SPATIAL, FUNCTIONAL AND GENETIC CHARACTERISTICS OF FIELD-PLANTED AND NATURALLY-REGENERATED POPULATIONS OF WHITE SPRUCE (*PICEA GLAUCA* (MOENCH) VOSS)

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ABSTRACT

Survival and growth depend on the genetic potential of plants to adjust to environmental changes. Plant response to spatial heterogeneity in the environment results from genetic differentiation and phenotypic plasticity within and among populations. This thesis aimed at examining the spatial, genetic and light-induced physiological differences within and among field-planted and naturally-regenerated populations of white spruce (*Picea glauca* (Moench) Voss) in the mixedwood section of the southern boreal forest of Saskatchewan.

The spatial and age structure of white spruce populations were studied in 52 stands. White spruce density increased with stand age in the 200-year chronosequence after fire. Tree height and diameter at breast height peaked at about 120 years after fire (26 m and 30 cm, respectively). Long term trends were examined only in fire-generated stands due to the lack of old clearcuts. Sapling density along a chronosequence after clearcutting exhibited similar patterns to that after fire, but peaked somewhat earlier. White spruce seedlings were present in various densities and heights along the entire chronosequence after fire, producing stands with uneven age structure. Seedling regeneration was mostly on the forest floor layer (72%) in younger plots and on logs (97%) in old plots. Seedlings in both regeneration types were evenly spaced at a young age. This pattern changed to random and clumped in older stands. Planted clearcuts formed more even-aged stands.

Physiological, morphological and growth responses to sun and shade treatments in the greenhouse were examined in white spruce seedlings collected from three naturally-regenerated (N1, N2 and N3) and three field-planted (P1, P2, and P3) stands. Seedling survival was greater in the sun than in the shade (100 versus 83%), and in the planted than in the naturally-regenerated populations (96 versus 86%). Dark respiration and light compensation points declined by 70 and

81% respectively, in shade- compared to sun-acclimated seedlings. Quantum yield, total chlorophyll content, specific leaf area and absolute water content increased by 45, 33, 32 and 50%, respectively, in response to shade. Terminal bud growth was not affected by light regime. Fewer and longer secondary branches were noticed in the shade compared to full sun. At light saturation (1,100 μmol m^{-2} s^{-1}), populations P1 and N3 showed similar photosynthetic responses under both light regimes (about 6 μmol m^{-2} s^{-1}). Populations P2, P3 and N2 performed more poorly in the sun than in the shade (8.2, 8.7 and 9.1 in shade, versus 5.1, 4.1 and 5.5 in full sun, respectively). Photosynthetic rate in N1 was greater in full sun than in shade (14.7 and 11.1 μmol m^{-2} s^{-1}, respectively). Differences in physiological responses to light among populations suggest the presence of more than one ecotype. N1 behaved like a true "sun population", showing the greatest plasticity in the measured physiological parameters, while the remaining populations behaved more like shade-adapted populations. The variation in physiological and morphological parameters within field-planted and naturally-regenerated populations was large, and did not show any obvious differences among populations.

Randomly Amplified Polymorphic DNAs (RAPD) analysis showed abundant polymorphism in all populations. Naturally-regenerated and the field-planted populations demonstrated similar within and among regeneration-type variation. Of the total genetic variation, 82.9% was due to intra-population variation, while inter-population variation and regeneration type accounted for 16.7 and 0.4% of the total variation, respectively. It appears that selection pressure during reforestation was not great enough to cause a significant decline in the genetic diversity of field-planted compared to naturally-regenerated white spruce.

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1. INTRODUCTION

The boreal forest of the Northern Hemisphere covers around eleven percent of the terrestrial surface of earth (Bonan and Shugart, 1989). In the last seventy years, the increase in clearcutting of productive forest has been accompanied by an increase in fire suppression measures (Carleton and MacLellan, 1994). In fact logging has replaced fire as primary disturbance in parts of the boreal forest (Brumelis and Carleton, 1988).

Spruces (*Picea glauca* (Moench) Voss, *P. mariana* (Mill) BSP, *P. rubens* (Du Roi) Dietr., *P. engelmannii* Engelm., and *P. sitchensis* Carr.) comprise about 55% of the total annual volume of harvested wood (Attree *et al.*, 1991) and of the tree seedlings used in reforestation in Canada (Margolis and Brand, 1990). White spruce alone represents 37% and 64 % of the total seedlings planted in Canada and Saskatchewan, respectively. White spruce wood is characterized by its light weight, moderate strength, good fiber quality and relatively low resin content (Attree *et al.*, 1991). These characteristics make white spruce the best pulp wood obtainable in North America (Morton and Lewis, 1917). White spruce wood is also used in the production of saw lumber for building construction, wall paneling, and the fabrication of boxes and crates (Attree *et al.*, 1991).

In the field, newly-planted or naturally-regenerated seedlings of white spruce experience a variety of environmental conditions among which is overtopping by the fast-regenerating aspen (*Populus tremuloides* Michx.) and other species that dominate the early stages after disturbance. The ability of white spruce seedlings to grow in low light and compete with other species determines its later presence or absence in the forest canopy. White spruce seedling survival after planting varies, ranging from over 90% (Brand, 1991) to as low as 34% (Hawkins *et al.*, 1995). Ontario Ministry of Natural Resources (1988) found that 40-60 % of white spruce

plantations did not meet reforestation targets. Krankina and Dixon (1992) suggested that survival rate is related to stock quality, site preparation, planting techniques and brush competition.

The wide distribution of white spruce in North America, its economic importance, large scale of timber harvesting and use in the forest industry, and potential impact of future climatic changes have increased concerns about the establishment, survival and growth of this tree. The importance of white spruce in determining the structure of the mixedwood forest suggests that the species deserves a special attention in forest management (Kazbems *et al.*, 1986). Because of its significance in the structure of the boreal forest, the presence of white spruce has effects on the plant, animal and insect communities, therefore the biodiversity of the boreal forest.

Effects of artificial selection and regeneration practices on the genetic diversity of white spruce have been discussed in the forestry literature. The extent to which artificial selection and regeneration methods affect the genetic diversity of white spruce, and, in turn, its physiological responses to stress, remain unclear. Plantations usually originate from collected seeds from natural forests, tree orchards or both. Collected seeds are cleaned and tested for germination. Seeds are then grown in either greenhouses for one year, or field nurseries for 2-3 years before transplanting to the field. Some studies suggest that seed sources are usually high in genetic diversity compared to native stands, due to the outcrossing nature and the low survival of inbred white spruce (Boyle, 1992). Others report a loss of genetic diversity associated with artificial selection (Rajora, 1996; El-Kassaby, 1992). This loss may affect evolutionary adaptation, and ultimately has impacts at the population and ecosystem levels. Unintentional selection during the reforestation process could result in loss of genotypes with the ability to acclimate to conditions in the field, e.g. light regime.

The present research was aimed at testing the following hypothesis: The spatial, functional and genetic dimensions of niche structure do not differ within and between field-planted and naturally-regenerated populations of white spruce in the boreal mixedwood forest of Saskatchewan. The objectives were 1) to describe the

spatial and age structure of naturally-regenerated white spruce populations in stands along a chronosequence developing after fire; 2) to contrast the spatial structure of white spruce seedling populations, and substrate properties in planted clearcuts and naturally-colonized clearcuts and burned areas; 3) to compare the growth and morphology of white spruce seedlings within and among populations selected from naturally-regenerated and field planted stands, concentrating on the physiological responses, and; 4) to measure the genetic variation among individuals in field-planted and naturally-regenerated white spruce seedling populations.

2. LITERATURE REVIEW

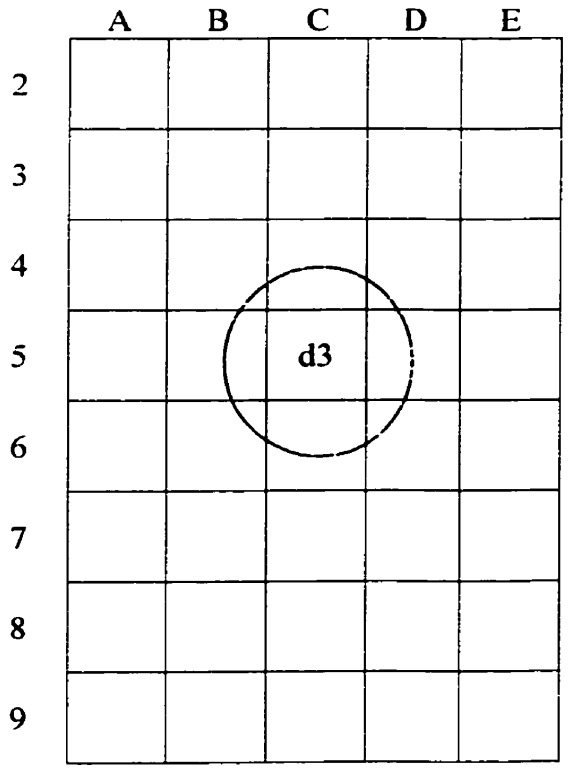
2.1. Boreal Forest

The boreal forest or taiga covers a large, circumpolar area of the Northern Hemisphere. The dominant conifer genera are *Picea* and *Pinus* and the deciduous genera include *Betula* and *Populus*. The dominant spruces in North America are *Picea glauca, P. mariana, P. rubens, P. engelmannii* and *P. sitchensis*. *Picea abies* (L.) Carr. and *P. excelsa* are common in Eurasia. Plant diversity in the boreal forest is relatively low when compared to other forest ecosystems like the temperate forest (Larsen, 1980).

Extreme low temperatures and short summers are important characteristics of the boreal forest (Aber and Melillo, 1991). The boreal forest is characterized by a gently sloping terrain, however the small differences in slope translate into significant changes in soil water characteristics, which is one of the major determinants of local and regional species distribution. Distinct forest types occur on relatively sandy soils, wet organic soils and mesic sites.

In North America, the boreal forest extends from Labrador and Newfoundland in the east, to the Rocky Mountains in the west and central Alaska on the north (Larsen, 1980). The boreal forest covers over one-half of Saskatchewan. The mixedwood section of the boreal forest, the focus of the current study, totals about 85,000 km^2. Beckingham *et al.* (1996) point out that moisture and nutrient regimes play an important role in species composition in the mixedwood forest. Based on the classification proposed by Beckingham *et al.*, the study areas in present research fall in the Low-bush Cranberry ecosite (Figure 2.1), characterized by a mesic moisture and medium nutrient regime. Tree species that dominate this ecosite are *Picea glauca* (white spruce) and *Populus tremuloides* (trembling aspen). Tree

species associated with white spruce on mesic sites include balsam fir (*Abies balsamea* (L.) Mill), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.). The understory plant species include bunchberry (*Cornus canadensis* L.), twin flower (*Linnea borealis* L.), sarsaparilla (*Aralia nudicaulis* L.), bishop's cap (*Mitella nuda* L.) and dewberry (*Rubus pubescens* Raf.) (Beckingham *et al.*, 1996).



Moisture regime	Nutrient regime
1. Very xeric	A. Very poor
2. Xeric	B. Poor
3. Subxeric	C. Medium
4. Submesic	D. Rich
5. Mesic	E. Very rich
6. Subhygric	
7. Hygric	
8. Subhydric	
9. Hydric	

Figure 2.1. Location of the Low-bush Cranberry ecosite (d3) on a moisture-nutrient grid (Beckingham *et al.*, 1996).

2.2. White Spruce Characteristics

White spruce (*Picea glauca* (Moench) Voss) belongs to the largest family of conifers, the Pinaceae (Attree *et al.*, 1991). It is one of the most widely distributed native conifers in North American boreal forest. White spruce extends from Alaska, where it is the dominant species in the Brooks Range at the northern treeline (Goldstein *et al.*, 1985) to Newfoundland in the east, and from the treeline south to

Montana and the New England States (Attree *et al.*, 1991) (Figure 2.2). It is a component of the hemlock-hardwoods forest in eastern Canada and the northeast U.S.A. (Braun, 1964).

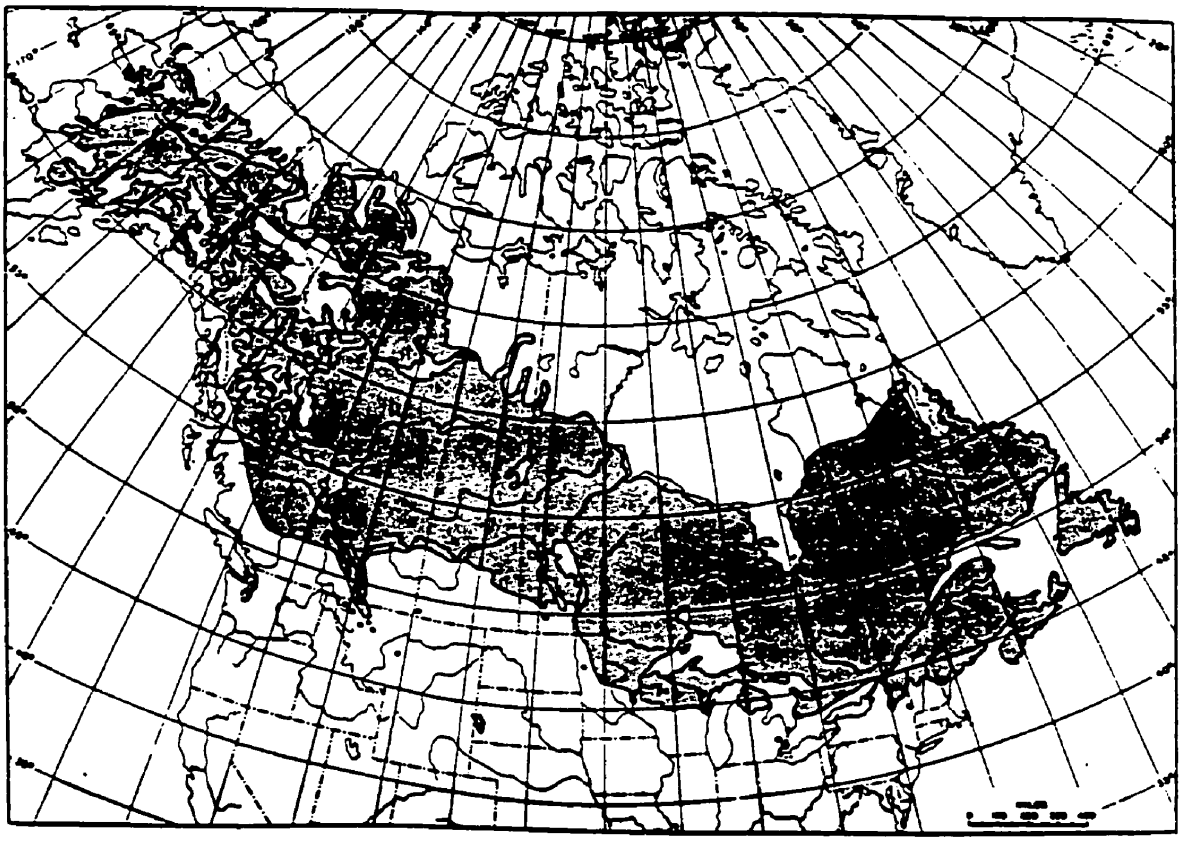


Figure 2.2. The range of white spruce in North American (Fowells, 1965).

Picea glauca grows under a wide range of climatic conditions ranging from the wet insular Nova Scotia to the semi-arid sites in southern Manitoba and the Cypress Hills of Saskatchewan (Nienstaedt and Zasada, 1990). It is considered one of the hardiest conifers, surviving in Alaska and parts of Canada, where minimal winter temperatures can reach -60 °C, and in the hot dry summers on the southern edge of its distribution in the prairie provinces, where mean annual precipitation is as low as 380 mm and July mean temperatures reach 24 °C or more (Fowells, 1965).

White spruce grows on a variety of soils, but performs best on Luvisol and Brunisol forest soils. White spruce tolerates wide ranges of pH, from 4.5 to 7.5, with symptoms of chlorosis appearing at pH 8.3 (Fowells, 1965). White spruce is a relatively shade tolerant species, classified 6.8 on a scale of 0 (intolerant) to 10 (very tolerant) (Rowe, 1955). Rapid, early growth is mainly achieved under good site conditions and full sunlight (Fowells, 1965). The high water consumption of spruce, and the lower water use efficiency when compared to other coniferous species such as pine, tend to restrict spruce to moist, more shaded environments (Korstain, 1925; Alexander, 1984; Carter and Smith, 1987).

White spruce exhibits determinate growth during the growing season, which averages 60 days per year. Trees usually reach 20m height (Attree *et al.*, 1991), although trees of 33 m height and diameter at breast height of around 136 cm were reported by Morton and Lewis (1917). Trees usually produce cones at 20 to 30 years. The optimum seed production is at 60 years (Fowells, 1965). Heavy cone production occurs about every seven years (Attree *et al.*, 1991). Trees mature between 70 and 100 years of age. White spruce is the longest lived tree in the boreal forest with a life span of 200 years on poor, dry sites and 300 years on mesic sites.

Seeds develop in one growing season and are shed in September. White spruce seeds experience conditional dormancy. Viable seeds from central Ontario only germinated when chilled for two weeks; in general an increase in chilling requirements was noticed with latitude (Coron *et al.*, 1990). In the field, the timing of germination varies within population and among seed sources. Optimum germination temperature for the boreal forest conifers is between 20 and 25°C (Farmer, 1997).

White spruce is easily killed by fire, due to its thin bark that provides little protection and its shallow roots. Seeds are not serotinous as in some other boreal species like jack pine (*Pinus banksiana* Lamb.), hence are killed instantly. Ehnes and Shay (1995) classified white spruce as a fire avoider. It is a shade-tolerant species that slowly invades burned areas (Rowe, 1983).

Soils of the boreal forest typically have poor nutrient status. The response of white spruce to nitrogen fertilization differs among studies. Brand and Janas (1988)

found that white spruce has low nutrient requirements during establishment, and applying fertilization and brush control to reduce competition around white spruce seedlings in cold soils provide little benefit. However, in warm soils, white spruce responds dramatically to brush control and brush control plus fertilization, but not to fertilizers alone. Durzan and Stewart (1967) could find no significant growth responses of white spruce to nitrogen fertilization, despite the high foliage nitrogen content in fertilized plants; the species seems to lack the ability to use high levels of nitrogen. On the otherhand, McAlister and Timmer (1998) observed that nitrogen application to bare root seedlings of white spruce stimulated growth by 104-180%.

2.3. Succession in the Mixedwood Section

Rowe (1961) concludes that the boreal forest is a disturbance forest, maintained in health by frequent fires to which most of its species are adapted. Disturbance determines the stage and the duration of succession. Disturbances in the boreal forest are mainly caused by fire or human impacts such as logging, although other disturbances may result from causes such as wind or diseases (Archibold, 1995).

The change in structure of boreal forest over time after disturbance, or succession, has been studied by Rowe (1961), Jarvis *et al.* (1966), Viereck (1973), Black and Bliss (1978), Larsen (1980), Day and Harvey (1981), Bergeron and Brisson (1990), Bergeron and Dansereau (1993) and Thorpe (1996a), among others. Elliot-Fisk (1988) lists some of the environmental changes that take place during succession in the boreal forest in response to canopy closure. These include an increase in thickness of the organic layer, and decreases in available nutrients, soil temperature, and soil drainage, resulting in anaerobic conditions and an increase in frost heave and thrust. These conditions, combined with low light levels, limit regeneration of white spruce, and favor regeneration of black spruce (*Picea mariana*) especially on wet sites (Bonan and Shugart, 1989).

In general, in a mesic stand, the shade intolerant and fast growing trembling aspen, and other deciduous hardwoods regenerate readily after disturbance and attain

an immediate dominance of the canopy (Bergeron and Charron, 1994). On sites where the organic layer is removed, white spruce seedlings may establish if seeds are available (Kazbems *et al.*, 1986). Any established white spruce seedlings are usually suppressed by aspen and remain for decades in subordinate position till gaps are formed (Oliver, 1978). Oliver and Larson (1996) suggested that during the period of aspen overmaturity (around 80 years, Kazbems *et al.*, 1986), white spruce is released from the understory and assumes dominance of the stand, while aspen dies back. Van Cleve and Viereck (1981) found that white spruce became the dominant tree at about 100 years after fire. At a stand age of 150 years, white spruce density commenced to decline as it became incapable of successfully reproducing itself due to increases in shade and moss layer thickness (Oliver and Larson, 1996). At this stage, balsam fir is released from the understory and eventually forms an uneven aged stand dominated by balsam fir (*Abies balasamea*) with scattered white spruce (Thorpe, 1996a).

2.4. Fire and Clearcutting

Fire is the major natural ecological factor controlling structure and function in the boreal forest. Fires caused by lightning account for 75% of the total area burned in Canada (Hardy and Franks, 1963). Fire frequency declines in the boreal forest towards the east. Fire return interval is 50 - 100 years in western boreal forest compared to 200 - 500 years in the east (Johnson and Rowe, 1975). Pre-suppression fire cycle was about 38 years in western boreal forest (Thorpe, 1996b). In recent decades, the increase in clearcutting of productive forest has been accompanied by an increase in fire suppression (Carleton and MacLellan, 1994). In those areas, logging has replaced fire as the primary disturbance (Brumelis and Carleton, 1988). Human overexploitation of the environment is expected to cause major changes in the world climate (Environment Canada, 1991). Climate change may have an impact on the frequency and intensity of disturbances in the boreal forest, particularly fire and insect infestations (Price and Apps, 1995). Hogg and Hurdle

(1995) predicted a drier climate and higher fire frequency for the southern boreal forest, similar to that of the aspen parkland zone.

A major effect of fire is the conversion of unavailable nutrients to soluble forms available to the plant, even though significant losses might occur from volatilization or leaching. The effect of fire varies greatly according to factors such as season, fuel quantity and quality, environmental conditions, severity and type of the fire, vegetation type, slope and soil (Van Wagner, 1983). For example, a spring fire, when the soil is moist, may only burn the fresh litter (L), leaving the FH (decomposing and humus layers) intact. In contrast, a severe fall fire can remove up to 50 cm of the organic material, possibly exposing the mineral soil, reducing infiltration and increasing surface runoff (Kimmins, 1997). Loss of structure and reduction in porosity might also occur in the case of severe fires. A fire that does not completely remove the LFH might improve soil moisture content and exert minimal effect on soil structure. Soil temperature increases after fire due in part to the removal of LFH and to the increase in the absorbed radiant energy due to soil darkening. The increase in temperature improves decomposition (Pritchett and Fisher, 1987).

The effect of clearcutting can be adverse depending on the stand characteristics, the harvest method and environmental factors. Following clearcutting, a general rapid increase in organic matter decomposition and a decrease in the litterfall inputs are noticed, resulting in a rapid reduction in the LFH layer (Pritchett and Fisher, 1987). Increased decomposition is mainly associated with the increase in temperature, and the decrease in some phenolic compounds found in litterfall which inhibits decomposer organisms, and with a decrease in mycorrhizae and an increase in free-living saprotrophs (Kimmins, 1997). The most obvious results, however, are a decrease in the water and nutrient storage capacity, and an increase in soil temperature.

The prime similarity between the effects of fire and clearcutting is the removal of the tree canopy and the associated changes in microclimate at the ground level (Carleton and MacLellan, 1994). These authors listed some of the differences between the two types of disturbances that will likely have an impact on regeneration

and subsequent vegetation cover. First, fire rarely kills trees in a uniform fashion, as is the case with clearcutting. Pockets of unburned trees might be left acting as centers of recolonization. Second, fire leaves standing dead trees that act as a seed bank, and modify habitat, notably by casting shade during the hot summer. Third, fire, by consuming the LFH, may kill or retard the regeneration of competitive plants that root in this layer. In contrast, clearcutting allows the persistence of this layer and the understory vegetation. The removal of logs and the use of heavy machinery cause soil physical disruption.

Thrasher-Haug (1997) found differences in the successional trajectory after clearcut relative to fire in the Saskatchewan mixedwood boreal forest. Some of the differences between the two types of disturbances included the increase in species diversity over an accelerated time span after clearcut relative to fire and, greater number of both late successional remnant and exotic species in recent clearcuts compared to burned sites.

The speed of tree regeneration after disturbances depends on many factors including seed availability and type of disturbance (Farmer, 1997). For example, disturbances exposing the mineral soil favor regeneration from wind-blown seeds while fire that does not completely remove the LFH will likely increase the number of trees sprouting from roots (Oliver and Larson, 1996). Carleton and MacLellan (1994) found that coniferous seedlings were more widespread in plots after fire than after clearcut, while aspen was more widespread after clearcut. They added that logging shifted stands from coniferous trees to deciduous trees. Of course this trend would not occur where significant restocking of cutareas with conifer seedlings was carried out.

2.5. Genetic Diversity

Noss (1990) defined biodiversity as the genetic variation among individuals, populations, species, communities, ecosystems and landscapes. Genetic diversity is the lowest level in this hierarchy, which enhances its importance. Genetic diversity is essential for both short-term adaptation to environmental changes and long-term

impacts on species and communities. Hence the impact of genetic diversity "percolates through all levels of biodiversity via the evolutionary process" (Templeton, 1995). The loss of biodiversity is of concern for three main reasons 1) ethical and esthetic; 2) economic benefit and 3) essential services provided by natural ecosystems (Ehrlich and Wilson, 1991).

Because all individuals in a population are similar enough to be considered one species, it is expected that the total variation in morphology, behavior, genetic material, and physiology among those individuals is therefore much lower than in a sample of the same number of individuals in a different species. Despite this, considerable variation can exist among or within populations of the same species. This variation could be the result of phenotypic response to a particular environment or due to genetic differences. The latter can impose differences in phenotypic traits independent of the environmental conditions, or impose limitation on phenotypic variability that can occur in response to environment (Clausen *et al.*, 1941). Thus, genetic diversity within a species is in some cases positively correlated with environmental variability, which may have an influence on species diversity.

Slatkin (1987) suggested that discrete populations or ecotypes arise from evolutionary forces such as limited dispersal of pollen and propagules, genetic drift and variable selection.

The genetic adaptation of species to different environmental conditions was recognized in early work by Turesson (1922). The fact that resource availability varies greatly over a wide range of spatial and temporal scales helps explain a large amount of the variation among populations. Factors such as soil nutrient availability, temperature and precipitation can have a major effect on variability within species (Grime, 1979; Woodward, 1987).

Clear differences in genetic variability between species from different successional stages have been found. A basic pattern seems to be that species with large ranges, high fecundity, an outcrossing mode of reproduction, wind pollination, a large generation time, and from habitats representing later stages of succession have great genetic variability (Zangerl *et al.*, 1977 ; Hamrick *et al.*, 1979).

Two methods are usually used to test for genetic diversity: provenance testing in common gardens (National Research Council, 1991) and molecular analysis (Mohan *et al.*, 1997). Provenance testing involves the transfer of individuals with differing provenance to a common environment, where physiological and morphological responses are tested. Molecular testing involves the survey of genetic diversity at the DNA level. Protein electrophoresis was one of the first methods used in the mid 1960s, but this method was limited to the protein coding genes (Templeton, 1995). Nowadays, such techniques as the random amplified polymorphic DNA's (RAPD), restriction fragment length polymorphism (RFLP's), microsatellites and amplified fragment length polymorphism (AFLP) are common tools for performing molecular genetic surveys (Mohan *et al.*, 1997).

2.6. Effect of Selection on Genetic Diversity in Conifers

Experience with genetic improvement of crop plants has demonstrated that selection and breeding are associated with reduction in genetic diversity (El-Kassaby, 1992). The loss of genetic diversity may increase the possibility of population extinction and reduce future adaptation through evolutionary change. On the other hand, heterozygosity or high genetic variation within a population is positively related to fitness (Meffe and Caroll, 1994).

The use of biotechnology in forests can have desirable or undesirable impacts on genetic diversity. Desirable effects could be increased productivity, thus reducing pressure on the land base. Biotechnology could be used as a tool to preserve genetic diversity and could be useful in developing biological control mechanisms. Undesirable effects include increased vulnerability to pests due to narrowing the genetic base, emergence of new pests (resistance to one pest may cause the emergence of others), reduction in biodiversity, and genetic pollution (Duchesne, 1993).

Conifers are still in their early stages of domestication, and thus, remain relatively genetically heterogeneous (Yeh *et al.*, 1986). Rajora (1996) determined the impact of artificial selection and plantations on genetic diversity of white spruce in

the Prince Albert Model Forest area of Saskatchewan. Results suggest that natural regeneration, artificial plantation and tree improvement selection caused reductions in the genetic diversity of 11-12%; 10-21% and 10-33%, respectively, when compared with natural old-growth populations. Rajora (1996) concluded that plantations and phenotypic selections of white spruce had a significantly narrower genetic base compared with the old-growth stands, and genetic diversity could only be maintained by natural regeneration. White spruce showed a loss of alleles when a limited number of trees were selected from natural populations on a phenotypic basis (Cheliac *et al.*, 1988).

On the other hand, Desponts *et al.* (1992) showed that selection of a restricted number of individuals from two natural populations of white spruce in southern Quebec reduce variability. No loss of alleles was noticed compared to the original provenance populations, despite the sizable reduction in number. They attributed their results to the high heterozygosity of coniferous species and the fact that white spruce is characterized by a high level of cross pollination and a low level of survival of seeds derived from inbreeding. Finally, they suggested that the second selection, in favor of individuals demonstrating a strengthened vigor, favored the most polymorphic genotypes.

Heterozygosity increases from seed to seedling to tree populations because of mortality in inbred individuals under the increased stress of competition (Ledig, 1986). Naturally-regenerated seedlings experience greater heterozygozity compared to plantations, as they are selected at earlier stages, while planted populations may show greater homozygosity at seedling stage due to the lower stress experienced in the nursery, leading to greater mortality in the field.

El-Kassaby (1992) found that the seed orchards containing phenotypic selection products of Sitka spruce (*Picea sitchensis*) populations showed the appearance of new rare alleles that were not seen in natural populations. The levels of heterogeneity were higher than those observed in natural stands.

Results for other species are variable. Douglas fir (*Pseudotsuga menziesii* Mirbel) showed a loss of alleles when a limited number of trees were selected from natural populations on a phenotypic basis (Cheliac *et al.*, 1988). No impact of

artificial selection was noticed on the genetic diversity or on the allele frequencies in Norway spruce (*Picea abies* L.) (Bergmann and Ruetz, 1991). In Scots pine (*Pinus sylvestris* L.) and jack pine (*P. banksiana* Lamb.), artificial selection exhibited a very small effect on genetic diversity (Knowles, 1985). The greatest allelic diversity in natural stands of loblolly pine (*Pinus taeda* L.) was present in the domesticated breeding populations (Williams *et al.*, 1995). Individuals had less genetic diversity, but their diversity did not decline as generations of improvement increased.

2.7. Acclimation to Light

Species populations occurring in different habitats can exhibit physiological and morphological differences in response to contrasting environmental conditions. Lambers *et al.* (1998) defined acclimation as the morphological and physiological adjustment by individual plants to compensate for the decline in performance following exposure to a single stress. The extent of this adjustment (plasticity) is related to both pre-treatment and genetic differences (Bazzaz and Carlson, 1982). Acclimation occurs within the lifetime of an individual, usually within days or weeks. Adaptation on the other hand is an evolutionary response, resulting from genetic changes in populations leading to morphological and physiological compensation for the decline in performance caused by stress.

Photosynthetic acclimation to light involves changes in the organization and investment in different components of the photosynthetic apparatus. These changes aim to improve plant performance in the prevailing light regime (Pearcy, 1998). The capacity of a species to acclimate to different light regimes depends on the stage of leaf development, especially on the stage of development of cell layers that increase the leaf thickness (Pearcy 1998).

The photosynthetic response to incident irradiance is divided into several components that are influenced by different physiological attributes of leaves. In the dark, the rate of CO_2 exchange is influenced by the rate of mitochondrial respiration. As light intensity increases, photosynthesis increases linearly at first. The slope of the linear region of the photosynthetic-light response curve is called the apparent

quantum yield (Figure 2.3). Quantum yield is influenced by leaf absorbance and the efficiency of the primary photochemical reaction and the photosynthetic electron transport. Above the linear region and below the light saturation point, is a convex region where absorbance and the internal distribution of light in the leaf influence the shape of the curve. At high irradiance, the rate of photosynthesis is saturated and the rate at which saturation occurs is determined in large part by the biochemical capacity of the leaf and the diffusional limitations to CO_2 flux (Stenberg *et al.*, 1995).

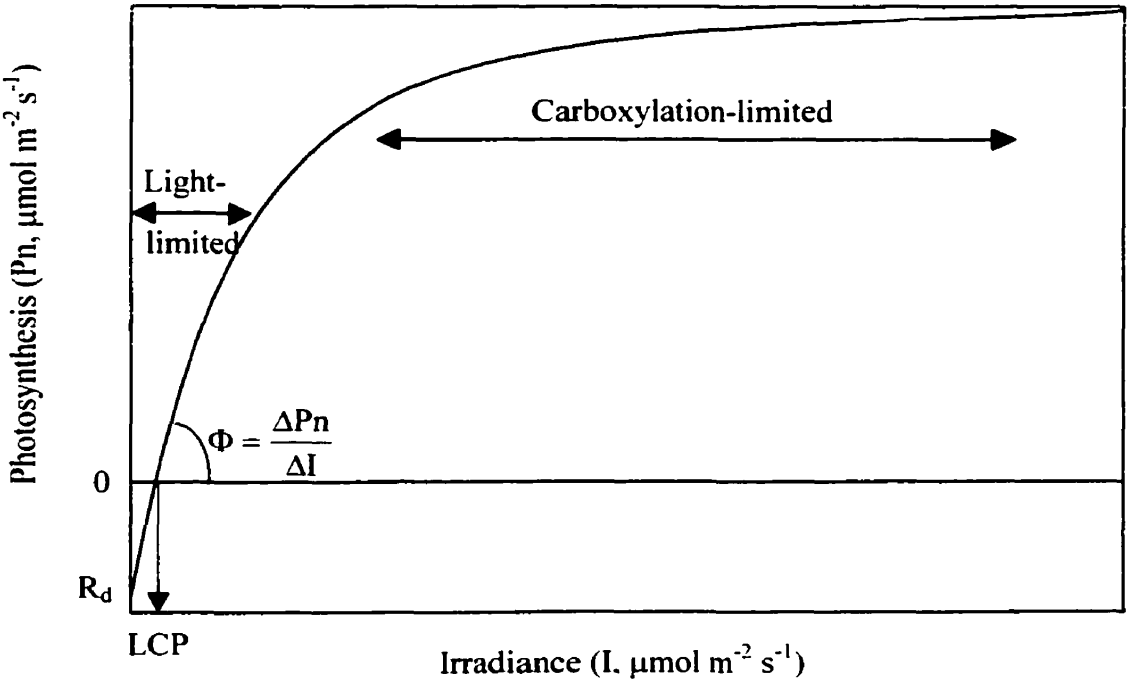


Figure 2.3. Typical response of photosynthesis to irradiance. Irradiance (I) where net photosynthesis (Pn) = 0 is the light compensation point (LCP), the initial slope of the line provides the quantum yields (ϕ), the intercept with the y-axis is the dark respiration (R_d). At low irradiance photosynthesis is light-limited; at high irradiance, it is carboxylation limited (adapted from Lambers *et al.*, 1998).

Shade-acclimated plants tend to fix more carbon than sun leaves under low irradiance (Björkman, 1981). Acclimation is achieved by having low respiration, resulting in a shift in the linear portion of the light response curve toward lower light

levels and producing a lower light compensation point rather than a change in the slope itself or a change in the quantum yield.

Full photosynthetic activity requires light, mainly because of the light regulation of the Rubisco enzyme (Portis *et al.*, 1986). Growth in high light results in greater Rubisco activity, PSII electron transport and cytochrome F capacity compared to leaves in the shade (Anderson and Osmond, 1987; Seemann, 1989). Moreover, Evans (1987) reported a linear relationship between maximum photosynthesis and Cytochrome F or PSII for plants growing under different light regimes. On the other hand, the relation between Rubisco and maximum photosynthesis was curvilinear at high Rubisco concentrations. The increase in Rubisco's activity in the sun could be the result of greater chloroplast concentration, or the increase in the number of chloroplasts or the number or volume of cells (Pearcy, 1998).

Consequently, plants adapted to high light intensity have high light saturation points. Maximum photosynthesis is usually greater in the sun versus the shade, when comparison is made on a leaf area basis. This is due to the increased cell volume per unit area. This difference will generally disappear on a mass basis except if a species from a shaded habitat experiences photoinhibitory damage. In this case a decline in the maximum photosynthesis on a per unit mass basis can be seen.

Sun-adapted plants have shorter leaves, more leaves per unit of branch length, and thicker and more numerous branches per seedling, when compared to shade-adapted species. The latter have high chlorophyll content on a per unit dry weight basis. The thin leaves of shaded seedlings apparently allow more efficient light utilization (Boardman, 1977). Leaf structure profoundly influences the degree of the convexity of the light response. More cell layers in sun leaves reduces the initial linear portion and make a gentle curve to the light-saturated photosynthetic rate (Stenberg *et al.*, 1995). The light saturated rate of net photosynthesis is inversely related to the specific leaf area (Oren *et al.*, 1986). Givnish (1988) summarized the differences in characteristics between shade and sun-acclimated leaves (Table 2.1).

Diurnal rates of photosynthesis, leaf conductance and transpiration vary with respect to light regimes. For example, seedlings of white spruce exhibited higher

Table 2.1. The general differences between shade- and sun-plants, acclimated to extreme irradiance levels (Givnish, 1988).

	Sun	Shade
Leaf-level		
Photosynthetic light response		
Light saturated rate	High	Low
Compensation point	High	Low
Saturation point	High	Low
Biochemistry		
N, Rubisco, and soluble protein content per mass	High	Slightly lower
Chlorophyll a / b ratio	High	Low
Chlorophyll / soluble protein ratio	Low	High
Anatomy and ultrastructure		
Chloroplast size	Small	Large
Thylakoid / grana ratio	Low	High
Morphology		
Leaf mass / area	High	Low
Leaf thickness	High	Low
Stomatal size	Small	Large
Stomatal density	High	Low
Palisade / spongy mesophyll ratio	High	Low
Mesophyll cell surface / leaf area ratio	High	Low
Leaf orientation	Erect	Horizontal
Plant level		
Fractional allocation to leaves	Low	High
Fractional allocation to roots	High	Low
Reproductive effort	High	Low

transpiration rates and stomatal conductance in gaps compared to shaded or open areas. Photosynthesis, however, was the highest in open areas (Carter and Smith, 1987). The light compensation and saturation points were positively correlated with light intensity. Light compensation point of white spruce changed from 34 for shaded to 44 $\mu mol\ m^{-2}\ s^{-1}$ for open habitats (1.3 times). Saturation points, on the other hand, were 149 and 1,933 $\mu mol\ m^{-2}\ s^{-1}$ in shaded and open habitats respectively (13 times). This proves the ability of spruce to acclimate to a range of light regimes.

The light environment of a forest understory is characterized by a very low level of diffused light that is interrupted by sunflecks lasting from a second to 15

minutes or more. Spruce needles had a low convexity during unilateral irradiance suggesting that the leaves are adapted to diffuse light. The importance of sunflecks on photosynthesis of understory vegetation has been well-documented (Lundegarth. 1921 ; Hodges and Scott, 1968). Sunflecks can contribute more than two-thirds of the photosynthetically active radiation (Pearcy, 1988).

Reich *et al.* (1998a and b) investigated the trade-offs involved in whole plant acclimation of white spruce to shade. Maximum photosynthesis was 25% greater at 25% of full light compared to 5%, and specific leaf area increased by around 30% in response to deep shade. Full light inhibited photosynthesis in Engelmann spruce (Kaufmann, 1976). furthermore full light is usually associated with elevated temperatures during the growing season, leading to superoptimal conditions for photosynthesis in spruces, such as red, sitka and white spruce (Neilson *et al.*, 1972; Goldstein *et al.*, 1985 and Alexander *et al.*, 1995).

Sims *et al.* (1994) studied plant acclimation to low light in *Alocasia macrorrhiza*, an understory species in the tropical forest. In the sun maximum photosynthesis increased by 2.5 times, but leaf area ratio was 60% smaller than in the shade. Sun-acclimated plants allocated 20% of the total biomass to the roots and 38% to the leaves versus 10% and 42% in the shade. Furthermore 35% of nitrogen in the leaves was used in photosynthetic components in the shade versus 30% in the sun.

2.8. Physiological Variation among Ecotypes

An ecotype is defined as a genetic subdivision of a species in response to variations in the environment of that species over its range (Kimmins, 1997). Ecotypic variation is well documented in literature. For example, Teich and Holst (1974) observed that growth of white spruce ecotypes from limestone areas was best on limestone parent materials, and granitic ecotypes on granitic soils, suggesting that these ecotypes have evolved by natural selection. Similar responses have been observed in other tree species. Black walnut (*Juglans nigra* L.) seedlings showed genetic variation in osmotic adjustment and tissue elasticity along a longitudinal

transect from New York to Iowa (Parker and Pallardy, 1985). Redbud (*Cercis canadensis* L.) seedlings originating from relatively xeric Kansas prairies had significantly more negative osmotic potentials than those from relatively mesic forest understory habitats in Indiana, at both early and later stages of a drought cycle (Abrams, 1988).

Quamme *et al.* (1982) suggested that the geographic distribution of some species may be related to their ability to supercool in response to cold stress. For example, because white spruce has a large geographical distribution in North America, where minimum temperature varies from near freezing to -60 °C, its ability to deep supercool should vary both seasonally and geographically (Simpson, 1993). In fact, Simpson (1993) found that the buds, foliage, and stem tissue became more hardy in the fall, and that trees originating from farther north hardened earlier in the fall, but were less hardy in the spring. In contrast, more northerly populations of sitka spruce (*Picea sitchensis*) lost hardiness later in the spring Cannel and Sheppard (1982).

Zine El Abidine *et al.* (1994) found that a lowland black spruce population from Ontario showed a slight, but significantly lower, relative water content and osmotic potential at the turgor loss point than an upland population, features that could be associated with water stress tolerance. However, upland and lowland populations from Quebec showed no significant differences in water relations parameters. They proposed that this lack of evident ecotypic differences in Quebec could have been due to: (1) the absence of natural obstacles for pollen transport, (2) the large within-populations variation could have masked any variation among populations, or (3) mesic conditions of the common garden which might not have induced different population responses.

Black cottonwood (*Populus trichocarpa* Torr.) clones from the moist, coastal climate of western Washington had light saturation at 600 μmol m^{-2} s^{-1} and an average net photosynthesis of 13.4 μmol m^{-2} s^{-1} compared with 800 and 18.2 μmol m^{-2} s^{-1} for a clone taken from the dry continental climate in eastern Washington (Bassman and Zwier, 1991). Furthermore, stomatal conductance in the western clone

did not decrease as the xylem pressure potential dropped when water stress was applied, and did not control water loss; stomatal conductance decreased sharply as xylem pressure potential dropped in the eastern clones. The latter had better water-use efficiency. Bassman and Zwier (1991) concluded that eastern and western Washington clones reflected adaptation to their native environment, and suggested that the introduction of the eastern Washington clones of *P. trichocarpa* into breeding programs is likely to yield lines with favorable growth characteristics combined with enhanced water use efficiency and adaptation to soil water deficit.

Johnsen and Major (1995) found that gas exchange and xylem water potential measured on 20-year-old black spruce trees from four full-sib families grown at three sites for two seasons (1991-92) showed that production was lowest at the driest site. One parent female (no. 59) produced progeny that had both higher growth rates and net photosynthesis than the progeny produced from a second parent female (no. 63), measured over a two-year period with contrasting rainfall on both a wetter and a drier site. However, progeny of the two females had similar stomatal conductance in both years and sites during the dry year. The genetic variation in photosynthesis and stomatal conductance was positively related to growth only on the dry site. They concluded that the genotype x environment interaction in growth appeared to be due to a relatively stable genetic difference in photosynthesis. On the dry site, however, water stress reduced photosynthesis below a threshold value at which point the genetic variation in photosynthesis affected productivity, resulting in genetic variation in the growth rate.

3. SPATIAL DISTRIBUTION OF WHITE SPRUCE ALONG A CHRONOSEQUENCE IN MIXEDWOOD FOREST

3.1. Introduction

Structure, functioning and composition are the elements of landscape study. Structure refers to the physical and temporal distribution of plant species in a stand. Following disturbance, species structure will change in a direction depending on factors such as site conditions, climate and type of disturbance. Studying a species structure and its causative factors along a chronosequence provides insight into the direction of changes in that species. Contrasting structural changes of white spruce along a chronosequence following fire and clearcut, could help forest managers develop techniques based on natural trends in the structure and function of the ecosystem (Higginbotham, 1995).

The present study was aimed at contrasting 1) the spatial and age structure of naturally-regenerated white spruce populations along a chronosequence developing after fire, and 2) the spatial structure of white spruce seedling populations, and environmental characteristics in field-planted clearcuts and naturally-colonized clearcuts and burned areas. White spruce tree and sapling density, height and diameter at breast height (DBH); seedling density, height and distribution pattern; and light regimes and soil characteristics along the chronosequence were used to characterize white spruce structure.

3.2. Materials and Methods

3.2.1. Stand characteristics and plot establishment

The study area is located in the mixedwood section of the southern boreal forest of Saskatchewan. The area falls within 53° 38' and 54° 41' latitude, and within 105° 00' and 106° 20' longitude (Figure 3.1, Appendix A). The climate is cool continental, characterized by long cold winters and short warm summers. The monthly average temperature varies between -20°C in January and 17°C in July and the annual average precipitation is around 450 mm (Beckingham *et al.*, 1996) with approximately 70 % falling as rain between June and August (Harris *et al*, 1989). Soils are mainly Orthic Gray Luvisols and Brunisolic Gray Luvisols (Table 3.1 and 3.2). Detailed site description is provided by Thrasher-Haug (1997) and Sulistiyowati (1998).

Vegetation on mesic sites is dominated by two coniferous tree species, white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill), and three deciduous tree species, trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.). Jack pine (*Pinus banksiana* Lamb.) occupies drier sites while black spruce (*Picea mariana* (Mill.) BSP) occupies wetter sites. The understory is dominated by bunchberry (*Cornus canadensis* L.), twin flower (*Linnea borealis* L.), sarsaparilla (*Aralia nudicaulis* L.), bishop's cap (*Mitella nuda* L.) and dewberry (*Rubus pubescens* Raf.) (Beckingham *et al.*, 1996).

With the use of forest inventory and topographic maps, 52 stands were established in and around Prince Albert Model Forest as part of a project on plant biodiversity (Thrasher-Haug, 1997). Stand selection was based on topography, age after fire or cutting, species composition and road accessibility. Age since disturbance was determined by measuring ages of the largest overstory white spruce and aspen. Balsam fir age was also measured when old trees were present. In each stand, a 40 x 20 m plot was established; plots were further divided into 32-5 x 5 m quadrats. Of the 52 stands, 36 stands were between zero and 201 years of age after fire, and 16 stands were between zero and 85 years of age after cutting. Nine stands

representing three age classes developed after fire (young, mature and old) and three young stands planted after clearcutting were further chosen for detailed sapling and seedling study (Table 3.1 and 3.2, Appendix B).

3.2.2. White spruce distribution along a chronosequence

Trees

White spruce tree density was recorded in each plot for all individuals exceeding 4 m height. Diameter at breast height (DBH at 1.3 m from the base) and tree height were measured with a diameter tape (cm) and an Abney hand level (Husch *et al.*, 1993), respectively.

Saplings

A sapling was considered such if the height was between 0.5 and 4 m. White spruce sapling density was recorded in each of the 52 plots. Sapling diameter at the base (DB, cm), and height (m) were measured in the 12 plots selected for intensive study. Outside seven established plots (excluding those in Prince Albert National Park), a total of 12 to 18 saplings that represented the height structure found within the plot were cut at the base. Sapling age, diameter and height of these saplings were used to predict age from size measurements within the 40 x 20 m plots developed after fire using multiple regression (Intercept = 0; R^2 = 80% and P = 0.0001; Appendix C).

$$\textbf{Sapling age}_{(years)} = \textbf{3.48 height}_{(m)} + \textbf{4.06 Diameter}_{(cm)} \qquad (3.1)$$

Seedlings

White spruce seedling density (<50 cm height) was recorded in each of the 12 plots selected for intensive study. Seedling pattern was mapped, and height (cm) was measured using a ruler. Photosynthetically active radiation (PAR, $\mu mol\ m^{-2}\ s^{-1}$) and substrate characteristics (LFH thickness, presence of logs or mineral soil) next to each seedling were recorded.

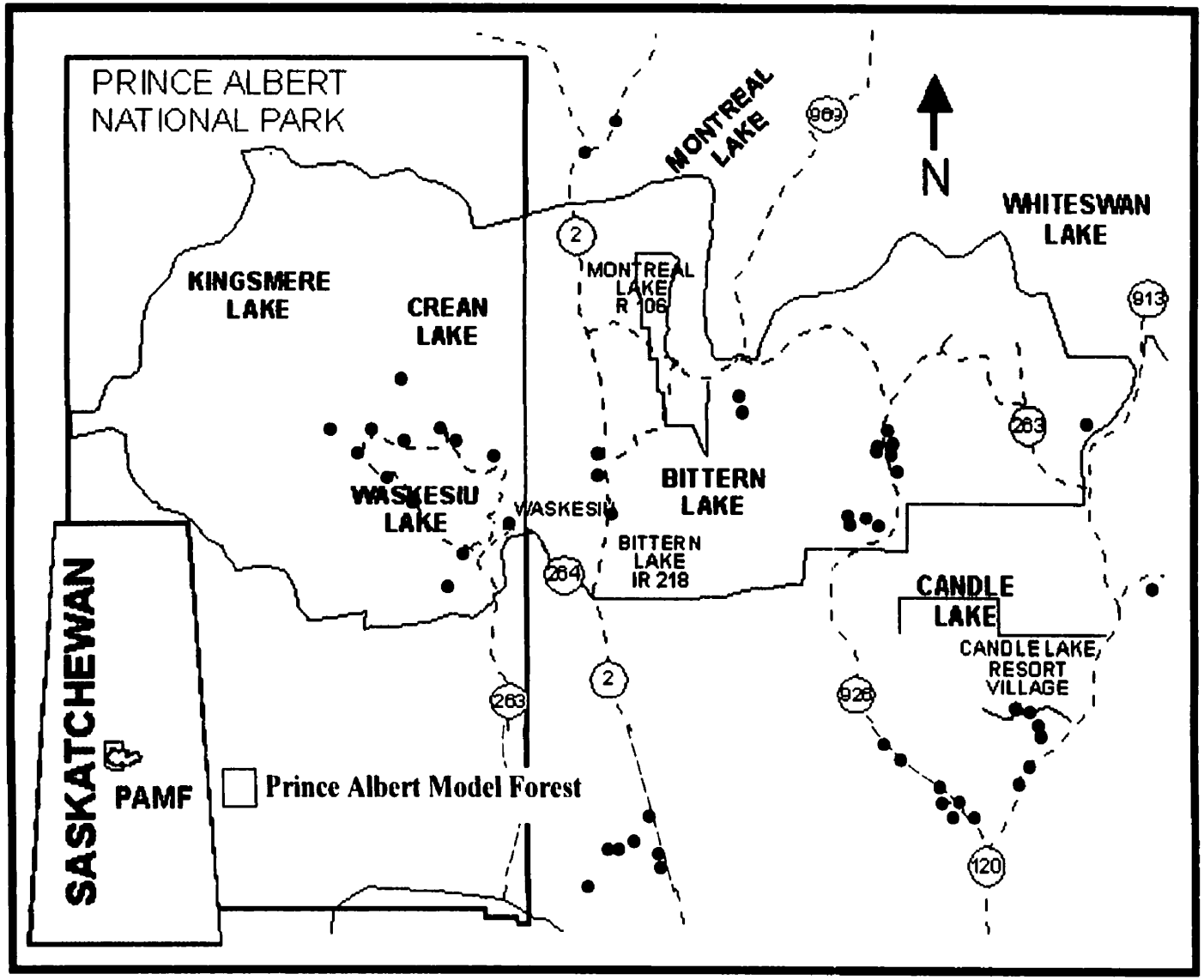


Figure 3.1. Map of the study region of the central boreal forest of Saskatchewan with locations of 52 plots. Adapted from Thrasher-Haug (1997).

Table 3.1. Age and soil characteristics in plots developed after fire in the mixedwood section of southern boreal forest of Saskatchewan. Adapted from Thrasher-Haug (1997).

Plot	Age	Soil type	Plot	Age	Soil type
9609	0	Orthic Gray Luvisol	9408	100	Orthic Gray Luvisol
9602	1	Brunisolic Gray Luvisol	9607	101	Orthic Gray Luvisol
9534[1]	5	Brunisolic Gray Luvisol	9604	102	Orthic Gray Luvisol
9613[1]	16	Brunisolic Gray Luvisol	9405	108	Orthic Gray Luvisol
9615	16	Brunisolic Gray Luvisol	9414	108	Orthic Gray Luvisol
9612[1]	43	Orthic Gray Luvisol	9525	110	Orthic Gray Luvisol
9614	49	Orthic Gray Luvisol	9407	111	Orthic Gray Luvisol
9523	63	Brunisolic Gray Luvisol	9429	116	Orthic Gray Luvisol
9521	66	Brunisolic Gray Luvisol	9608	124	Brunisolic Gray Luvisol
9535	75	Orthic Gray Luvisol	9520	127	Brunisolic Gray Luvisol
9524[2]	76	Orthic Gray Luvisol	9423	134	Orthic Gray Luvisol
9411	77	Orthic Gray Luvisol	9611	147	Eutric Brunisol
9412[2]	77	Eutric Brunisol	9422	150	Orthic Gray Luvisol
9409	78	Orthic Gray Luvisol	9606	150	Gray Luvisol
9413	86	Orthic Gray Luvisol	9402[3]	157	Brunisolic Gray Luvisol
9522	90	Brunisolic Gray Luvisol	9404	171	Orthic Gray Luvisol
9401[2]	93	Brunisolic Gray Luvisol	9403[3]	172	Brunisolic Gray Luvisol
9415	94	Orthic Gray Luvisol	9406[3]	201	Orthic Gray Luvisol

[1] young, [2] mature, [3] old age classes, selected for intensive study

Table 3.2. Year of stand harvest and planting with white spruce, stand age at time of sampling, soil characteristics and site preparation type in plots after cutting in central Saskatchewan mixedwood forest. Adapted from Thrasher-Haug (1997).

Plot	Harvested	Planted	Age	Soil type	Site preparation
9601	1996	-	0	Brunisolic Gray Luvisol	Prior to site preparation
9531[1]	1995	1995	2	Orthic Gray Luvisol	Delta disc trenched
9509	1993	-	2	Brunisolic Gray Luvisol	Drum chopped and disc trenched
9510	1993	-	3	Brunisolic Gray Luvisol	Drum chopped and V-plowed
9533[1]	1993	1993	4	Orthic Gray Luvisol	Delta disc trenched
9528	1987	1988	8	Orthic Gray Luvisol	Delta disc trenched
9507a[1]	1986	1988[2]	9	Orthic Gray Luvisol	Drum chopped and mounded
9507b	1986	1988	9	Orthic Gray Luvisol	Drum chopped and mounded
9527	1985	1986	11	Orthic Gray Luvisol	Delta disc trenched
9503	1983	1984[2]	12	Orthic Gray Luvisol	Delta disc trenched
9511a	1983	1986	12	Brunisolic Gray Luvisol	Mounded
9506	1972	1972[2]	23	Orthic Gray Luvisol	NA[3]
9505	1970	1970	26	Orthic Gray Luvisol	NA
9610	1968	-	28	Orthic Gray Luvisol	NA
9530	1955	-	40	Brunisolic Gray Luvisol	NA
9532	1910	-	85	Orthic Gray Luvisol	Cut by homesteaders

[1] young age class selected for intensive study
[2] plots cleaned manually of hardwood
[3] NA, not available

Environmental characteristics

In each of the 12 plots selected for intensive study, forest floor thickness (LFH, cm), photosynthetically active radiation next to the forest floor (PAR, μmol $m^{-2}s^{-1}$) and soil temperature (°C) at 5 cm depth, were measured at the center of the 5 x 5 m quadrats (32 readings per plot). Photosynthetic active radiation and soil temperature were measured with a Quantum Sensor and a Thermocouple thermometer, respectively (both from *LICOR, Inc.*). PAR was expressed as a percentage of incident radiation above the canopy measured in the open in nearby clearings. Environmental characteristics were measured between 24 May and 6 June of 1997. The photosynthetically active radiation (PAR) was re-measured in August 1998 (Appendix D). PAR measurements were carried out between 11:00 am and 2:30 pm in mature and old plots, and between 2:00 and 3:30 in recent burns and clearcuts.

3.2.3. Data analysis

White spruce density, diameter at breast height and height were regressed against stand age (chronosequence). Regression analysis was carried out using the Minitab statistical package. 'Lack of fit' test was performed to determine the appropriate order of the regression equation. Environmental parameters were analyzed by ANOVA, using the SAS statistical package (SAS, 1988).

Seedling pattern (random, clumped, even) was analyzed using Poisson distribution and Chi-square. Each plot was divided into 128-2.5 x 2.5 m quadrats. White spruce seedlings were counted in each quadrat. Seedling pattern was then evaluated with Chi-square calculation, and the null hypothesis was that plants are distributed randomly in a plot. In cases where the null hypothesis was rejected, the ratio of variance of the mean was used, based on the fact that the ratio of a variance of a Poisson distribution and the mean is equal to one in a random distribution. A ratio greater than one implies a clumped distribution while a ratio less than one implies a more evenly spaced distribution (Whittaker, 1975, Barbour *et al.*, 1987).

3.3. Results

3.3.1. Tree density, DBH and height

White spruce tree-density increased gradually along the chronosequences after fire and cutting (Figure 3.2). White spruce trees were first noticed in a 16 year-old plot after fire (444 stems ha^{-1}) and a 26 year-old plot after clearcutting (125 stems ha^{-1}). An exception occurred in a recent clearcut where 12.5 stems ha^{-1} were left on site after harvesting. Maximum density of white spruce (1,413 stems ha^{-1}) was in a stand aged 172 years after fire (Figure 3.2). Based on the regression, white spruce as a percent of total trees present on a site was around 15 % at 16 years and increased to 45 % at 200 years after fire (Figure 3.3). Measured values varied widely around the regression line; mature stands had up to 57% white spruce and older stands up to 84%.

The average tree height and DBH increased with age after fire to peak between 110 and 127 years of age (Figure 3.4). The largest trees averaged 26 m tall with a diameter at the breast height of about 30 cm. During the period of white spruce dominance (93 to 172 years after fire), the average tree height was 20 m and DBH was 17cm. The DBH and height of trees in clearcuts were within the range of those in fire-generated stands.

Correlation analysis indicated an insignificant inverse correlation between tree density and height, and tree density and DBH (R^2 = 6.8 and 16 %, P = 0.7 and 0.35, respectively). On the other hand, tree height and DBH were highly correlated (R^2 = 91%, P< 0.05).

3.3.2. Sapling density, age, DBH, and height

White spruce saplings were present in all sampled plots, except in recently-disturbed plots, some mature plots (77, 86, 100, 108, 111-124 years), and an old plot (150 years) after fire. In plots developing after cutting, sapling density peaked at 11 years (1,450 stems ha^{-1}). Maximum densities after fire were observed in 16- and 90-year-old plots (2,300 and 3,350 stems ha^{-1} respectively) (Figure 3.5).

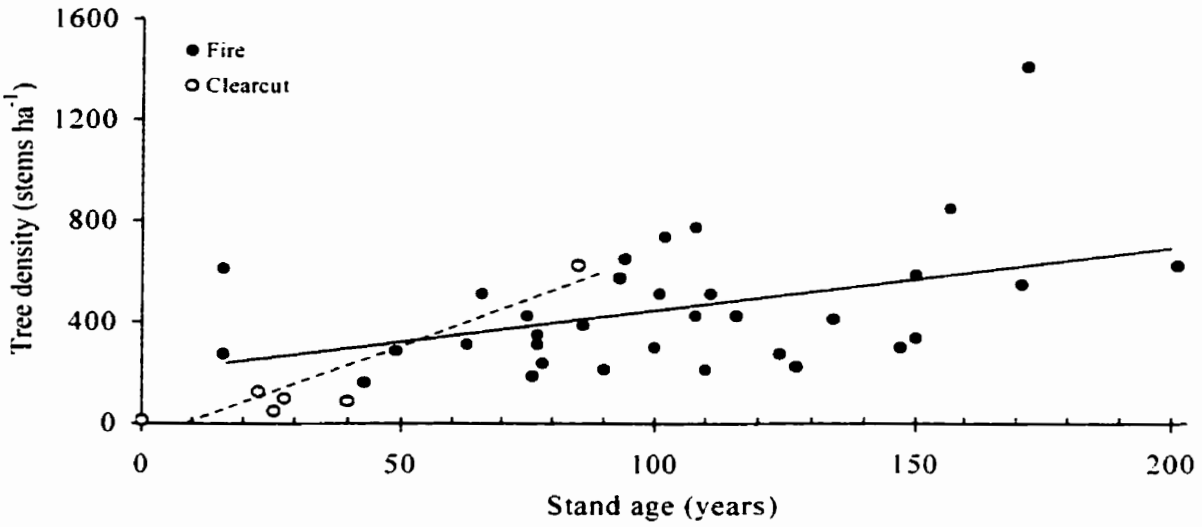


Figure 3.2. Tree density (ha^{-1}) of white spruce along a chronosequence after fire (33 stands) or clearcutting (6 stands). The remaining stands were too young to have trees in them. Linear regression lines were fitted for plots after fire (solid, density = 2.5 age + 199.7, $R^2 = 0.18$, $P<0.05$) and after cutting (dashed, $R^2 = 0.85$, $P<0.05$).

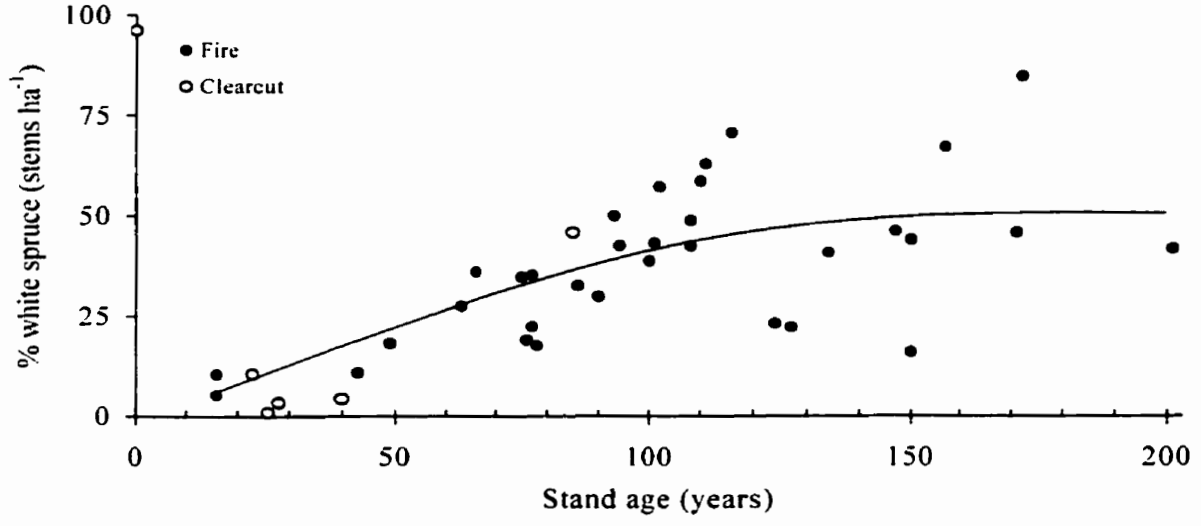


Figure 3.3. Tree density (ha^{-1}) of white spruce expressed as percent of total trees present (all species) along a chronosequence after fire (33 stands) or clearcutting (6 stands). Second order polynomial regression line was fitted for stands after fire (% white spruce = $-0.001\ age^2 + 0.54\ age$, $R^2 = 0.43$, $P < 0.05$).

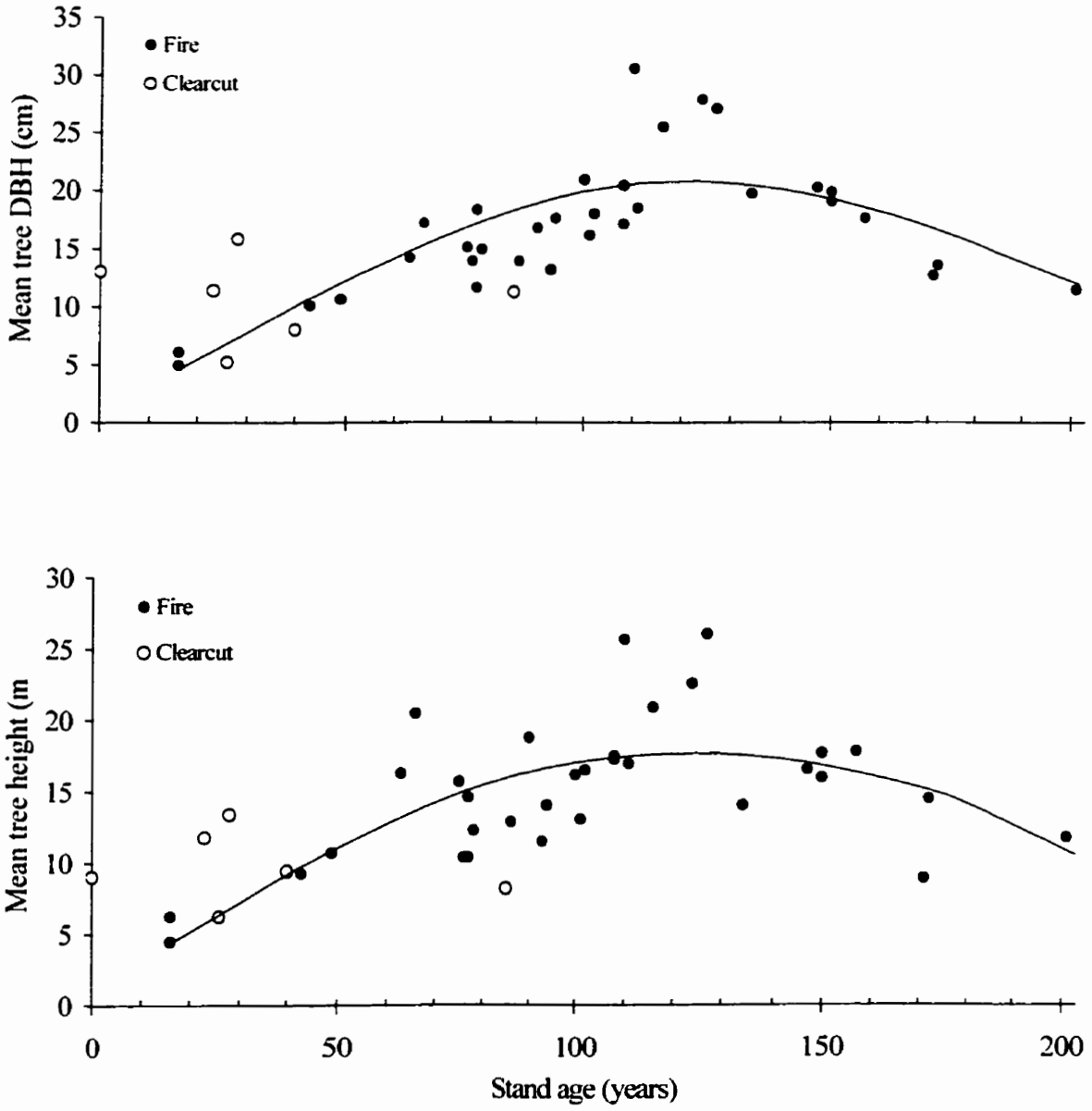


Figure 3.4. Mean tree diameter at breast height (DBH, cm) and height (m) of white spruce along a chronosequence after fire (33 stands) or clearcutting (6 stands). Second order polynomial regression line was fitted for plots after fire (DBH= -0.001 age^2 + 0.32 age, height = -0.001 age^2 + 0.29age, R^2 = 0.58 and 0.47 respectively, $P<0.05$).

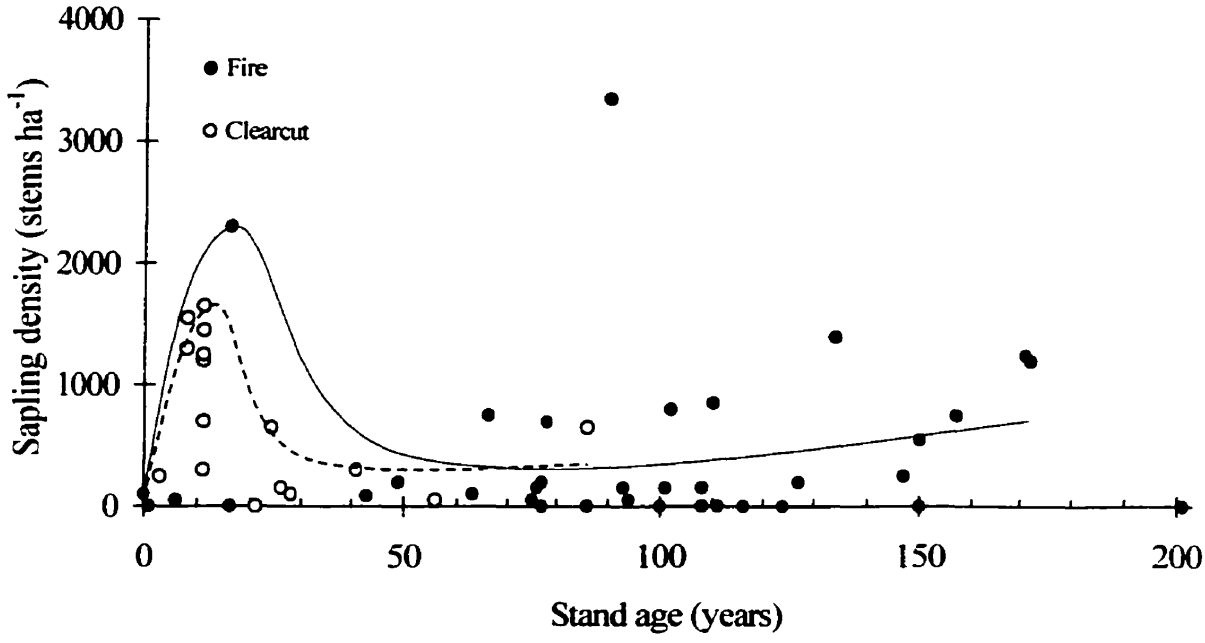


Figure 3.5. Sapling density (ha^{-1}) of white spruce along a chronosequence after fire (36 stands) or clearcutting (16 stands). Curves were fitted by eye for plots after fire (solid) and clearcutting (dashed).

Generally, sapling density along the chronosequence after fire resembled that after cutting, but trends were not as clear due to the small number of fire-generated stands in the 0-40 year range. The oldest saplings (24 years) were observed in a 43-year-old plot (Figure 3.6). These saplings averaged 2.5 ± 0.5 m tall and 3.8 ± 0.7 cm diameter at the base. Mean sapling height and DH were least between 93 and 157 years after fire (Figure 3.7). The pattern was similar to that of sapling age, which was expected since age was predicted from height and diameter. Saplings in planted clearcuts were 2 years older than stand age, because 2-year-old seedlings were planted after clearcutting. Saplings of similar age were generally bigger in clearcuts than in fire-generated stands. Diameter at the base and height of 11-year-old saplings after clearcutting were 3.6 cm and 1.7 m compared to 1.5 cm and 0.92 m for those developed after fire.

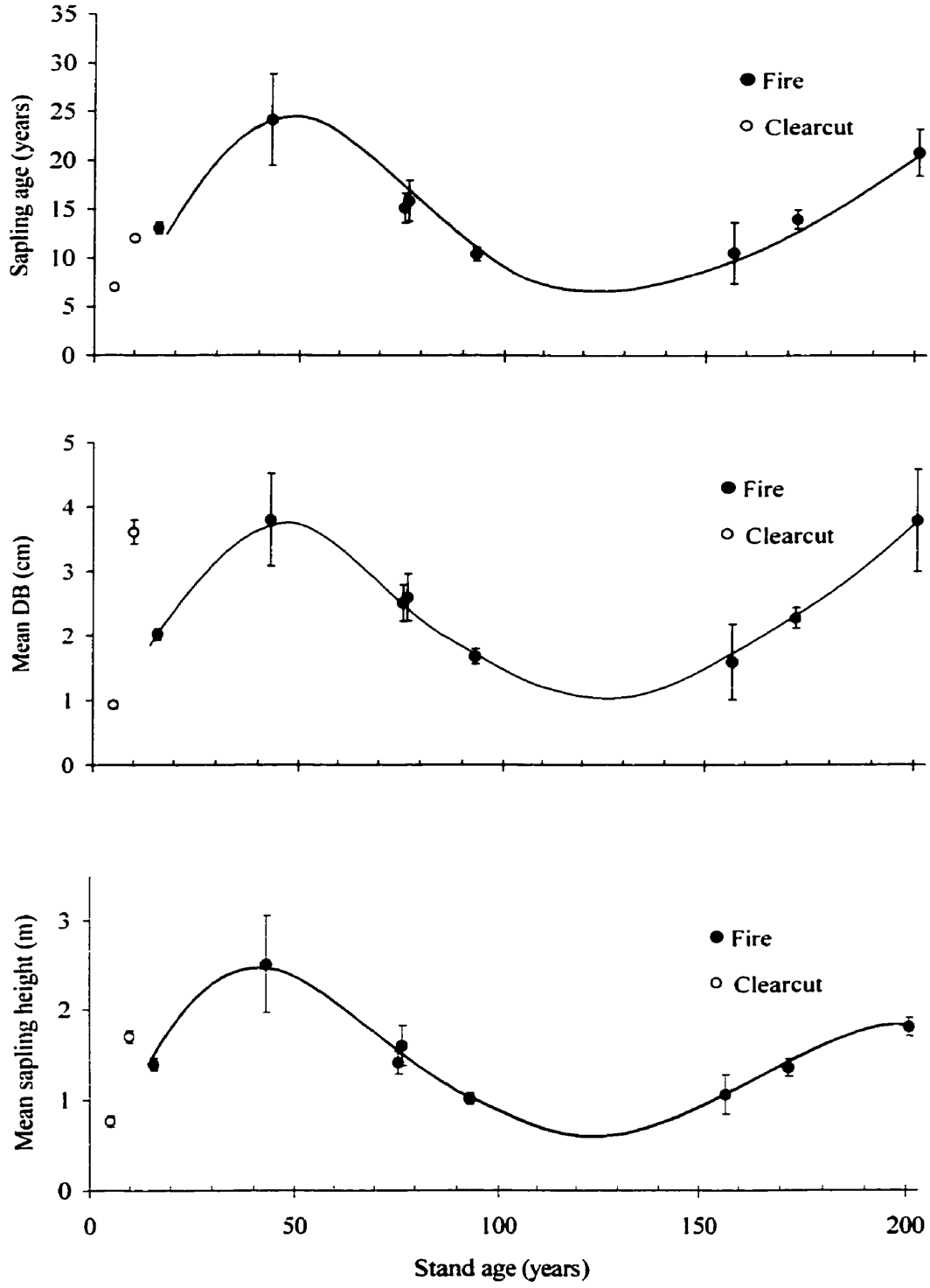


Figure 3.6. White spruce age (years), diameter at the base (DB, cm) and height (m) of saplings, and standard errors bars, in 10 stands along a chronosequence developing after fire or clearcutting. Fourth order polynomial regression lines were fitted for plots after fire (R^2 = 0.70, 0.28 and 0.41 respectively, P>0.05).

3.3.3. Photon irradiance, soil temperature and LFH thickness

Light intensity near the forest floor, expressed as percent of incident radiation above the canopy, declined along the chronosequence (Figure 3.7, Appendix E). Maximum intensities next to the forest floor were recorded in plots shortly after clearcutting (100 %) and after fire (64%). Minimum light intensity observed was 3.5 % in a 172-year-old plot after fire. Light intensity increased again in a 201-year-old plot (34 %).

The greatest mean soil temperature was measured in a 2-year-old plot after clearcut (14.9 °C). It differed significantly from the young plots after fire (4.5 °C). The lowest soil temperature was in a 201-year-old plot (3.5 °C). Corresponding air temperatures for these plots were 18, 11 and 17 °C respectively. Air temperature varied between 11 and 27 °C, and averaged 19.3 °C during the two-week period of data collection (Appendix E).

The LFH layer thickness increased along the chronosequence after fire (Figure 3.7, Appendix E), maximum thickness of 13 cm was measured in a 172-year-old plot, and the thinnest layer was 7.8 cm in a plot burned 5 years earlier. In comparison, the LFH layer in recent planted plots was not distinct, due to surface disturbance that exposed the mineral soil. In a 9-year-old planted plot, the LFH thickness varied from 1 to 10 cm, averaging 7.6 cm.

3.3.4. White spruce seedling structure along the chronosequence and environmental gradient

White spruce seedlings were present in all sampled plots except for a plot 43 years after fire, and a 9-year-old plot after clearcutting. The lowest density observed was 75 stems ha^{-1} in a 77-year-old plot while the greatest density was 737 stems ha^{-1} in a 93-year-old plot after fire (Figure 3.8). In a 2-year-old planted clearcut, white spruce seedlings were present at a density of 1,387 stems ha^{-1}. In an older clearcut (4-year-old), seedlings were 6 years of age and greater than 50 cm in height, thus were classified as saplings. As seedlings their density would have been 1,262 ha^{-1}, based on measured sapling density. In addition, 1,050 seedlings ha^{-1}

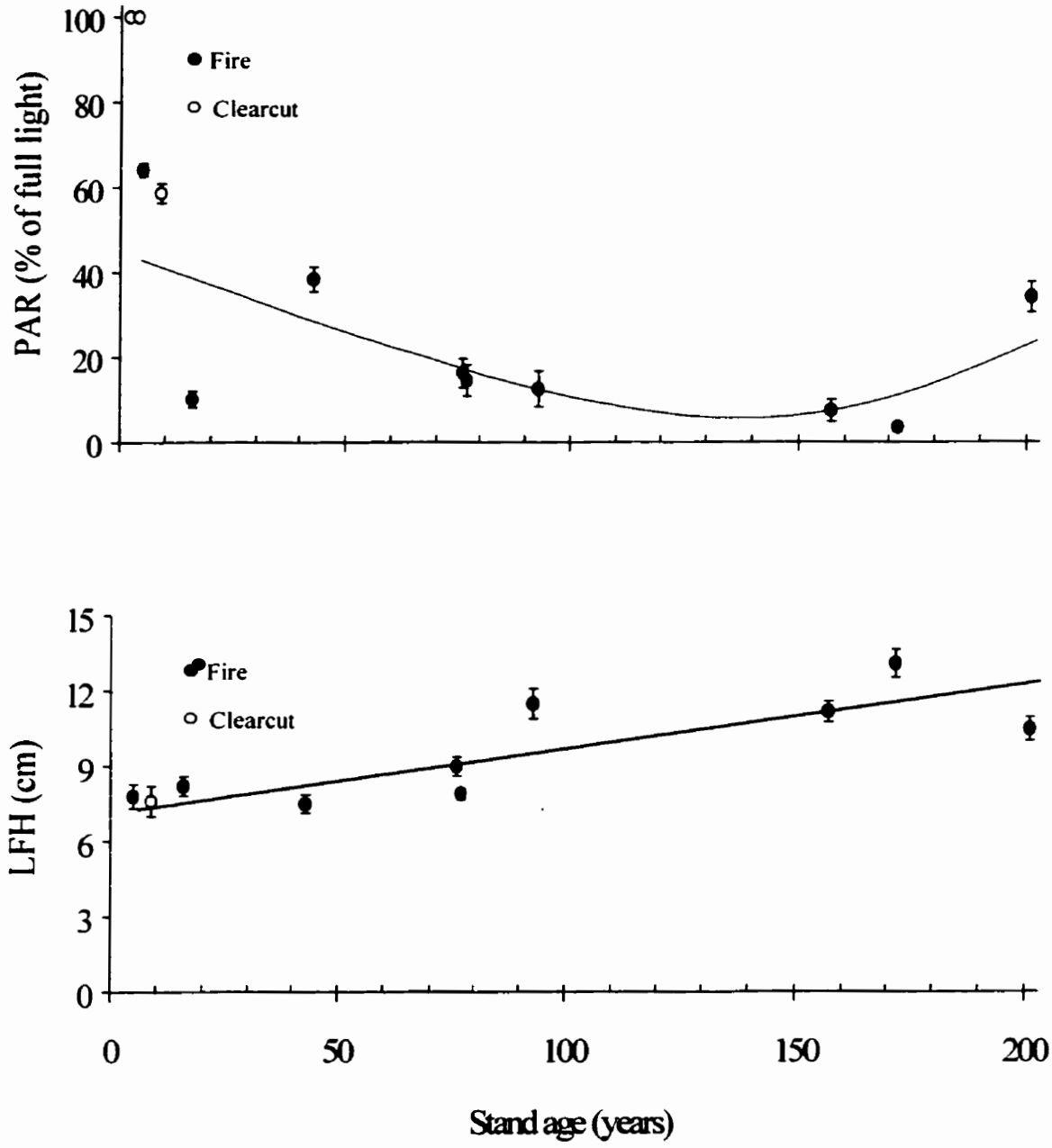


Figure 3.7. Photosynthetically active radiation (% of full light), soil temperature (°C) and forest floor thickness (LFH, cm), and standard error bars along a chronosequence in stands developing after fire or clearcutting. Second order or linear regression lines were fitted for plots after fire (PAR = 0.003 age^2 – 0.72 age + 51, LFH = 7.47 + 0.023 age, R^2 = 0.57 and 0.66 respectively, $P<0.05$).

regenerated naturally after planting in this plot. The 2 and 9-year-old plots after clearcut did not show any natural regeneration.

Seedlings were mostly observed in shaded microsites with irradiance of 6 to 30 % of full sunlight. Regressing seedling density against the percent of light near the seedling gave a significant negative relationship (Figure 3.9). Seedling pattern in relation to light, analyzed using Chi-square, indicated that seedlings were not located at random, rather they were concentrated in microsites with low light levels.

Average seedling height in plots after fire ranged between 18.5 ± 1.8 cm in a 157 year-old and 37 ± 1.8 cm in a 16 year-old plot (Figure 3.10). Seedling heights in clearcut stands were similar to those in fire-generated stands. The overall average coefficient of variation in seedling height was 41.5% in fire regenerated and 28% in planted clearcuts.

Results from Chi-square analysis were utilized as described by Whittaker (1975) to determine seedling pattern in mapped plots (Figures 3.11 to 3.20). Results showed that seedlings in old plots after fire were clumped together, while in younger plots seedlings were evenly spaced or random. In planted clearcuts, seedlings were evenly spaced in rows either on the side or on the top of the mounds created during site preparation. In the 4-year-old planted plot, saplings were randomly distributed. Naturally-regenerated seedlings in the 4-year-old clearcut were clumped to randomly spaced (Figure 3.18). Pattern analysis was not performed on a 9 year-old planted plot or a 43 year-old fire generated plot due to the absence of seedlings, or on 201 (Figure 3.12) and 77 (Figure 3.15) year-old plots after fire due to lack of sufficient data (Table 3.3).

Of the total number of seedlings in fire-generated stands, 70 % grew on logs and 30 % on the forest floor (LFH). Seedlings in the young age class (0 to 43 years) occurred mainly on LFH (72 %) rather than on logs (28 %) (Table 3.3). In old plots (>157 years) the recruitment was mainly on logs (97%). In mature stands (76 to 93 years), 52% of seedlings were on logs, and 48 % on LFH. In planted clearcuts, seedlings occurred on mineral soil.

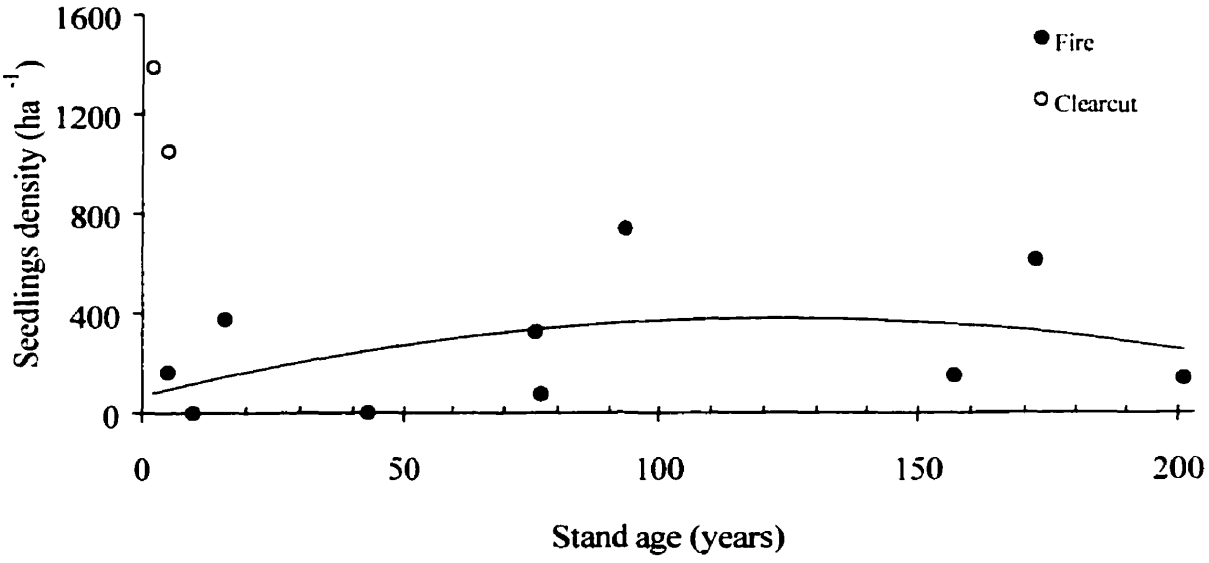


Figure 3.8. Seedling density (ha^{-1}) along a chronosequence in stands developing after fire or clearcutting. Second order polynomial regression was fitted for stands developing after fire (density = -0.021 age^2 + 5.1 age + 69. R^2 = 0.16, P>0.05).

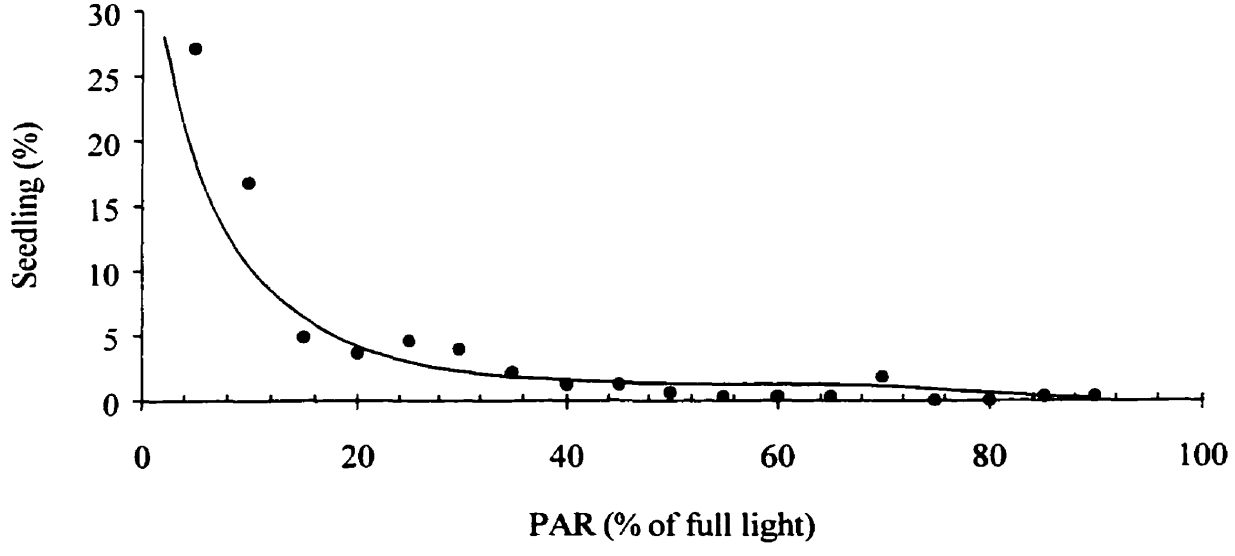


Figure 3.9. Distribution of white spruce seedlings (% of total population) in relation to light (% of full light) in stands developing after fire. Forth order polynomial regression line was fitted (% seedlings = 5E-06 PAR^4 - 0.001 PAR^3 + 0.1 PAR^2 - 3.2 PAR + 39.6, R^2 = 0.95, P<0.05).

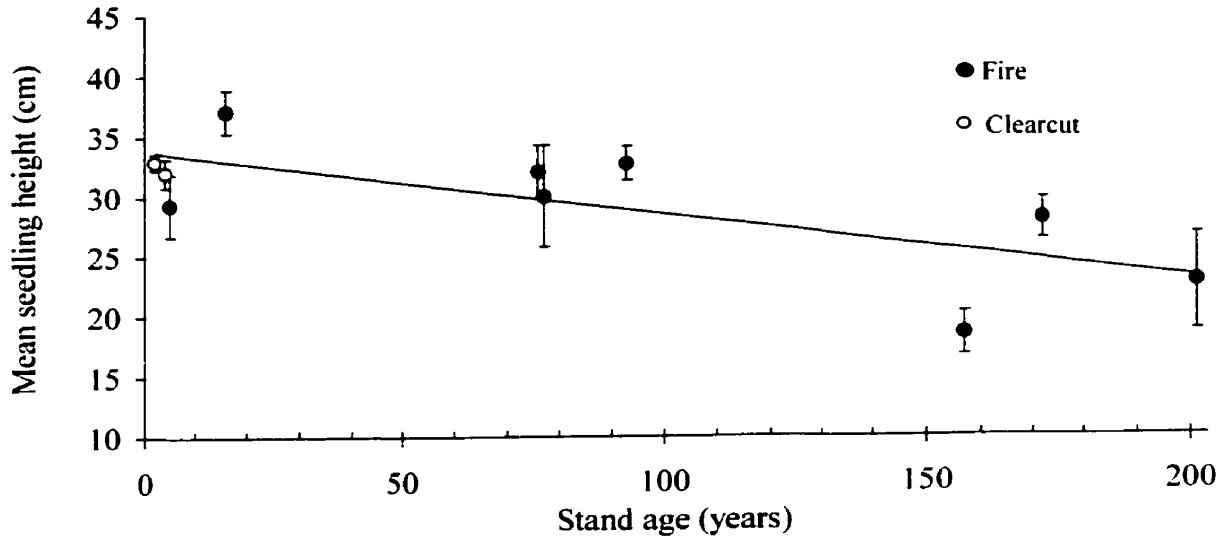


Figure 3.10. White spruce seedling-height (cm) and standard error along a chronosequence in stands developing after fire or clearcutting. Linear regression line was fitted for plots after fire (Height = 362.5 – 8.7 age. $R^2 = 0.70$, $P<0.05$).

Table 3.3. White spruce seedling density (ha^{-1}), and seedling pattern in the 20 x 40 m plots, and substrate preferences in stands after fire or clearcutting.

Stand age	Seedlings density (Stems ha^{-1})	Seedling pattern[1]	Substrate preference (% of seedlings)		
After fire			Log	LFH	Mineral
5	162	Evenly spaced	23	77	0
16	375	Evenly spaced	30	70	0
43	0	—	—	—	—
76	325	Random	38.5	61.5	0
77	75	—	17	83	0
93	737	Clumped	63	37	0
157	150	Clumped	83	17	0
172	612	Clumped	100	0	0
201	137	—	100	0	0
After clearcut			Log	LFH	Mound
2	1387	Evenly spaced	0	0	100[4]
4	1050 (1262)	Clumped-random (Random)[2]	2.4	1.2	96.4
9	0 (—)[3]	—	0	0	0

[1] seedling pattern was analyzed following Whittaker (1975).
[2] randomly distributed young saplings were found.
[3] sapling distribution not determined.
[4] 5 % were on the top, 31% on the bottom and 64% on the side of the mound.

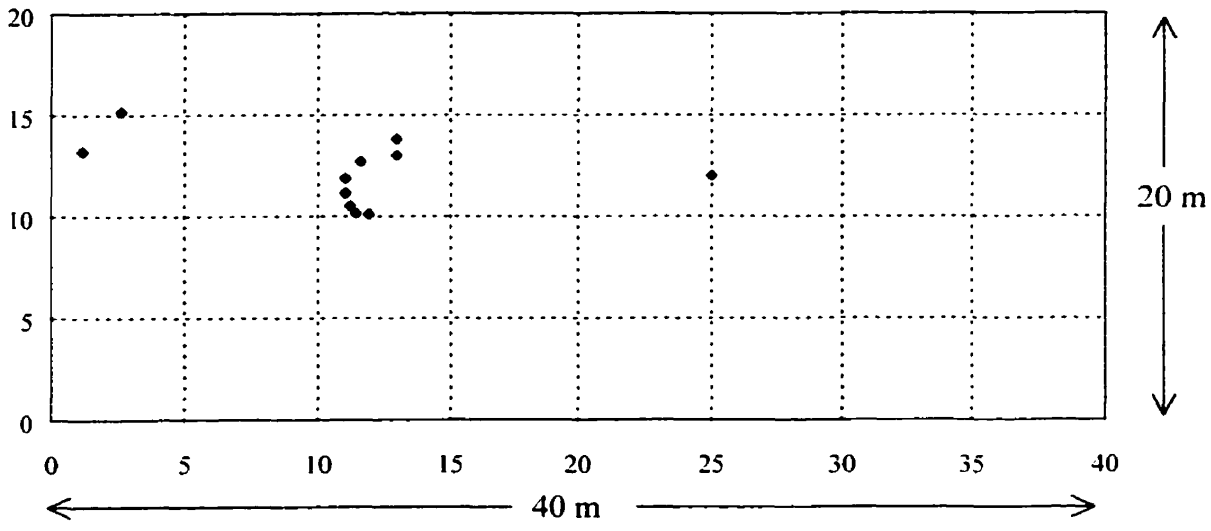


Figure 3.11. Distribution of white spruce seedlings in a 201-yr-old stand (94-06) after fire (40x20 m plot); ◆ seedlings on logs. Pattern was not calculated because of small sample size.

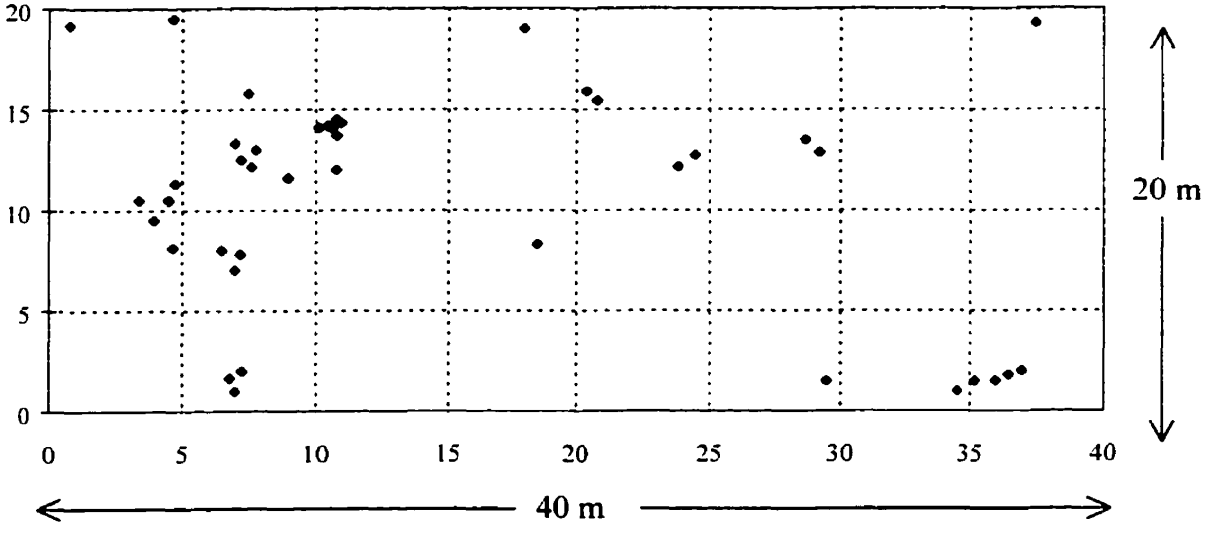


Figure 3.12. Clumped distribution of white spruce seedlings in a 172-yr-old stand (94-03) after fire (40x20 m plot); ◆ seedlings on logs.

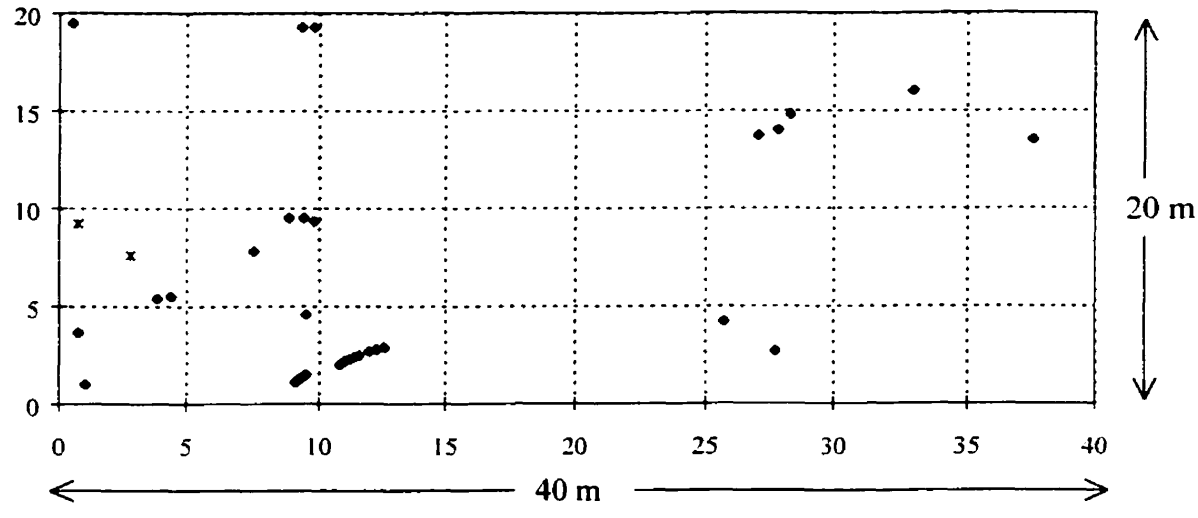


Figure 3.13. Clumped distribution of white spruce seedlings in a 157-yr-old stand (94-02) after fire (40x20 m plot); ◆ seedlings on logs: * on LFH.

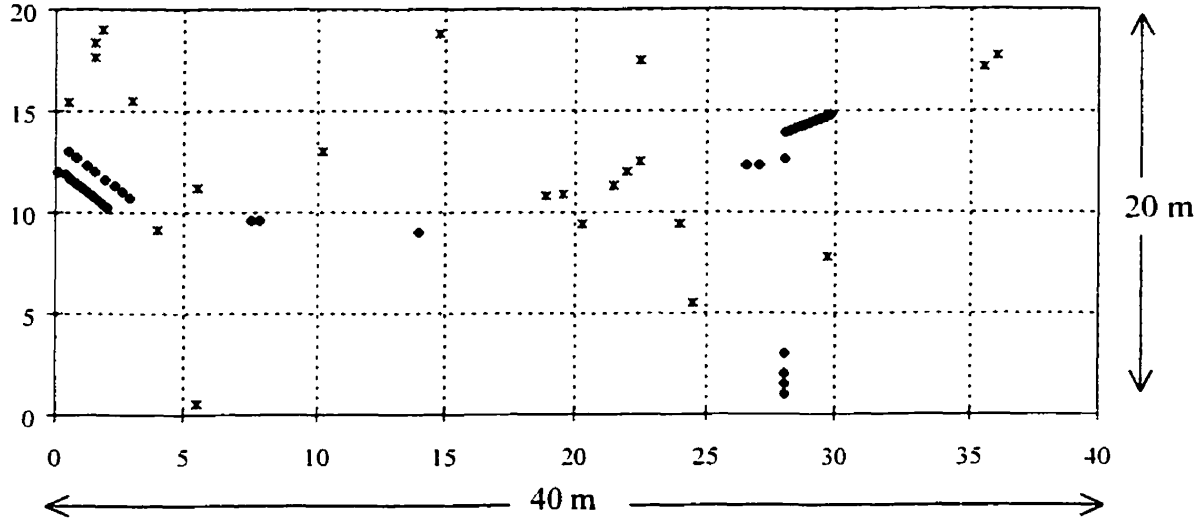


Figure 3.14. Clumped distribution of white spruce seedlings in a 93-yr-old stand (94-01) after fire (40x20 m plot); ◆ seedlings on logs; * on LFH

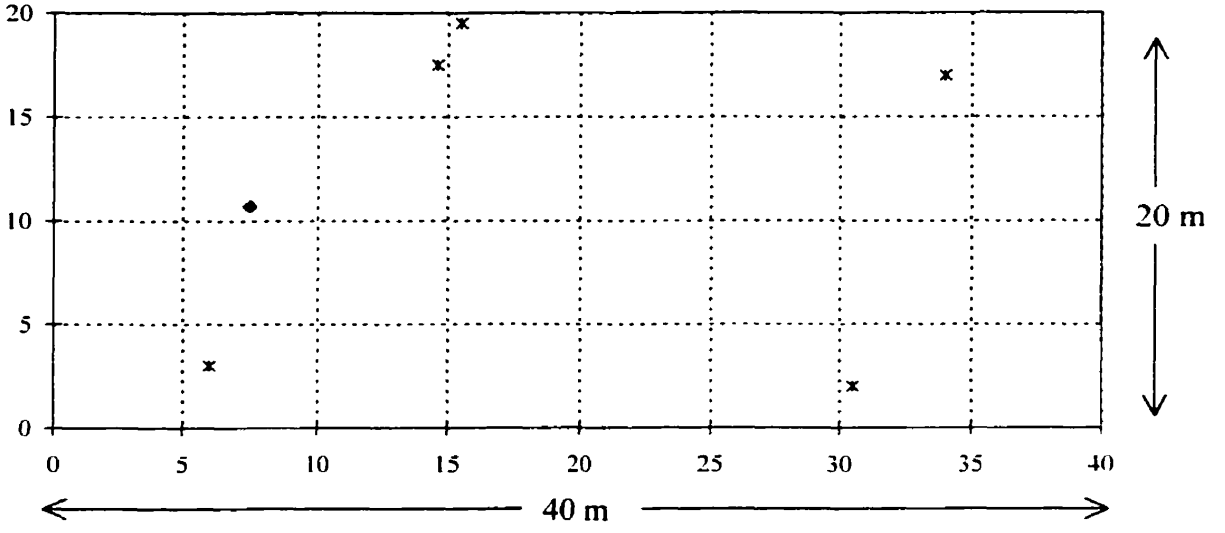


Figure 3.15. Distribution of white spruce seedlings in a 77-yr-old stand (94-12) after fire (40x20 m plot); ● seedlings on logs; * on LFH. Pattern was not calculated because of small sample size.

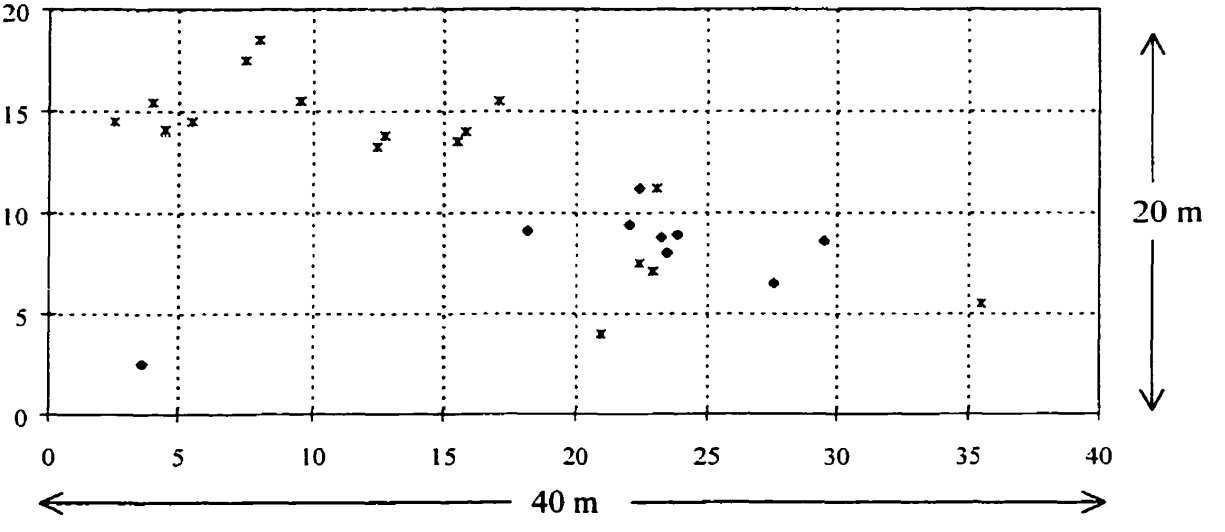


Figure 3.16. Random distribution of white spruce seedlings in a 76-yr-old stand (95-24) after fire (40x20 m plot); ● seedlings on logs; * on LFH.

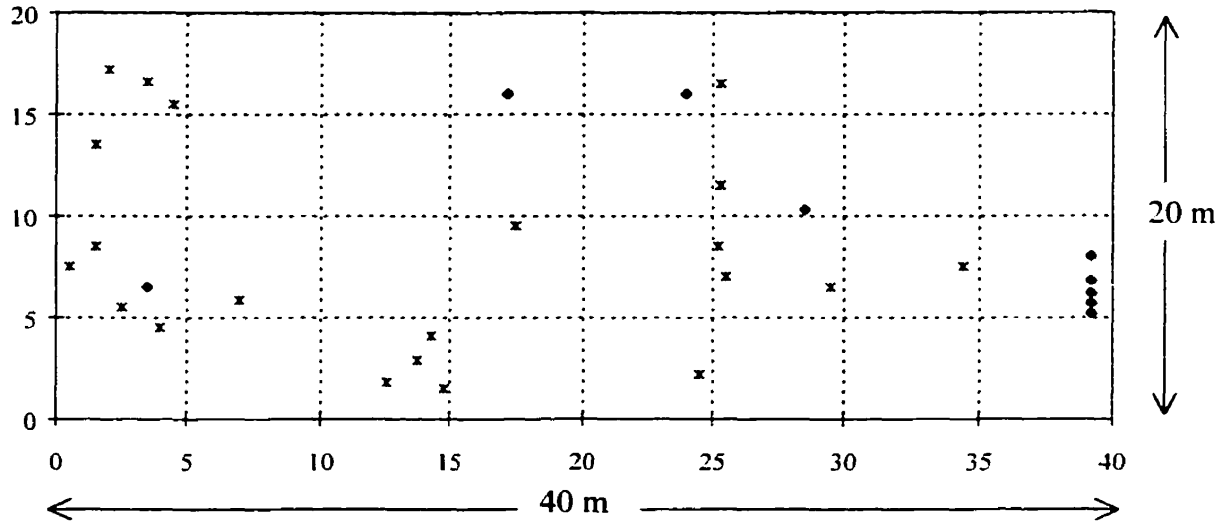


Figure 3.17. Evenly spaced white spruce seedlings in a 16-yr-old stand (96-13) after fire (40x20 m plot); ◆ seedlings on logs; * on LFH.

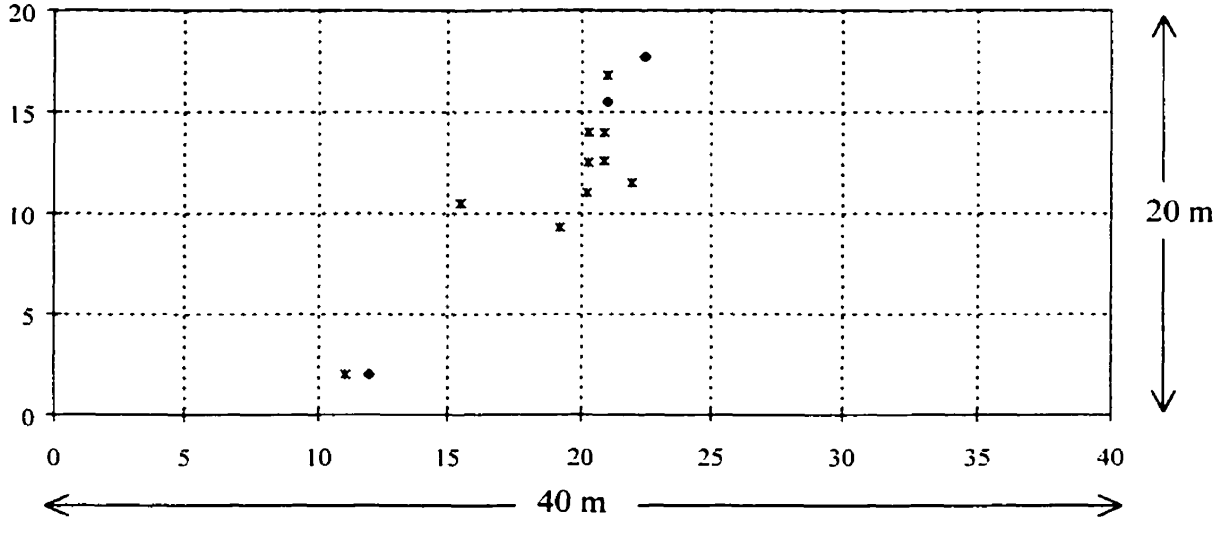


Figure 3.18. Evenly spaced white spruce seedlings in a 5-yr-old stand (95-34) after fire (40x20 m plot); ◆ seedlings on log; * on LFH.

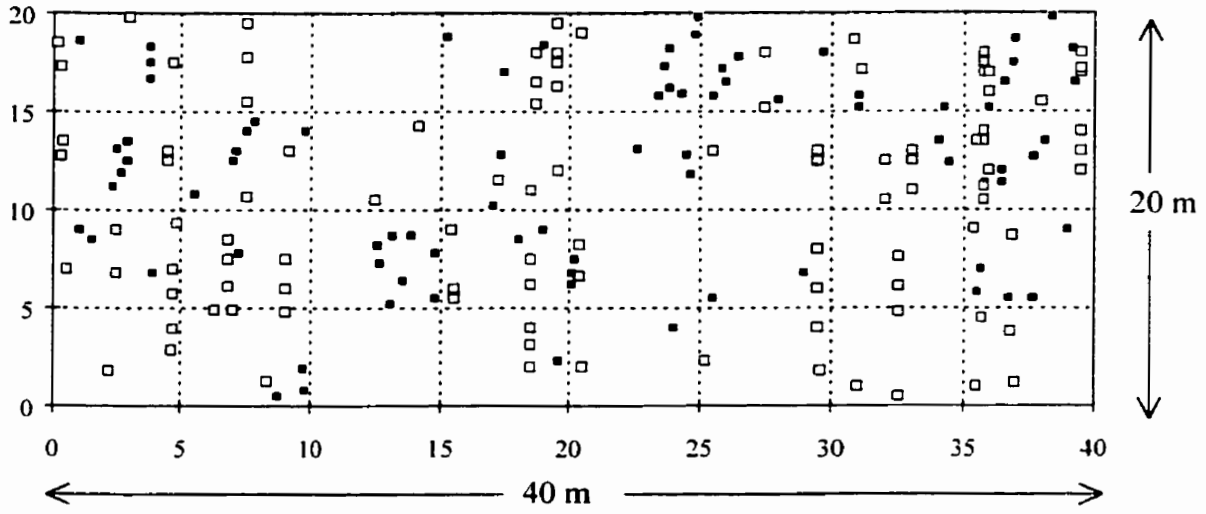


Figure 3.19. Random white spruce sapling □ and clumped to random seedling distribution ■ in a 4-yr-old planted stand (95-33); 40x20 m plot; all saplings and seedlings were on mineral soil.

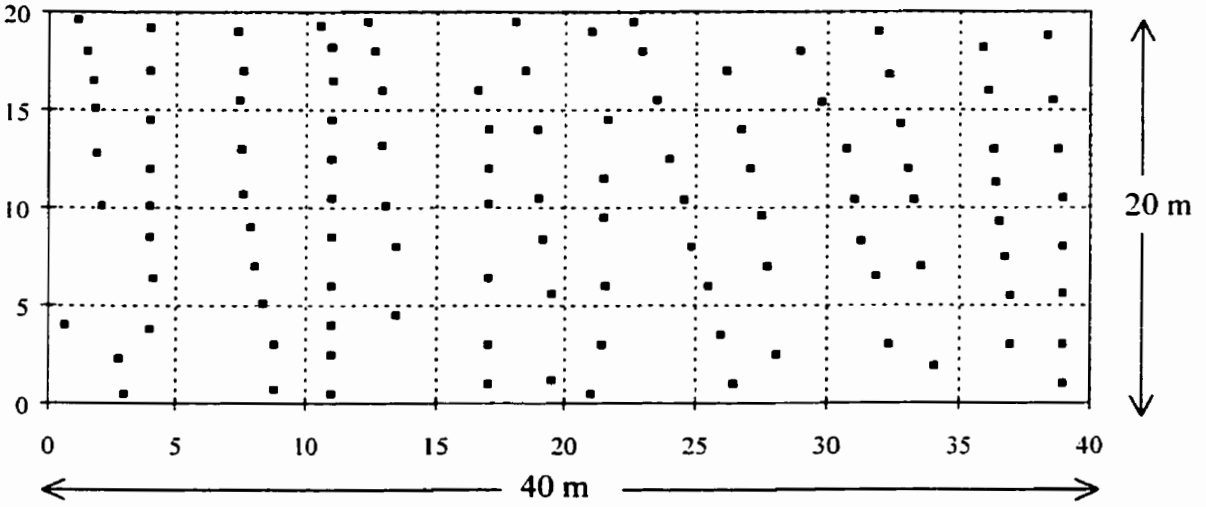


Figure 3.20. Evenly spaced white spruce seedlings in a 2-yr-old planted stand (95-31); 40x20 m plot ; all seedlings were on mineral soil.

3.4. Discussion

White spruce trees first appeared in recently disturbed areas. 16 years after fire and 23 years after clearcutting. Bergeron and Charron (1994) found that after disturbance. fast growing trembling aspen regenerated readily from root suckers and attained an immediate dominance of the canopy. White spruce, even though found recently after disturbances, were suppressed by aspen and remained for decades in a subordinate position until canopy gaps were formed (Oliver, 1978).

White spruce tree density in a 23 year-old plot after clearcut was 20% that of a 16 year-old plot after fire. but trees were 5 m taller. The 23 year-old-plot was planted in 1972 and was manually cleared of hardwood in 1994 (Thrasher-Haug, 1997), releasing white spruce from aspen competition for resources at an earlier stand age. This, in conjunction with an increase in nutrient mobilization after cutting (Pritchett and Fisher. 1987) and possibly a superior white spruce planting stock probably led to the greater growth. On the other hand. the greater density of white spruce at an earlier stand age after fire than after clearcut could be attributed to several factors including, clearcut stands being far from a seed source; site conditions being not conductive for seed germination and seedling establishment; tree harvest coinciding with a low seed production of nearby mature trees; or a combination of two or more of the mentioned factors (Galipeau *et al.*, 1996; Farmer, 1997).

In the current study, some trees were left on site after cutting, a practice carried out by timber companies to provide seed input, wildlife refuge and corridors. The fate of these trees varies with site and environmental conditions. Many reports showed that the shallow rooted white spruce was prone to wind and when left in the open were severely damaged (Kimmins, 1997).

In both clearcuts and burns, young white spruce were generally overtopped by trembling aspen by at least 2 m. This difference further increased until 77 years after fire before it dropped again (Sulistiyowati, 1998). White spruce dominated stands between 93 and 172 years, coinciding with a decline in deciduous trees. Oliver and Larson (1996) suggested that during the period of aspen overmaturity (about 80 years, Kazbems *et al.*,

1986), white spruce was released from the understory and assumed dominance of the stand, while aspen died back. Van Cleve and Viereck (1981) found that white spruce became the dominant tree at about 100 years after fire with a density of 500 stems ha^{-1}. Delaney (1995) reported that white spruce increased from 410 to 515 stems ha^{-1}, and softwood to hardwood ratio increased from 1 to 1.4 between 51 and 110 years in Manitoba's boreal forest. In the present study, white spruce followed a similar trend but with lower tree density (332 and 426 stems ha^{-1}) and softwood to hardwood ratio (0.4 and 0.7) for the same period. In a 172 year-old stand after fire, white spruce represented 84% of the total trees. However, as the stand grew older, and in the absence of major disturbances, white spruce density commenced to decline as it became incapable of successfully reproducing itself due to the increase in shade and thickness of the moss layer. This is usually noticed at 150 years after fire (Oliver and Larson, 1996). At this stage, balsam fir is released from the understory and eventually forms an uneven aged stand dominated with balsam fir with scattered white spruce (Thorpe, 1996). A similar successional pattern, from deciduous to coniferous composition along a chronosequence after fire was also observed in the southern Canadian boreal forest of Quebec (Bergeron and Dansereau, 1993).

The largest white spruce trees in the study sites averaged 26 m tall and 30 cm DBH. Johnson *et al.* (1995) reported 40 m tall white spruce, and Morton and Lewis (1917) found trees as large as 1.36 m DBH. However, they added that the average white spruce height and DBH reached in a forest stand is only 17 m and 50 to 68 cm respectively. A weak negative coefficient of determination was noticed when correlating white spruce tree density with height and DBH. Closely spaced trees are expected to be shorter and smaller in diameter than those in wider spaced stands over time (Scott *et al.*, 1998). Hann and Ritchie (1988) concluded that tree height growth is relatively independent of its degree of crowding and amount of foliage except at extremely narrow spacing. Tree DBH and height dropped in the old age classes, which is attributed to the increase in white spruce mortality with overmaturation.

White spruce sapling density probably peaked at an earlier age after clearcutting than after fire, as the stands were mainly planted either immediately after cutting or during the following growing season with two to three-year old seedlings. This likely

accelerated white spruce regeneration and succession. in comparison to stands after fire where regeneration depended mainly on seed dispersal from nearby trees. The seed bank of white spruce is depleted after fire (Harper, 1977; Farmer, 1997). Saplings from planted stands were taller than the naturally-regenerated saplings of the same age. Delaney (1995) reported that 7-year-old white spruce were 0.62 m tall while naturally-regenerated seedlings were 0.52 m. Hawkins *et al.* (1995) found that 10-year-old white spruce saplings were around 60% taller on mounded sites than on control sites.

Seedling density was greater in a 2 years after cutting (1,387 stems ha^{-1}) compared to 5 years after fire (162 stems ha^{-1}) because trees were planted. In the 4-year-old planted plot, seedlings density was 1262 stems ha^{-1}, corresponding to 90% of the density in the 2-year-old planted plot, assuming the same planting density. In addition, over 1,000 seedlings ha^{-1} regenerated naturally on the 4 year-old site. Carleton and MacLellan (1994) stated that the speed by which white spruce regenerates after disturbance depends on many factors, the most important being propagule availability and establishment, followed by competition and interaction with the environment. Delaney (1995) suggested that the original stocking rate should be between two and three thousands stems ha^{-1}. This is required to ensure the presence of 750 stems ha^{-1} at time of harvest in the boreal forest of Manitoba. Seedling survival after planting varies, ranges from over 90% after two growing seasons (Brand, 1991; Lowery and Zabubenin, 1995) to 65 % (Krankina and Dixon, 1992). Hawkins *et al.* (1995) found that mounded sites, planted with white spruce showed 90% survival compared to 34% on unmanaged sites. Ontario Ministry of Natural Resources (1988) found that 40-60 % of white spruce plantations did not meet reforestation targets. Krankina and Dixon (1992) suggested that survival is in fact related to stock quality, site preparation, planting techniques and brush competition.

White spruce seedlings were found in all burned plots selected for intensive study except for a 43 year-old plot. Nearby trees may have not reached sufficient maturity to provide seeds in that stand, or seed dispersal from near-by stands could have been limited. Farmer (1997) suggests that seed dispersal distance of white spruce is usually around 20 m in a closed stand.

White spruce seedling density was highest in stands aged 16. 93 and 172 years after fire. Galipeau *et al.* (1996) found that white spruce recruitment after fire was characterized by 2 peaks. one shortly after fire (5-20 years) and a second smaller peak at about 50 years. Lieffers *et al.* (1996) suggested that white spruce recruitment is site specific, and added that regeneration was immediate in stands close to seed trees. while a lag phase of 20-years was noticed in stands over 250 m away from seed source.

Seedling height varied within and among plots. The average coefficient of variation for height was 41.5 %, suggesting a continuous recruitment of the species over time as suggested by Lieffers *et al.* (1996). Also considering the variation in age of saplings (CV = 43.6), one can conclude that regeneration was generally continuous but with varying intensities along the chronosequence after fire. and that some seedlings in the understory may have died, creating an uneven aged stand. Oliver and Larson (1996) suggested that the pattern of seedlings growth in the understory depends greatly on the pattern of the overstory death, adding that younger trees. usually exhibit varying ages. heights and sizes because the overstory breaks up unevenly.

Distribution of seedlings in mature and old plots was clumped. This pattern also was reported by Delaney (1995). Seedlings in young plots were mainly evenly or randomly distributed. In older plots, seedlings were mostly found on decaying logs. In some cases. several individuals were established on the same log. The important role of logs for seedling establishment of white spruce is well known (Rowe. 1955; Kimmins. 1997). White spruce regeneration on logs increases in importance as stands age. Rowe (1955) found that 32% of white spruce seedlings regenerated on logs in older stands. Concentrations of seedlings on logs probably contributed to the clumpy pattern of seedlings in older plots. Barbour *et al.* (1987) suggested that a clumpy distribution reflects either the reproduction properties of a species, or the variability of microsites. They added that suitable microsites for a species tend to be more populated with that species. Williamson (1975) and Yeaton (1978) suggested that individuals compete and may die at the narrower spacing within clumps; consequently, surviving individuals may change from a clumped to a random distribution and then may approach a regular or evenly-spaced distribution as they grow older.

As stands age, light, temperature, and moisture regime gradually change next to the forest floor. As well, mineral soil becomes colder, because of insulating effects of the LFH, and this in turn reduce the number of microsites that species can grow in (Oliver and Larson, 1996). Place (1955) reported 5 cm of undecomposed litter inhibited establishment of white spruce while 7 cm was needed to inhibit the establishment of balsam fir. This was attributed to the heavier and longer seed of balsam fir, which supports more extensive radical growth in fir than in spruce seedlings.

Light intensity was about 100 % and 64 % of full light in recent clearcut and burned stands, respectively. Light transmittance dropped to below 20% in mature and old stands, coinciding with canopy closure, before it increased again in 201 years after fire. This opening of the canopy results from gap formation in older stands (Oliver and Larson, 1996). Brand (1991) found that light reaching seedlings was 80-100% in recent clearcut during the beginning of the growing season and dropped depending on the rate of seedling shading. Lieffers and Stadt (1994) reported that mixedwood stands dominated by hardwood transmitted the maximum light (11-40%) while pure stands of white spruce transmitted the least. The majority of seedlings in the canopy understory were found between 10 and 30 % of full light. Eis (1970) reported death of white spruce below 15% light, while Logan (1969) found that white spruce seedlings remained alive at 11 to 13% light. Light intensity below 8% of full light limits white spruce recruitment (Lieffers and Stadt, 1994).

Clearcuts exhibited a significantly higher soil temperature than recent burns. Brand (1991) found that soil temperature increased in scarified stands by 5°C, on average, relative to non-scarified stands during the end of May (soil temperature, 14 and 19 °C respectively). The forest floor acts as insulator against soil temperature and the consequence of its removal varies with disturbance type. Exposed mineral soils, on the other hand, tend to have greater diurnal and day-to-day variation in soil temperatures than soils with a forest floor, because of the greater radiation absorbance and emmittance during the day and night respectively (Pritchett and Fisher, 1987). Mineral soil was 3.7 and 7 °C warmer in clearcut and slash burned clearcut areas respectively, than in uncut forests (Viro, 1974). Pomeroy (1996) suggested that increase in soil temperature in clearcut stands is related to 1) the lack of cover in recent clearcuts,

resulting in a significant input of energy which in turns increases the flow through the soil; 2) to the removal of the forest floor and 3) the increase in compaction due to site preparation. This is usually accompanied by a smaller leaf and root area and less water interception, resulting in lower evapotranspiration. The latter is especially important for cooling the surface.

4. PHYSIOLOGY AND GROWTH OF PLANTED AND NATURALLY-REGENERATED POPULATIONS OF WHITE SPRUCE

4.1. Introduction

In transition from an open to a closed canopy, the one environmental factor that changes the most is light. The decrease in light is rapid close to the forest floor, and is likely to exert a strong influence on the distribution, establishment and success of species early stages of recruitment (Turton and Duff, 1992). The effect of light on growth is mostly through photosynthesis, and it is noticeable in seedlings that, when growing on forest floors, are exposed to variable light intensities because of the seasonal variation in forest canopy, changes in solar elevation, diurnal variation in irradiances, and short term variation over minutes or seconds.

"Photosynthesis is the most important process, by which radiation energy from the sun is fixed in plants and transformed into chemical energy, from which all links in food chain derive the energy required for carrying vital processes" (Larcher, 1995). Approximately 40% of the plant dry mass consist of carbon fixed by photosynthesis (Lambers *et al.*, 1998). Light regime affects photosynthetic activity, biochemistry, morphology and finally growth of the plants (Bazzaz, 1979).

Photosynthetic acclimation to light involves changes in the organization and the investment in different components of the photosynthetic apparatus. These changes aim to improve plant performance in the prevailing light regime (Pearcy, 1998). Physiological and morphological responses to varying light regimes differ not only among species, but also among populations within a species, and individuals within a population. These differences result from long term adaptation to the environment.

The main objective of the present study was to compare the growth and morphology of white spruce seedlings within and among populations selected from

naturally-regenerated and field-planted populations, concentrating on the physiological responses to light. The following physiological responses were determined: photosynthetic light response curves, stomatal conductance, dark respiration, quantum yield, light compensation point and total chlorophyll content. Morphological and growth parameters measured included specific leaf area, absolute water content, terminal bud growth, and number and length of secondary branches.

4.2. Materials and Methods - Greenhouse Experiment

4.2.1. Population selection and origin

Six stands located in the mixedwood section of the southern Saskatchewan boreal forest were selected for the study of the white spruce seedling characteristics. Three were naturally-regenerated stands after clearcut (N1, N3) or fire (N2), and three were planted stands (P1, P2, P3) (Figure 4.1). Site selection was based on stand type, year of disturbance and planting, availability of seedlings and seedling age (Appendix F).

Planted seedlings originated from seeds collected from nearby areas by the company Weyerhaeuser Canada. Provenance of population P1 is Big River South (seedlot 1207-02-82). Seeds for populations P2 and P3 originated from the Big River area (seedlots 1007-01-93-01 and ws1207b respectively). Seedlings of population P2 were grown in Armstrong, BC, and seedlings of population P1 and P3 were grown in the Prince Albert Tree Nursery, SK, before planting in the field.

4.2.2. Seedling collection and greenhouse condition

Forty seedlings were randomly collected at each site within an area of 1 to 2 ha, and transplanted, with the surrounding soil, into 3L plastic pots. At the time of collection in May - June 1997, seedlings from naturally-regenerated sites (N1, N2, N3) were 12±0.7, 13±0.6 and 11±0.4 cm tall, respectively, and ranged between three and five years of age. Seedlings collected from the field-planted sites P1 and P3 were 4 and 3 years old and 19.5±0.8 and 23±0.6 cm tall, respectively. Seedlings from site P2 were 16±0.5 cm tall and 2 years old.

Seedlings were transferred to the Agriculture Greenhouse, University of Saskatchewan, Saskatoon, SK. Just after collection in 1997, one-half of the seedlings in each population was repotted in 3L plastic pots filled with greenhouse mix (*Terra-Lite Redi-Earth, W. R. Grace Co. of Canada, Ajax, ON.*), while the other one-half was kept in the original forest soil. Slow release osmocote fertilizer (14-14-14, 27 g/pot) was applied to the greenhouse mix 12 July 1997. Seedlings were allowed to grow in the greenhouse until 2 October 1997, when they were moved to a cold chamber for hardening (4°C and 12 hr light, PAR about 300 μmol m^{-2} s^{-1}). On 4 November 1997, pots were taken to the field and covered with transparent plastic film to prevent desiccation. The film was removed on 9 December 1997, after which seedlings were covered with snow. On 2 April 1998, pots were moved back to the cold chamber (5°C and 14 hours of light, PAR about 300 μmol m^{-2} s^{-1}) to break dormancy before their final transfer to the greenhouse on 14 April 1998.

4.2.3. Soil characteristics

Properties of the forest soils in pots, including texture of the mineral soil, pH, bulk density, water holding capacity, organic matter and nitrogen content were measured during the fall of 1998, at the end of the experiment. Particle size analysis was based on the hydrometric method (Bouyoucos, 1962). The percentages of sand, silt and clay were used to classify soil texture, based on triangular diagram of Armson (1977). All soils were moderately coarse, sandy-loams. Soil pH was measured using a 1:2 soil:water slurry (Moore and Chapman, 1986). Soil bulk density (g cm^{-3}) was calculated as the mass of dry soil in a given volume using bulk density cylinder rings (Pritchett and Fisher, 1987). The water holding capacity was calculated as the mass ratio of saturated to dry soil.

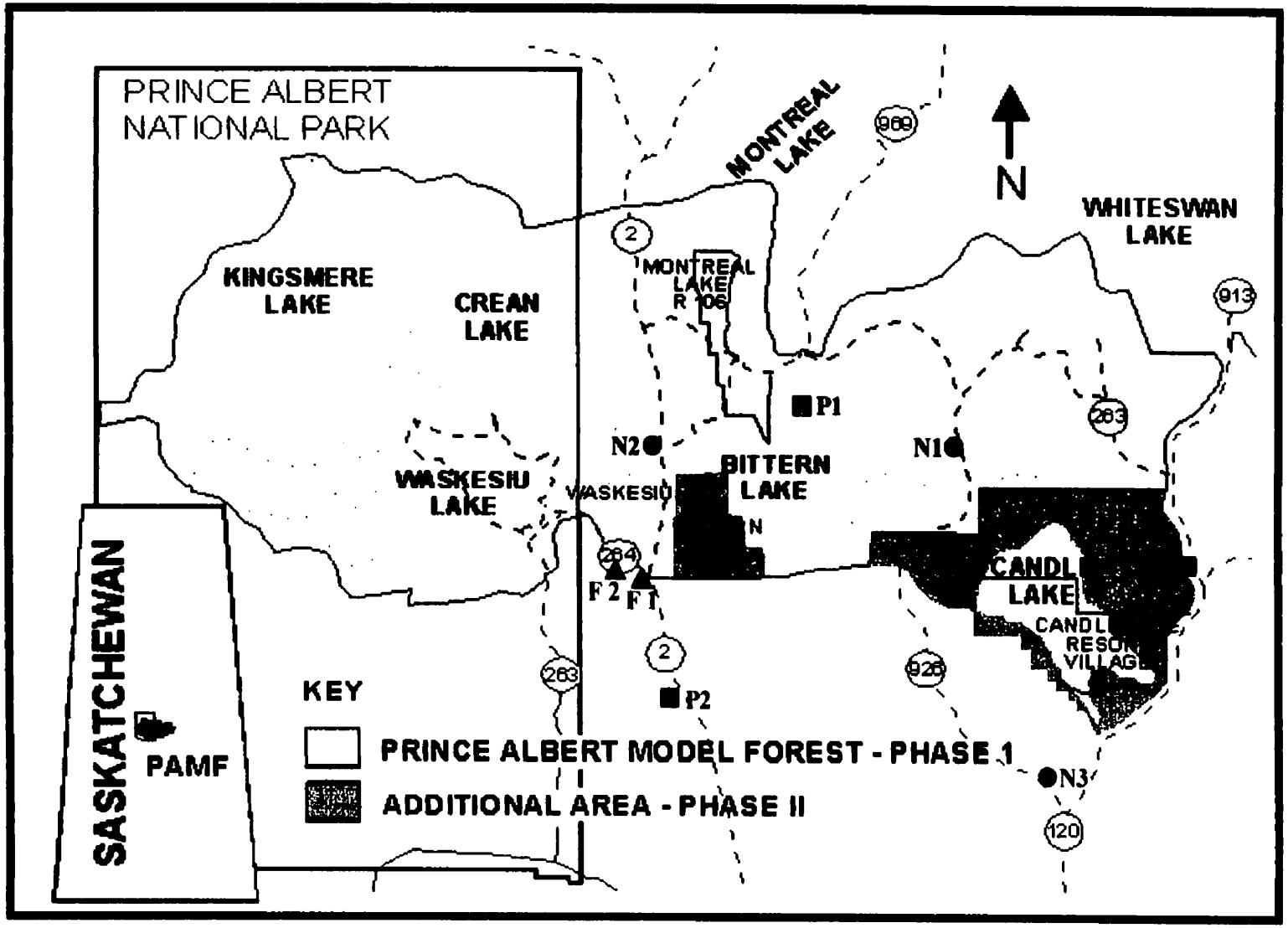


Figure 4.1. Location of the six stands from which white spruce seedlings were collected. Three naturally regenerated stands (N1, N2 and N3) and three field-planted stands (P1, P2 and P3). F1 and F2 are sites selected for field measurements.

The percentages of total soil nitrogen and carbon were determined in 0.2 g of finely ground soil samples using a *CNS – 2000 Elemental Analyzer (LECO Co.)*. Soil analysis was performed on three to five pots selected randomly from each population (Table 4.1).

Table 4.1. Soil pH, bulk density (BD), water-holding capacity (WHC), percent soil carbon (C) and nitrogen (N) and standard errors (SE), in field soil collected from six stands in central Saskatchewan boreal forest from which white spruce seedlings were collected, and in *Redi-Earth* greenhouse medium.

Population type	Soil pH n = 5 Range	BD (SE) n = 5 g cm^{-3}	WHC (SE) n=5 %	C (SE) n = 3 %	N (SE) n = 3 %
Planted					
P1	5.6-6.6	1.50 (0.02)	122.7 (1.36)	1.15 (0.30)	0.075 (0.01)
P2	5.5-6.5	1.32 (0.15)	131.1 (8.27)	0.73 (0.19)	0.050 (0.01)
P3	5.5-6.6	1.46 (0.02)	120.9 (1.76)	0.68 (0.12)	0.041 (0.01)
Natural					
N1	5.5-6.6	1.32 (0.14)	130.8 (8.93)	0.62 (0.11)	0.041 (0.01)
N2	5.7-6.5	1.51 (0.03)	119.9 (0.66)	0.82 (0.13)	0.058 (0.01)
N3	5.8-6.8	1.24 (0.05)	130.6 (0.14)	0.49 (0.001)	0.032 (0.01)
Redi-Earth	5.6-5.8	0.2 (0.003)	417.6 (6.4)	-	-

4.2.4. Light acclimation treatment

Shade frames (1m high x 1.7m long x 1.4m wide) were used to reduce light supplied to growing seedlings. The sides were covered with black polyethylene sheathing and the top with 3 layers of plastic shade cloth (Figure 4.2), reducing light intensity at the top of plants to around 10% of full sun. One-half of the seedlings from each population was transferred to the shade on 20 April 1998, while the rest were kept under full sun (sunlight plus artificial lights). The seedlings were allowed to acclimate to the light treatments for three months before physiological and growth measurements were conducted.

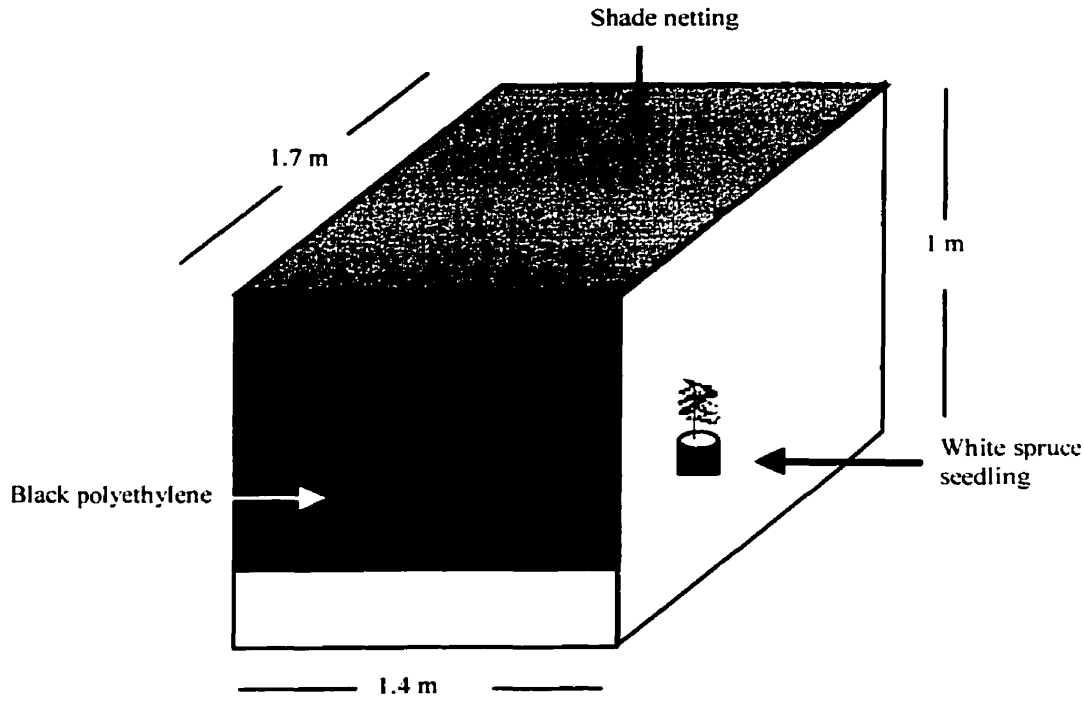


Figure 4.2. Schematic drawing of a shade frame used to produce low light conditions in the greenhouse.

4.2.5. Physiological and growth characteristics

Seedling survival

Seedlings that survived the winter were counted before applying of the light treatments in April 1998. Light treatment effects on seedling survival were recorded at the end of the experiment in early August 1998.

Gas exchange measurements

Net photosynthesis (CO_2 assimilation rate, μmol m^{-2} s^{-1}) and stomatal conductance (mol m^{-2} s^{-1}) were measured using a portable closed-type photosynthetic system *(LI-6200, LI-COR Inc.).* This system consisted of an infra-red gas analyzer, a computerized console, and a 0.25 L closed-type leaf chamber with sensors for leaf and air temperatures, light intensity, and relative humidity.

Photosynthesis was measured based on Fick's law, as the net exchange of carbon dioxide between the needle and the atmosphere:

$$\mathbf{Pn = g_{CO2}\,(Ca - Ci)} \qquad (\mu\text{mol m}^{-2}\text{ s}^{-1}) \qquad \mathbf{(4.1)}$$

where g_{CO2} is the stomatal conductance for CO_2 (mol m^{-2} s^{-1}) and Ca and Ci are the air and intercellular CO_2 concentrations (μmol mol^{-1}).

Stomatal conductance for H_2O was derived from the transpiration rate (estimated from the relative humidity fluctuation in the chamber) and the leaf and air temperature values (excluding the boundary layer conductance):

$$\mathbf{g_w = \frac{E}{(wi - wa)}} \qquad (\text{mol m}^{-2}\text{ s}^{-1}) \qquad \mathbf{(4.2)}$$

where E is the transpiration rate (mol m^{-2} s^{-1}) and wi and wa are the water mole fractions inside and the outside of the needles (mol mol^{-1}) (LI-COR, 1990).

Gas exchange measurements were performed on all seedlings at the end of July 1998. Only clear days were chosen to conduct the measurements. Pots were watered frequently to eliminate water stress. Greenhouse ventilation and lights were set to keep the air temperature, relative humidity and light as stable as possible. During measurements typical leaf temperature was between 25 and 27°C, relative humidity was around 50%, and CO_2 concentration of the air averaged 380 ppm.

An additional 60-watt halogen lamp was mounted over the seedlings to keep the incident light during the measurements as constant as possible. Photosynthesis was measured at the following photon irradiances: 0, 50, 150, 350, and 1,100 – 1,200 μmol m^{-2} s^{-1} to give light response curves.

The measurements were conducted by enclosing currently-growing needles of secondary branches in the closed chamber of the photosynthetic system. The measurements were based on three changes of either 15 seconds or 3 μmol mol^{-1} of carbon dioxide. This was done so that the sample would not remain in the chamber for more than 1 minute.

Individual seedlings were first measured in the dark by completely covering the chamber and then light intensity was increased in a stepwise fashion. Different light levels were achieved by adjusting layers of plastic shade cloth and by adjusting the distance between the seedling and the halogen lamp. At each light level the plant was allowed to equilibrate for several minutes; readings were recorded when the CO_2 exchange was stable.

Photosynthetic measurements were expressed on a projected leaf area basis. The needles enclosed in the chamber for physiological measurements were removed, and leaf area was measured using a *LI-3100 Area Meter (LI-COR, Inc.)*.

Indicators of shade tolerance

Shade tolerance indicators, calculated following Smith (1980) and Bazzaz and Carlson (1982) included: (1) quantum yield, (2) dark respiration, and (3) light compensation point.

Apparent* quantum yield (Φ) is the change in net photosynthesis (Pn) over the change in irradiance, calculated using the initial, linear portion of the photosynthesis-light curve (0- 50 μmol $m^{-2} s^{-1}$) in the equations

$$\mathbf{Pn = Rs_D + \Phi I} \qquad (\mu\mathbf{mol\ m^{-2} s^{-1}}) \qquad \mathbf{(4.3)}$$

$$\Rightarrow$$

$$\Phi = \frac{\mathbf{Pn - Rs_D}}{\mathbf{I}} \qquad \mathbf{(4.4)}$$

where Rs_D is the rate of respiration in the dark (μmol $m^{-2} s^{-1}$) and Pn (μmol $m^{-2} s^{-1}$) is the net photosynthesis at irradiance I (μmol $m^{-2} s^{-1}$).

Respiration rate was determined by setting I equal to zero in equation (3). Net photosynthesis at zero irradiance is equal to respiration rate (μmol $m^{-2} s^{-1}$).

$$\mathbf{Pn}_{(I=0)} = \mathbf{Rs}_{(D)} \qquad (4.5)$$

The light compensation point (Γ) was calculated from equation (4) by solving for the irradiance (I) at which gross photosynthesis (P_G) was equal to dark respiration (Pn = 0).

$$\mathbf{I} = \frac{-\mathbf{Rs}_D}{\Phi} \qquad (\mu\text{mol m}^{-2}\text{ s}^{-1}) \qquad (4.6)$$

Chlorophyll content

Chlorophyll content was determined on a fresh weight basis (μg mg^{-1}) during the fall of 1997 and 1998. Two to three needles were collected per seedling. Needles were weighed and placed in tubes containing 2.5 ml of N,N-Dimethylformamide (NNF). Tubes were stored in the dark at 4°C for 72 hr. Absorbance (A) of the NNF extract was measured at 664.7 and 647 nm using a spectrophotometer (Moran and Porath, 1980). Total chlorophyll content was calculated using the following equation:

$$\textbf{Total chlorophyll} = 17.9\ A_{(647)} + 8.08\ A_{(664.7)} \qquad (\mu\text{g ml}^{-1}) \qquad (4.7)$$

The total chlorophyll content was converted from μg ml^{-1} to μg mg^{-1} as follows:

$$\textbf{Total chlorophyll} = \frac{\textbf{Total chlorophyll}\ (\mu\text{g ml}^{-1}) \times 2.5\ \text{ml}}{\textbf{Fresh weight (mg)}} \qquad (\mu\text{g mg}^{-1}) \qquad (4.8)$$

Specific leaf area and absolute water content

Using several needles per seedling, fresh weight (mg) was measured, and the leaf area was estimated using the *LI-3100 Area Meter (LICOR, Inc)*. Samples were then dried in the oven for 72 hr at 75°C. Specific leaf area (SLA = leaf area / dry

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• Apparent because the quantum yield was measured on incident light basis and not absorbed light.

weight, $cm^2\ mg^{-1}$) and absolute water content, ((fresh weight – dry weight) / dry weight, $mg\ mg^{-1}$) were calculated.

Growth analysis

Length of the leader (terminal growth, cm), and number and length (cm) of the secondary branches of current-year growth were measured. These measurements were taken in August 1997 and 1998.

4.2.6. Experimental design and data analysis

Two light treatments (shade and full sun), two soil treatments (*Redi-Earth* and forest soil), and two regeneration types (naturally-regenerated and field-planted) were used. Three populations from each regeneration type were selected, with 40 seedlings randomly collected from each population. Two blocks were set up for the experiment. Soil treatment effect was excluded from the analysis, due to the high winter mortality of seedlings in the *Redi-Earth* medium. The remaining seedlings of the six populations were then equally divided and randomly arranged within the two blocks and two light treatments. The experimental design was a split-plot with light and regeneration type as the main and subplot treatment effects respectively.

The analysis was performed using the statistical package SAS. The split-plot design was handled using the general linear model (GLM). The Ls means statement was used to estimate the means in unbalanced data. Ls means are estimators of the class marginal means that would be expected had the design been balanced (no missing data) (Steel *et al.*, 1996). Means comparisons were performed using the probability of difference (Pdiff) for the unbalanced data and the least significant difference (LSD) for the balanced data. Analysis of variance was used to analyze photosynthesis, respiration, quantum yield, light compensation point, specific leaf area and absolute water content. Covariate analysis was performed on the terminal bud growth, the number and length of secondary branches and total chlorophyll content. Covariate analysis separates the effect of natural variation present in individual populations from that due to light treatment (SAS, 1988).

4.3. Materials and Methods - Field Experiment

Two sites located in the mixed-wood section of the southern Saskatchewan boreal forest were selected for gas exchange measurements (F1 and F2, Figure 4.1). Both sites were on the eastern side of Waskesiu Lake. Site 1 (F1) was located at the intersection of Highway 2 and Road 264 and site 2 (F2) was located about 7 km from the intersection on Road 264. Ten white spruce seedlings were marked at each site for the measurements. Five seedlings were from the understory and five were from the open (3 to 4 m away from the forest edge).

Gas exchange measurements were performed on clear days in August 1998. Photosynthesis was measured in a stepwise fashion, at photon irradiances of 0, 60, 350 μmol m^{-2} s^{-1} and at light saturation. The latter differed among sites, being about 2,000 μmol m^{-2} s^{-1} for site (F1) and about 1,100 at site (F2). A portable Halogen lamp with a maximum photon irradiance of about 900 μmol m^{-2} s^{-1} was mounted over the chamber. The lamp provided irradiance to the understory seedlings and kept the light as constant as possible. Air temperatures averaged 23 and 25°C, and CO_2 concentration of the air averaged 397 and 373 ppm in the understory and the open, respectively. Relative humidity was about 45% at the time of measurement.

Light response curves, apparent quantum yield, dark respiration and light compensation point were determined in a similar way as in section 4.2.5 of this chapter.

Data were analyzed with ANOVA using the SAS statistical package. The design was factorial with two sites (F1 and F2), and two light regimes (understory and open). Means were separated by the least square difference (LSD) at 5% probability.

4.4. Results - Photosynthesis and Growth in the Greenhouse

4.4.1. Seedling survival

Seedling survival over the winter was influenced by soil treatment. Of the seedlings potted in *Redi-Earth*, 97% died. The only surviving seedlings were from planted population P1. In forest soils, survival was significantly greater, being 91 % in field-planted populations (54 of 59 seedlings surviving) and 73% in naturally-regenerated populations (44 of 60 seedlings surviving).

Light treatment affected seedling survival and growth during the 1998 growing period (Table 4.2). An increase in seedling mortality and dieback of newly emerging needles and branches were noted in seedlings growing in the shade. This was not observed for seedlings growing in full sun; 100% of these survived. In the shade, 27% of the seedlings from naturally-regenerated populations died compared to 8% for seedlings from planted sites. The greatest seedling mortality occurred in the naturally-regenerated population (N1) with 43% mortality under shade.

4.4.2. Photosynthesis and stomatal conductance

Photosynthetic rates on a leaf area basis increased with irradiance over the measured range of 0 to 1,100 $\mu mol\ m^{-2}\ s^{-1}$ (Figures 4.3 and 4.4). At low light levels, shaded populations showed greater photosynthetic rates and steeper light response curves than seedlings growing in full sun. Seedlings growing in the shade saturated at about 200 $\mu mol\ m^{-2}\ s^{-1}$, with no further significant increase in photosynthesis at higher light intensities. At light saturation, shaded seedlings had either higher or similar values of photosynthesis compared to seedlings growing in full sun except for the naturally-regenerated population N1 which had greater photosynthesis at saturation in full sun than in shade treatment. P3 and N2 showed a significant negative effect of full sun on photosynthetic rates at saturation.

Table 4.2. Survival of naturally-regenerated and field-planted seedlings, collected from six stands in central Saskatchewan boreal forest, under shade or full sun treatments in the greenhouse.

Regeneration type		Total number of seedlings in each light treatment	Seedling Survival (%)	
			Shade	Full sun
Planted	P1	9	89	100
	P2	9	89	100
	P3	9	100	100
Mean			*93*	*100*
Natural	N1	7	57	100
	N2	7	71	100
	N3	8	88	100
Mean			*73*	*100*

At light saturation, photosynthetic rates varied among individual plants of the same population (Light response curves of individual plants in each population are shown in Appendix G). Values of the coefficients of variability (CV, Table 4.3) tended to be higher among individuals in the full sun than in the shade, in four of the six populations. Variability tended to be somewhat greater among field-planted than among naturally-regenerated populations. The number of observations (n) varied among populations, explaining the differences in trends of the CV compared to the SE values.

The overall average of photosynthetic rate at light saturation in field-planted populations was not significantly different from naturally-regenerated populations, either in the shade or full sun regimes.

Analysis of variance indicated that photosynthesis of populations within regeneration type and plants within populations were significantly different ($P<0.05$). Table 4.3 shows the Ls means and the standard errors of photosynthetic rates on a leaf area basis for the six populations under both light treatments (ANOVA table is in Appendix H). The maximum photosynthetic rate was noticed in

population N1 under both light regimes. Net photosynthesis of planted populations were not different ($P<0.05$) from each other either in the full sun or in the shade.

Stomatal conductance was measured at light saturation, and was similar in the shade and full sun treatment, and in the naturally-regenerated and the field-planted populations (Table 4.4). Furthermore, stomatal conductance did not differ ($P<0.05$) among the six populations in the shade. However, in full sun, population N1 had a greater ($P<0.05$) stomatal conductance than other populations, which agrees with the trend in maximum photosynthesis for this population. At light saturation, maximal photosynthetic rates were positively correlated with maximal stomatal conductance ($R^2 = 60\%$) indicating that, generally, populations with high photosynthetic rates had high stomatal conductance.

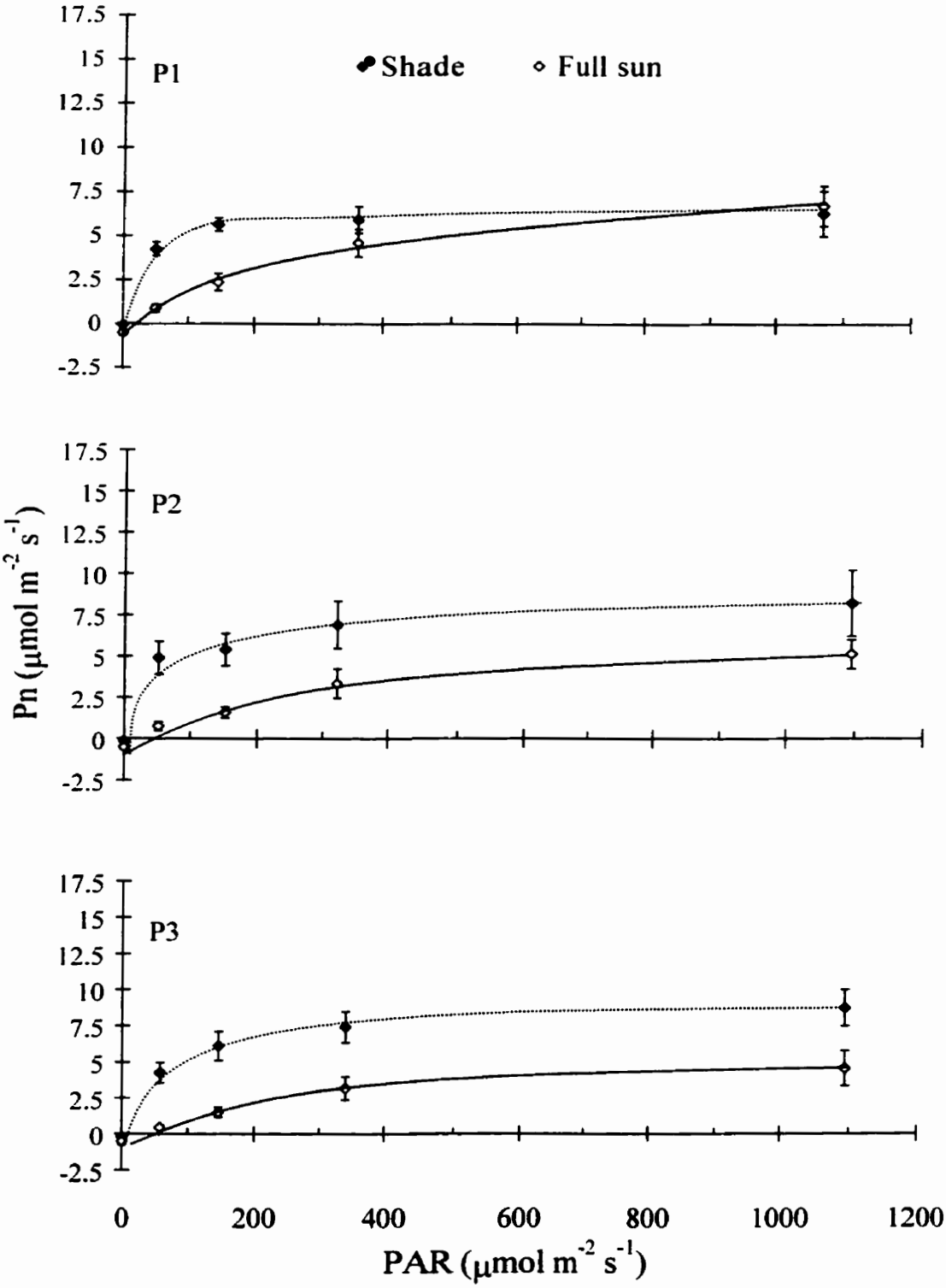

Figure 4.3. Photosynthesis in relation to photon irradiance (PAR) for the three populations of white spruce seedlings collected from field-planted sites and grown in full sun (straight line) or shade (dashed line). Curves were fitted by eye.

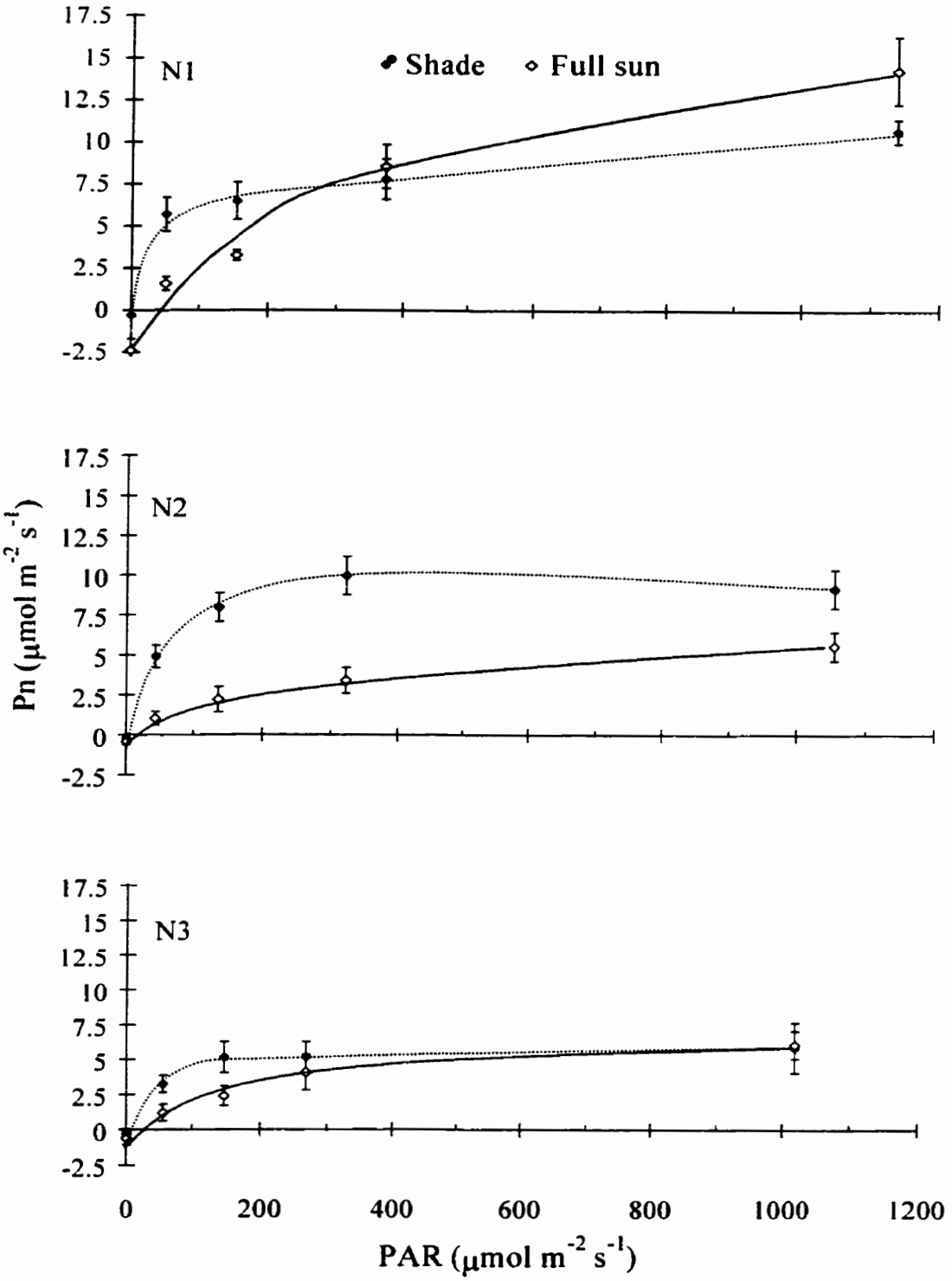

Figure 4.4. Photosynthesis in relation to photon irradiance (PAR) for the three populations of white spruce seedlings collected from naturally-regenerated sites and grown in full sun (straight line) or shade (dashed line). Curves were fitted by eye.

Table 4.3. Ls means and standard error (LSM(SE)), and coefficient of variation (CV) for maximum photosynthesis at light saturation (μmol m^{-2} s^{-1}), expressed on a leaf area basis in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type			
		Shade		Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	6.17 (1.41) a	48	6.47 (1.34) b	72
	P2	8.22 (1.41) a	44	5.15 (1.34) b	34
	P3	8.74 (1.26) a	51	4.12 (1.45) b*	62
Mean		***7.71 (0.78)***		***5.25 (0.79)***	
Natural	N1	11.1 (2.30) a	18	14.7 (1.52) a	50
	N2	9.19 (1.62) a	39	5.51 (1.52) b*	43
	N3	5.99 (1.52) a	86	5.99 (1.33) b	19
Mean		***8.76 (1.06)***		***8.70 (0.84)***	

Means within columns with similar letters are not significantly different at alpha 0.05.
*Means within rows are significantly different at alpha 0.05.

Table 4.4. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for stomatal conductance at light saturation (mol m^{-2} s^{-1}), expressed on a leaf area basis in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type			
		Shade		Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	0.32 (0.023) a	24	0.32 (0.023) b	23
	P2	0.33 (0.023) a	20	0.30 (0.023) b	23
	P3	0.32 (0.021) a	18	0.30 (0.023) b	19
Mean		***0.32 (0.003)***		***0.31 (0.007)***	
Natural	N1	0.37 (0.033) a	10	0.43 (0.024) a*	19
	N2	0.35 (0.024) a	13	0.30 (0.024) b	37
	N3	0.28 (0.023) a	34	0.29 (0.021) b	23
Mean		***0.33 (0.027)***		***0.34 (0.04)***	

Means within columns with similar letters are not significantly different at alpha 0.05.
*Means within rows are significantly different at alpha 0.05.

4.4.3. Dark respiration

The overall average respiration rate was 70% lower in the shade than in full sun, but the main effect of light was not significant (Appendix H). Analysis of variance indicated that light treatment did not influence rates of dark respiration to the same extent in every population. The average rate of dark respiration for one naturally-regenerated population (N1) in full sun was 2.46 μmol m^{-2} s^{-1} while the remaining populations ranged from 0.43 to 0.63 μmol m^{-2} s^{-1} (Table 4.5). Respiration of population N1 declined by 86% in response to shade, while the others showed about a 50% decline. The large variation among plants of the same population explains the lack of statistically significant differences in respiration among the remaining populations at both light treatments (note large CV values in Table 4.5). The coefficient of variation was lower among individuals in the shade than in the full sun for three of the six populations. Variability in dark respiration was similar among populations in the field-planted and the naturally-regenerated populations of the full sun, but tended to be lower for the naturally-regenerated populations in shade.

4.4.4. Apparent quantum yield

Apparent quantum yield was about 50% higher in the shade than in the full sun. The difference was statistically significant for all populations except the naturally-regenerated populations N1 and N3. In full sun, the average quantum yield was 100% greater in the naturally-regenerated populations than in the field-planted populations (0.044 and 0.022, respectively) (Table 4.6). In the shade, similar averages of quantum yields were observed in both regeneration types. The highest quantum yield was found in population N1 in full sun; quantum yield of N1 was significantly different from all other populations. Quantum yields of the remaining populations were not statistically different from each other. There was a regeneration effect on quantum yield, as shown by the significant differences between planted and naturally-regenerated populations in full sun. This variation was the result of high values for N1. The coefficient of variation was greater among individuals in full sun than in shade, except for P3 (CV, Table 4.6).

Table 4.5. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for dark respiration ($\mu molm^{-2} s^{-1}$), expressed in leaf area basis in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type			
		Shade		Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	0.261 (0.17) a	85	0.524 (0.25) b	83
	P2	0.263 (0.15) a	41	0.528 (0.25) b	58
	P3	0.233 (0.22) a	82	0.478 (0.27) b	80
Mean		***0.254 (0.17)***		***0.510 (0.2)***	
Natural	N1	0.328 (0.14) a	42	2.460 (0.28) a*	80
	N2	0.210 (0.13) a	70	0.430 (0.28) b	67
	N3	0.287 (0.11) a	27	0.631 (0.25) b	73
Mean		***0.275 (0.07)***		***1.210 (0.2) ****	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.

Table 4.6. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for the quantum yield (Φ), in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type			
		Shade		Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	0.061 (0.006) a	25	0.027 (0.005) b*	65
	P2	0.071 (0.006) a	22	0.024 (0.005) b*	23
	P3	0.062 (0.005) a	26	0.016 (0.007) b*	20
Mean		***0.064 (0.002)***		***0.022 (0.002) ****	
Natural	N1	0.071 (0.007) a	20	0.070 (0.008) a	64
	N2	0.062 (0.006) a	26	0.033 (0.006) b*	37
	N3	0.052 (0.006) a	32	0.030 (0.005) b	45
Mean		***0.061 (0.002)***		***0.044 (0.002)*** [†]	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.
[†] regeneration type average mean within columns are significantly different at alpha 0.05

Variability in quantum yield was generally greater among naturally-regenerated populations than among the field-planted seedlings in both light regimes.

4.4.5. Light compensation point

Light compensation point differed significantly between the two light treatments (Table 4.7). Shaded seedlings had an average light compensation point of about 4.3 compared to 23 μmol m^{-2} s^{-1} in seedlings growing in full sun. Field-planted populations were not statistically different from naturally-regenerated populations either in the full sun or in the shade regimes. The light compensation point did not differ significantly ($P<0.05$) among field-planted populations growing in full sun, but did differ among the naturally-regenerated populations. Population N1 exhibited higher light compensation in full light treatment while all populations were similar in the shade. Coefficients of variability (CV, Table 4.7) were greater among individuals in full sun than in the shade for all populations. This variability tended to be greater among the field-planted than among naturally-regenerated populations.

4.4.6. Chlorophyll content

Covariate analysis of total chlorophyll content on a fresh weight basis for needles, indicated that light treatment induced an increase ($P<0.05$) in the total chlorophyll content (Table 4.8, Appendix I). The average total chlorophyll content increased by 34% in response to shade (1.83 versus 1.2 μg mg^{-1}). Total chlorophyll content in field-planted populations was not significantly different from naturally-regenerated populations, either in the shade or full sun regimes. Chlorophyll content of populations within each regeneration type (natural and planted) did not differ significantly, neither in the shade nor in the full sun. The coefficient of variation (CV, Table 4.8) was greater among individuals in full sun than in shade. A similar pattern of variability was noticed among field-planted and naturally-regenerated populations.

Table 4.7. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for light compensation point (Γ; μmol m^{-2} s^{-1}), in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type: Shade		Acclimation type: Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	4.33 (0.11) a	15	19.41 (6.02) b*	70
	P2	3.71 (0.11) a	35	22.00 (6.12) ab*	76
	P3	3.71 (0.46) a	38	29.80 (6.30) ab*	55
Mean		***3.91 (0.34)***		***23.76 (3.14)****	
Natural	N1	4.50 (0.67) a	21	35.14 (6.80) a*	54
	N2	3.38 (0.61) a	21	13.03 (5.60) b*	60
	N3	5.52 (0.71) a	25	21.03 (6.7) ab*	70
Mean		***4.61 (0.51)***		***23.06 (6.4)****	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.

Table 4.8. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for total chlorophyll content (μg mg^{-1}), expressed in needle fresh weight in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type: Shade		Acclimation type: Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	1.814 (0.15) a	23	1.086 (0.14) a*	39
	P2	1.670 (0.15) a	25	1.069 (0.14) a*	39
	P3	1.930 (0.13) a	20	1.450 (0.15) a*	31
Mean		***1.805 (0.085)***		***1.20 (0.081)****	
Natural	N1	1.967 (0.19) a	19	1.315 (0.19) a*	38
	N2	1.877 (0.16) a	19	1.087 (0.16) a*	39
	N3	1.745 (0.16) a	22	1.306 (0.14) a*	28
Mean		***1.863 (0.100)***		***1.236 (0.107)****	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.

4.4.7. Terminal bud growth

Covariate analysis (Table 4.9, Appendix G) did not reveal any significant light or regeneration type treatment effects on terminal bud growth (increase in height). Terminal bud growth during the 1998 growing period in the greenhouse ranged from 0.87 cm (N1 in shade) to 3.45 (N3 in shade). The large variability (CV. Table 4.9) are behind the lack of significance in the results. This variability was higher among individuals in the shade than in the full sun in four of the six populations.

4.4.8. Number and length of secondary branches

The number of secondary branches developing from the axillary buds was lower in the shade than in full sun during the greenhouse study (Table 4.10), but was only significant in the field-planted populations. The field-planted populations had more secondary branches than the naturally-regenerated populations in full sun (62 and 28 respectively). The greatest number of secondary branches was found in the field-planted population P1 (83 branches) in the full sun. Population P1 differed significantly from all other populations. Light treatment had no significant effect on the number of secondary branches emerging in naturally-regenerated populations. Variability in the number of secondary branches was greater among individuals in the shade than in full sun treatment, and among naturally-regenerated than among field-planted populations (CV values, Table 4.10).

Secondary branches that developed in the shade were longer than those developed in full sun (Table 4.11). The difference was significant ($P<0.05$) in field-planted, but not in the naturally-regenerated populations. The number of secondary branches in field-planted populations were not different from naturally-regenerated populations, either in the shade or full sun regimes. Nevertheless, individual populations within each population type differed among each other under both light regimes. The coefficient of variability (CV, Table 4.11) was greater among individuals in full sun than in shade. Variability tended to be similar among field-planted and naturally-regenerated populations.

Table 4.9. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for the terminal bud growth (cm), in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type			
		Shade		Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	2.28 (1.33) a	164	2.78 (1.11) a	119
	P2	3.37 (1.21) a	101	1.56 (1.10) a	211
	P3	1.50 (1.07) a	214	1.88 (1.11) a	177
Mean		***2.38 (0.68)***		***2.08 (0.62)***	
Natural	N1	1.09 (1.54) a	282	1.89 (1.18) a	165
	N2	0.89 (1.27) a	319	2.88 (1.25) a	114
	N3	3.45 (1.16) a	82	2.16 (1.05) a	128
Mean		***1.81 (0.68)***		***2.31 (0.70)***	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.

Table 4.10. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for number of secondary branches emerged during the 1998 growing season, in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type			
		Shade		Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	29.45 (5.28) a	51	83.34 (4.66) a*	17
	P2	19.74 (6.12) a	88	57.24 (6.00) b*	31
	P3	21.71 (4.66) a	64	46.01 (5.05) b*	33
Mean		***23.63 (3.07)***		***62.20 (3.70)*†***	
Natural	N1	21.36 (6.98) a	65	24.64 (5.45) c	58
	N2	16.57 (5.67) a	77	31.13 (5.81) bc	49
	N3	16.87 (5.5) a	80	29.26 (4.86) c	44
Mean		***18.27 (3.7)***		***28.34 (3.34)***	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.
† regeneration type average mean within columns are significantly different at alpha 0.05

Table 4.11. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for secondary branches mean length (cm), in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type			
		Shade		Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	3.77 (0.34) a	25	2.59 (0.28) ab*	32
	P2	2.87 (0.31) ab	30	2.33 (0.29) b	37
	P3	3.66 (0.30) a	25	2.93 (0.31) ab	32
Mean		***3.43 (0.19)***		***2.62 (0.17)****	
Natural	N1	3.72 (0.31) a	17	3.38 (0.33) a	26
	N2	2.86 (0.34) ab	26	2.31 (0.35) b	40
	N3	2.62 (0.32) b	30	1.95 (0.29) b	39
Mean		***3.07 (0.21)***		***2.54 (0.2)***	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.

4.4.9. Specific leaf area and absolute water content

Light treatment caused a 32% increase in the overall specific leaf area for populations in the shade compared to full sun (Table 4.12). This increase was significant in both the naturally-regenerated and field-planted populations. The average specific leaf area was not different in the naturally-regenerated populations and the field-planted populations. The six populations did not exhibit any statistically significant variation among each other within light regime. Coefficient of variability (Table 4.12) was greater among individuals in the full sun than in shade. Variability also tended to be lower among naturally-regenerated than among planted populations in full sun.

Significantly higher absolute water content of needles was observed in the shade compared to full sun (Table 4.13) in all populations. Absolute water content of naturally-regenerated populations did not differ from field-planted populations in either light regime.

Table 4.12. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for specific leaf area ($cm^2\ g^{-1}$) in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type: Shade		Acclimation type: Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	64.7 (5.3) a	23	35.8 (5.1) a*	43
	P2	61.1 (5.3) a	24	42.3 (5.1) a*	36
	P3	53.9 (4.8) a	27	37.7 (5.5) a	44
Mean		***59.9 (3.0)***		***38.6 (3.0)****	
Natural	N1	72.2 (7.6) a	21	45.6 (5.8) a*	34
	N2	53.1 (6.9) a	29	45.3 (5.8) a	34
	N3	55.4 (6.0) a	26	38.3 (5.5) a	38
Mean		***60.3 (3.9)***		***43.1 (3.3)****	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.

Table 4.13. Ls means and standard error (LSM (SE)), and coefficient of variation (CV) for the absolute water content (mg mg^{-1}), in naturally-regenerated and field-planted populations of white spruce acclimated to shade or full sun in the greenhouse.

Regeneration type		Acclimation type: Shade		Acclimation type: Full sun	
		LSM(SE)	CV (%)	LSM(SE)	CV (%)
Planted	P1	3.43 (0.20) a	16	1.45 (0.17) a*	35
	P2	3.08 (0.18) a	16	1.56 (0.17) a*	33
	P3	3.27 (0.16) a	15	1.57 (0.18) a*	34
Mean		***3.26 (0.10)***		***1.53 (0.10) ****	
Natural	N1	3.57 (0.25) a	14	1.94 (0.19) a*	26
	N2	3.51 (0.23) a	15	1.66 (0.19) a*	30
	N3	2.81 (0.19) a	17	1.59 (0.18) a*	30
Mean		***3.29 (0.13)***		***1.73 (0.11) ****	

Means within columns with similar letters are not significantly different at alpha 0.05.
* Means within rows are significantly different at alpha 0.05.

The values of coefficient of variation for absolute water content (Table 4.13) were greater among individuals in full sun than in the shade. Variability also tended to be similar among naturally-regenerated and planted populations in both light treatments.

4.5. Results- Photosynthesis in the Field

Photosynthetic rates increased with photon irradiance at low light levels. Photosynthesis did not seem to saturate in any of the populations (Figure 4.5). At photon irradiance 800 μmol m^{-2} s^{-1}, the average net photosynthesis at site F1 was greater in the open than in the understory, but at site F2, the average photosynthetic rate in the open and the understory populations was similar.

Analysis of variance showed statistically significant light and site effects on all measured parameters (Table, 4.14, Appendix J). Respiration rates and light compensation points were lower ($P<0.05$) in the understory populations than in the open. The quantum yield of the understory population (F1) was significantly greater than the remaining populations.

Table 4.14. Means of respiration rate (R), apparent quantum yield (Φ) and light compensation point (Γ) in the open and the understory of two white spruce populations measured in the field.

Light	Site	R (μmol m^{-2} s^{-1})	Φ	Γ (μmol m^{-2} s^{-1})
Understory	(F1)	0.81 bc	0.054 a	14.9 c
	(F2)	0.50 c	0.036 b	14.2 c
	Means	***0.655***	***0.045***	***14.55***
Open	(F1)	1.68 a	0.031 b	53.4 a
	(F2)	1.05 b	0.036 b	30.8 b
	Means	***1.365****	***0.034****	***42.1****

Means within columns with similar letters are not significantly different at alpha 0.05.
* means within columns are significantly different at alpha 0.05

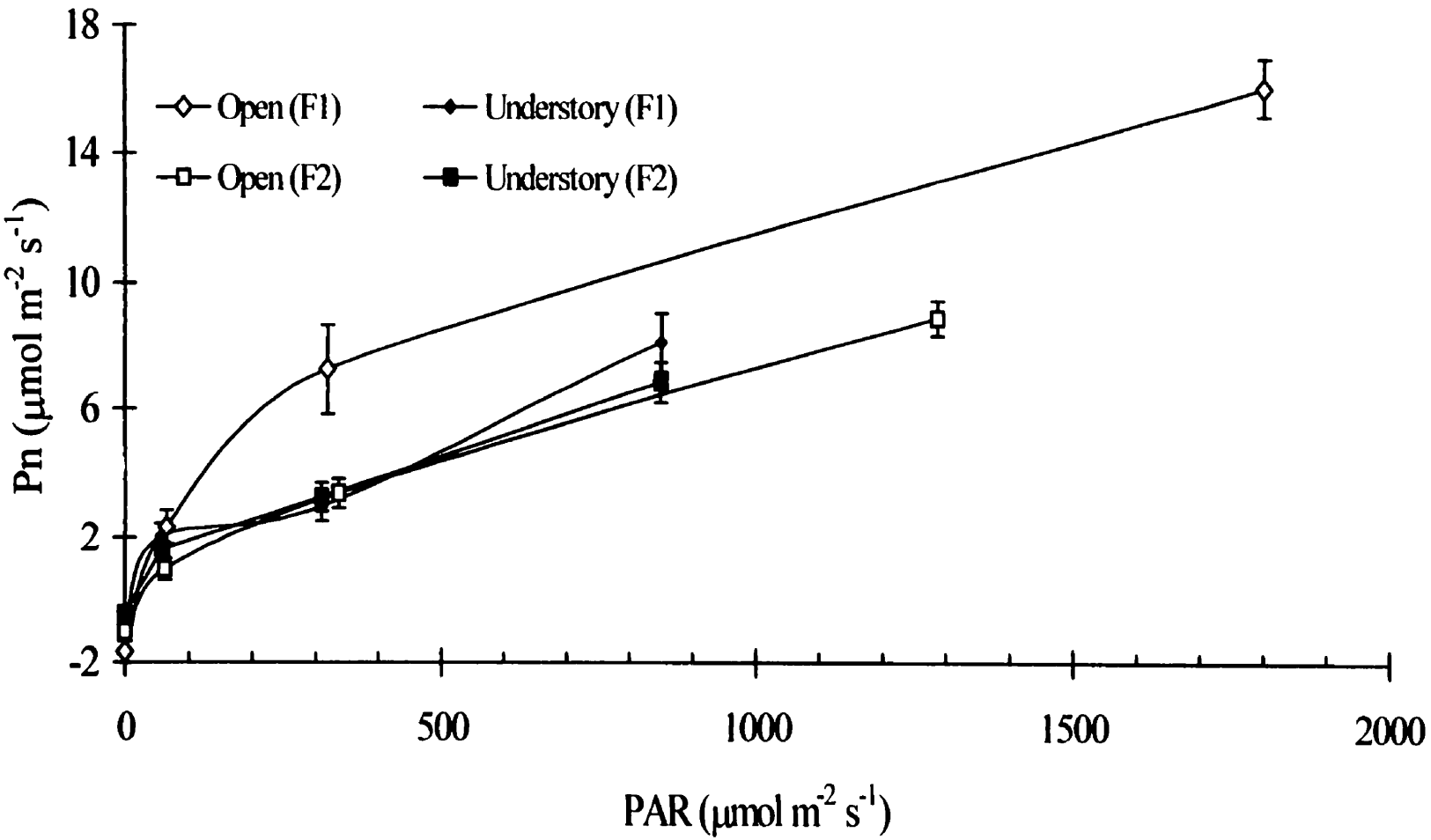

Figure 4.5. Field measurement of photosynthesis (Pn) in relation to photon irradiance (PAR) for white spruce seedlings at two sites (F1, F2). Seedlings were present in the understory or the open.

4.6. Discussion

4.6.1. Seedling survival

Winter seedling survival was influenced by soil treatment. Only 3% percent of seedlings potted in *Redi-Earth* survived the 1997 winter, compared to over 80% survival in seedlings potted in the forest soil. Winter desiccation probably caused the high mortality in seedlings potted in the *Redi-Earth*. The *Redi-Earth* mix is characterized by its high porosity, low bulk density (0.2 g cm^{-3}) and low water content per volume (0.83 g cm^{-3}) in comparison to forest soils (1.3 and 1.26 g cm^{-3}, respectively) (Table 4.1). Therefore, the *Redi-Earth* dries out faster than forest soil and as dry soils have a lower specific heat than wet soils, this results in a rapid temperature fall in cold weather especially in the absence of enough snow coverage (Pritchett and Fisher, 1987). In fact, great temperature fluctuations were recorded during the 1997 winter, coinciding with a year of an El- Niño, which resulted in a partial snow meltdown on few occasions. Consequently, winter desiccation in seedlings potted in *Redi-Earth* occurred, affecting root growth and ability to absorb water. Pritchett and Fisher (1987) suggested that a snow cover of 40 cm is required to prevent seedling desiccation in cold climates as snow acts as an insulator (Jones, 1994). Another possibility behind the high rates of winter mortality, is transplantation chock, however, seedlings were healthy at the time they were moved outdoor, in fall, 1997.

Seedling recovery in spring depends mainly on the length of the previous cold period, the temperature that at which a plant is stored (0'Reilly, 1989), the extent of water stress and the ability of the plant to recover from desiccation (Rose *et al.*, 1992). White spruce seedlings were able to restore spring growth after winter desiccation, however, a water potential below -1.5 MPa damaged the terminal buds or delayed their emergence. McMinn (1980) suggested that desiccation during winter can cause irreversible damage that is reflected in growth and survival.

In spring, seedlings that survived the winter were placed in the greenhouse where they received two light treatments (shade and full sun). Survival at the end of the growing season was 100 % in full sun. In the shade, survival was greater and

varied less in the field-planted than in the naturally-regenerated populations. This could be attributed to a) the different rate of shade adaptation in different populations; b) the fact that two of the three populations collected from field-planted sites were of the same origin and had similar responses to shade; and c) the selection process that field-planted seedlings experienced, like the artificial selection of seeds, and the natural selection that took place in the nursery and in the field after planting. The field-planted populations might have been selected for shade, or better acclimated to shade.

Björkman (1981) suggested that survival under low light depends on the balance between photosynthetic gain and respiration loss. Roussel (1948) found that Norway spruce seedlings were able to survive in 5% light, however 35-50% light intensities were required for optimum seedling growth. Teskey and Shrestha (1985) stated that greenhouses and growth chambers differ in their environment from that of the canopy understory. For instance, the high CO_2 levels next to forest floor could be responsible for the survival of seedlings under low light as some shade tolerant species could possess a higher CO_2 efficiency especially during the seedling stage, which is critical for the growth and development of the species.

4.6.2. Photosynthesis and stomatal conductance

The effect of light treatments on white spruce populations in the greenhouse was in part evaluated by comparing the light response curves and the photosynthetic rates at light saturation. In all populations, photosynthesis increased linearly at low irradiances due to the increase in the available energy (Lambers *et al.*, 1998), to point beyond which further increase in light caused little or no change in photosynthesis. At low light intensities, shaded plants showed steeper light response curves and greater rates of photosynthesis than plants growing under full sun, the greater photosynthetic efficiency in shade than in for seedlings grown in full sun, and the higher values of photosynthesis under shade are indications of light acclimation (Man and Lieffers, 1997). This acclimation reveals the great capacity of white spruce to maintain positive photosynthesis in low light environments at early stages.

Light response curves generally started to level off at about 200 μmol m^{-2} s^{-1} in shaded seedlings, and at higher light intensities in seedlings growing in full sun. Light saturation points vary with species. For example, white spruce seedlings (Bonan, 1993) and interior spruce (Bassman, 1989) saturated at about 400 μmol m^{-2} s^{-1}; red spruce seedlings at 250 μmol m^{-2} s^{-1} (Alexander *et al.* 1995); black spruce at 500 μmol m^{-2} s^{-1} (Leverenz, 1987) and Engelmann spruce at 1,000 μmol m^{-2} s^{-1} (Knapp and Smith, 1982). Light response curves of shaded Sitka spruce needles were more convex than those of sun needles (Leverenz and Jarvis, 1979).

At light saturation three types of light responses were observed for white spruce: 1) greater photosynthetic rates in full sun than in shade; 2) similar photosynthetic rates under both light treatments, and; 3) lower photosynthetic rates in full sun than in shade. The first response type was observed only in the naturally-regenerated population N1. The second type was found for the field-planted population P1 and the naturally-regenerated N3, while the third type of response was observed in the field-planted populations P2 and P3 and for the naturally-regenerated population N2.

While the linear portion of the light response curve is light limited, the light saturation point is CO_2 limited, reflecting the inability of the Rubisco enzyme to keep pace with the absorbed light energy. Rubisco activity is usually higher in sun than in shade populations, generally resulting in greater light saturation point and photosynthetic rates at light saturation in plants growing under full sun than in the shade assuming optimum environment (i.e. sufficient nitrogen, optimal temperature and available water; Larcher, 1995). Bazzaz and Carlson (1982) found that mid-successional species grew well under both high and low light regimes, but early successional species grew better in full sun and late successional species grew better in the shade. The authors concluded that populations that show a decline in photosynthetic capacity after growing in low light are less adapted to shade than populations with minimal or no change in photosynthesis. Teskey and Shrestha (1985) proposed that plants achieving similar rates of photosynthesis under high and low light are considered shade tolerant while those with reduced rates in the shade in

comparison to high light environment would be intolerant, depending on the difference in photosynthetic rates in both light regimes.

Photosynthesis at light saturation was 25% and 40% lower for white spruce and balsam poplar seedlings, respectively, when grown at 5% than at 25% full light suggesting that the differences in photosynthetic rates at saturation in seedlings grown at different light intensities decreased as tolerance of the species to shade increased (Reich *et al.*, 1998b). During the summer, photosynthesis of white spruce was higher in the understory than in the open, perhaps because of either light acclimation or lower temperature in the understory or both (Man and Lieffers, 1997).

When light response curves are considered, one can conclude that the six populations responded differently to shading. Similar behavior in full sun and in the shade was observed for populations P1 and N3 indicating the ability of these two populations to function equally under both light regimes. Photosynthesis of populations P2 and P3 which are of the same origin (Big River area) and N2 was less in full sun than in the shade, indicating greater adaptation of the photosynthetic system to low than high light intensities. Population N1 performed best under full light. These differences in photosynthesis of white spruce in response to light indicate differences in the capacity of each population to acclimate to shade.

In the shade treatment, mean photosynthetic rates at light saturation did not differ significantly ($P<0.05$) among the six populations. However, in full sun, photosynthesis of naturally-regenerated population N1 (14.7 $\mu mol\ m^{-2}\ s^{-1}$) was higher than the others, which were not significantly different from each other (about 5.5 $\mu mol\ m^{-2}\ s^{-1}$). Photosynthetic rate at saturation in white spruce seedlings grown in the shade was 8 $\mu mol\ m^{-2}\ s^{-1}$ (Reich *et al.*, 1998b). Maximal values of net photosynthesis under favorable environmental conditions at light saturation reported by various authors ranged from 10 to 15 $\mu mol\ m^{-2}\ s^{-1}$ (Bonan, 1993; Jiang *et al.*, 1995 ; Marsden *et al.*, 1996).

White spruce seedlings stored in the cold for six months showed greater photosynthetic rates on a projected leaf area basis at light saturation, when exposed to 500 $\mu mol\ m^{-2}\ s^{-1}$, than in full sun (8 and 6 $\mu mol\ m^{-2}\ s^{-1}$, respectively) (Camm *et*

al., 1993). The authors suggested that exposure of seedlings to high light intensities after cold storage can damage the photosynthetic membrane that in case of high illumination dissipates excess energy. This may decrease the photosynthetic capacity of the plant, and consequently, lower rates of photosynthesis (Binder *et al.*, 1988). Photoinhibition in full sun might have occurred in some populations, especially those exhibiting a large decrease in quantum yield in the sun compared to the shade.

The standard errors for mean photosynthesis in populations from naturally-regenerated sites were slightly greater than those of field-planted sites. This greater variability suggests greater within-population variation in the former. However, when comparing this variation using the coefficient of variation, it was not possible to find an obvious trend as the variation was equally high within populations in both regeneration-types. Based on the coefficient of variation, the conclusion is that photosynthesis within naturally-regenerated and field-planted populations is equally variable. Lack of differences among populations might be attributed to the similarity of environmental conditions in stands that led to the development of similar adaptive characteristics (Alexander *et al.*, 1995).

Neither light treatment nor population seemed to exert any effect on stomatal conductance at light saturation. Variations were large among plants within populations. The only noticeable trend was that photosynthetic rates and stomatal conductance were positively correlated (R^2 = 60%). This relationship agrees with the findings of Suresh *et al.* (1997), but disagree with Nobel (1976), who found that the stomatal resistance in shade acclimated leaves of desert lavender (*Hyptis emoryi Torr.)*, a shrub common to the north facing slopes of the Santa Rosa mountains, increased 14-fold when exposed for 30 minutes to high irradiance.

Stomatal conductance in the current study ranged between 0.27 and 0.43 mol m^{-2} s^{-1}. Marsden *et al*, (1996) reported that the maximum average values of stomatal conductance on projected leaf area basis were about 0.45 mol m^{-2} s^{-1} measured at 80% relative humidity and declined 2 fold at 30% in 3-year-old white spruce seedlings. Stomatal conductance values ranged between 0.2 and 0.25 mol m^{-2} s^{-1} at 1400 μmol m^{-2} s^{-1} PAR and 23°C in interior spruce seedlings (white spruce x Engelmann spruce hybrid) (Camm *et al.*, 1995). Jiang *et al.* (1995) reported values

of 0.25 mol m^{-2} s^{-1} in well-watered white spruce seedlings. Harper and Camm (1993) stated the importance of non-stomatal limitation to photosynthesis in white spruce, as they found a close relation between the net assimilation rate and mesophyll conductance while stomatal conductance was high under water stressed environment. Similar findings were noticed for yellow cedar (*Chamaecyparis nootkatensis* Spach.) (Grossnickle and Russel, 1991) and for black spruce after repeated drought cycles (Steward *et al.*, 1995). Steward *et al.*, (1995) concluded that it would be more efficient to select for high photosynthetic capacity than for stomatal sensitivity when breeding for increased drought resistance in black spruce seedlings.

4.6.3. Shade indicators

The respiration rate averaged 0.26 μmol m^{-2} s^{-1} in the shade and 0.8 μmol m^{-2} s^{-1} in the full sun treatment. The naturally-regenerated population N1 showed 7.5 times decrease in respiration rates in shade compared to full sun acclimated seedlings. A similar trend was reported by Bazzaz and Carlson (1982) for some mid-successional species. Respiration rates in the remaining populations were lower in the shade, but did not differ from the full sun treatment. This agrees with Man and Lieffers (1997), who found that white spruce seedlings had slightly higher respiration rates in the open than in the shade. Bazzaz and Carlson (1982) measured respiration rates in the shade-acclimated, late-successional plants that were not significantly different from those in sun-acclimated plants.

Shade-acclimated plants are characterized by lower respiration rates and light compensation points than sun acclimated plants (Kozlowski *et al.*, 1991). Teskey and Shrestha (1985) reported that the respiration rates found in shade tolerant American beech (*Fagus grandifolia* Ehrh.) averaged 0.3 μmol m^{-2} s^{-1} while those for the shade intolerant loblolly pine (*Pinus taeda* L.) averaged 0.7. Bonan (1993) reported respiration rates of 1.5 μmol m^{-2} s^{-1} for white spruce growing in Alaska. Luoma (1997) reported that even though photosynthesis varied significantly among populations of *Pinus sylvestris* from different latitudes, there was no significant variation in respiration rates. Pearcy (1998) explained that respiration is the result of growth and maintenance, thus greater growth rates and greater amounts of the non-

photosynthetic tissue, lead to greater respiration. In the shade, a positive carbon gain is maintained by lowering respiration rates. Lower respiration rates on a leaf area basis found in the shade could be related to lower protein content per unit area as compared to the sun.

The light compensation point did not differ among populations growing in the shade (average 4.3 μmol m^{-2} s^{-1}). However, in full sun, the naturally-regenerated population (N1) differed from the others. The maximal light compensation point in the full sun was 35 and the lowest was 13 μmol m^{-2} s^{-1} for N1 and N2, respectively. Man and Lieffers (1997) reported higher photosynthetic efficiency, lower light compensation points and lower light saturation in shade-grown than in open-grown white spruce seedlings. Taiz and Zeiger (1998) suggested that light compensation points for C3 plants growing in the shade generally range between 1 and 5 μmol m^{-2} s^{-1}, while those of sun plants range between 10 and 20 μmol m^{-2} s^{-1}. Light compensation values are closely related to the respiration rate of a plant: greater respiration rates lead to greater light compensation points. This explains the higher values found in N1 under full sun. The greatest decrease in light compensation point between the two light regimes occurred in N1. A similar trend was reported by Bazzaz and Carlson (1982) for some mid-successional species.

The apparent quantum yield, the slope of the linear region of the light response curve, was greater in the shade- than in the sun-grown seedlings. In the full-sun treatment quantum yield was greater in the naturally-regenerated populations (0.044) than the field-planted (0.022). In the shade, the quantum yield averaged 0.06. Greater variation in quantum yield was detected in the naturally-regenerated populations than in the field-planted populations. However, this variation was not paralleled by any differences among populations growing within the same light regime except for the naturally-regenerated population N1 growing in full sun.

Values of quantum yield reported in literature vary. For example, Teskey and Shrestha (1985) found that the quantum yield of the shade tolerant species American birch was 0.03 compared to 0.025 in the shade intolerant loblolly pine. Pearcy (1998) suggested that the minimum quantum requirement for the reduction of CO_2

under ambient CO_2 concentrations (330 ppm) is 8 photons which gives a value of quantum yield of 0.125 mol mol^{-1} photons. This assumes that all photons are used photochemically in electron transport; however, losses occur due to factors such as non-specific absorption, or to radiation-less decay which reduces the quantum yield.

In the absence of stress the maximum quantum yields of sun and shade adapted species or of species acclimated to various light regimes should not differ significantly. Differences in quantum yield between shade and sun environment could vary with stresses imposed on the plant by growing it in unsuitable light environment (Bazzaz and Carlson, 1982). Pearcy (1998) suggested that photoinhibition is the common factor behind the reduction of quantum yield in sun populations. Taiz and Zeiger (1998) suggested that C3 plants kept at low oxygen levels that inhibit photorespiration usually show a quantum yield of 0.1. However, in the field 0.05 is a more typical value depending on species, temperature and CO_2 concentration of the air.

Low light induced an increase in the total chlorophyll content expressed on fresh weight. The average total chlorophyll content increased by 34% in response to shade. An increase in total chlorophyll in response to shade is commonly observed. In the shade, total chlorophyll content increased when measured on a unit weight, but was similar to the sun when expressed on leaf area basis (Björkman, 1981). Pearcy (1998) suggested that doubling total chlorophyll does not translate into a doubling in photosynthesis as the relation between the two parameters is not linear, but logarithmic.

Differences in physiological responses to light among populations indicate the presence of more than one ecotype. N1 behaved like a true "sun population", showing the greatest plasticity in the measured physiological parameters, while the remaining populations behaved more like shade-adapted populations. This agrees with Björkman and Holmgren (1963), who found that clones from open habitats exhibited greater photosynthetic capacity in the sun than in the shade, whereas the quantum yields remained the same. In comparison, clones from shaded habitat had steeper light response curves and similar rates of photosynthesis at light saturation, suggesting that clones from such habitat had likely experienced photoinhibition, as

their photosynthetic apparatus could not probably tolerate high light. The authors concluded that differences in the physiological responses to light varied among ecotypes.

Ecotypic variation is well-documented in literature and it rises from long adaptation and acclimation to different climatic conditions (Teich and Holst, 1974; Berry and Björkman, 1980; Peck and Wallner, 1982; Barbour *et al.*, 1987 and Luoma, 1997;). The presence of different ecotypes permits a species to survive in a variety of different physical and biotic environments, while the genetic variability allows a population to adapt to the changing environmental conditions" (Kinmins, 1997).

4.6.4. Growth parameters

It was not possible to detect any significant differences in terminal bud growth among the six populations because of the large within-population variation in growth. Terminal bud growth in white spruce apparently varies greatly. Brand and Janas (1988) reported an annual growth of 7 cm in white spruce seedlings on a forest floor substrate on clearcut sites, and 8 cm growth in seedlings planted on scarified sites. Logan (1969) reported growth of only 2.5 cm over an 8-week period under light levels of 45% and 100% of full sun. Camm *et al.* (1995) reported that interior spruce seedlings (white spruce x Engelmann spruce hybrid) grew 11 cm in height after one growing season from planting. McMinn (1980) explained that growth rate in white spruce seedlings depends largely on its height. For example, growth of (2+0) bare-root white spruce seedlings in central interior of British Columbia was 9 cm in large seedlings (21 cm tall) after two growing seasons, while the growth was only 5 cm in shorter seedlings. This might explain the lower values found in this experiment as well as the large variation in standard errors. Seedlings ranged from 11 to 23 cm in height and between 3 and 5 years in age. Another factor that limits growth is winter storage. Low temperature may damage terminal buds or delay their emergence (Rose *et al.*, 1992). In the current study buds emerged in all seedlings in full sun, and in seedlings that survived under the shade.

Seedlings in full sun developed more secondary branches than in the shade. This type of response is well documented in the literature. For instance, sun plants have shorter leaves but more leaves per unit of branch length and thicker and more numerous branches per seedlings when compared with shade-adapted plants (Boardman, 1977). Number of needles per plant and the dry weight increased with an increase in light treatment (Logan, 1969). Man and Lieffers (1997) found that the length of white spruce needles was lower in the sun than in shade. The average number of secondary branches in populations from field-planted sites was higher under both light regimes than in populations from naturally-regenerated sites, however, the difference was only significant in the full light treatment. Similar to terminal bud growth, differences in seedlings height and age might explain the variability in the present study.

The overall specific leaf area increased by 32% in the shade. Changes in the specific leaf area values in response to shade depend on light intensity, the length of treatment and population characteristics. Boardman (1977) and Björkman (1981) concluded that the specific leaf area is inversely related to the daily sunlight under which the leaf develops. Sims *et al.* (1998) determined that the increase in specific leaf area in the shade reduces the resource investment per unit leaf area, allowing greater total leaf area production. This allows greater light capture and photosynthesis under low light, which is an indication of shade adaptation. Björkman (1981) reported that the leaf area increased from 121 to 293 $cm^2\ g^{-1}$ for *Pinus radiata* D. in the canopy. Man and Lieffers (1997) found that specific leaf area averaged 75.2 $cm^2\ g^{-1}$ in shade and 66.8 in full-light-grown white spruce seedlings. Specific leaf area was 35 $cm^{-2}\ g^{-1}$ in white spruce seedlings growing in high light (Bonan, 1993).

4.6.5. Greenhouse experiment versus field experiment

The field experiment was carried out to determine whether white spruce populations from the forest understory and from the open exhibited similar characteristics to populations grown in the greenhouse in the shade and the full sun.

Similar to the greenhouse-grown plants, white spruce populations in the field showed a steady increase in photosynthetic rates at low light levels. At the maximum measured irradiance (800 to 2,000 μmol m^{-2} s^{-1}), photosynthesis in field did not saturate. This did not agree with what was observed in the greenhouse experiment, where all populations saturated at relatively low light levels, except for the naturally-regenerated population N1. Response of N1 was similar to that of the field population F1. The photosynthetic light response curve of F2 tended to resemble that of the greenhouse populations P2, P3 and N2.

Differences in light saturation in white spruce are also reported in literature. Bonan (1993) reported that white spruce saturated at 400 μmol m^{-2} s^{-1} photon irradiance, while Carter and Smith (1987) found that white spruce seedlings saturated at 149 and 1,933 μmol m^{-2} s^{-1} in the shade and the sun, respectively.

Dark respiration rates of the understory populations were generally greater than those observed in the shade in the greenhouse, however in the open, values of dark respiration were in the range observed in the greenhouse.

Quantum yields in the field-grown plants fell within the range for those in the greenhouse. Light compensation points were generally higher in the field than in the greenhouse. Greenhouses and growth chambers differ in their environment from that of the canopy understory (Teskey and Shrestha, 1985). High CO_2 levels next to forest floor could be important for survival of seedlings under low light as some shade tolerant species could possess a higher CO_2 efficiency especially during the seedling stage, which is critical for the growth and development.

5. GENETIC CHARACTERISTICS OF PLANTED AND NATURALLY-REGENERATED SEEDLINGS

5.1. Introduction

The resilience of biotic communities in the face of natural and human-induced changes is dependent on the ability of their component species to adapt to new conditions. The gene pool in an ecosystem should be considered as a non-renewable resource. The present pool is the result of millions of years of natural selection. If a particular genotype is lost, its re-creation might take a long period of natural selection, or it might never be re-created. The new techniques of gene technology might recreate lost genotypes, however it would be impossible to create an already lost genotype, if all similar genotypes also have been lost.

After logging, a new forest establishes by natural regeneration or by planting. The aim of artificial regeneration is to replace the harvested stand with a well-stocked stand of high quality timber (Skrøppa, 1994). Such management has raised concerns about the genetic diversity of species. Molecular genetics provide a powerful tool for the study of changes in genetic diversity (Chalmers, 1992).

The objective of this study was to measure the genetic variation among individuals in field-planted and naturally-regenerated white spruce seedling populations, using Randomly Amplified Polymorphic DNAs (RAPD). Randomly Amplified Polymorphic DNAs is a tool based on the amplification of unknown DNA sequences using single, short random oligonucleotide primers (Williams *et al.*, 1990).

5.2. Materials and Methods

5.2.1. DNA extraction

Newly emerging needles were collected from 10 randomly-selected individuals in each of the six populations growing in the greenhouse (see section 4.2.1 for details on seedling collection). Needles of each seedling were frozen separately in liquid nitrogen and ground into fine powder with a mortar and pestle. DNA was isolated from these needles using the Cetyltriammonium Bromide (CTAB) procedure, modified from Procunier *et al.* (1991) and, Murray and Thompson (1980). Ground needles of each individual were transferred into a 50 ml centrifuge tube, and 15 ml of 1% CTAB solution (*Sigma Chemical, Co.*) was added. The tube was incubated for 10 min at 65°C. One volume of chloroform:isoamyl alcohol (24:1) was added and the solution was mixed thoroughly by inversion. The emulsion was then centrifuged for 10 min at full speed (2,000 rpm). The aqueous supernatant solution was transferred to a new tube and 1/10 volume of CTAB (65°C) was added. The chloroform:isoamyl centrifugation and removal of supernatant solution were repeated. The DNA in the supernatant solution was precipitated with 2 volumes of 95% ethanol (–20°C) and stored for 1 hour at 4°C. The solution was then centrifuged for 5 min and the ethanol was drained. The precipitated DNA was soaked with 10 ml of 75% ethanol (-20 °C) for 1 hour at 4°C to remove excess salt. Centrifugation was repeated and ethanol was drained. The DNA pellet was then allowed to dry at room temperature. The pellet was suspended in 200 µl of sterile distilled water. DNA concentration was determined using a spectrophotometer (*Gene Quanta RNA/DNA calculator, Pharmacia LKB Biochrom. Ltd.*). The concentration of DNA was adjusted to 0.5 µg μl^{-1}. RNA contamination was removed at the end with the addition of 10 µl of RNAase A.

5.2.2. DNA amplification

The RAPD primers used were obtained from *Operon Technology Inc. USA,* and the *Biotechnology Laboratory, University of British Columbia, Canada.* Over 50 single ten-base oligonucleotide primers were randomly selected and tested on 1 or 2

individuals from each population. Sixteen RAPD primers that showed good amplification (over four clear bands) were chosen for the study (Table 5.1).

Table 5.1. Name and sequence of the Operon Technology (OP) and University of British Columbia (UBC) PAPD primers used in the study.

Primer code	Sequence (5' to 3')
OPA-03	AGTCAGCCAC
OPA-08	GTGACGTAGG
OPA-11	CAATCGCCGT
OPA-15	TTCCGAACCC
OPA-16	AGCCAGCGAA
OPB-01	GTTTCGCTCC
OPB-04	GGACTGGAGT
OPB-06	TGCTCTGCCC
OPB-14	TCCGCTCTGG
OPB-18	CCACAGCAGT
OPC-10	TGTCTGGGTG
OPC-16	CACACTCCAG
OPD-03	GTCGCCGTCA
OPE-07	AGATGCAGCC
OPE-11	GAGTCTCAGG
519 (UBC)	ACCGGACACT

Polymerase Chain Reaction (PCR) conditions were based on a protocol modified from Williams *et al.* (1990). The optimum reaction mix found for white spruce needles contained 20 mM Tris-HCl (pH 8.4), 50 mM KCl, 2.2 mM $MgCl_2$, 100 µM each of dATP, dTTP, dCTP and dGTP, 0.6 µM of primer, 20 ng DNA template and 1 unit of Taq polymerase (*Gibco BRL*). Reaction was brought to a volume of 25 µl by adding sterile distilled water.

Amplification conditions included a preliminary 3 minutes denaturation at 94°C, followed by 40 cycles of 1 minute at 94°C, 1 minute at 37°C (annealing temperature) and 1.30 minutes at 72°C (elongation temperature). Amplification terminated with an incubation at 72 °C for 10 minutes. Solution was kept at 4°C until retrieval. PCR amplifications were conducted with a *Thermolyne, Amplitron II.*

PCR products were separated by electrophoresis in a 1% Agarose gel (*Sigma Chemical, Co.*). The gel was stained with 1% ethidium bromide. Bands were detected with ultra-violet light.

5.2.3. Data analysis

The RAPD profiles obtained from DNA amplification were photographed, and bands from each primer were scored visually for presence (1) or absence (0). Data were entered in a binary matrix. The Numerical Taxonomy and Multivariate Analysis System (NTSYS-PC version 2) was used to generate similarity matrices using Jaccard's similarity coefficient. The unweighted pair-group method of arithmetic averages (UPGMA) classification of the SAHN clustering method (sequential, hierarchic, non overlapping) was used to generate dendrograms (Ganeshan, 1997; Sokal and Sneath, 1963; Panchen, 1992)

Analysis of molecular variance (AMOVA) was used to partition the total genetic variation to between regeneration type (group), inter-population and intra-population variations. The phi-statistic (Φ_{st}) was used as an inter-population distance measurement (Ferdinandez, 1999; Huff, 1997). The analysis was performed using the AMOVA-PREP-1.01 (Miller, 1998) and the WINAMOVA-1.55 (Excoffier, 1993).

5.3. Results

Genetic diversity among and within populations of white spruce seedlings originating from field-planted and naturally-regenerated sites could be distinguished using random amplified polymorphic DNA (RAPD) primers. RAPD primers detected between 4 and 12 clear informative bands, and averaged around 8 loci per primer (Table 5.2, Figure 5.1). The size of the amplified product ranged from around 400 to 3,000 bp. A total of 136 clear informative loci (bands) were selected for the study of the genetic diversity. Of this total, 106 polymorphic loci were found, corresponding to 77% of the total loci tested. Populations were monomorphic only for primer OPA-03 (frequency=1) (Table 5.2 ; Figure 5.2).

Table 5.2. Primer name, number of clear informative loci and locus frequency used in the analysis of genetic diversity in white spruce seedlings .

Primer code	No of informative loci	Frequency
OPA-03	4	1.00
OPA-08	8	0.92
OPA-11	9	0.39
OPA-15	11	0.69
OPA-16	11	0.64
OPB-01	12	0.42
OPB-04	10	0.37
OPB-06	6	0.77
OPB-14	8	0.42
OPB-18	6	0.70
OPC-10	6	0.87
OPC-16	9	0.70
OPD-03	8	0.72
OPE-07	6	0.77
OPE-11	10	0.48
519 (UBC)	12	0.68
Total	**136**	

Dendrograms were generated with the UPGMA cluster procedure for individual populations (Figure 5.3) and for all 60 individuals (Figure 5.4) using Jaccard's coefficient. The coefficient varied from 0 in distant to 1 in two similar entities. The UPGMA classification for each population showed that there were no two identical individuals. Seedling 9 and 10 of the naturally-regenerated population (N1) had the highest similarity (85%), while, seedlings 9 of the naturally-regenerated population (N3) was the least similar (56%) to other individuals of N3 (Figure 5.3) and to all other individuals of the remaining populations (Figure 5.4). Individuals within populations generally overlapped; an exception was for the naturally-regenerated population (N1) (Figure 5.3). The dendrogram of population (N1) showed two distinct groups, the first included seedlings 1 to 3 and the second included the remaining seven individuals.

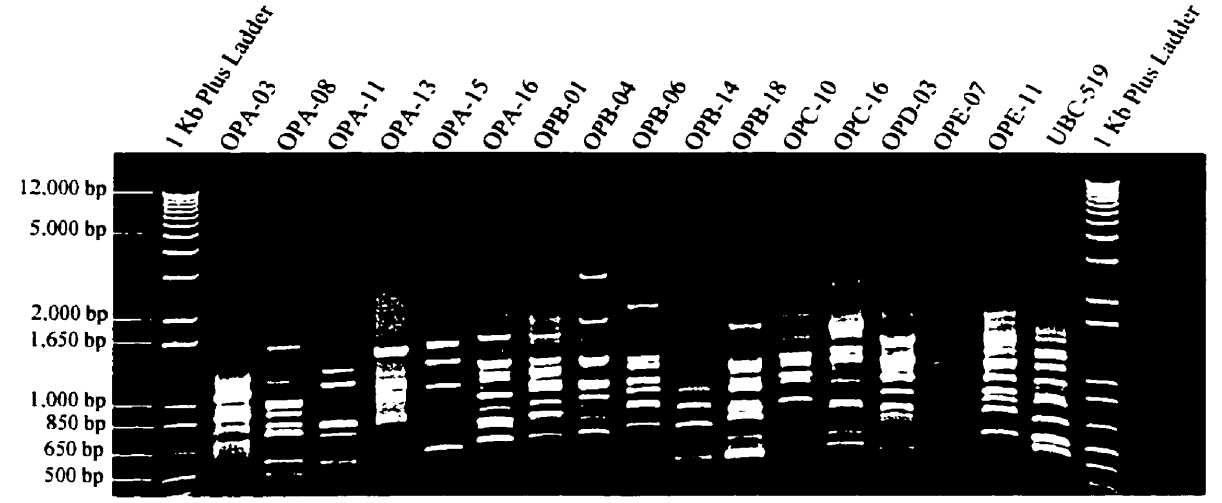

Figure 5.1. A sample of the amplification products of DNA extracted from seedling N1.1 of the naturally-regenerated populations N1; using Operon (OP) and UBC primers.

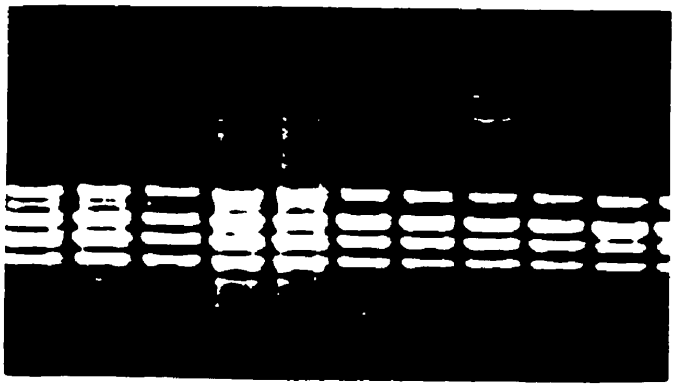

Figure 5.2. RAPD profiles of DNA samples using OPA-03 primer for 10 individuals of white spruce seedlings from the field-planted population P1.

The similarity among the seven individuals was relatively high and the seedlings were generally distinct in their classification (Figure 5.4).

A dendrogram generated by the UPGMA cluster analysis including all 60 seedlings from the six populations indicated that 50 to 70 % of individuals of naturally-regenerated origin were clustered with no overlapping (Figure 5.4). All individuals of the field-planted population P3 and 70 % of the individuals of P2 were clustered together. The remainder individuals including those of P1 were generally spread along the axis.

Variation within populations was studied using the sum of squares calculated by AMOVA (Table 5.3). The sum of squares overlapped among populations. Population N3 and P1 exhibited the highest intra-population variation. P3 had the least variation. which was 80% of the variation found in N3. AMOVA showed that variation among the field-planted populations was slightly greater (about 2%) than that of the naturally-regenerated populations (Table. 5.3).

Pairwise comparison using AMOVA revealed that the highest portion of the total variation was due to the intra-population variation (82.9%), compared to the inter-population variation and to the among regeneration type (group) that accounted for 16.7 and 0.4% of the total variation, respectively. Phi-statistic (Φ_{st}) which is equivalent to F-test in the analysis of variance, was used as an estimate of the distance between populations. All populations were significantly distant from each other (P=0.0001). The average distance among field-planted populations was 20% greater than that found among naturally-regenerated populations. The naturally-regenerated population N1 was the most distant from the field-planted populations P2 and P3 (0.24 and 0.26 respectively). The smallest distance was found between population P1 and N2 (0.107). The remaining populations had an average distance of 0.16 (Table 5.4).

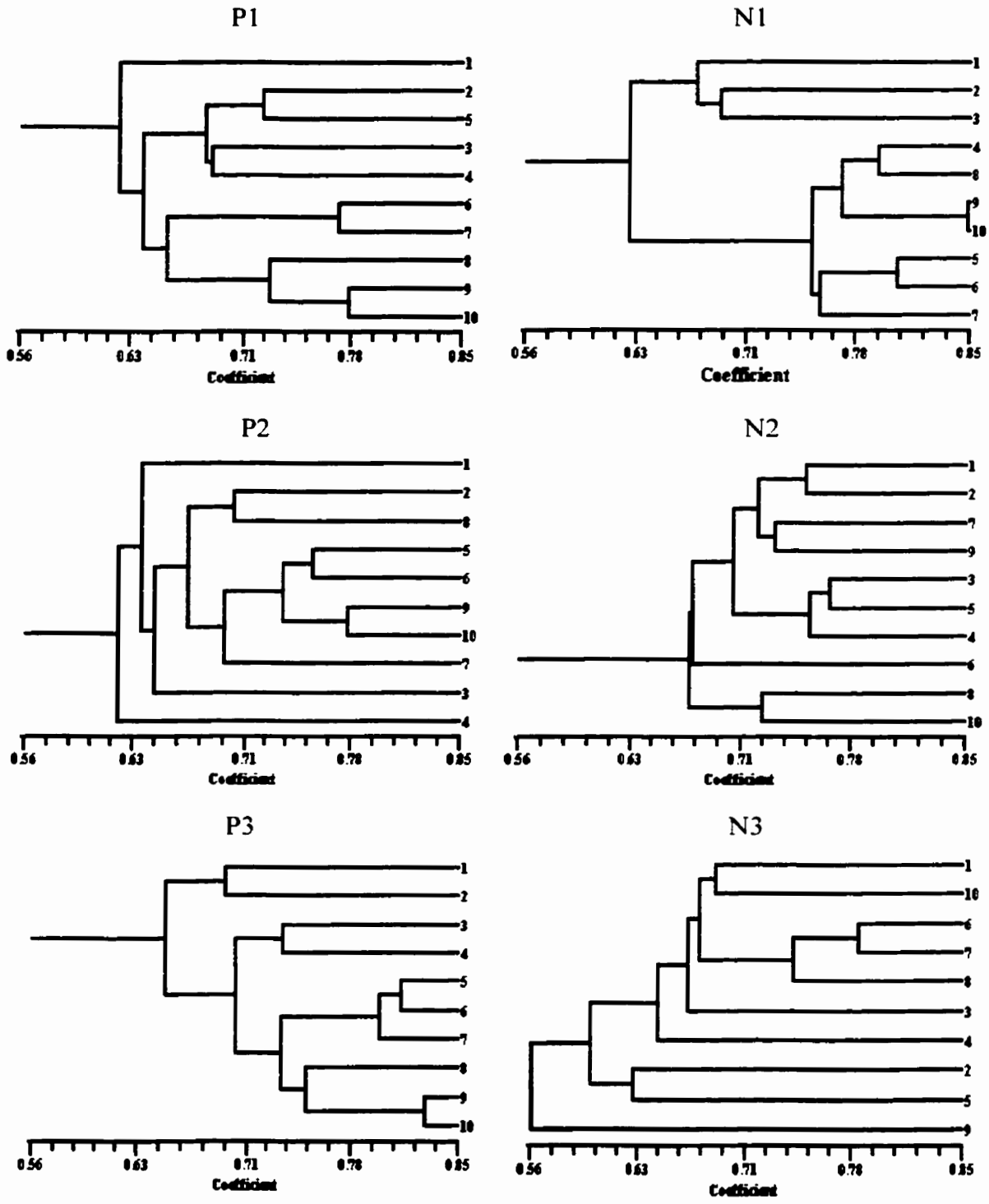

Figure 5.3. The unweighted pair-group method of arithmetic averages (UPGMA) classification based on Jaccard's similarity coefficient for individuals of naturally-regenerated populations (N1, N2, N3) and planted populations (P1, P2, P3).

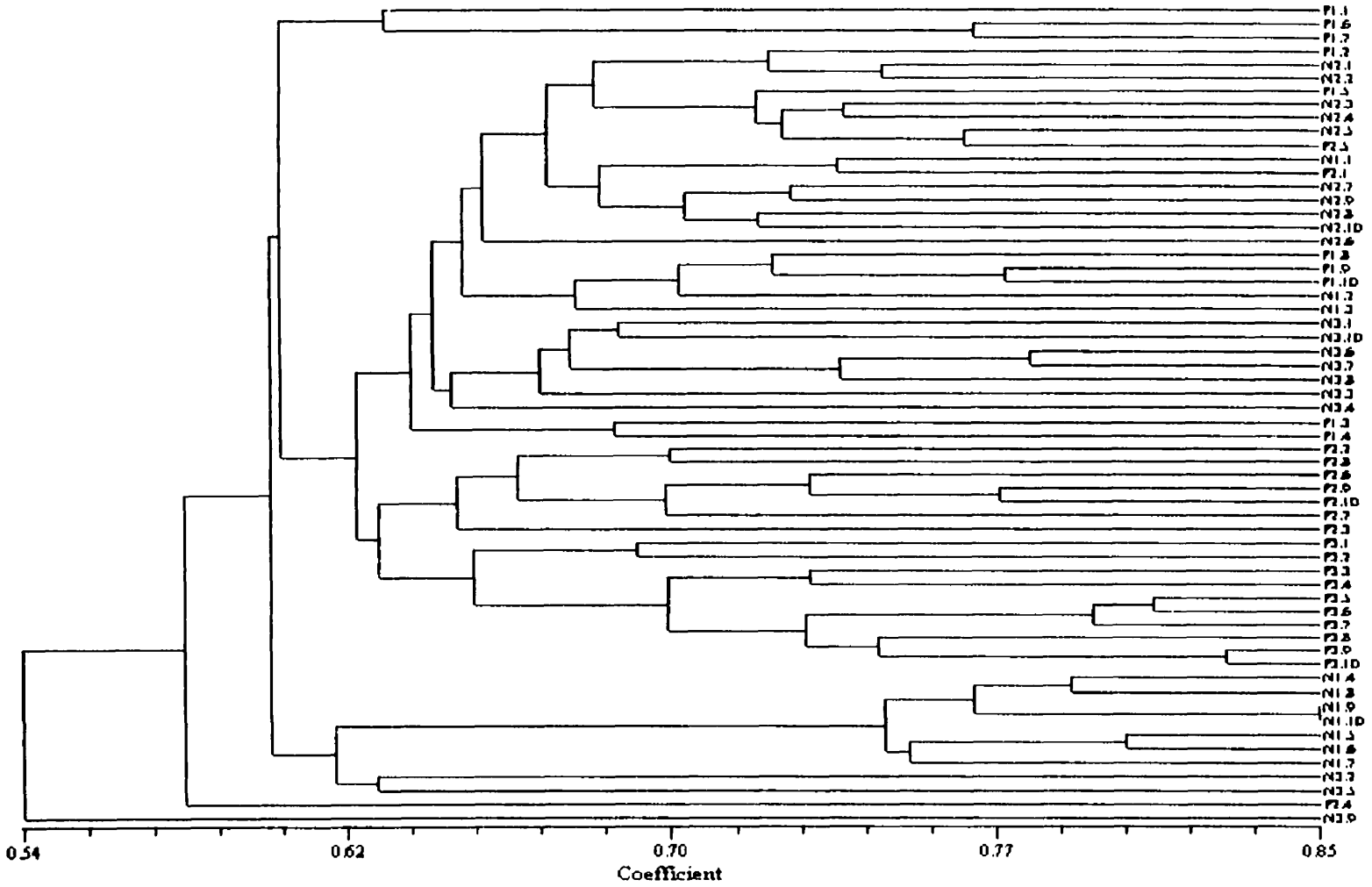

Figure 5.4. The unweighted pair-group method of arithmetic averages (UPGMA) classification based on Jaccard's similarity coefficients of individuals of planted populations (P1, P2, P3) and naturally regenerated populations (N1, N2, N3).

Table 5.3. Variation among individual seedlings of white spruce populations collected from field-planted and naturally-regenerated sites.

Regeneration type		No of individuals	Sums of Squares
Planted	P1	10	160.1
	P2	10	153.1
	P3	10	133.2
	Total	***30***	***555.1***
Natural	N1	10	141.6
	N2	10	145.6
	N3	10	165.8
	Total	***30***	***545.4***

Table 5.4. Inter-population distance (Φ_{st}) among white spruce populations collected from field-planted (P1, P2, P3) and naturally-regenerated (N1, N2, N3) sites. The analysis was determined by AMOVA; the upper-part of the matrix represents the P-value and the lower part shows the mean genetic distance.

	P1	P2	P3	N1	N2	N3
P1		0.000	0.000	0.000	0.000	0.000
P2	0.1698		0.000	0.000	0.000	0.000
P3	0.2147	0.1729		0.000	0.000	0.000
N1	0.1961	0.2438	0.2585		0.000	0.000
N2	0.1075	0.1206	0.2037	0.1553		0.000
N3	0.1099	0.1454	0.1407	0.1734	0.1178	
*Mean**	*0.159*	*0.2120*	*0.1981*	*0.2086*	*0.1521*	*0.1374*

* mean distance between individual populations (in heading row) and all other populations.

5.4. Discussion

Random amplified polymorphic DNA (RAPD) primers used to study the genetic variation within and among populations of white spruce appeared to give satisfactory results. This method is simple, inexpensive and results are generally reproducible with an average of eight clear bands produced per primer. RAPD

alleles are mostly dominant/recessive (present/absent band), and it is not possible to differentiate the heterozygotes from the dominant homozygous (Landry *et al.*, 1993). However, breeding populations in conifers rarely if ever the result of crosses between homozygotes. In fact, the levels of heterozygosity in Douglas fir were around 80% (El-Kassaby in personal communication with Carlson *et al.*, 1991).

RAPD primers showed abundant polymorphism in all populations, supporting Mosseler and Hughes (1992), who reported high levels of genetic heterogeneity in spruces of the boreal zone using RAPD markers, and Cheliak *et al.* (1988) using isozymes. The fragment sizes of the amplified products ranged from around 400 to 3000 bp. Fragments size produced using the primers in the current study are in agreement with Khasa and Dancik (1996) who used primers OPA-08 and OPB-06 to identify white spruce. However, the number of clear informative bands was 8 and 6 comparing to 10 and 7 reported by Khasa and Dancik using the OPA-08 and OPB-06 primers respectively. Moreover, two monomorphic bands were found in the amplification products of these primers in the present study. This agrees with the authors for OPB-06, but disagrees for OPA-08 where they reported one monomorphic band. OPA-03 was the only primer that showed four monomorphic bands in all tested individuals. This primer has the potential to be a marker for white spruce once tested on other spruce species and hybrids.

Dendrograms did not show the presence of any two identical individuals. Each individual showed a unique banding pattern. This is expected since white spruce is an outcrossing species in which inbred individuals do not usually survive (Cheliak *et al.*, 1985)

Based on the sum of squares (Table 5.3), the naturally-regenerated and the field-planted populations demonstrated similar variation within and among regeneration types. This variability shows that the selection pressure was not great enough to cause any decline in the genetic diversity of field-planted populations by forest management practices in the current study. Moreover, 82.9% of the total genetic variation was due to intra-population variation, while inter-population variation and regeneration type accounted for 16.7 and 0.4% of the total variation, respectively. Hamrick and Godt (1990) suggested that coniferous species are among

the most genetically variable plants. Hamrick *et al.* (1992) stated that woody species maintained more intra- then inter-populations variation than other species with other life forms. Huff *et al.* (1993) found that the within population variation in buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.) was 74 to 95% of the total variation. The authors attributed the results to the outcrossing nature of the buffalograss. Furnier *et al.* (1991) found that 3.8% of the total variation in the allozyme was due to differences among white spruce populations. Rajora *et al.* (1998) found that populations of white pine (*Pinus strobus* L.) from Newfoundland were as genetically variable as those from Ontario, adding that around 94% of the total genetic variation was due to intra-population variation. Yeh *et al.* (1986) found that 5.9 % of the observed genetic variation in black spruce in regions of Newfoundland was due to inter-population variation, while the remainder was caused by intra-population variation. Yeh *et al.* (1986) concluded that black spruce is an outcrossing species, and populations within a region are on average as similar to each other as they are to populations chosen at random from other regions of Newfoundland. This indicates that little genetic differentiation has occurred among populations of black spruce in the regions of Newfoundland. On the other hand, Mosseler and Hughes (1992) reported that the low general genetic variation in *Pinus resinosa* Ait. (red pine) could have resulted from habitat fragmentation due in part to the bottleneck of the species after the Holocene glaciation, and to the ability of red pine to self-pollinate, which promoted the loss of diversity through inbreeding in small populations.

All white spruce populations were significantly distant from each other. The average genetic distance was 0.163, while the greatest distance between two populations was 0.25. Average distances reported for white spruce populations in the current study were in some cases greater than those found by Yeh *et al.* (1986) for black spruce. The average distance among black spruce populations was 0.071 and the maximum distance was 0.14. This is evidence that non-specific differentiation occurs in many species. The distance among field-planted populations was 0.18 which was greater that that of the naturally-regenerated populations (0.15), even

though two the field-planted populations had similar seed provenance. This further demonstrates the large genetic variation among white spruce seedlings.

6. OVERALL SUMMARY AND CONCLUSIONS

Structure, function and composition are elements of ecosystem study at both the communities and landscapes scale. The structure and composition of the mixedwood section of the southern boreal forest of Saskatchewan were investigated previously (Thrasher-Haug, 1997; Sulistiyowati, 1998). The present research was aimed at contrasting the spatial, functional and genetic characteristics of field-planted and naturally-regenerated white spruce populations in the mixedwood section of the boreal forest of Saskatchewan. The following is a review of the specific objectives, and a summary of the corresponding results and conclusions of the research.

The first objective was to describe the spatial and age structure of naturally-regenerated white spruce populations in stands along a chronosequence developing after fire, and to compare this structure with that of clearcuts.

- White spruce tree-density increased gradually along the chronosequences after fire and cutting, although the latter was truncated because of the lack of old clearcut stands. White spruce density, expressed as percent of total trees present increased until 120 years after fire, coinciding with a decline in deciduous trees. White spruce density tended to increase along the entire chronosequence. Tree height and DBH peaked at about 120 years after fire. Seedlings were present even in the oldest stands, although others have concluded that the species is incapable of reproducing itself in the deep shade and moss layer (Oliver and Larson, 1996; Farmer, 1997).
- Sapling density in clearcuts appeared to peak at an earlier age than after fire. The stands were planted either immediately after cutting or during the following season, resulting in greater densities of white spruce at an earlier stand age. This

likely accelerated white spruce regeneration and succession. In comparison, stands after fire showed slower regeneration and relied mainly on seed input from nearby canopies. Sapling density along the chronosequence after fire resembled that after cutting, but trends were not as clear due to the small number of fire-generated stands in the 0-40 year age range.

- White spruce seedlings were present in various densities in all sampled plots after fire except for a 43-year-old plot. Seedlings were mostly observed in shaded microsites. Natural regeneration was observed in one 4-year-old clearcut, but was lacking in the remaining plots that were recently cut. White spruce regeneration seemed to depend on the presence of propagules at early stand ages, but on the presence of suitable microsites, especially those with favorable light, temperature and water regimes, and LFH thickness, in older stands.
- Field-planted seedlings were generally larger and had lower coefficients of variability in height than naturally-regenerated seedlings of the same age.
- The variability in white spruce seedling and sapling densities, heights and ages led to the conclusion that white spruce regeneration after fire was more or less continuous over time. The varying densities of saplings along the chronosequence suggests variation in recruitment into the sapling population over time. Planted stands were more even-aged.
- In recently disturbed plots, the difference between planted and naturally-regenerated seedlings was related to seedling density rather than spatial distribution. Seedlings in both regeneration types were evenly spaced. This pattern changed to random as the stands aged. In old plots after burn, seedlings were clumped together. The importance of woody debris was noticeable in old plots where the majority of seedlings regenerated on logs. Logs provide moisture during the summer, reduce the barrier to seedling establishment posed by mosses and litter, and provide an elevated environment for better light competition.
- Recent clearcuts were characterized by both higher light intensity reaching the forest floor and higher soil temperatures than recent burns.

The second objective was to compare the physiology, growth and morphology of white spruce seedlings within and among populations selected from naturally-regenerated (N1, N2 and N3) and field-planted (P1, P2, and P3) populations under greenhouse conditions. Physiological responses, particularly acclimation to light, were of primary interest.

- Seedling survival was 100 % at the end of the 15-week full-sun acclimation period and varied between 57% (N1) and 100% (P3) after a shade acclimation period. Survival in shade was greater and varied less in field-planted populations, which appeared to be relatively shade-tolerant.
- Photosynthesis increased linearly with increasing in photon irradiance, at low irradiances, due to the increase in the available energy. At low light levels, shaded populations showed steeper light response curves and greater rates of photosynthesis than populations grown under full sun treatment. Furthermore, populations acclimated to shade were characterized by lower respiration rates and light compensation points, and higher quantum yields. This reveals the capacity of all the white spruce populations studied to maintain positive photosynthesis in low light environments.
- At light saturation, the white spruce populations showed three types of photosynthetic responses. Similar behavior in the full sun and in the shade was noticed for populations P1 and N3, suggesting no acclimation in these two populations. Population P2 and P3, which are of the same origin (Big river area, SK.), and N2 performed poorer in the full sun treatment in terms of photosynthesis than in the shade showing a better adaptation of the photosynthetic system to low than high light intensities. Population N1 performed best under full light treatment and also did well in the shade treatment. It was the only population that had the ability to fully-acclimate to sun and shade conditions. The result suggests that there may be distinct physiological ecotypes in naturally-regenerated white spruce populations.
- The photosynthetic properties of four white spruce populations measured in the field were similar to those in the greenhouse experiment, confirming that greenhouse plants were responding "normally".

- Except for the naturally-regenerated population N1, that exhibited significantly greater photosynthesis at high light, stomatal conductance, dark respiration and light compensation points than the other populations in both light regimes, the remaining populations did not generally differ among each other within light regimes. Furthermore, N1 exhibited the greatest plasticity in physiological parameters in response to high and low light compared to other populations, a characteristic reported for some early- and mid-successional species. While most of the other populations showed a decline in quantum yields in full sun, N1 did not seem to be affected. The decline might have been the result of photoinhibition, which shade-tolerant species encounter once exposed to high irradiance.
- Low-light treatment induced a significant increase in the total chlorophyll content, specific leaf area and absolute water of white spruce needles. The growth of the terminal bud was not influenced by shade in either regeneration type. Fewer secondary branches developed in the shade than in the full sun treatment, but the difference was only significant in planted populations. Number of secondary branches was significantly greater in planted populations in full sun compared to naturally-regenerated populations, but this probably was because the planted individuals were initially larger. The length of secondary branches on the other hand was greater in the shade.
- The coefficient of variability was higher in sun than in the shade, indicating a greater within-population variation in the sun compared to the shade. This was true for all studied parameters except for the growth of the terminal bud and number of secondary branches, which varied more in shade. Grossnickle and Fan (1998) found that interior spruce (white x Engelmann spruce hybrid), exhibited clonal variation in gas exchange, but the magnitude of these differences depended on the selected atmospheric conditions. Intra-specific variation was also reported for other conifer species (Carter and Klinka, 1992).
- Within-population variation in field-planted and naturally-regenerated populations was large and did not show any obvious trend. For example, similar within-population variation was found in both regeneration types for stomatal

conductance, total chlorophyll content, length of secondary branches and absolute water content. There was higher variation within the field-planted populations in photosynthesis, respiration rate, light compensation point and specific leaf area. Quantum yield, terminal bud growth and number of secondary branches varied more within naturally-regenerated populations than within field-planted.

The third objective was aimed at measuring the genetic variation among individuals in field-planted and naturally-regenerated white spruce seedling populations.

- RAPD analysis showed abundant polymorphism in all populations. Dendrograms created using UPGMA cluster analysis did not show the presence of any two identical individuals. Each individual showed a unique banding pattern. This is expected since white spruce is an outcrossing species in which inbred individuals do not usually survive.
- Individuals within populations generally overlapped: The exception was the naturally-regenerated population (N1), with 70% of its individuals distinct from other individuals of the remaining populations.
- The naturally-regenerated and the field-planted populations demonstrated similar within and among regeneration type variation. This shows that the selection pressure during the process of reforestation was not great enough to cause any obvious decline in the genetic diversity of field-planted populations compared to naturally-regenerated populations. Moreover, 82.9 % of the total genetic variation was due to intra-population variation, while inter-population variation and regeneration type accounted for 16.7 and 0.4 % of the total variation respectively.

This research was aimed at testing the hypothesis that spatial, functional and genetic characteristics do not differ within and between field-planted and naturally-regenerated populations of white spruce. Based on the analysis of population structure, planted populations were similar to naturally-regenerated populations in

some respects, but differed in others. Spatial pattern of white spruce seedlings was similar in both regeneration types, but seedling physiology and morphology, and stand environment differed. Seedlings generally occupied shaded and protected microsites, in agreement with the findings of the physiological study, where both regeneration types performed equally or even better in the shade than in the full sun. There was a larger variation in physiological characteristics among naturally-regenerated than among field-planted populations. However, both regeneration types exhibited similar within population variation.

The large within-population variability shown by the DNA analysis corresponds with the large variation in physiological characteristics observed in the greenhouse. In general, there was a great within population variation in the measured genetic, physiological and morphological parameters that tended to mask some of the significant variations among populations. Despite the large within population variation, local adaptations to the environment in different populations were noticed, for example the naturally-regenerated population N1 performed best in full sun, and genetically, its individuals were mostly grouped together and were different from other individuals. Furthermore, full light seemed to exert similar negative effects on photosynthesis in P2 and P3.

The study of white spruce seedling characteristics in planted and naturally-regenerated populations was the focus of this thesis. Some ecological concerns regarding the impacts of current management practices on future forests emerged from the findings. Some of these concerns include the following:

1) Artificially-accelerated white spruce regeneration and succession could lead to even-age stands dominated by white spruce.
2) The greater uniformity in seedling densities, height and age in recently planted cutovers could leave them more vulnerable to disease and pests, and affect the future structural diversity of the forest. This in turn could affect the biodiversity of the whole forest community. In fact, stand uniformity may cause a decline in the available microhabitats below the levels required by many vertebrate species.

3) The variability among populations in response to sun and shade shows an adaptation to the local environment, and such variability could be behind some of the unsuccessful artificial regeneration on some sites.
4) The genetic diversity within and among populations should be assessed using molecular biology, accompanied with ecophysiological testing, because, evolutionary forces may act in different ways on the genes controlling these traits. Using genetic information as the only tool for conservation programs could be of limited value, while preservation of genotypes adapted to many sites throughout the species range is important.
5) The use of small numbers of seed provenances, or the use of cloned material in artificial-regeneration would impact the future genetic diversity, as well as the local adaptation of white spruce. For instance, despite the equally high genetic diversity in planted and naturally-regenerated populations in the present study, P2 and P3 were of the same origin, and as expected showed similar physiological responses to light treatment. Individuals of these two populations were grouped together in the cluster analysis. This shows that they were genetically closer to each other than to the other populations. Therefore, using a single seed source for reforestation may affect future white spruce genetic diversity that is difficult to assess at this stage, due to factors such as the high heterozygosity and longevity of this species. The use in reforestation of populations such as N1, which is capable of acclimating to both shaded sites and sunny open sites might be a successful strategy.

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APPENDIX A

Age and location of plots developed after fire in the mixedwood forest of central Saskatchewan.

Plot	Age	Latitude	Longitude	Location
9609	0	53 58' 45"	105 54' 30"	200 m N on 2 from Bittern Creek
9602	1	53 57' 30"	105 27'	95-26 resampled 926-Monday burn
9534*	5	54 14'	105 56'	Halfway House, junction of 2/Elaine Lake road
9613*	16	54 28' 30"	105 49"	3.6 km N on 2 east Weyakwin Lake turnoff
9615	16	54 41'	105 45'	7.6 km N on 2 past Weyakwin Lake turnoff
9612*	43	53 38' 45"	105 48'	3.2 km S on 2 from Clarine Lake turnoff
9614	49	53 39'	105 48'	3.3 km S in 2 from Clarine Lake turnoff
9523	63	53 57' 30"	105 27'	3.8 km N of Hannin Creek on 927
9521	66	53 55' 30"	105 28'	1.5 km west on road S of Hannin Creek on 926
9535	75	53 39'	105 55' 30"	9.1 km W on Clarine Lake road
9524**	76	53 44'	105 28'	17.5 km N on 926 from 926/120
9411	77	53 57'	106 05'	Waskesiu Lake, E
9412**	77	53 53'	106 06'	Waskesiu Lake, Narrows road and 263 junction
9409	78	53 42'	105 50'	Highway 2, south of Anglin Lake
9413	86	53 52'	106 10'	Waskesiu Lake, road to Helicopter pad
9522	90	53 58'	105 27'	5.6 km N of Hannin Creek on 926
9401**	93	53 49'	105 26'	Candle Lake, W side
9415	94	53 54'	106 05'	Waskesiu Lake, shortcut to Compound road
9408	100	53 56'	106 14'	Waskesiu Lake, Gravel pit road
9607	101	53 58' 30"	106 09'	5.2 km past marina on N Waskesiu road
9604	102	53 45' 30"	105 13' 15"	Candle Lake, 2.2 km E mini-golf in 265
9405	108	53 57'	106 14'	Waskesiu Lake, treebeard 57
9414	108	53 59'	106 10'	Crean Lake road
9525	110	53 43'	105 27'	5 km N on 926 from 926/120
9407	111	53 59'	106 20'	Waskesiu Lake, Narrows Camp ground site 53
9429	116	53 45'	105 13'	Candle Lake, Garbage dump
9608	124	54 02'	105 05'	Sasktel tower at Whiteswan Lake, 2.2 km from 913
9520	127	53 55'	105 27' 30"	400 m west on road S of Hannin Creek on 926
9423	134	53 46'	105 14'	Candle Lake, Northview road
9611	147	53 59'	106 16' 30"	Waskesiu Lake, Narrows Peninsula trail
9422	150	53 46'	105 15'	Candle Lake, Simon Lehne Drive to marina
9606	150	53 59'	106 14'	4.2 km off asphalt of N Waskesiu road
9402***	157	53 48'	105 26'	Candle Lake, W side
9404	171	53 58'	106 18'	Waskesiu Lake, treebeard trail
9403***	172	53 49'	105 24'	Candle Lake, W side
9406***	201	54 02'	106 14'	Crean Lake, Warden's cabin

* young, **mature, *** old age class selected for intensive study.

APPENDIX A
Continue

Age and location of cut plots in the mixedwood forest of central Saskatchewan.

Plot	Age	Latitude	Longitude	Location
9601	0	53 53'	105 00' 30"	7.8 km on 120 from 913/120
9531*	2	54 01'	105 40'	18.9 km NW on Bittern Lake road from 926
9509	2	53 58'	105 27'	5.6 km N of Hannin Creek on 926
9510	3	53 59'	105 27'	7.3 km N of Hannin Creek on 926
9533*	4	53 59'	105 55'	1.8 km on 2 past 926/2
9528	8	53 40' 30"	105 20'	750 m N of Snowcastle road/926
9507a*	9	53 41'	105 21'	7.4 km N on 926 from 926/120
9507b	9	53 41'	105 21'	7.4 km N on 926 from 926/120
9527	11	53 41' 30"	105 24'	10.25 km N on 926 from 926/120
9503	12	53 55' 45"	105 53' 30"	9.3 km N of turnoff to Waskesiu on 2
9511a	12	53 55'	105 30' 30"	3 km S of Hannin Creek in 926
9506	23	53 41'	105 51'	Clarine Lake (Tending for the Future sign)
9505	26	53 40' 30"	105 52'	Clarine Lake (Harvest 1970 sign)
9610	28	53 40' 30"	105 53'	6 km on Clarine Lake road (Harvest 1968 sign)
9530	40	53 43'	105 13' 30"	1.6 km NE past Candle Lake turnoff on 120
9532	85	53 41' 30"	105 15'	Heritage forest on 120, 2 km S of Candle Lake turnoff

* young stands selected for intensive study

APPENDIX B

Tree species density in the 40 x 20m plots selected for intensive study in the mixedwood section of the central Saskatchewan boreal forest.

	Stand age	White spruce	Trembling aspen	Balsam Poplar	Paper birch	Balsam fir
Old stands						
94-06	201	40	43	0	4	1
94-03	172	122	12	2	6	1
94-02	157	73	25	7	4	1
Mature stands						
94-01	93	51	33	3	9	1
94-12	77	25	42	3	0	1
95-24	76	12	68	2	1	3
Young stands						
96-12	28	18	118	0	0	0
96-13	16	42	356	1	0	0
95-34	5	0	0	0	0	0
Planted stands						
95-07a	10	0	0	0	0	0
95-33	4	0	0	0	0	0
95-31	2	0	0	0	0	0

APPENDIX C

Regression analysis of saplings age against saplings height and DBH outside plots selected for intensive study after fire in the mixedwood forest of central saskatchewan.

	df	SS	MS	F	P-value
Regression	2	3166.5	1583.2	144.4	0.00
Residual	76	833.3	11.0		
Total	78	3999.8			
R Square	80				
	Coefficients	Standard Error		t Stat	P-value
Intercept	0				
Height (m)	3.48	1.36		2.56	0.01
DBH (cm)	4.06	0.81		5.02	0.00

APPENDIX D

Environmental characteristics in plots developed after fire or clearcut in the mixedwood section of Saskatchewan boreal forest.

Stand type	Age	Sampling date	Light intensity ($\mu mol\ m^{-2}\ s^{-1}$)	Air temperature (°C)	Soil temperature (°C)	Light intensity ($\mu mol\ m^{-2}\ s^{-1}$)
		1997				August, 1998
After fire						
95-34	5	May. 24	630	10.5	4.50	-
96-13	16	May. 24	410	11	3.38	2000
96-12	43	May. 25	675	14.1	4.50	-
95-24	76	June. 5	860	27	8.60	850
94-12	77	May. 28	550	18	6.00	2000
94-01	93	June. 4	875	25	6.70	2000
94-02	157	Jun. 6	760	25	9.10	750
94-03	172	Jun. 4	725	20	5.20	1600
94-06	201	May. 26	120	17	3.50	-
After clearcut						
95-31	2	June. 6	130	18	14.90	-
95-33	4	May. 29	990	25.9	1070	2000
95-07a	9	June. 6	1016	20.4	13.20	-

APPENDIX E

Analysis of variance table of percent light reaching the forest floor in plots selected for intensive study, after fire and in different age classes (young, mature, old) of the mixedwood section of Saskatchewan boreal forest.

	DF	SS	MS	F-Value	P
Plot	8	98249	12281	73.9	0.0001
Age class	2	33155	16577	99.7	0.0001
Error	277	46041	166.2		

Analysis of variance table of soil temperature (°C) at 5 cm depth in plots selected for intensive study after fire, and in different age classes (young, mature, old) of the mixedwood section of Saskatchewan boreal forest.

	DF	SS	MS	F-Value	P
Plot	8	1095	136.9	55.7	0.0001
Age group	2	436.7	218.4	88.9	0.0001
Error	277	685.3	2.46		

Analysis of variance table of forest floor thickness (LFH, cm) in plots selected for intensive study after fire, and in different age classes (young, mature, old) of the mixedwood section of Saskatchewan boreal forest.

	DF	SS	MS	F-Value	P
Plot	8	918.8	114.8	17.75	0.0001
Age group	2	565.4	282.7	43.7	0.0001
Error	277	1805	6.47		

Analysis of variance table of percent light next to the forest in young planted versus naturally regenerated sites of the mixedwood section of Saskatchewan boreal forest.

	DF	SS	MS	F-Value	P
Stand type	1	41868.23	41868.23	111.86	0.0001
Error	190	71113.50	374.28		

APPENDIX E
Continued

Analysis of variance table of soil temperature (°C) at 5 cm depth in young planted versus naturally-regenerated sites of the mixedwood section of Saskatchewan boreal forest.

	DF	SS	MS	F-Value	P
Stand type	1	3762.14	3762.14	656.57	0.0001
Error	190	1088.69	5.73		

Analysis of variance table of forest floor thickness (LFH, cm) in young planted versus naturally-regenerated sites of the mixedwood section of Saskatchewan boreal forest.

	DF	SS	MS	F-Value	P
Stand type	1	1498.12	1498.12	140.06	0.0001
Error	190	2032.26	10.70		

Means of environmental parameters in three age classes after fire (young, mature, old) and young age class after clearcut of plots selected for intensive studying.

Age class	Light reaching forest floor (%)	Soil temperature (°C)	LFH thickness (cm)
Young (c)	86 *	12.9 *	2.5 *
Young (f)	37.6 a	4.1 c	8.2 c
Mature (f)	15.1 b	7.1 a	9.5 b
Old (f)	14.5 b	5.9 b	11.6 a
LSD (f)	3.66	0.39	0.64

(c) after clearcut, (f) after fire
* young (c) and young (f) are significantly different at alpha 0.05
within columns, means followed by the same letter are not significantly different at alpha 0.05

APPENDIX F

Year and type of disturbance and location, of six stands in central Saskatchewan boreal forest from which white spruce seedlings were collected.

Stand			UTM		Latitude	Longitude
Field Planted	**Year of planting and site preparation type**					
P1	1995	Drum chopper, Disk trenshed	455900	5984700	54° 01'	105° 40'
P2	1997	Disk trenshed	440400	5981200	53° 58'45"	105° 54'30"
P3	1996	Disk trenshed	492000	5973000	53° 90'	105° 20' 25"
Naturally regenerated	**Year and type of disturbance**					
N1	1989	Harvested (clearcut) in 1993	470200	5979800	53° 58'	105° 27'
N2	1993	Fire in 1992	438200	6010100	54° 14'	105° 56'
N3	1987	Harvested (clearcut) in 1987	473700	5948900	53° 41'30"	105° 24'

APPENDIX G

Photosynthesis in relation to photon irradiance for white spruce seedlings collected from three field-planted and three naturally-regenerated sites and grown in shade or full sun treatment under greenhouse condition.

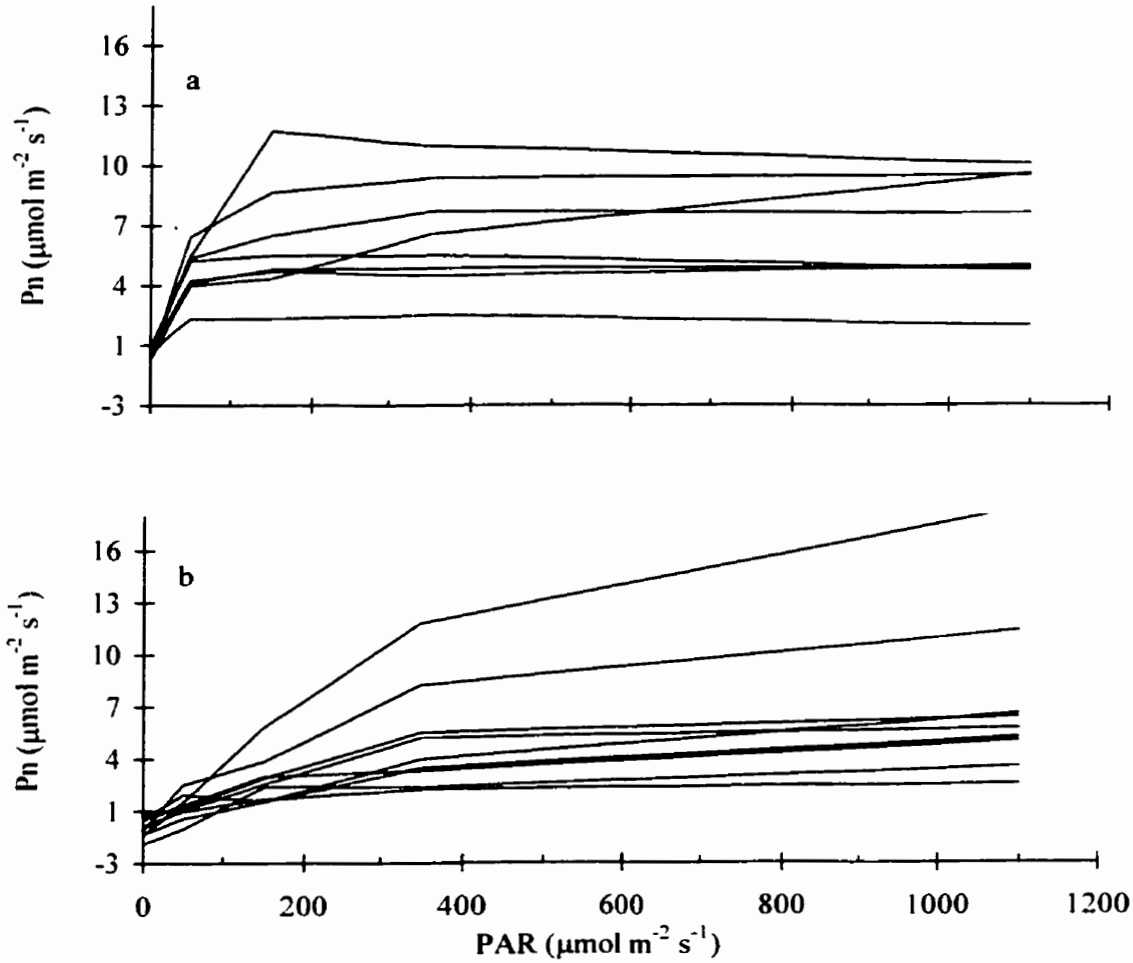

Figure 1. Photosynthesis (Pn) in relation to photon irradiance (PAR) for white spruce seedlings collected from field-planted site (P1) and grown in shade (a) or full sun (b).

APPENDIX G
Continued

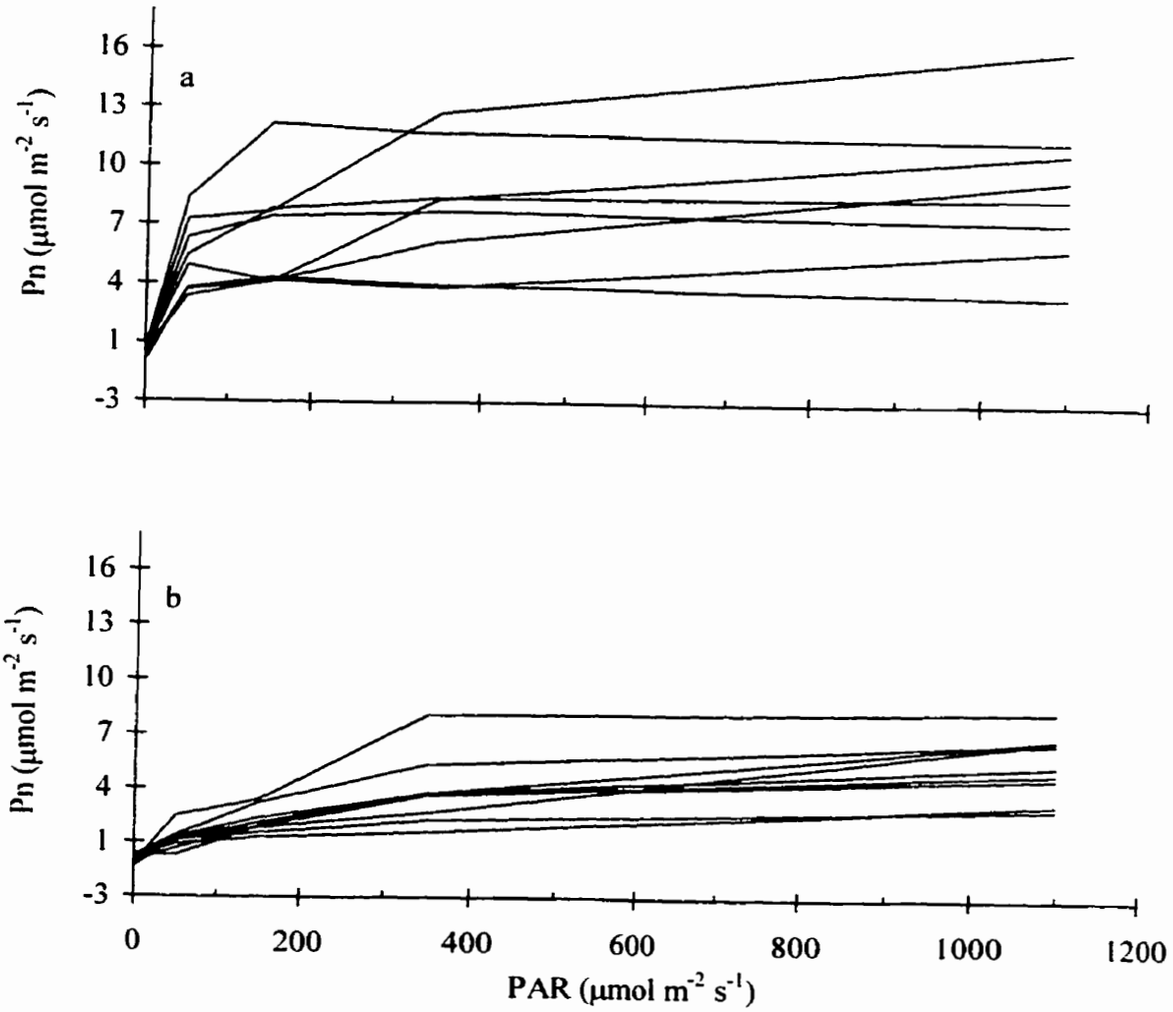

Figure 2. Photosynthesis (Pn) in relation to photon irradiance (PAR) for white spruce seedlings collected from planted site (P2) and grown in shade (a) or full sun (b).

APPENDIX G
Continued

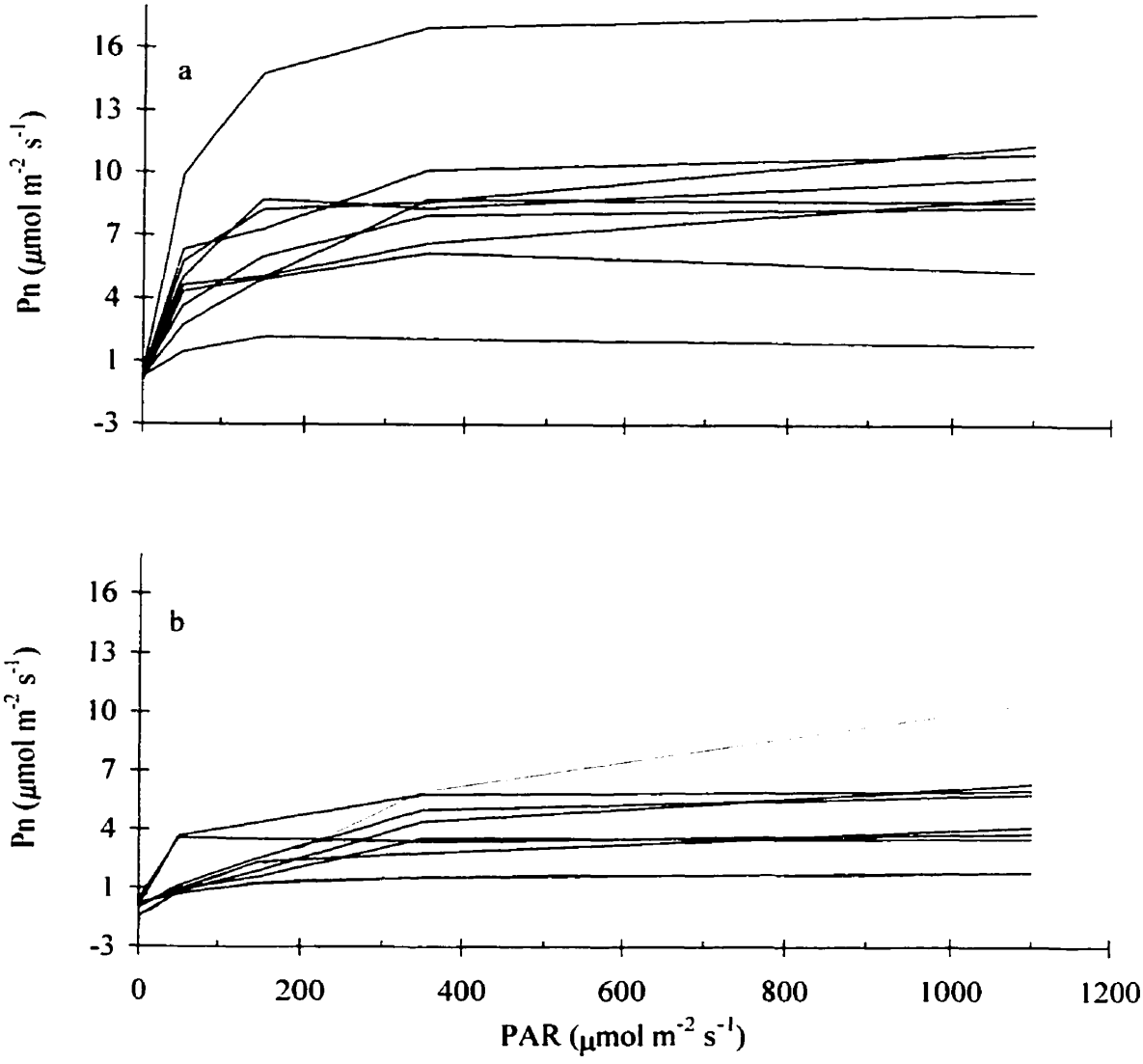

Figure 3. Photosynthesis (Pn) in relation to photon irradiance (PAR) for white spruce seedlings collected from planted site (P3) and grown in shade (a) or full sun (b).

APPENDIX G
Continued

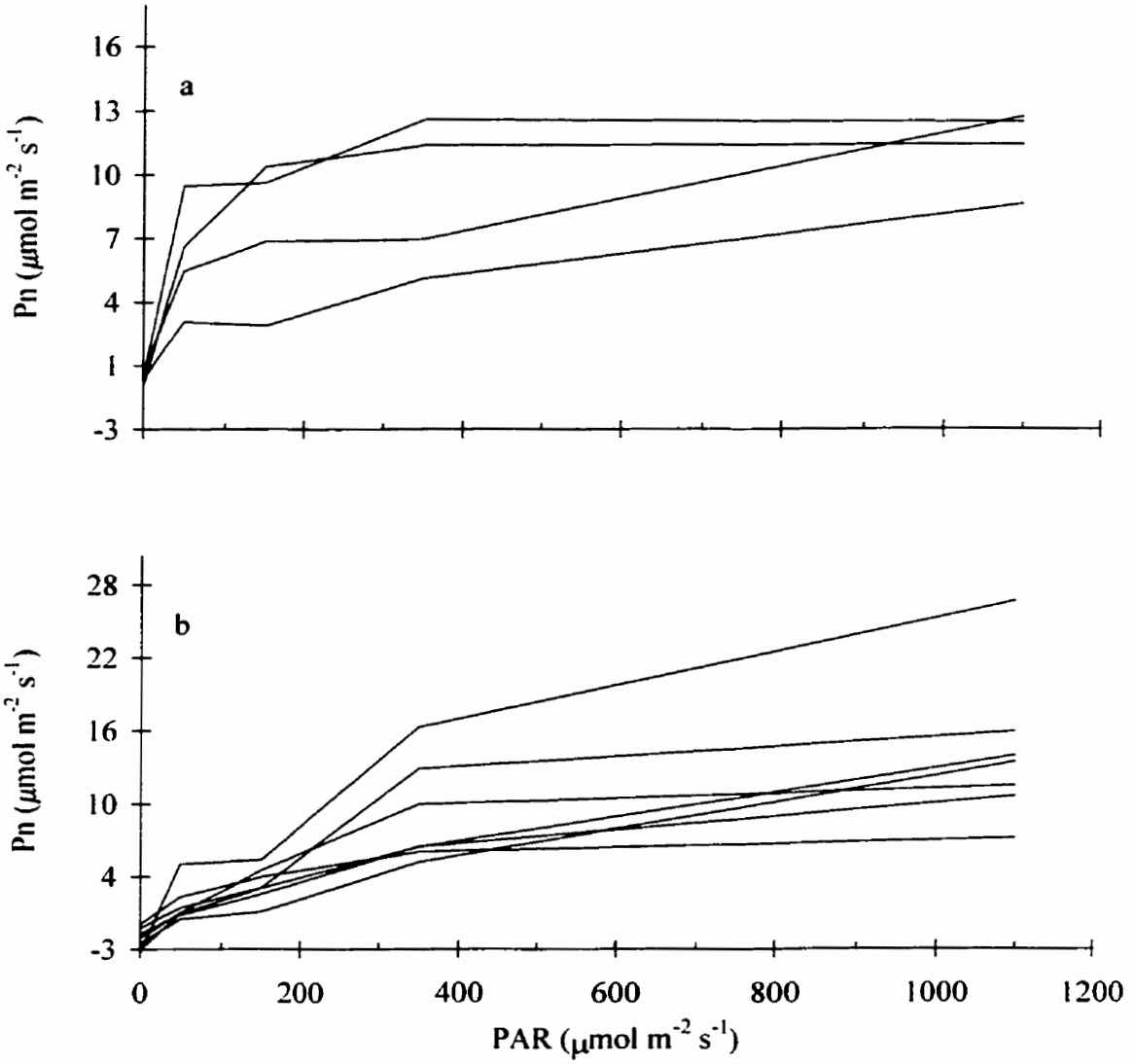

Figure 4. Photosynthesis (Pn) in relation to photon irradiance (PAR) for white spruce seedlings collected from naturally-regenerated site (N1) and grown in shade (a) or full sun (b).

APPENDIX G
Continued

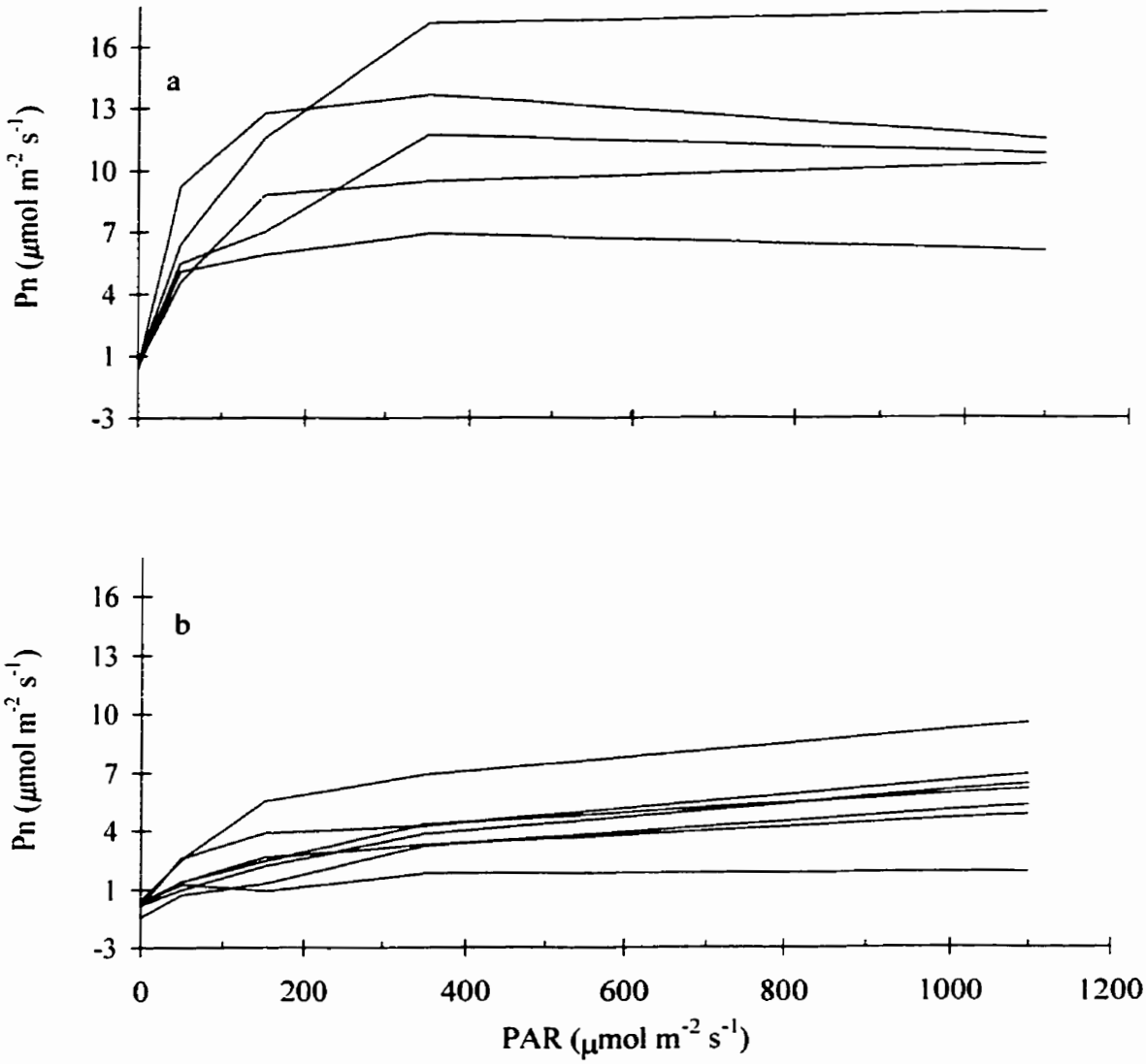

Figure 5. Photosynthesis (Pn) in relation to photon irradiance (PAR) for white spruce seedlings collected from naturally-regenerated site (N2) and grown in shade (a) or full sun (b).

APPENDIX G
Continued

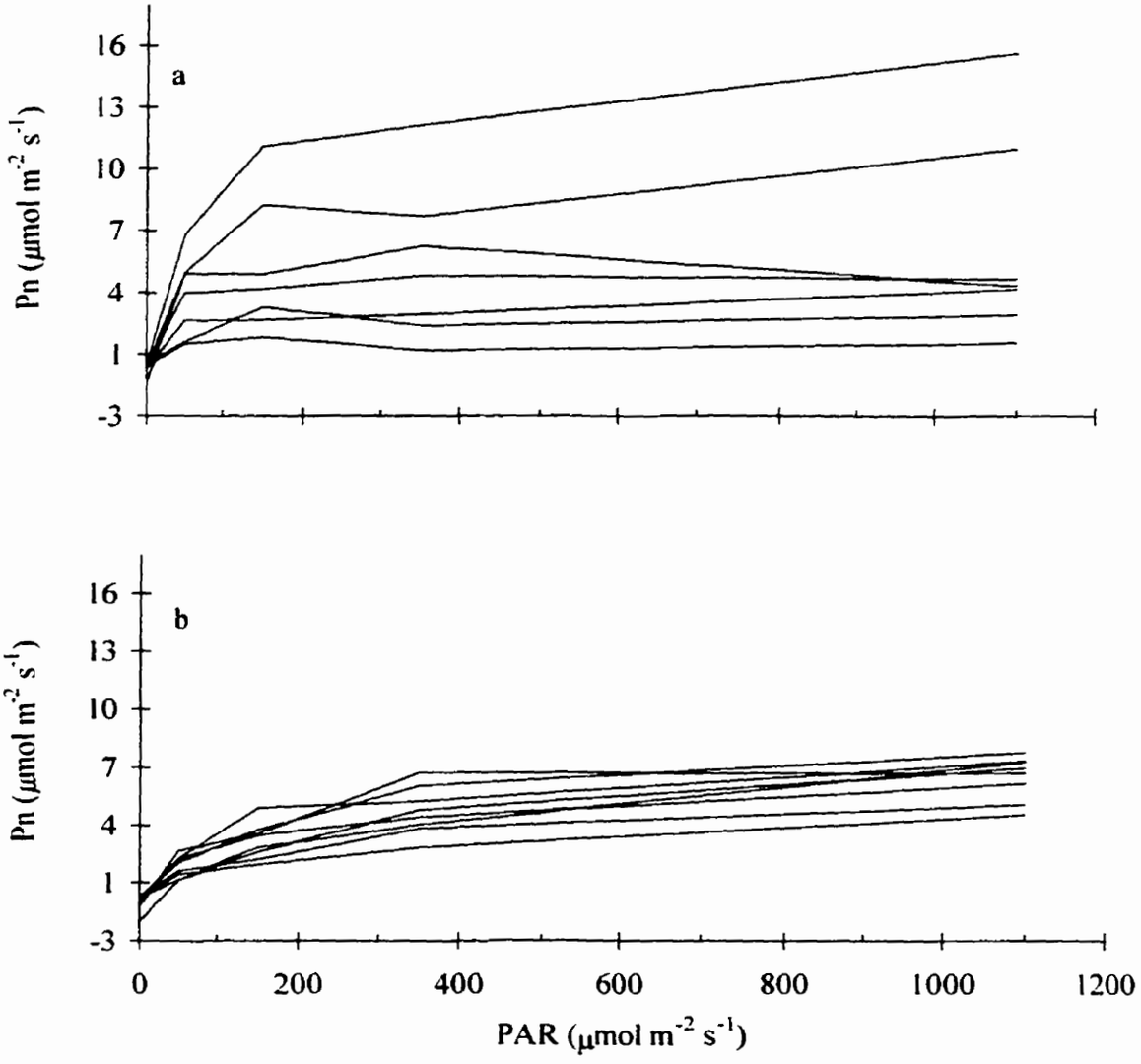

Figure 6. Photosynthesis (Pn) in relation to photon irradiance (PAR) for white spruce seedlings collected from naturally-regenerated site (N3) and grown in shade (a) or full sun (b).

APPENDIX H

Analysis of variance tables for the physiology and growth of three field-planted and three naturally-regenerated populations of white spruce acclimated to shade or full sun in the greenhouse.

Expectations of mean squares for the split- plot design (the appropriate denominators used in F-test)

Source	Type III expected mean square
Block	Var(error) + 3 var(pl(ligh*block*type*pop)) + 10 var(block*pop(light*type)) + 31 var(block*type(light)) + 63 var(block(light)) + 127.25 var(block)
Light	Var(error) + 3 var(pl(ligh*block*type*pop)) + 10 var(block*pop(light*type)) + 31 var(block*type(light)) + 63 var(block(light)) + q(light,light*type,light*pop(type))
Block(light)	Var(error) + 3 var(pl(ligh*block*type*pop)) + 10 var(block*pop(light*type)) + 31 var(block*type(light)) + 63 var(block(light))
Type	Var(error) + 3 var(pl(ligh*block*type*pop)) + 10 var(block*pop(light*type)) + 31 var(block*type(light)) + q(type,pop(type),light*type,light*pop(type))
Pop(type)	Var(error) + 3 var(pl(ligh*block*type*pop)) + 11 var(block*pop(light*type)) + q(pop(type),light*pop(type))
Light*type	Var(error) + 3 var(pl(ligh*block*type*pop)) + 10 var(block*pop(light*type)) + 31 var(block*type(light)) + q(light*type,light*pop(type))
Light*pop(type)	Var(error) + 3 var(pl(ligh*block*type*pop)) + 11 var(block*pop(light*type)) + q(light*pop(type))
Block*type(light)	Var(error) + 3 var(pl(ligh*block*type*pop)) + 10 var(block*pop(light*type)) + 31 var(block*type(light))
Block*pop(light*type)	Var(error) + 3 var(pl(ligh*block*type*pop)) + 11 var(block*pop(light*type))
Pl(ligh*block*type*pop)	Var(error) + 3 var(pl(ligh*block*type*pop))

APPENDIX H
Continued

Analysis of variance of net photosynthesis at light saturation (Pn, μmol m^{-2} s^{-1})

Source	DF	Type III SS	MS	F	P
Model	91	6341.44	69.69	51.29	0.00
Block	1	0.453	0.453	0.003	0.96
Light	1	100.87	100.87	0.81	0.53
Block(light)	1	124.53	124.53	2.64	0.24
Type	1	309.16	309.16	6.55	0.12
Population(type)	4	875.48	218.87	4.59	0.03
Light*type	1	92.19	92.19	1.95	0.29
Light*population(type)	4	390.74	97.68	2.04	0.17
Block*type(light)	2	94.19	47.09	0.98	0.41
Block*population(light*type)	8	381.22	47.65	0.84	0.56
Plant(light*block*type*population)	68	3830.78	56.33	41.46	0.00
Error	184	249.99	1.36		
Corrected total	275	6591.43			

Analysis of variance of stomatal conductance at light saturation (g_s, mol m^{-2} s^{-1})

Source	DF	Type III SS	MS	F	P
Model	91	1.803	0.0198	12.43	0.00
Block	1	0.011	0.011	0.184	0.74
Light	1	0.013	0.0127	0.211	0.72
Block(light)	1	0.061	0.061	1.46	0.35
Type	1	0.019	0.0192	0.464	0.56
Population(type)	4	0.194	0.0482	3.233	0.07
Light*type	1	0.0103	0.0103	0.248	0.66
Light*population(type)	4	0.0891	0.0221	1.486	0.29
Block*type(light)	2	0.083	0.0416	2.78	0.11
Block*population(light*type)	8	0.119	0.0149	0.886	0.53
Plant(light*block*type*population)	68	1.143	0.0168	10.45	0.00
Error	184	0.293	0.0016		
Corrected total	275	2.096			

APPENDIX H
Continued

Analysis of variance of dark respiration rate (Rs_D, μmol m^{-2} s^{-1})

Source	DF	Type III SS	MS	F	P
Model	91	247.34	2.72	26.68	0.00
Block	1	3.50	3.50	0.51	0.60
Light	1	26.48	26.48	3.88	0.29
Block(light)	1	6.83	6.83	2.07	0.28
Type	1	11.39	11.39	3.46	0.20
Population(type)	4	26.02	6.51	3.98	0.04
Light*type	1	5.02	5.02	1.52	0.34
Light*population(type)	4	20.51	5.18	3.14	0.07
Block*type(light)	2	6.61	3.31	2.03	0.19
Block*population(light*type)	8	13.09	1.64	1.11	0.36
Plant(light*block*type*population)	68	100.07	1.47	14.44	0.00
Error	184	18.74	0.102		
Corrected total	275	266.08			

Analysis of variance of quantum yield (Φ)

Source	DF	Type III SS	MS	F	P
Model	91	1.764	0.0196	23.1	0.00
Block	1	0.0041	0.0041	240.4	0.07
Light	1	0.053	0.053	5586	0.00
Block(light)	1	0.000002	0.000002	0.93	0.00
Type	1	0.0059	0.0059	29.6	0.03
Population(type)	4	0.170	0.0042	5.57	0.02
Light*type	1	0.118	0.118	58.58	0.01
Light*population(type)	4	0.0049	0.0012	1.60	0.26
Block*type(light)	2	0.00039	0.0002	0.25	0.78
Block*population(light*type)	8	0.0061	0.0008	0.73	0.66
Plant(light*block*type*population)	68	0.0698	0.0010	12.28	0.00
Error	184	0.015	0.00008		
Corrected total	275	0.191			

APPENDIX H
Continued

Analysis of variance of light compensation point (Γ, $\mu mol\ m^{-2}\ s^{-1}$)

Source	DF	Type III SS	MS	F	P
Model	91	32776.5	364.2	235.8	0.00
Block	1	15.11	15.11	17.18	0.15
Light	1	23887.8	23887.8	23738	0.00
Block(light)	1	0.882	0.882	0.806	0.46
Type	1	11.92	11.92	9.87	0.07
Population(type)	4	2855.45	713.86	131.78	0.00
Light*type	1	47.7	47.7	38.92	0.01
Light*population(type)	4	2819.5	704.9	129.1	0.00
Block*type(light)	2	2.19	1.09	0.194	0.82
Block*population(light*type)	8	42.71	5.34	0.313	0.95
Plant(light*block*type*population)	68	1141.9	17.0	11.03	0.00
Error	184	281.1	1.5		
Corrected total	275	33057.5			

Analysis of variance of specific leaf area (SLA, $cm^2\ mg^{-1}$)

Source	DF	Type III SS	MS	F	P
Model	23	0.012	0.0005	5.68	0.00
Block	1	0.0003	0.0003	4.077	0.29
Light	1	0.0077	0.0077	114.3	0.05
Bock*light	1	0.00007	0.0007	0.302	0.59
Type	1	0.00012	0.00012	0.54	0.48
Population(type)	4	0.00123	0.00031	1.353	0.32
Light*type	1	0.0001	0.0001	0.396	0.54
Light*population(type)	4	0.001	0.00021	0.939	0.47
Bock*light*population(type)	10	0.0023	0.00023	2.456	0.02
Error	66	0.0062	0.0001		
Corrected Total	89	0.01841			

APPENDIX H
Continued

Analysis of variance of absolute water content (mg mg^{-1})

Source	DF	Type III SS	MS	F	P
Model	23	64.65	2.81	11.49	0.00
Block	1	0.98	0.98	6.24	0.24
Light	1	54.88	54.88	350.7	0.03
Bock*light	1	0.16	0.16	0.62	0.44
Type	1	0.29	0.29	1.14	0.31
Population(type)	4	2.17	0.54	2.17	0.14
Light*type	1	0.14	0.14	0.55	0.47
Light*population(type)	4	1.03	0.26	1.03	0.43
Bock*light*population(type)	10	2.51	0.25	1.02	0.43
Error	66	16.14	0.24		
Corrected Total	89	80.79			

APPENDIX I

Covariate analysis tables for the physiology and growth of the three field-planted and three naturally-regenerated populations of white spruce acclimated to shade and full sun in the greenhouse.

Expectation of mean squares of covariate analysis for the split-plot design (the appropriate denominators used in F-test).

Source	Type III expected mean square
Block	Var(error) + 3.4223 var(Block*treat*pop(type)) + 20.534var(Block*treat) + 41.067 var(Block)
Treat	Var(error) + 2.6517 var(Block*treat*pop(type)) + 15.91 var(Block*treat)+ q(treat,treat*type,treat*pop(type))
Block*treat	Var(error) + 3.4438 var(Block*treat*pop(type)) + 20.663 var(Block*treat)
Type	Var(error) + 2.7255 var(Block*treat*pop(type)) + q(type,pop(type),treat*type,treat*pop(type))
Pop(type)	Var(error) + 3.291 var(Block*treat*pop(type)) + q(pop(type),treat*pop(type))
Treat*type	Var(error) + 2.928 var(Block*treat*pop(type)) + q(treat*type,treat*pop(type))
Treat*pop(type)	Var(error) + 3.4343 var(Block*treat*pop(type)) + q(treat*pop(type))
Block*treat*pop(type)	Var(error) + 3.5093 var(Block*treat*pop(type))

APPENDIX I
Continued

Covariate analysis of total chlorophyll content (T.chl. μg mg^{-1})

Source	DF	Type III SS	MS	F	P
Model	24	13.93	0.58	1.84	0.028
Chlorophyll 1997	1	1.24	1.24	3.95	0.051
Bock	1	2.30	2.30	40.13	0.088
Light	1	6.02	6.02	52.13	0.000
Block*light	1	0.056	0.056	0.354	0.564
Type	1	0.035	0.035	0.183	0.672
Population (type)	4	1.021	0.26	1.55	0.246
Light*type	1	0.0025	0.0025	0.0136	0.910
Light*population(type)	4	0.337	0.084	0.532	0.715
Bock*light*population(type)	10	1.548	0.1548	0.491	0.889
Error	63	19.84	0.315		
Corrected Total	87	33.76			

Covariate analysis of leader branch (terminal bud) growth (cm)

Source	DF	Type III SS	MS	F	P
Model	24	250.1	10.42	1.24	0.24
Height 1997	1	28.49	28.49	3.40	0.07
Bock	1	18.0130	18.01	2.41	0.37
Light	1	1.29	1.29	0.171	0.74
Block*light	1	7.48	7.48	0.815	0.39
Type	1	1.95	1.95	0.213	0.65
Population (type)	4	23.95	5.99	0.656	0.63
Light*type	1	6.61	6.61	0.718	0.41
Light*population(type)	4	43.57	10.90	1.18	0.37
Bock*light*population(type)	10	92.19	9.22	1.10	0.38
Error	62	519.91	8.37		
Corrected Total	86	770.00			

APPENDIX I
Continued

Covariate analysis of secondary branches that emerged during 1998

Source	DF	Type III SS	MS	F	P
Model	24	38347.10	1597.79	4.75	0.00
Branch count 1997	1	19.65	19.65	0.056	0.81
Bock	1	231.57	231.57	99.28	0.45
Light	1	12014.87	12014.87	5429	0.32
Block*light	1	4.96	4.96	0.0253	0.87
Type	1	4446.46	4446.46	17.39	0.00
Population (type)	4	4414.95	1103.74	5.39	0.00
Light*type	1	4092.43	4092.43	20.9	0.00
Light*population(type)	4	1924.28	481.07	2.52	0.11
Bock*light*population(type)	10	1897.92	189.79	0.56	0.83
Error	62	20838.52	336.10		
Corrected Total	86	59185.61			

Covariate analysis of secondary branches length emerged during 1998 (cm)

Source	DF	Type III SS	MS	F	P
Model	24	41.77	1.74	1.67	0.0548
Branch length 1997	1	0.004	0.004	0.004	0.94
Bock	1	2.37	2.37	0.68	0.56
Light	1	8.55	8.55	2.59	0.35
Block*light	1	3.30	3.30	4.7	0.049
Type	1	0.614	0.614	0.75	0.39
Population (type)	4	13.40	3.35	4.92	0.016
Light*type	1	0.436	0.436	0.64	0.44
Light*population(type)	4	0.982	0.245	0.36	0.83
Bock*light*population(type)	10	6.70	0.670	0.64	0.77
Error	62	64.65	1.043		
Corrected Total	86	106.43			

APPENDIX J

Analysis of variance tables for the physiological characteristics of white spruce seedlings from the open and forest understory habitats, measured under field conditions at two sites.

Analysis of variance of dark respiration (Rs_D, μmol m^{-2} s^{-1})

Source	DF	SS	MS	F	P
Model	19	37.77	1.988	10.23	0.00
Light	1	7.48	7.48	38.50	0.00
Site	1	3.38	3.38	17.38	0.00
Plant	4	11.57	2.89	14.89	0.00
Light*site	1	0.363	0.363	1.87	0.17
Light*plant	4	3.157	0.789	4.06	0.00
Site*plant	4	4.92	1.23	6.33	0.00
Light*site*plant	4	6.91	1.73	8.89	0.00
Error	40	7.77	0.194		
Corrected Total	59	45.54			

Analysis of variance of quantum yield (Φ)

Source	DF	SS	MS	F	P
Model	19	0.029	0.0015	17.93	0.00
Light	1	0.00198	0.00198	23.7	0.00
Site	1	0.00069	0.00069	8.2	0.00
Plant	4	0.0109	0.00272	32.6	0.00
Light*site	1	0.00185	0.00185	22.0	0.00
Light*plant	4	0.0043	0.0011	12.7	0.00
Site*plant	4	0.0021	0.00052	6.2	0.00
Light*site*plant	4	0.0069	0.0017	20.2	0.00
Error	40	0.00335	0.0001		
Corrected Total	59	0.0319			

APPENDIX J
Continued

Analysis of variance of light compensation point (Γ μmol m^{-2} s^{-1})

Source	DF	SS	MS	F	P
Model	19	31478.9	1656.8	15.0	0.00
Light	1	3015.4	3015.4	27.3	0.00
Site	1	617.6	617.6	5.6	0.02
Plant	4	12112.7	3028.2	27.5	0.00
Light*site	1	8847.1	8847.1	80.2	0.00
Light*plant	4	1921.5	480.4	4.3	0.00
Site*plant	4	2830.8	707.7	6.42	0.00
Light*site*plant	4	2133.9	533.5	4.8	0.00
Error	40	4409.3	110.2		
Corrected Total	59	35888.3			