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REGENERATION AND ECOPHYSIOLOGY OF WHITE SPRUCE IN ASPEN-DOMINATED BOREAL MIXEDWOODS

BY

RONGZHOU MAN ©

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled REGENERATION AND ECOPHYSIOLOGY OF WHITE SPRUCE IN ASPEN-DOMINATED BOREAL MIXEDWOODS submitted by RONGZHOU MAN in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

The ecophysiology of white spruce (*Picea glauca* (Moench) Voss.) and the use of shelterwood silvicultural systems to regenerate white spruce were examined in aspen (*Populus tremuloides* Michx.)-dominated boreal mixedwoods in central Alberta. Photosynthetic responses to light and temperature in potted seedlings grown for two years in open sites and in the understory of aspen suggested that white spruce has a strong ability to acclimate to low light environment by increasing photochemical efficiency and decreasing light compensation and saturation points. Understory seedlings also had higher light-saturated net photosynthetic rate, transpiration, stomatal conductance and dark respiration than open-grown seedlings in spring and especially in autumn when night frosts were frequent. In saplings, photosynthesis commenced in early April despite frozen soil and night frosts and stopped abruptly in late October when minimum air temperature dropped to -10 ~-15 °C. Existence of an overstory canopy greatly reduce the fluctuation of net photosynthesis of understory saplings during periods of drought and high temperature in the summertime compared to saplings on open sites. In spring and fall, when overstory aspen is leafless, white spruce saplings are photosynthetically active and able to use the high light resources despite low soil temperature (in spring) and night frosts.

In regeneration trials, microclimates, seed germination and seedling establishment in the first two years after planting were compared under various levels of canopy residual: two shelterwood seeding cuts (low and high canopy residuals), one conventional clearcut and

one control (uncut). Each overstory treatment was subdivided into three site preparation treatments (blading, mixing and control). The partial canopy of the shelterwoods offered a more benign environment: increased light transmission and soil and air temperatures in comparison with the control, and less environmental extremes (higher humidity, cooler maximum, warmer minimum and reduced risk of night frosts) compared to the clearcut. Shelterwoods had earlier budflush, higher terminal leader survival, greater height growth, and better seed germination and recovery of photosynthesis than the clearcut and the control. Effects of site preparation were also apparent, especially in soil temperature and seed germination. Seedlings in shelterwoods can be expected to establish better than those in clearcuts and uncut stands.

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GENERAL INTRODUCTION

In the boreal mixedwood forests of western Canada, the major tree species are trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Monench) Voss.), but lodgepole pine (*Pinus contorta* Dougl.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.) and paper birch (*Betula papyrifera* Marsh.) are frequently found intermixed in these forests (Rowe 1972). These stands are usually even-aged and originate after fire. Rapid early growth and vigorous root suckering of aspen enable it to dominate the sites right after the disturbance and form a canopy over the spruce. In contrast to aspen, spruce is considered to be a moderately shade tolerant species; it can occur soon after disturbance or may slowly establish under the canopy of aspen over several decades (Nienstaedt and Zasada 1990). Being long-lived, white spruce becomes the dominant canopy tree in late successional stages when aspen dies out (Nienstaedt and Zasada 1990).

Foresters have a variety of ways to remove mature stands and create favorable environmental conditions for the new generation (Smith 1986). In boreal mixedwoods, the most popular sivilcultural practices are clearcut coupled with site preparation and planting. Shelterwood and other silvicultural systems, however, are also being considered (Lieffers *et al.* 1996).

1.1 Clearcut

Clearcuting removes the entire stand in one cut, creating a site fully exposed to light, with minimal protection of the site from climatic extremes (Smith 1986). Regeneration of white spruce by clearcuting has economic and management advantages. However, white spruce seedlings planted on clearcuts are frequently reported to have slow growth for several years after planting; this slow growth, commonly referred to planting check, has been suggested to be caused mainly by the extreme environmental conditions on clearcuts (Mullin 1963, Vyse 1981, Burdett *et al.* 1984). The following discusses some of the important environmental conditions on clearcut sites.

1.1.1 High radiation

Light intensity on the forest floor increases dramatically after clearcutting. There are reported positive responses of advanced regeneration to overstory removal (Ferguson and Adams 1980, McCanghey and Ferguson 1988). Increased growth and photosynthetic rate have also been documented in released white spruce (Berry 1982, Yang 1989, Lieffers *et al.* 1993, Navratil *et al.* 1994). This benefit could be probably gained only by understory trees that are well above the ground surface, approximately 1.0 m height depending upon height and density of ground vegetation (Oke 1987, Stathers 1989). Temperature and humidity below this height are typically more extreme because of greater energy input during the day and loss during the night (Oke 1987). For young natural or newly planted seedlings, strong light may lead to photoinhibition and photooxidation of photosynthetic systems, which could be exacerbated by high frequency and severity of night frosts near the ground surface (Powles 1984).

1.1.2 Temperature extremes and water stress

Removal of the overstory canopy increases input of solar radiation during the day and losses of longwave radiation at night (Spittlehouse and Childs 1992). Thus, clearcut sites typically have higher daytime temperature, lower night temperature, especially at positions near the ground surface (Oke 1987). High temperature may increase respiration and decrease rate of net photosynthesis (Sorensen and Ferrell 1973, Alexander *et al.* 1995). Increased daytime temperature also decreases relative humidity and increases vapor pressure deficit. This speeds up loss of water by transpiration and increases water stress. In many cases, water stress is one of the major reasons for the failure of spruce plantations (Grossnickle 1988, Burdett 1990). High temperatures near soil surface also increases soil evaporation, leaving the surface layer of soil dry which results in poor seed germination and seedling survival (Marquis 1979).

Low night temperatures increase the risk of frost, especially near the ground surface. High frequency and severity of night frosts (temperatures below 0°C) can cause damage to young seedlings by ice crystal formation within cells (Levitt 1980) and increase the risk of photoinhibition and photosynthetic destruction on sunny days following the frost (Lundmark and Hällgren 1987). In white spruce seedlings, severe frost can cause a 50% reduction in growth (Nienstaedt 1985) and late frost in spring may kill newly flushed shoots.

1.1.3 Vegetation competition

Competition from shrubs, hardwoods and herbs can be frequently be a problem in white spruce plantations (Lieffers *et al.* 1993). Aspen suckers and *Calamagrostis canadensis* (Michx.) Beauv. grow well on open sites and normally outgrow white spruce seedlings. Herbaceous vegetation may slow down the growth rates of planted seedlings in the first few years after planting but rarely causes significant mortality and failure of regeneration, while shrub and grass competition may cause mortality or elimination of planted seedlings (Eis 1981, Eis and Craigdallie 1983). Grass litter, compacted by snow, can crush conifer seedlings (Blackmore and Corns 1979) or act as an insulator, reducing spring soil temperatures (Hogg and Lieffers 1991). However, some light covering of plants may offer protection to young seedlings (Stiell 1976).

1.2 Shelterwood

Shelterwood systems remove the old stand in several cuts and provide protection for the regenerating even-aged seedlings. In recent years, there has been renewed interest in shelterwood methods (Kabzems and Lousier 1992, Waldron and Kolabinski 1994) because of increased environmental concern over clearcutting and the reported poor regeneration of white spruce on clearcuts (Navratil *et al.* 1991). A typical shelterwood harvest system include preparatory, seeding and removal cuts (Smith 1986), but a two-stage uniform shelterwood system combining the preparatory and seeding cuts is most commonly applied (Hannah 1988, Waldron and Kolabinski 1994).

1.2.1 Microclimates in shelterwoods

Existence of a partial overstory canopy in shelterwoods creates different microclimates from those on clearcut sites.

Light is generally limited in the understory and could be the factor limiting a development of understory white spruce. Comparatively, aspen-dominated mixedwoods transmit more light through their canopy than conifer-dominated stands. In the boreal forests of western Canada, light transmission in mid summer is less than 10% of incoming solar radiation in spruce-dominated stands and highly variable in aspen-dominated stands, from 14 to 40% of full sunlight depending on the successional stage (Lieffers and Stadt 1994). In aspen stands, the irradiance is above the compensation point but below the saturation point of white spruce (DeLong 1991, Greenway 1995). In aspen-dominated stands, understory white spruce may also be able to utilize high light resources in spring and fall when aspen is leafless (Ross *et al.* 1986, Constabel and Lieffers 1996), depending upon if white spruce is photosynthetically active during these periods. Reduction of the overstory canopy in shelterwoods increases light transmission in the understory.

Environmental conditions under the partial canopy of shelterwoods are less extreme compared to those on clearcuts (Holbo and Childs 1987). Thus, shelterwoods can ameliorate the harsh conditions created by clearcutting. Lower net radiation during the day and less loss of longwave radiation during the night result in lower daytime air temperatures and higher night temperatures compared to clearcuts (Valigura and Messina 1994), which will reduce daytime heating and nighttime freezing (Mahrt 1985). Lower daytime temperatures, in turn, reduce vapor pressure deficits which reduce transpiration rates in seedlings and improve seedling water relations (Childs and Flint 1987, Dalton and Messina 1995), even in the presence of competition from the overstory canopy for soil water (Dunlap and Helms 1983). Low light intensity reduces photoinhibition caused by high radiation and freezing temperatures (Lundmark and Hällgren 1987, Tucker *et al.* 1987, Dang *et al.* 1992).

During the early growing season, soil temperatures under a forest canopy are likely lower than those in the exposed mineral soil of clearcut sites (Childs *et al.* 1985, Brand and Janas 1988). Low soil temperatures in early spring may reduce water uptake and cause water stress. Several reports have shown the poor growth of newly-planted white spruce seedlings at low soil temperatures (Goldstein *et al.* 1985, Grossnickle and Blake 1985, Grossnickle 1988, Brand 1990).

1.2.2 Growth of white spruce under shelterwood canopies

Plants have the ability to maximize carbon accumulation by morphological and physiological adjustments in plant form and function. Under low light environments, plants tend to increase their ability to capture light by increasing their specific leaf area and carbon partitioning to the shoots relative to roots (Lewandowska and Jarvis 1977, Mitchell and Arnott 1995).Therefore, understory plants may have longer, wider, thinner and widely-spaced leaves than open-grown plants. Some plants also show a shift from diameter growth to height growth (Mitchell and Arnott 1995).

In general, plants under low light conditions have large photosynthetic apparatus and high concentration of light-harvesting pigments (Lewandowska and Jarvis 1977, Michell and Arnott 1995) but low amounts of electron carriers (Boardman *et al.* 1975). This results in high efficiency of light utilization at low light intensity, low light compensation and saturation points, and low photosynthetic capacities compared to the same species grown under high light conditions (Boardman 1977). However, in a study in northwestern Washington by Hodges and Scott (1968), four shade-tolerant species in a partially-shaded edge of a 40-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand had greater average daily net photosynthetic production than the same species in an adjacent open area, while two relatively shade-intolerant species showed greater net photosynthesis in the open areas. Higher photosynthesis of trees grown in low light conditions than in high light conditions has been also reported in many other shade-tolerant species (Jarvis 1964, Logan and Krotkov 1969, Keller and Tregunna 1976, Leverenz and Jarvis 1980).

White spruce is a shade-tolerant species; its photosynthetic system can reach the compensation point at 100 μmol m^{-2} s^{-1} or less and saturation point around 600 μmol m^{-2} s^{-1}(DeLong 1991, Greenway 1995). In the juvenile stage, white spruce is able to reach maximum height growth in less than 50% of full light (Logan 1969, Stiell 1976, Lieffers and Stadt 1994) but foliage production and diameter growth may be reduced.

Observations on white spruce saplings (1.5 to 3.0 m tall) showed an increased light-saturated net photosynthetic rate after release from an overstory canopy (Lieffers *et al.* 1993, Greenway 1995). These saplings were well above the zone near ground surface with extreme environmental conditions (Oke 1987, Stathers 1989). It is not clear how white spruce seedlings within the stressful zone respond photosynthetically to high light conditions in clearcuts.

1.2.3 Residual density of overstory canopies

Environmental conditions under shelterwood canopies are controlled mainly by the residual density of the overstory canopy. Reduction of the residual canopy increases light transmission, which may increase seedling growth as well as environmental extremes and growth of competing vegetation. In shelterwood management, the residual density of the overstory canopy is controlled to maintain the growth of understory crop trees and to minimize environmental extremes and growth of shade-intolerant competitors, such as *Calamagrostis canadensis* and *Epilobium angustifolium* L. (Lieffers and Stadt 1994). The basal area of residual shelterwood, depending upon shade-tolerance of the desired understory trees, the crown density of the overstory canopy, environmental conditions and management objectives, can be from a few m^2 to over 30 m^2/ha (Hannah 1988, DeLong 1991). For example, a 50-60% crown cover or 10 to 20 m^2 basal area of residual canopy is probably necessary for frost protection (Stathers 1989) and a total basal area of 10 to 15 m^2/ha (of which a minimum of 4 to 6 m^2/ha mature white spruce) should be left after the first cut of a two stage shelterwood system in boreal mixedwoods to obtain satisfactory natural regeneration of white spruce (Waldron 1966, Waldron and Kolabinski 1994).

1.3 Site preparation

Prescribed burning and chemical and mechanical site preparation are three approaches to modify microclimates and reduce competition for seed germination and establishment of planted seedlings (Örlander *et al.* 1990, Spittlehouse and Childs 1992). In boreal mixedwoods, different mechanical site preparations, such as trenching, blading, ploughing, mixing and mounding, are commonly used (Lieffers and Beck 1994). Positive treatment effects of mechanical site preparation include improvements of temperature, density, moisture, and gas exchange in the soil, and relative humidity and air temperature near ground surface (Stathers 1989, Örlander *et al.* 1990). Improvements may also be seen both in nutrient availability in the soil (Munson *et al.* 1993) and nutrient status of plants (Macdonald *et al.* 1996), especially in a short period after site preparation treatment. Removal of nutrient reserves in forest humus by blading, however, could decrease nutrient status of planted seedlings in the long run (Munson *et al.* 1993, Macdonald *et al.* 1996).

1.4 Production of new stands

Regeneration of white spruce on clearcut sites or under partial forest canopies can be obtained by planting, protecting advanced regeneration and natural or artificial seeding.

1.4.1 Planting

Restoration of white spruce after harvesting can be obtained by planting with either container or bareroot seedlings. Time for planting depends upon the type of seedling stock used. Spring stock, which will flush shortly after planting, can be planted up to the summer solstice, whereas summer stock, which will not flush until the next spring, can be planted from June 21 to Aug. 15 (Scagel 1993). Whatever seedling type or planting time is used, newly planted seedlings are susceptible to environmental extremes, particularly water stress due to the lack of intimate root-soil contact (Rietveld 1989). Recovery of normal seedling water status depends largely on the growth of new roots (Grossnickle and Blake 1987). As carbohydrates for root growth come from both carbohydrate reserves and current photosynthesis in white spruce (Van Den Driessche 1987), improvement in photosynthesis of seedlings right after planting may increase survival and growth of planted seedlings, especially in seedlings that have undergone a prolonged cold-storage and have partially depleted carbohydrate reserves.

1.4.2 Protection of advanced regeneration

In aspen-dominated boreal mixedwoods, white spruce frequently recruits under the developing aspen canopy (Lieffers *et al.* 1996). Protection of the existing understory white spruce, while harvesting the mature overstory may reduce reforestation costs and shorten the rotation length (Brace and Bella 1988). In general, understory white spruce responds positively to removal of the hardwood overstory, but a short period of shock may occur if understory white spruce is suddenly exposed to high irradiance (Greenway 1995).

1.4.3 Seeding

New stands can also be produced by natural or artificial seeding provided there are enough suitable seedbeds. White spruce can germinate on a wide variety of seedbed types and exposures (Jarvis *et al.* 1966). But the most favorable seedbeds are mineral soil, mixed soil and humus, and decayed wood (Jarvis *et al.* 1966, Waldron 1966, Eis 1967, Horton and Wang 1969, Bell 1991, DeLong 1995). In undisturbed stands of boreal mixedwood forests, naturally exposed mineral soil is very rare and regeneration of white spruce is usually inadequate without the aid of site preparation (Lees 1962, 1963, 1970, Kabzems 1971). Mechanical site preparation treatment is routinely applied to increase seedbed receptivity.

Field germination is usually affected by temperature. The optimum temperature for germination of white spruce is around 20 °C (Stiell 1976, Bell 1991). Temperatures above 35 °C may slow the rate of germination (Fraser 1971, Coyea 1988). Light may promote germination of white spruce, particularly at low temperatures (Patten 1963), but germination is usually best in the shade under field conditions (Tear 1979, Putman and Zasada 1986, Bell 1991).

Newly germinated white spruce seedlings are very susceptible to environmental stresses and survival declines rapidly in the first few years after germination (Tear 1979, Tear *et al.* 1982). Water stress and unsuitable seedbeds are believed to be the major cause of seedling mortality in white spruce (Sutton 1969, Tear *et al.* 1982). Also high temperature may cause damage to young seedlings by overheating, desiccation or both (Örlander *et al.* 1990) and night frosts can kill newly flushed, succulent shoots.

Smothering and crushing from deciduous leaf litter, primarily from trembling aspen and paper birch have adverse effects on white spruce seedling survival and it take several years for seedlings to be large enough to avoid being smothered or crushed by fallen leaves (Gregory 1966, Dominy and Wood 1986).

1.5 Overview of studies

The general purpose of this thesis was to further the understanding of the growth of understory white spruce and examine use of a two stage shelterwood silvicultural system combined with site preparation to regenerate white spruce. The specific objectives were to determine: (1) the differences of photosynthetic parameters in white spruce seedlings grown under an aspen canopy and on open site and if these differences change with season (Chapter 2); (2) seasonal variation of photosynthetic capacity in white spruce saplings, particularly in spring and fall when overstory aspen is leafless (Chapter 3); and (3) effects of residual canopy and site preparation in a shelterwood seeding cut on microclimates (Chapter 4), seed germination and seedling growth under different levels of residual canopies and ways of site preparation (Chapter 5), and recovery of photosynthesis in planted white spruce under different canopy residuals and site preparations (Chapter 6). As white spruce is considered to be a shade-tolerant species, I expected that it has the abilities to acclimate photosynthetically to the low light environments and adapt to the seasonality of light under aspen-dominated overstory canopies. I also expected reduced extremes of environmental conditions under shelterwood canopies in comparison with clearcuts, which would lead to better establishment of white spruce seedlings.

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CHAPTER 2

SEASONAL PHOTOSYNTHETIC RESPONSES TO LIGHT AND TEMPERATURE IN WHITE SPRUCE (*PICEA GLAUCA*) SEEDLINGS PLANTED UNDER AN ASPEN (*POPULUS TREMULOIDES*) CANOPY AND IN OPEN CONDITIONS.

2.1 Introduction

An overstory of deciduous trees with an understory of shade-tolerant conifers is a common forest structure in young temperate and boreal forest stands. The understory has a very different environment than open sites and there is wide seasonal variation. During the period when the deciduous trees have leaves the conifers are in a low light environment. Understories also have higher relative humidities, lower midday temperatures and lower frequency of night frosts than open environments (Childs and Flint 1987). Because of the shade cast by boles and canopies, understories are also protected from high radiation on the days following frosts; high radiation is known to exacerbate the effects of frost on the photosynthetic system (Strand and Öquist 1985, Lundmark and Hällgren 1987, Örlander 1993).

Aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench.) Voss.) mixedwoods are a widespread forest association in North America. In these forests the periods of leaf-off in the spring and autumn provide high light in the understory compared to the summer (Constabel and Lieffers 1996). The periods of overstory leaf-off have been shown to be important in the annual carbon accumulation of Douglas-fir understory saplings in the red alder forests of the Pacific Northwest (Emmingham and Waring 1977). Little is known about the seasonality of photosynthesis of white spruce in boreal forests, especially in the spring and autumn when soils are cold and night frosts are common. There is little understanding about photosynthetic efficiencies during these periods relative to the summer. In addition, it is not clear if spruce seedlings sheltered by an overstory have different photosynthetic parameters than those grown in open conditions. Although some work has been done on morphological and physiological differences between sun- and shade-grown conifers, the interest was either comparison among different shading

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treatments (Higginbotham and Tear 1978, Leverenz and Jarvis 1980, Mitchell and Arnott 1995) or examination of the acclimation of seedlings or trees upon release from shaded conditions (Tucker and Emmingham 1977, Tucker *et al.* 1987, Lieffers *et al.* 1993). There is little information on the differences of shade-tolerant coniferous seedlings between open sites and in the understory, particularly in white spruce.

In general, plants in low light conditions tend to have large leaf surfaces (by increasing specific leaf area and allocating more carbon to shoots) for absorption of light, high water use and photosynthetic efficiencies, low respiration, low compensation and saturation points, and low light saturated photosynthetic rate (Boardman 1977). However, many shade-tolerant trees show higher light-saturated photosynthetic rates when grown under low light intensities than under high light intensities (Jarvis 1964, Hodges and Scott 1968, Logan and Krotkov 1969, Keller and Tregunna 1976, Leverenz and Jarvis 1980, Mitchell and Arnott 1995), probably by physiological adjustment in foliage (Mitchell and Arnott 1995). Observations on white spruce saplings showed a higher light-saturated photosynthetic rate on open sites than in the understory by the difference before and after the removal of overstory canopy (Lieffers *et al.* 1993, Greenway 1995).

The objectives of this study were to: (1) determine the variations in gas exchange and photosynthetic responses to light and temperature in white spruce seedlings in spring before aspen had leaves, in summer, and after aspen leaf fall in autumn; (2) compare gas exchange and photosynthetic parameters of white spruce seedlings from open and understory sites; and (3) determine how the differences change with season. I expected different gas exchange and photosynthetic parameters between understory and open-grown seedlings due to different growing conditions.

2.2 Materials and methods

2.2.1 Study area and experimental seedlings

The field study site was located 25 km southwest of Edmonton, Alberta, Canada (53°22'N; 113°45'W). Two sites were selected: a pure aspen stand with averages of 12 m height and 15 cm dbh; and a cleared site, 150 m away from the aspen stand. Annual precipitation from a nearby weather station is 468.2 mm (30 years average from 1961 to 1990), over 50% of which is received from June through August. The soil texture of both open and understory sites was fine sand. In open site, the major shrub species, *Rosa acicularis* L., was about 1 m high and sparsely scattered on the sites. Dominant grasses were *Bromus inermis ssp. pumpelliamus* and *Agropyron trachycaulum* (Link) Malte. Under the aspen canopy, the shrub layer was dominated by *Almus crispa* (Ait.) Pursh, *Amelanchier alnifolia* Nutt., *Rosa acicularis* L., and *Corylus cornuta* Marsh. The major herbaceous species in the understory were *Aralia nudicaulis* L. and *Epilobium angustifolium* L.

White spruce seedlings were grown in 60 ml styroblock containers in greenhouse for one growing season and were overwintered outside. Fifty seedlings were transplanted to 20 cm, 4L unglazed clay pots (1 seedling/pot in a 3:1 mixture of loam soil and peat moss by volume ratio) in mid-May, 1994 and grown outside for two weeks before being transported to the field sites. Seedlings were randomly divided into two groups of 25 seedlings, and the 25 seedlings and pots were buried to the soil level in each site. Seedlings were grown during 1994, overwintered on the sites and periodically examined during their growth. All seedlings were watered during periods of drought and fertilized with a balanced fertilizer (20:20:20) three times a year to ensure good nutrient supply.

2.2.2 Records of environmental conditions

Air temperature at seedling height (30 cm above the ground) and soil temperature at 10 cm depth were measured in both open and understory sites with a 101 thermistor (Campbell Scientific Co., Ltd., Logan, UT). Sensors for air temperature were shielded from direct radiation. Maximum, minimum and average temperatures were recorded on a daily basis by a CR21 datalogger (Campbell Scientific Co., Ltd., Logan, UT). Photosynthetic photon flux density (PPFD) under the aspen canopy was measured on sunny days between 1000 and 1400 h solar time at 1.3 m above ground with a hand-held integrating radiometer (Sunfleck Ceptometer, model SF-80, Decagon Services, Inc., Pullman, WA). At each sampling date, twenty locations were randomly chosen in the stand. At each location, the observer rotated taking 12 readings at 30° intervals. These were averaged for each sampling location. Above canopy light was estimated beside the stand in the open before and after understory measurement.

2.2.3 Measurement of photosynthetic responses

During the growing season of 1995, photosynthetic responses to light and temperature were determined on the potted seedlings from the open site and aspen understory in three seasons: April 25 to May 3, August 3 to August 11 and September 25 to September 30. In each period, six seedlings were randomly chosen from each site and transported to the laboratory. To minimize the effects of water stress, all targeted seedlings were fully watered both one week and one day before the determinations of photosynthetic responses.

Lateral branches of the youngest available foliage were selected for analysis of gas exchange; for the spring measurement, this meant that foliage from the previous season was used. Photosynthetic light response curves were measured at four leaf temperatures (5, 15, 25, 35 °C). For the spring observations, pots were placed in a growth chamber at 5 °C for a day before measurements. The clay pots were then placed in an insulated container to maintain this soil temperature during measurement. Soil temperature was maintained at 20 °C for the summer and autumn measurements by keeping seedlings in the laboratory for a day before measurement and putting them in the insulated container during measurement. Leaf temperature was measured with a fine copper-constantan thermocouple (Omega Engineering, Stamford, CN) placed on the bottom side of the foliage. The thermocouple was connected to a datalogger (CR21X, Campbell Scientific Co., Ltd, Logan, UT). The insulated pots, the seedlings and the cuvette were all placed inside an insulated chamber where cooled or warmed air (as needed) was blown over the cuvette to maintain the appropriate leaf temperature.

Gas exchange was measured with an open system, portable infrared gas analyzer (LCA-2), conifer cuvette and air supply unit (Analytical Development Corp., Hoddenson, England). Light was calibrated with a Li - Cor quantum sensor (Li - 190 SB, Li- Cor, Ltd., Lincoln, NE) placed inside the leaf cuvette. The light source was a 500 watt quartz halogen lamp (T-3, the Edge, Bellevue, WA). A clear acrylic water bath was placed between the lamp and the cuvette. Different light intensities were achieved by the use of neutral density filters and by adjusting the distance between the lamp and the cuvette. Air was drawn from a uniform supply of ambient air. Silica gel desiccant was used to decrease water content at low temperatures and ferrous sulfate ($FeSO_4.7H_2O$) to enhance water content at high temperatures in order to obtain relatively constant vapor pressure deficit across the four leaf temperatures. For each seedling, photosynthetic light response was measured at leaf temperatures of 5, 15, 25, 35 °C in spring and 25, 15, 5, 35 °C in summer and autumn. At each temperature, gas exchange was measured at eight PPFD's (0, 50, 100, 200, 400, 600, 800, 1100 μmol m^{-2} s^{-1}) from low to high, after a 20-minute period for dark acclimation. In a preliminary experiment, similar readings were obtained when the orders of temperatures and PPFD's were reversed. Gas exchange rates were recorded when readings were stable at each irradiance. Following gas exchange analyses, needles were removed from the sampled shoot, dried for 48 h at 70 - 80 °C and weighed.

Net photosynthetic rate (NA; μg $g^{-1}s^{-1}$), stomatal conductance to H_2O (g_s; mmol $g^{-1}s^{-1}$), transpiration rate (E; mg $g^{-1}s^{-1}$) and intercellular CO_2 concentration (C_i) were calculated as described by Caemmerer and Farquhar (1981). Mesophyll conductance to CO_2 (g_m; mmol $g^{-1}s^{-1}$) was determined as g_m=A/C_i (Jones 1985). Instantaneous water use efficiency of photosynthesis (WUE; μmol CO_2 $mmol^{-1}$ H_2O) was calculated as WUE=A/E.

The nonlinear monomolecular model described by Causton and Dale (1990) was fitted to the data using PROC NLIN in SAS. The fitting was done on data from individual seedling and seedling groups pooled for each combination of seedling type, season and leaf temperature. Derived parameters of light saturated rate of net photosynthesis (A_{max}; μg $g^{-1}s^{-1}$), light compensation point (LCP; μmol photons m^{-2} s^{-1}), dark respiration rate (R_d; μg $g^{-1}s^{-1}$) and photochemical efficiency (PE; μg CO_2 g^{-1}/μmol photons m^{-2}) were determined from the light response curves of individual seedlings as in Causton and Dale (1990). Light saturation point (Q_{sat}; μmol photons m^{-2} s^{-1}) for an individual seedling was calculated from the fitted light response curve when NA reached 95% of A_{max}.

2.2.4 Seedling morphology

Bud flush, needle color and frost damage were checked periodically for both open-grown and understory seedlings in the field. In early November, 1995, six seedlings from the open site and understory were moved into the greenhouse. After new needles fully expanded in early March of 1996, height increment and needle length were measured on each leader cohort of each year, from 1993 to 1996. Projected leaf area was determined by scanning leaves with DeskScan II image scanning software on a ScanJet 3c scanner (Hewlett Packard, Palo Alto, CA). Needle areas were calculated from the captured image using SigmaScan, window 2.0 (Jandel Scientific, San Rafael, CA). Specific leaf area was calculated as the ratio between leaf area and leaf dry weight (48 h at 70-80 °C).

2.3 Results

2.3.1 Seedling environments

Minimum air temperatures on the open site were generally below 0°C before June and after mid-September and maximum air temperatures frequently exceeded 30 °C from mid-May to mid-September (Figure 2.1-a). Minimum air temperatures were higher and maximum temperatures lower in understory than in open site (Figure 2.1-b). Irradiance was low in the aspen understory, but there was periods of high light in early spring and late fall when the overstory aspen was leafless (Figure 2.2).

2.3.2 Light response parameters

Photosynthetic response curves were generally steeper and higher in understory than in open-grown seedlings, especially in spring and fall (Figure 2.3).

The light-saturated rate of net photosynthesis (A_{max}) was highest at 15 °C in spring and 25 °C in summer in both open and understory seedlings (Figures 2.3 and 2.4). In the autumn, however, the optimum leaf temperature for A_{max} differed slightly between two seedling types, 15 °C in understory seedlings and 25 °C in open-grown seedlings. The shift of optimum temperature in A_{max} appears to coincide with the change of ambient air temperature (Figure 2.1-a). Light compensation point (LCP), light saturation point (Q_{sat}), and dark respiration (R_d) generally increased with temperature for all three seasons (Figure 2.4). The LCP and R_d both increased rapidly with temperature in the spring but remained relatively constant until 35 °C in the summer and autumn. In contrast, photochemical efficiency (PE) was relatively constant with temperature in all three seasons.

The A_{max} and PE increased from spring to summer and decreased thereafter especially in open-grown seedlings, whereas LCP, R_d and Q_{sat} were highest in spring (Figure 2.4).

Understory seedlings generally had higher PE and lower LCP and Q_{sat} than open-grown seedlings for all temperatures and seasons (Figure 2.4). The A_{max} was generally higher in understory than in open-grown seedlings at all leaf temperatures and seasons. These differences, however, were significant only in spring and autumn. The R_d was slightly higher in open-grown than in understory seedlings in summer, but the pattern was reversed at most leaf temperatures in spring and autumn.

2.3.3 Gas exchange at saturating light

Water use efficiency (WUE) and stomatal conductance to water vapor (g_s) generally decreased with increasing leaf temperature in the summer and autumn, but g_s was insensitive to temperature in the spring (Figure 2.5), whereas transpiration (E) steadily increased with leaf temperature in all seasons. Change in mesophyll conductance (g_m) with leaf temperature followed the same trends as A_{max}. In all three seasons, g_m had a maximal value at leaf temperatures from 15 to 25 °C.

Seasonally, E, g_s and g_m were highest in summer and depressions of these parameters were obvious in spring and autumn, especially in open-grown seedlings (Figure 2.5). The WUE was nearly constant across the three seasons, except for higher WUE at 5 °C in spring.

Understory seedlings had higher WUE and g_m than open-grown seedlings. As in A_{max}, the difference in g_m was small in summer and large in spring and autumn, whereas the difference in WUE was relatively constant across seasons. The E and g_s were similar in the two types of seedlings in spring and summer, but significantly higher in the understory than in open-grown seedlings at many temperatures in the autumn.

2.3.4 Seedling morphology

There were no significant differences in height growth and needle length between open-grown and understory seedlings for the leader and foliage which initiated in the greenhouse but flushed in the field (1994 column, Table 2.1). Seedlings began to differentiate in the second year (1995) after buds that had formed in the field flushed, with more height increments and longer needles in understory seedlings. Specific leaf area of these needles showed a similar trend: understory seedlings were generally higher than open-grown seedlings and the difference was highest in the second year (1995) for the needles that formed and grew in the field. Buds flushed first in understory seedlings, followed one week later by open-grown seedlings both in the field and in the greenhouse after seedlings were brought in from the field. In late May 1995, about 50% of newly flushed terminal buds in open-grown seedlings were killed by late frosts (see Figure 2.1-a). In the spring of 1995, seedlings were chlorotic on the open site and green in the understory site. The differences in needle length, color, and shoot growth between open and understory seedlings decreased after seedlings were returned into the greenhouse (1996).

2.4 Discussion

Depression of photosynthesis in spring and autumn was greater in open-grown than understory seedlings. The reasons for this are not clear but may relate to the greater frequency of night frost and higher intensity of solar radiation in the open site compared to the understory (Figures 2.1 and 2.2). Cold nights are often followed by clear days with high irradiance. Light or even heavy frosts frequently occurred before the measurements for the light response curves were done in spring and autumn (Figure 2.1-a). Freezing air temperatures inhibit the light-saturated rate of photosynthesis and increase the susceptibility of photosynthetic systems to photoinhibition (Lundmark and Hällgren 1987, Lundmark *et al.* 1988). Understory seedlings would be less affected by the night frosts because of relatively higher minimum temperature during the night under the canopy (Figure 2.1-b) and shading by the aspen canopy in the following day (Lundmark and Hällgren 1987, Örlander 1993). The pronounced effects of freezing temperature on open-grown seedlings by photoinhibition and subsequent photooxidation was likely responsible for the discoloration of open-grown seedlings compared to the dark green color of understory seedlings as Lundmark and Hällgren (1987) observed in *Pinus sylvestris* L. and *Picea abies* L.

In summer, A_{max} was still higher in understory than open seedlings; however, the difference was not significant at any leaf temperature. This contrasts with the observation on white spruce saplings in which A_{max} increases with increasing irradiance (Lieffers *et al.* 1993). Relatively high A_{max} in understory seedlings could be a result of acclimation of white spruce seedlings to understory environments, less environmental stresses in the understory, or both. Studies of photosynthetic light acclimation in tree seedlings reveal different photosynthetic responses to light conditions between shade intolerant and tolerant species; in shade intolerant trees, A_{max} is higher in sun-grown than shade-grown seedlings, whereas responses of shade-tolerant trees are variable (Kramer and Kozlowski 1979). As a strategy to maintain growth in low light environments, higher rates of A_{max} by low-light phenotypes than by high-light phenotypes have been found in many shade-tolerant tree species (Jarvis 1964, Hodges and Scott 1968, Logan and Krotkov 1969, Keller and Tregunna 1976, Leverenz and Jarvis 1980). Microclimates on open sites are more extreme: low night temperature, high daytime temperature and low relative humidity, especially at seedling height. White spruce seedlings are sensitive to environmental stresses; their A_{max} decrease when grown in low relative humidity even for well-watered seedlings (Marsden *et al.* 1996).

White spruce exhibited photosynthetic acclimation to understory low light environments as noted by the lower light compensation and saturation points (LCP and Q_{sat}) and higher photochemical efficiency (PE) in understory seedlings than open-grown seedlings. The light compensation point of understory seedlings obtained in this study was lower than that of understory white spruce saplings (Greenway 1995), indicating a stronger ability of white spruce seedlings for net assimilation at low light conditions.

The need for higher temperature to achieve maximum photosynthesis in the summer, compared to spring and autumn, was similar to the trend found in *Picea sitchensis* Carr. (Neilson *et al.* 1972) and *Pinus taeda* L. (Strain *et al.* 1976). The reduction of net photosynthesis above the optimum temperature appeared to be caused by a rapid increase in dark respiration rate (Figure 2.4), as reported in *Pseudotsuga menziesii* (Mirb.) Franco by Sorensen and Ferrell (1973) and in *Picea rubens* Sarg. by Alexander *et al.* (1995). Decreased stomatal conductance appeared to play a minor role. In spring, respiration rates appeared to be higher than in summer and autumn, probably because of: (1) repair to chloroplast, chlorophyll, enzyme and electron transport systems that had been altered or damaged during the winter (Martin *et al.* 1978, Öquist *et al.* 1978, Gezelius and Hallén 1980, Öquist *et al.* 1980) and recovery of these components in spring is an energy-demanding process; (2) high bud respiration during budbreak in spring (Bachelard and Wightman 1973, Bhella and Roberts 1975). High respiration and low net photosynthesis resulted in LCP being much higher in spring than in summer and autumn.

The growth of seedlings in pots brings up two important discussion points. The restricted rooting of seedlings in pots has been shown to reduce NA by reducing sink strength at the root (Arp 1991). I discount the possible relationship of pot effects with lower NA in open-grown seedlings because both open-grown and understory seedlings were grown in the same size pots and the higher NA was observed on larger understory seedlings. Secondly, the pots may result in some water stress in open-grown seedlings. Seasonally, seedlings on the open site were expected to experience more water stress in summer, but larger differences of NA between open-grown and understory seedlings were seen in spring and fall. This suggested that water stress due to the pots was not important.

The results of this study have several ecological implications. (1) There is sufficient light under aspen canopy for photosynthesis of white spruce seedlings. In all seasons, except spring, light intensity under the aspen canopy was generally below the saturation point for the spruce but much higher than the compensation point (Figure 2.2). (2) With relatively high photosynthetic rates, understory seedlings can take advantage of high light periods in spring and autumn when overstory aspen is leafless despite lower photosynthetic rates at high temperatures. The periods when aspen trees are leafless are probably important in the annual carbon budget for the understory spruce. (3) The low LCP and high PE of white spruce seedlings in summer suggests acclimation to the normal conditions of low light during aspen and shrub leaf-on. (4) Understory seedlings can maintain healthy growth by morphological and physiological acclimation to understory environments, whereas open sites appear to be less suitable for establishment of white spruce seedlings. Besides discoloration and poor photosynthetic activity in spring and autumn, open-grown seedlings also showed short needles and restricted shoot growth. These characteristics are typical of white spruce 'planting check' and may last several years in the field (Mullin 1963, Burdett *et al.* 1984).

2.5 Literature cited

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Table 2.1. Foliage and leader characteristics of white spruce seedlings from understory and open sites: 1993 - first year in greenhouse; 1994 - buds formed in greenhouse and foliage flushed outside and expanded in the field; 1995 - buds formed and foliage flushed and expanded in the field; 1996 - buds formed in the field and foliage flushed and expanded in the greenhouse. Means and SE (in brackets) of six seedlings and probability of two-tailed Student's *t*-test are presented.

Growth	Seedlings	1993	1994	1995	1996
Height increment (cm)	Understory	6.67 (1.06)	5.58 (0.75)	10 (1.36)	14.8 (3.71)
	Open	6.33 (0.76)	7.07 (0.47)	5.17 (0.85)	10.63 (1.50)
	P	0.7996	0.1232	0.0131	0.3223
Needle length (cm)	Understory	1.59 (0.13)	1.52 (0.16)	1.55 (0.18)	1.98 (0.15)
	Open	1.50 (0.07)	1.64 (0.10)	0.67 (0.03)	1.51 (0.12)
	P	0.5557	0.5391	0.0007	0.0345
Specific leaf area (cm^2g^{-1})	Understory		73.70 (5.20)	76.50 (3.30)	75.22 (4.62)
	Open		65.26 (1.08)	55.50 (1.37)	66.85 (2.02)
	P		0.1431	0.0001	0.1279

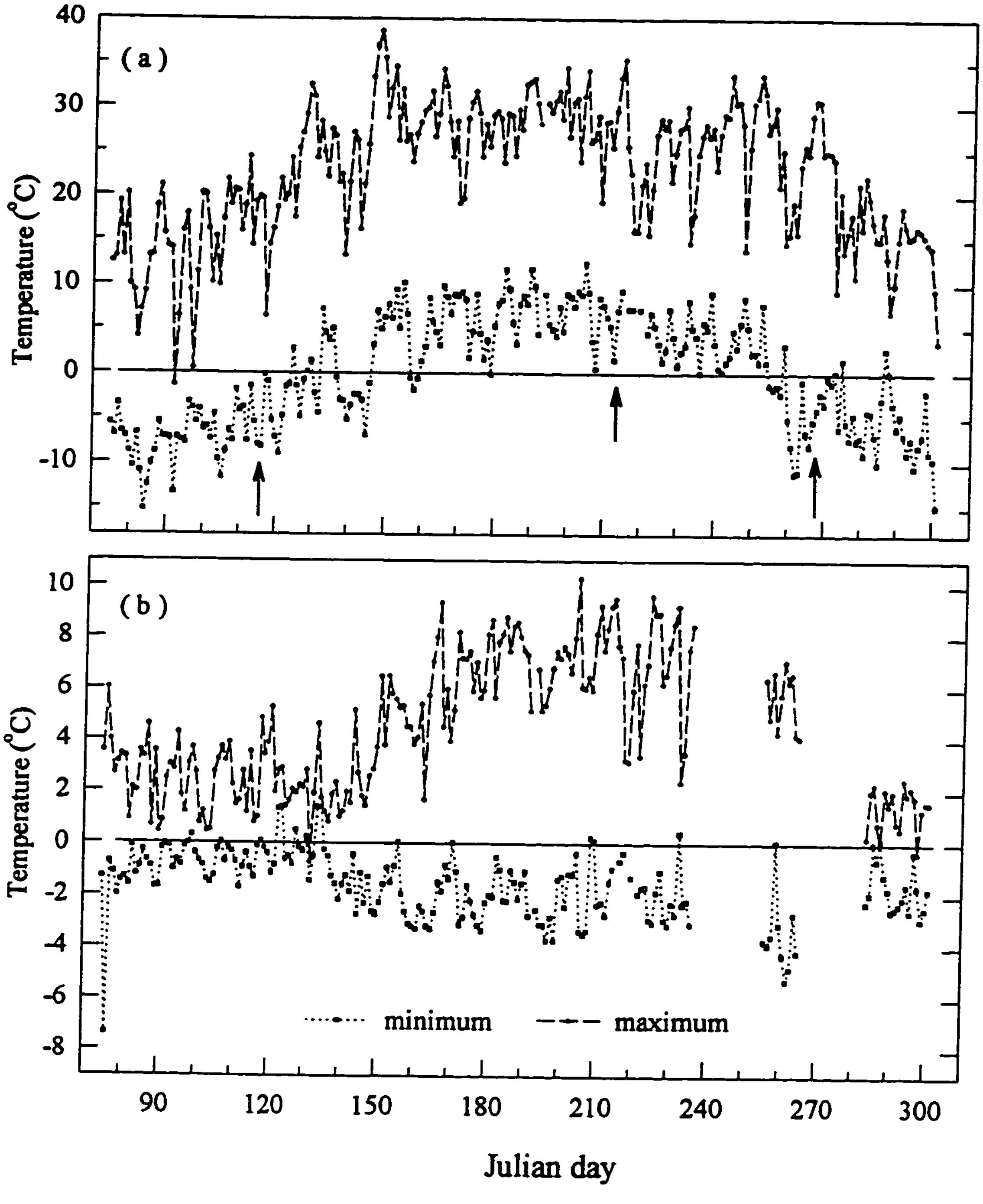

Figure 2.1 Daily maximum and minimum temperatures, at 30 cm above the ground during the growing season of 1995. (a) absolute temperature at the open site; (b) difference in temperature between the two sites (understory=0). The arrows point to the starting date of measurements in photosynthetic response.

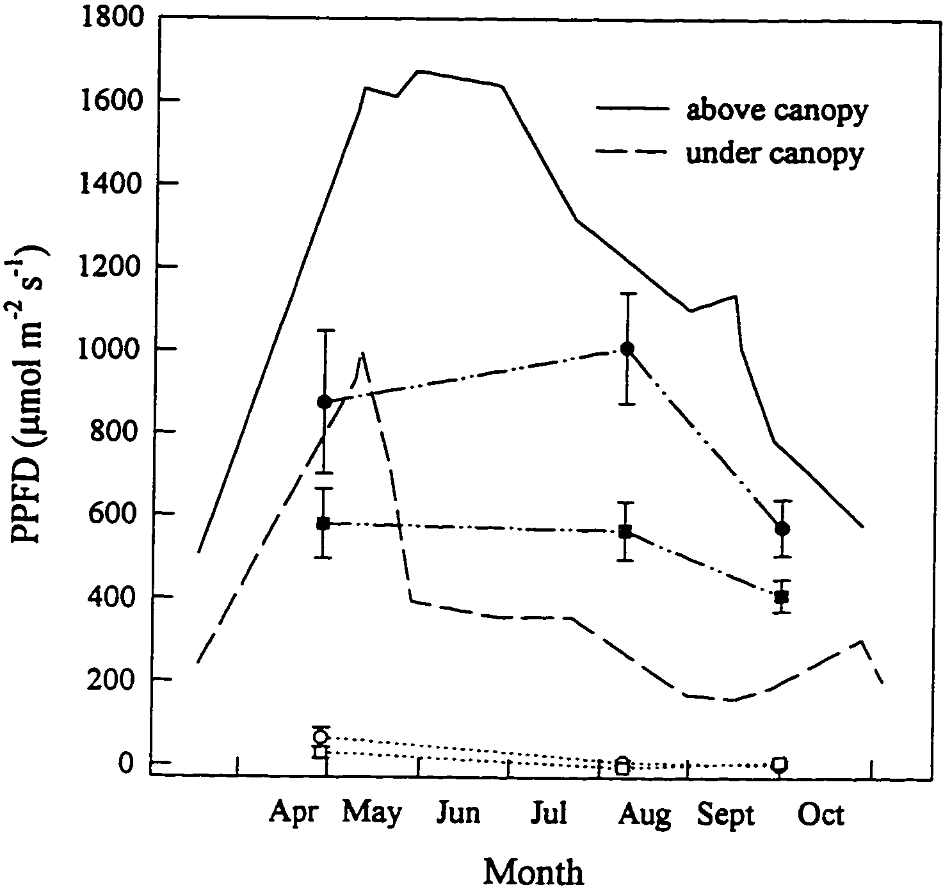

Figure 2.2 Seasonal variations of mean stand photosynthetic photon flux density (PPFD) at mid-day above and under the canopy of aspen stand on clear days, and mean light compensation point (open symbols) and light saturation point (filled symbols) for open-grown (circles) and understory (squares) white spruce seedlings at optimum temperatures for A_{max} (25 °C in summer and 15 °C in spring and fall). Bars=±SE, n=6.

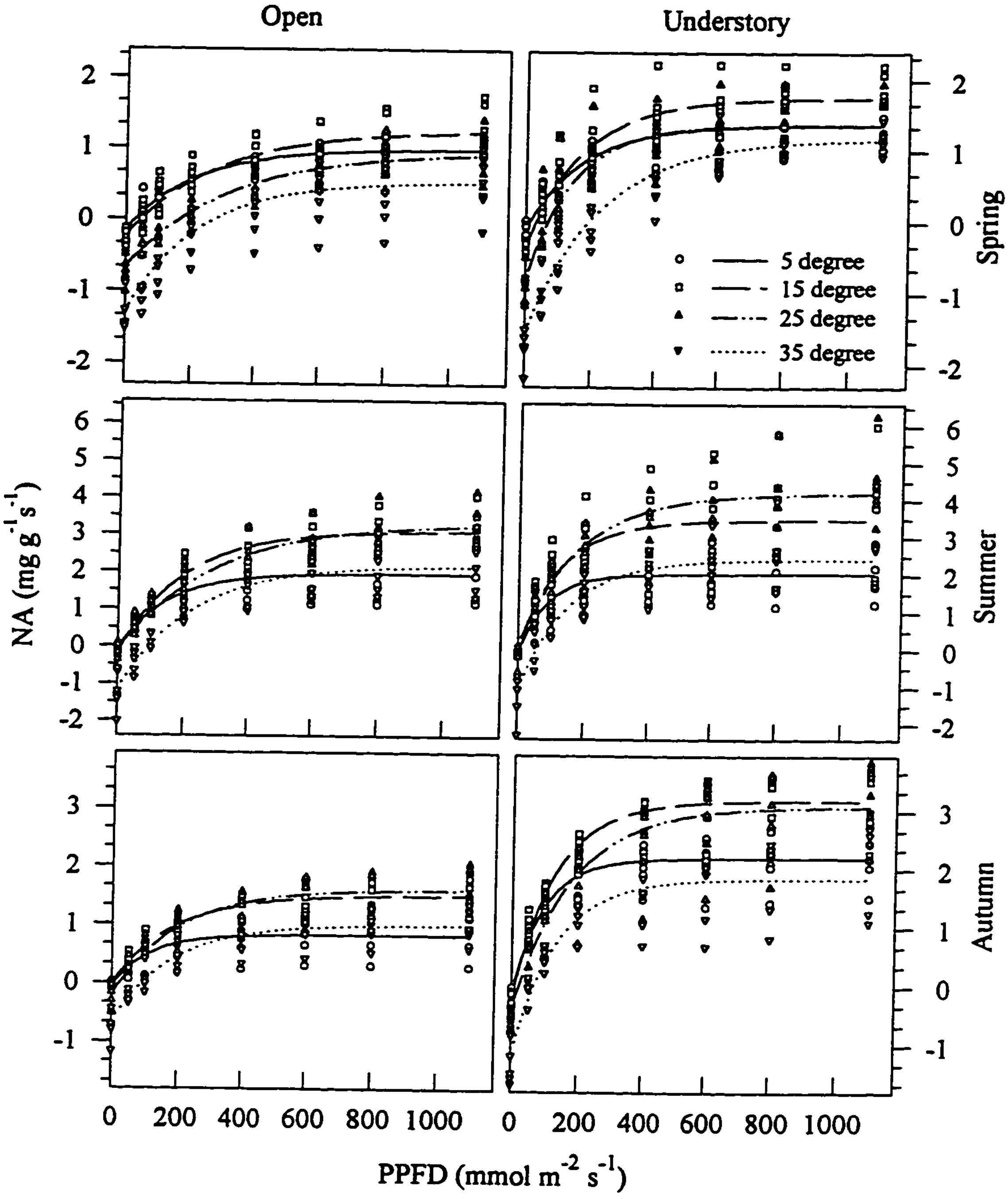

Figure 2.3 Light response (net photosynthetic rate - NA vs photosynthetic photon flux density - PPFD) of photosynthesis of open and understory white spruce seedlings at four leaf temperatures and in three seasons. Curves are fitted on the seedlings pooled for each combination of seedling type, temperature and season.

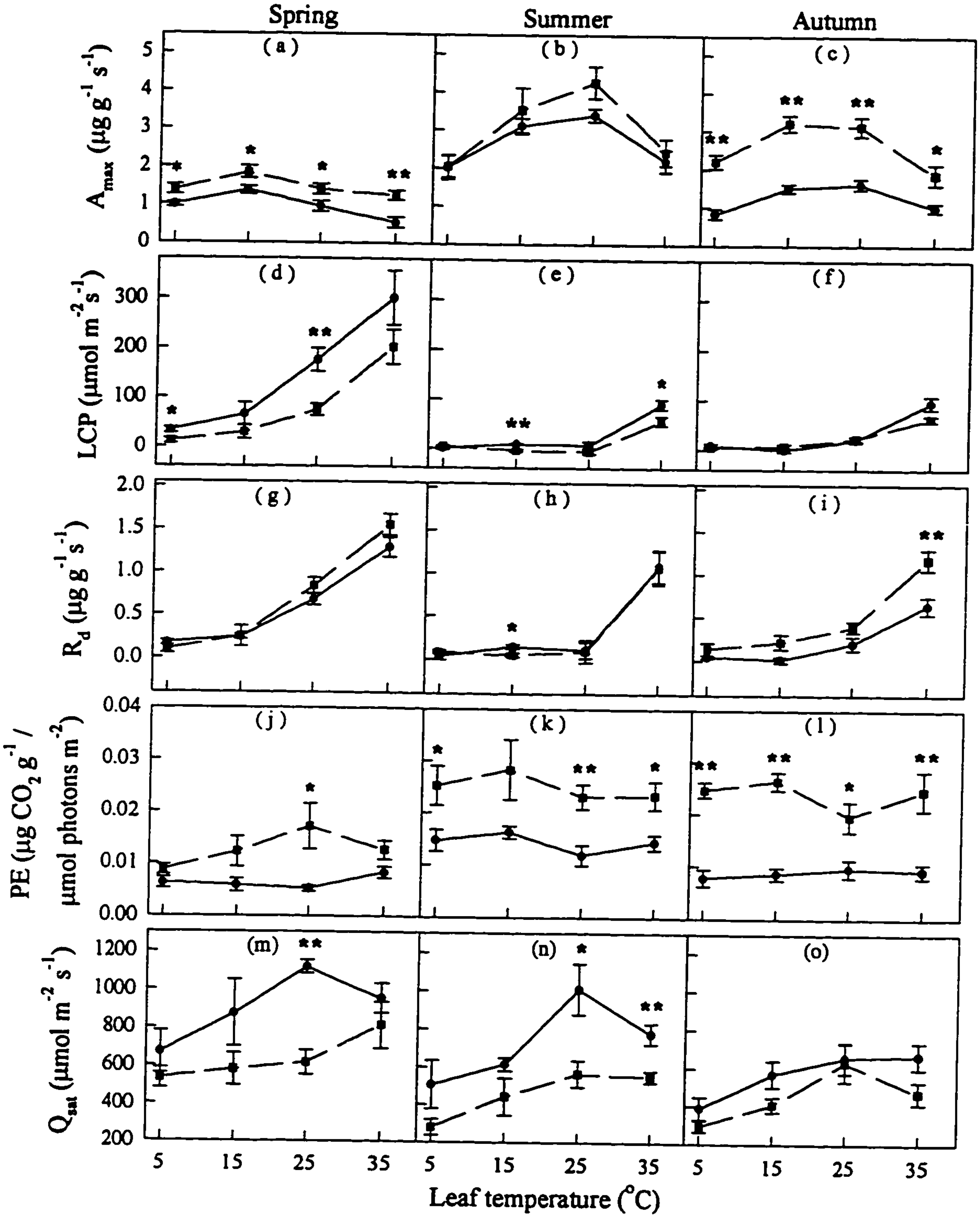

Figure 2.4 Changes in light response curve parameters (mean±SE, n=6) with leaf temperature for open (circles) and understory (squares) white spruce seedlings in spring, summer and autumn. (a), (b) and (c) light saturated rate of net photosynthesis (A_{max}); (d), (e) and (f) light compensation point (LCP); (g), (h) and (i) dark respiration (R_d); (j), (k) and (l) photochemical efficiency (PE); (m), (n) and (o) light saturation point (Q_{sat}). The value of P according to two-tailed Student's *t*-test is indicated by * ($P<0.05$) and ** ($P<0.01$).

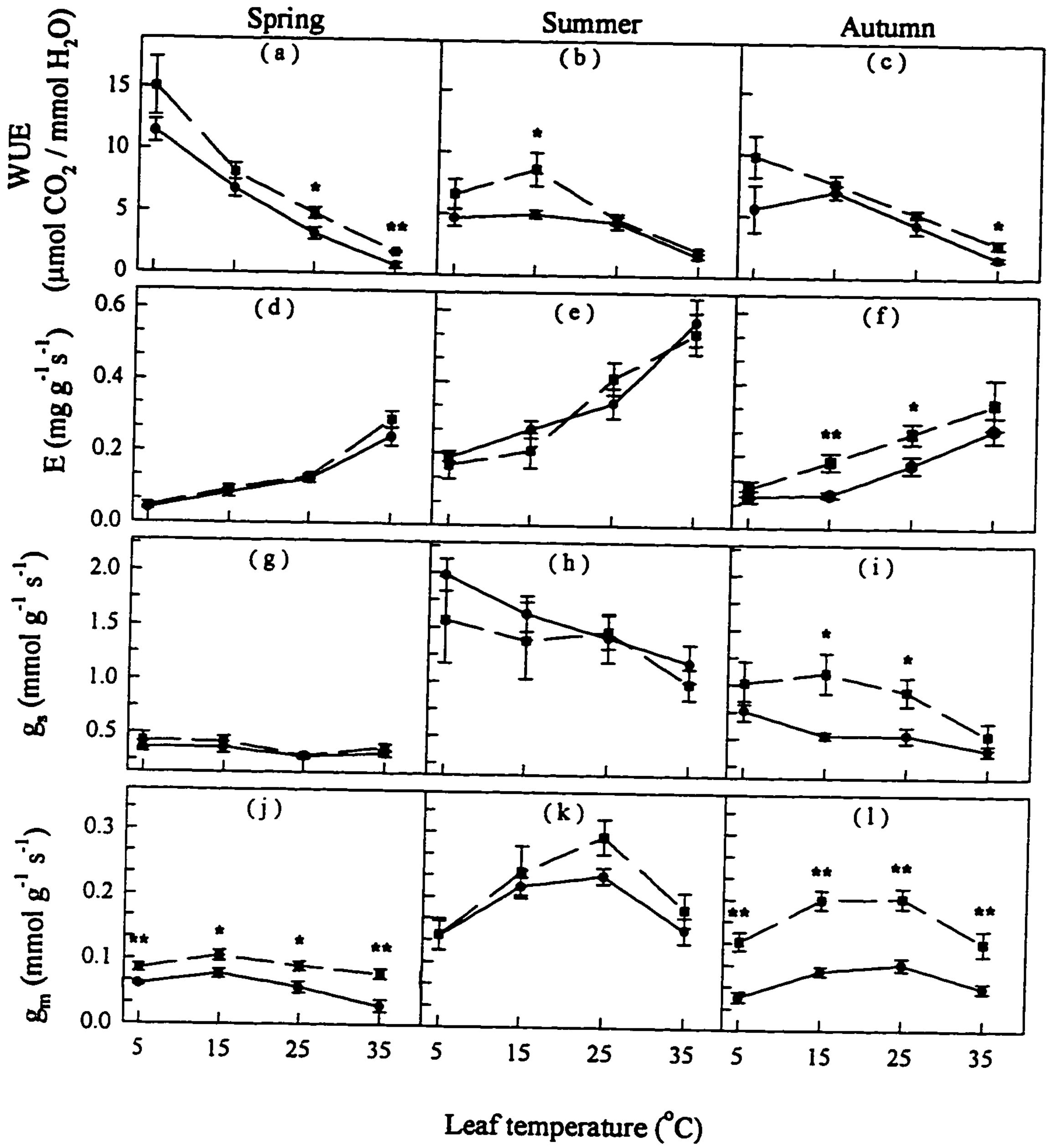

Figure 2.5 Changes in gas exchange parameters (mean±SE, n=6) at saturating light (1100 μmol m^{-2} s^{-1}) with leaf temperature for open (circles) and understory (squares) white spruce seedlings in spring, summer and autumn. (a), (b) and (c) water use efficiency (WUE); (d), (e) and (f) transpiration (E); (g), (h) and (i) stomatal conductance to H_2O (g_s); (j), (k) and (l) mesophyll conductance to CO_2 (g_m). The value of P according to two-tailed Student's *t*-test is indicated by * ($P<0.05$) and ** ($P<0.01$).

CHAPTER 3
PHOTOSYNTHESIS OF WHITE SPRUCE (*PICEA GLAUCA*) AND JACK PINE (*PINUS BANKSIANA*) SAPLINGS IN RELATION TO SEASON AND TEMPERATURE

3.1 Introduction

Conifers have the potential for carbon assimilation throughout the year. In regions with moist and mild autumn, winter and spring conditions, photosynthesis is significant in spring and autumn, and even in winter (Helms 1965, Fry and Philips 1977, Boltz *et al.* 1986). In areas with very cold winters, coniferous photosynthesis is usually depressed completely by subfreezing temperatures (Bourdeau 1959, Schulze *et al.* 1967, Jurik *et al.* 1988, Strand 1995). In the boreal forests of Alberta, winter is cold and long, and it is assumed that most of the annual photosynthesis takes place in the warmest months of the year from May to September.

In mixedwoods dominated by aspen (*Populus tremuloides* Michx.) there is a wide variation of light reaching the understory over the season. There are periods of high light during the periods when aspen is leafless (Ross *et al.* 1986, Constabel and Lieffers 1996). These times are, however, accompanied by low night temperatures and relatively cold soils. Lieffers and Stadt (1994) found that the growth of understory white spruce (*Picea glauca* (Moench) Voss.) is higher in hardwood-dominated stands than in softwood-dominated stands, and suggested that growth of the spruce is related to the light regimes under the canopy. Moreover, the higher light regimes when the overstory aspen are leafless during spring and fall should also be considered. It is not clear if white spruce is photosynthetically active during spring and autumn and is able to take advantage of these high light resources.

Due to the lag between soil and air temperatures, photosynthesis of conifers in spring and fall is probably most limited by their abilities to take up water from cold soil in spring (Jurik *et al.* 1988) and tolerate night frosts in autumn. Cold soil reduces root conductance

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and can induce water stress (Teskey *et al.* 1984). Jurik *et al.* (1988) reported that net photosynthesis in white pine (*Pinus strobus* L.) was undetectable when soil temperature was below 2 °C, and recovery of photosynthesis closely followed the increase of soil temperature. In Scots pine (*Pinus sylvestris* L.), photosynthesis started in spring when the soil was still frozen (Troeng and Linder 1982); however, the authors believed the water for transpiration came from storage in the stem. In the autumn, frost resistance of conifers increases gradually with shortening photoperiod and decreasing temperature (Levitt 1980). In northern Sweden, field-grown Scots pine seedlings showed relatively high photosynthetic rates after a night frost as low as -8 °C (Lundmark *et al.* 1988). However, photosynthesis was greatly reduced after a 12-day period of artificial freezing stress at light/dark temperatures of -5/0 °C (Öquist *et al.* 1980).

The objectives of this study were to determine 1) the seasonal patterns of photosynthetic activity, particularly in the spring and the autumn, of white spruce saplings in open and understory sites, and 2) the photosynthetic rates of white spruce over a range of temperatures. Jack pine (*Pinus banksiana* Lamb.), usually growing on open sites, was also assessed for comparison. I expected high photosynthetic rates of white spruce during the leaf-off periods of overstory aspen in spring and autumn. I also expected the protection of overstory canopy on understory white spruce and different seasonal patterns of photosynthesis between white spruce and jack pine.

3.2 Materials and Methods

3.2.1 Study site and trees

The field site was located at the University of Alberta Forest Science Research Station near Devon, 25 km southwest of Edmonton, Alberta, Canada (53°22'N, 113°45'W). Measurements of seasonal patterns of net photosynthesis at saturating light were carried out on 20-year-old open-grown and understory white spruce saplings (4-6 cm in dbh and 3-5 m in height) and 30-year-old, widely spaced open-grown jack pine (10-15 cm in dbh, 6-8 m in height, and less than 100 trees/ha in stem density). These open white spruce and jack pine were about 100 m apart. Understory white spruce grew under the canopy of a

80-year-old pure aspen stand (20 to 40 cm in dbh, 14 to 18 m in height, and about 25 m^2 /ha basal area), and open-grown white spruces were from the edge trees of a small plantation (over 2000 trees/ha). On open sites, the major shrub species, *Rosa acicularis* L., was about 1 m high and sparsely scattered on the sites. Dominant grasses were *Bromus inermis ssp. pumpelliamus* and *Agropyron trachycaulum* (Link) Malte. Under the aspen stand, the shrub layer was dominated by *Alnus crispa* (Ait.) Pursh., *Amelanchier alnifolia* Nutt., *Rosa acicularis* L., and *Corylus cornuta* Marsh. At ground level, major herbaceous species were *Aralia nudicaulis* L. and *Epilobium angustifolium* L. Annual precipitation measured at a nearby weather station was 468.2 mm averaged from 1961 to 1990, with June and July being the months with highest precipitation. Average slope was less than 2% on open sites and about 5% (south-facing) in aspen understory. The soil consisted mainly of fine sand.

3.2.2 Environmental measurements

Air temperature at 1.3 m above ground and soil temperature at 10 cm depth were measured in both the aspen understory and the open site using 101 thermisters (Campbell Scientific Co., Ltd., Logan, UT), with two samples at each location. These positions were chosen to represent the height at which branches were sampled and the depth where majority of the tree roots were distributed. Sensors for air temperature were shielded from direct radiation. Daily maximum, minimum and average temperatures were recorded using a datalogger (CR 21, Campbell Scientific CO., Ltd., Logan, UT).

Photosynthetic photon flux density (PPFD) under the aspen canopy was measured on sunny days with a hand-held integrating radiometer (Sunfleck Ceptometer, Model SF-80, Decagon Services, Inc., Pullman, WA). At each sampling time, PPFD measurements were made at 1.3 m above ground between 11:00 and 13:00 solar time. Fifteen locations were randomly chosen in the stand and at each location 12 PPFD readings were taken in a circle and averaged. Irradiance under the aspen canopy was the average of the 15 locations. Light conditions on the open site were determined by averaging the PPFD readings taken outside the stand before and after understory measurements.

3.2.3 Field measurement of gas exchange

Seasonal patterns of net photosynthesis at saturating light were measured in current and one-year-old needles in jack pine and open and understory white spruce during two growing seasons. Six trees were randomly chosen for each species and location at each time. One twig from each sampled tree was selected 1.5-2.0 m above the ground from the south side of the crown. Gas exchange in one-year-old needles was measured before July in 1994 and for the entire growing season in 1995. Measurement on current needles started when they were fully expanded.

Gas exchange was measured between 1000 and 1600 solar time on sunny days at saturating light (full sunlight for open-grown white spruce and jack pine and over 1000 μmol $m^{-2}s^{-1}$ PPFD for understory white spruce where natural light was supplemented by a quartz halogen lamp), using a portable gas analysis system (LCA-2) equipped with a conifer cuvette (Analytical Development Corp., Hoddesdon, England). Air flow rate was set at 8 ml/s and relative humidity of incoming air was adjusted so that the relative humidity in the cuvette during measurements was approximately equal to the relative humidity of ambient air. Following gas exchange measurements, the sampled shoots were clipped and sealed in a plastic bag for determination of leaf area. Projected leaf areas of the needles were measured with a Li-3100 leaf area meter (Li-Cor., Lincoln, NB).

3.2.4 Photosynthetic response to leaf temperature

Net photosynthesis was measured at leaf temperatures of 5, 15, 20, 25, and 35 °C and a PPFD of 900 μmol m^{-2} s^{-1} in white spruce and jack pine seedlings that had been grown at 22 °C and 16 h photoperiod for seven months in a greenhouse. During the measurements, the entire seedling and cuvette were enclosed in a temperature-controlled chamber. Light from a 500 watt quartz halogen lamp (T-3, The Edge, Bellevue, WA) was filtered through a flowing water bath. Irradiance was measured with a Li-Cor quantum sensor (Li-190 SB, Li-Cor, Ltd., Lincoln, NB) placed inside the cuvette. Leaf temperature was monitored with a fine copper-constantan thermocouple (Omega Engineering, Stanford, CT) placed in contact with the foliage and connected to a datalogger (CR 21X, Campbell Scientific CO., Ltd., Logan, UT). Silica gel desiccant was used to decrease water content at low temperatures and ferrous sulfate ($FeSO_4.7H_2O$) to enhance water content at high temperatures in order to obtain relatively constant vapor pressure deficit across the five leaf temperatures. Net photosynthesis was measured sequentially from low to high temperatures, with readings recorded when they were stable. Projected leaf area was measured with a Li-3100 leaf area meter (Li-Cor., Lincoln, NB). Results were expressed relative to the highest value obtained within the temperature range.

Net photosynthesis at saturating light (A_{max}; μmol m^{-2} s^{-1}) and stomatal conductance to water vapor (g_s; mmol m^{-2} s^{-1}) were calculated based upon the formulas given by Caemmerer and Farquhar (1981). Two-tailed Student's *t*-test was used to compare the means of A_{max} and g_s on comparable sampling dates among jack pine and open-grown and understory white spruce, and between current and one-year-old needles for each species and location. Percent A_{max} and g_s in temperature-response experiment were arcsine-squareroot transformed before comparison was made between white spruce and jack pine seedlings (Little and Hills 1978).

3.3 Results

3.3.1 Seasonal photosynthesis

In 1995, minimum air temperature was generally below 0 °C before mid-May and after mid-September (Figure 3.1). In April there was an abrupt increase in air temperature. Increase in soil temperature lagged that in air temperature, especially in the aspen understory. In both years, aspen began leaf flush in late April. By mid-May, newly flushed leaves were about half their fully expanded size. In the autumn, aspen began shedding leaves in early September and about 50 % of leaves were off in late September. In the understory of aspen, there were peaks of irradiance in autumn and especially in spring (Figure 3.2), when the trees were leafless.

In 1995, net photosynthesis of both white spruce and jack pine became positive in early April (Figure 3.3) when maximum daily air temperatures were around 15 °C (Figure 3.1).

The main recovery of A_{max}, depending upon species and location, occurred in April and early May, a period with low soil temperature (temperatures at 10 cm depth were slightly below or near 0 °C until mid-April on the open site and until early May in the understory) and night frosts (minimum temperature -5 °C or lower frequently occurred before early May). From early April to late May, net photosynthesis at saturating light (A_{max}) was lower in the understory than open-grown white spruce, except for one measurement in late April (see comparison at the bottom of Figure 3.3-a). Between the two species, white spruce regained its photosynthetic capacity quicker than jack pine according to direct (see the bottom of Figure 3.3-c) or relative comparison (percent of maximum of the season; 64% for open-grown white spruce and 26% for open-grown jack pine for an average of three measurements before mid-May, 1995), but an apparent depression was seen in May in both open-grown and understory white spruce.

In the two years, A_{max} fluctuated considerably in the two species, especially in summertime. The open-grown white spruce showed the widest day to day variation in A_{max}. Rainfall records from a nearby weather station and our temperature measurements showed that most of the depressions in photosynthesis were in periods of drought (e.g., rainfall was low before the sampling dates of July 19 and September 12, 1995 and July 26, 1994) and peaks of hot days (e.g., in late May and early to mid September, 1995).

In the autumn, both jack pine and white spruce maintained relatively high photosynthetic capacity until late October despite frequent night frosts as low as -7°C. In both years and for both species, A_{max} abruptly dropped to near 0 after several days of heavy frosts in late October: -15 °C in 1994 and -10 °C in 1995. Additional gas exchange measurements in November, 1994 indicated no photosynthetic activity or stomatal conductance. Between the two species, A_{max} was lower in jack pine than in white spruce by direct (the bottom of Figure 3.3-c) or relative comparison (percent of maximum for the season; 78% for white spruce and 65% for jack pine for the average of the eight measurements after mid September in the two years).

Stomatal conductance (g_s) showed the same seasonal pattern as that of A_{max} in the two species (Figure 3.4), an apparent recovery in spring with increases in air temperature, a great fluctuation in summertime during periods of drought and high temperature, and a quick decline in late October after several cold nights.

Current needles exhibited a seasonal pattern of A_{max} similar to that of one-year-old needles. In white spruce, the rates of A_{max} in current foliage were generally higher than in one-year-old foliage (Figures 3.3-a and 3.3-b), but similar differences were not observed in jack pine until September (Figure 3.3-c). A comparison of A_{max} among jack pine and open and understory white spruce indicated that open-grown white spruce usually had a higher rates of A_{max} and g_s than jack pine, but the reverse usually occurred during the periods of drought and high temperature (see the bottom of Figure 3.3-c for both one-year-old and current needles). A_{max} was also higher in open-grown than understory white spruce saplings, except on those sampling dates with less rainfall and high daytime temperature (see the bottom of Figure 3.3-a for both one-year-old and current needles).

3.3.2 Photosynthetic response to leaf temperature

Relative rate of A_{max} (% of highest value obtained over the range of temperature) increased with temperature from 5 to 20 °C and decreased thereafter in both white spruce and jack pine (Figure 3.5-a), whereas change of relative g_s with leaf temperature was less clear (Figure 3.5-b). With the increases of leaf temperature (Figure 3.5-c), g_s showed a pattern similar to A_{max} in jack pine but remained relatively constant in white spruce. Comparatively, white spruce seedlings had higher relative A_{max} and g_s than jack pine seedlings at leaf temperature of 5 °C, whereas jack pine had slightly higher g_s at leaf temperatures above 15 °C.

3.4 Discussion

The results show that A_{max} recovered in the spring when soil temperature at 10 cm was low (0 to 2 °C) in both white spruce and jack pine. This was also the case in *Pinus sylvestris* L. during recovery of photosynthesis in spring (Troeng and Linder 1982), but different from the observation on *Pinus strobus* L. where activation of photosynthesis did not start until soil temperature at 10 cm was above 2 °C (Jurik *et al.* 1988). In conifers, recovery of photosynthesis after a cold winter is considered to be mainly limited by their ability to take up water from cold soil (DeLucia and Smith 1987, Jurik *et al.* 1988). In April and early May 1995, the steady increase in g_s (Figure 3.4) and A_{max} (Figure 3.3) in the understory white spruce (Figure 3.3-a) suggests the trees were able to absorb water and were able to gear up their photosynthesis despite near 0 °C soil temperatures (Figure 3.1). Earlier research has shown that root conductance to water decreased rapidly at soil temperatures less than a specific threshold, e.g. 7 °C in *Pinus contorta* Dougl. (Running and Reid 1980), 5 °C in *Picea engelmannii* (Parry) Engelm. (Kaufmann 1975) and 2.5 °C in *Abies amabilis* (Dougl. ex Loud.) Forb. (Teskey *et al.* 1984). However, Kramer (1942) and Teskey *et al.* (1984) note that there is still some water movement even at soil temperatures near 0 °C. Another possible way of getting water for transpiration is the use of stored water in the stem that becomes available in mild spring days when soil is still frozen (Troeng and Linder 1982). In saplings, this is a small volume of water and would be exhausted in a short time as in 1995. There was significant photosynthesis of understory white spruce for at least a month when soils were near 0 °C. Trees might be able to absorb water directly from soil or replenish the tissue water depleted during the day by taking water from soil during the night (Lopushinsky and Kaufmann 1984). It may also be possible that the soil was warmer than 0 °C above 10 cm, which would allow water uptake by the roots concentrated in surface layers in white spruce (Kabzems and Lousier 1992).

In spring, the recovery of photosynthesis in jack pine was slow compared to that of white spruce (see the bottom of Figure 3.3-c). The reason for this is not clear, but may be related to relatively lower photosynthetic capacities at low temperatures in jack pine (Figure 3.5-a) or slow recovery of its photosynthetic system, which can be altered during cold weather. Cold weather may affect chloroplast structure (Senser *et al.* 1975), chlorophyll content (Martin *et al.* 1978), photosynthetic enzyme activity (Öquist *et al.* 1980) and photosynthetic electron transport (Martin *et al.* 1978, Öquist *et al.* 1980). Low soil temperature in spring might have had more restriction on water absorption of jack pine than on white spruce. In white spruce, slower recovery of A_{max} and g_s in understory than open-grown trees was probably related to the slower rise of soil temperature in spring under the aspen canopy.

The decline of photosynthesis in the autumn corresponded with the decrease in air temperatures and photoperiod. Minimum daily temperatures were below 0 °C by mid September. Low temperature has direct inhibitory effects on photosynthetic systems (Strand and Öquist 1985). Photoinhibition and photooxidation caused by freezing temperatures and high irradiance also results in the depression of photosynthesis of conifers (Öquist *et al.* 1987). Abrupt decline of photosynthesis to near zero shortly after some very cold night frosts suggests that these cold night temperatures are related to the final shutdown of photosynthesis in the autumn. The critical temperature for the cessation of photosynthesis seems to be around -10 to -15 °C, which was in general agreement with earlier reports in conifers (Bourdeau 1959, Bamberg *et al.* 1967, Troeng and Linder 1982). Coincident cessation of photosynthesis in late October in both years, however, suggests that other factors such as photoperiod or associated changes in hormones (Jurik *et al.* 1988) might be also involved.

The fluctuation of A_{max} in the two species appeared to be caused by drought and high temperatures according to rainfall records from a nearby weather station and our temperature measurements. High temperatures increase dark respiration (Alexander *et al.* 1995) and decrease stomatal conductance (Goldstein *et al.* 1985). In this study, stomatal closure might be part of the cause for the decrease of A_{max} during the periods of drought and hot days in the field-grown trees (Figures 3.3 and 3.4), but not for the seedlings in well watered conditions (Figure 3.5). Smaller fluctuations of A_{max} in jack pine than in white spruce were probably related to its higher resistance to water stress than white spruce (Grossnickle 1988). In white spruce, the existence of an overstory aspen canopy apparently reduces the variability of A_{max}, perhaps by ameliorating temperature and moisture extremes (Marquis 1979) and consequent improvements of water relations (Childs and Flint 1987, Dalton and Messina 1995).

This study clearly shows that spring and autumn are important periods for photosynthesis of white spruce saplings. The data suggest spruce has an ability to rapidly regain photosynthetic capacity in spring and tolerate freezing temperature in autumn. This suggests that understory white spruce can take advantage of spring and autumn periods of high light. Photosynthesis during these periods is likely important for annual carbon accumulation of white spruce under the canopy of aspen. For jack pine, there was proportionally lower A_{max} during the spring and fall, which suggests a reduced ability to take advantage of high light resources when the deciduous species are leafless. These data suggest that white spruce is well adapted to positions below a deciduous canopy such as aspen and part of the reasons for the relatively low shade tolerance and low competitive abilities of jack pine under a deciduous canopy relates to its reduced abilities for photosynthesis in the periods of high light in the spring and fall when temperatures are low.

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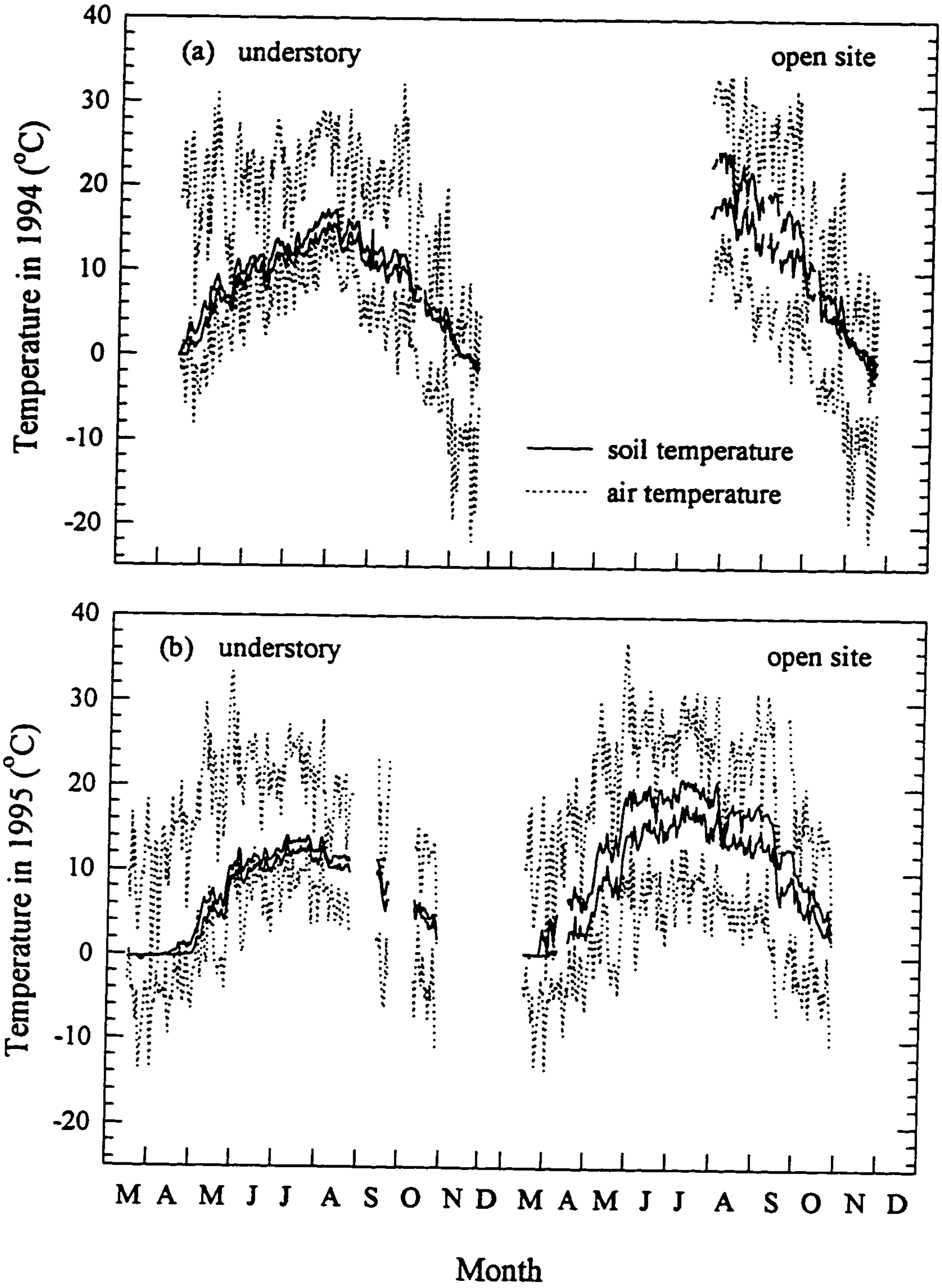

Figure 3.1 Maximum and minimum air and soil (10 cm) temperatures under a *P. tremuloides* canopy and on an open site: (a) 1994; (b) 1995.

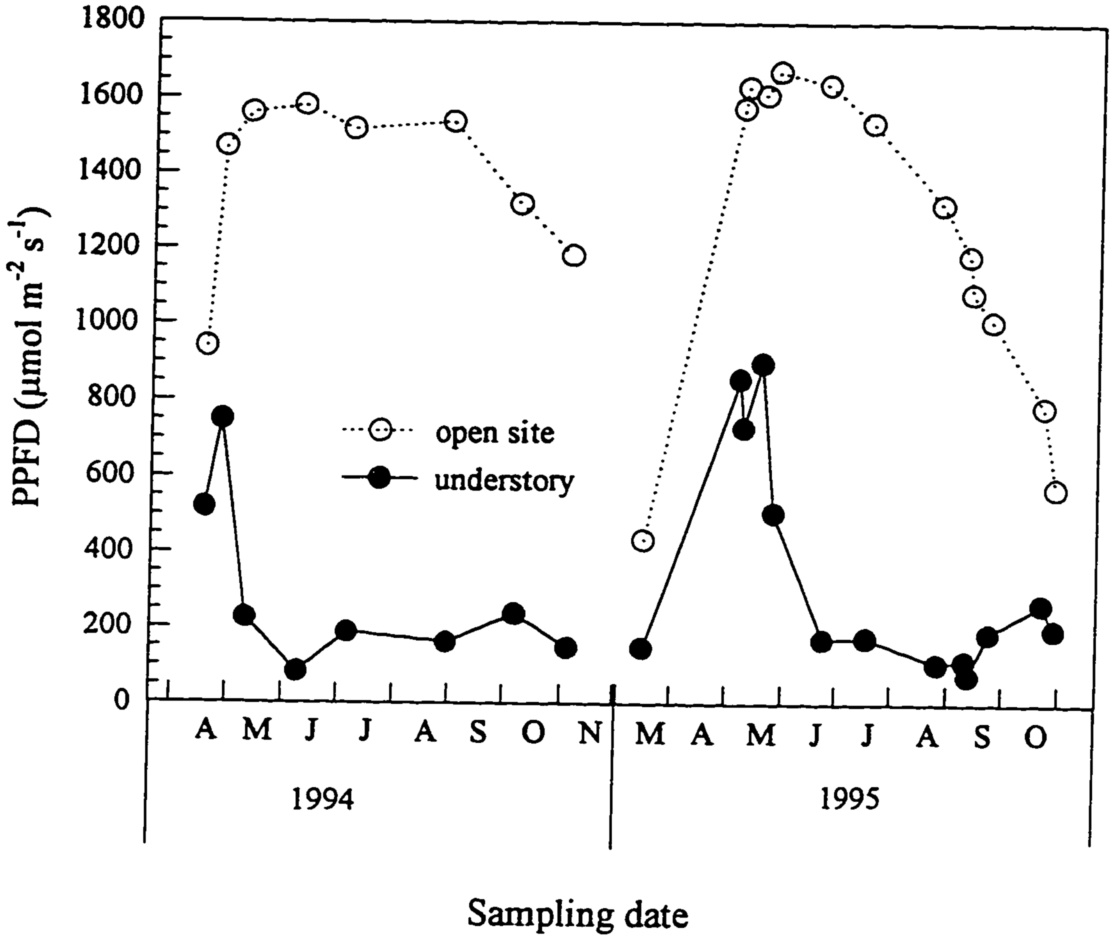

Figure 3.2 Seasonal observations of photosynthetic photon flux density (PPFD) on sunny days under a *P. tremuloides* canopy and on an open site in 1994 and 1995.

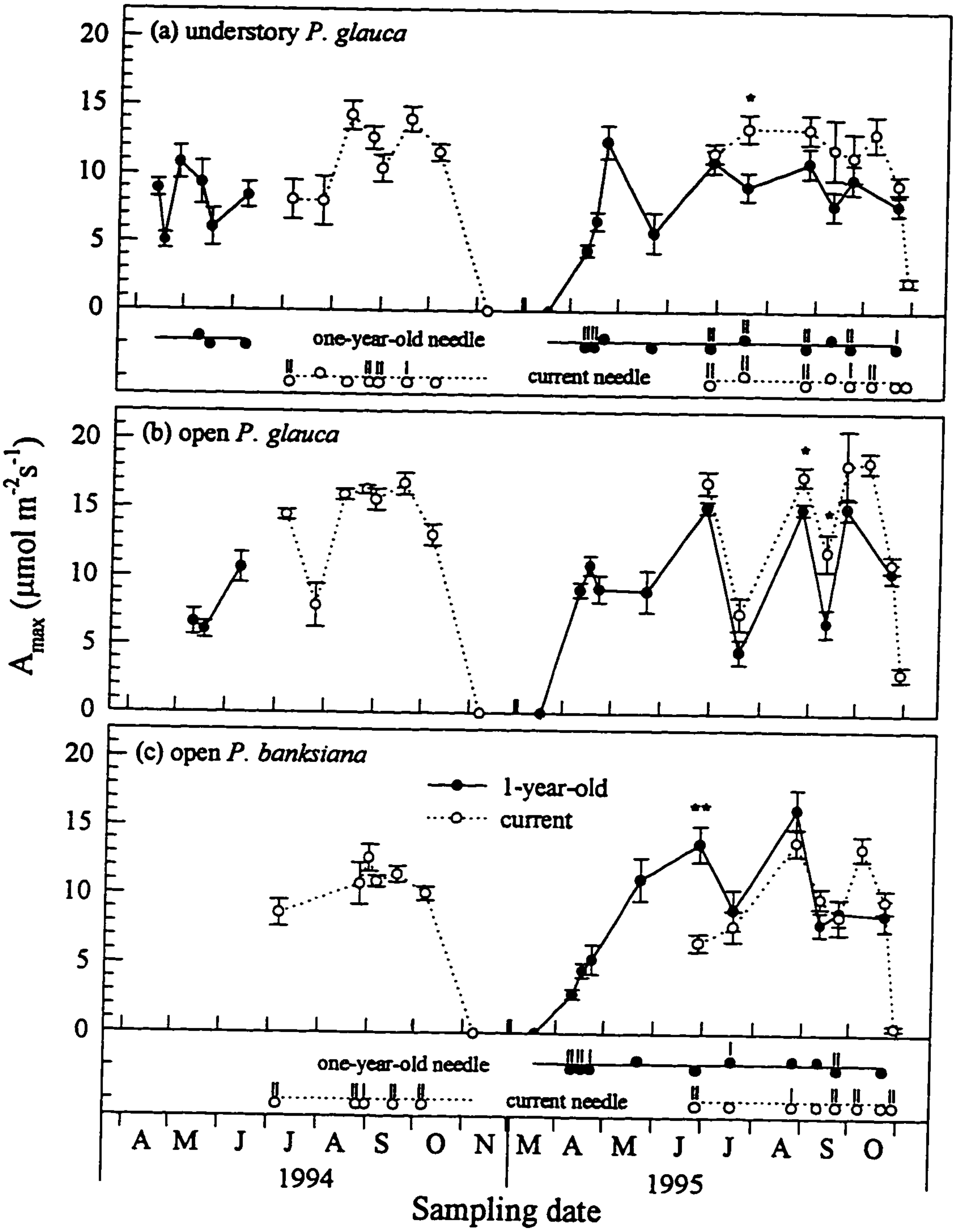

Figure 3.3 Seasonal patterns of A_{max} (mean±SE,n=6) in current and one-year-old foliage: (a) understory *P. glauca*; (b) open *P. glauca*; (c) open *P banksiana*. Significant difference between current and one-year-old needles is indicated by * ($P<0.05$) and ** ($P<0.01$). Comparisons between understory and open *P. glauca* are presented at the bottom of graph (a) and between open *P. glauca* and open *P. banksiana* at the bottom of (c). A circle above or below the reference line represents higher and lower A_{max} compared to the open *P. glauca*, respectively. Significant differences are marked by l ($P<0.05$) and ll ($P<0.01$).

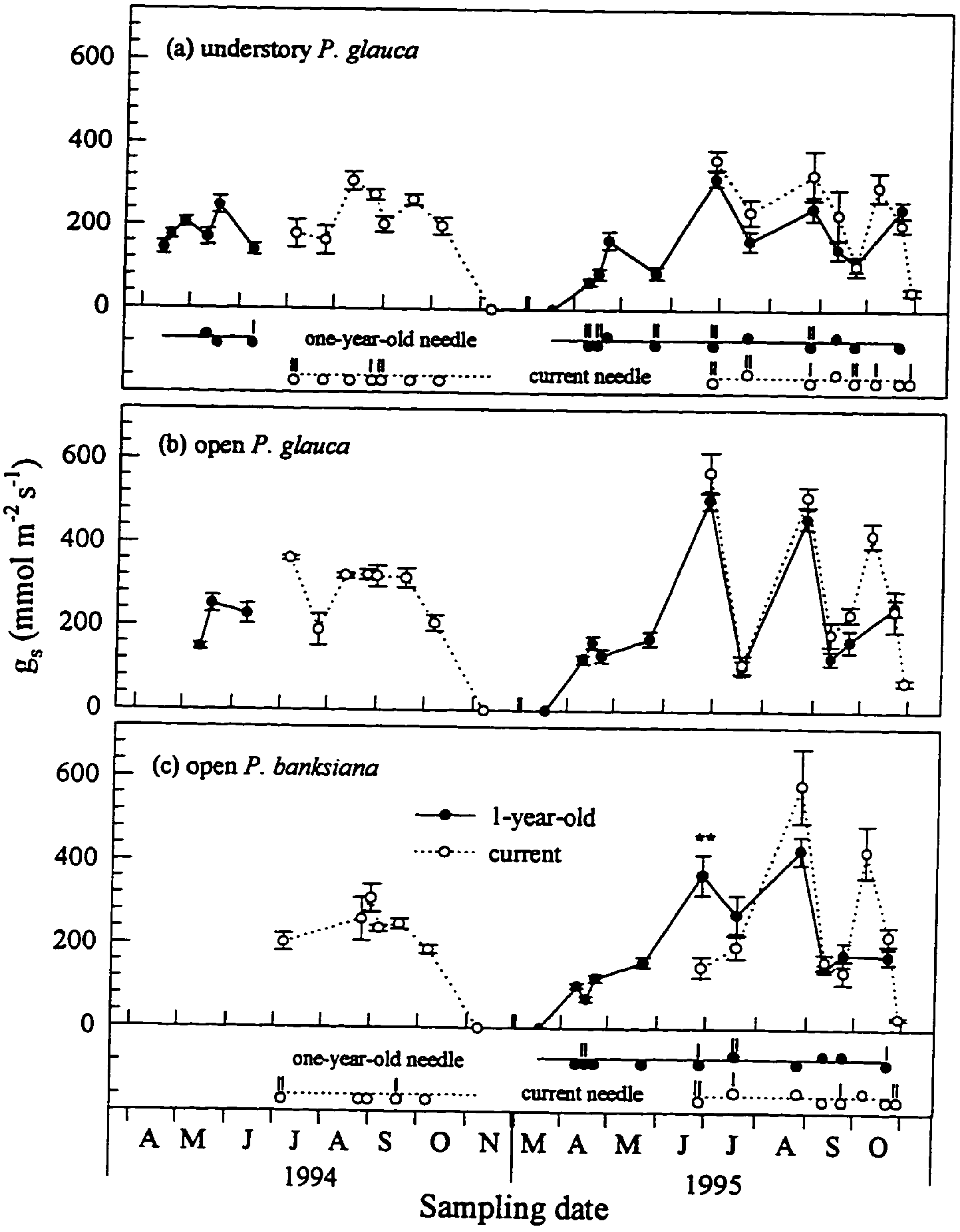

Figure 3.4 Seasonal patterns of g_s (mean±SE,n=6) at saturating light in current and one-year-old foliage: (a) understory *P. glauca*; (b) open *P. glauca*; (c) open *P banksiana*. Significant difference between current and one-year-old needles is indicated by * (P<0.05) and ** (P<0.01). Comparisons between understory and open *P. glauca* are presented at the bottom of graph (a) and between open *P. glauca* and open *P. banksiana* at the bottom of (c). A circle above or below the reference line represents higher and lower g_s compared to the open *P. glauca* , respectively. Significant differences are marked by I (P<0.05) and II (P<0.01).

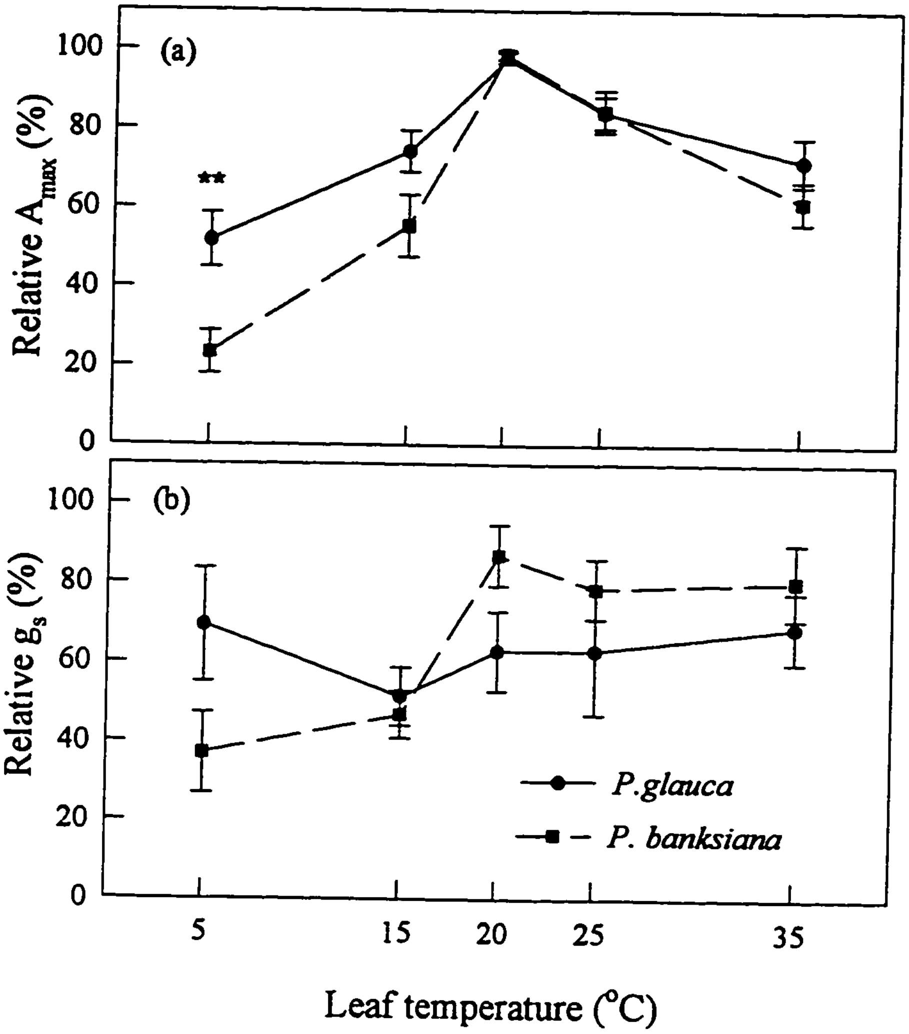

Figure 3.5 Relative rates of photosynthesis (A_{max}%) and stomatal conductance (g_s%) (mean±SE, expressed as a percentage of the highest value) in relation to leaf temperature in seven-month-old *P. glauca* and *P. banksiana* seedlings. Significant differences between two species are indicated by * (P<0.05) and ** (P<0.01).

CHAPTER 4

MICROCLIMATES IN THE UNDERSTORY OF BOREAL MIXEDWOODS IN RELATION TO CANOPY RESIDUAL AND SITE PREPARATION TREATMENTS

4.1 Introduction

Microclimates under a full forest canopy are thought to have a high night temperature, low daytime temperature, high relative humidity, reduced wind, and high moisture content in the surface layers of the soil in comparison with those on open sites (Marquis 1979). These environmental conditions are ideal for survival of young seedlings, except that light transmission in conifer-dominated boreal mixedwoods is low, often less than 10% of above-canopy light (Ross *et al.* 1986, Lieffers and Stadt 1994, Constabel and Lieffers 1996). This level is low for optimal growth of white spruce seedlings (Lieffers and Stadt 1994). In contrast, complete removal of the overstory canopy greatly increases solar radiation reaching the forest floor, but results in a seedling environment which is more extreme because most of the energy and water exchange is concentrated near the ground surface (Spittlehouse and Childs 1992). Extremely high daytime temperatures have negative impacts on physiological processes or cause direct damage to young seedlings. High frequency of night frosts combined with strong solar radiation may inhibit the photosynthetic systems (Lundmark and Hällgren 1987). Vegetative competition can frequently be a problem for conifers planted in clearcuts (Lieffers *et al.* 1993), and the dry surface soil may be a poor substrate for seed germination and establishment (Marquis 1979).

In a shelterwood system, the old stand is removed in a series of cuts while simultaneously establishing the next stand of trees in the understory. The residual trees moderate the regeneration environment of seedlings. There have been several attempts to adapt the shelterwood system for regeneration of white spruce in boreal mixedwood forests (Lees 1962, Lees 1963, Lees 1970a, Lees 1970b, Waldron 1959, Youngblood and Zasada 1991). Recent surveys of these trials showed that shelterwood cutting combined with

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scarification provided satisfactory regeneration of white spruce in these forests (Waldron and Kolabinski 1994), although reduced growth was found in some cases (Kabzems and Lousier 1992). Unfortunately, environmental conditions were not monitored in these cutting experiments or examined in relation to different methods of site preparations.

This study examined the effects of shelterwood cutting and site preparation treatments on seedling environmental components, including light quantity within the photosynthetically active radiation wavelengths and light quality (Red:Far Red ratio), air temperature, relative humidity, and soil temperature and moisture. I expected that existence of overstory canopies in shelterwoods reduces environmental extremes compared to clearcuts, e.g., lower daytime temperatures, higher humidity and night temperatures, and reduced risk of night frosts.

4.2 Materials and Methods

4.2.1 Site Description

The study site was located in the Weldwood FMA, 65 km northwest of Edson, Alberta, Canada (53°42' N, 117° 05' W), with an average slope of about 5% and an average elevation about 1050 m above sea level. The dominant soil type is a Brunisolic Gray Luvisol developed in a thin veneer of loam to sandy loam textured, fluvial sediments, underlain by clay loam to clay textured, morainal parent material (Proudfoot 1994). Climate is subhumid and continental, with long, cold winters and mild summers. Annual precipitation is approximately 500 mm. The site was covered by a mature aspen-white spruce mixedwood prior to cutting treatment. Under the canopy the shrub layer was mainly composed of *Rosa acicularis* Lindl. and *Viburnum edule* (Michx.) Raf. Major herbaceous species were *Aralia nudicaulis* L., *Cornus canadensis* L., *Epillobium angustifolium* L., *Mertensia paniculata* (Ait) G. Don., *Pyrola asarifolia* Michx. and *Rubus pubescens* Raf.

4.2.2 Experimental Design and Treatments

A split-plot design randomized in two blocks was laid out to investigate the effects of cutting and site preparation treatments. The type of canopy residual was the main plot, whereas the type of site preparation was the subplot. There were four canopy residuals in each block: two levels of shelterwood seeding cuts - high canopy residual (16.6 m^2/ha aspen and 3.6 m^2/ha white spruce) and low canopy residual (8.7 m^2/ha aspen and 3.8 m^2/ha white spruce), one conventional clearcut (complete canopy removal) and one control (18.0 m^2/ha aspen and 12.5 m^2/ha white spruce). Each main plot was 150 m x 150 m; the outer 25 m served as a buffer leaving a 1 ha sampling plot in the centre. Cutting was done in the winter of 1993/1994. In the early summer of 1994, each canopy treatment plot was subdivided into three types of mechanical site preparation: blading, mixing and control (i.e. no scarification). These subplots were 100 m long and 33 m wide and subtreatments were randomly assigned. Blading removed organic litter ("LFH" horizon) and part of the upper mineral soil to a depth of 11 to 13 cm, exposing "Ae" horizon. In the mixing treatment, the mixed layer, 10 to 13 cm deep, was composed of materials from "LFH" and "Ae" horizons. Both blading and mixing were done by a Thomas 233 Skidsteer loader fitted with either a 1.60 m hydraulic angle tilt blade or a MJ-1.40 Merri-crusher mixing head.

4.2.3 Measurements of Seedling Environments

Measurements of PPFD (photosynthetic photon flux density) were made on sunny days at 1.3 m above the ground between 10:00 and 14:00 solar time in late June 1994, at 15 locations in each subplot. At each location, 12 PPFD readings were taken in a circle and averaged. PPFD in open locations was recorded at the start and finish of sampling for each subplot to calculate canopy light transmission as a percentage of above canopy light.

The Red:Far Red ratio (R:FR, 654-664/724-734 nm) was measured between 10:00 and 15:00 solar time on clear days with a portable spectroradiometer (Li-Cor. 1800, Lincoln, NB) in late June, 1994. Nine locations were sampled at 1.3 m height in each plot. The spectrometer was mounted and leveled before scan.

Daily mean, maximum and minimum air temperatures at 0.50 and 1.40 m above the forest floor were measured in the canopy treatments of clear cut, high canopy residual and the control, using type 101 thermistors (Campbell Scientific, Inc., Logan, UT). These heights were chosen to represent a typical seedling height and the standard height for measurement of air temperature. The temperature measurement, two samples from each canopy treatment started in late May, 1994 and continued throughout the growing season of 1995. A type 201 RH thermistor probe (Campbell Scientific Inc., Logan, UT) was added at 0.50 m height in the beginning of 1995. All temperature and humidity sensors were suspended in the centre of a horizontal white PVC pipe (5.0 cm diameter and 30 cm long for temperature sensors and 8.0 cm diameter and 50 cm long for RH sensors) to shield them from direct radiation. Small holes were drilled at bottom of the pipes to prevent heat and water buildup. Sensors were connected to a datalogger (CR21, Campbell Scientific Inc., Logan, UT) and daily mean, maximum, and minimum temperatures and relative humidities were stored. Absolute humidity (g H_2O vapour/m^3 air) was calculated as described by (Oke 1987) and daily range of air temperature as the difference between maximum and minimum temperatures.

Instantaneous measurements of soil temperature were made in the three site preparation strips under all cutting treatments at depths of 0.10 and 0.30 m below the soil surface on May 5, 19, July 22, August 2, and Sept. 20, 1995. Ten thermocouples (24 -gauge copper/constantan) at 0.10 m depth and 5 at 0.30 m depth in each site preparation subplot were installed. Locations for soil temperature assessment were chosen randomly within the correct treatment zone. At each installation, a sod was removed to the correct depth and thermocouples were horizontally inserted into the soil before replacing the sod. At each sampling date, readings were taken by blocks over a one to two hour period at mid day with a microprocessor thermometer (Model HH21, Omega Engineering Inc., Stamford, CT).

A time domain reflectometer (moisture - point TK-917, Gabel Cor., San Diego, CA) was used to measure soil moisture (% v/v). Three locations were measured in each subplot on July 28, August 2, 1994 and on July 11, 1995. Measurement was done at three depth segments, 0 - 15, 15 - 30 and 30 - 60 cm. At each sampling date, measurement was taken by block. Due to poor soil-probe contact in the upper layer, only readings from depths of 15 - 30 and 30- 60 cm were analyzed.

4.2.4 Data Analysis

The general linear models procedure available in SAS Release 6.11 (SAS Institute Inc., 1995) was used to test for treatment effects on soil temperature and moisture. The differences among the treatments were analyzed on each sampling date. Whenever differences were detected, orthogonal contrasts were performed for comparison of treatments.

4.3 Results

4.3.1 Light

Average light transmission at 1.30 m above the forest floor was 100% in the clearcut, 73 % in low residual, 46 % in high residual and 20 % in the control. The decrease of light intensity was accompanied by a decrease in R:FR ratio: 1.09 in the open, 0.92 in the low residual, 0.91 in the high residual and 0.51 in the control.

4.3.2 Air Temperature and Humidity

At seedling height (0.50 m), reduction of canopy residual (high canopy residual and clearcut) increased maximum and daily range of temperatures and risk of frost and decreased minimum temperature compared to the controlled canopy (Figure 4.1, Table 4.1). On average, maximum temperature was about 2 °C warmer in the high residual and 2.5 to 3.5 °C warmer in the clearcut than that in the control. Daily range of temperature was about 2.5 to 3 °C higher in the high residual and 5 to 6 °C higher in the clearcut than that in the control. Of 312 days of observations over two years, 50 night frosts below 0 °C were recorded in the uncut, 53 in the high residual, and 79 in the clearcut. In total, there were 43 frosts below -2 °C in the clearcut and 30 frosts below -2 °C in the high residual, but only 19 frosts of that severity in the uncut. Minimum temperature averaged over the entire sampling period was about 0.5 °C lower in the high residual and 2.2 °C lower in the clearcut than that in uncut.

There was less impact of canopy residual on air temperature at 1.40 m height compared to 0.50 m height (Table 4.1). Average temperatures in the high residual and clearcut were closer to the temperatures in the uncut treatment. Also, the maximum and minimum temperatures were not as extreme as at the 0.50 m height.

Absolute and relative humidity decreased as cutting intensity increased (Figure 4.2, Table 4.2). Mean RH averaged over the whole sampling period was 3.5% and 7.3 % lower in the high residual and in the clearcut, respectively, than the control. The average minimum RH was 2.9% lower in the high residual and 8.1% lower in the clearcut compared to the uncut treatment (Table 4.2). Over the entire sampling period, mean absolute humidity (g H_2O vapor/m^3 air) was 7.39 in the control, 7.19 in the high residual and 6.85 in the clearcut.

4.3.3 Soil Temperature and Moisture

Different methods of site preparation had a significant impact on soil temperatures (Table 4.3). At all sampling dates, soil temperature in the control was significantly different from those in blading and mixing treatments, while the difference between blading and mixing was much less pronounced. Seasonal patterns of soil temperature at both 0.10 and 0.30 m depths were similar, with temperature highest in blading and lowest in control from spring to summer (Figure 4.3). The difference gradually decreased after July and almost disappeared in August. By mid-September, the pattern reversed, with temperature highest in control and lowest in blading.

The effect of canopy residual on soil temperature was significant only at 30 cm depth in mid summer. Mean soil temperature in the uncut control was apparently lower than those in the cutting treatments, but temperatures were similar among the clearcut and shelterwoods (Table 4.3).

In general, the soil moisture regime was higher in the clearcut than under the forest canopies (Table 4.4). This treatment effect was significant only at the depth of 16-30 cm in the summer of 1994 when soil moisture was low. Soil moisture was not affected by different methods of site preparation and there was no significant interaction between cutting and site preparation.

4.4 Discussion

4.4.1 Light

Light transmission through the shelterwood canopy (46% in the high residual and 73% in the low residual) was approximately equivalent to 750 to 1200 μmol m^{-2} s^{-1} at noon in mid-summer. The lower level of the range is still close to the saturation point of net photosynthesis for white spruce seedlings (Greenway 1995, Chapter 2), suggesting ample light for growth of understory white spruce. Several reports have indicated a reduced growth response of shade tolerant young trees to increasing light at >40% of above-canopy light, including white spruce (Lieffers and Stadt 1994, Wang *et al.* 1994). The decrease of R:FR ratio through the forest canopy observed in this study was in agreement with the findings by Haeussler and Tappeiner (1993). Low R:FR ratio has been reported to improve photosynthesis in Black Valentine plants (*Phaseolus vulgaris* cv.) (Hoddinott and Hall 1982) and in some tropical tree seedlings (Kwesiga *et al.* 1986), but inhibit seed germination in red alder (*Alnus rubra* Bong.) (Bormann 1983).

4.4.2 Air Temperature and Humidity

In this study, the increases in the maximum and daily range of air temperature and the decrease in the minimum temperature after partial or complete canopy removal were consistent with the general belief that an overstory canopy increases the interception of net radiation during the day and decreases the outgoing longwave radiation losses at night (Mahrt 1985, Holbo and Childs 1987). These treatment effects become larger at positions near the soil surface (Stathers 1989) in the shelterwood and especially in the clearcut treatments. The greater diurnal variation near the ground may result in stress on establishing seedlings. Temperatures above optimum increase transpiration and respiration, leading to reduction in net photosynthesis (Chapter 2) and water stress when water supply is restricted. At night, canopy reduction increases the frequency of frost occurrence (Valigura and Messina 1994). The shelterwood site (high canopy residual) showed little increase in frost frequency compared to the uncut control, suggesting that a partial canopy can provide nearly the same protection from low temperature as uncut stands. This is similar to Hungerford and Babbitt (1987). Shading by the overstory canopy is also beneficial to the protection of white spruce seedlings from photoinhibition caused by an interaction between freezing temperature and high radiation (Lundmark and Hällgren 1987).

The decreases in relative humidity (RH) in the shelterwoods and clearcut appeared to be accounted for by both the increase in daytime temperature and the reduction in absolute humidity associated with canopy residual (Tables 4.1 and 4.2). Reduction of the canopy reduces the addition of moisture to the atmosphere through transpiration and increases convection near ground surface, which all lead to the reduction of air moisture content. A decrease in RH or an increase in the vapor pressure deficit generally causes an increase in transpiration of tree seedlings (Teskey *et al.* 1986, Fits and Teskey 1988, Marsden *et al.* 1996) and leads to seedling water stress when water supply is limited. White spruce stomata are sensitive to atmospheric humidity and increased VPD reduces stomatal conductance and net photosynthesis (Marsden *et al.* 1996) even in well-watered seedlings.

4.4.3 Soil Temperature and Moisture

Reduction of the overstory canopy reduces soil water consumption by tree transpiration, but, to a lesser extent, increases soil evaporation (Spittlehouse and Childs 1992). This may explain the higher soil moisture at the depth of 16-30 cm on the clearcut sites during a dry period. No significant change was observed at the depth below 30 cm probably due to reduced root density of trees.

The lack of a residual canopy effect on soil temperature was not in agreement with the observations that shelterwood overstories decrease soil temperature compared to soil temperature in the open (Childs *et al.* 1985, Childs and Flint 1987, Valigura and Messina 1994). In this study, there was a trend for increased soil temperatures with a decrease in the residual canopy from control to high residual. However, mean temperatures in the clearcuts were usually lower than or equal to those in shelterwoods. This was probably due to a large amount of logging slash on open sites (Landhäusser, unpublished data), which may block incoming solar radiation reaching the soil surface.

It was interesting to note the seasonal changes in the ranking of mean soil temperatures in relation to site preparation (Figure 4.3). Heat conductivity of mineral soil is greater than that of organic matter. With high inputs of solar radiation from late spring to late summer, mineral soil in the blading was warmer than that of the mixed layer in the mixing treatment and the organic layer in the control. But in the fall, heat loss from soil was also faster in the blading than in the mixing and the control, resulting in the opposite soil temperature pattern among the three treatments from that in spring and summer. This result is similar to findings of Örlander *et al.* (1990). Soils of the boreal forests are often considered too cold for optimum conifer growth (Silversides *et al.* 1986), especially during the initiation of photosynthesis in early spring (Chapter 3). Higher soil temperature can improve photosynthetic and relative growth rates of white spruce seedlings (Brand 1990). Higher soil temperature in blading in spring and early summer may also promote seed germination and seedling growth.

In summary, the shelterwoods have higher relative and absolute humidity, cooler maximum and warmer minimum temperatures and reduced risk of night frosts compared to the clearcut. Light transmission under the shelterwood canopies was sufficient to saturate photosynthetic apparatus of understory white spruce. Soil moisture under the shelterwood canopies was lower than the clearcut only during periods of low rainfall and there was no difference in soil temperatures compared to clearcuts, given the heavier slash loading on clearcuts. In general, the partial canopy offered a more benign environment for spruce seedling recruitment than the clearcut.

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Table 4.1. Air temperature differences (°C) and frost occurrences at 0.50 and 1.40 m heights for 1994 and 1995 in brackets. Temperatures in the clearcut and high residual are expressed as daily differences between the control and cutting treatments and averaged over the sampling period.

temperature	clearcut		high residual		control	
(height)	(0.50	1.40)	(0.50	1.40)	(0.50	1.40)
average maximum	3.65	2.89	2.11	1.69		
	(2.68	2.40)	(2.19	1.32)		
average minimum	-2.35	-0.86	-0.61	-0.11		
	(-2.21	-0.92)	(-0.40	-0.19)		
average daily range	6.0	3.75	2.72	1.81		
	(4.88	3.68)	(2.59	1.44)		
total frost occurrence:						
< 0 °C	31	21	25	20	23	22
	(48	29)	(28	26)	(27	25)
< -2 °C	20	15	15	8	8	8
	(23	17)	(15	11)	(11	9)

Table 4.2. Relative humidity differences (RH) and absolute humidity (AH) at 0.50 m in 1995. RH values are expressed as daily differences between control and cutting treatments averaged for the sampling period. AH is the seasonal average of the actual daily mean AH.

humidity	clearcut		high residual		control	
	mean	minimum	mean	minimum	mean	minimum
average RH (%)	-7.3	-8.1	-3.5	-2.9		
average AH (g/m^3)	6.85	2.45	7.19	3.02	7.39	3.39

Table 4.3. Probability values and comparisons for soil temperature under two blocks (B), four levels of canopy residuals (C: CT-control, HR-high residual, LR-low residual and CC-clearcut) and three site preparation treatments (S: CN-control, BL-blading and MX-mixing) in 1995.

Source	May 5	May 19	July 11	Aug 2	Sept 20
0.10 m depth					
B	0.3604	0.7632	0.8975	0.2615	0.0198
C	0.5314	0.2562	0.1179	0.1781	0.3615
B*C	0.0257	0.2000	0.0353	0.1052	0.0988
S	0.0134	0.0147	0.0009	0.0253	0.0118
C*S	0.5177	0.2828	0.5624	0.6701	0.3984
C*B*S	0.0001	0.0002	0.0459	0.0510	0.1506
Contrasts for treatment differences of soil preparation					
CT vs. BL+MX	0.0072	0.0051	0.0003	0.0084	0.0086
BL vs. MX	0.1377	0.5577	0.9246	0.9150	0.0708
0.30 m depth					
B	0.5739	0.4424	0.9651	0.8343	0.5004
C	0.4366	0.0678	0.0299[#]	0.2673	0.2926
B*C	0.0323	0.1248	0.2392	0.5528	0.1825
S	0.0055	0.0001	0.0022	0.4619	0.0058
C*S	0.4046	0.1069	0.4843	0.4084	0.5239
C*B*S	0.0577	0.2407	0.1053	0.2053	0.6408
Contrasts for treatment differences of site preparation					
CT vs. BL+MX	0.0031	0.0001	0.0001	-	0.0032
BL vs. MX	0.0823	0.0257	0.3504	-	0.0916

[#] Mean separation for cutting treatment on July 11

Contrast	CT vs. HR+LR+CC	CC vs. HR+LR	HR vs. LR
Pr > F	0.0085	0.3032	0.4052

Treatments	CT	HR	LR	CC
Means (°C)	9.72	11.76	12.16	11.52

Table 4.4. Probability values and comparisons of treatment means for soil moisture under two blocks (B), four canopy residuals (C: CT-control, HR-high residual, LR-low residual and CC-clearcut) and three site preparation treatments (S: CN-control, BL-blading and MX-mixing).

			Sources:					
dates (cm)	depth (% v/v)	mean	B	C	B*C	S	C*S	B*C*S
28/06/94	16-30	14.8	0.9112	0.0137[#]	0.6762	0.2100	0.6268	0.4039
	31-60	26.8	0.1117	0.4356	0.1465	0.7018	0.4725	0.6999
02/08/94	16-30	19.1	0.4317	0.2435	0.2374	0.2016	0.2326	0.2715
	31-60	21.7	0.3812	0.1677	0.6023	0.5912	0.6876	0.0138
12/07/95	16-30	21.5	0.1855	0.5046	0.0692	0.6005	0.5935	0.0369
	31-60	26.9	0.1652	0.3407	0.1591	0.5810	0.7959	0.1563

[#] mean separation for the 16-30 cm depth in relation to cutting treatment on June 28, 1994

treatments	CT	HR	LR	CC
means (% v/v)	12.32	14.14	12.39	20.34

contrasts	CC vs. HR+LR+CT	CT vs. HR+IR	LR vs. HR
Pr > F	0.0038	0.3951	0.2093

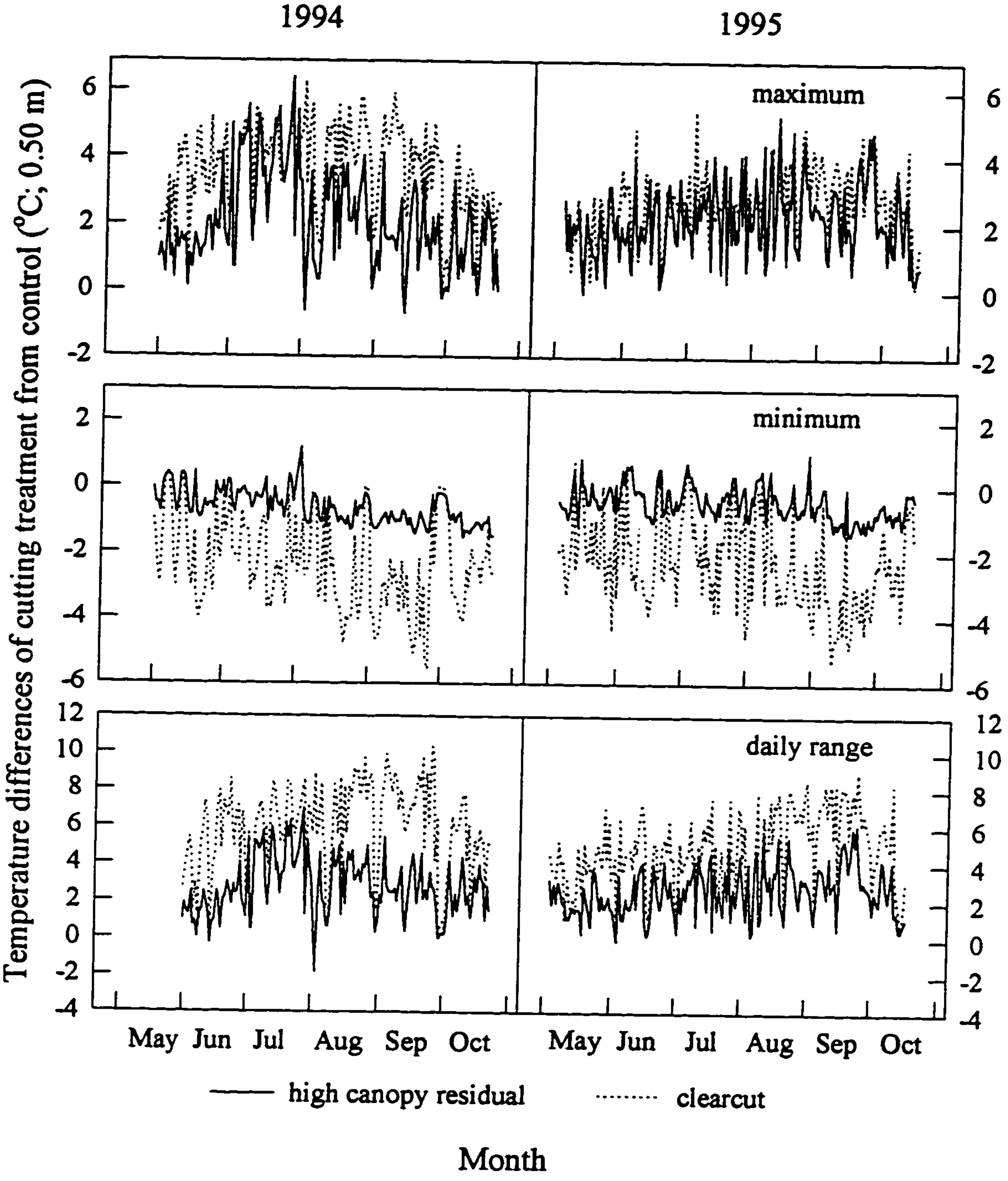

Figure 4.1 Temperature differences at 0.50 m height for 1994 and 1995 at site 1. Maximum, minimum and daily range of temperatures were expressed as the differences between the control and the cutting treatments.

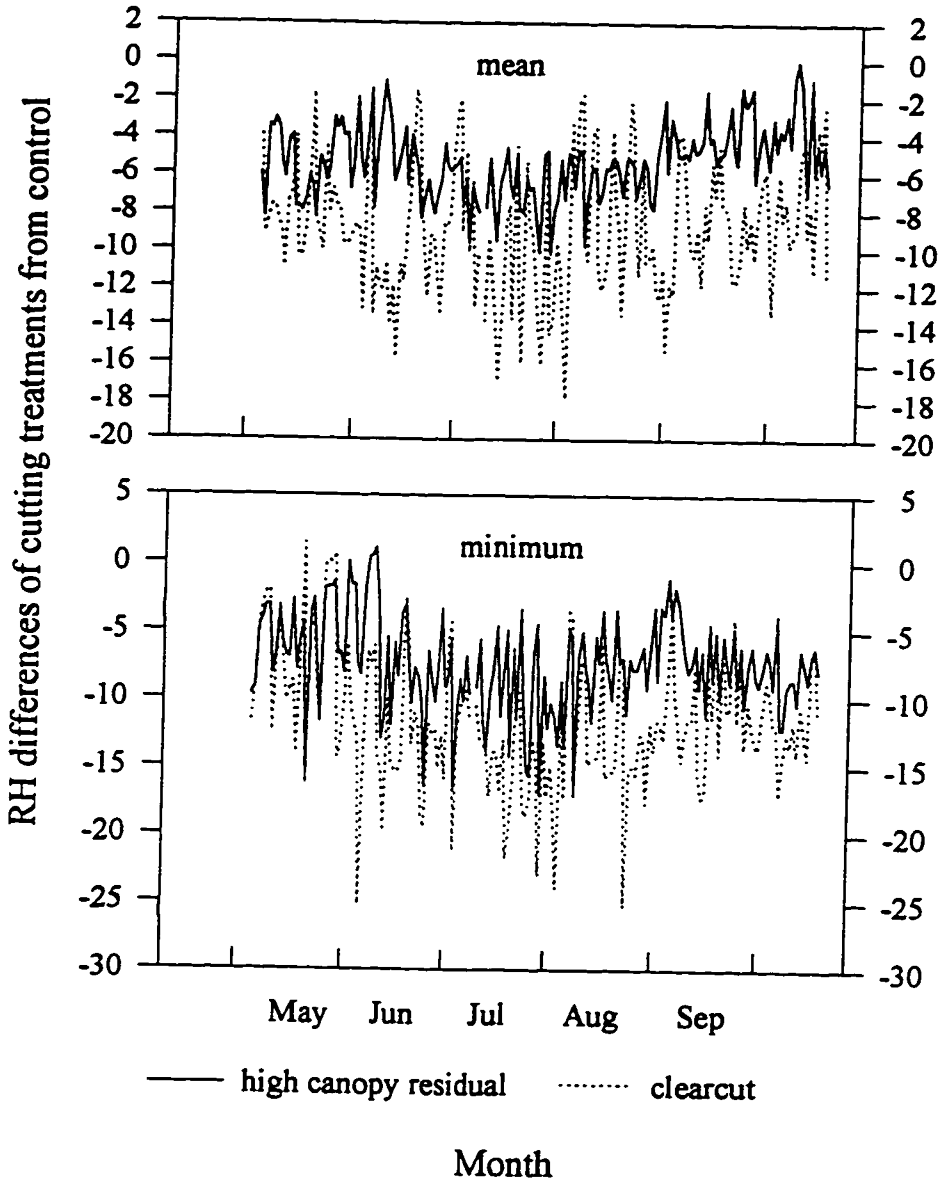

Figure 4.2 Relative humidity in 1995 at site 1. Daily mean and minimum relative humidity (RH) were espressed as the difference between the control and the clearcut or shelterwood treatments.

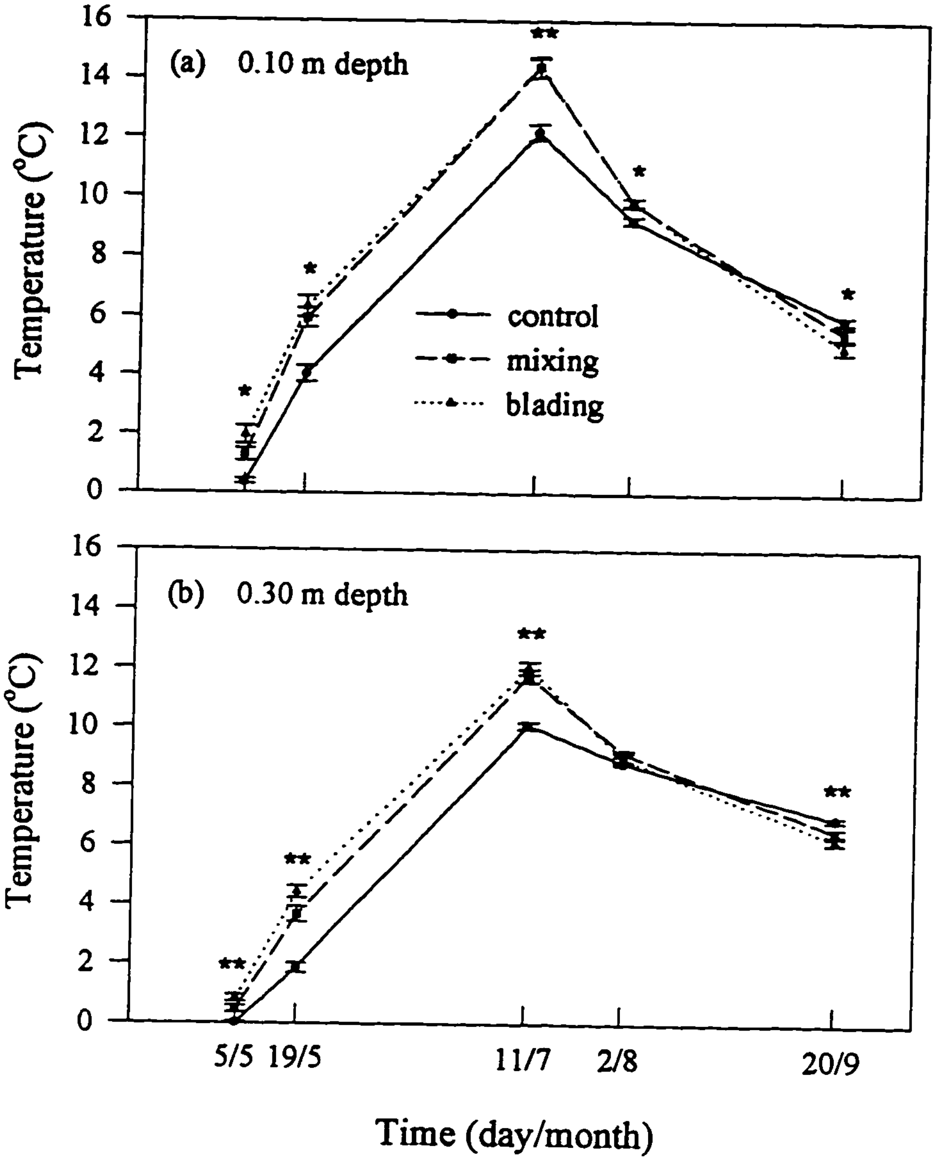

Figure 4.3 Seasonal change in mean soil temperatures at 0.10 and 0.30 m depths in relation to three methods of site preparation. Significant differences are indicated by * ($P<0.05$) and ** ($P<0.01$).

CHAPTER 5

GERMINATION, SURVIVAL AND GROWTH OF PLANTED WHITE SPRUCE SEEDLINGS UNDER FOUR CANOPY RESIDUALS AND THREE SITE PREPARATION TREATMENTS

5.1 Introduction

Seed germination and seedling establishment of white spruce (*Picea glauca* (Moench) Voss.) requires a source of viable seed, a suitable seedbed and favorable environmental conditions (Kabzems and Lousier 1992). Under field conditions, water and temperature conditions at the soil surface are believed to be the most important factors controlling seed germination and early survival of white spruce seedlings (Sutton 1969, Tear *et al.* 1982). Since first-year seedlings are small and have shallow roots (Eis and Craigdallie 1983, Bell 1991), drought is believed to be the major cause of seedling mortality during the early stages of seedling establishment (Eis 1967, Lees 1970). White spruce has a wide temperature range for germination, from 7 to 35 °C, with an optimum temperature around 20 °C (Fraser 1971, Bell 1991). Higher temperatures damage germinants by stem girdling and drought (Day 1963). Some light might improve germination of white spruce (Heit 1968) but germination is usually better in partial shade under field conditions. This is true for fully exposed sites with high temperature and soil moisture loss (Place 1955, Putman and Zasada 1986, Bell 1991).

White spruce germinates on a wide variety of seedbeds, including mineral soil, mixed soil and humus, decayed wood, litter, duff, humus, lichen or moss (Bell 1991), but the most favorable seedbeds are mineral soil, mixed soil and humus, and decayed wood (Jarvis *et al.* 1966, Waldron 1966, Eis 1967, Horton and Wang 1969, Bell 1991, DeLong 1995), presumably because of their superior water retention capacity (Place 1950). In undisturbed forest floor, mineral soil and mixed soil and surface layers of decomposed humus are relatively rare (Griffith 1931, Rowe 1955, Day 1964, Dobbs 1972), and site preparation is often employed to provide adequate seedbeds and improve microenvironments. Unfortunately, any improvement in seedbed receptivity is also beneficial to competitive vegetation. Shelterwood methods could regenerate shade-tolerant trees and inhibit shade-intolerant competitors (Lieffers *et al* 1993). In boreal mixedwoods, white spruce can recruit and develop in the understory of aspen-dominated forests (Lieffers and Stadt 1994). Mature aspen-dominated mixedwoods can transmit as much as 40% light (Lieffers and Stadt 1994). Partial removal of forest canopies allows more solar radiation to reach to the forest floor and raise soil temperatures, compared with uncut forest, but does not increase environmental extremes excessively in comparison with complete canopy removal (Chapter 4). Under shelterwood canopies, seed germination and seedling survival are improved for white spruce (Eis 1967, Lees 1972). Seedling growth in the reduced light intensity is not affected severely, particularly in height (Gustafson 1943, Logan 1969, Lieffers and Stadt 1994). Planted white spruce seedlings grew better in aspen understory than in open sites in the fully exposed areas with summer drought and frequent frosts in early and late growing season (Chapter 2).

This study was designed to compare the effects of different levels of overstory residuals and site preparation treatments on seed germination and performance of planted white spruce seedlings (bud flush, terminal bud damage and height growth). Due to the improvements of environmental conditions by overstory canopy and site preparation treatments (Chapter 4), I expected that seed germination and seedling performance (bud flush, terminal bud damage and height growth) were better under shelterwood canopies and treated sites.

5.2 Materials and methods

5.2.1 Site description

Two sites were selected and established in the Weldwood FMA near Edson, Alberta, Canada. Site 1 was located in 65 km northwest of Edson (53°42' N, 117° 05' W) and site 2 about 15 km southeast of site 1. Average slope was about 5% in site 1 and 8% in site 2. Dominant soil type is Brunisolic Gray Luvisols. Climate is subhumid and continental, with long, cold winters and mild summers. Annual precipitation is approximately 500 mm, with about 70% of this falling as rain. The sites were covered by mature aspen-white spruce mixedwood, approximately 15-25 m^2/ha aspen (*Populus tremuloides* Michx.), 7-15 m^2/ha white spruce and a small amount of balsam poplar (*Populus balsamifera* L.), black spruce (*Picea mariana* (Mill.) B.S.P) and lodgepole pine (*Pinus contorta* Dougl.) prior to cutting treatment. Under the canopy, the shrub layer was mainly composed of *Rosa acicularis* Lindl. and *Viburnum edule* (Michx.) Raf. Major herbaceous species were *Aralia nudicaulis* L., *Cornus canadensis* L., *Epilobium angustifolium* L., *Mertensia paniculata* (Ait) G. Don., *Pyrola asarifolia* Michx. and *Rubus pubescens* Raf.

5.2.2 Experimental design and treatments

The overall experiment was a split-plot design randomized in two blocks. Canopy residual was main plot, whereas type of site preparation was subplot. There are four levels of canopy residuals: two shelterwood seeding cuttings - high canopy residual and low canopy residual, one conventional clearcut (complete canopy removal) and one control (uncut). The main plots were 150 m x 150 m, the outer 25 m served as a buffer leaving a 1 ha sampling plot in the centre. Cutting was done in 1993/1994 winter at site 1 and 1995/196 winter at site 2. The cutting treatment was not consistent between the two sites. At site 1, residual basal area was 30.5 m^2/ha in control (18 m^2/ha aspen and 12.5 m^2/ha white spruce), 20.2 m^2/ha in high canopy residual (16.6 m^2/ha aspen and 3.6 m^2/ha white spruce), and 12.5 m^2/ha in low canopy residual (8.7 m^2/ha aspen and 3.8 m^2/ha white spruce), whereas similar cutting treatments left 35.4 m^2/ha (23.8 m^2/ha aspen, 7.8 m^2/ha white spruce and 3.8 m^2/ha other trees), 28.6 m^2/ha (19.8 m^2/ha aspen, 5.9 m^2/ha white spruce and 2.9 m^2/ha other trees) and 22.7 m^2/ha (14 m^2/ha aspen, 5.8 m^2/ha white spruce and 2.9 m^2/ha other trees) basal areas at site 2 .

Each main treatment plot was subdivided into three subplots (100 m long and 33 m wide) at site 1. Plot layout was same at site 2 except in one of clearcut where subplots were separated from each other by a 30 m wide untreated zone. Three site preparation treatments, mixing, blading and control (i.e. no scarification), were randomly assigned to each of the subplots. A Thomas 233 Skidsteer loader, fitted with a 1.60 m hydraulic angle tilt blade, was used to remove the LFH horizon and part of the upper mineral soil to the depth of 11 to 13 cm exposing the Ae horizon. The mixing treatment was done with the same loader fitted with a MJ - 1.40 Merri-crusher mixing head. The mixed layer, 10 to 13 cm deep, was composed of LFH and Ae horizons.

5.2.3 Seeding

The seeding trial was carried out at site 1 in 1995. Ten spots in each subplot were chosen in the areas representative of each site preparation treatment. These seeding spots were more or less uniformly distributed in two rows within the subplot and about 15 m apart from each other. At each distance, the closest acceptable microsite was selected. Seeding was made on June 12 with seeds collected locally, and 100 sound seeds were spread in an area of 0.2 m^2. A germination survey was carried out afterwards, two times in 1995 (July 11 and September 19) and one time in 1996 (September 25). At each time, the number of live seedlings were carefully determined for each seeding spot and cumulative germination rate was calculated as the ratio of total living seedlings to total sowed seeds. Seedling survival from the first to second fall was calculated as the ratio of the number of live seedlings in the fall of second year to the number of live seedlings observed in the fall of first year within the subplot.

A survey of natural seedlings was also done in 5 1x1 m quadrates of each of the above microsites at the end of summer in 1996.

5.2.4 Planting

Two types of container stock were planted: spring stock which would flush in the first growing season after planting and summer stock which delayed budflush until the spring of next year. At site 1, there were 10 planting spots in each subplot and each of them was about 2 m away from the seeding spots. Planting was made in mid-June, 1994, with 1+0 container-grown summer stock, which averaged 18.1±0.5 cm in height and 0.4±0.1 cm at root collar. Seeds were collected locally. Planting spots were about 1 m^2 with 5 seedlings planted at the edge of the spot.

Planting was replicated at site 2 with spring stock. Fifteen spots were systematically chosen from the areas representative of site preparation treatment and arranged in three row in each subplot. Planting was made in late May, 1996, with four seedlings planted within a 1 m^2 planting spot.

5.2.5 Bud flush

Timing of bud flush of planted stock was periodically checked on the summer-planted seedlings at site 1 in the spring of 1995 (from mid-may to early June). At each time, the number of flushed seedlings was recorded for all planting spots. Terminal buds were checked on May 18, May 25 and June 2, while lateral and top laterals were checked on May 18 and May 25.

5.2.6 Growth

Height growth of seedlings after planting was measured in fall, 1996 at the two sites. At site 1, seedlings planted in early summer, 1994, did not flush in the first year so that measurements were taken on the growth in the second (1995) and third (1996) field year. At site 2, however, only growth in 1996 was available. Height increment (HI) of the seedlings was defined as the length of the leader when it was fully extended and relative height increment (RHI) as the ratio of height increment of the seedling by the end of current year to the total height of the seedling at beginning of the year. Both HI and RHI of all live seedlings were measured and averaged for each planting spot.

Terminal bud damage was assessed by the percent of seedlings with damaged terminal bud in total planted seedlings in each subplot at the end of growing season (1995 and 1996 seasons at site 1 and 1996 season at site 2).

5.2.7 Data analysis

The general linear models procedure available in SAS Release 6.11 (SAS Institute Inc., 1995) was applied to test the treatment effects of canopy residual and site preparation on seed germination (%) and seedling growth. Percent germination rate of seeding spots was arcsine-squareroot transformed (Little and Hills 1978). Both germination rate and seedling growth were repeatedly measured at site 1. However, the overall experimental design at a specific location and time was a randomized split-plot, with two blocks, 4 main-plot treatments, three subplot treatments, and 10 samples at site 1 and 15 at site 2. Analysis was performed for all combinations of site and time. Effects were considered statistically significant when the probability of a Type I error was 0.05 or less. Whenever a significant difference was detected, orthogonal contrast was performed for comparison of treatment means.

Counts of budflush and terminal bud damage were analyzed with a log-linear model from the categorical data modeling procedure in SAS. Data were combined across seedling spots within the subplot to produce an adequately large sample size. The fitting started with a saturated model and the best-fit partial model was obtained by gradually removing the nonsignificant random components. If a significant association occurred between dependent variables (budflush or terminal bud damage) and treatments (canopy residual or site preparation), a separate best-fit model was built by creating a new variable (combining the dependent variable and treatment effect) to compare the means from different treatment levels. Contrasts were made between treatment levels within seedling categories (flush or nonflush for budflush and healthy or damaged for terminal bud).

5.3 Results

5.3.1 Germination

Total germination rate for seeded spots at site 1 averaged only 1.9% on July 11, one month after sowing, and increased to 7.7% in the fall, according to the survey conducted on September 19 (Figure 5.1). The seed germination between the first and second year was about 0.2%. Surveys conducted at the end of third summer (1996) after site preparation treatment did not find any naturally germinated seedling, suggesting a negligible error due to natural seedling ingress.

Germination rate differed significantly between treated (blading and mixing) and untreated (control) seedbeds, whereas the difference between blading and mixing treatments was generally small (Figure 5.1 and Table 5.1). Highest germination rate or the number of germinated seedlings per seeding spot usually occurred in blading, followed by mixing and control (Figure 5.1). This trend was consistently observed over time in the first year. However, the mixed seedbed had the greatest number of seeds which germinated in the second year.

Effects of canopy residuals was not significant except on July 11, one month after sowing. However, some general trends could be observed (Figure 5.1 and Table 5.1). Germination was highest in the high residual, followed sequentially from high to low by low residual, clearcut and control.

Survival of one-year-old seedlings through their first winter was also higher in prepared seeding spots of blading and mixing than in those of control (Figure 5.1). Mean survival rate was about 53.3% in control, and as high as 91.9% and 83.9% in blading and mixing, respectively. Overstory canopy residual also affected seeding survival, with an average of 89.0% in high residual, 91.9% in low residual, 73.2% in clearcut and only 62.3% in control.

5.3.2 Bud flush of planted seedlings

At site 1, budflush was significantly affected by canopy residual (Figures 5.2 and 5.3, Table 5.2). Both terminal and lateral buds of planted white spruce seedlings flushed earlier in shelterwood treatments than in the control and clearcut. The highest number of flushed seedlings was usually observed in high residual, followed by low residual, control and clearcut. This difference decreased gradually to near zero in early June when all live seedlings were flushed. Lateral buds in general flushed before terminal buds. Site preparation generally had no significant influence on the time of budbreak, except on May 18 when flush of lateral buds was delayed in controlled seedbeds.

5.3.3 Growth of planted seedlings

At both sites, height and relative height increments (HI and RHI) were higher in the shelterwood treatments than in the control and clearcut, and seedling growth was generally best in the low residual although the treatment effect was not large enough to be significant (Figures 5.4 and 5.5, Table 5.3). Effects of site preparation on seedling growth was also nonsignificant. However, reduced seedling growth in controlled spots at site 1 was noted in the second growing year after buds which had formed in the field flushed.

Analysis of variance with the log-linear model showed that terminal bud damage was closely related to canopy residual and site preparation. In the first year of seedling growth at site 1, the terminal bud damage was lower in blading than in control and mixed seedbeds. But mixing had the lowest amount of terminal bud damage in the second year of seedling growth at site 1 and first year of seedling growth at site 2.

The treatment effect of canopy residual on terminal bud damage was not consistent among the cutting treatments between the two sites (Figure 5.6, Table 5.4). At site 1, different overstory canopies had similar rates of bud damage in the spring of 1995, except the clearcut with significantly higher rate of bud damage. Terminal bud damage dramatically increased in the second year, especially in control and clearcut. At site 2, however, the damage of terminal buds appeared to decrease steadily with the reduction of canopy residual in their first year of field growth.

5.4 Discussion

5.4.1 Germination

Results of this study reconfirm that seed germination in white spruce is greatly influenced by seedbed type. In general, germination and early seedling survival require moisture-retentive seedbeds to allow roots to establish (Place 1955). Undisturbed forest floor is usually covered with thick organic layers which readily dry out during rainless days, whereas water content is usually higher and more stable in mineral soil (Dobbs 1972). White spruce seeds resting on organic layer in the control treatment are likely to experience periodic drought, which may kill germinating seeds and maintain dormancy in ingerminated seeds (Place 1955). In this study, germination was generally best in blading and poorest in untreated seeding spots. This is in agreement with previous experiments and observations (Griffith 1931, Blyth 1955, Crossley 1955a, Crossley 1955b, Place 1955, Rowe 1955, Quaite 1956, Ackerman 1957, Lees 1963, Wagg 1964, Jarvis 1966, Waldron 1966, Clark 1969, Dobbs 1972, Tear 1979, Putman and Zasada 1986, Packee 1990). The mean germination rate on mineral soil exposed by blading was only 10.4 % by the end of first growing season, compared to 20% noted by Tear (1979) and 13-53% by Place (1955) in white spruce. Seeds that remained dormant and germinated in the next year were very limited (0.2%). It was very likely that some of the seeds germinated and died during the growing season and were never counted on July 11 or September 19 of the first year, or September 25 in the second year, due to the high mortality of newly germinated white spruce seedlings (Tear 1979). The change of best seedbed from blading in the first year to mixing in the second year might be an indication that seedbed remains receptive longer in mixing treatment than in blading treatment.

Partial canopies in shelterwoods (high and low canopy residuals) produced better germination and seedling survival than control and clearcut treatments as indicated by the differences in treatment means (Figure 5.1). Full sunlight in clearcut apparently was not optimal for field germination of white spruce and the poor germination was likely attributed to increased heating and periodic drought (Place 1955, Waldron 1966, Eis 1967). In Calling Lake, Alberta, air temperature near the forest floor is frequently over 40 °C on fully exposed sites on sunny days of mid-summer (Coyea 1989). Temperatures above 35 °C have been shown to be detrimental to the germination of white spruce (Fraser 1971, Coyea 1989). The low germination in control was probably due to low light intensity and temperature at soil surface.

Field germination of white spruce generally occurs in June and July (Eis 1965, Waldron 1966). In Alberta, germination of white spruce can occur throughout most of the growing season, from late June or early July until August or early September (Rowe 1955, Jarvis *et al.* 1966, Tear 1979). The first germination survey conducted in early July might be in the time when seed germination had just started, with only 1.9% seeds germinated. This was slow in comparison with germination of white spruce in the central interior of British Columbia where 100 % of seeds germinated within three weeks after sowing (Eis 1965).

This germination delay might be caused by a less favorable distribution of summer precipitation.

5.4.2 Bud flush

Buds flushed earlier under the shelterwood canopies. The treatment effect was most apparent when about 50% of live seedlings flushed (Figures 5.2 and 5.3). This is similar to another field study where the bud flush was delayed in the cleared sites compared to sites under aspen canopies (Marsden *et al.* 1996). Cleared sites are characterized by low night temperatures, high daytime temperatures, and high solar radiation, which might inhibit photosynthetic systems, especially in late fall and early spring when night frosts are frequent (Chapter 2). Direct impacts of extreme environmental conditions in clearcuts such as low night temperatures and low mid-day humidity were most likely the reasons for the delay of budbreak in spring. However, low photosynthetic rates caused by low night temperatures and high solar radiation should also be responsible for the delayed budflush in the clearcut (Marsden *et al.* 1996).

5.4.3 Growth

White spruce is considered to be a shade tolerant species (Nienstaedt and Zasada 1990). The annual height increment of natural spruce saplings increased at light transmission from 10% to 40% but remained approximately the same at light levels over 40% (Lieffers and Stadt 1994). In the present study, light transmission under the shelterwood canopies was between 40 to 80% of incoming light. Lower height increment in the control is attributed to the low light transmission through the full forest canopy, and in the clearcut to extreme microenvironments (Chapter 4). The high daytime temperatures and low mid-day humidity in clearcut might cause seedling water stress and damage and reduce growth rates, particularly for newly outplanted seedlings with limited new root growth after planting (Grossnickle and Blake 1987, Grossnickle and Heikurinen 1989). In addition , photoinhibition caused by freezing temperatures and strong light could also suppress photosynthetic capacities in late fall and early spring and reduce growth rates for the seedlings planted in the open area (Man and Lieffers 1996). Under these environmental stresses, growth of open-grown white spruce seedlings is likely suppressed compared to seedlings under a partial canopy of aspen (Chapter 2, Russell 1963 cited in Kabzems and Lousier 1992). Unlike the observations of Burdett *et al.* (1984) and Vyse (1981), planted seedlings did not show reduced height growth in the second growing season after the buds which had formed in the field flushed (site 1). This suggest little planting check.

There was a noticeable difference in terminal bud damage between the two sites. A close inspection of the damage at site 1 revealed bud damage under forest canopies (shelterwood and especially control) was caused mainly by a fungus, which was active in environments with low light transmission and high humidity. This fungus attacked young tissue and damaged or even killed seedlings. Terminal bud damage in the clearcut was mainly caused by late frost in spring as Clements *et al.* (1972) reported in young white spruce plantation at Ontario, where frost damage to terminal buds was most prevalent for open-grown trees and shorter trees. At site 2, seedlings in shelterwoods suffered more from a fungus than those at site 1, probably due to higher canopy residuals. However, seedlings in clearcut did not experience the frost period in late spring which had killed the terminal buds of many newly flushed seedlings in clearcut at site 1.

In conclusion, shelterwoods had better seed germination and seedling growth, earlier buds flush, and less terminal bud damage than control or clearcut although not all of these treatment effects were strong enough to be significant. Between two shelterwood canopies, bud flush and seed germination, which are assumed sensitive to water stress (Tear *et al.* 1982, Rose *et al.* 1992, Marsden *et al.* 1996), were better in high canopy residual. Seedling growth, which is likely limited by light intensity under forest canopy (Lieffers and Stadt 1994), however, was usually better in low residual. Among the site preparation treatments used in this study, both blading and mixing significantly improved seed germination but only the mixing treatment significantly reduced terminal bud damage of planted seedlings compared to the seedlings in the controlled seedbed.

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Table 5.1. Probability values and comparisons for seed germination under four canopy residuals (CT-control, HR-high canopy residual, LR-low canopy residual and CC-clearcut) and three site preparation (CN-control, BL-blading and MX-mixing).

Source	July 11 (1995)	Sept. 19 (1995)	Sept. 25 (1996)	New germination in 1996
B	0.1246	0.9716	0.9513	0.2303
C	0.0420	0.2375	0.2975	0.2809
B*C	0.7688	0.1018	0.0153	0.5361
S	0.0006	0.0007	0.0001	0.0839
S*C	0.2509	0.2055	0.1776	0.5568
B*S*C	0.0429	0.4234	0.2405	0.0982
Contrast				
Canopy residual				
CT vs HR+LR+CC	0.0361	--	--	--
CC vs HR+LR	0.0361	--	--	--
HR vs LR	0.0998	--	--	--
Site preparation				
CN vs BL+MX	0.0002	0.0002	0.0001	--
BL vs MX	0.2568	0.1933	0.0506	--

Note: B-block; C-canopy residual; and S-site preparation

Table 5.2. Probability values and comparisons for budflush with log-linear model

	Terminals			Laterals	Top laterals
Source	May 18	May 25	June 2	May 18	May 25
B	0.0258	0.0139	0.1075	0.0941	0.6997
C	0.0017	0.0010	0.0056	0.0000	0.1093
B*C	0.9484	0.0894	0.0017	0.3872	0.5298
S	0.9613	0.1350	0.3164	0.0980	0.2576
B*S	0.9577	0.9384	0.9160	0.5484	0.9519
C*S	0.9939	0.9984	0.9550	0.5526	0.9973
B*C*S	0.9994	0.9427	0.9928	0.2286	0.9947
L	0.0000	0.0000	0.0000	0.0000	0.0000
B*L	0.0088	0.0000	--	0.0022	0.0002
C*L	0.0001	0.0000	0.0000	0.0000	0.0000
S*L	--	--	--	0.0001	--
B*C*L	--	0.0003	0.0000	0.0390	0.0000
C*S*L	--	--	--	--	--
B*C*S*L	--	0.0721	--	0.0037	--
LIKELIHOOD RATIO	0.2536	0.1092	0.6642	0.1117	0.2908
Contrast					
Canopy residual:					
CT vs HR	0.0039	0.0000	0.9967	0.0000	0.0000
CT vs LR	0.0801	0.0000	0.0817	0.0000	0.0361
CT vs CC	0.3759	0.4008	0.0002	0.0000	0.0000
CC vs HR	0.0014	0.0000	0.0001	0.0000	0.0000
CC vs LR	0.1382	0.0000	0.0110	0.0000	0.0000
HR vs LR	0.0878	0.3785	0.0390	0.5936	0.0094
Site preparation:					
CN vs BL	--	--	--	0.0386	--
CN vs MX	--	--	--	0.0149	--
BL vs MX	--	--	--	0.7702	--

Note: B-block, C-canopy residual (CT-control, HR-high canopy residual, LR-low canopy residual and CC-clearcut), S-site preparation (CN-control, BL-blading, and MX-mixing), and L-seedling budflush (flush or nonflush).

Table 5.3. Probability values for height increment (HI) and relative height increment (RHI) under four canopy residuals (CT-control, HR-high canopy residual, LR-low canopy residual and CC-clearcut) and three site preparation (CT-control, B-blading and M-mixing).

Source	site 1				site 2	
	first year		second year		first year	
	HI	RHI	HI	RHI	HI	RHI
B	0.5292	0.0684	0.3857	0.2316	0.9059	0.9837
C	0.4242	0.1759	0.1503	0.1357	0.0901	0.1842
B*C	0.0435	0.6294	0.4155	0.6542	0.5515	0.5213
S	0.5689	0.1409	0.3845	0.7419	0.6487	0.1619
S*C	0.1910	0.9157	0.8214	0.9545	0.6842	0.8843
B*S*C	0.6121	0.2086	0.0861	0.1832	0.0009	0.0001

Table 5.4. Probability values and comparisons for terminal bud damage with log-linear model.

Source	Site 1		Site 2
	1995	1996	1996
B	0.9571	0.4297	0.9228
C	0.0285	0.2840	0.0000
B*C	0.0431	0.3437	0.0026
S	0.1009	0.7048	0.0059
B*S	0.9925	0.7678	0.4986
C*S	0.9966	0.8910	0.0161
B*C*S	1.0000	0.9998	0.0023
L	0.0000	0.0004	0.0000
B*L	--	0.0000	--
C*L	0.0031	0.0000	0.0000
S*L	0.0291	0.0168	0.0005
B*C*L	0.0088	0.0003	0.0005
C*S*L	--	--	0.0001
B*C*S*L	--	--	0.0000
LIKELIHOOD RATIO	0.1527	0.0609	0.1566
Contrast			
Canopy residual:			
CT vs HR	0.8133	0.0000	0.4606
CT vs LR	0.9007	0.0000	0.0000
CT vs CC	0.1068	0.0000	0.0000
CC vs HR	0.0111	0.0000	0.0000
CC vs LR	0.0871	0.0018	0.0007
HR vs LR	0.5616	0.0019	0.0000
Site preparation:			
CN vs BL	0.1159	0.7162	0.1987
CN vs MX	0.0937	0.0091	0.0005
BL vs MX	0.2591	0.0406	0.0007

Note: B-block, C-canopy residual (CT-control, HR-high canopy residual, LR-low canopy residual, and CC-clearcut), S-site preparation (CN-control, BL-blading, and MX-mixing), and L-terminal leader status (live or dead).

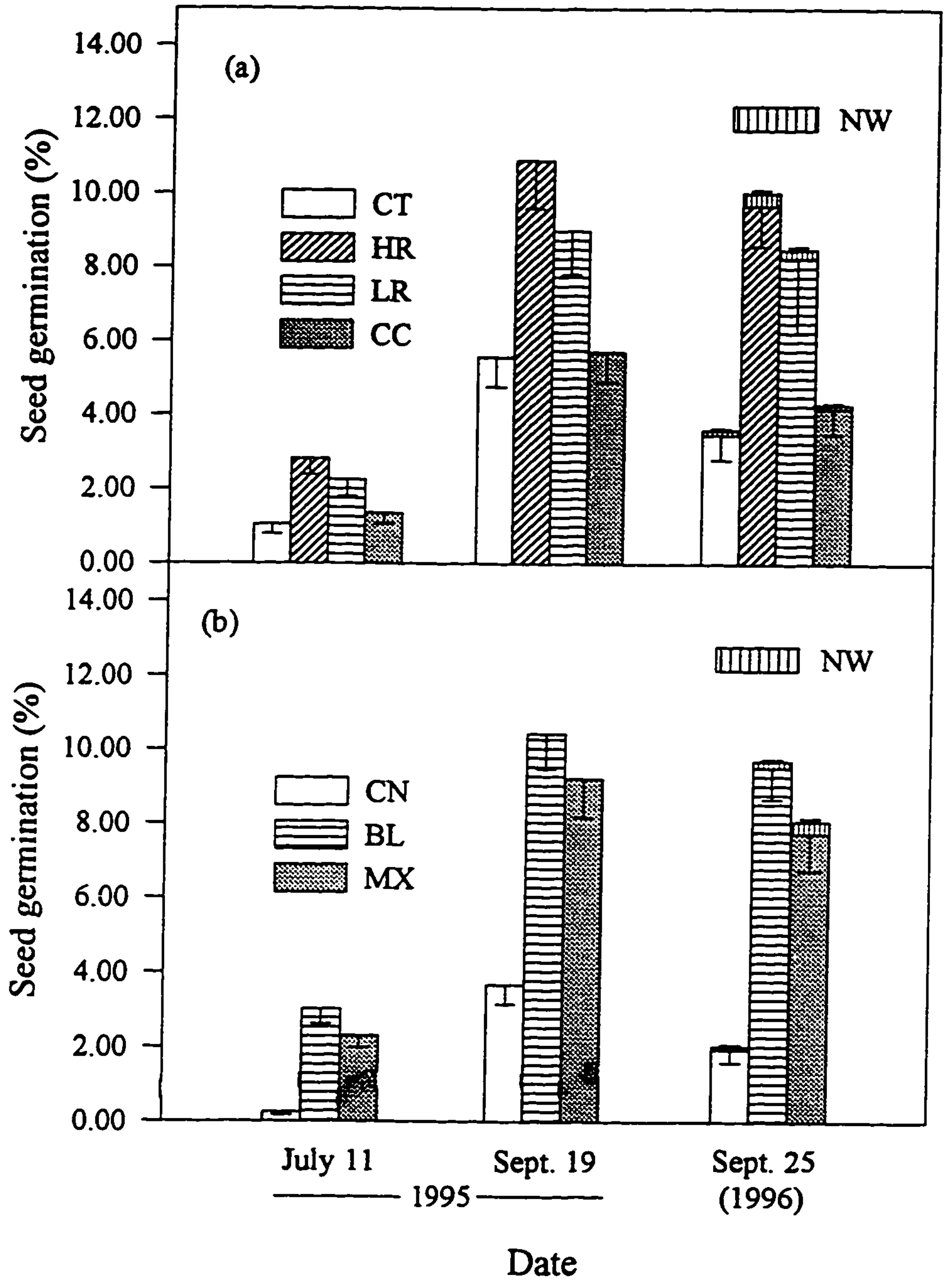

Figure 5.1 Mean cumulative germination and SE of seeding spot at different time after sowing at site 1 (seeds sowed in 1995): (a) canopy residual (CT-control, HR-high canopy residual, LR-low canopy residual, and CC-clearcut), and (b) site preparation (CN-control, BL-blading, and MX-mixing). NW represents the seeds germinated in 1996.

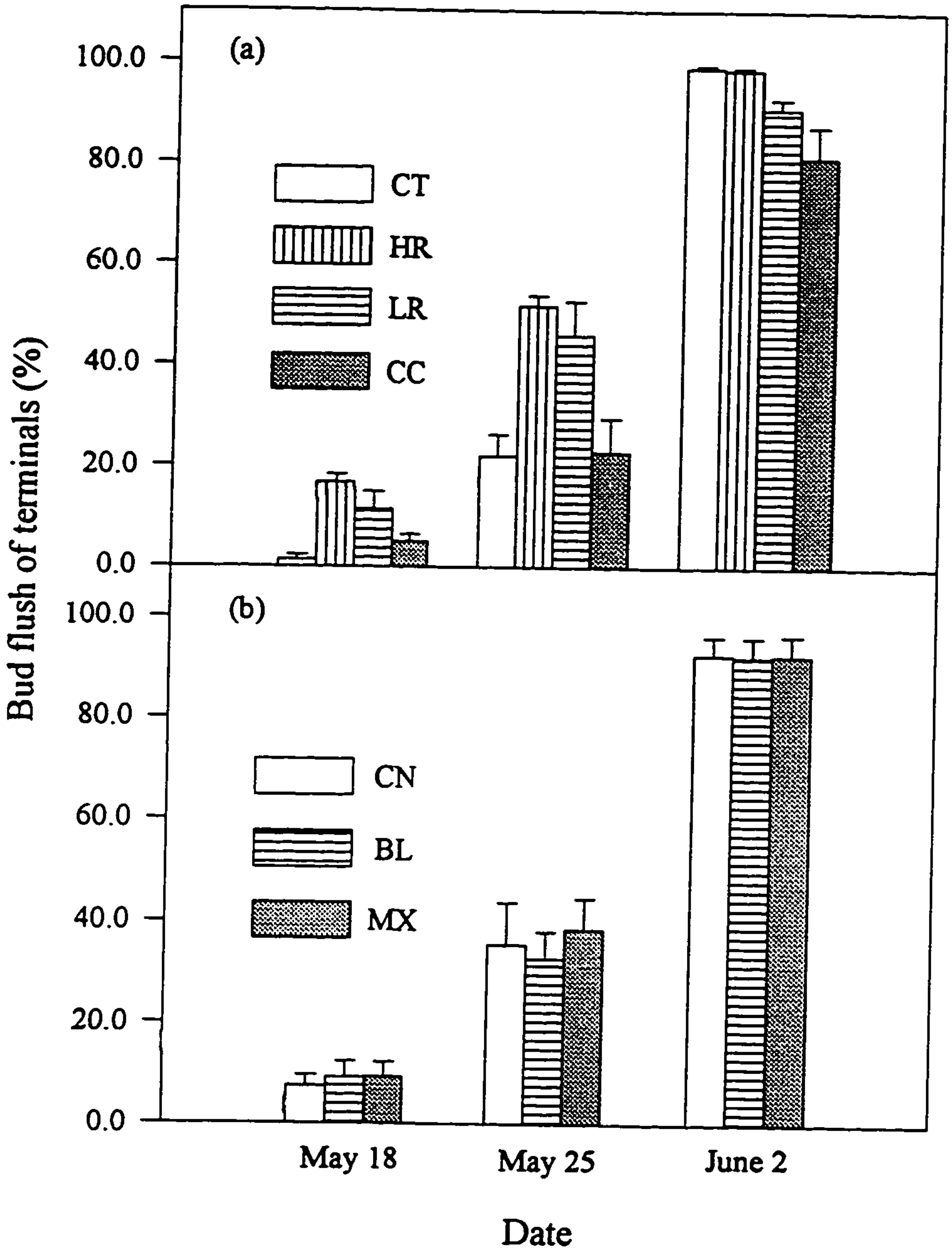

Figure 5.2 Mean and SE of cumulative percent budflush of terminals in subplot during first budflush of 1994 seedlings in the field at site 1: (a) canopy residual (CT-control, HR-high canopy residual, LR-low canopy residual and CC-clearcut), and (b) site preparation (CN-control, BL-blading and MX-mixing).

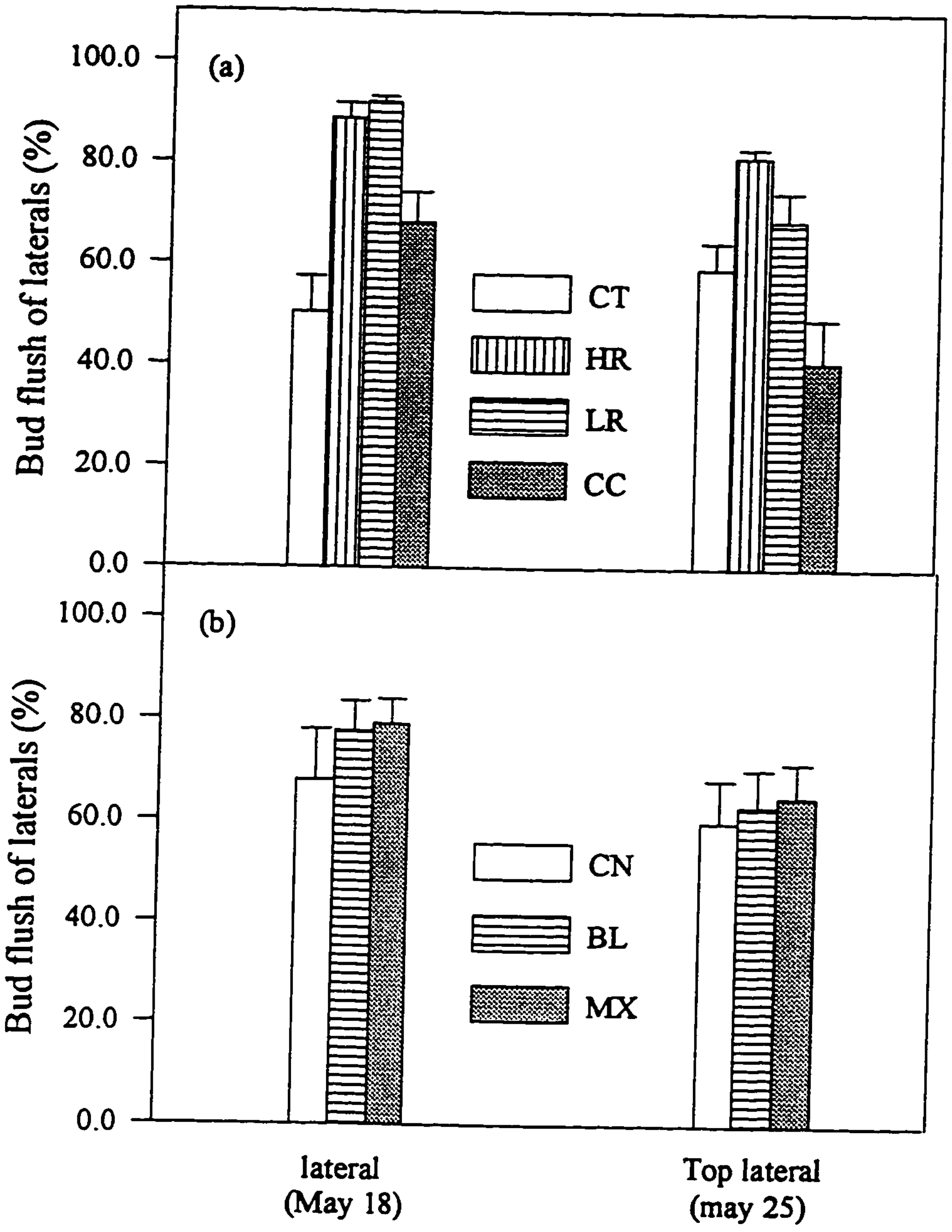

Figure 5.3 Means and SE of cumulative percent budflush of lateral and top lateral buds in subplot during first budflush in the field at site 1: (a) canopy residual (CT-control, HR-high canopy residual, LR- low canopy residual and CC-clearcut), and (b) site preparation(CN-control, BL-blading, and MX-mixing).

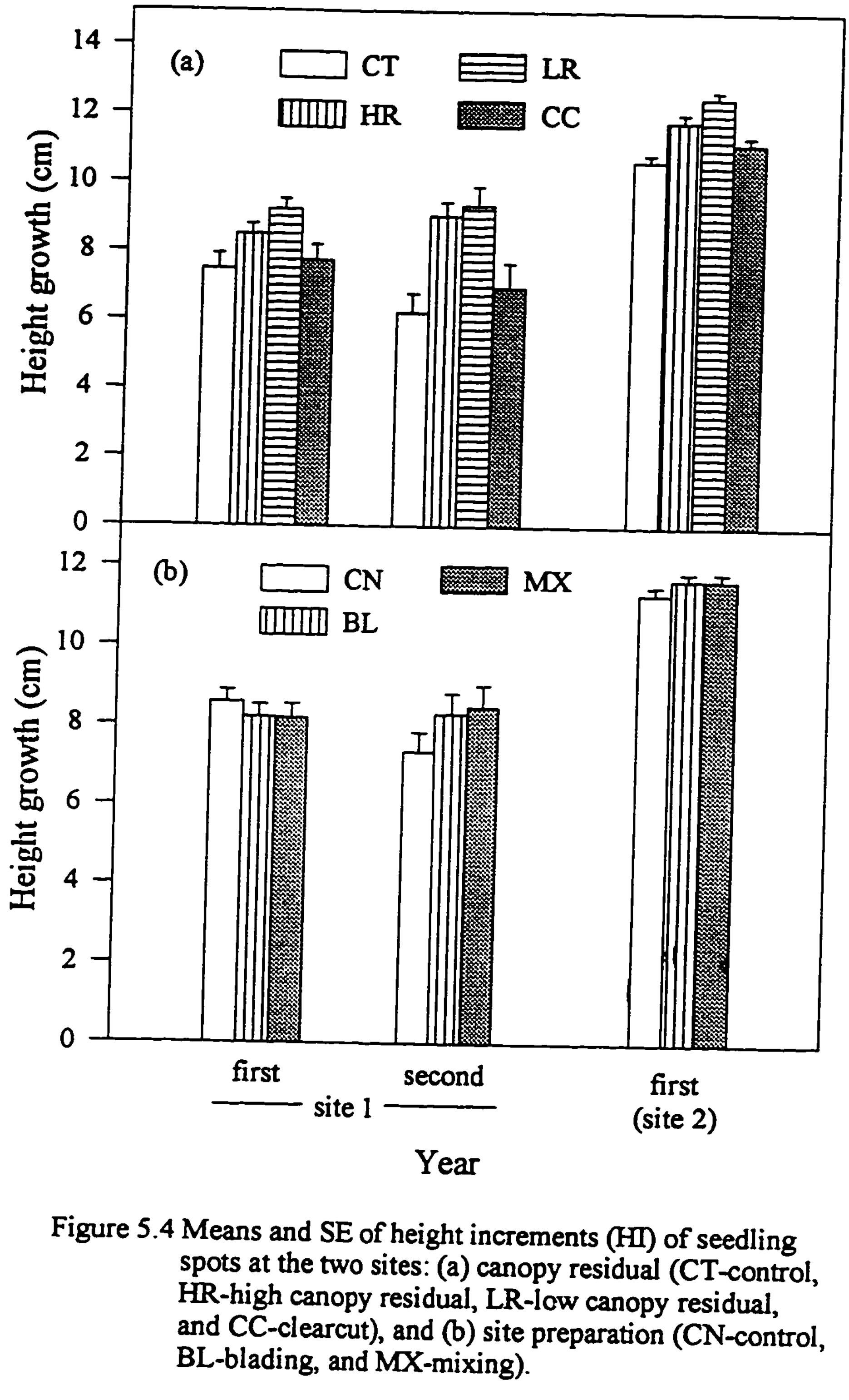

Figure 5.4 Means and SE of height increments (HI) of seedling spots at the two sites: (a) canopy residual (CT-control, HR-high canopy residual, LR-low canopy residual, and CC-clearcut), and (b) site preparation (CN-control, BL-blading, and MX-mixing).

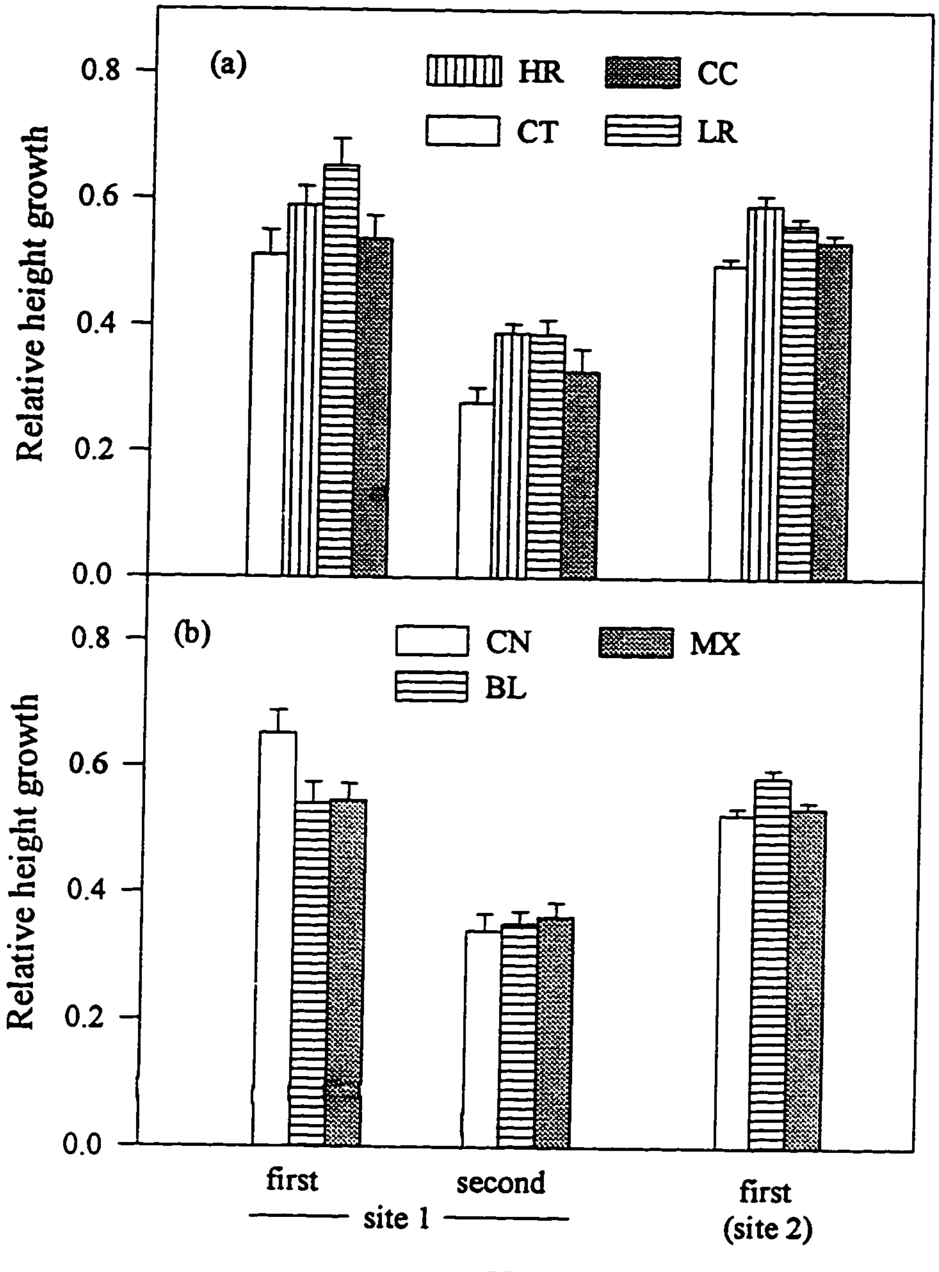

Figure 5.5 Means and SE of relative height increments (RHI) of seedling spots at the two sites: (a) canopy residual (CT-control, HR-high canopy residual, LR-low canopy residual, and CC-clearcut), and (b) site preparation (CN-control, BL-blading, and MX-mixing).

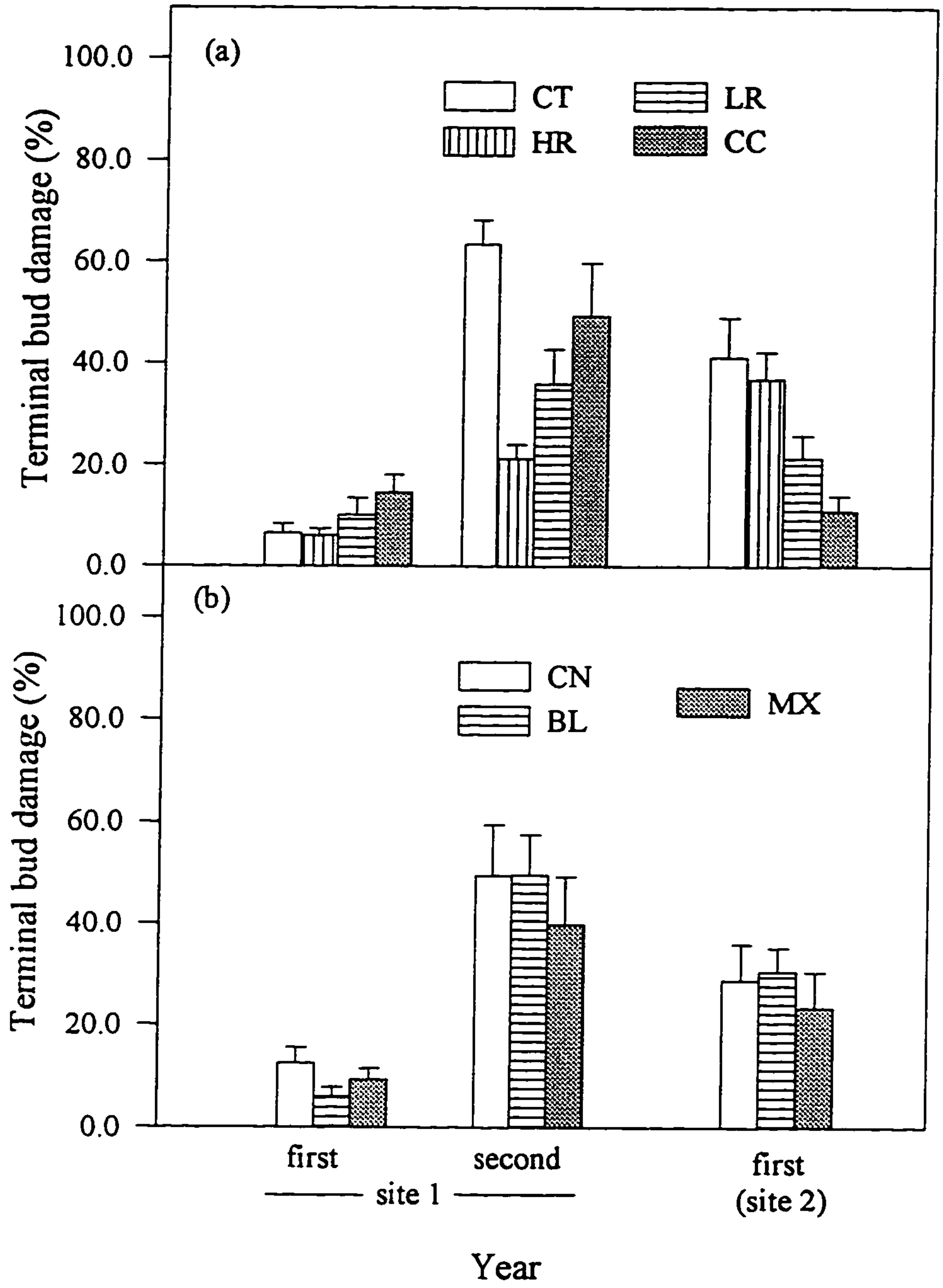

Figure 5.6 Means and SE of terminal bud damage in subplot at the two sites: (a) canopy residual (CT-control, HR-high canopy residual, LR-low canopy residual, and CC-clearcut), and (b) site preparation (CN-control, BL-blading, and MX-mixing).

CHAPTER 6

GAS EXCHANGE OF WHITE SPRUCE SEEDLINGS AFTER PLANTING UNDER CANOPY RESIDUAL AND SITE PREPARATION TREATMENTS

6.1 Introduction

Planting check, the slow growth of planted seedlings in the first few years, has been widely reported for white spruce plantations on clearcuts (Vyse 1981, Burdett *et al.* 1984, Mullin 1963, Nienstadt and Zasada 1990). At minimum, this slow growth means the loss of several growing seasons, but in many cases it also results in plantation failure if heavy beds of vegetation establish quickly and overtop the trees (Eis 1981). Poor initial establishment is most likely related to environmental stresses, especially water stress because of the lack of good contact between soil and roots in newly planted seedlings (Burdett 1990, Grossnickle 1988a).

Survival and growth of newly planted seedlings depends on root growth to re-establish intimate root-soil contact and normal water uptake from surrounding soils (Rietveld 1989). Carbohydrates for new root growth can come from current photosynthesis or carbohydrate reserves (Philipson 1988), depending upon species and site conditions (Rietveld 1989). Vapaavuori *et al.* (1992) demonstrated that new root development in white spruce depended on both current photosynthesis and carbohydrate reserves. Jiang *et al.* (1994) also observed new root development at the same time as increasing rate of net photosynthesis in outplanted white spruce seedlings. Therefore, a rapid reestablishment of photosynthetic capacity is critical for the establishment of outplanted white spruce seedlings, especially for overwintered planting stock where prolonged storage can partially deplete carbohydrate reserves.

Environmental conditions under a forest canopy are less extreme compared to open sites; warmer minimum night temperatures, cooler daytime temperatures, higher levels of humidity and lower evaporative demand reduce frost occurrence and ameliorate water stress (Chapter 4). Low light intensity under a canopy can also decrease the photoinhibition and subsequent photooxidation caused by an interaction between subfreezing temperatures and high irradiance (Lundmark and Hällgren 1987, Orlander 1993), particularly in late spring and early fall (Chapter 2). There was an improved water status in loblolly pine seedlings under a shelterwood canopy compared to seedlings on open sites (Dalton and Messina 1995). In white spruce, studies of water relations were conducted on seedlings planted on open sites (Grossnickle and Blake 1985, Grossnickle and Blake 1986, Grossnickle and Blake 1987, Grossnickle 1988a, Grossnickle 1988b, Grossnickle and Heikurinen 1989). It is not clear if a shelterwood canopy can enhance water status and early photosynthesis of planted white spruce seedlings compared to the seedlings in clearcuts. It has been noted that white spruce seedlings planted in understories experience less planting check than those on clearcut sites (Mullin 1963). A study by Marsden *et al.* (1996) showed that white spruce seedlings grown under high vapor pressure deficit (VPD) had lower photosynthetic capacity than seedlings grown under low VPD. Partial removal of the forest canopy by shelterwood cutting allows more irradiance to reach the forest floor and raises soil temperature, but does not increase environmental extremes excessively compared with uncut forests (Chapter 4). These conditions are favorable for germination and survival of white spruce seedlings (Eis 1967, Lees 1972). This study compares the photosynthesis, stomatal conductance and water use efficiency of white spruce seedlings planted under various levels of canopy residual and site preparation treatments in the early period of establishment after planting (from the time immediately after planting to two years later). I expected that shelterwoods promoted the recovery of gas exchange of planted white spruce seedlings.

6.2 Materials and methods

6.2.1 Study sites and treatments

Two study sites were established in the Weldwood Forest Management Area near Edson, Alberta, Canada: site 1 was about 65 km northwest of Edson (53°42'N, 117°05'W) and site 2 about 15 km southeast of site 1 (53°38N, 116°58'W). Average slope was less than 5% in site 1 and between 5-10% at site 2. Dominant soil type at the two sites was Brunisolic Gray Luvisols. Climate is subhumid and continental, with long, cold winters and mild summers. Annual precipitation is approximately 500 mm. Both sites were covered by mature aspen-white spruce mixedwood prior to cutting treatment. Under the canopy, the shrub layer was mainly composed of *Rosa acicularis* Lindl. and *Viburnum edule* (Michx.) Raf. Major herbaceous species were *Aralia nudicaulis* L., *Cornus canadensis* L., *Epilobium angustifolium* L., *Mertensia paniculata* (Ait) G. Don., *Pyrola asarifolia* Michx. and *Rubus pubescens* Raf.

A split-plot with two replicate blocks was established at each site to investigate the effects of canopy residual and soil preparation treatments, with canopy residual as the main plot and site preparation as the subplot. There were four levels of canopy residuals, two shelterwood seeding cuts (high and low canopy residuals), one conventional clearcut (complete canopy removal) and one control (uncut). Each main plot was 150 m x 150 m, the outer 25 m served as a buffer leaving a 1 ha sampling plot in the centre. Cutting was done in 1993/1994 winter at site 1 and in 1995/1996 winter at site 2. Cutting treatments were slightly different between two sites. At site 1, basal area of remaining trees was 30.5 m^2/ha (12.5 m^2/ha white spruce) in the control, 20.2 m^2/ha (3.6 m^2/ha white spruce) in high canopy residual and 12.5 m^2/ha (3.8 m^2/ha white spruce) in low canopy residual, whereas similar cutting treatments at site 2 left 35.4 m^2/ha (7.8 m^2/ha white spruce), 28.6 m^2/ha (5.9 m^2/ha white spruce) and 22.7 m^2/ha (5.8 m^2/ha white spruce) basal area.

Within each canopy treatment plot, three types of mechanical site preparation were employed: blading, mixing and control (i.e. no scarification). Subplots, 100 m long and 33 m wide, were set up in early summer of 1994 at site 1. Plot layout at site 2 in early summer of 1996 was the same except in one of the clearcuts where subplots were separated from each other by a 30 m wide untreated zone. Blading removed organic litter ("LFH" horizon) and part of top mineral soil to the depth of 11 to 13 cm, exposing the "Ae" horizon, while in the mixing treatment the mixed layer, 10 to 13 cm deep, was composed of materials from "LFH" and "Ae" horizons. Both blading and mixing were done by a Thomas 233 Skidsteer loader fitted with either a hydraulic angle tilt blade (160 cm wide) or a MJ Merri-Crusher mixing head (140 cm wide).

6.2.2 Seedlings

White spruce seeds were collected 60 km south of the sites and raised at a B.C. Ministry of Forests nursery in Ladner. The container grown seedlings (PSB 4-15B, 1 + 0) from a subsample of the seedling population (n=60) averaged 18.1 ± 0.5 cm in height and 0.4 ± 0.1 cm in root collar diameter when planted. Two types of seedling stock were used: spring stock, which flushed shortly after planting, and summer stock, which did not flush until the following spring. At site 1 summer stock was planted in the middle June of 1994 and early July of 1995. At site 2, both spring and summer stocks were used, with spring stock planted in late May and summer stock in early July of 1996. Planting was done in seedling spots chosen randomly from the correct treatment zone within each site preparation treatment. There were 10 seedling spots at site 1 and 15 at site 2 within each subplot. Seedlings were planted within 1 m^2 planting spot. At each spot, five seedlings were planted at site 1 and four seedlings at site 2 so that seedling population in subplots was 50 at site 1 and 60 at site 2. In the blading treatment, seedlings were planted in such a way that the whole root system of seedlings was in mineral soil, whereas in mixing and control subtreatments about a third of the root plug was in mineral soil.

6.2.3 Seedling environments

Daily mean, maximum and minimum air temperatures and relative humidities at seedling height (0.50 m above ground) were measured in the canopy treatments of clear cut, high canopy residual and control, with 101 thermisters and RH-thermistor probes (Campbell Scientific, Inc., Logan, UT). At site 1, measurements of seedling environments replicated in two blocks were continued for two growing seasons from 1994 to 1995 (Chapter 4), whereas monitoring of microclimates at site 2 was done in one block from the time of planting (end of May) to late September. All temperature and humidity sensors were suspended in the centre of a horizontal white PVC pipe (5.0 cm diameter and 30 cm long for temperature sensors and 8.0 cm diameter and 50 cm long for RH sensors) to shield them from direct radiation. Small holes were drilled at bottom of the pipes to prevent heat and water buildup. Sensors were connected to a datalogger (CR21, Campbell Scientific Inc., Logan, UT).

6.2.4 Measurements of gas exchange

In the growing season of 1996, gas exchange was measured on the seedlings from three canopy residual (control, high canopy residual and clearcut) and two site preparation (control and blading) treatments at different times after planting, immediately after at site 2 and one (95 seedlings) and two years later (94 seedlings) at site 1. At site 1, photosynthesis was measured in late May, mid-August, and late September. Spring measurement was on one-year-old foliage and summer and fall measurements on current foliage. All sample shoots were taken from top laterals except second-year-seedlings where only terminals were available in springtime. At each sampling date, five seedling spots were randomly chosen from subtreatment cell and one seedling from one each spot was selected. Measurements were made by block to reduce daily variation in temperature and moisture between treatments.

At site 2, photosynthesis measurements were 3, 12, 27, 82, 101, and 106 days after planting (June 3, June 12, June 27, August 20, September 19, and September 24, 1996) on spring stock and 3, 17, 25, 45, 66, and 71 days after planting (July 8, July 22, July 30, August 19, September 19, and September 24, 1996) on summer stock. Measurements of photosynthesis in spring stock were taken on terminals for the first three measurements (June 3, June 12 and June 30) and then on top laterals after current needles were fully developed. Only terminals were measured in the summer stock. Because of limited seedlings and frequent measurements, photosynthesis was sometimes measured more than one time on the same terminals before a new shoot was chosen.

Gas exchange at saturated light level was measured using a portable gas analysis system (LCA-2) equipped with a conifer cuvette (Analytical Development Corp., Hoddenson, England). Air flow rate was set at 8 ml/s. Relative humidity of incoming air was adjusted by using silica gel desiccant so that the relative humidity in the cuvette during measurements was approximately equal to the relative humidity of ambient air. Light source was from a quartz halogen lamp positioned on the top of the cuvette to provide light to over 1000 μmol $m^{-2}s^{-1}$. Following gas exchange measurements, the sampled shoots were frozen for leaf area determinations. Projected leaf areas of the shoots were determined with DeskScan II image scanning software on a ScanJet 4c scanner (Hewlett Packard, Palo Alto, CA). Needle areas were calculated from the captured image using SigmaScan Pro for windows (Jandel Scientific, San Rafael, CA).

6.2.5 Data analysis

Light-saturated net photosynthesis (A_{max}; µmol m^{-2} s^{-1}), transpiration (E; mmol m^{-2} s^{-1}) and stomatal conductance to H_2O (g_s; mmol m^{-2} s^{-1}) were calculated as described by Caemmerer and Farquhar (1981). Instaneous water use efficiency (WUE; µmol CO_2 $mmol^{-1}$ H_2O) was calculated as WUE=A/E. The general linear models procedure available in SAS Release 6.11 (SAS Institute Inc., 1995) was used to test the treatment effects of canopy residual and site preparation on photosynthesis of white spruce seedlings after planting at specific time and location except for the measurements at site 2 in September when only data from one block was available and a two way ANOVA model was employed to analyze data in these two measurements.

6.3 Results

Reduction of canopy residual increased daytime temperature and VPD and reduced relative humidity and nighttime temperature (see Figures 4.1 and 4.2 for site 1 and 6.1 for site 2). Thus shelterwood had higher humidity, lower VPD, cooler maximum and warmer minimum temperatures and reduced risk of night frosts in spring and fall compared to the clearcut, whereas differences between high canopy residual and control were generally small according to the temperature data from both sites.

In the first year after planting, light-saturated net photosynthesis (A_{max}) was 8 µmol m^{-2} s^{-1} in the summer stock only three days after planting and remained relatively stable during the rest of growing season (Figures 6.2-a and 6.2-e). The A_{max} in spring stock was below 6 µmol m^{-2} s^{-1} about a month after planting but an increase was apparent thereafter (Figures 6.2-b and 6.2-f). By late August, both summer and spring stocks reached a similar photosynthetic capacity (around 8 µmol m^{-2} s^{-1}). The decline of A_{max} was rapid in late September when minimum temperatures dropped to several degrees below 0°C

(Figure 6.1).

Seasonal pattern of A_{max} was similar in the second (Figures 6.2-c and 6.2-g) and third year (Figures 6.2-d and 6.2-h) seedlings: showing an increase from May to August and a decrease thereafter. In mid-August, all seedling types (include both spring and summer stocks of first year seedlings and second and third year seedlings) showed similar photosynthetic rates (around 8 μmol m^{-2} s^{-1}). In late September, old seedlings (one and two years after planting) had higher A_{max} than newly planted seedlings (first growing season in the field).

Stomatal conductance to H_2O (g_s) followed a similar pattern to that of A_{max} (Figures 6.2 and 6.3), whereas an apparent increase in water use efficiency (WUE) was noted from summer to fall for all types of seedlings (Figure 6.4). Decrease of g_s in the fall were greater than that of A_{max}.

Seedlings in clearcut generally had lower A_{max} and WUE than those in control or high canopy residual for all types of seedlings (Figures 6.2 and 6.4, Tables 6.1 and 6.2). The g_s was also lower in seedlings in the clearcut treatment (Figure 6.3, Table 6.3). When seedlings got older, the differences of g_s among the treatments appeared to reverse (from Figures 6.2-a, 6.2-b, 6.2-c to 6.2-d).

Effects of site preparation on gas exchange of planted white spruce seedlings were less apparent than those of canopy residual (Figures 6.2, 6.3, and 6.4, Tables 6.1, 6.2 and 6.3). The A_{max} and g_s seemed higher in blading than in control treatments (Figures 6.2 and 6.3), particularly in first year seedlings. This difference tended to decline as seedlings got older. The WUE of the second and third year seedlings appeared to be higher in blading than in control treatment (Figure 6.4), but no clear trend was seen in first year seedlings.

6.4 Discussion

Newly planted seedlings may need several weeks to achieve a positive carbon balance because of seedling distress from lifting, handling, storing, shipping, and planting and less favorable environmental conditions at planting sites (Marshall 1985, Vapaavuori *et al.* 1992). In this study, however, resumption of high rates of photosynthesis of white spruce seedlings after their planting took place immediately in both spring and summer stocks, indicating little transplanting stress. Similar phenomenon was also observed by Wang (unpublished data) in three-year-old bareroot spring stock planted either in June or July in Devon, Alberta (almost the same altitude as my sites). Quick recovery of photosynthetic capacity can provide more carbohydrates for new root growth and promote establishment of planted seedlings (Rietveld 1989). High photosynthetic capacity after planting in this study may be an indication of little physiological planting check in these planted white spruce seedlings (see Chapter 5 for seedling growth).

Spring stock had relatively low A_{max} shortly after planting compared to summer stock. The period of low A_{max} immediately after planting coincided with a drought spell in June (Figure 6.1-b) and the time of budbreak and shoot elongation. Reduced resistance to water stress (Colombo and Teng 1992) and increased respiration (Bachelard and Wightman 1973, Bhella and Roberts 1975) during budbreak and rapid shoot elongation may results in lower rates of net photosynthesis. In addition, seedlings in a dormant state are more stress-resistant than those in an actively growing state (Rietveld 1989). Higher A_{max} and g_s in second and third year seedlings than first year seedlings after frosts in the fall might indicate an increase of stress resistance with the progress of establishment, although these seedlings were planted at different sites.

Seedlings in clearcut showed consistently lower A_{max} than those in the high canopy residual and control despite cool wet years in 1995 and 1996. Water stress can easily develop in newly planted seedlings (Rietveld 1989), even if seedlings are in well-watered conditions (Sands 1984). White spruce is a species susceptible to water stress because of slow new root growth after planting (Grossnickle and Blake 1987), high relative water content at turgor loss point (Grossnickle and Blake 1987, Colombo and Teng 1992), and stomata sensitivity to change in VPD (Grossnickle and Blake 1986, Marsden *et al.* 1996). Seedlings in clearcuts experience high daytime temperatures, low relative humidity and high evaporative demands (Chapter 3), which all contribute to the development of more water stress in open-grown seedlings. Strong radiation in clearcuts may also cause photoinhibition in planted seedlings. White spruce seedlings grown under an aspen canopy had a higher A_{max} than seedlings in open sites (Chapter 2). Marsden *et al.* (1996) showed a reduced A_{max} when seedlings were grown at high VPD.

In the first year seedlings, the differences in A_{max} between open-grown (clearcut) and understory (high canopy residual and the control) seedlings appeared to increase late in the growing season when minimum air temperatures began to drop below 0°C (Figure 6.1). Similar phenomenon was also noted in white spruce seedlings planted under aspen canopy and in open site (Chapter 2). Freezing air temperatures inhibit the light-saturated rate of photosynthesis and increase the susceptibility of photosynthetic systems to photoinhibition (Lundmark and Hällgren 1987). Higher minimum temperature and low intensity of irradiance in the understory would reduce the photoinhibition caused by an interaction between freezing temperature and solar radiation (Lundmark and Hällgren 1987, Lundmark *et al.* 1988, Dang *et al.* 1992). Faster decrease of g_s than A_{max} after frosts might suggest that stomatal opening is more sensitive to freezing stress than the photosynthetic systems.

Seedlings in the blading performed slightly better than those in the control. Scarification removes vegetation and the organic layer and may improve light and soil moisture (Spittlehouse and Childs 1992) and nutrient availability for a short period after site preparation treatment (Macdonald *et al.* 1996). For the newly planted seedlings, however, lack of water for transpiration is probably the most limiting factor (Rietveld 1989).

In conclusion, the results showed that there was an apparent improvement in photosynthetic capacity of white spruce seedlings planted in shelterwoods in comparision with seedlings in the clearcut. This should translate to improved seedling establishment and reduction in the severity of planting check. However, reduced light availability under shelterwood could result in reduced seedling growth (Youngblood and Zasada 1991, Kabzems and Lousier 1992). Secondly, high rates of net photosynthesis right after planting suggested that the integrity of photosynthetic systems in outplanted white spruce seedlings can be maintained during transplanting. Resumption of photosynthetic capacity after planting, depending upon environmental conditions at sites and seedling status, can take place immediately after planting, which may be critical for survival and growth of planted white spruce seedlings.

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Table 6.1 Probability values for light-saturated net photosynthesis of white spruce seedlings immediately after planting (at site 2) and one and two years later (at site 1) under three canopy residual (C: CT-control, HR-high canopy residual and CC-clearcut) and two site preparation treatments (S: CN-control and BL-blading) in the growing season of 1996.

	First year seedlings (Spring stock, Site 2)				First year seedlings (Summer stock, Site 2)			
Source	JN3	JN12	JN27	A17	J8	J22	J30	A17
B	0.2964	0.1913	0.3210	0.6516	0.1480	0.7037	0.9878	0.0997
C	0.6471	0.0854	0.6629	0.0453	0.3482	0.3902	0.2174	0.3409
B*C	0.1006	0.0219	0.0322	0.6255	0.1637	0.1740	0.1542	0.3099
S	0.0065	0.0056	0.0807	0.8536	0.3772	0.1080	0.1037	0.2755
S*C	0.0522	0.0163	0.5586	0.8352	0.3041	0.7714	0.8753	0.7321
S*C*B	0.8967	0.9838	0.2927	0.1006	0.7297	0.3786	0.4476	0.0480
	S19	S24			S19	S24		
C	0.0003	0.0002			0.5721	0.0025		
S	0.1695	0.2141			0.1048	0.0324		
S*C	0.0015	0.0794			0.0672	0.0137		

	Second year seedlings (Site 1)			Third year seedlings (Site 1)		
Source	May	Aug	Sept	May	Aug	Sept
B	0.5695	0.8520	0.5951	0.2239	0.9351	0.3908
C	0.1279	0.4502	0.2894	0.0450	0.3358	0.0211
B*C	0.0044	0.3504	0.5221	0.8757	0.6634	0.8221
S	0.1298	0.9703	0.7319	0.3578	0.1659	0.4657
S*C	0.0115	0.9159	0.9947	0.3815	0.9550	0.1574
S*C*B	0.9868	0.1281	0.3402	0.1012	0.0634	0.3825

Note: B-block, C-canopy residual, and S-site preparation. Time of measurement was June 3, June 12, June 27, August 17, September 19, and September 24 in spring stock and July 8, July 22, July 30, August 17, September 19, and September 24 in summer stock. Data on September 19 and September 24 were from only one block.

Table 6.2 Probability values for water use efficiency at saturating light in white spruce seedlings at different times after planting (immediately after at site 2 and one and two years later at site 1) under three canopy residual (C: CT-control, HR-high canopy residual and CC-clearcut) and two site preparation treatments (S: CN-control and BL-blading) in the growing season of 1996.

	First year seedlings (Spring stock, Site 2)				First year seedlings (Summer stock, Site 2)			
Source	JN3	JN12	JN27	A17	J8	J22	J30	A17
B	0.9814	0.3658	0.2822	0.1793	0.4375	0.4240	0.8561	0.1903
C	0.9828	0.0582	0.7941	0.3635	0.4792	0.2430	0.3482	0.6419
B*C	0.1871	0.3437	0.1586	0.3452	0.7582	0.0969	0.0417	0.3034
S	0.1966	0.2915	0.1307	0.3080	0.4344	0.0640	0.4687	0.3653
S*C	0.2688	0.7491	0.8302	0.3430	0.6910	0.1047	0.0593	0.8654
S*C*B	0.0536	0.4385	0.0264	0.0304	0.0048	0.6041	0.4596	0.0006
	S19	S24			S19	S24		
C	0.0001	0.0001			0.0167	0.8976		
S	0.0987	0.0199			0.6144	0.5640		
S*C	0.2558	0.8708			0.6368	0.0545		

	Second year seedlings (Site 1)			Third year seedlings (Site 1)		
Source	May	Aug	Sept	May	Aug	Sept
B	0.8093	0.0632	0.9153	0.7859	0.4757	0.4941
C	0.1750	0.0212	0.2119	0.1361	0.3395	0.7359
B*C	0.2316	0.7024	0.3457	0.7628	0.2534	0.2808
S	0.9300	0.5808	0.1938	0.4028	0.0933	0.2696
S*C	0.9865	0.3719	0.2123	0.6375	0.8891	0.6006
S*C*B	0.1450	0.0508	0.7237	0.0217	0.0678	0.0550

Note: B-block, C-canopy residual, and S-site preparation. Time of measurement was June 3, June 12, June 27, August 17, September 19, and September 24 in spring stock and July 8, July 22, July 30, August 17, September 19, and September 24 in summer stock. Data on September 19 and September 24 were from only one block.

Table 6.3 Probability values for stomatal conductance at saturating light in white spruce seedlings at different times after planting (immediately after at site 2 and one and two years later at site 1) under three canopy residual (C: CT-control, HR-high canopy residual and CC-clearcut) and two site preparation treatments (S: CN-control and BL-blading) in the growing season of 1996.

	First year seedlings (Spring stock, Site 2)				First year seedlings (Summer stock, Site 2)			
Source	JN3	JN12	JN27	A17	J8	J22	J30	A17
B	0.1027	0.5997	0.1058	0.8228	0.0581	0.0343	0.0873	0.1815
C	0.2845	0.1166	0.5092	0.1791	0.2667	0.0071	0.3129	0.6290
B*C	0.3519	0.6996	0.0188	0.7934	0.0457	0.9121	0.0819	0.1660
S	0.1124	0.0701	0.1029	0.3606	0.2160	0.5333	0.0181	0.9009
S*C	0.8908	0.4221	0.0601	0.7686	0.0806	0.2911	0.1574	0.3636
S*C*B	0.3894	0.5181	0.8284	0.0046	0.9380	0.5941	0.9163	0.3299
	S19	S24			S19	S24		
C	0.0249	0.0598			0.2668	0.0013		
S	0.0115	0.0371			0.1623	0.0096		
S*C	0.0915	0.1495			0.2446	0.0087		

	Second year seedlings (Site 1)			Third year seedlings (Site 1)		
Source	May	Aug	Sept	May	Aug	Sept
B	0.3635	0.5108	0.2412	0.5452	0.0446	0.0361
C	0.2999	0.4636	0.7348	0.6710	0.0159	0.2658
B*C	0.8949	0.0427	0.1189	0.0255	0.8759	0.3220
S	0.6706	0.2638	0.1448	0.4252	0.9434	0.7156
S*C	0.7754	0.0592	0.6914	0.0598	0.8500	0.7736
S*C*B	0.0368	0.7395	0.2779	0.6908	0.3338	0.8215

Note: B-block, C-canopy residual, and S-site preparation. Time of measurement was June 3, June 12, June 27, August 17, September 19, and September 24 in spring stock and July 8, July 22, July 30, August 17, September 19, and September 24 in summer stock. Data on September 19 and September 24 were from only one block.

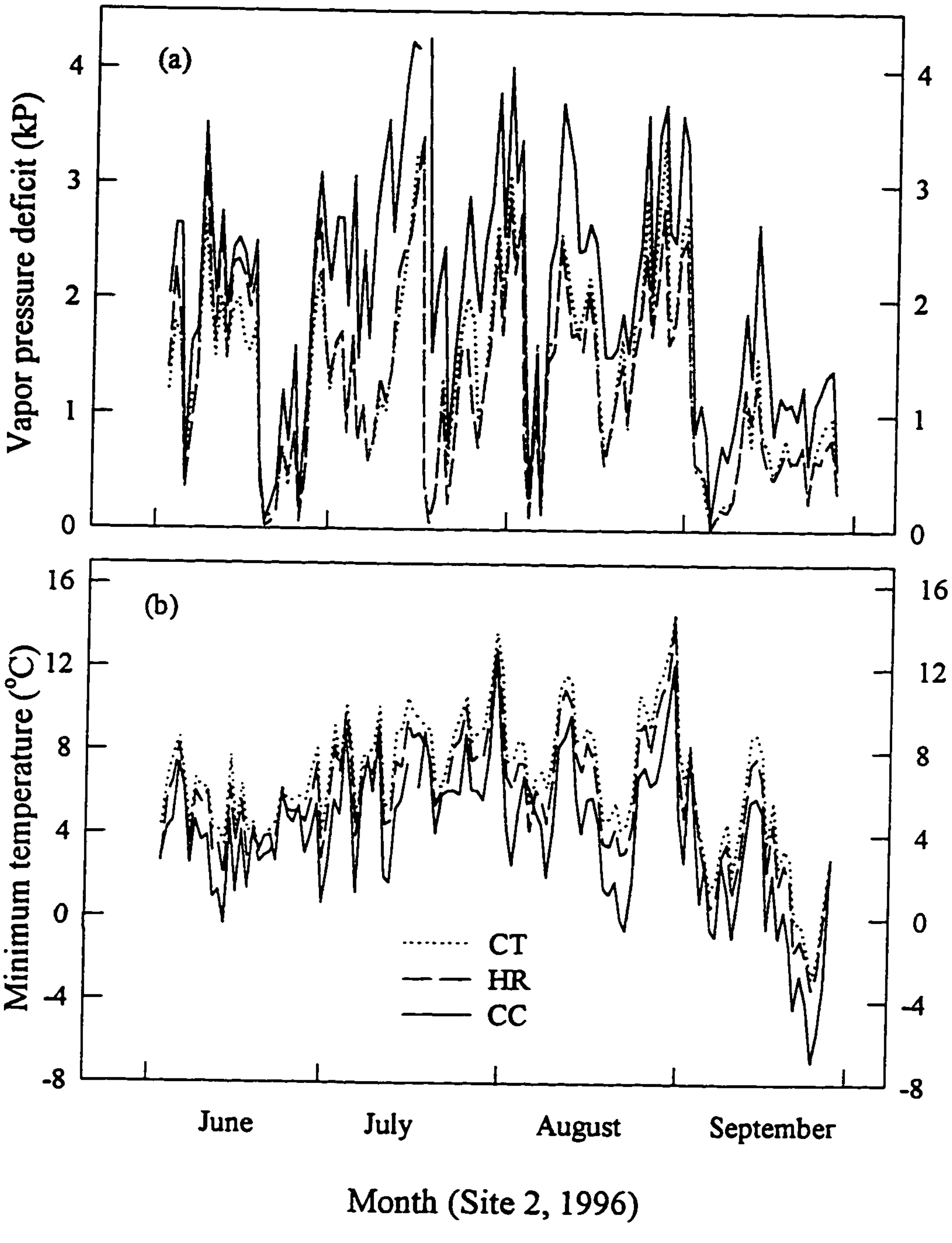

Figure 6.1 Daily maximum vapor pressure deficit (a) and minimum temperature (b) at site 2 under three levels of canopy residual (CT-control, HR-high canopy residual and CC-clearcut).

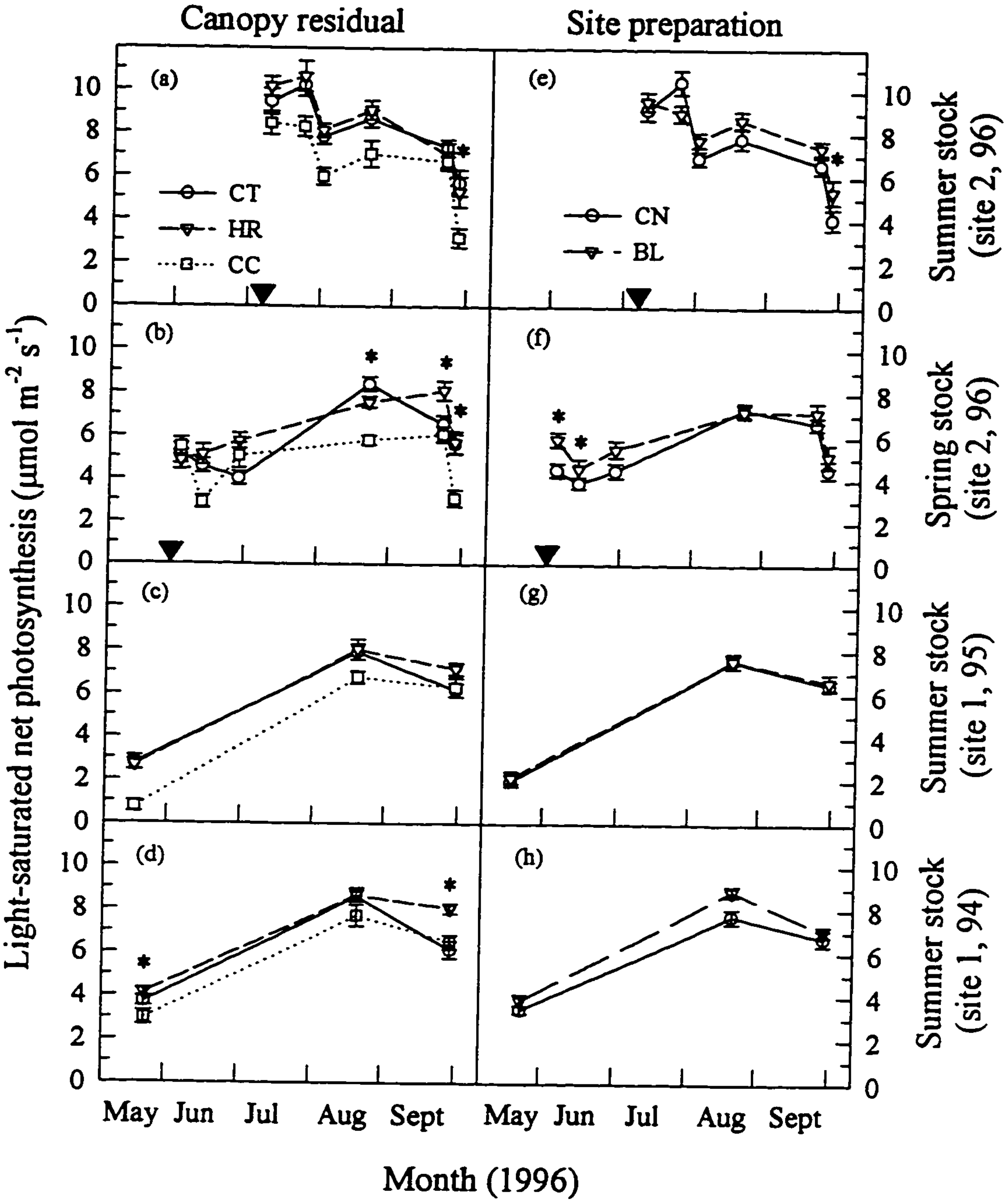

Figure 6.2 Photosynthesis of white spruce seedlings (mean± SE, n=20 for canopy residual and 30 for site preparation) after planting under three canopy residual (CT-control, HR-high canopy residual and CC-clearcut) and two site preparation (CN-control and BL-blading) treatments. Stock type, site and year of planting are depicted on the right. The symbol ▼ indicates the planting time for seedlings at site 2. Significant difference is indicated by * ($P<0.05$).

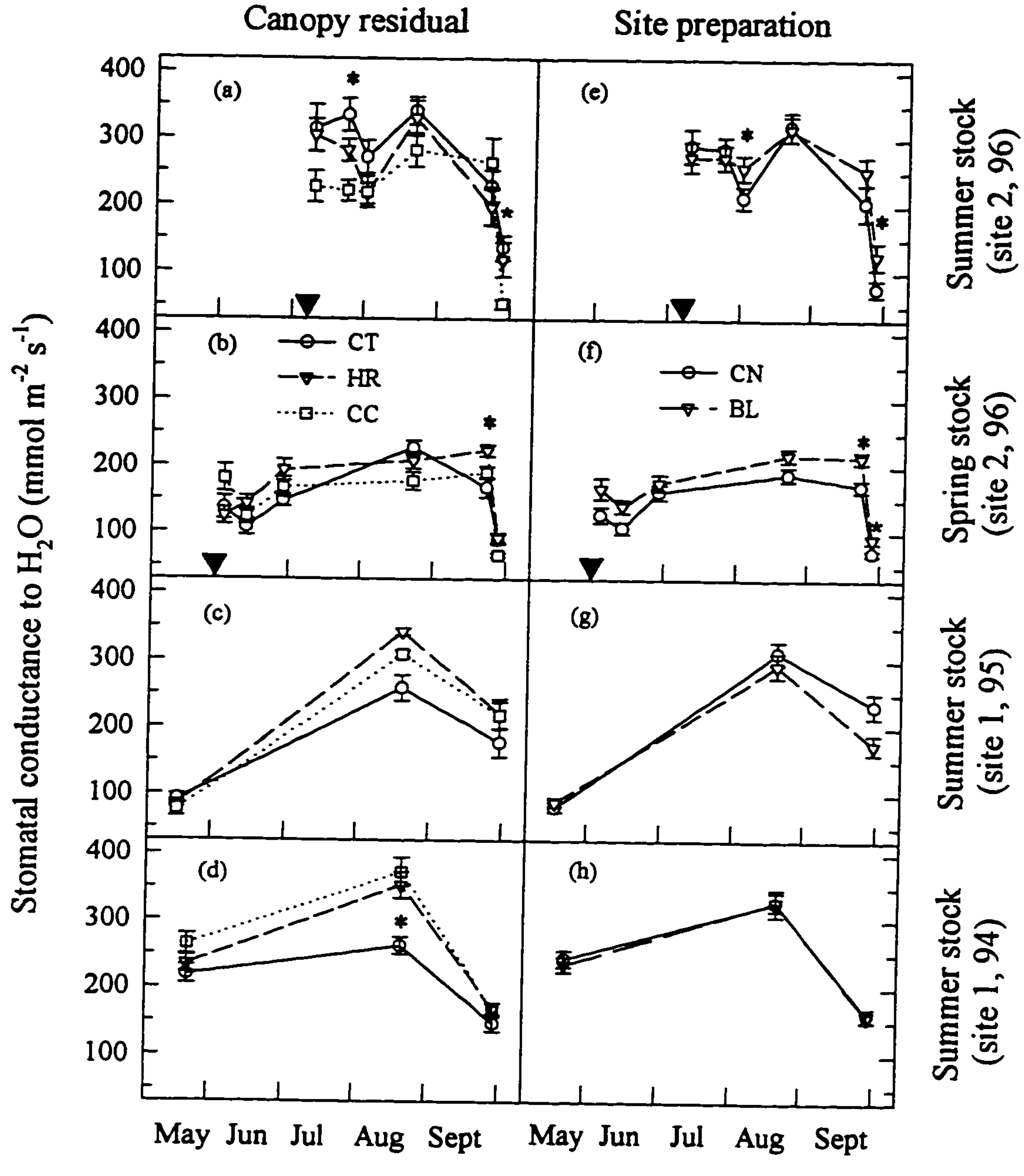

Figure 6.3 Stomatal conductance to H_2O of white spruce seedlings (mean ± SE, n=20 for canopy residual and 30 for site preparation) after planting under three canopy residual (CT-control, HR-high canopy residual and CC-clearcut) and two site preparation (CN-control and BL-blading) treatments. Stock type, site and year of planting are depicted on the right. The symbol ▼ indicates the planting time for seedlings at site 2. Significant treatment effect is indicated by * (P<0.05).

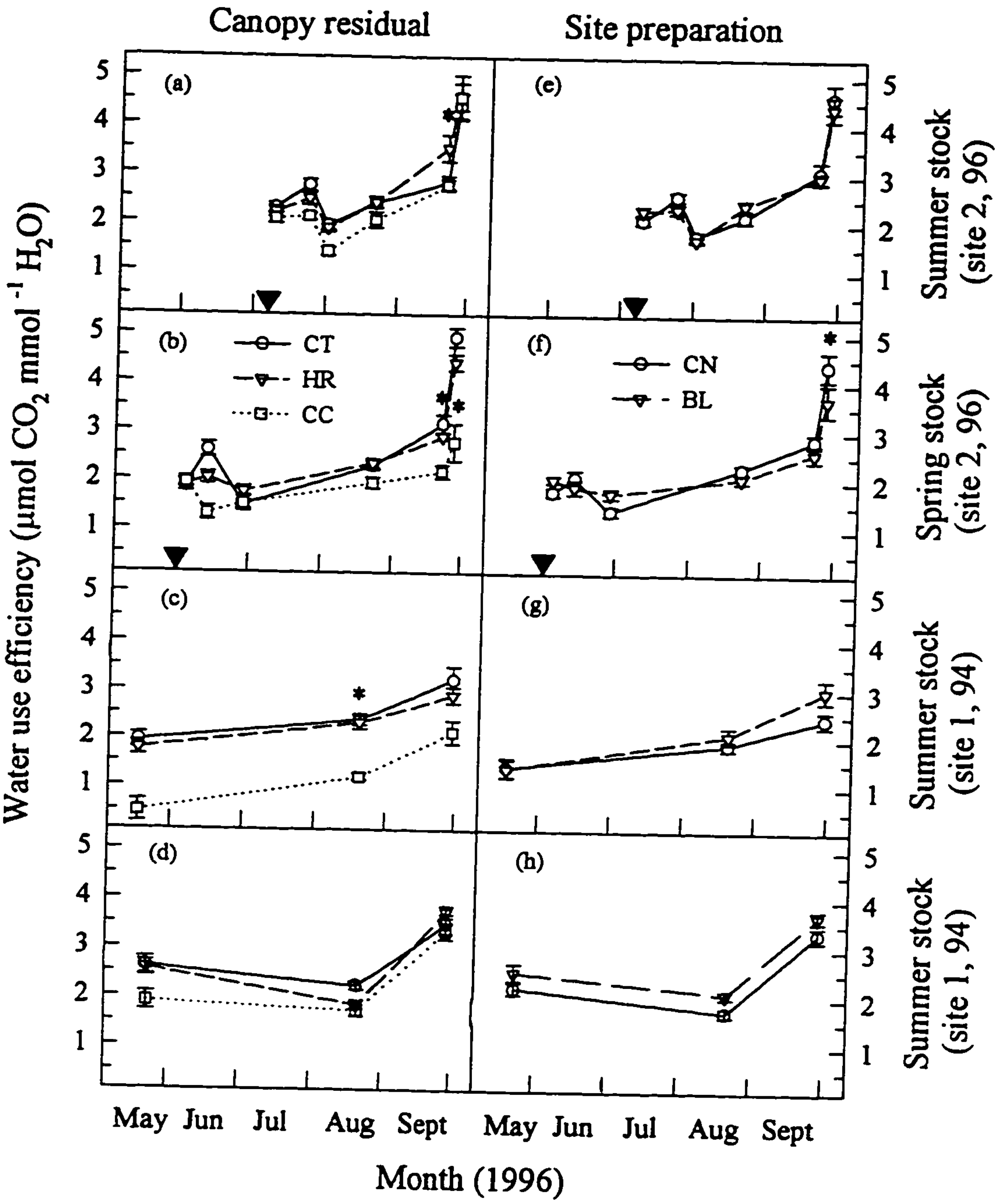

Figure 6.4 Water use efficiency of white spruce seedlings (mean± SE, n=20 for canopy residual and 30 for site preparation) after planting under three canopy residual (CT-control, HR-high canopy residual and CC-clearcut) and two site preparation CN-control and BL-blading) treatments. Stock type, site and year of planting are depicted on the right. The symbol ▼ indicates the planting time for seedlings at site 2. Significant treatment effect is indicated by * ($P<0.05$).

CHAPTER 7
SYNTHESIS

7.1 Summary and conclusions

The overall objective of this dissertation was to advance understanding of the ecophysiology of understory white spruce. The application of this knowledge is to develop silvicultural systems that are capable of initiating white spruce under partial canopies in boreal mixedwoods (Lieffers and Beck 1994, Lieffers *et al.* 1996, Brace and Bella 1988, Navratil *et al.* 1994, Youngblood 1990). Chapter 2 determined the light and temperature responses in white spruce seedlings grown in an aspen understory and in open conditions; Chapter 3 examined the seasonal photosynthesis in white spruce saplings; and Chapter 4, 5, and 6 reported the effects of canopy residual and site preparation on microclimates, seed germination, recovery of photosynthesis after planting, and survival and growth of planted seedlings.

In Chapter 2, seasonal photosynthetic response of open-grown and understory white spruce seedlings to light and temperature showed that understory seedlings had lower compensation and saturation points and higher photochemical efficiency than the seedlings grown in open conditions. Light intensity is low in summer due to leaf development of the overstory canopy (Chapters 2 and 3), but understory white spruce was able to acclimate photosynthetically to seasonal variation of light in the aspen understory and maintained a positive carbon balance by decreasing its compensation points to near zero (Chapter 2). This study demonstrated that white spruce has a stronger ability in utilizing low light than previously reported (DeLong 1991, Greenway 1995).

In general, light resources are limited in the understory and may be the factor limiting the development of understory plants (Smith 1986). Aspen-dominated stands transmit more light than spruce-dominated stands, particularly as the stands age (Constabel and Lieffers 1996). There are also periods of high light under aspen canopies in spring and fall when overstory aspen is leafless (Constabel and Lieffers 1996). My work showed that white spruce saplings were capable of photosynthesizing in the spring and fall despite the frequent night frosts and low soil temperatures (near 0°C) in springtime (Chapter 3). White spruce grown in aspen-dominated stands likely have more carbon gain and growth than those grown in spruce-dominated stands.

Living under an aspen canopy may provide white spruce some protection from environmental extremes. Understory saplings had a slightly lower but much more stable photosynthetic capacity than open-grown trees during periods of lower rainfall and high daytime temperatures (Chapter 3). In seedlings, understory spruce had more active photosynthesis than open-grown spruce in spring and fall when night frosts were frequent (Chapters 2 and 6). This study has also demonstrated that understory white spruce seedlings could have a higher photosynthetic capacity than open-grown seedlings in summer although this difference decreased if photosynthesis was expressed on a leaf area basis. White spruce seedlings are sensitive to water stress, especially shortly after transplanting. Marsden *et al.* (1996) have demonstrated a decreased photosynthetic capacity for seedlings grown under high VPD. Thus open-grown white spruce seedlings may be unable to utilize the high light resources due to environmental stresses. Open-grown saplings seemed to be less affected by freezing stress than seedlings, probably due to increased cold-resistance and reduced temperature extremes because of their greater height (Chapter 4).

Under the shelterwoods, environmental conditions were more benign than in the clearcuts: higher relative and absolute humidity, cooler maximum and warmer minimum temperatures and reduced risk of night frosts (Chapter 4). Increased light transmission under partial canopy boosted photosynthesis for both existing and planted white spruce in comparison with uncut forests. Therefore, seedlings under shelterwood canopies had earlier budflush, better height growth, less terminal bud damage, and higher rates of photosynthesis immediately after and up to two years after planting than seedlings in clearcuts (Chapters 5 and 6). Among the residual densities used in this study, 20 m^2/ha provided better conditions for white spruce seedlings than either higher or lower residual density in terms of budflush, seed germination and leader survival of planted seedlings. Lower residual canopy, however, provided more light and therefore could promote seedling growth (Chapter 5). Foresters may need a balance between seedling protection and growth in shelterwood management. On harsh sites, a higher canopy residual may be necessary; otherwise, a lower canopy residual should be used to produce better seedling growth. In this project, site preparation significantly increased soil temperatures in spring and early summer. It also improved seed germination and terminal leader survival of planted seedlings (only mixing) compared to the controlled seedbed (Chapters 4 and 5).

For white spruce seedlings transplanted in clearcuts, planting check, i.e., a slow growth in the period after planting, is common and considered to be caused by the extreme conditions on clearcuts (Vyse 1981, Burdett *et al.* 1984, Mullin 1963). In this study, planted seedlings did not show an apparent check, based upon the high photosynthetic capacity right after planting (Chapter 6) and stable height growth from the first to second year after buds which had formed in the field flushed (Chapter 5). This was probably due to the better nursery production techniques for seedling in recent years, more favorable climate than normal, good growing sites, or the combination of all these factors. Seedlings under shelterwood canopies had higher photosynthesis and growth than seedlings on clearcuts, which might mean less planting check and better establishment of planted seedlings. Comparing the spring and summer stocks used in this study, the summer seedlings had higher photosynthesis in the period immediately after planting than spring seedlings, but the difference may be negligible in the long run.

When looking back to the whole study, I feel that part of it could be done differently. Maximum light in light response measurements was 1100 μmol m^{-2} s^{-1}, which was probably high enough to saturate the photosynthetic systems of white spruce. But it is not known how the species, especially the understory trees, responds to the light above that level, from 1100 to 1700 μmol m^{-2} s^{-1}, the high lights in the summer. Secondly, it would has been better to measure soil moisture content in the seasonal photosynthetic measurement so that summer drought did not have to be inferred from precipitation records. In the shelterwood study, I would have had stronger conclusions and more systematically statistically analysis if microclimate, budflush, height growth and photosynthetic measurements had been replicated equally and continued for a longer period at the two sites even though this might not be physically possible.

7.2 Some suggestions for the future research

This study demonstrated that white spruce is photosynthetically active in spring and fall when overstory aspen is leafless. However, the importance of these periods in the annual carbon budget of understory white spruce relative to the summer is still unknown. Quantitative determination of carbon accumulation during these periods requires modeling of photosynthesis and the complete carbon budget of the tree. At the foliage level, rate of photosynthesis is an interaction among light availability, environmental conditions, and photosynthetic ability and physiological status of the foliage. In the understory, light is highly variable over space and time and a number of attempts have been made to characterize the light transmission through boreal mixedwood canopies (Ross *et al.* 1986, Lieffers and Stadt 1994, Constable and Lieffers 1996). A light transmission sub-model incorporating this information has to be built before modeling of photosynthesis could be done. This light sub-model should be able to predict changes of light over time (diurnal and seasonal) and space (for different heights of understory trees) on a stand level given the composition, density and height of overstory trees and understory shrubs and herbs. Photosynthetic ability of foliage is determined by photosynthetic parameters of compensation point, saturation point, photochemical efficiency and light-saturated photosynthetic rate, which change with environmental conditions and physiological status of the foliage. Thus, a number of sub-models need to be established to simulate the relations of these parameters with environmental conditions and physiological status of foliage. This thesis focused on the changes of these parameters with temperature and season and differences between open and understory seedlings. More work is required to investigate the changes of these parameters with needle age, tree height, position and direction of the needles in the crown, and light conditions in the understory. Further development of the model should consider carbon loss through respiration at different times of year by foliage (during night), by stem, and by roots. Finally, biomass production and its allocation within a tree has to be evaluated to predict carbon balance and growth of understory white spruce given the size of a tree, overstory canopy, and environmental conditions. As a special case, the model will be also valid for white spruce growing on open sites.

A better understanding of effects of environmental conditions on photosynthetic ability of white spruce is required. In contrast to the observations on white spruce saplings (Lieffers *et al.* 1993, Greenway 1995), understory seedlings showed a consistently higher photosynthetic capacity than open-grown seedlings. Greater depression of photosynthetic capacity in open-grown seedlings suggests a significant effect of photoinhibition caused by freezing temperatures and strong radiation on the open site in spring and fall when night frosts were frequent (Lundmark and Hällgren 1987, Dang *et al.* 1992, Örlander 1993). Marsden *et al.* (1996) observed a negative effect of low relative humidity on photosynthetic capacity of white spruce seedlings. Further investigations on the effects of environmental conditions, such as low soil moisture, low supply of nutrients, elevated CO_2 concentration and low light conditions in understory, on photosynthetic parameters of white spruce will be helpful in understanding response of white spruce to environmental conditions and increasing the suitability of photosynthetic model and should be made in future research.

The development of planting check needs to be clarified. It has been frequently reported that white spruce seedlings planted in clearcut have slower growth after planting and water stress has been suggested to be one of the major causes (Grossnickle 1988, Burdett 1990, Colombo and Teng 1992, Marsden *et al.* 1996). However, the relationship between water relations of trees and planting check is not known. On the other hand, planting check normally lasts several years after planting. The decrease of planting check with time is probably due to the improvement of water relations with time in transplanted seedlings (Rietveld 1989). However, changes in microclimates with height as seedlings grow (Oke 1987, Stathers 1989) may also be important on the sites with extreme environmental conditions near ground surface.

The relationship between photosynthesis and other physiological characteristics of seedlings shortly after planting and long term seedling performance needs to be addressed. Studies suggest that growth of new roots is critical to survival and growth of newly planted seedlings (Rietveld 1989) and carbohydrates for new root growth come from both current photosynthesis and carbohydrate reserves in white spruce (Vapaavuori *et al.* 1992, Jiang *et al.* 1994). In this study, planted seedlings did not show any apparent slow growth during the first two years in the field, and photosynthesis of these planted seedlings also recovered quickly after planting and remained high compared with the results of other studies (Jiang *et al.* 1994). Investigations of the effect of photosynthesis shortly after planting and carbohydrate reserves on new root growth, water relations, and growth of planted seedlings are therefore necessary in the future studies.

The ability of white spruce saplings to photosynthesize in early spring when soil was nearly frozen was remarkable. This is consistent with the observation in *Pinus sylvestris* (Troeng and Linder 1982), but inconsistent with many other studies (Kaufmann 1975, Running and Reid 1980, Teskey *et al*, 1984, DeLucia and Smith 1987, Jurik *et al.* 1988). Since the soil solution may freeze several degrees below 0°C (Marshall and Holmes 1979), white spruce might have the capacity for water uptake at very cold soil temperatures (near 0°C). However, a clear image about the relationship between soil temperature and water absorption of white spruce on seasonal basis should be made in further investigations.

Seasonal observation of photosynthesis in white spruce saplings poses another interesting question. Studies have shown that conifers could have net carbon accumulation in spring, fall and even in winter, depending upon the temperature (Bourdeau 1959, Schulze *et al.* 1967, Jurik *et al.* 1988, Strand 1995, Schaberg *et al.* 1995). In white spruce saplings, recovery and decline of photosynthesis in spring and fall were also highly related to the air temperature, especially nighttime temperature. It is not known if photosynthesis of white spruce might be maintained into the winter period with the increase of air temperature due to global warming (earlier recovery in spring and later stop in the fall).

Different residual densities of overstory canopy need to be tried in the future to determine the optimal canopy residual in the first cut of a two-stage shelterwood systems in boreal mixedwoods. Some work of modelling is necessary. Efforts should be made to establish the connections among photosynthesis, water relations, root growth, and growth of planted seedlings at different canopy densities. Competition status of seedlings should also be assessed in the new studies to gain more insights into the treatment effects of canopy residual and site preparation. Some attention should be paid to seedling growth and changes of environmental conditions, particularly light, with the recovery of canopy cover of overstory after the first cut. While we have gained more experience in the shelterwood system, we should be aware that other silvicultural systems, such as single tree selection and group selection, may have potential application in some stands of boreal mixedwoods (Lieffers *et al.* 1996) and should be tried in future research.

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APPENDIX 1

Means and stand errors of the parameters of the monomolecular models from open and understory seedlings at four leaf temperatures and in three seasons.

Seedlings		Understory				Open			
Temperature		5	15	25	35	5	15	25	35
Spring	a	4.9455 (0.2083)	6.3231 (0.3249)	4.9621 (0.3146)	4.2489 (0.3861)	3.5443 (0.1392)	4.5028 0.3768)	3.4239 (0.3497)	1.4537 (0.3495)
	b	0.0640 (0.0575)	0.1807 (0.0631)	0.4640 (0.0701)	0.8353 (0.0753)	0.1425 (0.0419)	0.1709 (0.0663)	0.5350 (0.0712)	1.4560 (0.2091)
	c	0.0058 (0.0010)	0.0057 (0.0011)	0.0069 (0.0012)	0.0044 (0.0007)	0.0047 (0.0006)	0.0036 (0.0009)	0.0032 (0.0006)	0.0045 (0.0010)
Summer	a	6.9704 (0.4037)	12.5321 (0.8969)	15.1555 (0.6060)	8.7213 (0.5777)	7.3210 (0.4241)	11.1253 (0.3469)	11.9248 (0.5919)	7.8445 (0.5375)
	b	0.0268 (0.0880)	-0.0216 (0.1219)	-0.0258 (0.0542)	0.3665 (0.0765)	0.0337 (0.1074)	0.0450 (0.0373)	0.0152 (0.0393)	0.4022 (0.0595)
	c	0.0068 (0.0017)	0.0076 (0.0025)	0.0054 (0.0009)	0.0067 (0.0013)	0.0112 (0.0030)	0.0050 (0.0006)	0.0033 (0.0005)	0.0043 (0.0007)
Fall	a	7.9270 (0.2441)	11.4916 (0.2976)	11.1292 (0.5276)	6.6388 (0.4035)	2.9604 (0.1954)	5.4151 (0.1900)	5.7626 (0.2576)	3.5774 (0.1984)
	b	0.0611 (0.0543)	0.0683 (0.0402)	0.1244 (0.0601)	0.4949 (0.0682)	0.0573 (0.1099)	0.0047 (0.0460)	0.1185 (0.0511)	0.5004 (0.0537)
	c	0.0104 (0.0014)	0.0076 (0.0008)	0.0056 (0.0010)	0.0075 (0.0013)	0.0087 (0.0025)	0.0053 (0.0008)	0.0050 (0.0008)	0.0055 (0.0008)