmental variables were determined, after removing the spatial effects. This was achieved by regressing the residuals of the variables of interest. The amount of the variation in white spruce abundance that is attributable to each set of variables is given by the  $R^2$  value of each partial regression. The proportion of variation in white spruce abundance explained solely by each set of variables (spatial versus environmental), the proportion explained by both sets together and the proportion of unexplained variation were then calculated and reported in a summary table. The effects of the biotic, abiotic and distance to seed source on white spruce abundance in each cohort, including cohort 3 (seedlings), were depicted as bar charts of white spruce abundance per distance, biotic and abiotic class.

#### **4.3.4 Age – Size Relationships of White Spruce**

Height and DBH of white spruce on each site were regressed against age to determine the amount of variation in height and DBH accounted for by age. The data were log-transformed producing a power-law relationship. Simple regressions were also carried out between height and DBH for each site. Height by age regressions were also performed separately on cohorts one and two on each site to determine the degree to which height varies with age over time. Height distributions of white spruce were also produced to illustrate the variation in height and coefficients of variation were calculated for all white spruce, and the two cohorts, on each site.



### **4.3.5 Growth of White Spruce**

#### Early Growth and Factors Affecting Growth

The difference between the number of growth rings at the base versus breast height (1.25m) of each tree greater than 1.4 m tall was calculated and frequency distributions were produced to determine the number of years it took each tree to grow above the lower vegetation canopy, or 1.25 m. These differences were also regressed against height to show the variation in the early growth of these trees. This measure of early growth, and the height and DBH, of each tree were regressed against age and the residuals were used to give the initial growth, height and DBH of each tree after accounting for the influence of age. These residuals were entered into stepwise multiple regressions with biotic and abiotic factors to determine what factors, other than age, may have been affecting the growth of these trees.

#### Suppression

The heights (log-transformed) of all trees from both sites were regressed against their ages (log-transformed) to determine the mean growth rate of white spruce in this area based on a power-law relationship. Height was used as a measure of growth as DBH was highly correlated with height. The regression was adjusted to begin at zero cm and zero years, which corresponds to a height of 1 cm in 1 year. This growth curve was used to determine growth suppression of each tree. If a tree did not reach the predicted height for its age, based on the growth curve, then the tree was considered suppressed. Conversely, white spruce occurring above the growth curve were considered free to

grow. Frequency distributions of the percent of unsuppressed white spruce, per age class, were produced for each site.

#### **4.3.6 Mortality**

Age distributions of dead white spruce were produced for each site. These distributions indicate the age at which death of white spruce occurred. However, time since death, and thus time of establishment, is unknown. Thus these age distributions are only used to depict general patterns of mortality. The data for the two sites was then pooled, as relatively little mortality occurred on the MAINLAND site. The percent of dead trees in the pooled data was then expressed by white spruce density class to gauge the influence of intraspecific competition on mortality.

## CHAPTER 5

### RESULTS

#### 5.1 Description and Summary of Study Sites and Adjacent Old Growth Forest

##### 5.1.1 Old Growth

###### MAINLAND

The old growth forest adjacent to the MAINLAND study site was mixed wood with high and low density phases of white spruce and aspen. In the old growth adjacent to transects D through F (Fig. 3.3) many mature aspen had fallen, resulting in a fairly open canopy with high shrub cover of beaked hazelnut (*Corylus cornuta*). Mean cover of white spruce and aspen in areas dominated by spruce were 60% and 40% respectively (Table 5.1). Where aspen dominated, its mean cover was 80%, while that of spruce was 10%. Overall, white spruce density adjacent to the MAINLAND site was 95 trees/ha and aspen density was 212.5 trees/ha.

###### PENINSULA

The old growth forest adjacent to the PENINSULA study site was dominated by white spruce. Aspen and black spruce were present to a lesser degree. Balsam fir was also present further away from the burn, closer to the tip of the peninsula. Mean canopy cover of white spruce was 85% and aspen was 10% (Table 5.1). Spruce density was 372.5 trees/ha and aspen density was 41.3 trees/ha.

The most common species, in decreasing order of cover, are presented in Table 5.2. Herbaceous cover on both sites was similar to that of the burned sites, although later successional species such as *Mitella nuda* (common mirewort), *Linnaea borealis* (twinflower) and *Pyrola sp.* (wintergreen) had greater abundance in the old growth forest. Shrub cover was virtually non-existent in the old growth adjacent to the PENINSULA site, while shrub cover in the old growth adjacent to the MAINLAND site was extremely high. Moss cover was much higher adjacent to the PENINSULA site than the MAINLAND site. *Hylocomium splendens* (stair-step moss) was the dominant moss species in the peninsula old growth.

Considering the much greater density of white spruce adjacent to the PENINSULA site, in addition to the fact that the PENINSULA plots were closer to the old growth, it is apparent that seed availability must have been much greater adjacent to the PENINSULA site.

### **5.1.2 Biotic Characteristics of the Study Sites**

Aspen heights on both sites averaged 15 to 16 metres. Aspen density was very similar between sites (4614/ha on the MAINLAND and 4685/ha on the PENINSULA), while birch density was higher on the MAINLAND site (975/ha) than the PENINSULA site (400/ha) (Table 5.3 a). In terms of basal area, aspen covered slightly more area on the MAINLAND site (2930.2 m<sup>2</sup>/ha) than on the PENINSULA site (2650.33 m<sup>2</sup>/ha). T-tests of aspen and birch basal areas on the MAINLAND site versus the PENINSULA site indicated that aspen basal areas between the two sites were not significantly different (t-statistic = 0.741, p = 0.4608), whereas birch basal areas were significantly different (t-

statistic = 2.985,  $p = 0.0038$ ). In general, deciduous canopy cover was higher on the MAINLAND site (mean = 53.65%) than the PENINSULA site (mean = 37.02%), while white spruce cover was much higher on the PENINSULA site (mean = 23.81%) than on the MAINLAND site (mean = 6.34%) (Table 5.3 b). The cover of tall shrubs, which mostly consisted of *Corylus cornuta*, on the MAINLAND site was also quite high (mean = 27.83%), while the PENINSULA site had only trace amounts (mean = 0.52%).

Seedbed conditions also differed quite substantially (Table 5.3 b). As a result of the higher deciduous canopy and shrub cover on the MAINLAND site, its mean cover of leaf litter was 89.17%, versus 42.19% on the PENINSULA site. The percent cover of rotting logs was similar on both sites, although slightly higher on the PENINSULA site (mean = 8.66% on the MAINLAND and 9.60% on the PENINSULA). Moss cover was higher on the PENINSULA site (mean = 10.2% versus 5.4%) and was often associated with rotting logs. The presence of rotting logs and moss cover likely served as an advantage for germinating white spruce in the absence of mineral soil. Approximately 84% of white spruce seedlings (cohort 3) germinated on logs and over 90% germinated on logs of the highest decay class.

Herbaceous species and low shrub composition was similar between sites. However, relative cover differed between sites. The two group discriminant analysis showed that the two sites were significantly different in terms of herb and low shrub understory vegetation ( $T^2 = 40.84$ ,  $p < 0.001$ ). The three most dominant species on both sites were *Aralia nudicaulis*, *Mertensia paniculata* and *Rubus pubescens* (Table 5.4). The higher cover of *Ribes oxycanthoides*, *Rosa acicularis* and *Bromus ciliatus* on the MAINLAND site indicates a drier, more competitive habitat than the PENINSULA site.

The PENINSULA site had higher cover of *Carex utriculata*, *Equisetum arvense*, *Petasites palmatus*, *Cornus canadensis* and mosses indicating a moister and more hospitable habitat for white spruce.

The results of the biotic PCA analyses for the MAINLAND and PENINSULA sites differed as a result of the lower cover of birch and shrubs on the PENINSULA site (Fig. 5.1). On the MAINLAND site, greater birch and moss cover were associated with the negative (left) end of the first PCA axis, while greater shrub and aspen and poplar cover were associated with the positive (right) end. On the PENINSULA site, greater moss cover was associated with the negative end of the first axis, while deciduous cover was highest in plots at the positive end. Thus plots with negative numbers along the first PCA axis (left end) may be interpreted as having less interspecific competition, while positive numbers (right end) may represent plots with more interspecific competition. The first PCA axis for the MAINLAND site accounts for 34.99% of the variation described by the biotic variables, while the PENINSULA PCA axis accounts for 24.01%.

### 5.1.3 Abiotic Characteristics of the Study Sites

The abiotic factors measured were more similar between sites than the biotic factors (Table 5.5). The two group discriminant analysis indicated that the two sites were significantly different in terms of the abiotic variables ( $T^2 = 31.17$ ,  $P = < 0.001$ ). Mean elevation differed by 3.69m between sites, with the MAINLAND site being higher than the PENINSULA site. However, the MAINLAND site had an elevational range of 16.8m, while the PENINSULA site had a range of 7.9 m. The mean slope of the plots on the MAINLAND site also greater (13.33%) than on the PENINSULA site (6.86%). There

was an increase in elevation at the middle of the MAINLAND site that was quite apparent in the field (Fig. 5.2). Conversely, the PENINSULA site had smaller elevational differences, although it was more complex topographically, with many small depressions and ridges (Fig. 5.3). Mean soil moisture content was slightly higher on the PENINSULA ( $M = 9.38\%$ ,  $P = 10.5\%$ ) site and the sand:clay ratio was slightly higher on the MAINLAND site. The mean percent sand, silt and clay indicate that the MAINLAND site was a sandy loam, whereas the PENINSULA site was more of a sandy clay loam. The PENINSULA site was also more variable in terms of soil texture ( $CV = 87.9\%$ ) than the MAINLAND site ( $CV = 69.9\%$ ). The higher elevation above the water table and the lower soil moisture indicate that the MAINLAND plots receive less moisture than the PENINSULA plots. A greater abundance of moist microsites on the PENINSULA site may have provided better conditions for white spruce recruitment. The greater topographic complexity of the PENINSULA site may explain the high and low density phases of regenerating white spruce, as elevation was significantly negatively correlated with white spruce abundance. Organic matter depth, pH and conductivity were very similar between sites. Mean organic matter depth was 4.19 cm on the MAINLAND site and 4.01 cm on the PENINSULA site. Mean pH was slightly higher on the MAINLAND site (6.7 vs. 6.43) and mean conductivity was slightly higher on the PENINSULA site (60.92 vs. 59.58  $\mu\text{S}/\text{cm}$ ).

The abiotic PCA results are very similar between sites (Fig. 5.4). Negative values represent dry, sandy plots that are slightly higher in elevation with steeper slopes. Positive values represent plots with greater soil moisture, percent clay content and conductivity. Thus the PCA axis represents a complex moisture-nutrient status gradient.

The first PCA axis of the MAINLAND site accounts for 23.85% of the variation in abiotic variables, while that of the PENINSULA site accounts for 28.28% of the variation.

#### **5.1.4 White Spruce in the Study Sites**

The two sites studied were within approximately 260 m of each other, were burned by the same fire, were both close to the lakeshore, and thus shared many similarities. However, there were also some important differences between the two sites, which resulted in different patterns of white spruce recruitment. The density of regenerating white spruce was much higher on the PENINSULA site (6205/ha) than on the MAINLAND site (990/ha), presumably as a result of greater white spruce density in the old growth adjacent to the PENINSULA site. However, the proportion of live spruce was higher on the MAINLAND site (96%) than on the PENINSULA site (79%) (Table 5.6 a), suggesting that white spruce mortality was density dependent. In the field, the MAINLAND site appeared to be quite homogenous, with regenerating white spruce relatively evenly distributed. On the PENINSULA site there were obvious high and low density phases of regenerating white spruce. The tendency for dead spruce to occur in plots with higher densities of white spruce was also quite apparent at both sites suggesting a relatively high degree of intraspecific competition.

When broken down into cohorts it became apparent that the first cohort to become established (ages 25-39) was slightly larger on the PENINSULA site, while on the MAINLAND site white spruce tended to belong to later establishing cohorts (Table 5.6 a). Thus the PENINSULA site appears to have had faster recruitment rates than the



MAINLAND site, which is likely attributable to the closer and denser seed source on the peninsula. Conversely, the greater abundance of white spruce in the later cohorts on the MAINLAND site versus the PENINSULA site suggests that the greater distance from seed source on the mainland slowed recruitment rates. Mean age and size of white spruce were also slightly higher on the PENINSULA site (Table 5.6 b and c), partly as a result of faster recruitment rates.

## **5.2 Age Distributions of White Spruce**

Although total recruitment was higher on the PENINSULA site, the two sites showed similar patterns of recruitment in that the majority of white spruce established between 5 and 15 years post-fire. Thus 25 to 35 year old white spruce show the highest abundance (Figs. 5.5 and 5.6). However, recruitment was higher on the PENINSULA site during this initial period of recruitment, (CV (coefficient of variation) = 37.35%), while on the MAINLAND site recruitment was more continuous (CV = 48.05%). On the MAINLAND site 53% of white spruce recruited within the first 14 years following the fire, 35% established during the intermediate years and 12% germinated within the last 4 years (Table (5.6 a)). On the PENINSULA site 64% of white spruce recruited within the first 14 years following the fire, 21% established during the intermediate years and 8% germinated within the last 4 years (Table (5.6 a)).

In the absence of the seedlings the CV on the PENINSULA site was 27.41% while the MAINLAND CV was 35.97%, once again indicating that recruitment was more continuous on the MAINLAND site. The cumulative frequency distributions show that, overall, recruitment was more rapid on the PENINSULA site than the MAINLAND site

(Fig. 5.7). This difference in the rate of recruitment is likely a result of the closer and denser seed source on the PENINSULA site. It is also possible that moister seedbeds with less leaf litter provided better conditions for white spruce establishment on the PENINSULA site. In addition, competition from shrubs was almost non-existent on the PENINSULA site.

Both sites had a large cohort of four year old seedlings, possibly resulting from a recent mast year. The majority of these seedlings were observed in moist areas, on the shadier south side of wetlands and on moss covered decaying logs. The seedlings occurring under aspen canopies were at risk of being smothered by leaf litter before overtopping the lower vegetation, being outcompeted by surrounding vegetation, or dessicating, on the drier hill top sites. Seedlings occurring on the shaded south sides of wetlands were more likely to survive as there was very little surrounding vegetation at these sites to compete for light or to contribute to smothering by leaf litter. These moister areas also protect seedlings from dessication. The proliferation of older, taller spruce beside wetlands provides evidence for such a conclusion. Thus the seedlings are likely to contribute to recruitment only at certain select microsites.

## **5.3 White Spruce Establishment**

### **5.3.1 Spatial Autocorrelation**

All variables that were assessed for spatial autocorrelation on the MAINLAND site were significantly, and positively, spatially autocorrelated (Table 5.7). Negative numbers are interpreted as positively autocorrelated because the inverse of Euclidean distance was used. On the PENINSULA site, only the abiotic PCA axis and white spruce

abundance of cohort 2 were significantly spatially autocorrelated (Table 5.7). The biotic variables on the PENINSULA site were not significantly autocorrelated. In general, the degree of spatial autocorrelation of the data was quite low, as Mantel's statistic ranges from  $-1$  to  $+1$ . Cohort 2 on the MAINLAND site had the highest  $r_m$  ( $-0.11296$ ). The absence of spatial autocorrelation for the biotic PCA axis of the PENINSULA site is not surprising. There is little variation in the biotic component, as birch and shrubs are only present in trace amounts. For cohort 1 on the PENINSULA site, spatial autocorrelation is not significant because distance to seed source did not play a large role in the recruitment of cohort 1, as evidenced by the prolific recruitment of white spruce early on throughout the PENINSULA site.

### **5.3.2 Correlations Between Variables After Removing Spatial Effects**

On the MAINLAND site the partial Mantel statistic was significant for positive correlations between the variation in white spruce abundance of cohort 1 and the variation in both the biotic and abiotic PCA axes (Table 5.8). The variation in cohort 2 was also positively correlated with the variation in the biotic and abiotic PCA axes, although the biotic PCA axis was not quite statistically significant ( $p = 0.072$ ). The variation in cohort 2 and the abiotic variation were the most highly correlated on the MAINLAND site, although the correlation was quite low ( $r_m = 0.133$ ). These results show that regardless of spatial effects, such as distance to seed source, the variation in spruce abundance of both cohorts on the MAINLAND site tended to be correlated with the variation in both the biotic and abiotic factors.

The variation in white spruce abundance of cohort 1, on the PENINSULA site, showed a tendency towards a positive correlation with the biotic variation between plots, although not quite significant ( $p = 0.074$ ) (Table 5.8). The variation in the abiotic PCA axis was not correlated with the variation in cohort 1. The variation in cohort 2 abundance was correlated with both the biotic and abiotic PCA axes. The variation in cohort 2 abundance and the variation in the biotic PCA axis had the highest significant positive correlation ( $r_m = 0.181$ ). The variation in abundance of cohort 2 and the abiotic variation were less closely associated ( $p = 0.054$ ). Thus, regardless of plot positions within the PENINSULA site, the variation in abundance of white spruce in cohort 1 appears to be affected only by the variation in the biotic variables. Similarly, the variation in the abundance of cohort 2 was more related to the variation in the biotic variables than to abiotic variation.

When the same variables used in the partial Mantel tests were used in simple Mantel tests that do not include a geographic location matrix, similar results were obtained (results not presented). The same variables showed positive significant correlations. Thus spatial effects did not have strong influences on the correlations between the variations in spruce abundance and the environmental variables.

### **5.3.3 Factors Affecting Establishment**

The summary table of the multiple regressions indicates that the abundance of MAINLAND cohorts 1 and 2 were both affected by the biotic variables, whereas only cohort 2 was affected by distance to seed source (Table 5.9). Cohort 1 on the PENINSULA site could not be predicted, to any significant degree, by any of the

variables, while cohort 2 was affected by both the abiotic variables and distance to seed source. These general trends are supported by the partial Mantel results. However, the regressions consider all variables together and thus clarify which variables are best able to predict white spruce recruitment.

The summary table of the partial regression results (Table 5.10) shows the proportion of variation in white spruce abundance accounted for by each set of variables; spatial versus environment (biotic and abiotic), after the effects of the other have been removed. For cohort 1, on the MAINLAND site, the environmental variables were most important in predicting white spruce abundance, accounting for 15% of the variation in abundance. For cohort 2 the spatial variables were most important, explaining 18% of the variation in abundance of white spruce, while the environmental variables accounted for 10.3% of the variation.

As with the multiple regressions, abundance of PENINSULA cohort 1 could not be predicted by any of the variables. The variation in cohort 2 abundance on the PENINSULA site was best predicted by spatial variables, while environmental variables accounted for 10.2% of the variation.

The multiple and partial regression results suggest that distance to seed source was most important for cohort 2 and was more important on the MAINLAND site than the PENINSULA site. Biotic effects were more important on the MAINLAND site, while abiotic effects were more important on the PENINSULA site. However, none of the variables were important in predicting white spruce abundance of cohort 1 on the PENINSULA site. Overall, the abundance of white spruce in cohort 2 on the MAINLAND site was best predicted by the variables measured ( $R^2 = 39.4\%$ ).

### MAINLAND cohort 1

The multiple regression of white spruce abundance in cohort 1 on the MAINLAND site, indicates that 24.5% of the variation in abundance was accounted for by all four factors (biotic PCA axis, abiotic PCA axis, x coordinates (location between transects A and H) and y coordinates (distance from old growth)) (Table 5.11 a). When spatial effects were removed, the partial regression results for cohort 1 indicate that 16.7% of the variation in abundance was accounted for by the biotic and the abiotic, although only the biotic was a significant predictor (Table 5.11 b). In the partial regression of the spatial variables, after accounting for the biotic and abiotic, neither x nor y coordinates were significant (Table 5.11 c). Thus the abundance of cohort 1 on the MAINLAND site was primarily affected by the biotic. The negative partial regression coefficient of the biotic PCA axis (-0.097) indicates that white spruce abundance in cohort 1 increased with decreasing values of the biotic PCA axis, or with increasing aspen, poplar and shrub cover and increasing birch and moss.

### MAINLAND cohort 2

For cohort 2 on the MAINLAND site, the total variation in abundance that was accounted for by all four factors was 39.4% (Table 5.12 a), slightly more than for cohort 1. The partial regression results show that the biotic and abiotic accounted for 14.5% of the variation in white spruce abundance, after accounting for space (Table 5.12 b). Only the biotic was a significant predictor of abundance, although the abiotic was approaching significance ( $p = 0.0801$ ). The spatial variables accounted for 23.3% of the variation in abundance, after accounting for environmental effects, although only the distance from

old growth was a significant predictor (Table 5.12 c). Thus white spruce abundance in cohort 2, on the MAINLAND site, increases as aspen, poplar and shrub cover decreases or birch increases and distance to the old growth seed source decreases.

#### PENINSULA cohort 1

White spruce abundance of cohort 1 on the PENINSULA site was not predicted to any significant degree by any of the four variables (Table 5.13). The  $R^2$  of the multiple regression was only 2.6%.

#### PENINSULA cohort 2

For cohort 2, on the PENINSULA site, 25.5% of the variation in abundance was accounted for by all four factors (Table 5.14 a). The partial regression results show that 12.1% of the variation in the abundance of cohort 2 was accounted for by the biotic and abiotic, after accounting for spatial effects, with only the abiotic being significant (Table 5.14 b). The variation accounted for by the spatial variables, after accounting for the biotic and abiotic, was 15.2%, with only distance from old growth being significant (Table 5.14 c). The positive partial regression coefficient of the abiotic PCA axis (0.063) indicates that white spruce abundance of cohort 2, on the PENINSULA site increases with increasing moisture and nutrients. As with cohort 2 on the MAINLAND site, cohort 2 abundance on the PENINSULA site increases at shorter distances to the seed source.

### 5.3.4 Interpretation of Results

The effects of the biotic, abiotic and distance to seed source on each cohort, including cohort 3 (seedlings), are depicted in Figures 5.8 through 5.13. These figures illustrate the main trends given by the Mantel and Regression results.

#### Distance to Seed source

It is apparent that distance from seed source has a greater effect on later cohorts (Figs. 5.8 and 5.11) on both sites and less of an overall effect on the PENINSULA site (Fig. 5.11). The absence of a significant distance effect immediately post-fire (Tables 5.11 and 5.13) suggests that fire severity may have been low and a sufficient amount of unburned seed source trees may have been present within the study sites to reseed these areas. The lower effect of distance on the PENINSULA versus the MAINLAND may be attributable to the denser and closer seed source on the PENINSULA. The mainland would have had less seeds to start with and further distances to travel, thus limiting it more by dispersal distance.

#### Environmental effects – Biotic

White spruce abundance increases with increasing birch and moss cover and decreasing aspen, poplar and shrubs for all cohorts on the MAINLAND site (Fig. 5.9). The biotic variables do not predict white spruce abundance on the PENINSULA site (Tables 5.13 and 5.14). The ability of the biotic to predict white spruce abundance on the MAINLAND site (Table 5.11 and 5.12) could be a result of the influence of shrub and birch cover on white spruce establishment. Shrubs and birch were indicators on the



MAINLAND site, whereas very few shrubs or birch were present on the PENINSULA site.

#### Environmental effects - Abiotic

White spruce abundance tended to increase with increasing moisture and nutrients for cohorts 2 and 3 on both sites (Figs. 5.10 and 5.13), although the abiotic variables are only capable of predicting white spruce abundance of cohort 2 on the PENINSULA site (Table 5.14). This trend is not apparent for cohort 1 on either site, suggesting that the establishment of white spruce immediately post-fire was not limited by moisture availability. The greater ability of the abiotic to predict white spruce abundance in cohort 2 on the PENINSULA site is most likely a result of the high degree of abiotic variability between plots caused by the complex topography of this site.

### **5.4 Age – Size Relationships of White Spruce**

#### **5.4.1 Regressions of Height and DBH by Age**

There was a great deal of variability in white spruce height and DBH for trees of similar ages (Figs. 5.14 and 5.15). Thus something other than age, such as environmental factors, was having a strong effect on the size of white spruce at these sites. A log-log linear curve fit the data for the relationships between height and DBH by age. Thus much more variation in height and DBH was apparent, as trees grew larger and older. The regression of DBH against age had a lower  $R^2$  (83 % for both sites) than the regression of height against age (MAINLAND = 87% and PENINSULA = 89%) for both sites. Thus environmental effects may have had more of an influence on DBH than on height.

The regression of DBH by height for the PENINSULA site (Fig. 5.16 b) has a lower  $R^2$  (88%) than for the MAINLAND site (92%, Fig. 5.16 a). Therefore white spruce on the PENINSULA site had a more variable growth form than on the MAINLAND site. The slope is also greater for the PENINSULA site, suggesting a taller, thinner growth form.

When broken down into cohorts it became more apparent that height variation was much greater for older trees (cohort 1) than for younger trees (cohort 2) at both sites (Fig. 5.17 and 5.18). Variability in height increases as trees grow older as a result of the divergence of individual trees towards either a suppressed state or a “free to grow state” depending, in part, on environmental conditions. The lower  $R^2$  values for the MAINLAND versus the PENINSULA for both cohorts suggest that white spruce heights on the MAINLAND site were more variable and thus more affected by environmental conditions, particularly shrub cover, than on the PENINSULA site.

#### **5.4.2 Height Distributions**

The coefficient of variation was highest for the MAINLAND height distribution (MAINLAND = 251% vs. PENINSULA = 181%, Fig. 5.19), further evidence for more variable growth, possibly resulting from higher shrub cover. White spruce heights averaged between 2 and 3 metres. All were less than 12 metres tall, well below the aspen canopy, which averaged 15 m. When depicted as the cumulative proportion of trees by height (Fig. 5.20) it becomes apparent that the MAINLAND site has a greater proportion of shorter trees than the PENINSULA site. This was to be expected, as white spruce recruitment rates were slower on the MAINLAND site. Competition from *Corylus*

*cornuta* on the MAINLAND site also may have reduced overall white spruce growth, whereas shrubs are very rare on the PENINSULA site.

The height distributions for cohort 1 on both sites had higher coefficients of variation (MAINLAND = 1.42, PENINSULA = 1.06) compared to cohort 2 (MAINLAND = 1.23, PENINSULA = 0.57) (Figs. 5.21 and 5.22). These results support the regressions by confirming a greater variability in height for older trees (cohort 1). The increase in height variability for cohort 1 is more pronounced on the PENINSULA site. It is possible that shrub cover may have been higher on the PENINSULA site when cohort 1 was establishing.

## 5.5 Growth of White Spruce

### 5.5.1 Early Growth

On average, established white spruce individuals that were aged at the base and at 1.25 metres (at least 1.5 metres tall) took 12 to 13 years to grow to 1.25 m at both sites (Fig. 5.23). Over 97% reached 1.25 m in 20 years or less. Figure 5.24 shows that the number of years it took each tree to grow to breast height is significantly positively related to total tree height. Thus individuals that are able to rapidly overtop surrounding vegetation have a better chance of reaching the overstory canopy.

The early growth, from ground level to 1.25 m, was quite variable, especially on the PENINSULA site (MAINLAND CV = 97%,  $R^2 = 31.2\%$  and PENINSULA CV = 86%,  $R^2 = 20.5\%$ ). This may be a reflection of an etiolation response of white spruce on the PENINSULA site. Because intraspecific competition between white spruce was more of a factor on this site, individuals in denser plots may have increased height growth in an

attempt to reach adequate light levels for continued growth. This is in agreement with the earlier results showing white spruce growth forms on the peninsula site to be more variable, taller, and thinner.

When early growth, height and DBH against age residuals were regressed against the environmental variables, no strong trends were apparent. This suggests that growing conditions at these sites vary substantially over time. Thus data collection from one year was not sufficient to represent average growing conditions that each tree had been subject to.

### 5.5.2 Suppression

The growth model derived from the regression of height against age of all trees is shown in Fig. 5.25. The equation used to derive this growth model is  $\log(\text{height (cm)}) = 1.609 \log(\text{age (years)})$ . The mean heights of the empirical data are shown as circles (Fig. 5.25). Growth at age 1 is made to equal a height of 1 cm. Age at breast height (1.25 m) equals approximately 20 years of age in the growth model, which is confirmed by the empirical data for age at breast height (Fig. 5.23) and by Eis (1967). Furthermore, the mean heights of trees  $> 1.5$  m in height tend to be above the modelled heights. Thus this growth model is rather conservative and therefore we can be confident that any trees occurring below the modelled regression line are almost certainly suppressed.

As white spruce age increases the proportion of unsuppressed trees increases (Figs. 5.26). Thus trees that established soon after the fire have experienced better growing conditions. As time since fire increases, competition from shrubs and other trees increases and seedbed conditions may become less favourable. Therefore, white spruce

establishing later (cohort 2) had less chance of overtopping the understory and sub-canopy, while cohort 1 was able to establish more successfully before tall shrubs and other spruce became well established. It is also possible that suppressed trees in cohort one have died and fallen over, leaving no trace.

The trend for later recruiting white spruce to be more suppressed than older white spruce is stronger on the MAINLAND site. This could be a result of increasing competition with increasing shrub cover.

## **5.6 Mortality**

On both sites, the majority of deaths for standing dead white spruce occurred between the ages of approximately 10 to 30 years (Figs 5.27). However, time since fire is unknown, as time of death was not ascertained. High mortality between the ages of 10 to 30 years indicates that these trees were already well established suggesting competition for light may have been the cause of death. Mortality is much higher on the PENINSULA site (253 vs. 29), which also had a greater component of regenerating white spruce.

Mortality on both sites (expressed as percent dead) was much higher in plots with greater spruce densities (Fig. 5.28). Plots with less than 12 trees, per 10 x 10 m, had less than 5% mortality, while plots with greater than 80 trees had close to 30% mortality. These results suggest that resources became more limiting as white spruce grew and began to interfere with one another. Thus intraspecific competition for limiting resources, such as light, would have become more of an issue as white spruce developed larger canopies. The greater densities of white spruce on the PENINSULA site and the greater mortality on the PENINSULA site support such a conclusion. It is important to note that

mortality of seedlings went undetected, as rapid decay of seedlings would have obliterated such evidence. Additionally, fallen dead trees that had begun to decay were not considered, thus mortality may have been underestimated in dense plots.

Table 5.1. Density, basal area and mean % cover of trees in the oldgrowth forest adjacent to the study sites.

	Mainland			Peninsula		
	Density (trees/ha)	Basal area (m <sup>2</sup> /ha)	Mean cover (%)	Density (trees/ha)	Basal area (m <sup>2</sup> /ha)	Mean cover (%)
White spruce	95	12.17	10-60	372.5	36.55	85
Trembling aspen	212.5	18.23	4-80	41.3	3.31	10
White birch	12.5	1.04	trace	22.1	1.51	5
Balsam poplar	1.5	0.11	trace	4.7	0.38	1

Table 5.2 Common vegetation in the old growth forests adjacent to the study sites.

Mainland	Peninsula
<i>Corylus cornuta</i>	<i>Hylocomium splendens</i>
<i>Rosa acicularis</i>	<i>Mertensia paniculata</i>
<i>Aralia nudicaulis</i>	<i>Aralia nudicaulis</i>
<i>Fragaria virginiana</i>	<i>Rubus pubescens</i>
<i>Pyrola</i> sp.	<i>Mitella nuda</i>
<i>Mertensia paniculata</i>	<i>Cornus canadensis</i>
<i>Cornus canadensis</i>	<i>Galium triflorum</i>
<i>Rubus pubescens</i>	<i>Lathyrus</i> sp.
<i>Linnaea borealis</i>	<i>Linnaea borealis</i>

Table 5.3 a). Comparison of tree densities on the MAINLAND and PENINSULA study sites.

	Mainland		Peninsula	
	Density (trees/ha)	Basal area (m <sup>2</sup> /ha)	Density (trees/ha)	Basal area (m <sup>2</sup> /ha)
Aspen (live)	3019	2623.2	3080	2413.75
Aspen (dead)	1595	307	1605	236.58
Percent live aspen	65%	89.50%	66%	91.08%
Birch (live)	875	267.64	370	126.8
Birch (dead)	100	10.44	30	1
Percent live birch	90%	96.25%	93%	99.22%

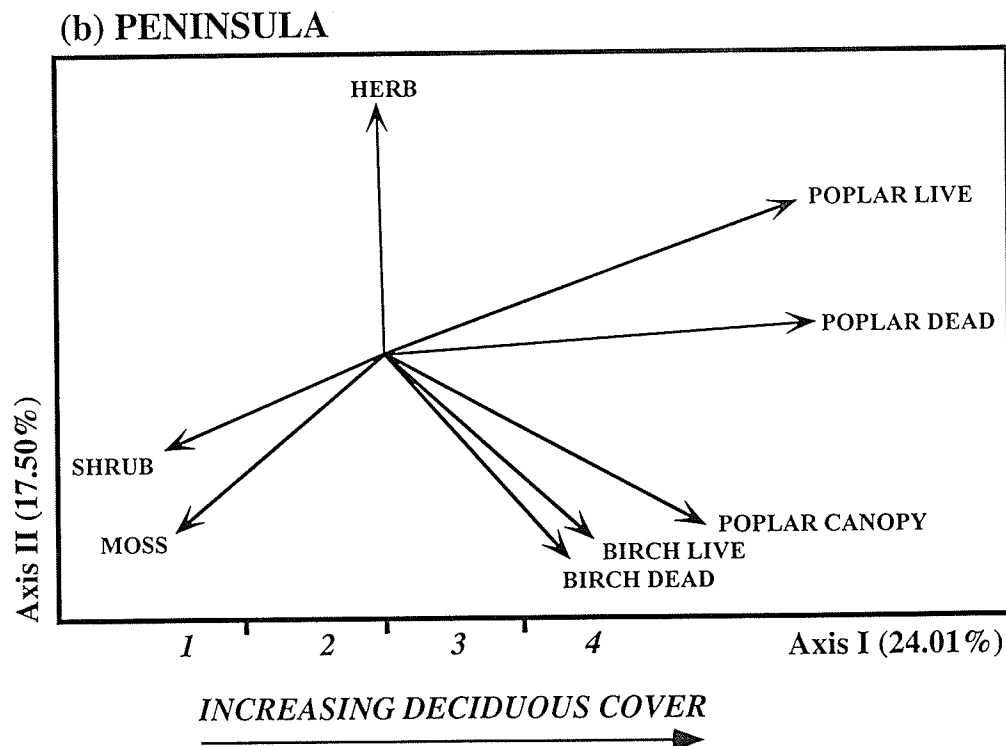
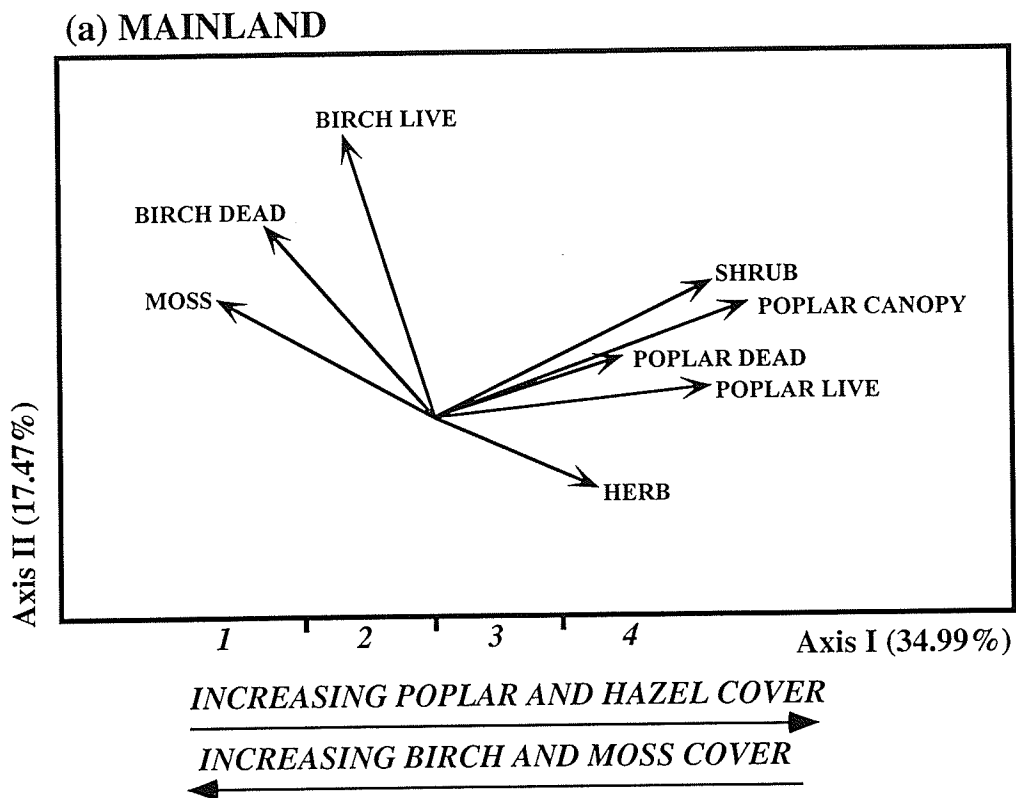
Table 5.3 b). Comparison of canopy and seedbed cover on the the MAINLAND and PENINSULA study sites.

	Mainland		Peninsula	
	Mean %cover	Standard error	Mean %cover	Standard error
Spruce canopy	6.34	1.36	23.81	2.89
Upper deciduous canopy	53.65	3.07	37.02	2.28
Shrub canopy	27.83	2.40	0.52	0.21
Herb canopy	44.61	1.80	40.57	2.48
Broadleaf litter	89.17	1.01	42.19	4.86
Decayed wood	8.66	0.79	9.60	1.15
Undecayed wood	1.65	0.31	3.45	0.68
Moss	5.43	0.64	10.21	1.56



Table 5.4 Dominant low shrub, herb and moss species on the MAINLAND and PENINSULA study sites (in descending order of percent cover).

Mainland	Peninsula
<i>Aralia nudicaulis</i>	<i>Aralia nudicaulis</i>
<i>Mertensia paniculata</i>	<i>Mertensia paniculata</i>
<i>Rubus pubescens</i>	<i>Rubus pubescens</i>
<i>Rosa acicularis</i>	<i>Pleurozium</i>
<i>Fragaria virginiana</i>	<i>Cornus canadensis</i>
<i>Viola canadensis</i>	<i>Symphoricarpos albus</i>
<i>Brachythecium</i>	<i>Brachythecium</i>
<i>Symphoricarpos albus</i>	<i>Fragaria virginiana</i>
<i>Ribes oxycanthoides</i>	<i>Viola canadensis</i>
<i>Pleurozium</i>	<i>Ribes triste</i>
<i>Cornus canadensis</i>	<i>Carex utriculata</i>
<i>Ribes triste</i>	<i>Equisetum arvense</i>
<i>Maianthemum canadense</i>	<i>Oryzopsis asperifolia</i>
<i>Mnium</i>	<i>Aster ciliolatus</i>
<i>Oryzopsis asperifolia</i>	<i>Linnaea borealis</i>
<i>Aster ciliolatus</i>	<i>Aulacomnium</i>
<i>Bromus ciliatus</i>	<i>Rosa acicularis</i>
<i>Apocynum androsaemifolium</i>	<i>Petasites palmatus</i>
<i>Galium boreal</i>	<i>Halicomium</i>
<i>Lathyrus ochroleucus</i>	<i>Mnium</i>



**Figure 5.1.** Principal component analysis results (axis I vs. II) for biotic data, (a) MAINLAND site and (b) PENINSULA site. Italicized values (1-4) on axis I signify divisions of the ordination used in Figures 5.9 and 5.12.

Table 5.5 Comparison of abiotic variables on the MAINLAND and PENINSULA study sites.

	Mainland		Peninsula	
	Mean	Standard error	Mean	Standard error
Elevation (m)	678.93	0.55	675.24	0.19
Slope (%)	13.33	0.82	6.86	0.52
Soil moisture (%)	9.38	0.33	10.50	0.45
Sand (%)	64.28	1.05	57.91	1.38
Silt (%)	18.07	0.63	20.59	0.72
Clay (%)	17.65	0.78	21.50	1.02
Organic matter depth (cm)	4.19	0.15	4.01	0.17
pH	6.70	0.05	6.43	0.07
Conductivity (uS/cm)	59.58	2.61	60.92	3.44

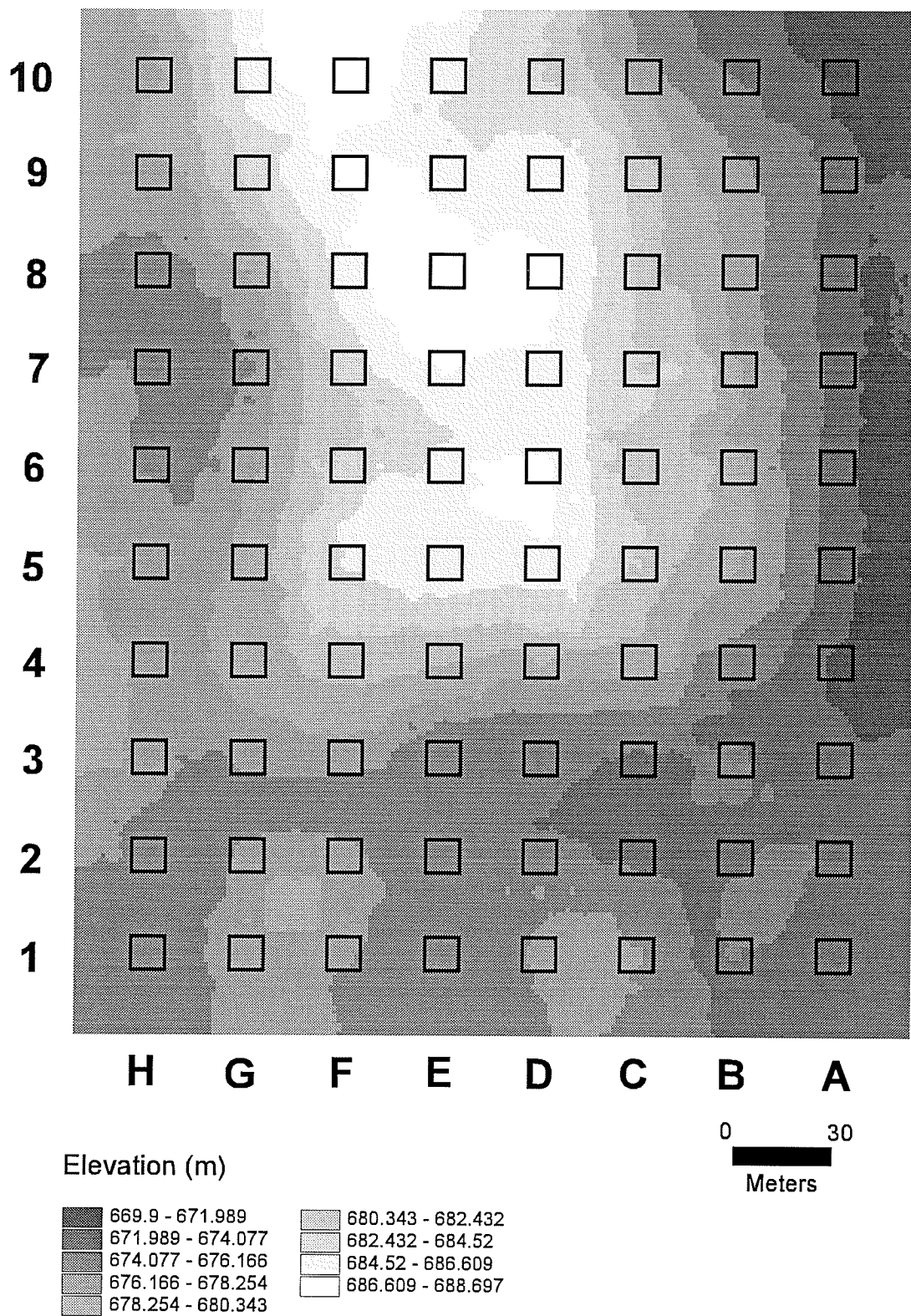


Figure 5.2 a) MAINLAND site digital elevation model

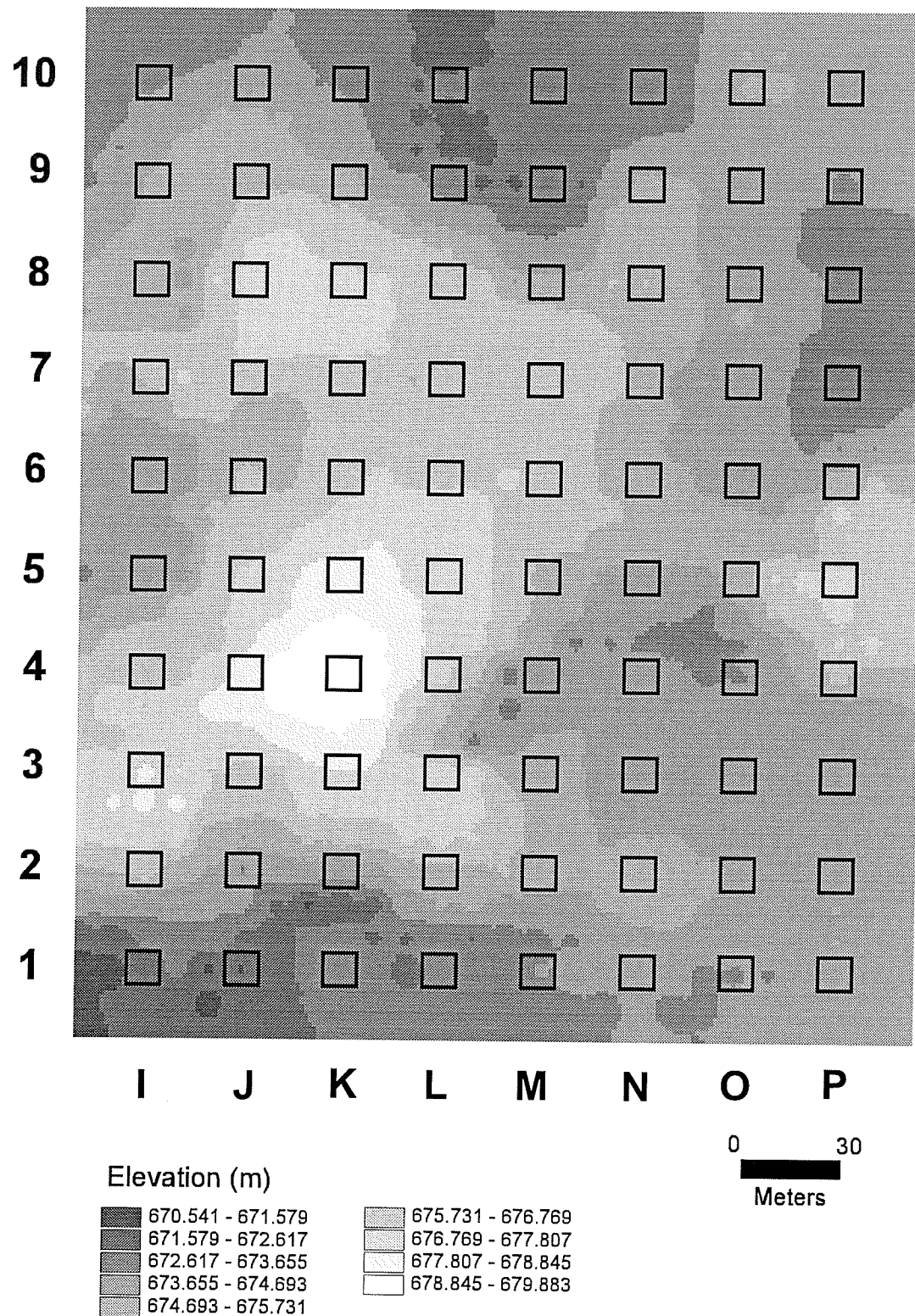
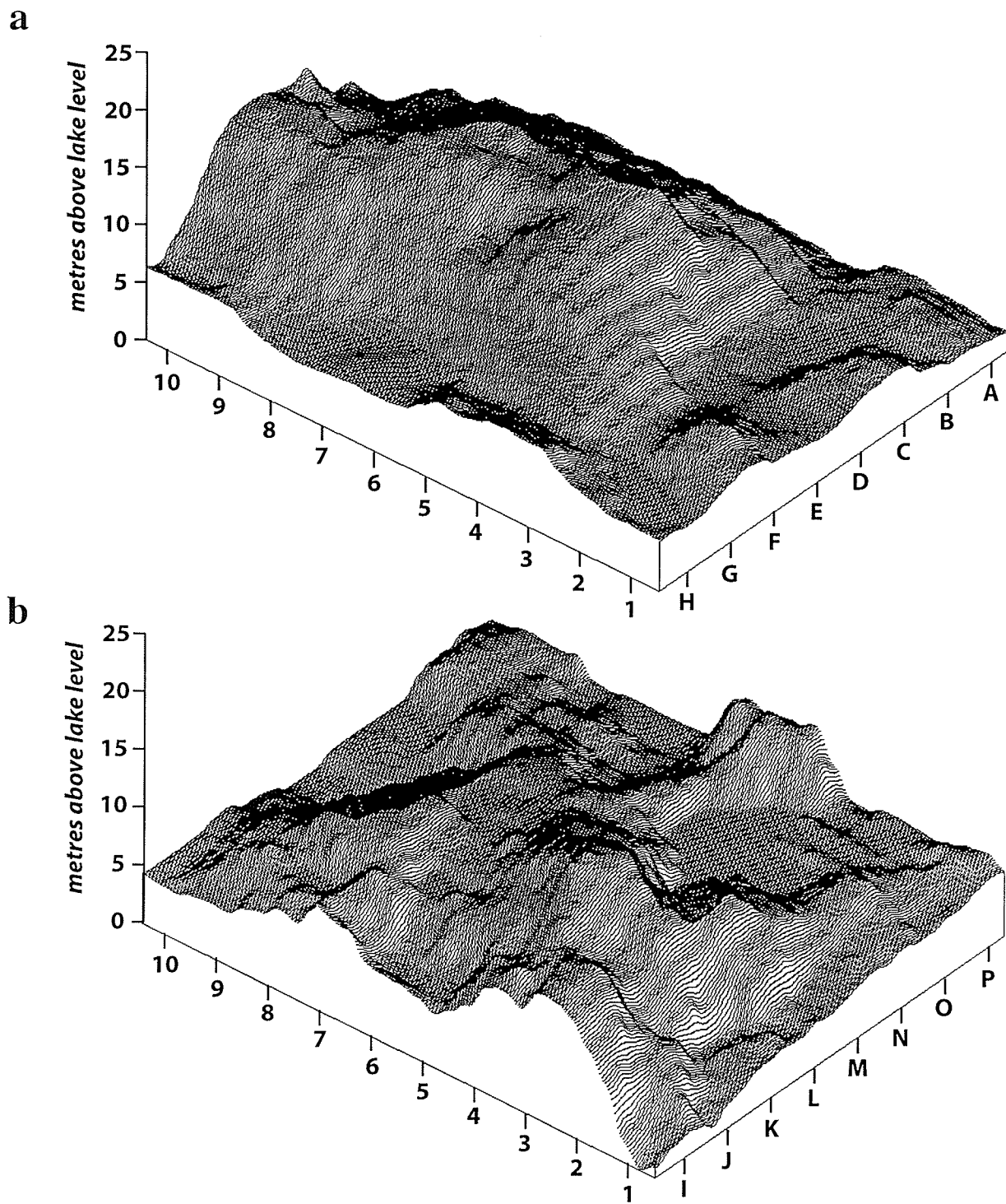
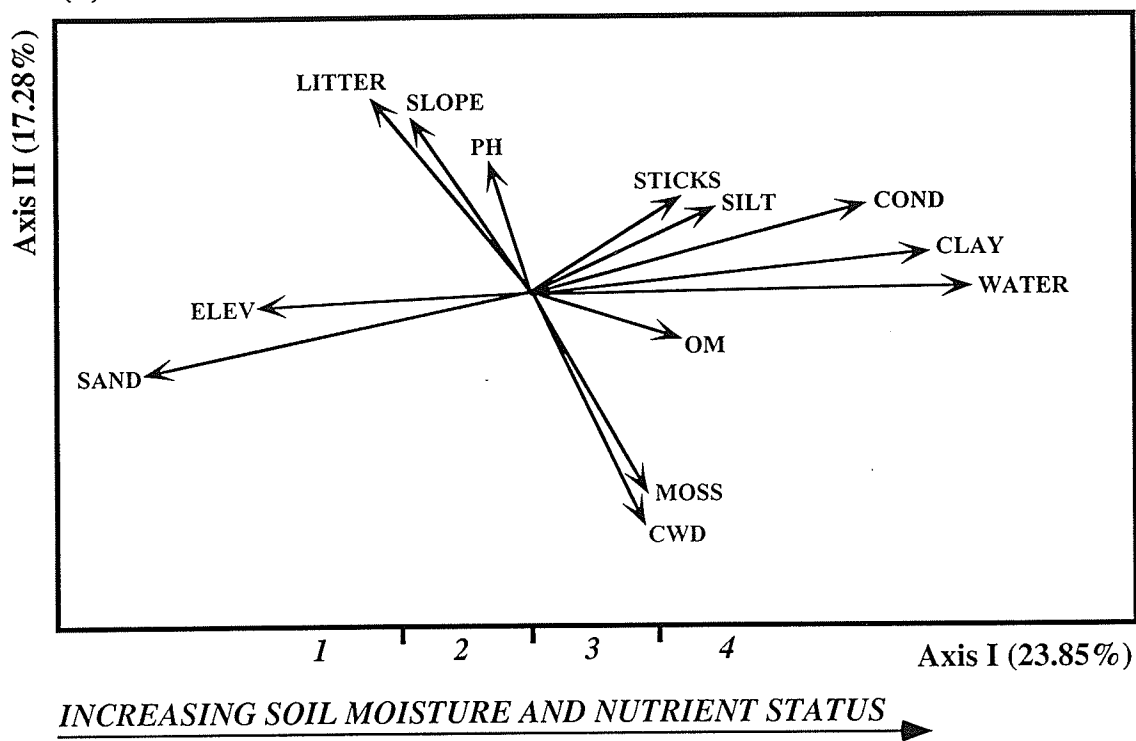


Figure 5.2 b) PENINSULA site digital elevation model

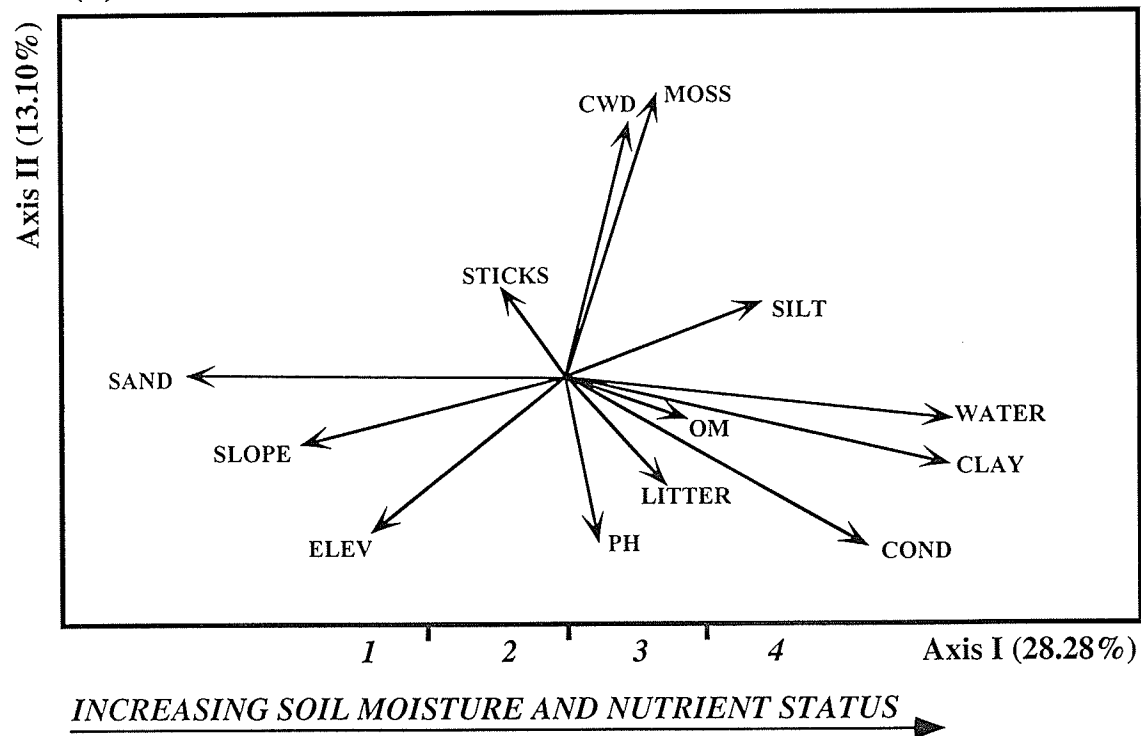


**Figure 5.3.** Surface digital elevation model profiles for the two study plots; a) MAINLAND; b) PENINSULA. Elevations are relative to the surface lake-level of Childs lake, which approximates the location of the ground watertable.

(a) MAINLAND



(b) PENINSULA



**Figure 5.4.** Principal component analysis results (axis I vs. II) for abiotic data: (a) MAINLAND site, (b) PENINSULA site. Italicized values (1-4) on axis I signify divisions of the ordination used in Figures 5.10 and 5.13.

Table 5.6 a). Comparison of white spruce densities and abundance on the MAINLAND and PENINSULA study sites.

	Mainland		Peninsula	
	trees/ha	#trees/10x10m plot	trees/ha	#trees/5x5m plot
Total white spruce	990	791	6205	1241
Live	954	763	4895	979
Dead	36	28	1310	262
Cohort 1 (ages 25-39)	508	407	3190	638
Cohort 2 (ages 5-24)	333	266	1320	264
Cohort 3 (ages 3&4)	113	90	385	77
% live spruce of total		96		79
Cohort 1 (% of live)		53		64
Cohort 2 (% of live)		35		21
Cohort 3 (% of live)		12		8

Table 5.6 b). White spruce demography data for the MAINLAND study site.

	Standard		Median	CV	Skewness	
	Mean	error			index	Kurtosis
Height (m)	2.13	0.083	1.25	1.08	1.34	1.46
DBH (cm)	3.09	0.123	2	1.1	1.55	2.4
Age (yrs)	22.01	0.383	26	0.49	-0.48	-1.22
Age at 1.25m (yrs)	17.85	0.28	17	0.3	-0.06	-0.64

Table 5.6 c). White spruce demography data for the PENINSULA study site.

	Standard		Median	CV	Skewness	
	Mean	error			index	Kurtosis
Height (m)	2.87	0.085	2.4	0.79	0.05	0.19
DBH (cm)	3.45	0.112	2.5	0.88	1.44	2.61
Age (yrs)	25.15	0.362	28	0.37	-1.03	-0.03
Age at 1.25m (yrs)	18.76	0.17	19	0.23	-0.22	-0.48



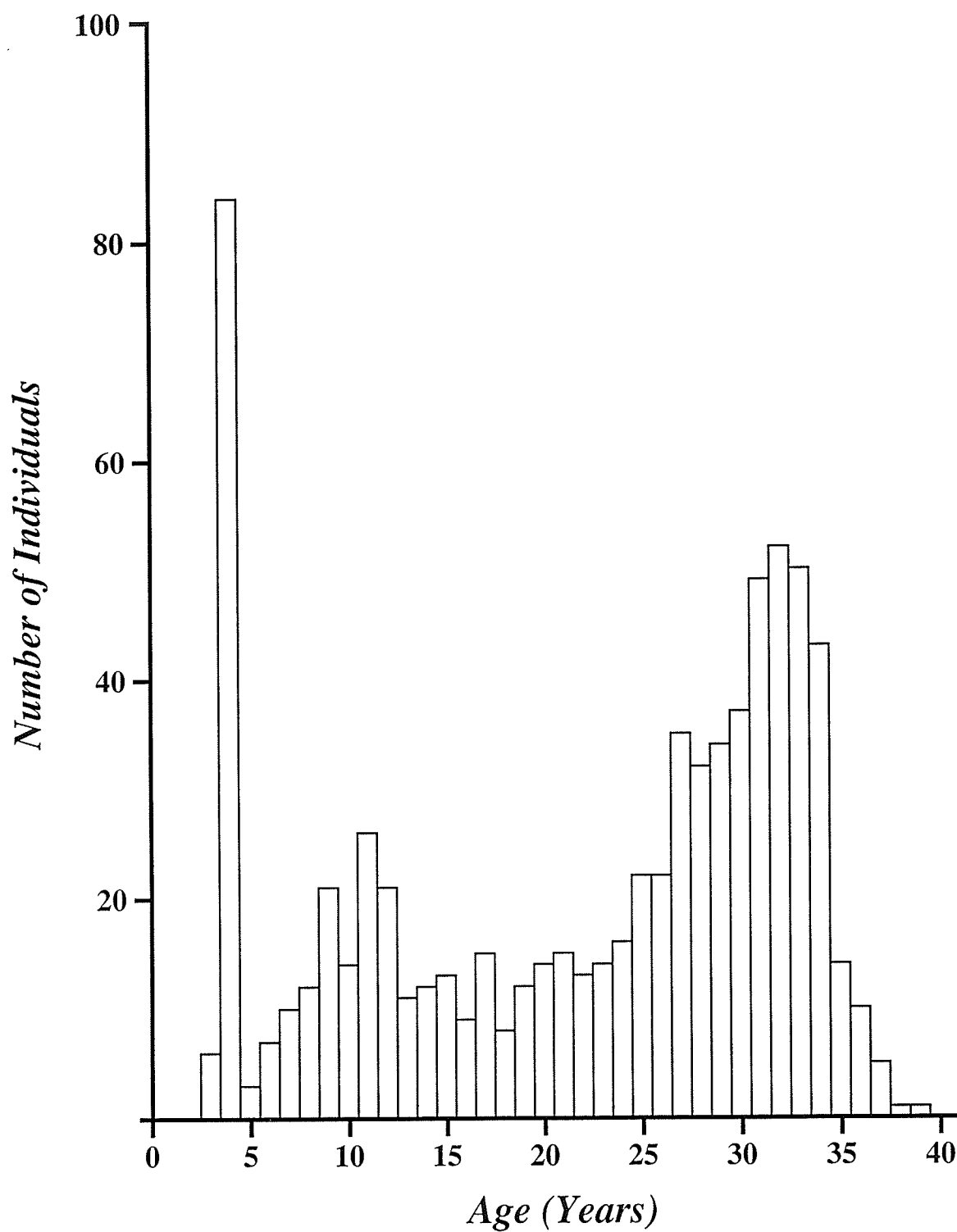


Figure 5.5 MAINLAND site. Age distribution of white spruce ( $n = 673$ ).

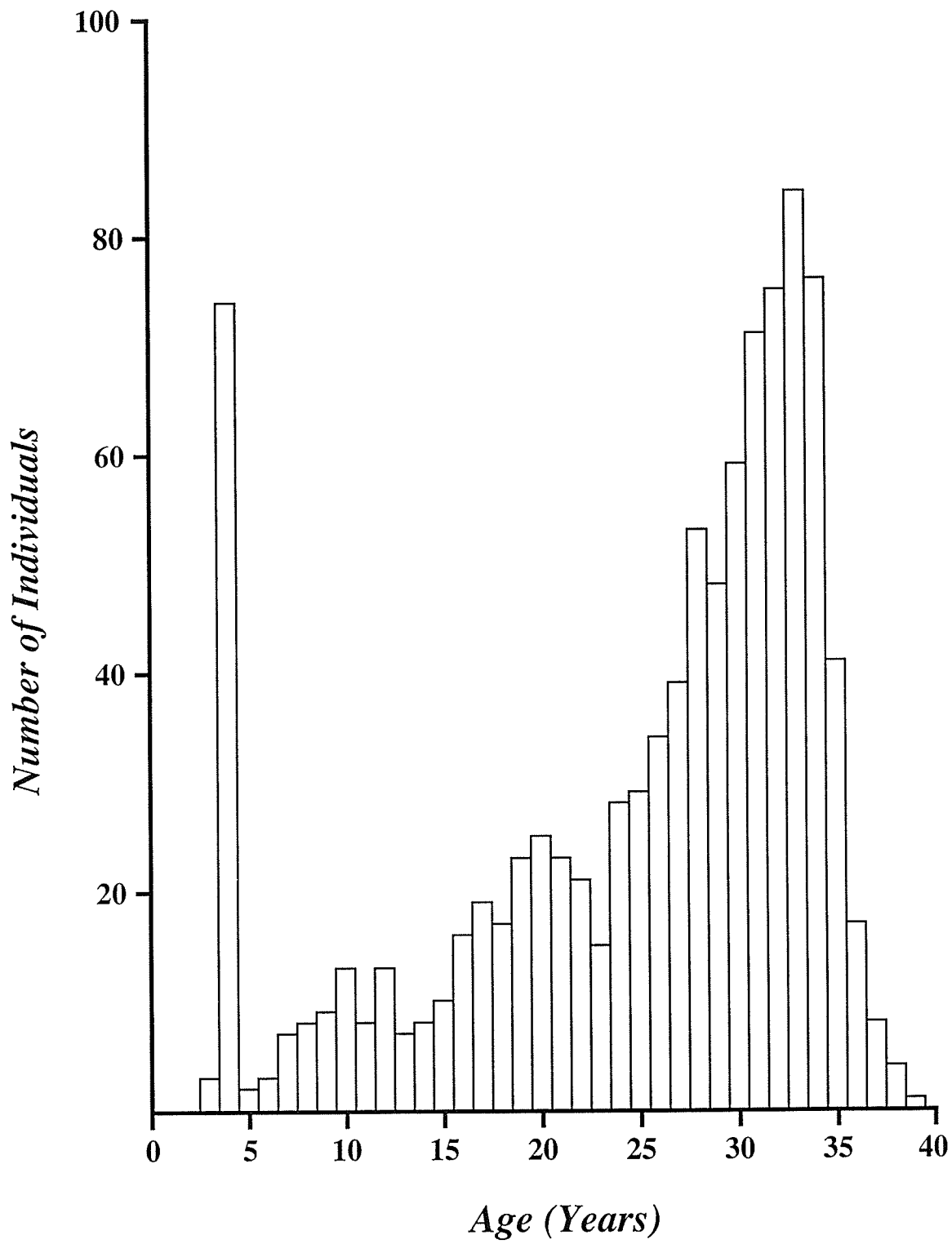


Figure 5.6 PENINSULA site. Age distribution of white spruce ( $n = 979$ ).

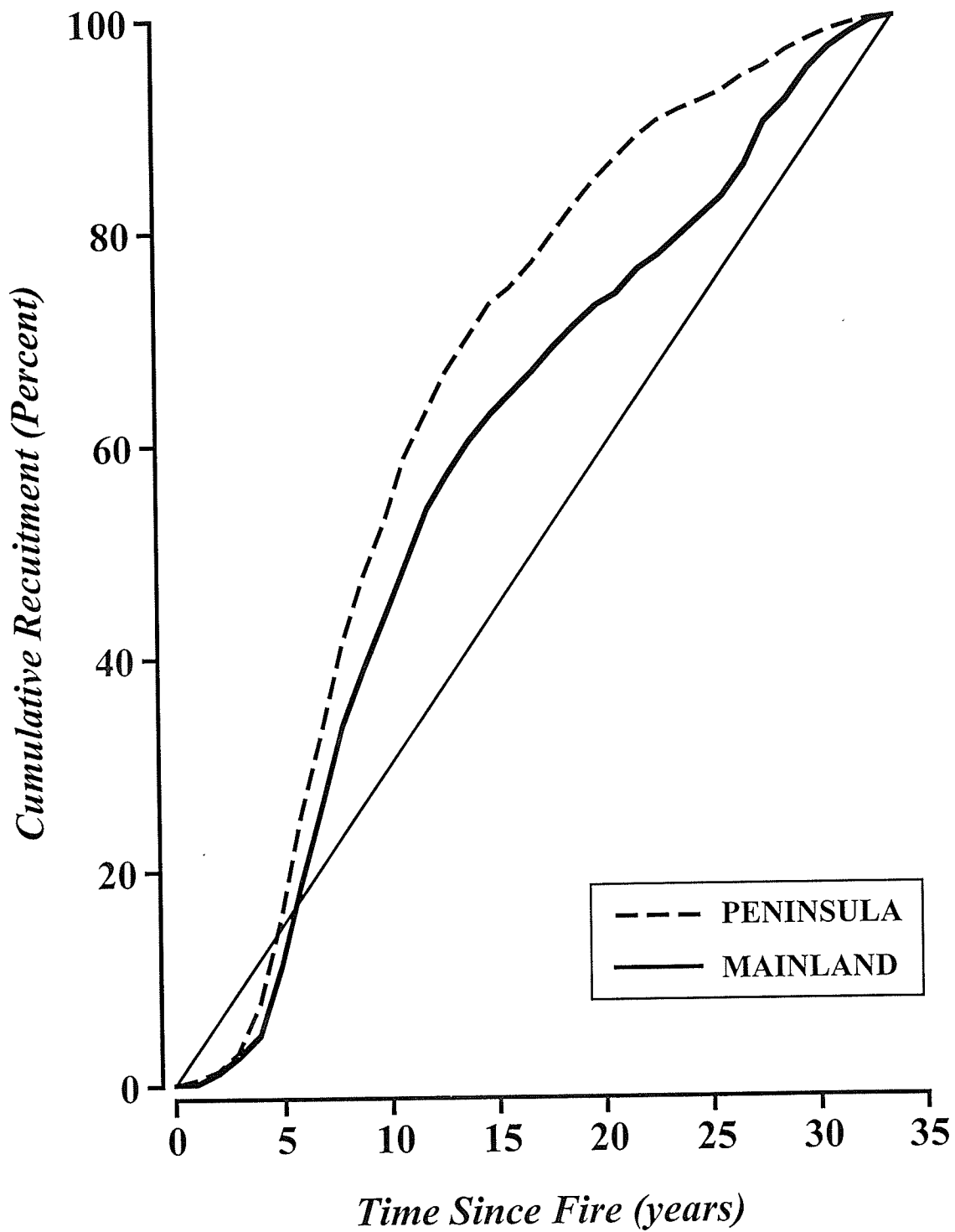


Figure 5.7. Cumulative age distributions (time since fire, years) for the MAINLAND and PENINSULA sites.

Table 5.7. Mantels statistics and associated p values for determination of spatial autocorrelation within variables on the MAINLAND and PENINSULA study sites (using inverse Euclidean distances).

	Mainland		Peninsula	
	r	p	r	p
BioticPCA axis 1	-0.052	0.028*	-0.036	0.120
Abiotic PCA axis 1	-0.111	0.001*	-0.073	0.007*
White spruce abundance of cohort 1	-0.102	0.002*	-0.042	0.071
White spruce abundance of cohort 2	-0.113	0.001*	-0.084	0.001*

Table 5.8. Partial Mantels statistics and associated p values for correlations between cohorts 1 and 2 and biotic and environmental PCA axis scores, after removal of spatial effects, on the MAINLAND and PENINSULA sites (using inverse Euclidean distances).

	Mainland		Peninsula	
	r	p	r	p
Cohort 1 x biotic	0.104	0.012*	0.111	0.074
Cohort 1 x abiotic	0.094	0.023*	0.004	0.465
Cohort 2 x biotic	0.092	0.072	0.181	0.017*
Cohort 2 x abiotic	0.133	0.019*	0.094	0.054
Environment x biotic	0.034	0.285	0.052	0.187

\*significant at  $\alpha = 0.05$

Table 5.9. Summary table of multiple regressions reporting regression coefficients.

	Mainland		Peninsula	
	Cohort 1	Cohort 2	Cohort 1	Cohort 2
Abiotic	0.022	0.041	-0.018	0.062*
Biotic	-0.097*	-0.062*	0.027	-0.007
x coordinates	-0.042	0.005	-0.007	-0.017
y coordinates	-0.026	-0.067*	-0.012	-0.045*

\* significant at  $\alpha = 0.05$

Table 5.10. Summary of partial regressions partitioning the variation in white spruce abundance accounted for by each set of variables.

	Mainland		Peninsula	
	Cohort 1	Cohort 2	Cohort 1	Cohort 2
Environmental	15%	10.3%	-	10.20%
Shared environmental & spatial	2%	10.7%	-	2%
Spatial	7.9%	18.4%	-	13.3%
Unexplained	75.1%	60.6%	97.4%	74.5%
R <sup>2</sup>	24.9%	39.4%	2.6%	25.5%

Table 5.11 a) Multiple regression results for the prediction of white spruce abundance in cohort 1 on the MAINLAND site.

white spruce abundance =

$$0.936 + 0.022(\text{environment}) - 0.097(\text{biotic}) - 0.042(\text{x coord. (A-H)}) - 0.026(\text{y coord. (dist. to old gr.)})$$

R<sup>2</sup> = 24.9%

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	3.529	4	0.882	5.88	<0.001
Error	10.658	71	0.15		

Table 5.11 b) Partial regression results for the prediction of white spruce abundance in cohort 1 on the MAINLAND site after removing spatial effects.

white spruce abundance residuals = 0.022(environment residuals) - 0.097(biotic residuals)

R<sup>2</sup> = 16.7%

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	2.135	2	1.067	7.31	<0.001
Error	10.658	73	0.146		

	t-ratio	Probability
Abiotic	0.78	0.438
Biotic	-3.6	< 0.001

Table 5.11 c) Partial regression results for the prediction of white spruce abundance in cohort 1 on the MAINLAND site after removing biotic and abiotic effects.

regression equation not significant

R<sup>2</sup> = 9.5%

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	1.118	2	0.559	3.83	0.056
Error	10.658	73	0.146		

Table 5.12 a) Multiple regression results for the prediction of white spruce abundance in MAINLAND 2 on the mainland site.

white spruce abundance =

$$0.743 + 0.041(\text{environment}) - 0.062(\text{biotic}) + 0.005(\text{x coord. (A-H)}) - 0.067(\text{y coord. (dist. to old gr.)})$$

$R^2 = 39.4\%$

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	4.783	4	1.196	11.5	<0.001
Error	7.366	71	0.104		

Table 5.12 b) Partial regression results for the prediction of white spruce abundance in cohort 2 on the MAINLAND site after removing spatial effects.

white spruce abundance residuals =  $0.041(\text{environment residuals}) - 0.062(\text{biotic residuals})$

$R^2 = 14.5\%$

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	1.247	2	0.623	6.18	0.006
Error	7.366	73	0.101		

	t-ratio	Probability
Abiotic	1.77	0.08
Biotic	-2.76	0.007

Table 5.12 c) Partial regression results for the prediction of white spruce abundance in cohort 2 on the MAINLAND site after removing biotic and abiotic effects.

white spruce abundance residuals =  $0.005(\text{x coord. (A-H)}) - 0.067(\text{y coord. (dist. to old gr.)})$

$R^2 = 23.3\%$

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	2.241	2	1.121	11.1	<0.001
Error	7.366	73	0.101		

	t-ratio	Probability
x coord. (A-H)	-4.7	0.755
y coord. (dist to old gr.)	0.314	< 0.001

Table 5.13 Multiple regression results for the prediction of white spruce abundance in cohort 1 on the PENINSULA site.

white spruce abundance =

$$0.900 - 0.018(\text{environment}) + 0.027(\text{biotic}) - 0.007(\text{x coord. (I-P)}) - 0.012(\text{y coord. (dist. to old gr.)})$$

R<sup>2</sup> = 2.6%

	Sum of	Degrees of	Mean		
	Squares	Freedom	Square	F-ratio	P
Regression	0.317	4	0.079	0.448	0.74
Error	12.03	68	0.177		



Table 5.14 a) Multiple regression results for the prediction of white spruce abundance in cohort 2 on the PENINSULA site.

white spruce abundance =

$$0.800 + 0.062(\text{environment}) - 0.007(\text{biotic}) - 0.017(x \text{ coord. (I-P)}) - 0.045(y \text{ coord. (dist. to old gr.)})$$

$R^2 = 25.5\%$

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	2.494	4	0.623	5.81	<0.001
Error	7.295	68	0.107		

Table 5.14 b) Partial regression results for the prediction of white spruce abundance in cohort 2 on the PENINSULA site after removing spatial effects.

white spruce abundance residuals =  $0.062(\text{environment residuals}) - 0.007(\text{biotic residuals})$

$R^2 = 12.1\%$

	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	1	2	0.5	4.8	0.02
Error	7.295	70	0.104		

	t-ratio	Probability
Abiotic	3.08	0.003
Biotic	0.235	0.815

Table 5.14 c) Partial regression results for the prediction of white spruce abundance in cohort 2 on the PENINSULA site after removing biotic and abiotic effects.

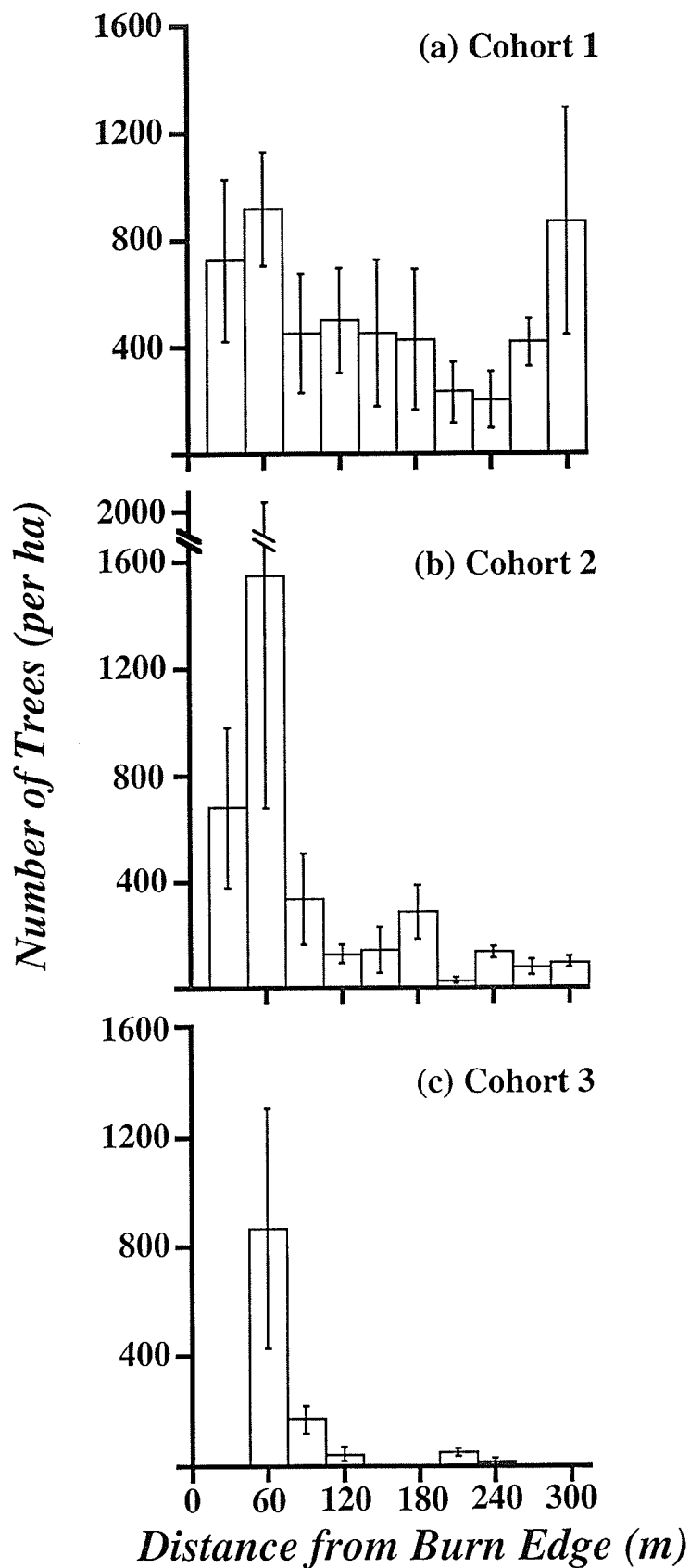
Wh. Spr. abundance resids. =  $-0.017(x \text{ coordinate (I-P)}) - 0.045(y \text{ coordinate (dist. to old gr.)})$

$R^2 = 15.2\%$

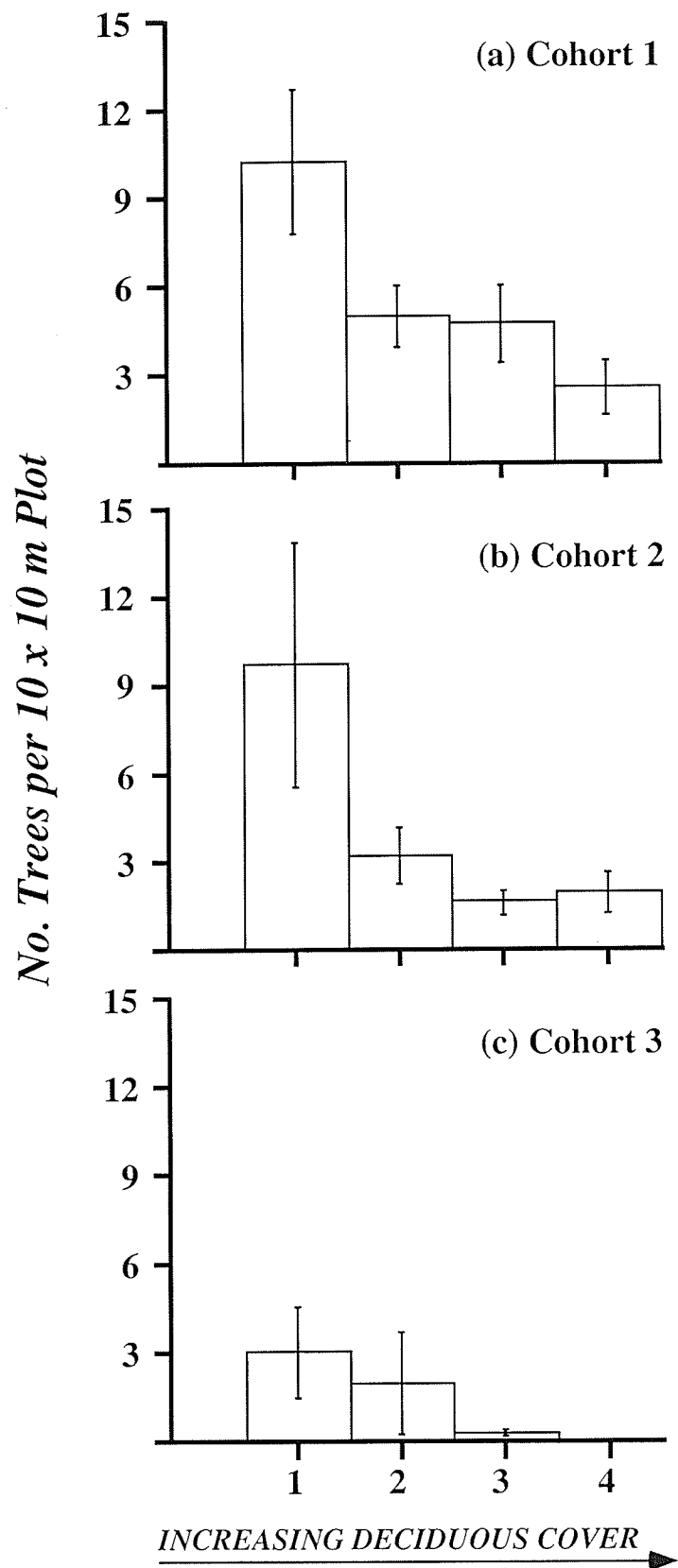
	Sum of Squares	Degrees of Freedom	Mean Square	F-ratio	P
Regression	1.306	2	0.653	6.26	0.006
Error	7.295	70	0.104		

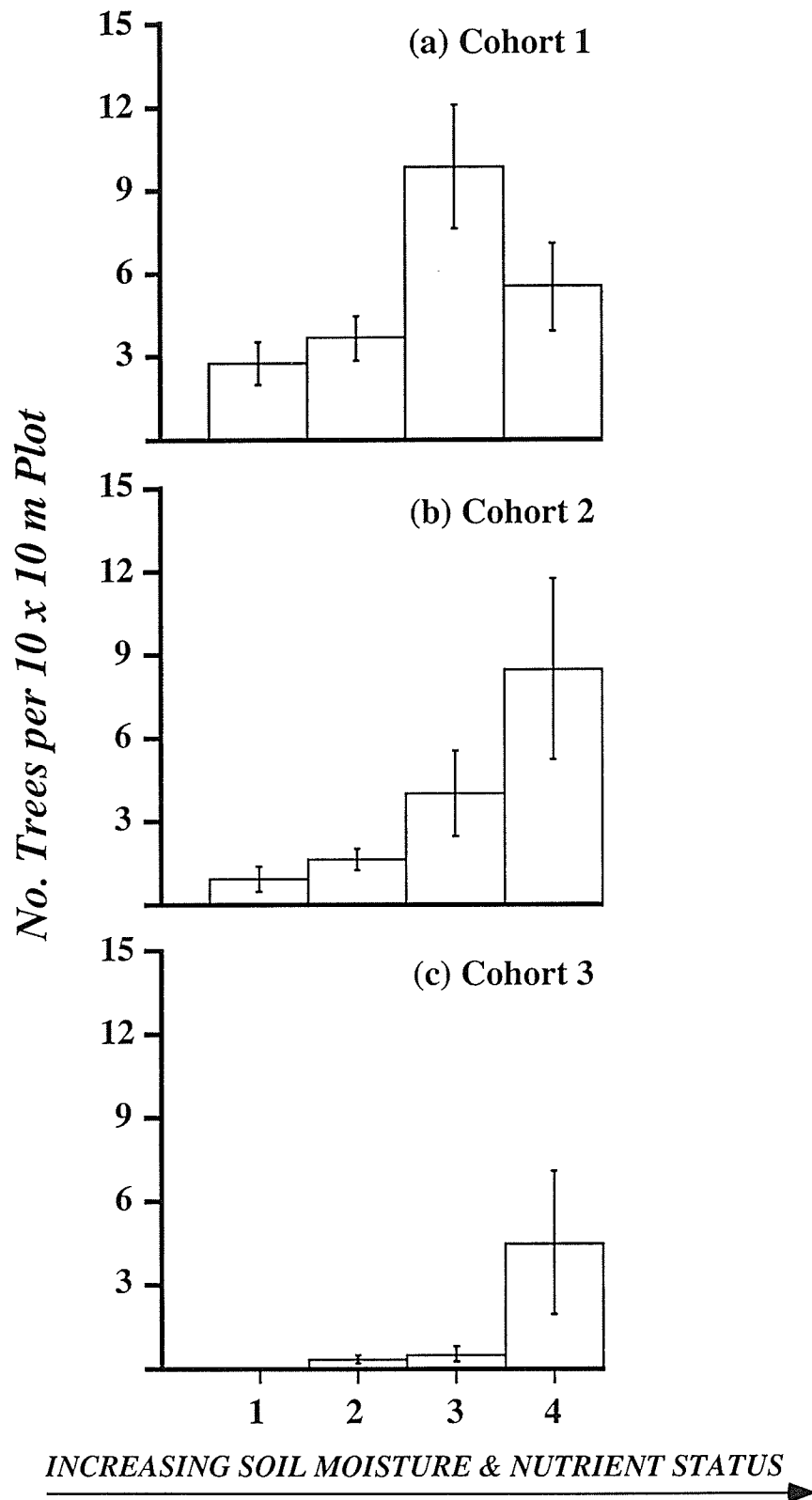
	t-ratio	Probability
x coord. (I-P)	-3.32	0.003
y coord. (dist. to old gr.)	-0.979	0.001



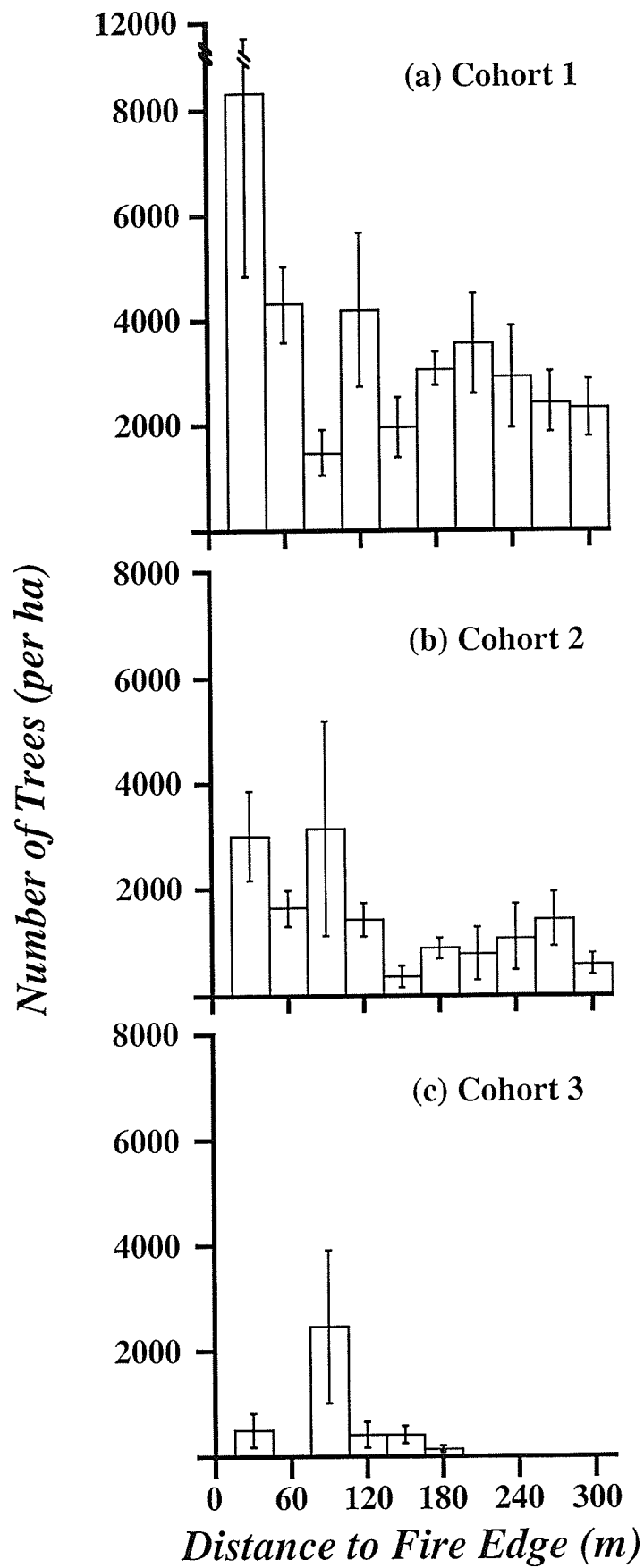
**Figure 5.8** MAINLAND site. White spruce density (mean  $\pm$  s.e. no. trees per ha) as a function of distance from burn edge (meters) for: (a) cohort 1, ages 25-39; (b) cohort 2, ages 5-24; (c) cohort 3, ages 1-4.



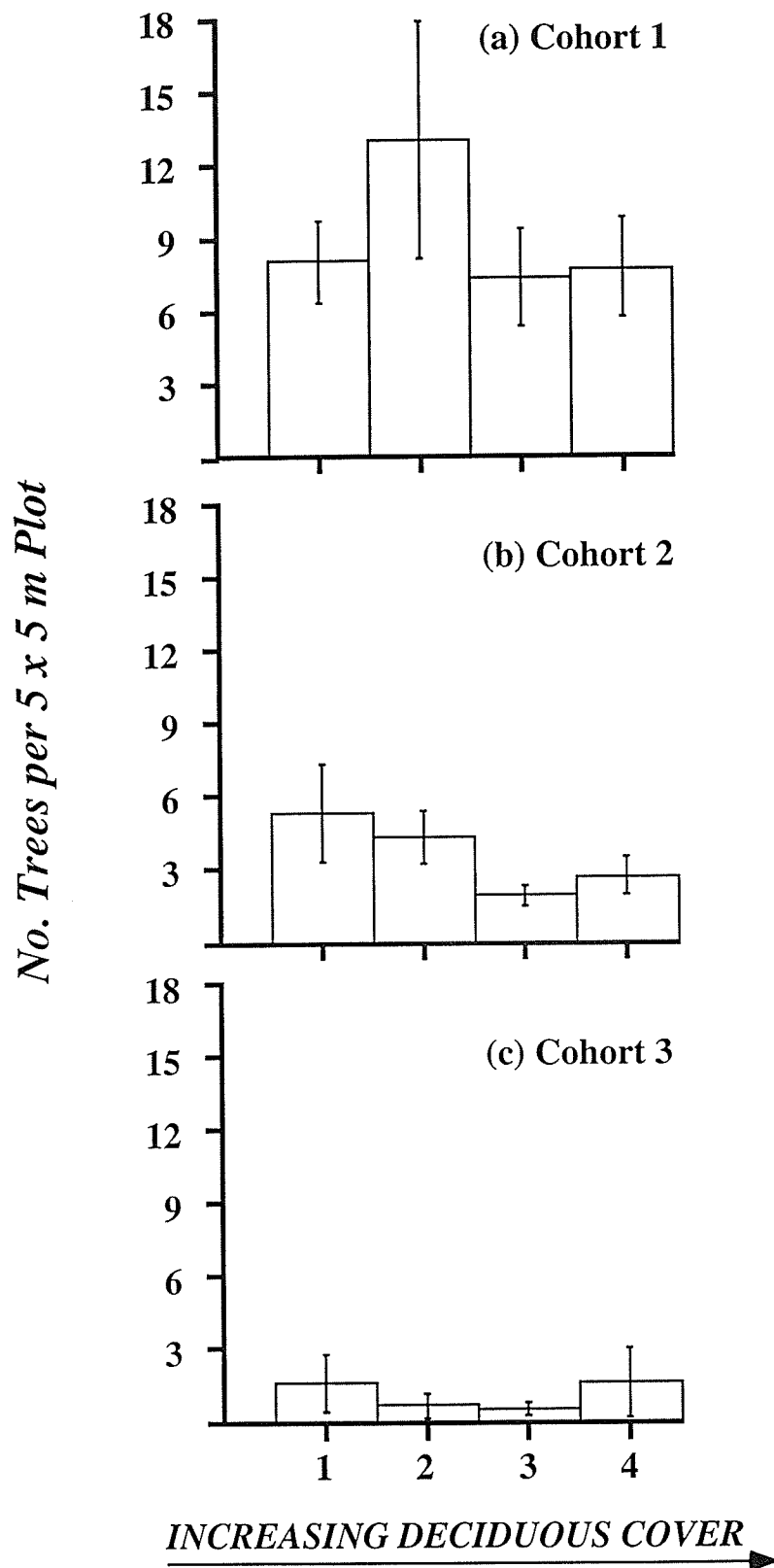
**Figure 5.9.** MAINLAND site. White spruce density (no. trees per 10x10 m plot, mean  $\pm$  se) for three cohort classes (1 = ages 25-39, 2 = ages 5-24, 3 = ages 1-4) along the principal axis of the biotic PCA (Fig 5.1 (a)). The principal axis is divided into 4 classes based on component scores: 1 = scores  $< -1.5$  ( $n = 13$ ); 2 = scores  $-1.5$  to 0 ( $n = 22$ ); 3 = scores 0 to 1.5 ( $n = 28$ ); 4 = scores  $> 1.5$  ( $n = 13$ ).



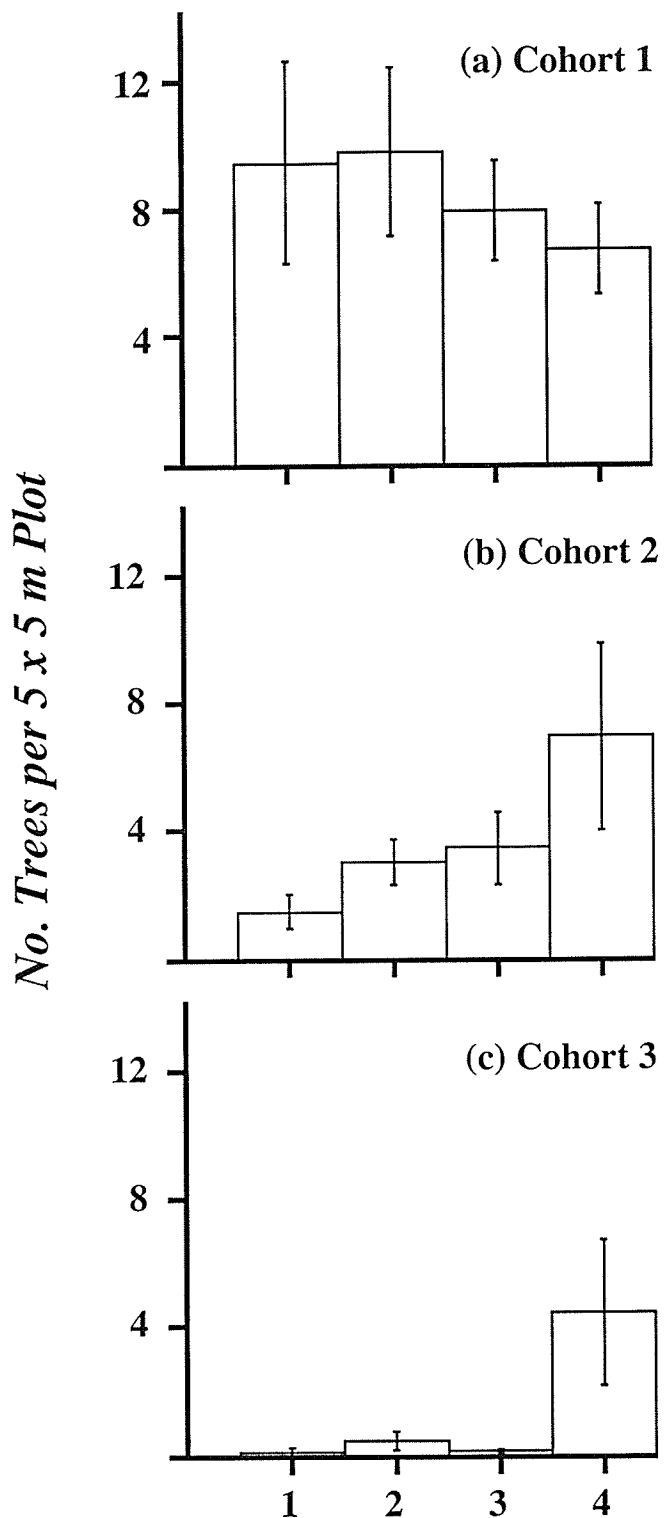
**Figure 5.10.** MAINLAND site. White spruce density (no. trees per 10x10 m plot, mean  $\pm$  se) for three cohort classes (1 = ages 25-39, 2 = ages 5-24, 3 = ages 1-4) along the principal axis of the abiotic PCA (Fig 5.4a). The principal axis is divided into 4 classes based on component scores: 1 = scores  $< -1.5$  ( $n = 14$ ); 2 = scores  $-1.5$  to 0 ( $n = 28$ ); 3 = scores 0 to 1.5 ( $n = 18$ ); 4 = scores  $> 1.5$  ( $n = 16$ ).



**Figure 5.11.** PENINSULA site. White spruce density (mean  $\pm$  s.e., no. trees per ha) as a function of distance from burn edge (meters) for: (a) cohort 1, ages 25-39; (b) cohort 2, ages 5-24; (c) cohort 3, ages 1-4.



**Figure 5.12.** PENINSULA site. White spruce density (no. trees per 5x5 m plot, mean  $\pm$  se) for three cohort classes (1 = ages 25-39, 2 = ages 5-24, 3 = ages 1-4) along the principal axis of the biotic PCA (Fig 5.1b). The principal axis is divided into 4 classes based on component scores: 1 = scores  $< -0.5$  ( $n = 23$ ); 2 = scores  $-0.5$  to 0 ( $n = 15$ ); 3 = scores 0 to 0.5 ( $n = 20$ ); 4 = scores  $> 0.5$  ( $n = 15$ ).



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**Figure 5.13.** PENINSULA site. White spruce density (no. trees per 5x5 m plot, mean  $\pm$  se) for three cohort classes (1 = ages 25-39, 2 = ages 5-24, 3 = ages 1-4) along the principal axis of the abiotic PCA (Fig 5.4b). The principal axis is divided into 4 classes based on component scores: 1 = scores  $< -2$  ( $n = 11$ ); 2 = scores  $-2$  to  $0$  ( $n = 32$ ); 3 = scores  $0$  to  $2$  ( $n = 16$ ); 4 = scores  $> 2$  ( $n = 14$ ).

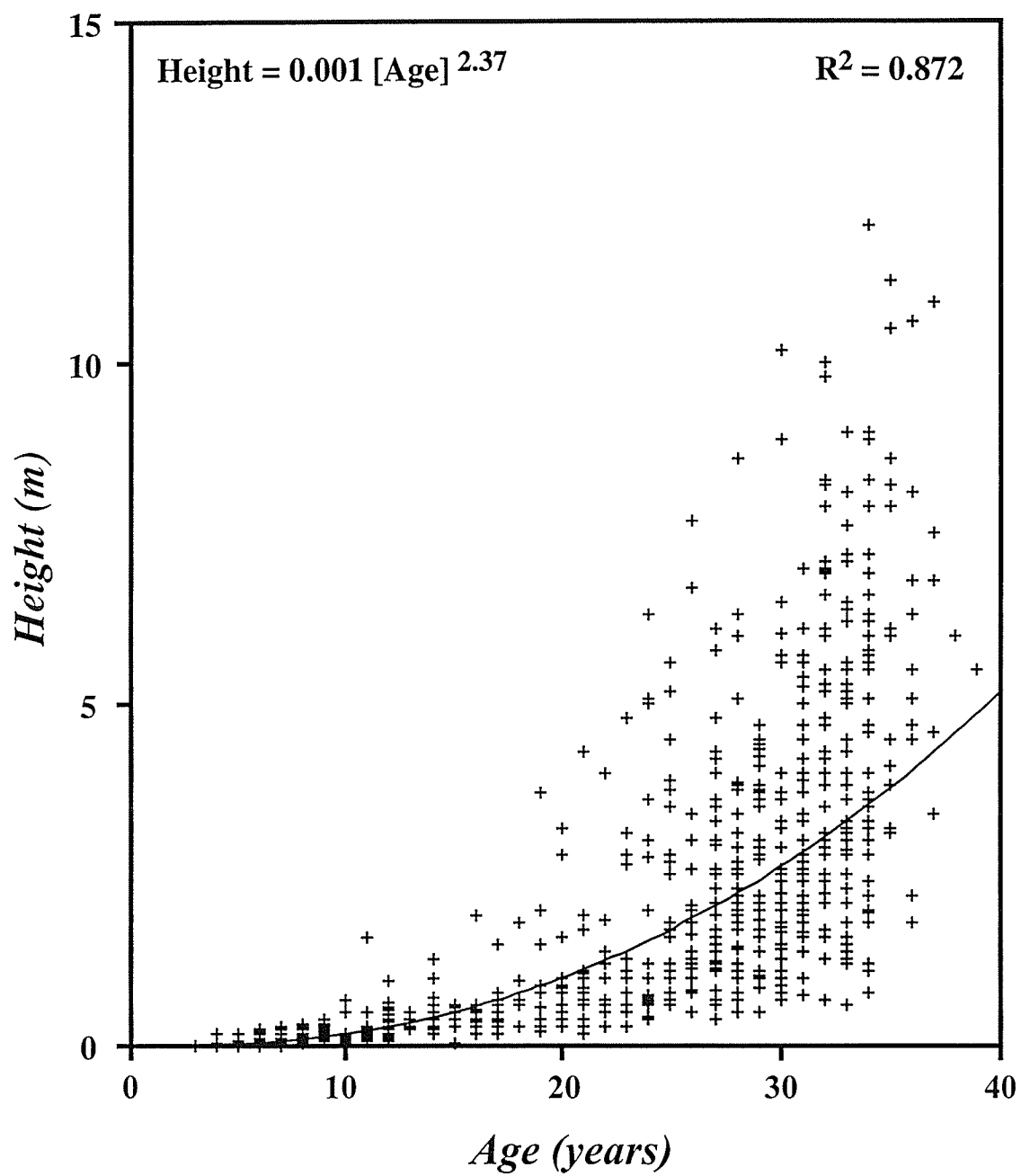
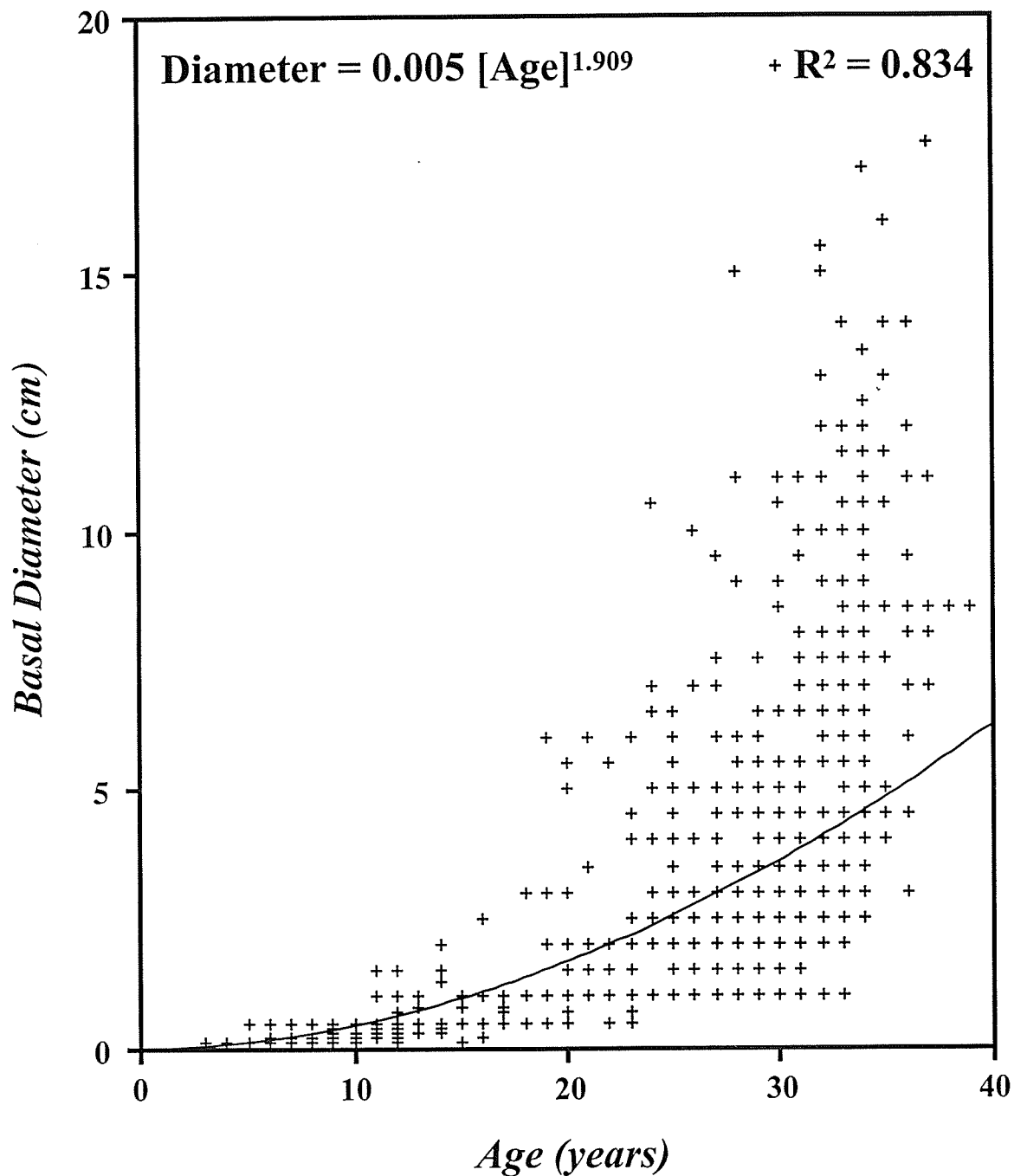
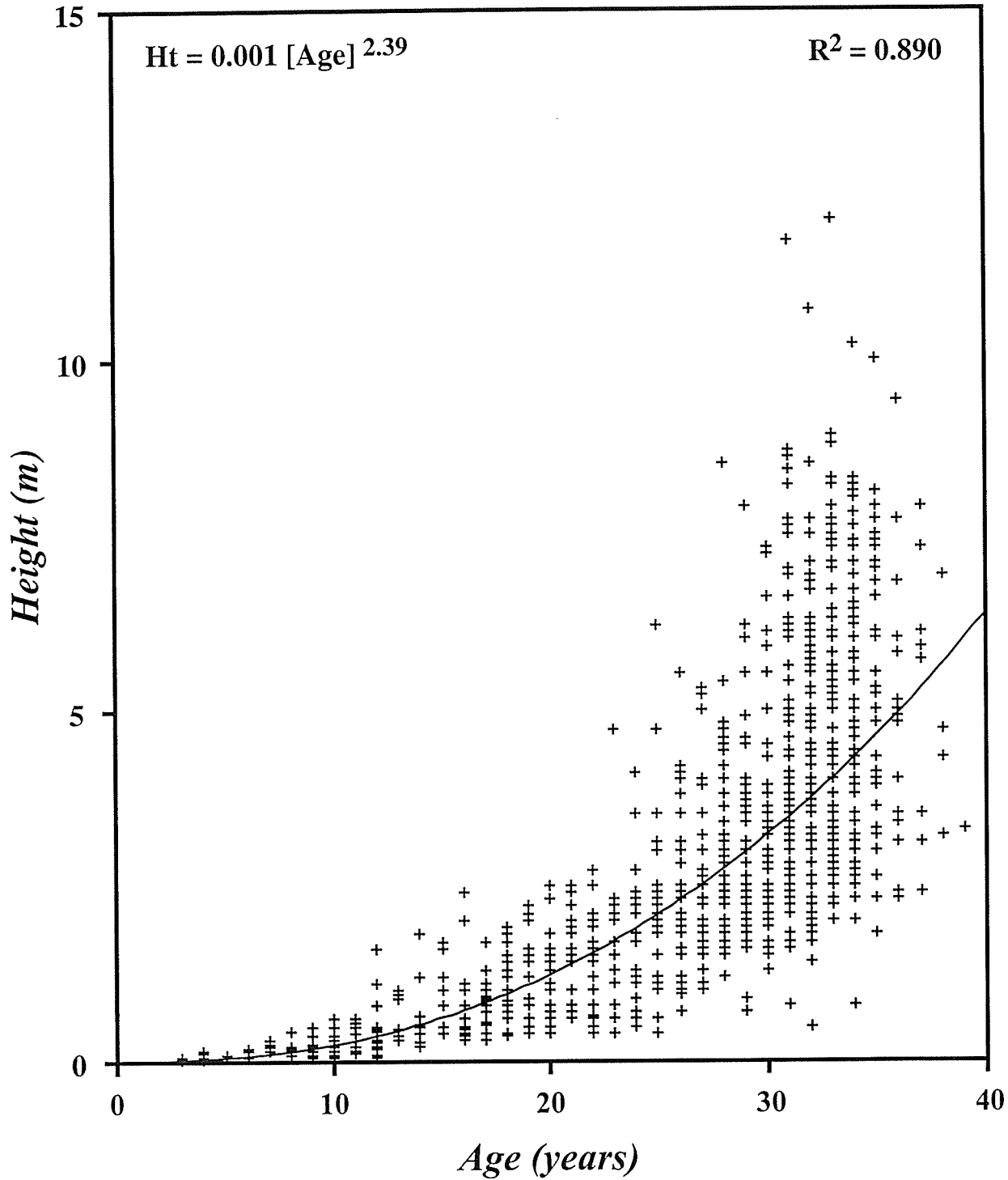


Figure 5.14a. MAINLAND site. Height (m) as a function of age (years) for white spruce ( $n = 763$ ). Data are fit to a power-law (log-log) curve.





**Figure 5.14b.** MAINLAND site. Diameter at tree base (cm) as a function of age (years) for white spruce ( $n = 763$ ). Data are fit to a power-law (log-log) curve.



**Figure 5.15a.** PENINSULA site. Height (m) as a function of age (years) for white spruce ( $n = 979$ ). Data are fit to a power-law (log-log) curve.

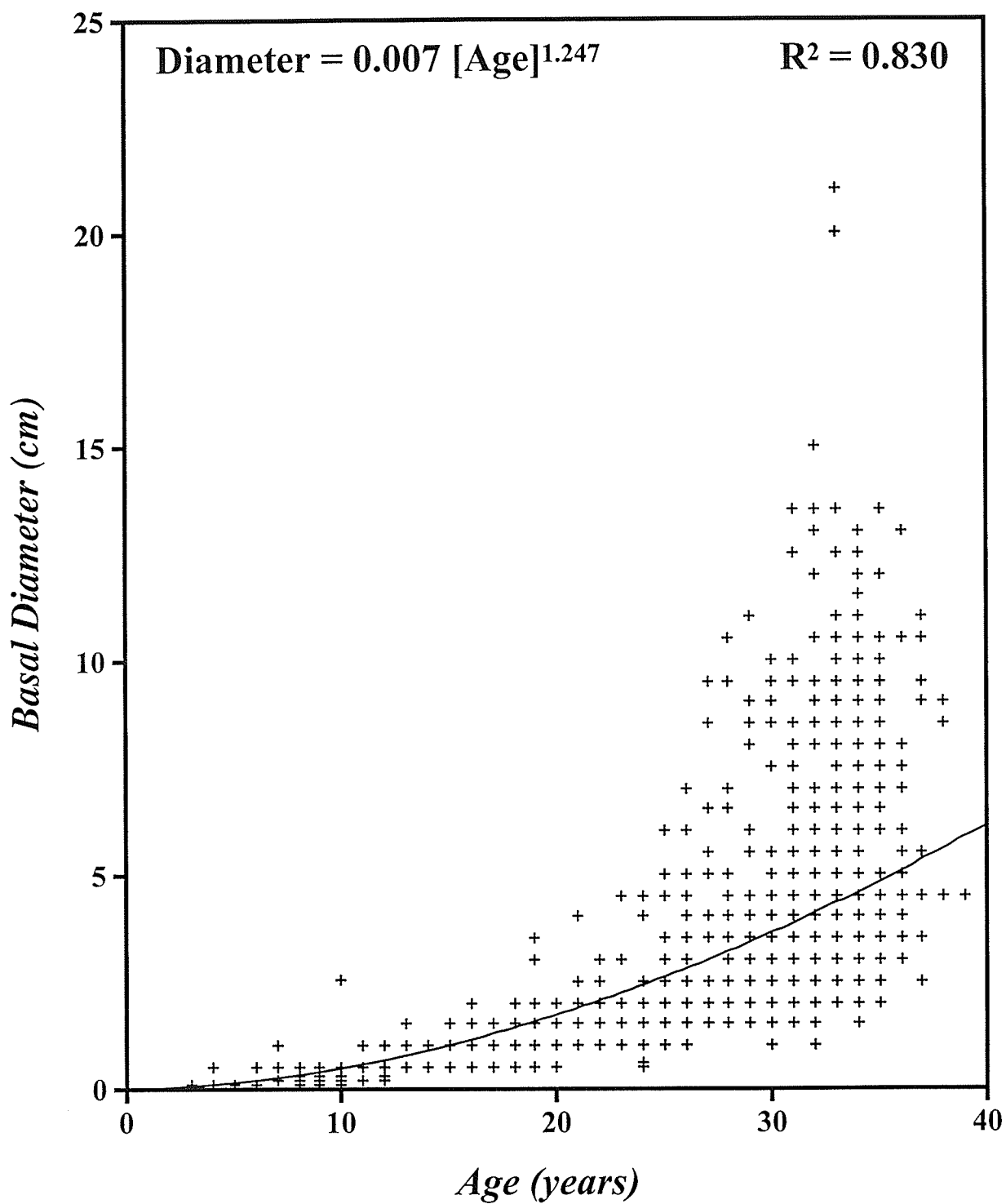


Figure 5.15b. PENINSULA site. Diameter at tree base (cm) as a function of age (years) for white spruce ( $n = 979$ ). Data are fit to a power-law (log-log) curve.

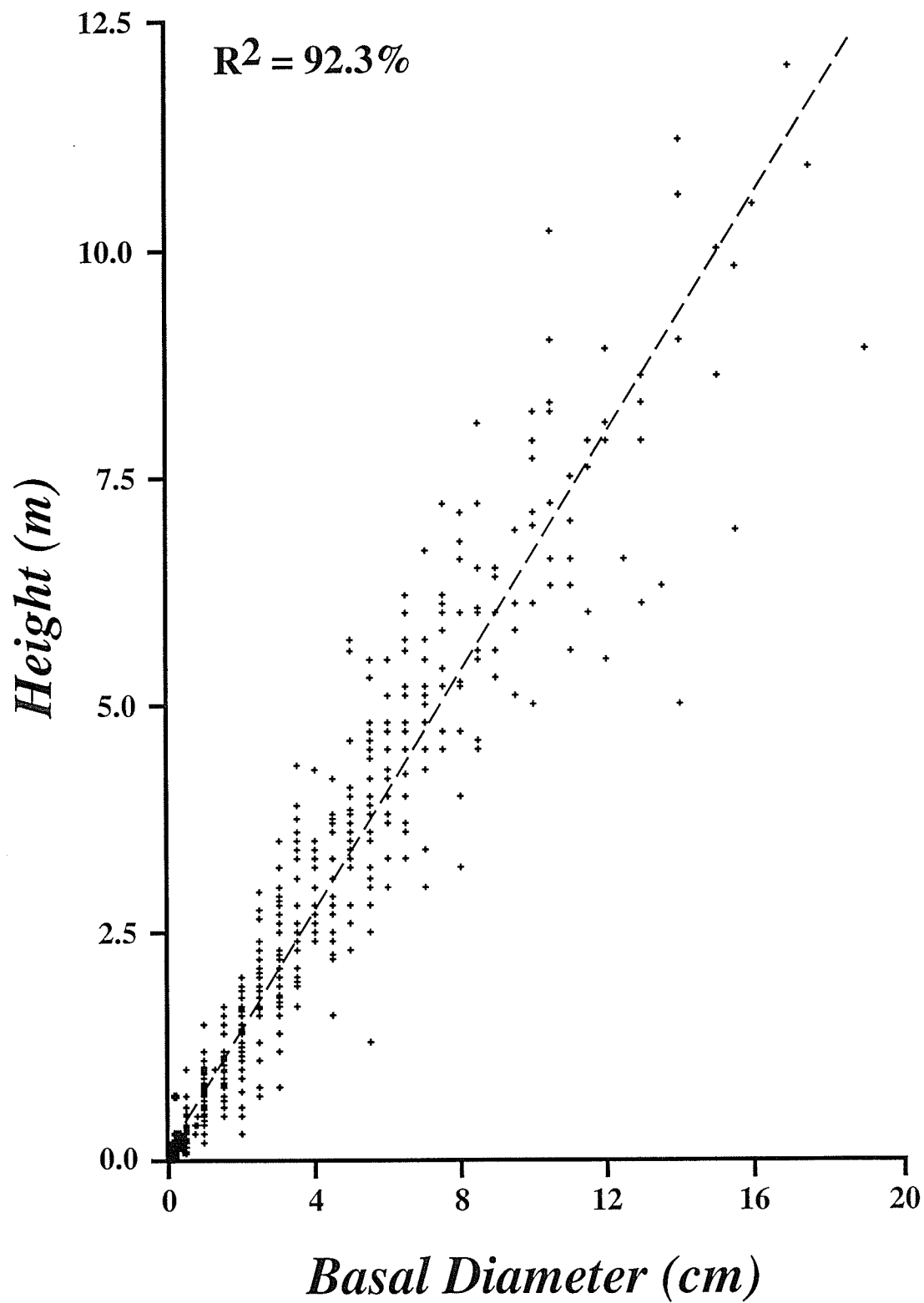


Figure 5.16a. MAINLAND site. Height (m) as a function of tree basal diameter (cm) for white spruce ( $n = 763$ ). The fitted line was obtained using linear regression, forced through the origin.

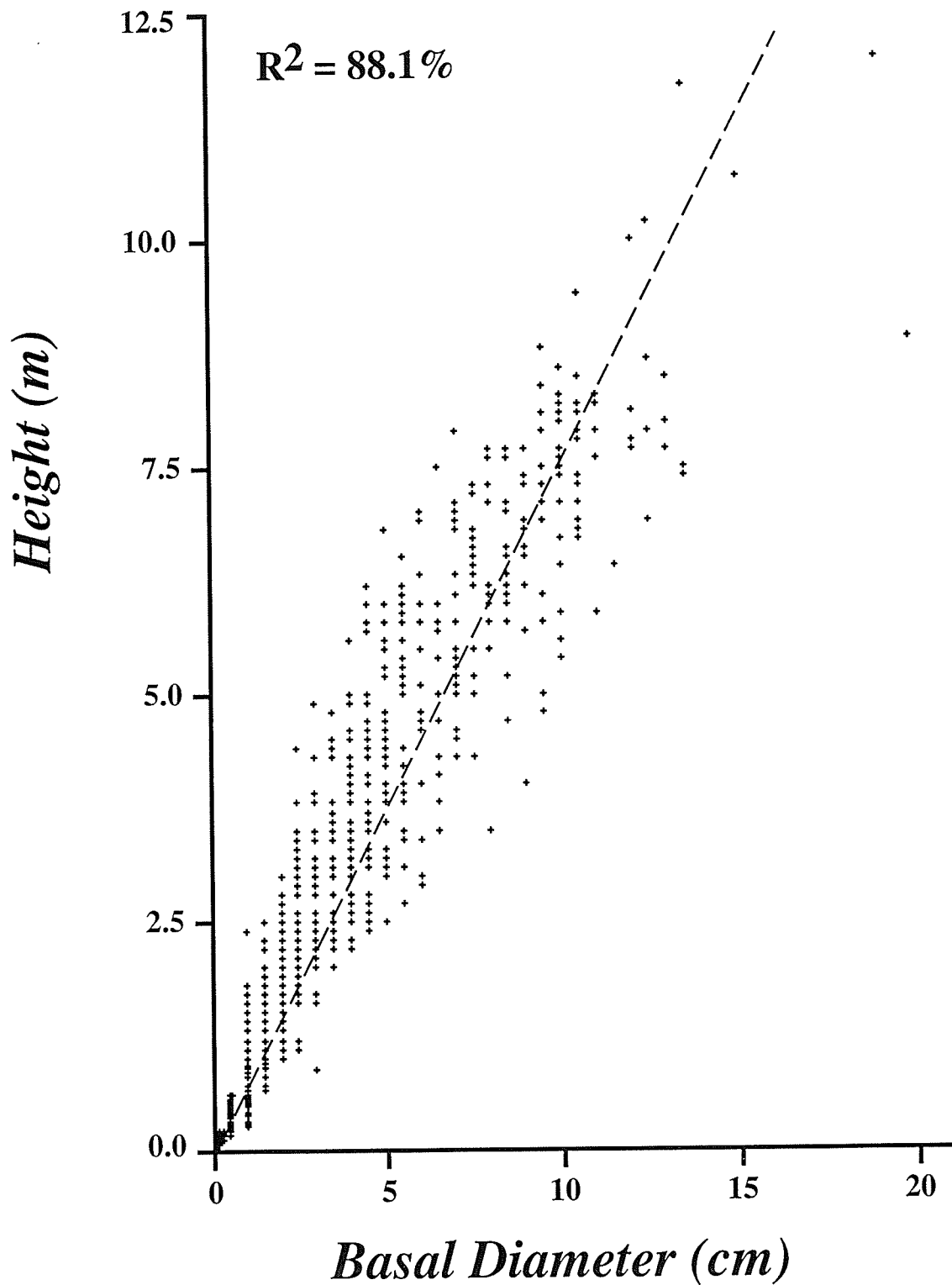
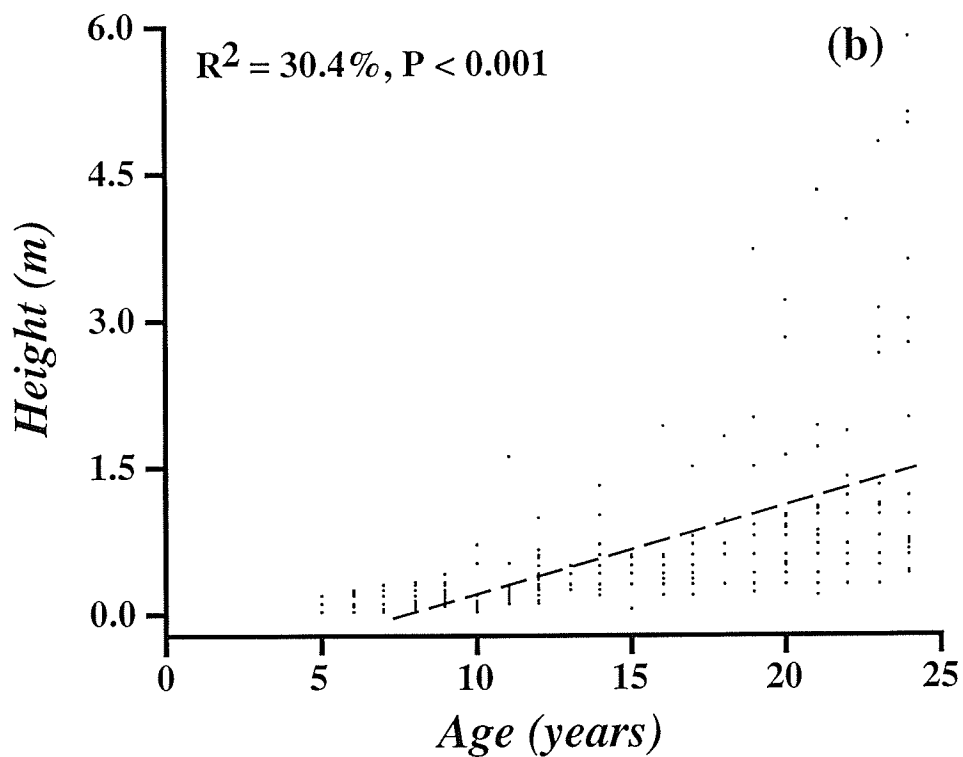
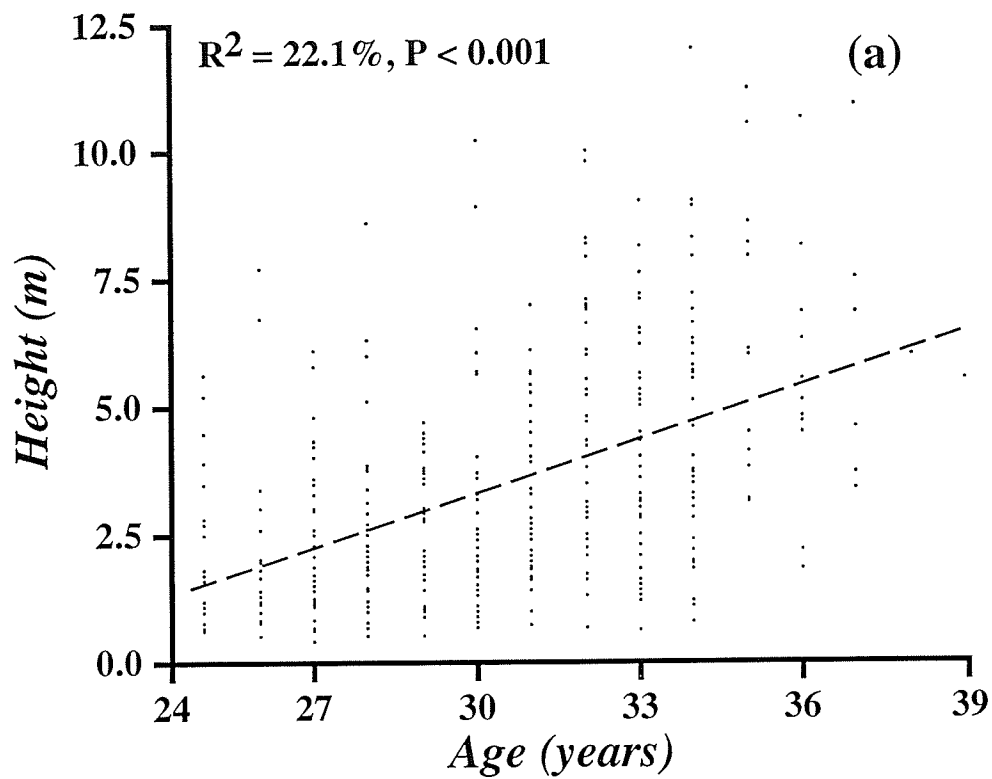


Figure 5.16b. PENINSULA site. Height (m) as a function of tree basal diameter (cm) for white spruce ( $n = 979$ ). The fitted line was obtained using linear regression, forced through the origin.



**Figure 5.17.** MAINLAND site. Height (m) of white spruce as a function of tree age (years), fitted to a linear model using regression: (a) cohort 1 (ages 25-39,  $n = 407$ ); (b) cohort 2 (ages 5-24,  $n = 266$ ).

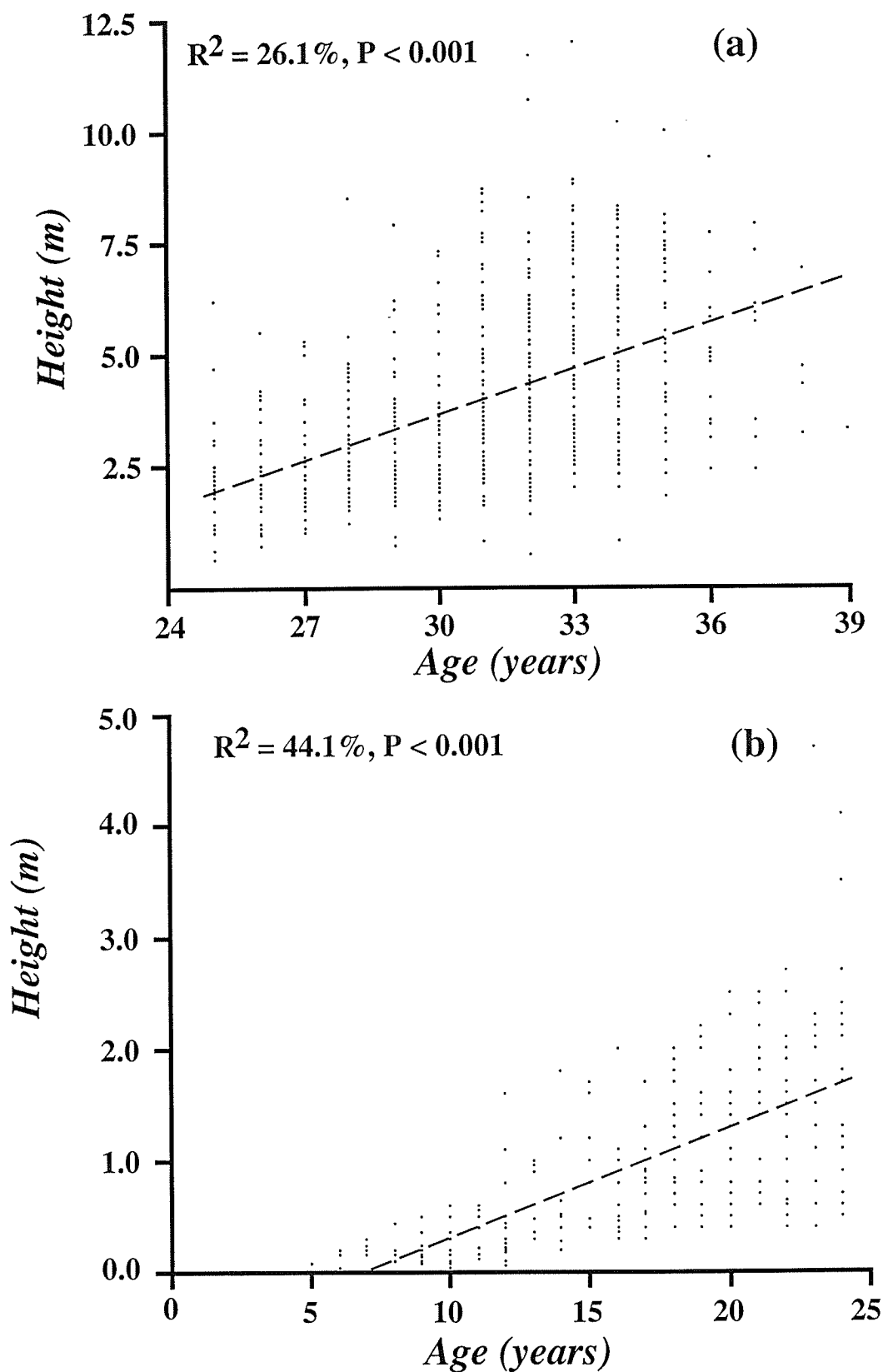
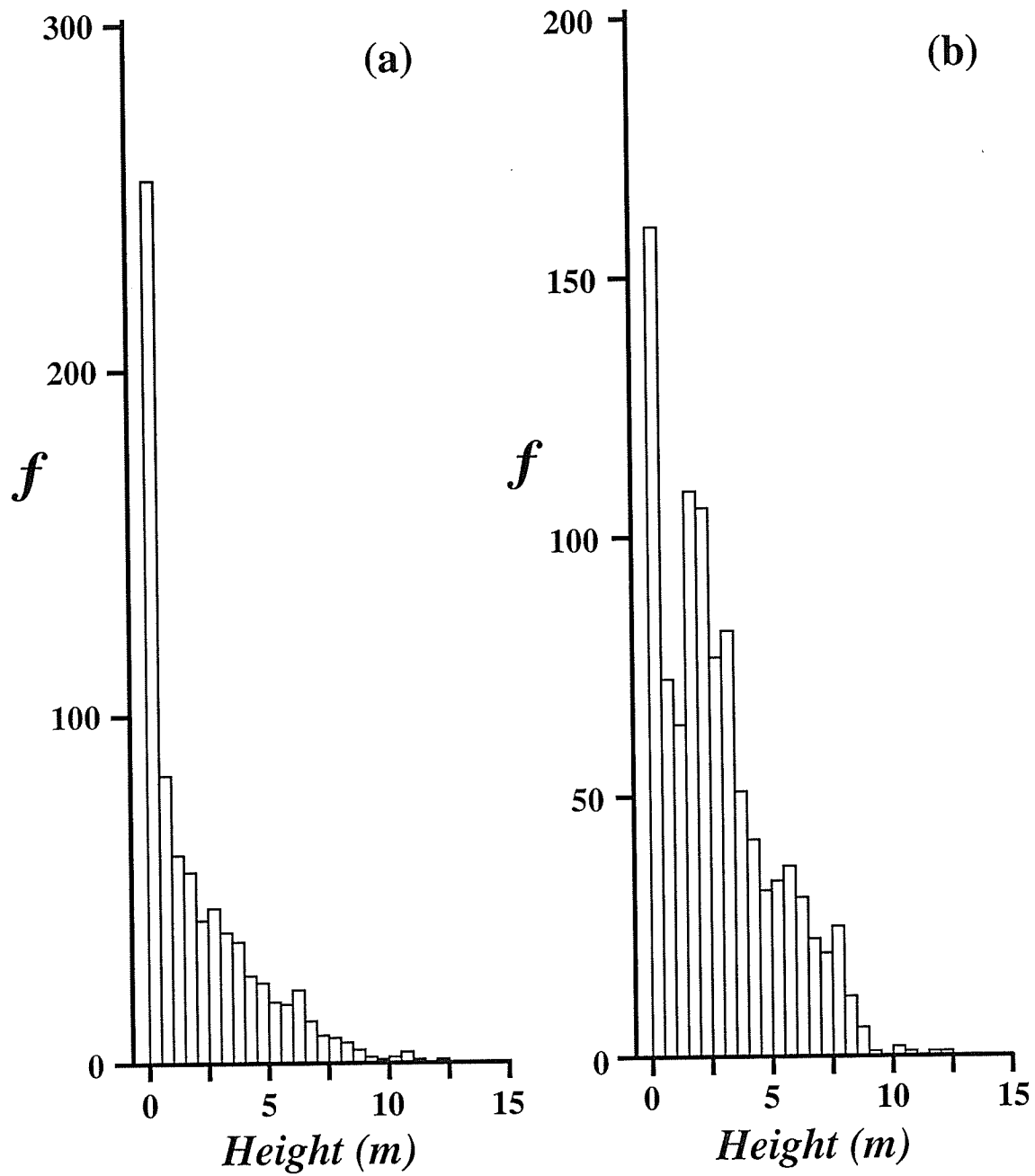


Figure 5.18. PENINSULA site. Height (m) of white spruce as a function of tree age (years), fitted to a linear model using regression. (a) cohort 1 (ages 25-39,  $n = 638$ ); (b) cohort 2 (ages 5-24,  $n = 264$ ).



**Figure 5.19.** Frequency distributions of white spruce heights (meters) for (a) MAINLAND site (b) PENINSULA site.



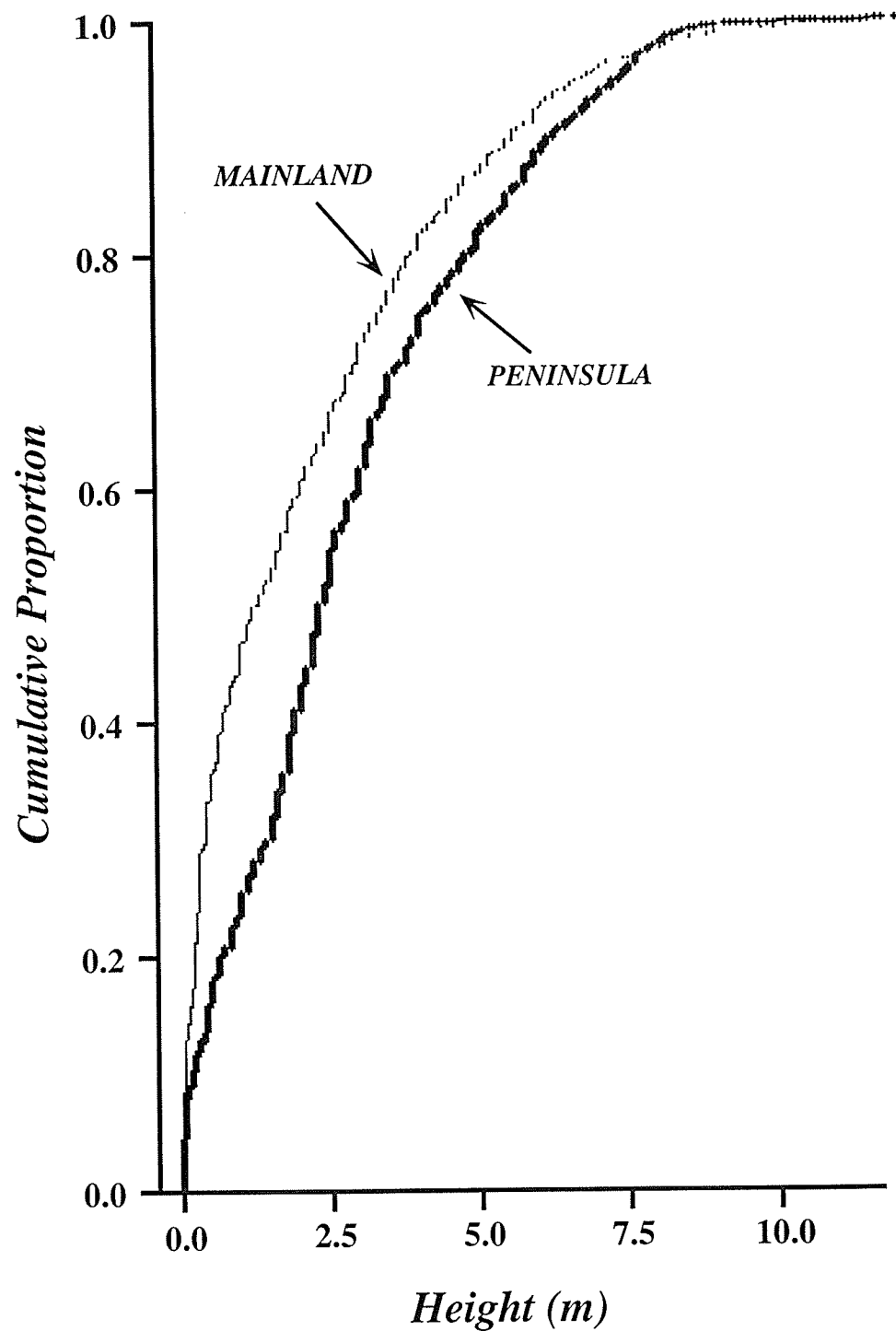
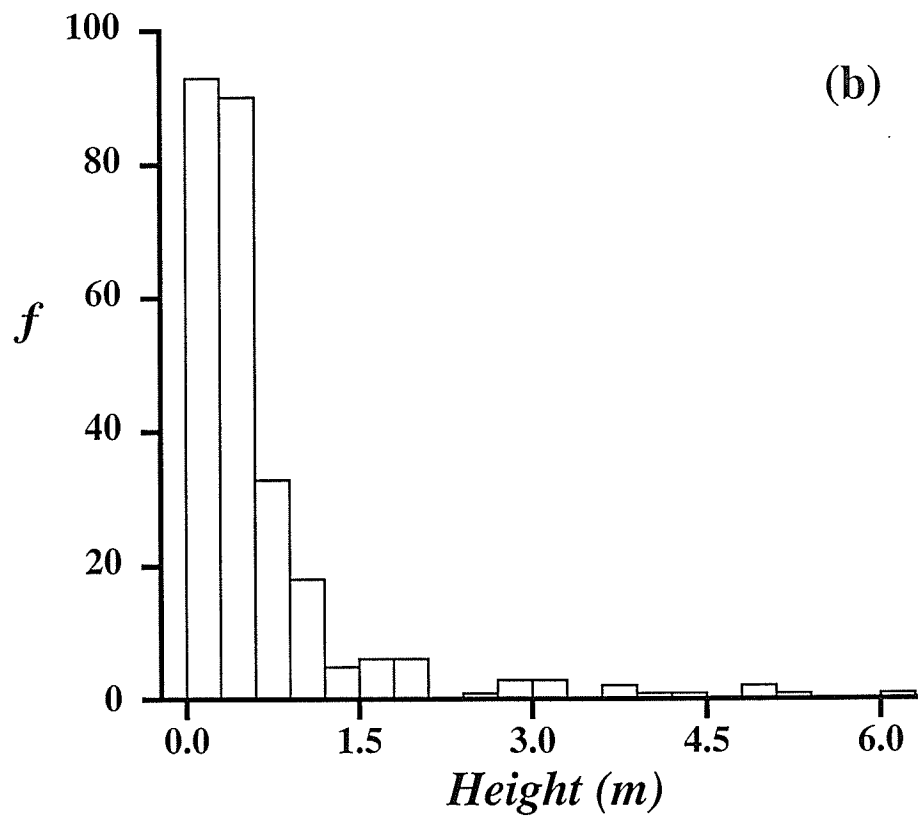
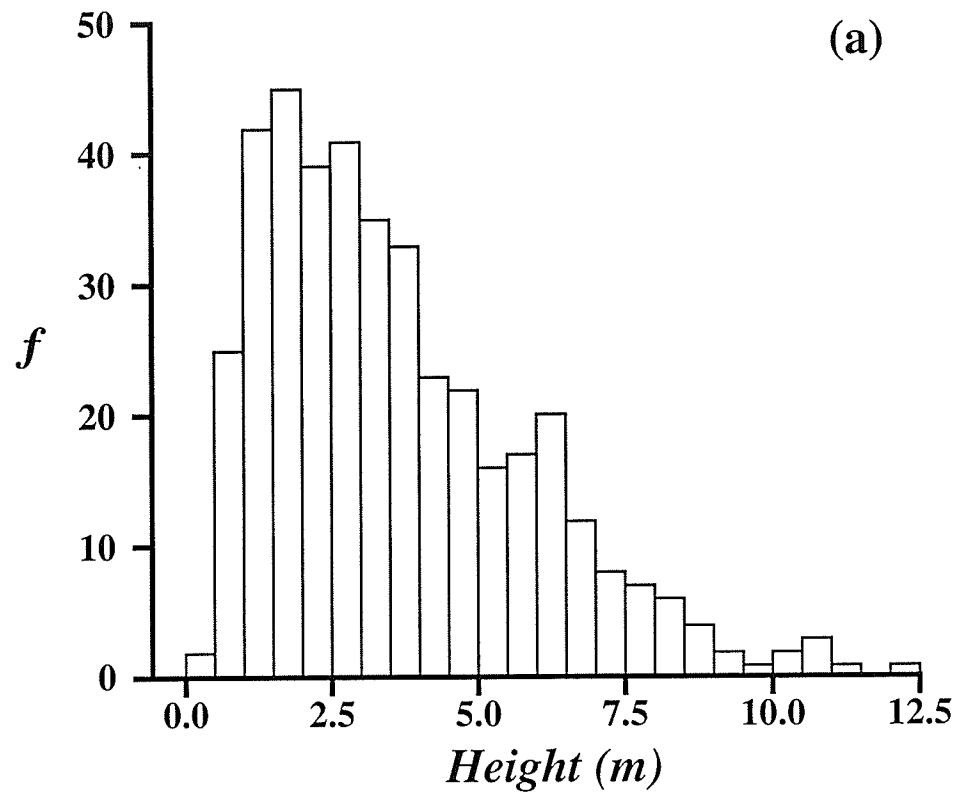


Figure 5.20. Cumulative height distributions of white spruce at the MAINLAND and PENINSULA sites.



**Figure 5.21.** MAINLAND site. Frequency distribution of white spruce tree heights, in meters: (a) cohort 1 (ages 25-39,  $n = 407$ ); (b) cohort 2 (ages 5-24,  $n = 266$ ).

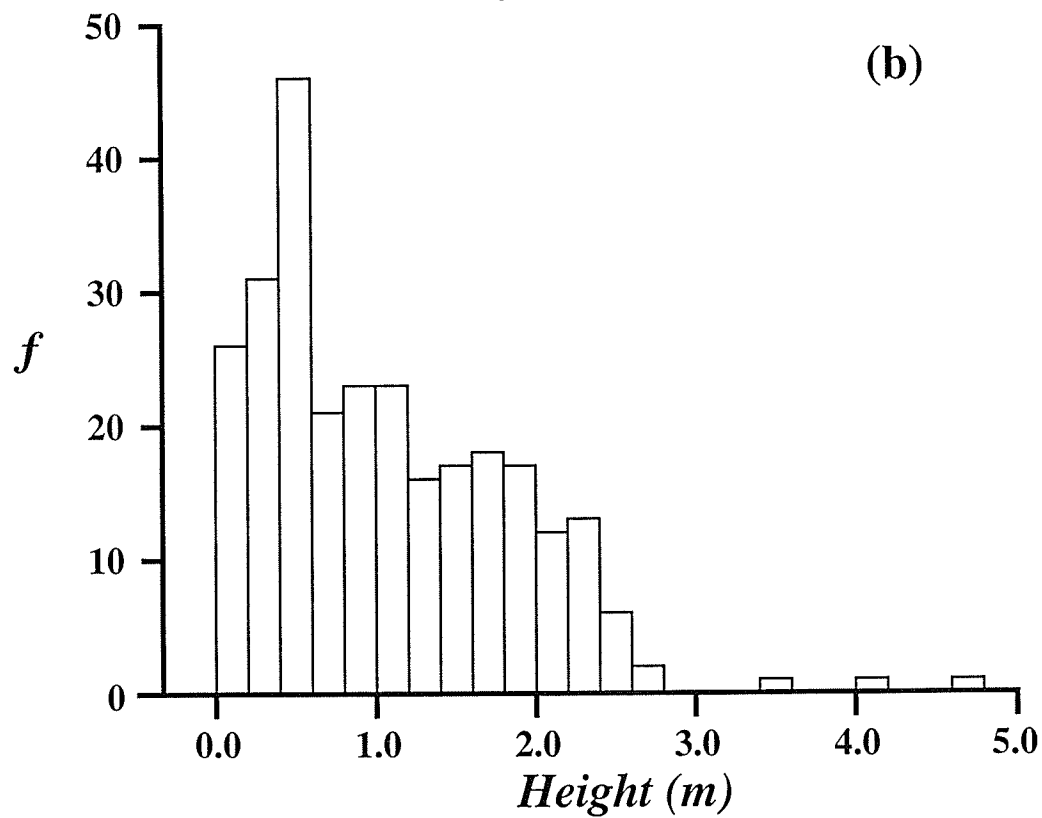
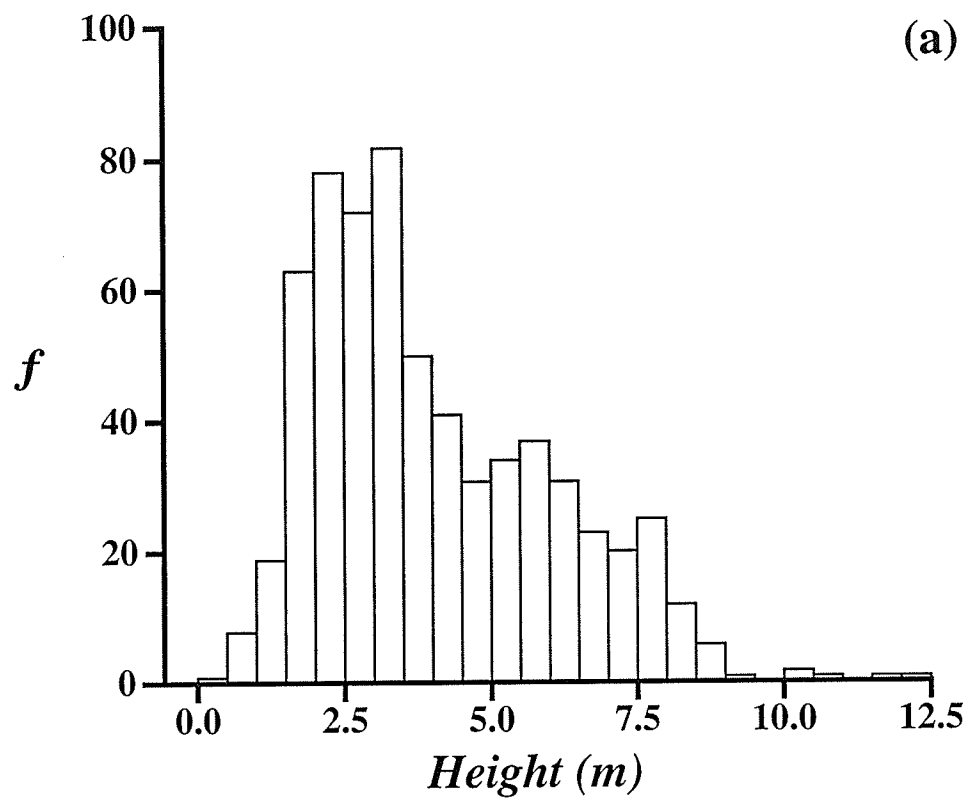
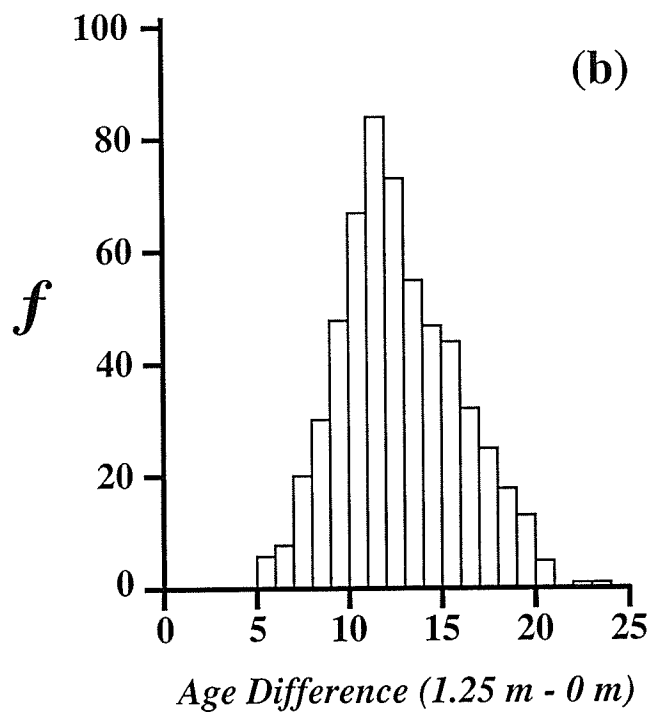
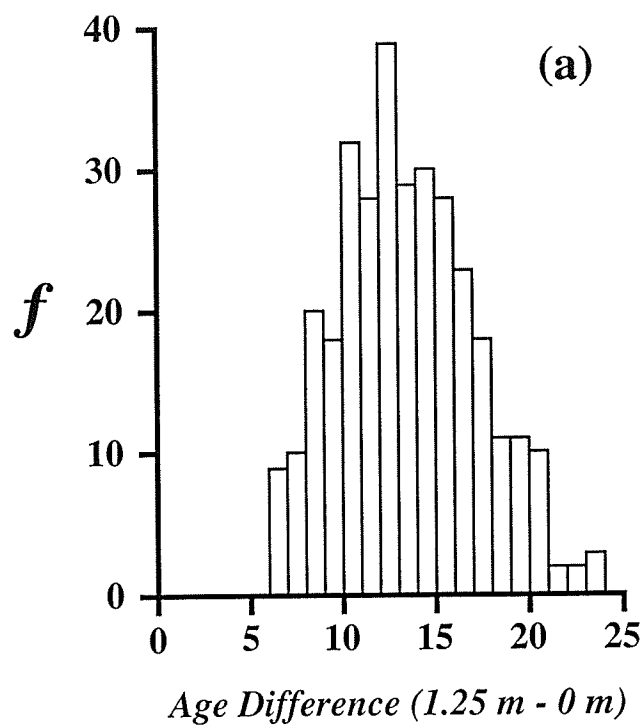
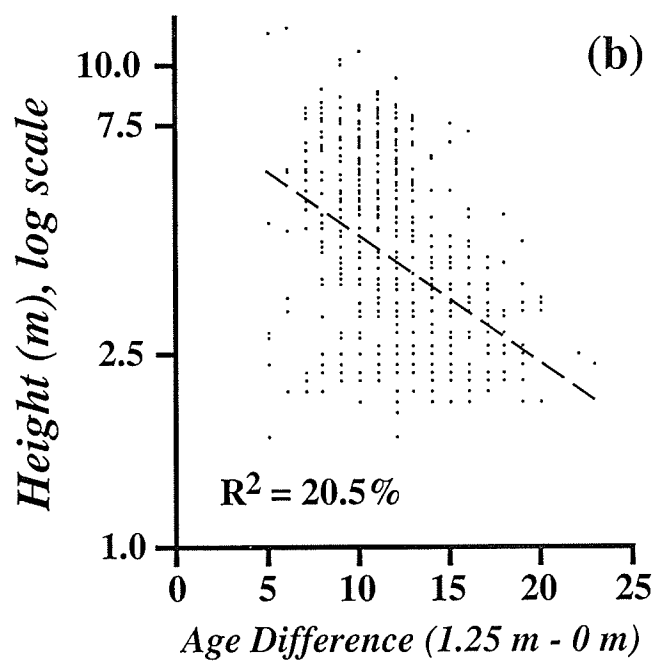
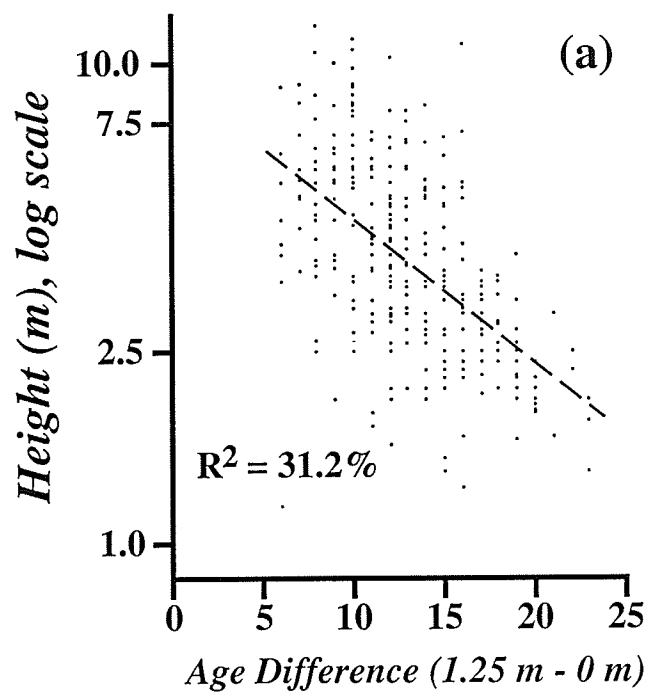


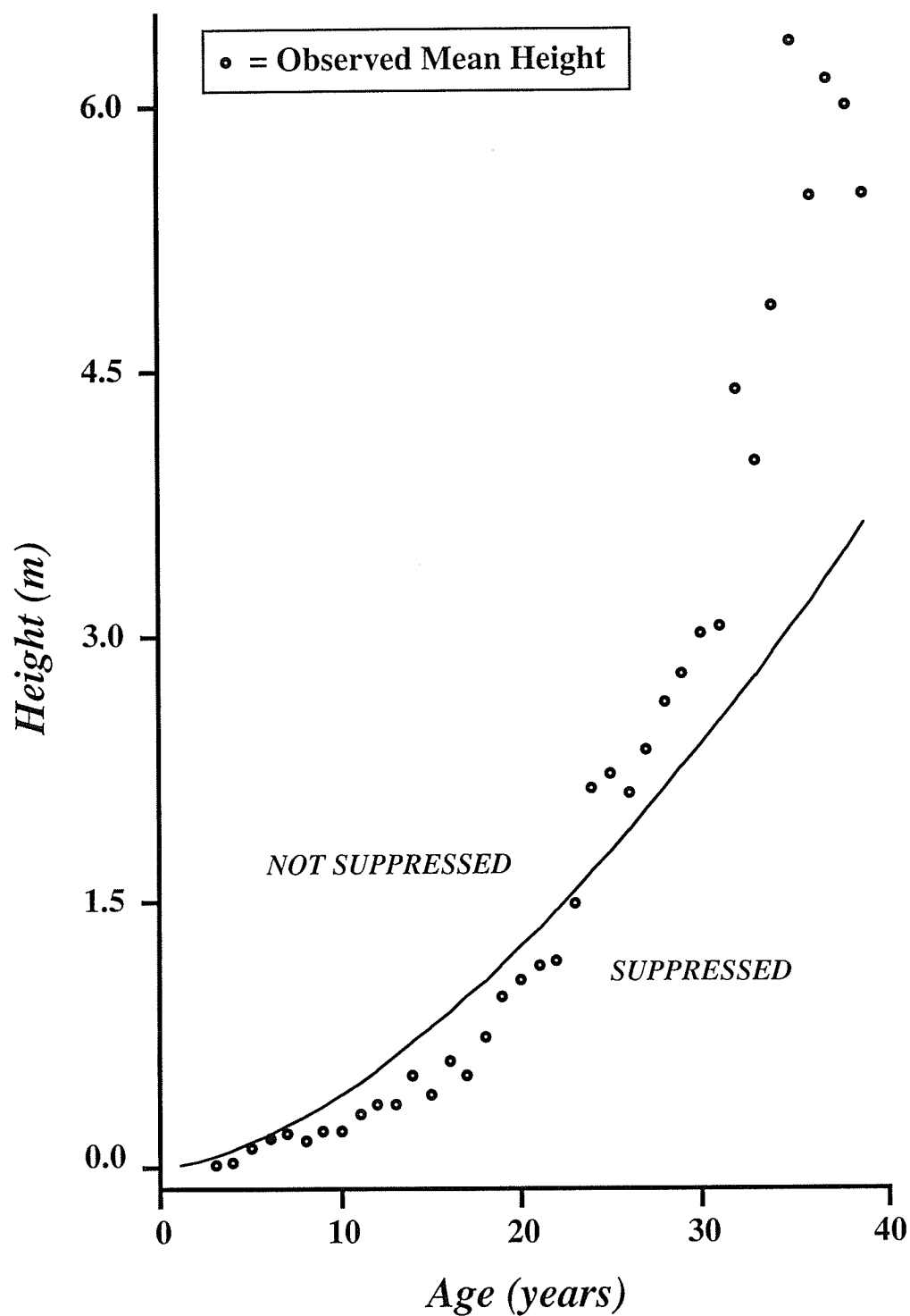
Figure 5.22. PENINSULA site. Frequency distribution of white spruce tree heights, in meters. (a) cohort 1 (ages 25-39,  $n = 638$ ); (b) cohort 2 (ages 5-24,  $n = 264$ ).



**Figure 5.23.** Frequency distribution of early growth (stem age difference between 1.25 m and base) for white spruce: (a) MAINLAND site ( $n = 323$ ); (b) PENINSULA site ( $n = 577$ ).



**Figure 5.24.** Early growth of white spruce (see Figure 5.23) as a function of current tree height (m, log scale): (a) MAINLAND site ( $n = 323$ ); (b) PENINSULA site ( $n = 577$ ).



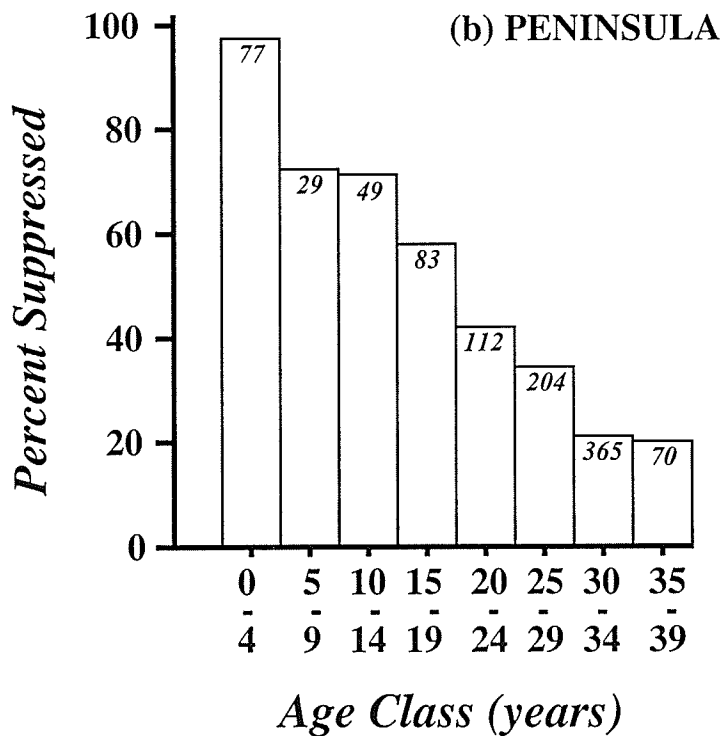
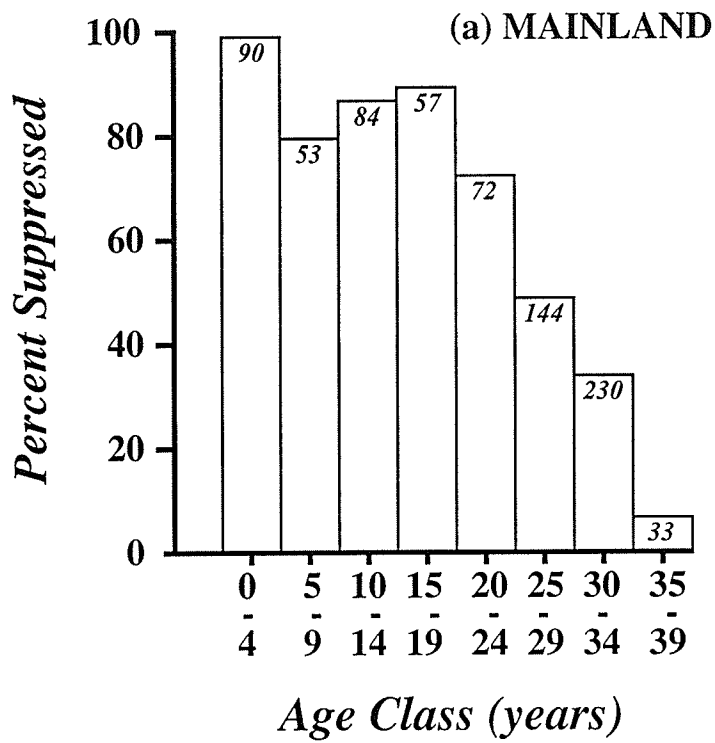
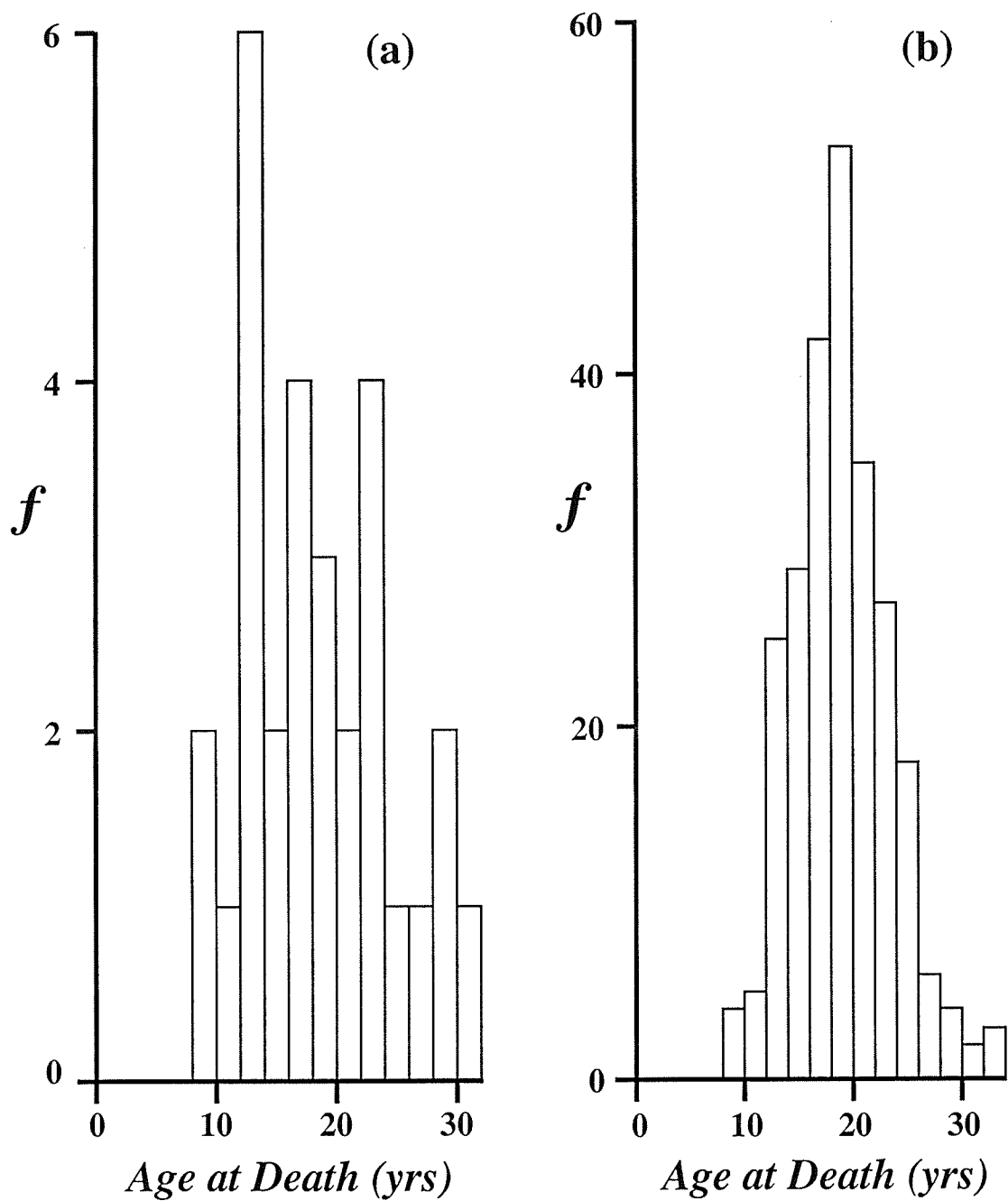
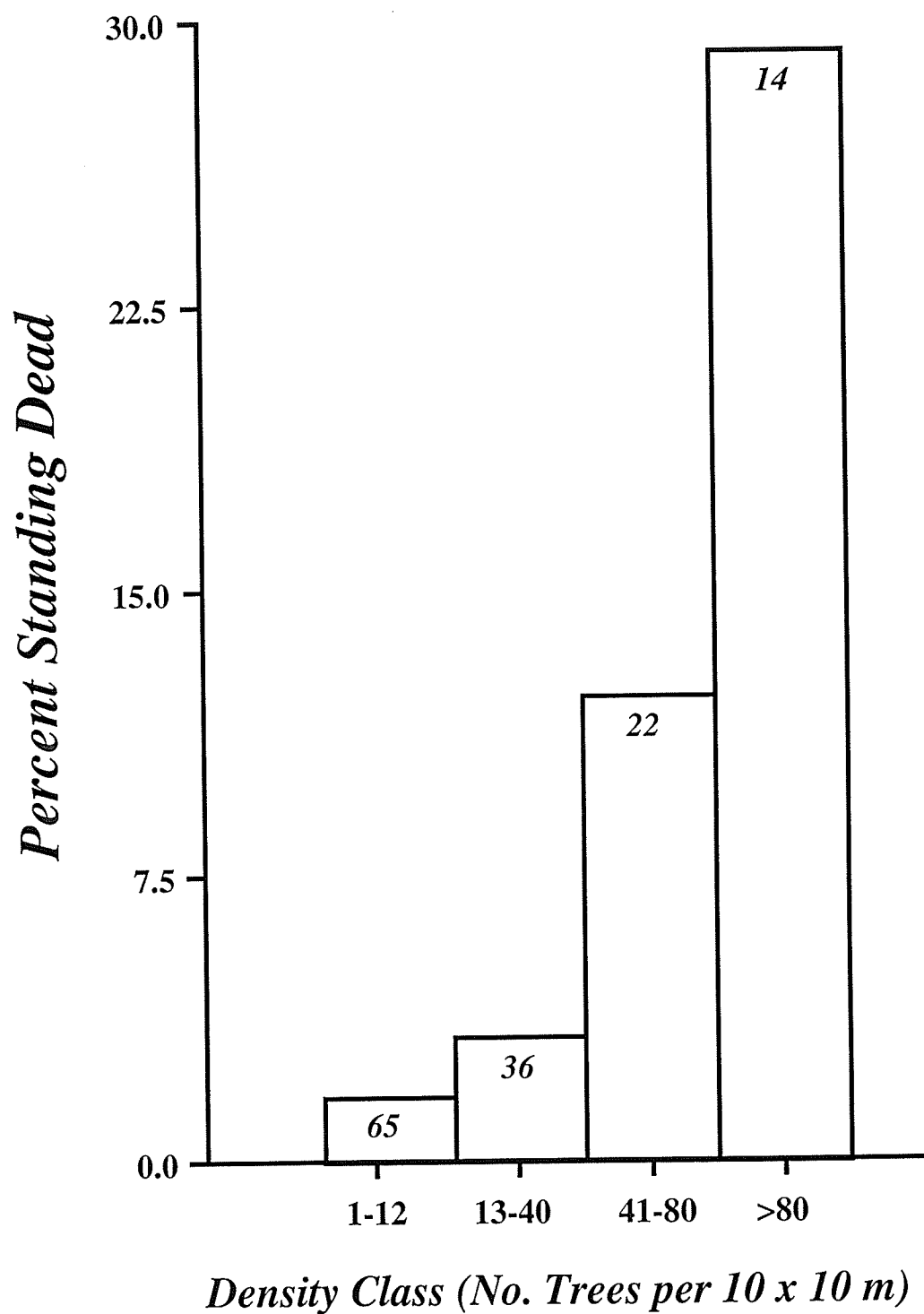


Figure 5.26. Percent suppressed white spruce trees in eight age classes, for (a) MAINLAND site; (b) PENINSULA site. Suppression is defined using the model summarized in Figure 5.25. Values in italics are the number of trees in each age class.



**Figure 5.27.** Frequency distributions of age at death (years) for standing dead white spruce trees at (a) MAINLAND site ( $n = 29$ ), and (b) PENINSULA site ( $n = 253$ ).





**Figure 5.28.** Percentage standing dead white spruce as a function of local stand density (number of individuals per 10 x 10 m plot). Data for the MAINLAND and PENINSULA sites are combined. Italicized values in bars are the number of plots in each of the four density classes.

## **CHAPTER 6**

### **DISCUSSION**

#### **6.1 Seed Source Distance Effects and White Spruce Recruitment**

Overall, white spruce recruitment was much higher on the PENINSULA site. The old growth seed source adjacent to the PENINSULA site was closer and denser than the MAINLAND site, while the old growth next to the MAINLAND site had a higher component of aspen and shrubs. Following establishment of the first cohort, there was a gradual decline in recruitment on the MAINLAND site, whereas the PENINSULA site experienced a steeper decline. Both seed source distance and the environmental variables influenced these patterns of recruitment to varying degrees over time. First the effects of seed source distance will be explored.

##### **6.1.1 Cohort 1**

Neither site was significantly limited by seed source distance while the first cohort was establishing. The MAINLAND site was more limited by the environmental variables, while the PENINSULA site did not appear to be limited by the environmental or spatial variables

There was a lag of approximately five years before white spruce recruitment became prolific at both sites. MacDonald et al. (2001) observed most recruitment of white spruce to occur within the first five to seven years following fire. They suggest that any delay in recruitment, immediately post-fire, could result from a delay in mast seeding such that seed would not become available for several years following fire. They also suggest

that an apparent delay in recruitment could be an artifact of missing rings, which they overcame by using cross-dating techniques.

A delay in masting is an unlikely explanation for the delay in recruitment on these sites. Just south of Duck Mountain, Riding Mountain experienced a moderate white spruce seed crop in 1962 with cone crop production reported as being the highest between 1954 and 1963 (Waldron 1965). A nearby climate station in Dauphin, Manitoba reports that temperatures were 2° F below normal, sunshine was nine hours below normal and precipitation was 2.6 inches above normal in 1962. These conditions delayed the period of peak seed fall of white spruce in Riding Mountain until mid-September. It is likely that Duck Mountain also experienced a mast year in 1962. If this was the case, the weather information obtained from Dauphin would suggest that the peak period of seed fall in Duck Mountain was delayed in 1962. Temperature and precipitation during the germination period in 1963 were average, although hours of sunshine from June to August were well below normal (Waldron 1965). Considering the close proximity of the old growth forest to the two study sites and the possibility of a mast year in 1962, seedbed conditions and weather were more likely responsible for any delay in white spruce recruitment.

Others have observed delayed recruitment of white spruce following fire, even using cross dating techniques (Bergeron and Charron 1994). Lieffers et al. (1996) observed some white spruce stands to have immediate recruitment while there was a lag of up to 20 years in others. They observed variable periods of recruitment with some stands displaying a relatively short period of recruitment, from 15 to 20 years, while in others white spruce continued to establish for up to 60 –80 years. Galipeau et al. (1997)

also observed a lag in immediate recruitment, with the first wave of white spruce establishing between 10 to 25 years post-fire and a second wave establishing 40 to 50 years post-fire, with recruitment continuing for approximately 70 years. Bergeron and Charron (1994) observed a five year delay in establishment of white spruce following fire, using cross-dating techniques. Their results support the delay in recruitment observed at Duck Mountain. They suggest that stand composition may be more a reflection of fire behaviour than time since fire.

While high intensity fires expose mineral soil immediately following fire, low intensity fires do not and therefore may cause a lag in recruitment (Lieffers et al. 1996). Indeed, following low intensity fires a large amount of charred duff may remain, which is a very poor seedbed (Nguyen-Xuan et al. 2000). The blackened and porous nature of charred duff promotes extreme temperature and moisture fluctuations. If fire severity was low in some areas of these sites the lack of recruitment immediately post-fire may reflect an inability to establish on charred duff. Thus seedbed conditions rather than seed source distance appear to be more of an influence on the recruitment of cohort 1.

The ability of white spruce to establish will also partly depend on the understory composition that develops immediately post-fire. The lower shrub cover on the PENINSULA site could be responsible for the more rapid recruitment of white spruce at this site, not only as a result of lower competition but also as a result of more successful dispersal. Indeed, white spruce that establishes within a relatively short time period may precede the establishment of hardwood species by several years (Youngblood 1995). Such patterns of recruitment would give white spruce establishing on the PENINSULA site a head start, in terms of early growth and survival.

### 6.1.2 Cohort 2

White spruce recruitment on both study sites started to decrease after approximately 15 years post-fire. Cohort 2 on both sites was limited by seed source distance, although the environmental variables also influenced recruitment. Seed source proximity is most often cited as the determining factor for spatial patterns of white spruce and conifer recruitment especially when seed is dispersing into full canopies (LePage et al. 2000; Asselin et al. 1999; Beach and Halpern 2001; Kneeshaw and Bergeron 1996; Galipeau et al. 1997; Greene and Johnson 2000). Canopies may act as physical barriers and their structure alters air currents, which may either capture or repel dispersing seeds (LePage et al. 2000; Schupp and Fuentes 1995).

The number of seeds dispersing into the study sites 15 years following fire may have been lower than immediately post-fire, as the growing aspen canopies may result in decreased wind speeds and increased variability in wind direction (Stewart et al. 1998). Although some seed will have dispersed in the spring and fall, when aspen trees were bare, shorter distances traveled through full canopies may have decreased white spruce recruitment of cohort 2 at farther distances from the old growth seed source.

The decrease in recruitment observed in this study could also be a result of an inability of white spruce to germinate on the seedbeds present and/or mortality of seedlings growing under poor conditions. It is likely that both played a role in decreasing recruitment. Considering the greater decline on the PENINSULA site, poor growing conditions are a more likely scenario. The PENINSULA site had much higher recruitment of cohort 1 than the MAINLAND site. Therefore, cohort 2 on the

PENINSULA site would have had to compete for light with earlier establishing white spruce from cohort 1. Thus mortality would have been higher on the PENINSULA site.

Lieffers et al. (1996) related periods of lower white spruce recruitment to a decrease in light availability under already established white spruce. They observed shorter periods of recruitment (15 to 20 years) in stands with higher spruce basal areas. The decrease in recruitment in this study was highest between 15 and 30 years post fire. During this period of time white spruce that established in cohort 1 could begin to shade out white spruce establishing in cohort 2. Higher spruce cover on the PENINSULA site may have reduced light to levels that were too low to support higher levels of recruitment during this period. Thus density-dependent mortality, caused by competing white spruce, may have been more of a contributing factor to the decrease in recruitment seen on the PENINSULA site. An inability to establish on the seedbeds present may have been more of a factor on the MAINLAND site.

The growing broadleaf component would have worsened seedbed conditions by the time cohort 2 began to establish at both sites, in addition to presenting a barrier to dispersal. A period of lower white spruce recruitment following the initial flush was observed by Galipeau et al. (1997) 25 years post-fire, which they attributed to inhibition of establishment caused by high shrub and herbaceous cover. Thus increasing shrub cover may have been responsible for decreasing rates of recruitment in cohort 2.

### 6.1.3 Cohort 3

There were many four year old white spruce within cohort 3, which is most likely representative of a mast year. The high levels of establishment observed, support the theory that decreasing recruitment rates are related to mortality rather than poor seedbed suitability. However, the majority of seedlings were observed in moist areas, surrounding wetlands and on moss covered logs of later stages of decay. Thus both seedbed conditions and density-dependent mortality are probably responsible for decreasing recruitment to varying degrees, depending on specific microsite conditions and white spruce densities.

## 6.2 Environmental Effects and White Spruce Recruitment

As discussed, the MAINLAND site was more limited by distance to seed source than was the PENINSULA site such that white spruce recruitment was higher on the PENINSULA site than on the MAINLAND site. It is also possible that seedbed limitations were more problematic on the MAINLAND site. The MAINLAND site had more competition from *Corylus cornuta*, more broadleaf litter, less moss and was slightly drier than the PENINSULA site.

The spatial distribution of regenerating white spruce on the PENINSULA site also tended to be more heterogeneous than on the MAINLAND site. High and low density phases of white spruce were very pronounced on the PENINSULA site. The greater heterogeneity on the PENINSULA site was likely due to its greater topographic complexity, which in turn would have made the soil moisture on this site much more spatially variable and therefore more limiting.

### **6.2.1 Birch**

The biotic variables entered in the PCA analysis represented the abundance of deciduous, shrub, herbaceous and moss cover. An interesting point to note is that white spruce abundance on the MAINLAND site was related to the presence of birch along the first PCA axis. High N-availability has been observed under birch, whereas high Ca-availability has been observed under aspen (Pare et al. 1993; Brais et al. 1995). The maintenance of high N-mineralization rates may be viewed as an important determining factor of white spruce recruitment, as N-availability is typically low under coniferous canopies. Indeed, birch has been stated as having an “almost legendary reputation as a soil improver” (Binkley and Giardini 1998). Therefore, the occurrence of white spruce under birch may have been related to a nutrient gradient, which affected the spatial distribution of white spruce recruitment on the MAINLAND site.

### **6.2.2 Broadleaf Litter**

The greater recruitment rates of white spruce on the PENINSULA site versus the MAINLAND site may partly be a result of differences in the surrounding canopy cover, which had a much higher deciduous component on the MAINLAND site as a consequence of its higher shrub cover. White spruce may require a protective cover of vegetation (Kneeshaw and Bergeron 1997). In addition, deciduous litter may limit the development of a moss cover. Moss cover may decrease soil temperature and nutrient uptake (Van Cleve and Yarie 1986).

However, the mechanical barrier and lower moisture holding capacity presented by leaf litter inhibits regeneration of white spruce (Parker et al. 1997). White spruce



germinants have difficulty extending a tap root through organic layers thicker than 5 cm. This inability to reach moister substrates contributes to drought induced mortality (Parker et al. 1997). Furthermore, mortality caused by crushing of white spruce seedlings by deciduous leaf litter may be very high (Galipeau et al. 1997; Delong et al. 1997; Kneeshaw and Bergeron 1997; Lieffers et al. 1996), especially for seedlings less than 5 years old or less than 5 inches tall (Gregory 1996). Thus the lower shrub cover on the PENINSULA site may have benefited establishing white spruce.

The broadleaf litter variable entered into the abiotic PCA analysis was associated with the drier end of the PCA axis, which supported less regenerating white spruce; further evidence for a detrimental effect of litter on the MAINLAND site. On the PENINSULA site the broadleaf litter variable was less influential in the abiotic PCA analysis. Thus other factors may have contributed to the higher white spruce recruitment on the PENINSULA site.

### **6.2.3 Moss**

Higher recruitment rates on the PENINSULA site may have been related to its greater moss cover. The PENINSULA site had much greater moss cover and the MAINLAND site showed a tendency for white spruce to establish on mossy areas rather than areas with high deciduous cover. Mosses that remain moist and are not too thick may provide receptive seedbeds and allow regenerating conifers to escape dessication and competition from other species (Parker et al. 1997). Reduced amounts of herbaceous competitors on moss seedbeds reduce shading and increase soil moisture availability. The rough surface of mosses may also capture seeds and hold them until sufficient water is

imbibed for germination (Johnson and Fryer 1992). Additionally, physical support provided by moss shoots could facilitate seed penetration and prevent seedlings from mechanical injury. Mosses do not only provide protection from crushing by falling deciduous leaf litter but the elevated position of moss colonies may also shed litter onto surrounding microdepressions (Parker et al. 1997).

However, it is important to note that deep moss mats (>5 cm) may prevent contact between seedlings and soil and shade germinating seeds (Harmon and Franklin 1989). Moss also has a negative effect on the soil thermal regime, which may slow down plant nutrient uptake (Van Cleve and Yarie 1986). Thus depending on environmental conditions moss may be an unfavourable seedbed (LePage 2000). As moss cover and thickness increase with age, the benefits of such a seedbed may decrease (DeGrandpre et al. 1993). Thus thickening of the moss layer may have been partially responsible for the precipitous decrease in recruitment on the peninsula site, especially if the high recruitment in cohort 1 resulted from the presence of mossy seedbeds of shorter moss communities. MacDonald et al. (2001) report decreased recruitment of white spruce to occur at approximately 10 years post-fire, which they also attribute to thickening of the moss layer up to a point that interferes with seedling establishment.

Youngblood (1995) observe a decrease in recruitment 30 years post-fire. However, they report that white spruce does germinate on thick mats of moss and that a decrease in recruitment reflects low survival rates. This lends weight to the argument that density-dependent mortality had a strong influence on the decrease in white spruce recruitment of cohort 2 on the PENINSULA site. Thus both seedbed conditions and

intraspecific competition may have been preventing establishment and promoting mortality of cohort 2 on the PENINSULA site.

#### **6.2.4 Decaying logs**

Coarse woody debris was not a strong component of the abiotic PCA analysis. However, seedbeds with high cover of decaying logs were also highly correlated with moss cover. Since moss cover in the biotic PCA analysis was highly associated with white spruce abundance, the strong relationship between moss and decaying logs in the PCA's suggests that white spruce germinants may have benefited from the presence of decaying logs.

A propensity for white spruce to germinate on logs under aspen canopies has been attributed to higher temperatures, a more stable water supply and higher photosynthetic rates, as well as lower soil strength, which promotes root penetration (DeLong et al. 1997; Beach and Halpern 2001; Lieffers et al. 1996). Decaying logs elevate seedlings even more so than moss colonies and thus further decrease competition, increase light levels and reduce crushing by leaf litter (DeLong et al. 1997; Harmon and Franklin 1989). Furthermore, such an elevated position may prevent flooding of seedlings by standing water. This may explain the high abundance of third cohort seedlings on moss covered logs surrounding wetlands at both sites. Freshly fallen logs colonized by young mosses or disturbed surfaces of older logs may increase recruitment (Harmon and Franklin 1989), however, decay stage has also been found to have no effect on recruitment rates (Beach and Halpern 2001). Within these study sites white spruce germinating on logs tended to be dependent on both the degree of moss cover and the

stage of decay. Older, softer logs with shorter moss communities supported the greatest number of white spruce germinants.

#### **6.2.5 Moisture and nutrients**

The abiotic variables which formed a moisture and nutrient gradient in the PCA analyses had the strongest effect on later establishing white spruce on the PENINSULA site and a weak effect on the MAINLAND site. White spruce abundance increased with increasing moisture, clay content and conductivity and decreased with increasing sand content, elevation and slope. White spruce regeneration may be associated with both sandy, loamy soils (Galipeau et al. 1997) and with fine textured soils of silt and clay (Kneeshaw and Bergeron 1996). Coarser soils have better aeration, drainage and stability, while clay soils are more fertile and have denser vegetation. Of course such results must be interpreted in the context of the specific study site. The soils of the MAINLAND and PENINSULA sites tended to be coarse, sandy loams, thus lending themselves to dryness. Therefore, moisture availability is very important on these sites. Furthermore the variable topography of these sites produces extreme microsites on dry hillslopes and beside wetlands. Thus changes in elevation and slope will have magnified effects on soil moisture, especially on the more topographically complex PENINSULA site. It is likely that this effect is not as strong for the initially establishing cohorts because the number of seeds available for germination may have been much higher.

An interesting point to note is the higher abundance of *Equisetum arvense* on the PENINSULA site. It has been reported that the presence of this species is correlated with better white spruce establishment, growth and survival compared to that under aspen

(Cater and Chapin 2000). This is believed to result from greater nitrogen availability in patches of *Equisetum arvense*. These findings emphasize that the high degree of variability in white spruce recruitment under different conditions results from complex interactions that may be apparent only at smaller scales of observation.

### 6.3 Seedling Survival

Survival rates of white spruce are typically lower for younger individuals (Xiaohong et al. 2001). During the first year of establishment drought stress may lead to high mortality rates due in part to poor root to soil contact (Marsden et al. 1996; Eis 1967). Some vegetation cover may prevent dessication by protecting seedlings from wind, erosion and frost damage and increasing shade and humidity (Groot 1999; Comeau et al. 1993). Thereafter seedling mortality tends to be greater on moist, rich sites as a result of frost heaving and increasing competition that may physically damage seedlings or severely decrease light levels. Given the cool moist conditions in the Duck Mountains, mortality after the first year may be quite high.

Early competition between white spruce and shrubs and herbs is important because the effects of competition are cumulative and have a strong impact on seedlings, which may not be apparent until the fourth growing season or later (Jobidon 2000). Thus even though we found a high abundance of 4 year old seedlings, any effects of competition with mosses or herbs may have been undetectable. Furthermore, many of the abundant germinating seedlings on moss covered logs may become overcrowded and die as a result.

As time since fire progresses, broadleaf litter and moss cover thickens resulting in taller thinner seedlings in response to steeper light gradients (Parker et al. 1997). This leads to lower mechanical strength and greater vulnerability to mortality by leaf crushing. However, it also leads to a higher root:shoot ratio, which may confer better survival during drought stress. Considering the moist climate and high leaf litter at these sites it seems likely that crushing by leaf litter could have been responsible for any decreases in recruitment resulting from seedling mortality.

## **6.4 White Spruce Growth, Suppression and Mortality**

### **6.4.1 MAINLAND**

In general, white spruce on the MAINLAND site tended to be shorter at a given age. Stand density and light interception are most often used to predict growth (Lieffers et al. 1999; Messier et al. 1999). Understory competition, soil moisture, nutrients and slope may also be useful in predicting white spruce growth and mortality (Wang 1995). The canopy under which white spruce regenerates influences understory composition, moisture, light and soil temperature (Kneeshaw and Bergeron 1997). White spruce regenerating under deciduous canopies, such as aspen and birch, must compete with faster growing trees, shrubs and herbs. Higher understory cover decreases light and root growing space, thereby decreasing productivity. Thus white spruce growing under the thick shrub layer of *Corylus cornuta* on the MAINLAND site would have been subject to slower growth. More suppressed growth of later establishing white spruce (cohort 2) could be a result of increasing shrub cover, increasing litter and decreasing light availability (Lieffers et al. 1996). These results are supported by Hostin and Titus (1996)

who report that suppression of white spruce height growth is most pronounced underneath the shrub layer, which tends to be thickest several decades following fire (DeGrandpre 1997).

Conversely, earlier establishing white spruce that have overtopped the sub-canopy may be growing under adequate light conditions to maintain healthy growth. Aspen canopies transmit 15 – 40% light above the shrub layer (1.3 m), sufficient light for acceptable growth of white spruce saplings (Constabel and Lieffers 1996). Growth of white spruce under 40% light is similar to that under open grown white spruce and growth has actually been reported to decrease under full light (Lieffers and Stadt 1994). The greater proportion of unsuppressed trees in cohort 1 on the MAINLAND site likely resulted from overtopping the shrub layer. This is also supported by the fact that aspen canopies typically do not suppress white spruce growth (Hostin and Titus 1996).

The steeper slopes and therefore drier slopes of the MAINLAND site may also have been responsible for shorter white spruce heights. Slopes of greater than 10% have been reported to decrease white spruce productivity (Wang et al. 1995). Ultimately, the slower recruitment rates onto the MAINLAND site would have resulted in shorter white spruce.

#### **6.4.2 PENINSULA**

White spruce on the PENINSULA site tended to be taller and have more variable and thinner growth forms. White spruce on the PENINSULA site may have required a taller growth form to compete for light with neighboring white spruce. Although height

may decrease with increasing stand density, a greater proportion of white spruce within a stand has been found to result in greater white spruce heights (Huang and Titus 1999).

The higher variability in height for the earlier establishing white spruce (cohort1) also suggests that the increasing white spruce densities may have been influencing white spruce growth on the PENINSULA site. Another possibility is that shrub cover may have been more abundant when cohort 1 was establishing thereby introducing further variability in height.

The trend towards greater suppression of cohort 2 suggests that intraspecific competition between white spruce, on the more densely populated PENINSULA site, was contributing to suppression of later establishing white spruce. Indeed light transmittance through white spruce may be one half to one tenth that under aspen canopies (Constabel 1995).

Moisture and elevation are additional factors that may be responsible for greater heights of white spruce on the PENINSULA site. Greater soil moisture decreases drought stress experienced by white spruce growing under high light conditions (Wright et al. 1998). Thus white spruce growing in the low density plots on the moister PENINSULA site may have been able to attain greater heights.

The higher growth rates on the PENINSULA site also result in white spruce being more subject to mortality (Xiaohong et al. 2001; Lieffers et al. 1999; Messier et al. 1999). In an effort to reach sufficient light levels for healthy growth, competing white spruce may succumb to mortality before adequate heights are reached. This conclusion is supported by the fact that white spruce on the denser PENINSULA site had much higher mortality rates of 10 – 30 year old individuals than on the MAINLAND site. These



findings are in agreement with Xiaohong et al. (2001) who found that white spruce survival is greater in stands with a higher proportion of aspen, such as those found on the MAINLAND site.

## CHAPTER 7

### SUMMARY AND CONCLUSIONS

#### 7.1 Major Findings

The highest amount of variation in white spruce recruitment that was explained by spatial and environmental variables was 39.4% for cohort 2 on the MAINLAND site, leaving 60.6% of the variation unexplained. Asselin et al. (2001) report 64% unexplained variation in predicting conifer recruitment. They suggest that the unexplained variation may reflect variation in non measured factors such as stochastic variation, germination bed, shade, humidity, soil temperatures, thickness of the organic layer, nutrient availability and competition. Also fire-wide differences that influence percent cover of optimum seedbeds, interaction of drought and mast years, density of small residual stands and topography contribute to unexplained variation of tree recruitment from burn edges (Greene and Johnson 2000). However, these variables were not measured during the early stages of recruitment.

Asselin et al. (2001) also found that spatial variables accounted for more than two times the variation accounted for by the environmental variables measured. Others agree that distance to seed source is the most important variable to consider when predicting regeneration success of white spruce and other conifer species (Galipeau et al. 1997; Beach and Halpern 2001), while environmental effects are much less useful (Kneeshaw and Bergeron 1996). Spatial variables were more important than the environment in predicting white spruce recruitment of cohort 2 on the MAINLAND and PENINSULA sites, although environmental variables also proved to be important. The environmental

variables were more important than the spatial variables in predicting white spruce abundance of MAINLAND cohort 1.

## **7.2 Seed Source Proximity versus Seedbed Suitability**

The initial pattern of seed dispersal determines potential recruitment rates. However, the contribution of seed source proximity changes with changing environmental effects on individuals at different life stages (Nathan and Muller-Landau 2000). Processes subsequent to dispersal, such as seedbed influences on germination and survival, may erase or alter initial patterns of dispersal causing the final pattern of recruitment to be spatially unrelated to dispersal. For wind dispersed seeds, such as white spruce, there may be a conflict between small seed size, which promotes dispersal, and large seed size, which promotes seedling survival (Schupp 1995). Furthermore, sites that promote seed deposition, such as rough or raised surfaces of logs and moss, may promote seedling establishment but not growth (Nathan and Muller –Landau 2000).

The influence of seed source proximity on white spruce recruitment of cohort 2 on both sites is especially strong considering the fact that even after passing through the environmental filter relationships between distance and abundance were still significant. For cohort 1 on the MAINLAND site the effects of environmental factors may have masked the initial patterns of seed dispersal, such that the present patterns of white spruce recruitment reflect environmental conditions. The prolific seed dispersal onto these sites and the ability of environmental variables to predict white spruce recruitment has allowed for the specific effects of seedbed and competition to be more precisely determined.

### 7.3 MAINLAND cohort 1

White spruce abundance of cohort 1 on the MAINLAND site was mainly influenced by biotic factors, such as birch, shrub and moss cover. The detrimental effects of high shrub cover were to be expected. However, discrepancies in the literature between the advantages and disadvantages of moss cover continue to persist. For these sites moss cover was advantageous. The protection from crushing by leaf litter that mosses can confer to establishing white spruce seedlings is most likely responsible for these results.

The tendency for white spruce to occur with birch on the MAINLAND site was unexpected. The positive influence that birch may have on nutrients and nitrogen availability suggests that white spruce regeneration may be more dependent on nutrient availability than usually given credit. Although nutrient availability has been stated as being important, its ability to determine white spruce recruitment success is not well known, as it is a difficult variable to quantify and one in which the scale of study is extremely important.

The importance of the effects of species on the environment, rather than direct competition between species has also been noted for white spruce recruiting into patches of *Equisetum arvense* (Cater and Chapin 2000). Further evidence for the importance of such interactions is provided by the theory that heterogeneity of recruitment is determined immediately following fire, by the spatial variation in fire intensity, which determines survival of below ground parts of understory species (Kneeshaw and Bergeron 1997; Coates et al. 1994; Bergeron and Charron 1994; Wurtz and Zasada 2001). The dependence of spatial patterns of recruitment on fire severity, topography,

seed bearing survivors and nutrient availability requires study on multiple spatial scales (DeGrandpre et al. 1993).

#### **7.4 MAINLAND cohort 2**

The limiting effect of seed source on cohort 2 on the MAINLAND site was likely a result of the greater distance to seed source in combination with the barrier to dispersal presented by the growing aspen canopy. The effect of the biotic variables on cohort 2 is similar to that for cohort 1. However, the combined effects of lower rates of seed arrival and worsening of seedbed conditions and competition from *Corylus cornuta* cover, resulted in an overall decrease in recruitment rates of cohort 2. Crushing of white spruce seedlings by aspen litter in the Duck Mountains has been previously reported (Dyck 1994).

The growth suppression of cohort 2 on the MAINLAND site emphasizes the effects of changing environmental conditions over time. The increasing cover of shrub and herb layers resulted in suppressed growth of cohort 2. Conversely, cohort 1, which had already overtopped the subcanopy layers, was “free to grow”.

#### **7.5 PENINSULA cohort 1**

Recruitment of cohort one on the PENINSULA site was very successful and thus the variables measured were not observed to have a significant limiting effect. It is likely that seed dispersal was highly prolific and seedbed conditions were sufficient for white spruce recruitment.

## **7.6 PENINSULA cohort 2**

Recruitment of cohort 2 on the PENINSULA site was limited mainly by distance to seed source and moisture and nutrient availability. These results stress the importance of complex topographical effects on white spruce recruitment through its influence on soil moisture, in addition to lending support to the importance of nutrient dynamics. The lower elevation, and thus closer position to the water table, and lower slopes on this site result in greater moisture availability.

The decrease in recruitment on the PENINSULA site likely reflects the high degree of density-dependent mortality on this site such that dispersal patterns may have been masked (Nathan and Muller-Landau 2000; Houle 1994). Many of the seeds that disperse short distances will succumb to mortality once a certain density threshold is reached, whereas seeds dispersing greater distances will have more space for growth and survival. Cohort 2 on the PENINSULA site will also have been subject to worsening of seedbed conditions and decreased dispersal capabilities as a result of the growing aspen canopy.

Changing environmental effects on white spruce growth are also apparent on the PENINSULA site. As a result of increasing white spruce densities on the PENINSULA site, cohort 2 height growth is suppressed, whereas cohort 1 was receiving more light and therefore was able to increase growth in an attempt to out compete neighboring white spruce.

## **7.7 MAINLAND and PENINSULA Cohort 3**

Cohort 3 was mainly affected by moisture and nutrients, although distance from seed source and biotic factors were influential, particularly on the MAINLAND site. It can be inferred from these results that abiotic variables are more limiting during early stages of establishment, while biotic factors become more important as seedlings struggle to grow and survive. The high abundance of four year old seedlings supports the theory that undisturbed forest floors can be an excellent seedbed for white spruce regeneration (Wurtz and Zasad 2001). Furthermore the high levels of seedling recruitment stress the importance of mortality in determining white spruce regeneration success.

## **7.8 Further Research**

The relative importance of seed source proximity, seedbed suitability and competition will change over time. Germination of seeds, establishment of seedlings and growth and survival of saplings each may require their own unique habitats (Schupp and Fuentes 1995). Conflicts between the needs and responses of white spruce at different developmental stages to seedbeds, light, water and competition reduce the abundance and spatial heterogeneity of recruits. Such conflicts are widespread in natural systems, although little attention has been paid to this issue (Schupp 1995).

Long-term studies that assess the changing needs and responses of white spruce to inter-related variables are required to further our understanding of white spruce recruitment success. Studies that examine such issues on a range of spatial scales would be particularly useful in determining the importance of specific environmental variables that vary with different scales of measurement.

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**APPENDIX I**  
**MAINLAND data**

10	-3.807	2.939	2.026	-1.454	-0.471	-1.897	0.239	0.14
9	2.036	0.083	0.246	-1.57	-1.352	-0.526	-1.801	-0.317
8		2.067	-0.844	2.656	0.154	1.381	0.765	0.295
7			-1.483	0.446	1.076	0.02	0.692	0.334
6		-1.463	-0.97	-3.077	-2.324	0.372	-1.037	0.91
5	-2.144	-0.912	-0.521	0.036	-0.082	-1.023	1.267	0.112
4	-0.098	-0.809	0.269	0.765	2.055	1.28	2.746	-0.876
3	0.122	3.012	-1.26	0.337	-2.304	-2.211	-0.122	-0.336
2	0.574	0.791	-1.995	1.938	-1.993	-3.779	-0.618	1.693
1	-3.086	0.423	1.143	-0.437	3.054	0.9	2.907	4.697
	<b>H</b>	<b>G</b>	<b>F</b>	<b>E</b>	<b>D</b>	<b>C</b>	<b>B</b>	<b>A</b>

### BURN EDGE

Figure. I.1 a) MAINLAND biotic PCA axis scores

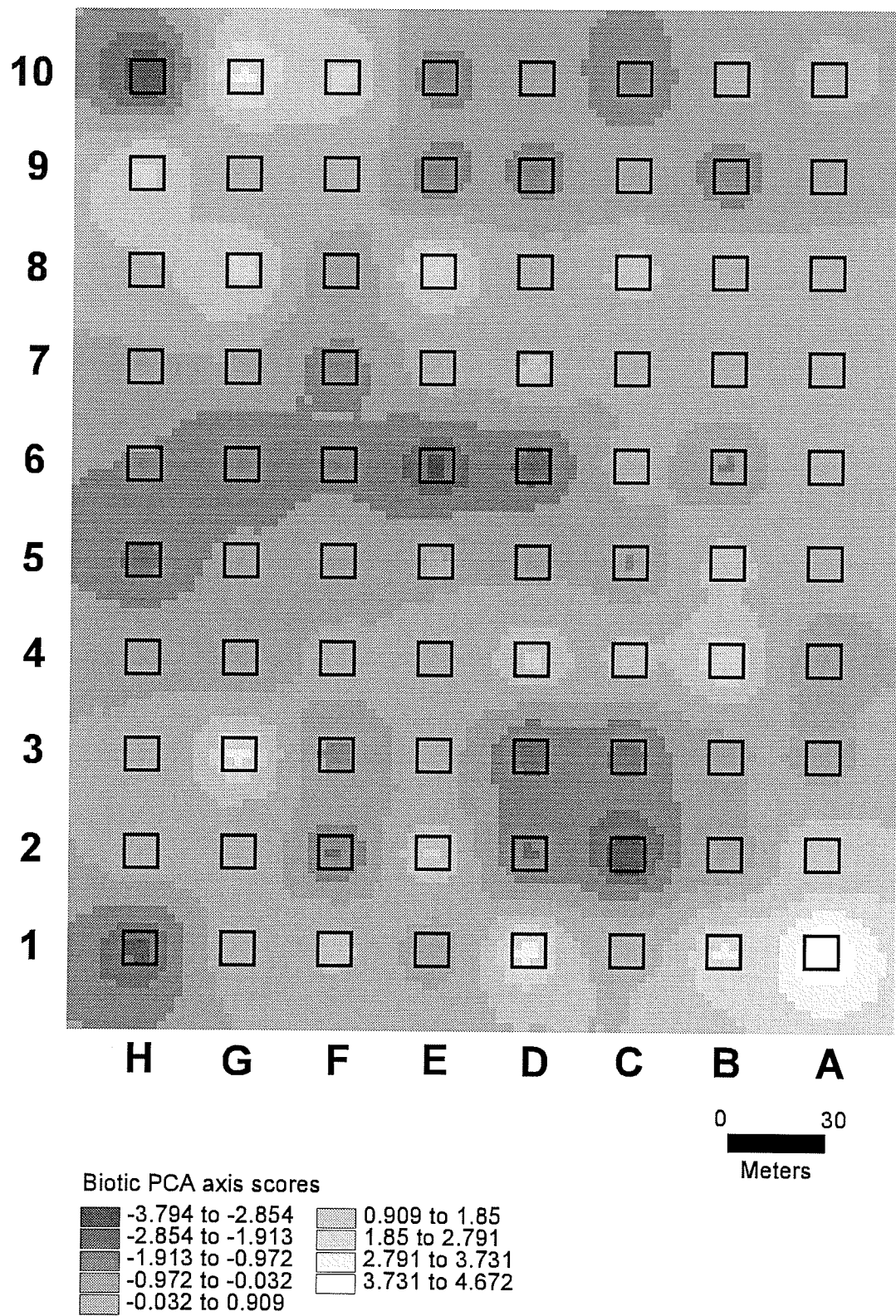


Figure I.1 b) MAINLAND surface interpolation of the biota.

10	0.27	-3.865	-2.089	-1.425	-0.719	0.658	0.131	1.111
9	-1.146	-2.236	-1.24	-0.332	-1.372	-2.269	0.026	2.125
8		2.842	-2.234	-0.756	0.391	-1.135	0.987	0.83
7			-1.66	-2.651	-1.928	-1.701	0.578	-0.249
6		-0.537	-1.087	-0.654	-0.005	-0.531	-1.248	-0.568
5	-0.864	-0.006	3.055	-2.32	-1.696	-1.579	-3.752	-1.052
4	1.244	-0.68	-3.028	1.349	-0.313	-1.089	-1.127	2.78
3	-1.441	-0.702	-0.864	2.594	-0.519	0.654	1.7	4.627
2	0.463	3.175	0.214	0.63	3.654	2.08	2.85	1.816
1	0.464	2.285	1.872	2.661	4.242	-0.415	-0.243	0.971
	H	G	F	E	D	C	B	A

### BURN EDGE

Figure. I.2 a) MAINLAND abiotic PCA axis scores

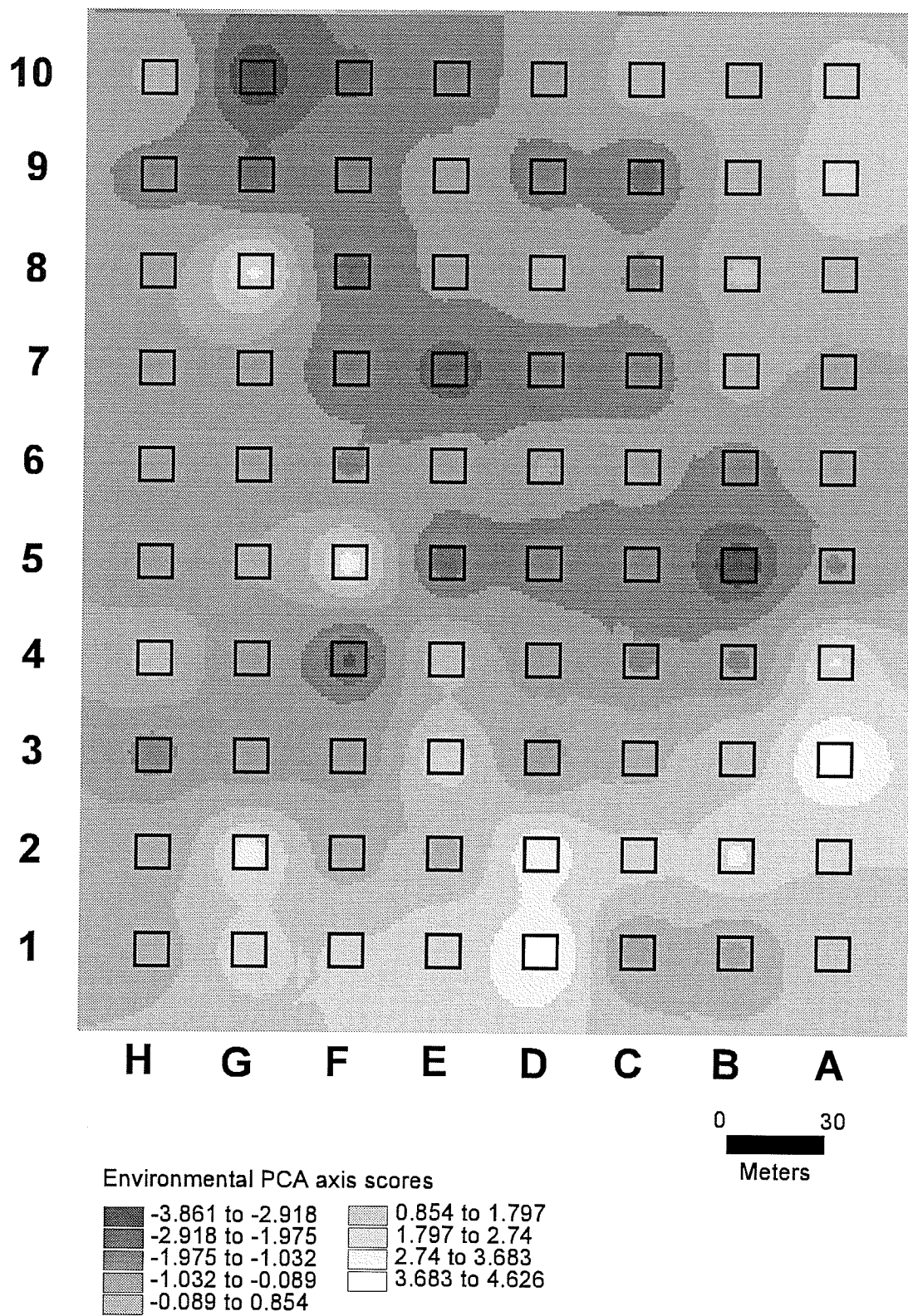


Figure 1.2 b) MAINLAND surface interpolation of the abiotic.



									SUM
10	22				1	2	13	38	76
9	5	6	2		6	5	2	12	38
8		1	5	2	2	3	4	7	24
7			6			6	1	5	18
6		9	12	10	17	4	2	2	56
5	18	12			10	5		2	47
4	13	14	9	6	4	1	2	3	52
3	8	7	3	2	9	21	25	1	76
2	22	13	12	20	78	54	58	8	265
1	53	13	7	20	1	8	6	3	111
	H	G	F	E	D	C	B	A	TOTAL = 763

### BURN EDGE

Figure. I.3 a) LIVE WHITE SPRUCE ABUNDANCE / 10 X 10 M PLOT ON MAINLAND

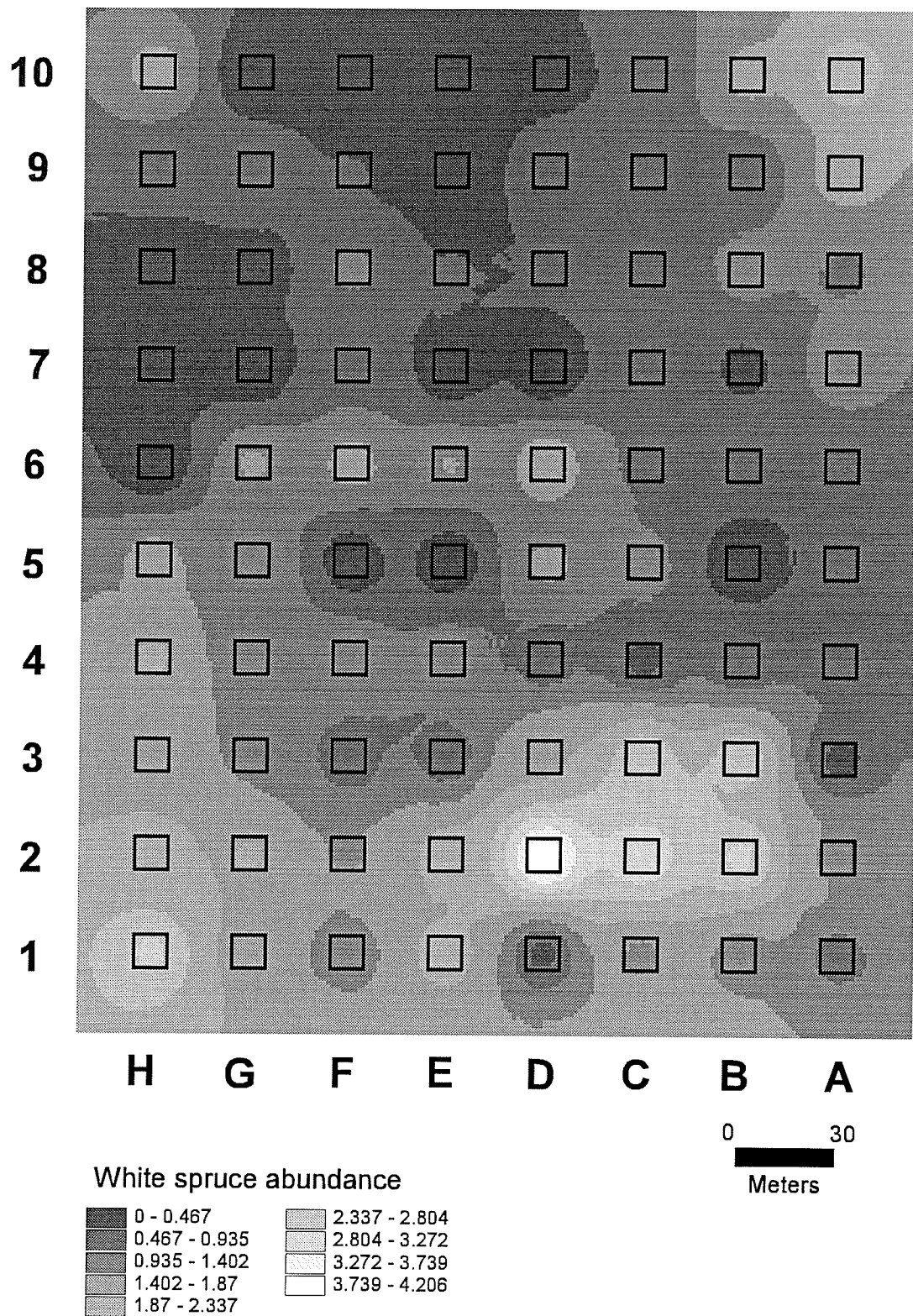


Figure I.3 b) MAINLAND total white spruce abundance (log-transformed).

											SUM	
10	21								2	11	35	69
9	5	6	2			6			5	2	7	33
8			2			2			1	2	7	14
7			6						6		2	14
6		4	4	8		13			3	1	1	34
5	17	11				4			3		1	36
4	9	14	7	4		4					2	40
3	5	3	3	1		3			6	15		36
2	13	9	11	11		21			2		6	73
1	27	6	6	13					2	3	1	58
	H	G	F	E	D	C	B	A				407

### BURN EDGE

Figure. I.4 a) WHITE SPRUCE coh 1 ABUNDANCE / 10 X 10 M PLOT ON MAINLAND

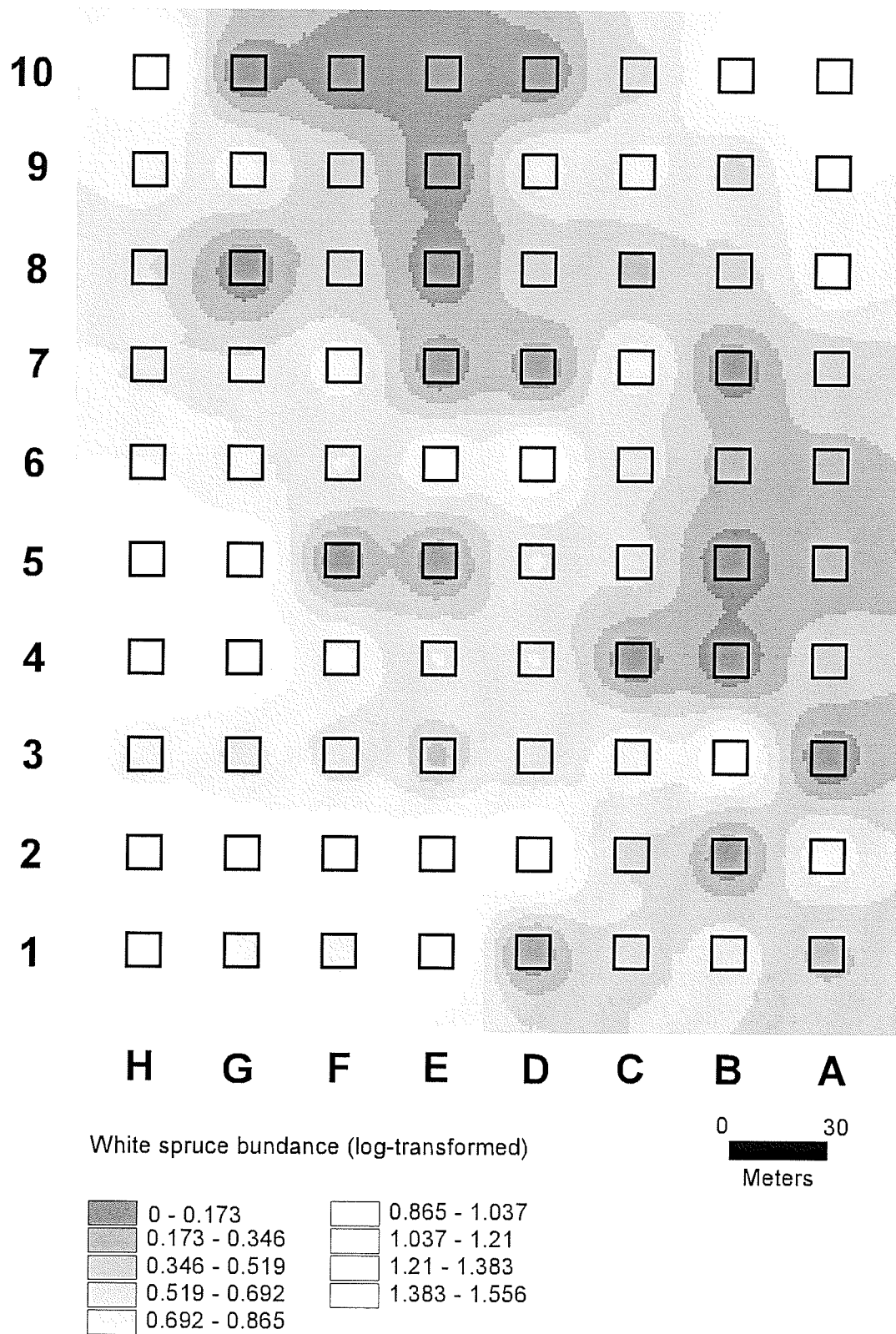


Figure I.4 b) MAINLAND COHORT 1 surface interpolation of white spruce abundance.

									SUMS
10	1				1		2	3	7
9								5	5
8		1	3	2		2	1		9
7								1	1
6		5	8	2	4	1	1	1	22
5	1	1			6	2		1	11
4	2		2	2		1	1	1	9
3	1	4		1	2	10	7	1	26
2	9	3	1	9	40	39	20	2	123
1	26	7	1	7	1	6	3	2	53
	H	G	F	E	D	C	B	A	266

### BURN EDGE

Figure. I.5 a) WHITE SPRUCE coh 2 ABUNDANCE / 10 X 10 M PLOT ON MAINLAND

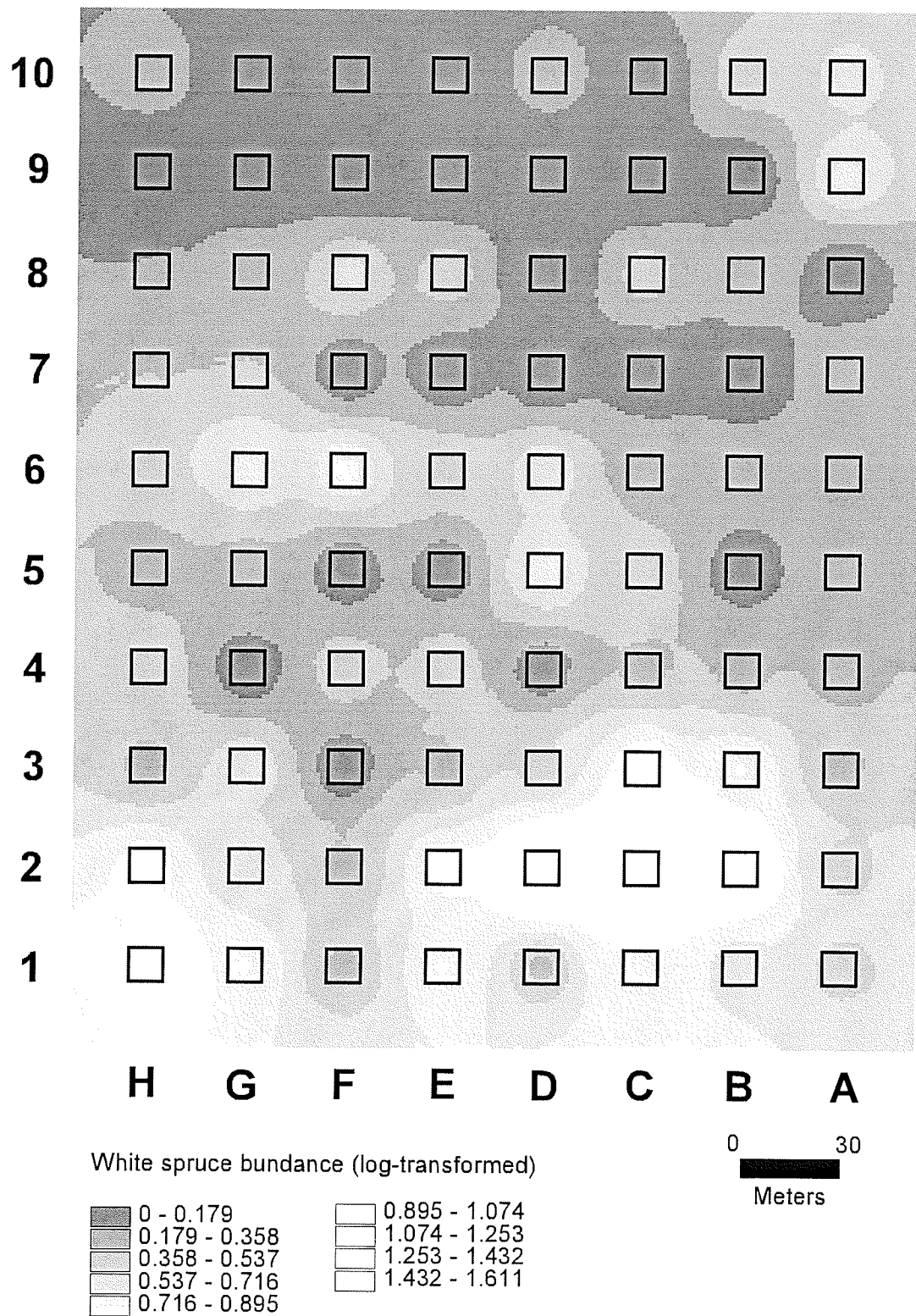


Figure I.5 b) MAINLAND COHORT 2 surface interpolation of white spruce abundance.

								SUM	
10								0	
9								0	
8						1		1	
7						1	2	3	
6								0	
5								0	
4	2					1		3	
3	2			4	5	3		14	
2		1		17	13	38		69	
1								0	
	H	G	F	E	D	C	B	A	90
BURN EDGE									

Figure. I.6 a) WHITE SPRUCE coh 3 ABUNDANCE / 10 X 10 M PLOT ON MAINLAND



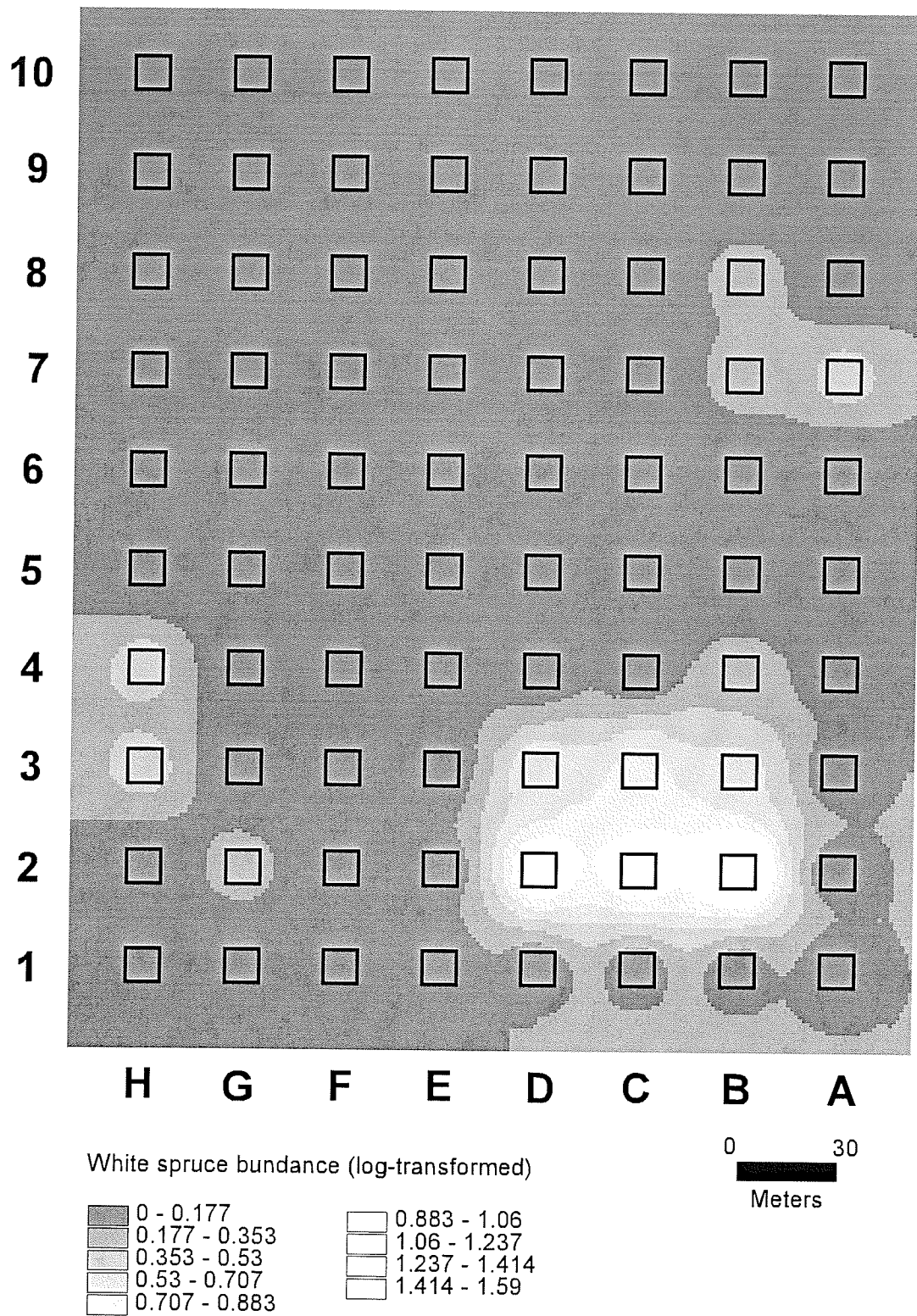


Figure I.6 b) MAINLAND COHORT 3 surface interpolation of white spruce abundance.





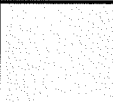
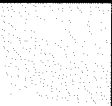
								SUM	
10						2	6	8	
9								0	
8			1					1	
7								0	
6								0	
5						1		1	
4					1			1	
3	1						1	2	
2		1		1	12			14	
1	1							1	
	H	G	F	E	D	C	B	A	28
BURN EDGE									

Figure. I.7 a) DEAD WHITE SPRUCE ABUNDANCE / 10 X 10 PLOT ON MAINLAND

**APPENDIX II**

**PENINSULA DATA**

10	-2.428	-0.293	0.347			-3.268	-0.312	1.273
9	4.89	-0.657	-0.414	-0.478		0.958	0.486	
8	0.33	-0.309	-0.813	0.009	0.666	-0.99	-1.067	
7	-1.326	0.386	-0.251	-1.479	-0.92	-0.803	-0.086	
6	0.478	0.864	0.261	0.134	0.421	1.543	0.154	-0.34
5	-0.178	-1.202	0.314	1.436	0.35	3.195	0.383	0.69
4	4.554	0.394	1.491	0.24	0.387		-0.278	0.077
3	1.189	-0.513	-1.109	-0.62	1.825	-3.338	2.121	-0.261
2	1.45	-0.269	-0.131	0.148	-0.75	0.053	-0.818	-0.437
1	0.432	-1.345	-1.736	-0.27	-1.34	-1.672	-0.845	-0.568
	I	J	K	L	M	N	O	P

### BURN EDGE

Figure. II.1 a) PENINSULA biotic PCA axis scores

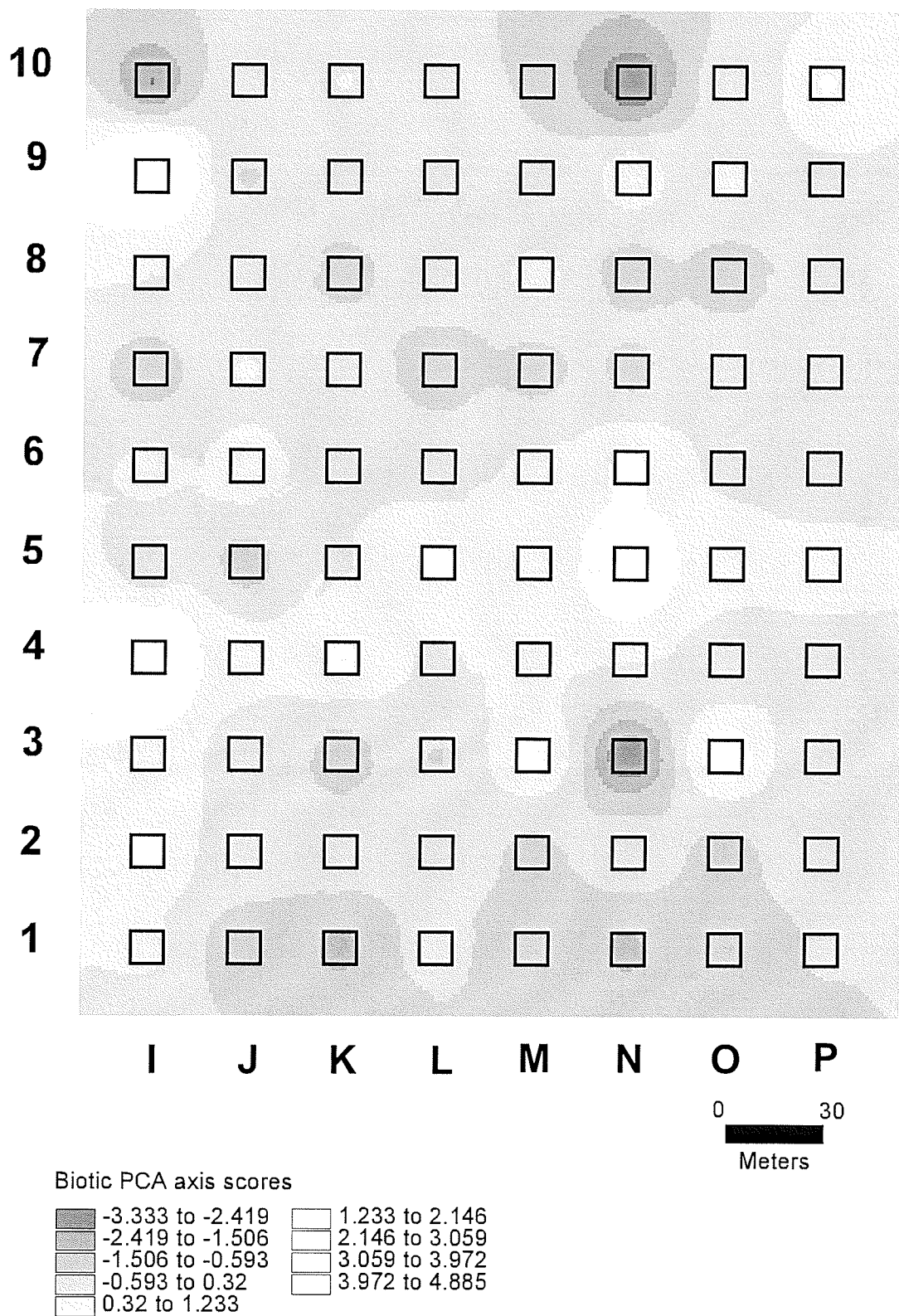


Figure II.1 b) PENINSULA surface interpolation of the biota.

10	1.126	-0.019	-0.357			5.357	-0.689	-0.892
9	0.114	-0.688	-0.53	2.602		-2.706	0.068	
8	-0.525	-2.272	0.72	-2.734	0.81	-2.107	-0.049	
7	-1.66	-0.545	-1.818	-0.442	-0.29	0.264	1.267	
6	3.059	0.644	1.167	0.914	-0.238	0.281	0.62	2.15
5	4.406	2.59	-3.176	-1.842	0.96	-0.857	2.743	-1.883
4	-1.75	-2.53	-3.036	-0.849	0.218		3.97	-1.148
3	-0.711	-2.477	-2.645	-1.112	-0.582	3.599	3.505	2.025
2	-0.828	-1.231	-0.733	-2.812	0.84	3.334	3.313	3.9
1	-2.507	-0.52	-1.172	-0.311	-1.277	-1.812	0.636	-0.835
	I	J	K	L	M	N	O	P

### BURN EDGE

Figure. II.2 a) PENINSULA abiotic PCA axis scores

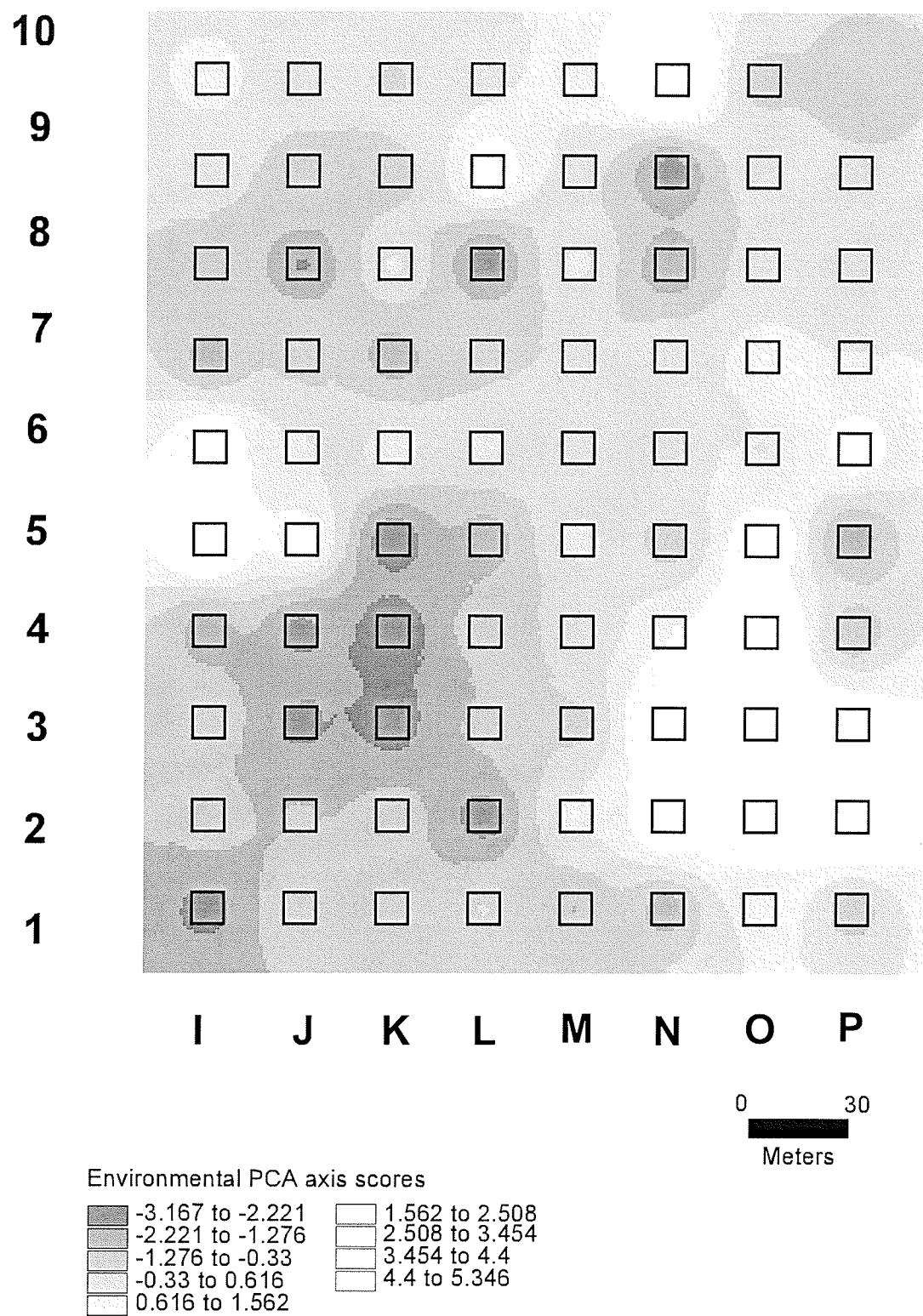


Figure II.2 b) PENINSULA surface interpolation of the abiotic.

									SUM
10	6	4	6			4	16	7	43
9	22	10	3	11		5	6		57
8	1	5	4	3	7	7	42		69
7	6		1	12	13	11	32		75
6	9	7	8	3	17	14	13	10	81
5	13	11	5	9	1	1	5	8	53
4	42	11	5	3	4		27	13	105
3	5	8	6	8	5	70	27	12	141
2	14	7	11	23	10	19	13	22	119
1	43	1	4	93	7	43	35	10	236
	I	J	K	L	M	N	O	P	TOTAL = 979

### BURN EDGE

Figure. II.3 a) LIVE WHITE SPRUCE ABUNDANCE / 5 X 5 M ON PENINSULA

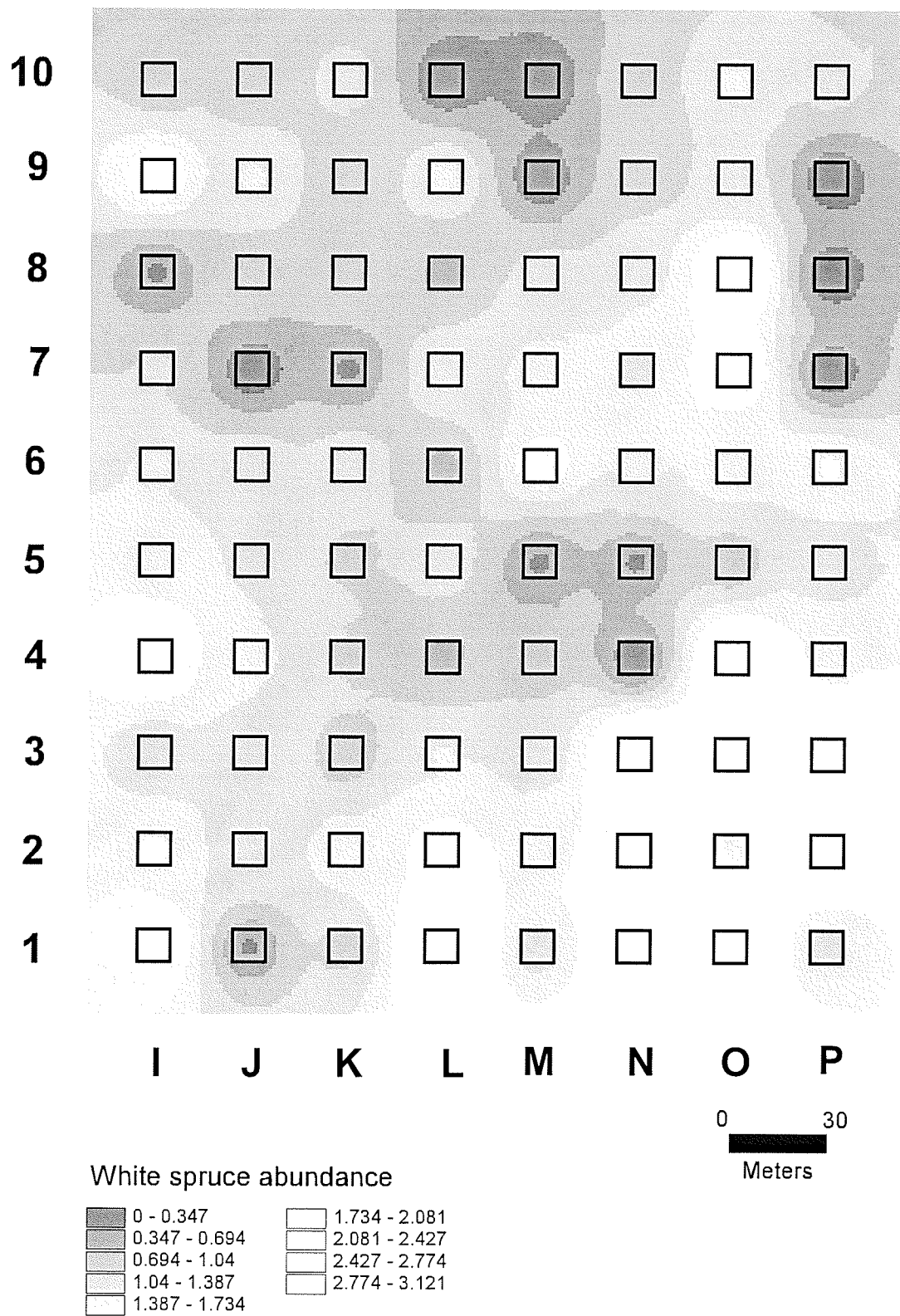


Figure II.3 b) PENINSULA total white spruce abundance (log-transformed).



								SUM	
10	6	4	3			1	15	6	35
9	13	8	2	4		5	4		36
8	1	4	2	3	6	5	30		51
7	5		1	11	11	10	24		62
6	6	5	6	3	13	13	10	5	61
5	9	10	4	8		1		7	39
4	33	9	4	3	1		14	9	73
3	2	7	6	4	3			7	29
2	9	5	8	19	7	14	9	15	86
1	38	1	3	77		30	17		166
								638	

### BURN EDGE

Figure. II.4 a) WHITE SPRUCE coh 1 ABUNDANCE / 5 X 5 M ON PENINSULA

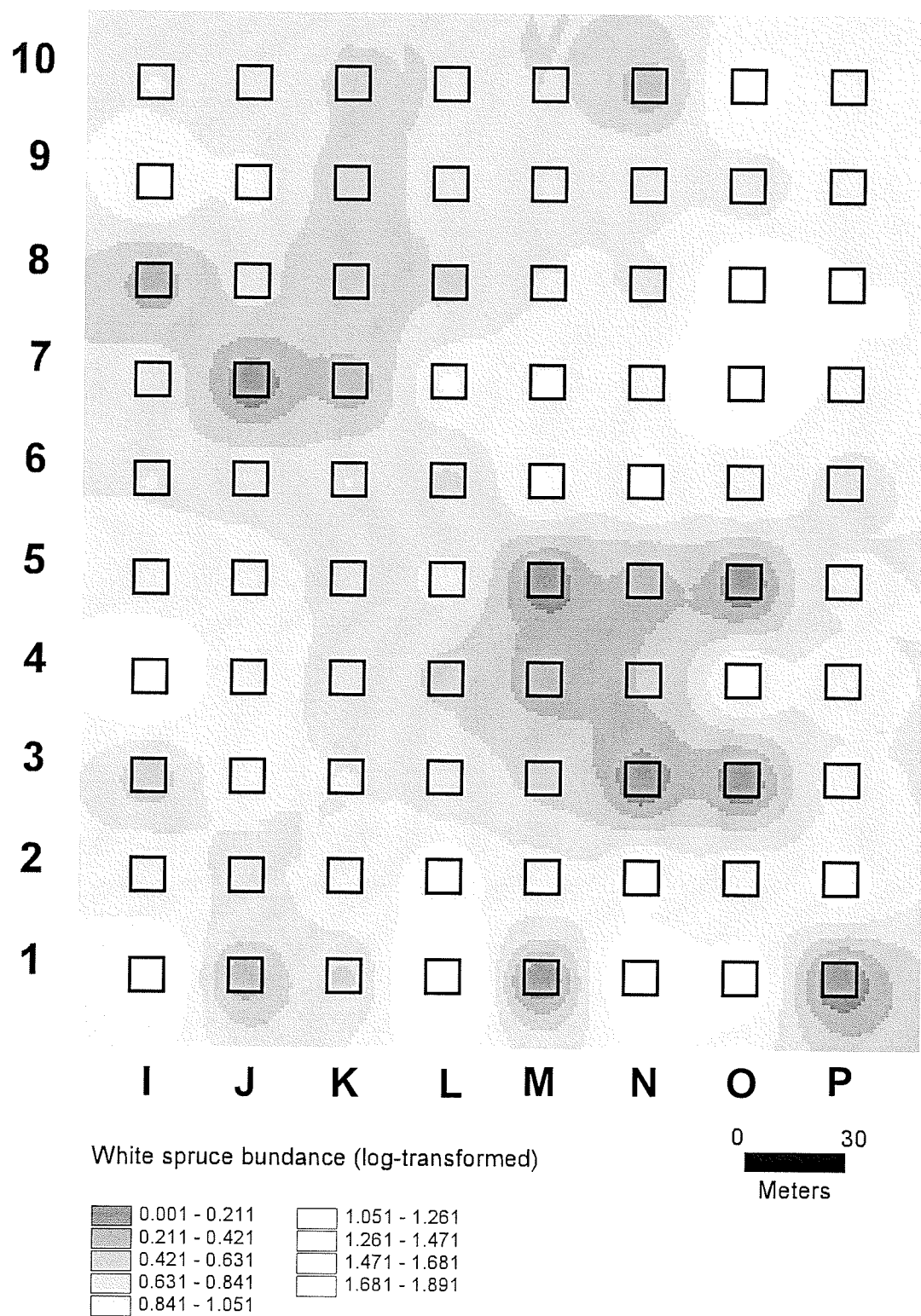


Figure II.4 b) PENINSULA COHORT 1 surface interpolation of white spruce abundance.

								SUM	
10			3			3	1	1	8
9	9	2	1	7			2		21
8		1	2		1	2	12		18
7	1			1	2	1	8		13
6	3	2	2		2	1	3	4	17
5	4	1						1	6
4	9	2	1		3		6	4	25
3	3	1		4	2	44	5	4	63
2	5	2	3	4	3	5	4	7	33
1	5		1	16	6	13	18	1	60
	I	J	K	L	M	N	O	P	264

### BURN EDGE

Figure. II.5 a) WHITE SPRUCE coh 2 ABUNDANCE / 5 X 5 M ON PENINSULA

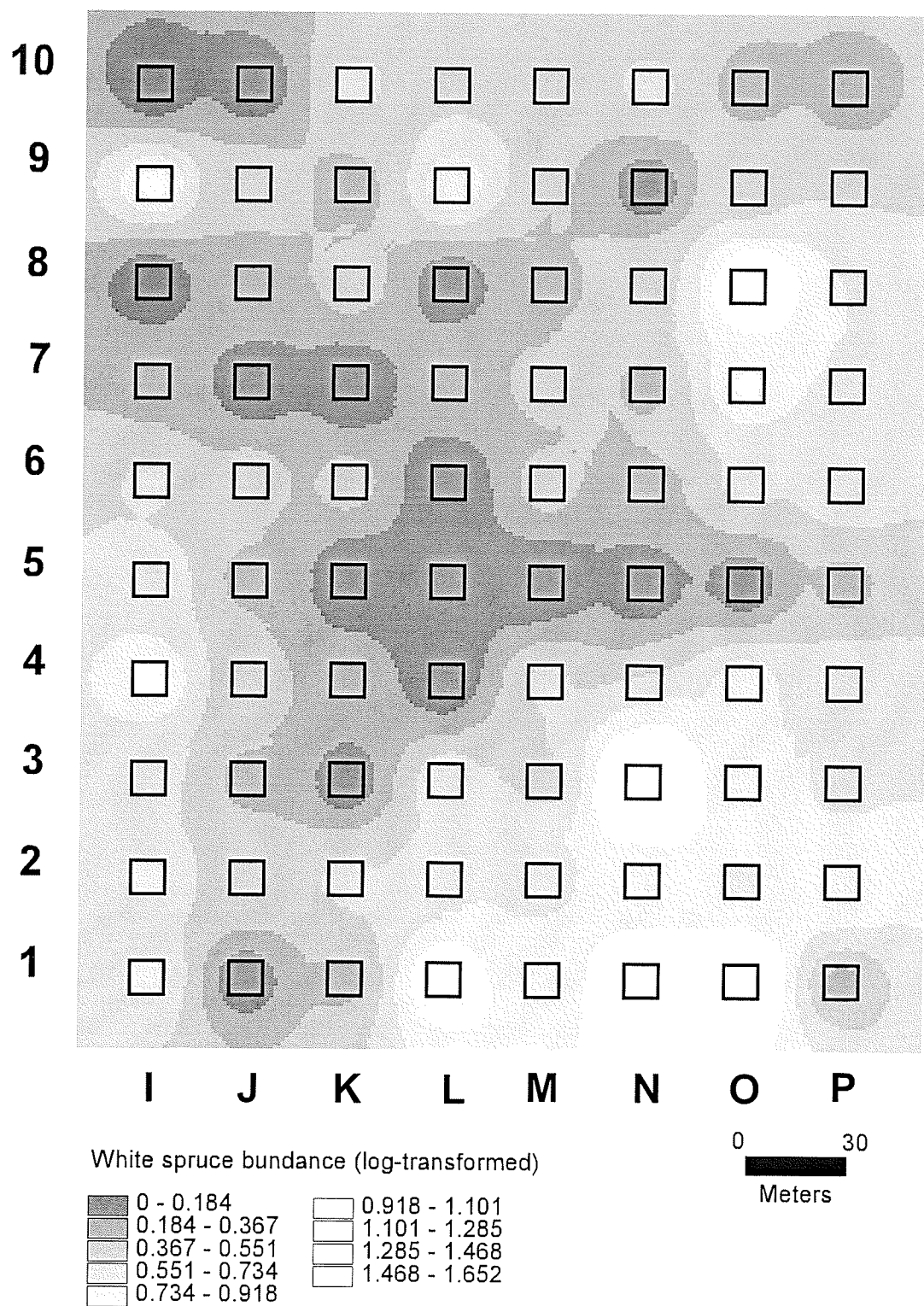


Figure II.5 b) PENINSULA COHORT 2 surface interpolation of white spruce abundance.

								SUM	
10								0	
9								0	
8								0	
7								0	
6					2		1	3	
5			1	1	1		5	8	
4							7	7	
3						26	22	49	
2								0	
1					1		9	10	
	I	J	K	L	M	N	O	P	77
BURN EDGE									

Figure. II.6 a) WHITE SPRUCE coh 3 ABUNDANCE / 5 X 5 M ON PENINSULA

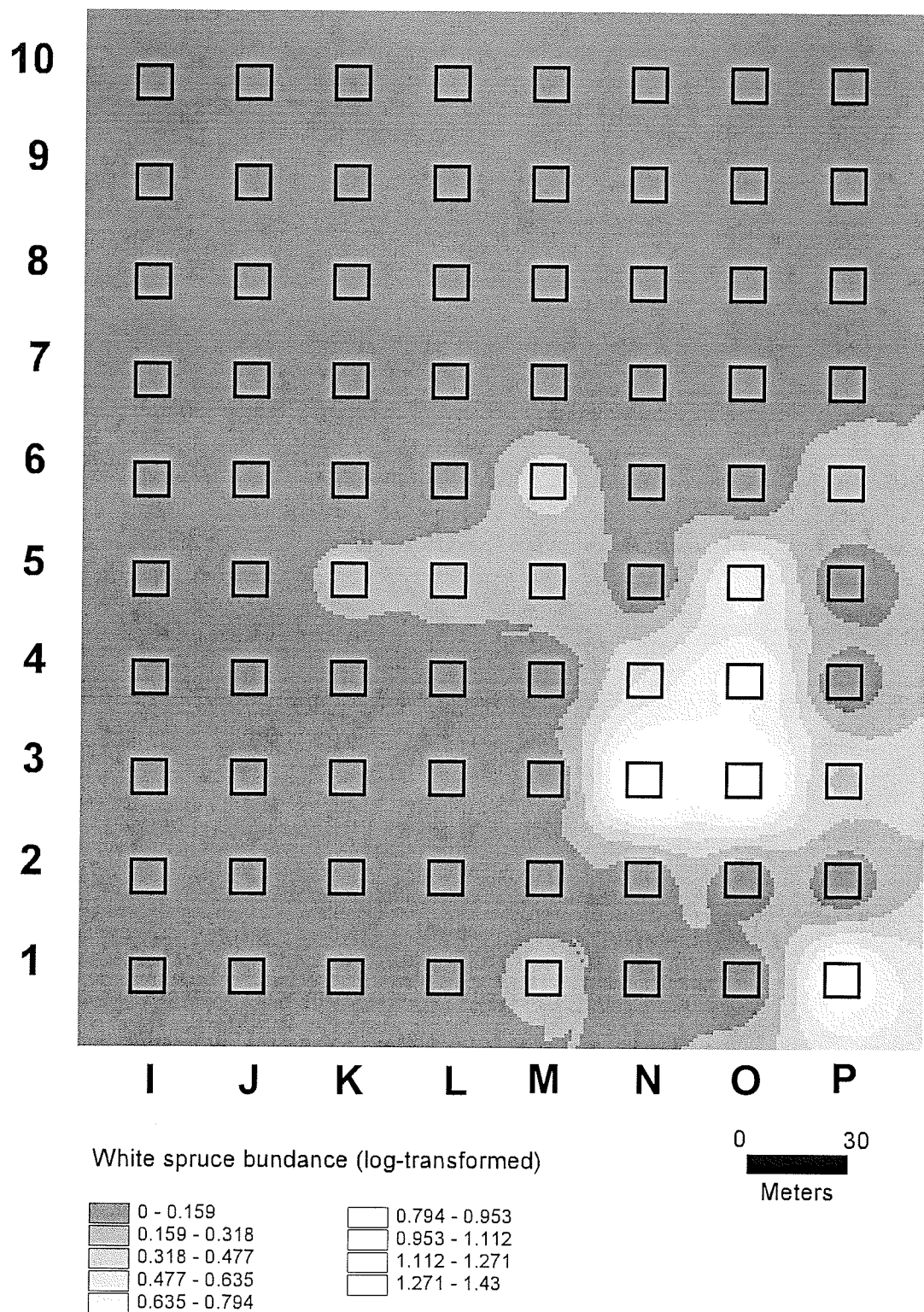


Figure II.6 b) PENINSULA COHORT 3 surface interpolation of white spruce abundance.

								SUM	
10						1		1	
9	1							1	
8						17		17	
7	2		3		2	17		24	
6	1	1		8	1	1	2	14	
5	2	2	1					5	
4	18	6	1			9	2	36	
3		1	1	8			1	11	
2	1		1	5	5		9	21	
1	14		37		56	25		132	
	I	J	K	L	M	N	O	P	
									262

### BURN EDGE

Figure I 7 a) DEAD WHITE SPRUCE ABUNDANCE / 5 X 5 M PLOT ON PENINSULA