Seasonal Changes in Gas Exchange and Foliar Nitrogen of three Conifer Species Growing on an Ontario Boreal Mixedwood Site

by

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ABSTRACT

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Key Words: seedling growth, growing season, photosynthesis, stomatal conductance, transpiration, foliar nitrogen concentration, nitrogen use efficiency, water use efficiency, specific leaf area, ecophysiology, northwestern Ontario

Jack pine, black spruce and white spruce are three vital species of the Ontario boreal mixedwood forest. The purpose of this study is to compare and contrast the ecophysiological characteristics of each species and to examine changes that occur in these characteristics over a growing season. Ecophysiological measurements (photosynthesis, stomatal conductance and transpiration) were taken on six trees each of jack pine, black spruce and white spruce from three blocks, at three times during the growing season (July, August and September). Foliar N concentration was also determined for each measured seedling in July and September. For all three species, photosynthetic rates were highest in September and lowest in July. Overall, rates were consistently highest for jack pine, even in partially shaded conditions. White spruce had its best performance in the lower light conditions, likely due to its shade tolerance. Black spruce performed in between the jack pine and white spruce. Jack pine had the lowest specific leaf areas, nitrogen use efficiencies and the highest water use efficiencies. For all three species, water use efficiency was lowest in July. Foliar nitrogen concentration and photosynthesis were only weakly correlated in this study.

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INTRODUCTION

Forest managers are under constant pressure to change and improve management practices and procedures. The source of this pressure is an ever increasing public awareness of the ecological, economic and social need to manage forests in a more ecologically sensitive and sustainable manner (Colombo and Parker 1999, Scarratt 2001).

Colombo and Parker (1999) state that the Canadian forest industry relies heavily on forest management practices that are based on past experience and not on a solid understanding of plant physiological processes in relation to environment. Plant physiology research is required to develop our understanding of ecophysiologically based forest management practices. For all plant species, growth is a function of how physiological processes respond to their physical environment. It follows that knowledge of these responses is necessary for the continuing development of forestry in all forest regions.

The boreal mixedwood forest is a diverse and complex forest. Because of its complexity, it is difficult to manage, and requires unique practices for sustainable management. Weingartner and MacDonald (1996) argue that the boreal mixedwood forest has been poorly managed in the past and, therefore, requires further study, especially at the physiological level.

The boreal mixedwood forest is a significant component of the Canadian forests, making up approximately one third of the productive forestland of the boreal forest (Brace and Bella 1988, MacIsaac *et al.* 1999, Navratil *et al.* 1996,

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Stelfox 1995). Typical boreal mixedwood sites support highly productive and diverse forest communities dominated by trembling aspen [*Populus tremuloides* Michx.] and white spruce [*Picea glauca* (Moench) Voss] along with white birch [*Betula papyrifera* Marsh.], balsam fir [*Abies balsamea* (L.) Mill.], jack pine [*Pinus banksiana* Lamb] and black spruce [*Picea mariana* (Mill.) B.S.P.] in varying combinations (Arnup 2001, Cameron *et al.* 1999, MacDonald 1996).

Because of the favourable conditions for multiple species, boreal mixedwood forests are often complex in structure and composition. Mixed stands often develop canopy stratification by species due to the different autecologies of the component species (Smith *et al.* 1997). The presence of a mixture of hardwood and coniferous tree species adds variability and diversity to a site, but also results in serious implications for the management of mixedwoods. For example, some have argued that the species composition, age structure, and successional relationships of boreal mixedwood stands, and their response to different levels of canopy removals, present opportunities to implement modified harvest methods (e.g. two-stage harvesting [Kenney and Towill 1999], specialized thinnings, or variable-canopy retention [MacDonald and Cormier 1998]).

Traditionally, boreal mixedwoods have been clearcut and planted to a single species (Scarratt 2001), but alternative harvesting and silvicultural operations are now options for management of boreal mixedwoods. These modified operations often result in partial canopies or residual stems being left on site, which affect a seedling's microclimate and growing conditions. The Ontario Ministry of Natural Resources (OMNR) is currently developing boreal

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mixedwood management guidelines. These guidelines recommend retaining a residual overstory on site through various methods of harvest, during all stages of mixedwood development (W. D. Towill, pers. comm., November 2002)[1]. It will be important to know how regeneration of mixedwood species responds to variable environmental conditions created by residual overstories.

Several research projects were established in the boreal mixedwood forests of Canada, as the need for a better understanding of these complex ecosystems was realized. The EMEND (Ecosystem Management Emulating Natural Disturbance) project in northwestern Alberta (Sidders and Spence 2001), and the SAFE (Silviculture and Forest Ecosystem Management) project in northwestern Quebec are two examples (OMNR 2001). Both projects, however, are somewhat empirical trials that do not include an assessment of physiological aspects.

In northwestern Ontario, the Black Sturgeon Boreal Mixedwood Research Project (BSBMRP), was established in 1993 to increase our understanding of ecological processes and relationships in boreal mixedwoods (Scarratt 2001). This project is a multi-agency (Canadian Forest Service, OMNR and Bowater Inc.) research initiative designed to examine of the complex and dynamic ecosystems that make up boreal mixedwoods and to examine alternatives to clearcutting. The study reported here represents a small component of the BSBMRP. The experiment was originally designed to examine the effects of silvicultural systems on key ecophysiological traits of planted conifer seedlings.

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[1] W.D. Towill. Senior Forest Practices Specialist – Northwest Region. Ontario Ministry of Natural Resources.

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This goal was abandoned, however, after a large fire destroyed a substantial portion of the study area in the spring of 1999.

A modified experiment was proposed to utilize the unburned portion of the original experiment. This new experiment focuses on comparative seasonal variation in ecophysiological characteristics of three typical boreal mixedwood species. Although more limited in scope and inference space, the modified experiment is still within the original objectives of the BSBMRP and the ecophysiological information gained will be important to those planning the future management of boreal mixedwood forests.

Among the several research projects in Canada that focus on boreal mixedwoods, the BSBMRP is unique. Mixedwoods in northwestern Ontario differ greatly from those in other regions of Canada and Ontario, in their stand structure, soils, and fire cycles. As such, mixedwood research and operations that are applied to mixedwoods in other regions are not necessarily applicable in northwestern Ontario (W. D. Towill, pers. comm., November 2002).

Although ecophysiological studies of boreal mixedwood species have been carried out in the past, many have been carried out in western Canada (Lieffers *et al.* 1996b, DeLong *et al.* 1997, Man and Lieffers 1999), or have focused on mature western species (Brix 1981, Dang *et al.* 1992, Man and Lieffers 1997), or on seedlings growing under controlled greenhouse conditions (Stewart *et al.* 1994, Tan and Hogan 1995, Brown *et al.* 1996, Poorter and Evans 1998). Fewer ecophysiological studies have been carried out on all three fundamental species of the eastern boreal forest (Robinson *et al.* 2001), and rarely in studies designed to compare and contrast the ecophysiological

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responses of these three important conifers (jack pine, black spruce, and white spruce). Ecophysiological studies that examine seasonal changes in gas exchange have also been done in the past, but they have usually focused on the winter and spring months, and not on changes that occur within a growing season (Strand 1995, Man and Lieffers 1997, Schwarz *et al.* 1997). Studies have also been done on mixedwood species, but have often taken place in other regions of Canada.

The main objective of this particular study, therefore, is to examine and compare the ecophysiological characteristics of three coniferous boreal tree species (two from the genus *Picea* and one from the genus *Pinus*) growing on a boreal mixedwood site in northwestern Ontario. The specific objectives are to examine how the seasonal changes in gas exchange of jack pine differs from the black and white spruce and how the performance of all three species changes in variable light conditions.

Jack pine, a pioneer, shade intolerant species was expected to have the highest rates of photosynthesis, stomatal conductance and transpiration, especially at higher light levels. As the most shade tolerant species of the two boreal spruces studied, white spruce was expected to have the lowest rates of gas exchange at the higher light levels. Gas exchange of black spruce was expected to be greater than white spruce, but less than jack pine, due to its shade tolerance.

For seasonal changes, I expected photosynthetic rates to be lowest for all three species in July when air temperatures and vapor pressure difference (VPD) are high and precipitation is low, causing water to become a limiting

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factor. The month of August was expected to yield the most optimal growing conditions (*i.e.* temperature and moisture) for the seedlings. Although the silvics and responses of these three species to the environment are well known, the fine details of the responses of these three species are not clear. In undertaking this research, I hoped to elucidate some of these subtle details.

I found that photosynthetic rates were highest for all three species in September and lowest in July. Jack pine consistently had the highest rates of gas exchange, even in partially shaded conditions, although white spruce showed its highest rates of photosynthesis in the lower light conditions. Black spruce performed intermediately. Jack pine had the lowest specific leaf areas, nitrogen use efficiencies and the highest water use efficiencies. WUE was lowest for all three species in July. Foliar nitrogen concentration and photosynthesis were only weakly correlated in this study. The results of this study contribute to the continued development and improvement of boreal mixedwood management in northwestern Ontario.

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LITERATURE REVIEW

CANADIAN BOREAL FOREST

In Canada, the boreal forest extends across the entire country, from British Columbia to Newfoundland. The Canadian boreal forest comprises 18 % of the world's boreal forest, and covers approximately 200 million hectares. It is composed mainly of black spruce, white spruce, trembling aspen, balsam poplar [*Populus balsamifera* L.], white birch, balsam fir, and jack pine (Weetman 1995).

The boreal mixedwood forest is dominated by trembling aspen and white spruce, but also includes white birch, balsam fir and black spruce in varying combinations (MacDonald 1996, Cameron *et al.* 1999). MacDonald and Weingartner (1995) define a boreal mixedwood stand as a tree community on a boreal mixedwood site in which no single species exceeds 80 % of the basal area.

The boreal mixedwood forest is an important and complex component of this forest region. Mixedwoods are common throughout the boreal region, except in the lowlands south and east of Hudson's Bay, and are the most widespread forest type in Canada (Rowe 1972). In western Canada, from the Prairie Provinces to British Columbia, about one third of the productive forest land is made up of mixedwoods (Stelfox 1995, Navratil *et al.* 1996, Brace and Bella 1988, MacIsaac *et al.* 1999). In British Columbia and Alberta, mixedwoods account for 35% (Comeau 2000), and 50% (Stelfox 1995, Navratil *et al.* 1996) of forest land, respectively. Further east, the boreal forest represents about 54%

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of Ontario's forested land (Morris and Duckert 1999), 50% (15.8 million hectares) of which is mixedwoods (McClain 1981, Towill 1996).

Mixedwood forests often grow on relatively rich soils, which is evident in their ability to support numerous tree species. Although adapted to a variety of soil types (Sims and Uhlig 1996), boreal mixedwood forests typically occur on deep, well-drained, moist, fertile soils of high productivity (Sims and Uhlig 1996, Cameron *et al.* 1999). Tills, as well as soils of lacustrine, alluvial, and aeolian origin support boreal mixedwood forests (Morrison and Wickware 1996). The primary natural disturbance agents of mixedwood forests are fires and insect outbreaks (Johnston 1996, Armson 1988). The species composition of mixedwood stands depends strongly on the intensity of overstory and forest floor disturbance and the availability of seed sources or vegetative reproductive organs (Lieffers *et al.* 1996a).

Because of the conditions favouring multiple species, boreal mixedwood forests are often diverse and complex in composition and structure. This complexity is a result of the different autecologies and physiologies of the main tree species in mixedwood forests and the highly variable terrain and soils on which they occur. Most mixed stands eventually develop a distinct structure and canopy stratification by species because of the different growth rates and morphology of species (Smith *et al.* 1997). These factors all add to the diversity of the boreal mixedwoods and have important implications for forest management (Armson 1988).

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SILVICS OF STUDY SPECIES

Jack Pine

Jack pine is the most widely distributed *Pinus* species in Canada (Rudolph and Laidly 1990, Farrar 1995). It is a shade intolerant pioneer species inhabiting areas that have been recently disturbed with mineral soil exposure. It usually grows in even-age pure or mixed stands with black spruce, white birch and trembling aspen. It can, however, grow on less fertile and drier soils than other native species in its range (Rudolph and Laidly 1990).

In its first 20 years, jack pine is the fastest growing conifer, besides tamarack [*Larix laricina* (Du Roi) K. Koch), in the North American boreal forest. This is attributable in part to a higher rate of photosynthesis (A) or nutrient use efficiency (NUE) than other coniferous species (Sullivan *et al.* 1997). Average annual juvenile height growth can reach 1 m, with seedlings normally reaching breast height (1.3 m) in 5 to 8 years. Although it is one of the most shade intolerant trees in its native range, partial shade to reduce surface temperatures and E may be beneficial to seedling establishment and early growth. Soon after establishment, however, seedlings exhibit maximum growth and survival under full sunlight (Rudolph and Laidly 1990, Arnup *et al.* 1995). The species develops poorly under a cover of broadleaved trees, especially trembling aspen (Bell 1991). Unlike black and white spruce, jack pine is less sensitive to planting check, a stress that is placed on newly planted trees as a result of nutrient deficiency and moisture stress (Rudolph and Laidly 1990).

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Black Spruce

Black spruce is one of the most economically important and widespread conifer species in Canada (Viereck and Johnston 1990, Farrar 1995). It is moderately shade tolerant (Farrar 1995) and it grows on a variety of sites and soil types, although upland sites are generally of higher productivity than lowland sites. On upland sites, it forms pure stands, occurs in mixture with jack pine, white spruce, balsam fir, white birch, and trembling aspen. On lowland sites it forms pure stands, or occurs with tamarack and other lowland species (Viereck and Johnston 1990).

The early growth of planted black spruce seedlings is inherently slow. Depending on the site, average annual height growth can vary between 2.5 cm and 15 cm. Ten years after planting, upland black spruce plantations typically reach an average height of between 1.5 and 4.0 m (Viereck and Johnston 1990). As black spruce is susceptible to planting check, and because of its slow growth, it is often at a disadvantage when in competition with other vegetation. Trembling aspen usually outgrows black spruce within a few years on most sites (Arnup *et al.* 1995).

White Spruce

White spruce has the ability to grow under a wide variety of site conditions, including extreme climate ranges and soils, and as a result, it is found in all forested regions of Canada, except along the Pacific coast (Farrar 1995). White spruce is typically more demanding of nutrients than associated

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conifers. It is found most frequently in mixed stands where it is often a major component, along with black spruce, balsam fir, white birch and trembling aspen. It is intermediate in shade tolerance, being equally or more tolerant than black spruce and significantly more tolerant than trembling aspen and jack pine (Nienstadt and Zasada 1990, Farrar 1995).

Regeneration of white spruce in the understory occurs on a variety of sites, although best growth is attained at full light intensity. Early growth of white spruce seedlings is even slower than black spruce seedlings, with average annual height growth of about 2 cm. In the open, it may take white spruce as long as 10 to 20 years to reach breast height (*i.e.* 7-15 cm/year). White spruce is also sensitive to planting check, even more so than black spruce (Nienstadt and Zasada 1990).

MIXEDWOOD MANAGEMENT

In the past ten years, there has been an increased demand for boreal hardwoods such as trembling aspen and white birch, and with this demand, the management of mixedwood forests has become more economically feasible (Lieffers and Beck 1994, MacDonald 1996). Clearcutting has traditionally been the standard method of harvest for boreal mixedwoods, and is currently the dominant form of harvest in Canada (Youngblood and Titus 1996). It is thought to be a suitable method of harvest in the boreal forest as it somewhat emulates large-scale disturbances, such as fire, that are such an integral part of the boreal forest. Most boreal tree species have evolved reproductive strategies to take advantage of the conditions created by natural disturbances, such as increased

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irradiance and temperature (Youngblood and Titus 1996). Some species (jack pine and black spruce) often regenerate after stand replacing disturbance as even age pure stands (Smith *et al.* 1997).

The presence of a mixture of tree species on a site, especially a mixture of hardwood and coniferous tree species, causes serious implications for the management of mixedwoods. Mixedwood stands can be some of the most challenging types of forests to manage, as managers must be concerned about the specific silvicultural requirements of different species, their different economic values, and their individual growth projections and allowable cuts (Lieffers and Beck 1994). In the past, with the high demand for conifers and lack of market demand for hardwoods, conversion of mixedwoods to single-species conifer stands was widely attempted, but was often unsuccessful.

Attempts to establish white spruce and Engelmann spruce [*Picea engelmanni* Parry ex Engelm.] in large clearcuts have failed in the past (Ronco 1970, Lieffers and Stadt 1994, Constabel and Lieffers 1996, Lieffers *et al.* 1996a, Marsden *et al.* 1996, Carlson and Groot 1997, DeLong *et al.* 1997, Man and Lieffers 1999). Failure has often been attributed to competition from deciduous tree species and grasses, late spring frosts and planting check (Carlson and Groot 1997). Planting check is likely a result of moisture stress and mineral nutrient deficiency experienced by seedlings shortly after planting (Burdett *et al.* 1984, Carlson and Groot 1997, Man and Lieffers 1999). Although planting check rarely lasts more than one or two seasons, it can put the planted seedlings at a disadvantage in the competition for resources with other vegetation (Burdett *et al.* 1984). Often manual cleaning or herbicide

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applications are required to release the conifer seedlings from competing vegetation, such as shade intolerant species such as trembling aspen, fireweed [*Epilobium angustifolium* L.] and red raspberry [*Rubus idaeus* L.] (Lieffers and Beck 1994, Groot *et al.* 1996, Smith *et al.* 1997), which may be expensive.

Once free of competition, growth of crop trees often respond positively to the flush of nutrients made available after logging as a result of accelerated mineralization of forest floor materials and the addition of fine slash to the forest floor (Kimmins 1997). This growth enhancement, or "assart effect", continues until nutrients from the readily decomposed organic matter have been taken up by plants, immobilized by microbes or soil chemical reactions, or lost from site by leaching or volatilization. The assart effect can cause nutrient demanding species to grow well initially on poor sites, but once this transient period of high resources is over, nutrient availability and growth may actually decline to levels lower than those before the harvest occurred (Kimmins 1997).

Although single-species stands are ecologically appropriate in the boreal forest, public support for large-scale clearcuts and extensive planting of monocultures is lacking. There has recently been an increase in public pressure to manage forests to maintain biodiversity and natural ecosystem processes (Lieffers and Beck 1994, Lieffers 1995, Scarratt *et al.* 1996). Comeau (2000) gives a number of reasons for managing mixedwoods, including: 1) their widespread natural occurrence throughout the boreal forest, 2) their value as a visual resource, 3) their greater structural and species (plant and animal) diversity than single-species forests, 4) the possibility that they may suffer reduced incidence of, and mortality from disease and insect outbreaks, 5) they

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can provide a greater wood yield and possible better economic returns than pure stands, 6) they may be more readily sustainable than growing single-species stands, 7) hardwood leaves can improve nutrient availability, 8) hardwoods can serve as valuable nurse crops for conifers and, 9) government regulations may require management of mixtures.

The need for knowledge of mixedwood forest ecosystems and their management was recognized more than 20 years ago and since then several symposia on the topic of boreal mixedwoods have been held. Although several research projects have also been developed in the boreal mixedwood forests of Canada (OMNR 2001, Sidders and Spence 2001, Scarratt 2001), overall, studies on boreal mixedwood forests in Ontario are lacking and there is an evident need for research to improve our understanding of them (Cameron *et al.* 1999). Because of the great variability in the composition and structure of boreal mixedwoods in Canada, mixedwood knowledge gained from other regions in Canada is not necessarily applicable or transferable to mixedwood forests in northwestern Ontario (W. D. Towill, pers. comm., November 2002). A new approach to the management of boreal mixedwoods in Ontario requires a better understanding of the ecophysiology of characteristic species of these ecosystems.

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OVERSTORY INFLUENCES ON UNDERSTORY ENVIRONMENT

Although widespread, clearcutting is generally not suitable for sustainable management of mixedwoods, mainly due to conflicts between silvicultural objectives. Since trembling aspen and white spruce often mature at different times, timing of harvest is a problem. If the aspen is harvested when it is mature, then the spruce is immature, whereas if the spruce is harvested at maturity, then the aspen is overmature (Lieffers and Beck 1994).

As noted earlier, alternative silvicultural systems (EMEND, SAFE) are presently being tested with boreal mixedwoods that harvest only some of the overstory (Sauder 1995). Pulkki (1996) presented five alternative harvesting approaches intended for boreal mixedwoods. These include strip-cutting, removal of most of the hardwoods while leaving the softwoods, removal of the overstory while protecting advance regeneration, patch cutting, and selection thinning. Although these operations are quite variable, they all involve leaving a portion of residual forest canopy. The OMNR's boreal mixedwood management guidelines for northwestern Ontario also suggest retaining some residual overstory vegetation on site through various methods of partial harvesting during all stages of mixedwood stand development. However, the harvest method best suited to a given stand depends on the age and structure of the stand at the time of harvest (*i.e.* stand initiation, stem exclusion, canopy transition and gap dynamics), as well as the species composition (*i.e.* aspen dominated, softwood dominated, birch-leading, etc.).

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Intact forest canopies have a prominent influence on understory microclimate by reducing transmittance and altering spectral quality of solar radiation, decreasing air temperature, increasing humidity, and intercepting precipitate. Canopy disturbances increase light transmittance, increase air and soil temperature, reduce humidity and increase amount of precipitation that reaches the forest floor. Overstory vegetation can moderate the harsh conditions that are often created by clearcutting by reducing vapour pressure deficits (VPD), irradiance and soil water content (Dalton and Messina 1995). Even in the presence of competition from the overstory for soil water, the water status of underplanted seedlings may be improved. However, the favorable environments for survival that are created by residual stems may be associated with a reduction in growth (Dalton and Messina 1995).

Partial cut silvicultural systems are being increasingly applied in the management of boreal mixedwoods to tailor the forest understory environment to the requirements of mid-tolerant or shade tolerant crop tree species (*i.e.* black spruce, white spruce), while reducing the growth of more shade intolerant competing vegetation (Lieffers and Stadt 1994). Greene *et al.* (2002) suggest that light transmission at seedling height should be greater than 25 percent of full sunlight, and state that aspen stands with less than 1200 stems/ha would provide suitable light levels for conifer seedlings. Unfortunately, they also state that underplanting is unlikely to be practised widely, because too few blocks will meet the available light requirement.

Man and Lieffers (1999) studied morphological and physiological responses of planted white spruce seedlings under four canopy densities and

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found that overstory vegetation could be used to improve environmental conditions and white spruce regeneration. They found that when the canopy density was decreased, light transmission, maximum air temperature and frost frequency increased, while minimum air temperature and relative humidity (RH) decreased. A partial overstory provided higher humidity, reduced severity and incidence of night frosts, and more moderate diurnal temperature fluctuations, all of which were beneficial to the establishment of white spruce. The highest rate of seedling mortality occurred in the clearcut as a result of water stress. Man and Lieffers (1999) concluded that the reduced light transmission could reduce photoinhibition and increase resource partitioning to aboveground growth, and that a partial canopy can be used to modify the extreme environmental conditions associated with clearcuts and therefore promote white spruce regeneration.

Lieffers and Stadt (1994) investigated light transmission through overstory aspen canopies and found that white spruce could attain acceptable annual leader growth (between 9 and 25 cm) at light levels between 15 and 40% of full sunlight. At light intensities above 40 %, white spruce could add more biomass, but its competitive status is reduced by the greater development of bunchberry [*Cornus canadensis* L], fireweed and other low shrubs. The percent cover of bunchberry was positively correlated with the amount of transmitted light (Lieffers and Stadt 1994). Constable and Lieffers (1996) confirm that light transmission through the overstory is an important factor controlling the development of understory trees and competing vegetation.

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Fully exposed, open environments exhibit more heterogeneous microclimates, and more extreme environmental conditions for seedlings. Clearcuts are characterized by high air and leaf temperatures, low humidity levels and high wind speeds, all of which increase the potential for a seedling's risk of dehydration (Marsden *et al.* 1996). Humidity levels around a seedling determine the rate of E by affecting stomatal conductance (g_s) and the evaporative power of the atmosphere, and can alter the influence of soil moisture stress on seedling growth. Under shaded conditions, higher humidity in the seedling environment tends to favour higher g_s and uptake for A. If higher g_s under greater humidity also results in higher E, increased seedling water loss may occur under shaded conditions. As a result, humidity levels surrounding the leaf have a strong influence on photosynthetic rate, through effects on g_s (Marsden *et al.* 1996).

Marsden *et al.* (1996) studied white spruce growing under a full canopy and a 50 percent canopy of aspen three metres in height, and growing in the open. They found that absolute humidity differences (AHD) between the air and the leaf were lower under full or partial aspen canopies than in clearcuts and that only a moderate canopy of aspen is required to increase humidity around the seedling. They also found that under low AHD conditions, net assimilation (NA) was higher, as was water use efficiency (WUE) of white spruce seedlings. These results agree with those of Kaufmann (1976, 1977) in that at high AHD conditions, g_s is considerably reduced.

Ronco (1970) performed a study on potted Engelmann spruce seedlings, growing in the open, in partial and in full shade, produced with the use of

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cheesecloth. He found that most seedling mortality occurred during the first winter, once the seedlings were covered by snow, and not by drought, frost heaving or herbivory. The amount of mortality was significantly reduced when the seedlings were partially shaded during the previous summer. When spruce seedlings were grown in the open, severe chlorosis developed and persisted for many years, whereas when grown in the shade, seedlings remained a normal green colour (Ronco 1970). High light intensities may have inhibited A and contributed to high mortality in the open-grown seedlings.

Ronco (1970) also found that shaded pines and spruces had higher rates of A than those seedlings growing in the open. He also found that the shade tolerant spruces became light saturated at about one-third of full sunlight. Ronco (1970) concluded that drought-induced water deficits were not the principal cause of Engelmann spruce mortality and that the solarization of unshaded seedlings appeared to be responsible for high mortality rates.

Pons and Bergkotte (1996), however, stated that shading reduces both photosynthetic and transpiration rates in plants and postulated that a reduction of A in shaded leaves is an important factor in the reduction of accumulation of dry matter. They also speculated that a reduction of E in shaded leaves is an important factor in regulating export of N from nearly mature leaves.

Zhang *et al.* (1997) studied the effects of abrupt changes in light conditions on loblolly pine [*Pinus taeda* L.] seedlings and found that shading significantly decreased A and leaf dark respiration. It was ascertained that photosynthetic acclimation to exposure to lower light levels was reached in 25 days. When the foliage was removed from shade and exposed to high light,

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maximum net A and dark respiration gradually increased. Within a week, maximum net A had recovered to more than 90 % of that of unshaded branches. They also found that shade reduced g_s and E, but had no effect on internal CO_2 concentration (C_i) or leaf N concentration. Unshaded foliage had a greater increase in specific leaf weight (leaf weight per unit leaf area) than did shaded foliage, suggesting that light intensity significantly affected the accumulation of photosynthate in leaves. When shaded foliage was exposed to high light, specific leaf weight increased, relative to that of unshaded foliage. Shading also increased chlorophyll content, but this level returned to that of unshaded foliage when re-exposed to high light. More chlorophyll in the leaves under low light conditions allows for more efficient absorption of radiation (Zhang *et al.* 1997). This rapid photosynthetic acclimation to a change in light intensity has important implications for forestry practices such as thinning.

PLANT GAS EXCHANGE

The species that compose the boreal mixedwood forests of Ontario have diverse silvical characteristics. It is these differences that contribute to the diversity and complexity of mixedwood forests. Foresters and ecologists often place jack pine and white spruce at opposite ends of the light, nutrient and microsite requirement spectra, with jack pine being less tolerant of shade and less demanding of water and nutrients. Black spruce is generally viewed to fall between jack pine and white spruce along this environmental gradient.

For all plant species, growth is a result of a number of physiological processes. Knowledge of these processes and their responses to the

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environment is important for the management of the boreal forest. The primary physiological, or gas exchange, processes are g_s and net A (Grossnickle *et al.* 2001).

Photosynthesis

The most important physiological process for all plants is A. In fact, Kozlowski *et al.* (1991) call A the most important chemical process in the world, with the major objective of most silvicultural and agricultural practices being to assure a high rate of A. Although growth is not necessarily closely correlated with photosynthetic rate, it is strongly dependent on carbohydrates produced by A.

Photosynthesis is the process by which light energy is trapped by chlorophyll in green plants and used to produce simple sugars from CO_2 and H_2O. It consists of the reduction of CO_2 and recombination of the carbon into carbohydrates through the use of light energy, by the splitting of water. The major processes of A include: 1) trapping of light energy by chloroplast pigments, 2) splitting of water and release of O_2 and high-energy electrons used to reduce $NADPH^+$, 3) generation of chemical energy in ATP and reducing power in $NADPH_2$, and 4) use of the reducing power of $NADPH_2$ and energy stored in ATP to fix CO_2 in phosphoglyceric acid and reduce it to triose phosphate, from which glucose and other carbohydrates are synthesized (Kozlowski *et al.* 1991). Net A is the amount of CO_2 assimilated minus that lost by respiration, the process of oxidation of carbohydrates produced by A (Grossnickle *et al.* 2001).

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Photosynthesis generally occurs in foliage, but it can also occur, to a lesser degree, in other plant parts. The maximum rate of net A varies widely among tree species and provenances, between sun and shade leaves, throughout the day and during the growing season. Decreases of net A with increasing needle age have also been observed in some species (Zine El Abidine *et al.* 1995, Kimmins 1997, Man and Lieffers 1997). Photosynthetic rate differences are a result of interactions between plant processes and environmental factors such as light intensity, air and soil temperature, water supply, external CO_2 concentration, and soil water and nutrient availability conditions (Kozlowski *et al.* 1991).

Stomatal Conductance

CO_2 required for A is taken into the plant through stomata of leaves by diffusion. Stomata are pairs of specialized epidermal cells that regulate the exchange of CO_2 and water vapor between the leaf and atmosphere. CO_2 enters the intercellular spaces within the leaf where it dissolves in water and penetrates through the mesophyll cell walls. It then diffuses to chloroplasts where A occurs (Lambers *et al.* 1998). Stomata vary in size and density among species. Stomata link A to external factors such as air temperature and relative humidity. Stomatal conductance to water vapor is dependent on the aperture of stomata, with greater g_s associated with greater opening of stomatal pores. Whitehead (1998) states that there is a general linear dependence of g_s on E.

Stomata open and close in response to the internal plant photosynthetic response and the environment around the plant, thus regulating how the plant

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responds to its environment (Lambers *et al.* 1998, Grossnickle 2000). As the primary avenue for gas exchange, the environmental factors that influence g_s, therefore, also affect A (Kozlowski *et al.* 1991, Sullivan *et al.* 1997, Lambers *et al.* 1998, Grossnickle 2000). Man and Lieffers (1997) found that g_s and photosynthetic capacity had similar seasonal patterns in jack pine and white spruce. Dang *et al.* (1992) found that g_s decreased in parallel with net A in black spruce following frosts.

Transpiration

Transpiration (E) is the rate of water vapour loss per unit leaf area, per unit time, through the cuticle and stomata of plant leaves. While it is an inevitable side effect of A, it is also a major factor in maintaining a leaf's energy balance. As water evaporates from the stomata, it cools the leaf. In the absence of E, leaf temperature may quickly reach lethal levels (Lambers *et al.* 1998). When stomatal pores are open, they inevitably allow water loss (Mauseth 1995). Transpiration is strongly dependent on g_s and atmospheric humidity, hence the strong linear correlation between g_s and E. There must be a compromise in leaves, between regulating stomatal aperture to allow CO_2 to enter the plant without excessive water loss (Schulze and Caldwell 1995).

Although E is an unavoidable consequence of A, differences among plant species exist in the efficiency with which water is used. This is known as plant water use efficiency (WUE), which is the ratio between the carbon gain in A and water lost in E (Kimmins 1997, Lambers *et al.* 1998). Instantaneous WUE can

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be determined by dividing A by E. Lambers *et al.* (1998) provided a range of WUE values of between two and 11 mmol/mol for woody plants.

A plant's WUE depends on g_s and the difference between vapour pressure in the leaf's intercellular air spaces and that in the air (VPD). WUE normally increases with decreasing g_s because decreased g_s inhibits the diffusion of water vapor more than it inhibits CO_2 uptake. A study done by Wang *et al.* (1998) found that the highest values of WUE were not due to high rates of A, but rather to very low rates of g_s under severe water stress. Temperature also affects leaf vapour pressure, which therefore affects plant WUE (Lambers *et al.* 1998).

Internal plant factors may also influence WUE. Livingston *et al.* (1999) found that a decreased N supply led to increased g_s and therefore a lower WUE. Fertilized seedlings had a significantly higher WUE than those that were N stressed. Environmental effects on WUE have been studied in a variety of plant species. Sizeable variations in WUE have been described between species, sites, climatic conditions, and methods used to calculate it (Field *et al.* 1983, Kimmins 1997).

Foliar Nitrogen

Nitrogen accounts for less than 1% of the dry weight of a plant, but N and N-containing compounds are extremely important physiologically. The most plentiful plant compounds are the amino acids found in protoplasm and the enzymes that catalyze biochemical reactions. Other important nitrogenous

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compounds include nucleic acids, nucleotides and chlorophyll (Kozlowski *et al.* 1991, Grossnickle 2000).

Nitrogen is classified as an essential element, as a plant cannot complete its life cycle without it (Ballard and Carter 1985, Field and Mooney 1986, Grossnickle *et al.* 2001). It is often the macronutrient that most commonly limits plant growth. The highest concentration of N occurs in meristems and other physiologically active tissues. The amount of N present in a tree varies with age, developmental stage and the physiological activity of the tissue (Kozlowski *et al.* 1991, Zine el Abidine 1995, Kimmins 1997). For example, Sullivan *et al.* (1997) found that foliar N concentrations were higher in young jack pine trees than in old jack pine trees.

Average foliar N concentrations can vary between 1 and 3 % of dry weight. Of this amount, approximately 75% is allocated to the chloroplast (Lambers *et al.* 1998). Deciduous species normally have a higher foliar N percentage than coniferous species (Pereira 1995). A study done by Miller *et al.* (1981) found foliar N concentrations in the range of 1.6 to 2% of foliage dry weight for Corsican pine [*Pinus nigra* var. *maritime* (Ait.) Melv.]. Mitchell and Hinckley (1993) obtained average concentrations of 1.25 and 1.58% for Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco), whereas Brix (1981) reported a range of 0.95 to 1.16% for unfertilized Douglas-fir. Korol (2001) found average leaf N concentrations of 1.09% for grand fir [*Abies grandis* (Dougl.) Lindl.] and 1.62% for western red cedar [*Thuja plicata* Donn], with varying percentages in between these values for other conifer species of the northwestern United States. Lamhamedi and Bernier (1994) suggested that the

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optimum foliar N concentration should be 1.61% for containerized black spruce seedlings, although their estimated critical concentration is 1.20%.

Ballard and Carter (1985) evaluated the nutrient status of forest stands in British Columbia and examined the foliar nutrient concentration for five western conifers. They ranked the N concentrations for each species from very severely deficient to adequate. For white spruce, trees with an average of 1.05% foliar N concentration were considered to be severely deficient, trees with 1.30% were considered to have a slight moderate deficiency and trees with a foliar N concentration of 1.55% had adequate levels of this element. The N values for the remaining four species were quite similar to white spruce, although western redcedar [*Thuja plicata* Donn ex D. Donn] had slightly higher values for all levels of N concentration and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] had slightly lower values (Ballard and Carter 1985).

Gas Exchange and Foliar N

Nitrogen is a major nutrient determining the productivity of hardwood and coniferous forest species. A detailed knowledge of the response of trees to available nutrients is needed to improve the efficiency of forest management and to increase productivity on nutrient-poor sites (Chandler and Dale 1995). The photosynthetic machinery accounts for more than half of the N in a leaf, which is why A has been shown to be strongly affected by N availability (Evans 1998, Lambers *et al.* 1998, Poorter and Evans 1998). The A-N relationship is inherently complex, because A integrates a series of environmentally sensitive

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physiological processes with leaf anatomy and structure (Field and Mooney 1986).

In the leaf, 70-80% of N is in proteins, 10% is in nucleic acids, 5-10% is in chlorophyll and lipoproteins, and the rest is in free amino acids (Field and Mooney 1986). One particular protein in the leaf is Rubisco (ribulose-1, 5-bisphosphate carboxylase/oxygenase), the primary enzyme of the dark reactions of C_3 A, used to attach CO_2 to a CO_2-acceptor molecule. Leaves contain extensive amounts of Rubisco, although not all of it contributes to A (Lambers *et al.* 1998). Rubisco is assumed to contain 15% N and it can compose up to 30% of the protein in a leaf, making it the most abundant protein on Earth (Mauseth 1995, Brown *et al.* 1996). Nitrogen is also found as protein in the thylakoid membranes of the chloroplast, often as pigment-protein complexes. In contrast to Rubisco, which functionally represents the dark reaction of A, thylakoid proteins function as part of the light reactions (Evans 1989).

Because A is strongly dependent on N, maximum photosynthetic rate (A_{max}) is often positively correlated with leaf N concentration. Under conditions of N limitation, the entire process of A is down regulated, with subsequent declines in Rubisco and chlorophyll concentration and rates of A_{max} and g_s (Lambers *et al.* 1998). Maximum g_s is strongly correlated with leaf N because of the functional relationship between g_s and A_{max} and between A_{max} and leaf N. The connection between A and leaf N clearly reflects the large investment of N in the photosynthetic machinery (Yin 1993, Lambers *et al.* 1998).

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Many studies of the relationship between gas exchange and N in tree species have focused on western species, usually around 20 to 30 years of age. Some studies have been performed on younger trees, but many of these studies have been carried out under controlled greenhouse conditions. For example, Korol (2001) performed a study on 11 coniferous species of the northwestern United States. She found maximum rates of A of these mature trees ranged from 3.1 $\mu mol/m^2/s$ to 14.1 $\mu mol\ CO_2/m^2/s$, with the shade-tolerant species generally having lower rates of A_{max} than the shade intolerant species. Maximum g_s ranged from 0.045 to 0.37 mol $H_2O/m^2/s$. Both A and g_s increased with leaf N. Mitchell and Hinckley (1993) studied N effects on gas exchange in 25 year-old Douglas-fir and Brix (1981) studied this relationship in Douglas-fir seedlings that were grown in a greenhouse, and both reported similar results to those of Korol (2001).

Brown *et al.* (1996) found that when seedlings of western conifers growing in a greenhouse were nitrogen fertilized, photosynthetic rates varied with foliar N concentrations in a species-specific manner. All species showed initial increases in A with increasing N, but the maximum rates of A achieved varied with species. Western hemlock had the lowest rates, and Sitka spruce [*Picea sitchensis* (Bong.) Carr] had the highest rates of A. This study also found that A increased linearly with g_s and concluded that the increase in photosynthetic rate with foliar N concentration was likely more a result of carboxylation capability than a result of increased g_s. A similar experiment performed by Johnsen (1993) found net A for black spruce seedlings generally

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increased with increasing foliar N concentration. Johnsen (1993) also found that in most cases, there was a general decrease in foliar N concentration with increased seedling dry weight.

Chandler and Dale (1995) found an increase in A, g_s and total chlorophyll with increasing N concentration for Sitka spruce [*Picea sitchensis* (Bong.) Carr]. They attributed this partly to a reduction in g_s with N deficiency and partly to greater chlorophyll and carotenoid concentrations, which improve the light-harvesting activity of A (Chandler and Dale 1995). Similar results have also been found for Norway spruce [*Picea abies* (L.) Karst.] (Strand 1995), radiata pine [*Pinus radiata* D. Don] (Sheriff and Mattay 1995), Corsican pine (Miller *et al.* 1981) and jack pine (Tan and Hogan 1995). Tan and Hogan (1995) reemphasized that the relationship between A, g_s and N strongly depends on species.

Photosynthetic Nitrogen Use Efficiency

Photosynthetic, or instantaneous, nitrogen use efficiency (PNUE or NUE) considers the instantaneous use of N for photosynthetic carbon gain, and is generally defined as the ratio of A to leaf N content (Birk and Vitousek 1986, Lambers *et al.* 1998). Garnier *et al.* (1995) found that plants that had a low NUE tended to invest more of their leaf N in non-photosynthetic compounds. A greater N concentration in the foliage normally results in a decrease in NUE, and vice versa, which suggests a phenotypic response of increased NUE under conditions of low N availability (Schulze and Caldwell 1995). Birk and Vitousek (1986) also found that NUE decreased as N availability increased.

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Poorter and Evans (1998) found an interesting correlation between NUE and specific leaf area (SLA), the leaf area per unit leaf mass (Lambers *et al.* 1998). Species with a high SLA regularly had a high NUE. Poorter and Evans (1998) gave several explanations for this phenomenon, including the possibility that there could be differences in light absorption by the leaf, variation in the activation state or specific activity of Rubisco and/or a variation in the amount of light needed to saturate A. However, they concluded that fast growing species with high SLA most likely allocated comparatively more N to photosynthetic components and functions.

Seasonal Changes in Gas Exchange

Gas exchange processes such as A, g_s and E are also highly influenced by air and soil temperature, humidity and water availability. As such, these processes are affected by seasonal changes in these microclimate variables, especially in the spring and autumn months. Photosynthesis of jack pine and white spruce in the spring and autumn is likely most restricted by low soil temperature in the spring and below freezing air temperatures at night in the autumn (Man and Lieffers 1997). Man and Lieffers (1997) also found that A of 20 to 30 year-old open-grown and understory white spruce and jack pine in Alberta began in mid-April, when maximum daily air temperatures were around 15°C. White spruce regained its photosynthetic capacity slightly ahead of jack pine. Photosynthetic rates of both species fluctuated considerably in the summertime, with lowest values occurring mainly during periods of drought and high temperatures. Seasonal variation in A was greater in white spruce than

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jack pine, and g_s exhibited a very similar seasonal pattern to that of A. Zine el Abidine *et al.* (1995) attributed seasonal decline in photosynthetic rates of black spruce to the aging of foliage, as well as declining minimum night temperature and day length. Constable and Lieffers (1996) state that seasonal trends of light transmission through canopies are a result of the type and age of the canopy, but also a result of differing solar elevations. This may also help explain seasonal trends of gas exchange.

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MATERIALS AND METHODS

GENERAL STUDY SITE DESCRIPTION

The Black Sturgeon Boreal Mixedwood Research Project is situated in the north central portion of Ontario, southwest of Lake Nipigon, approximately 120 km northeast of Thunder Bay, Ontario (Cameron *et al.* 1999). The study site is located on the Black Sturgeon Road, 46.5 km north of highway 11/17 (Figure 1).

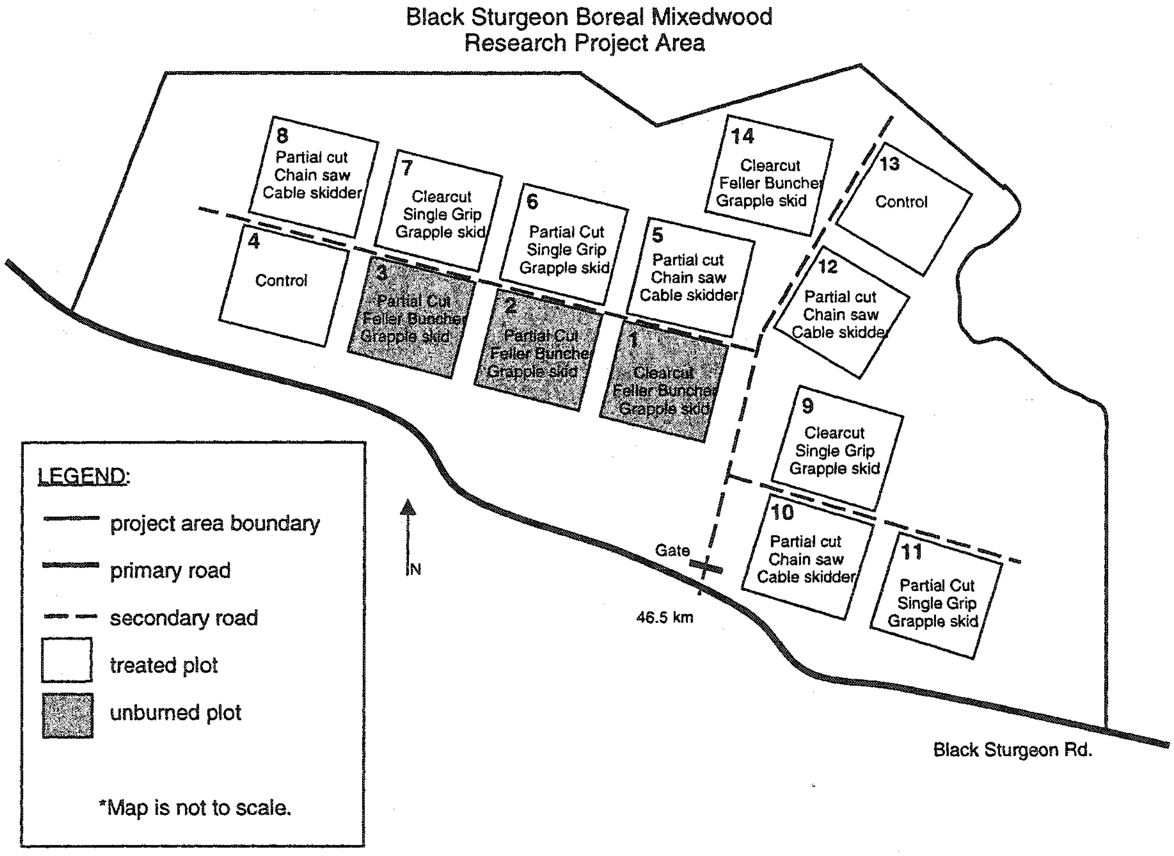

Figure 1. Map of the Black Sturgeon Boreal Mixedwood Research area, including study blocks.

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The study site is located on an extensive, relatively flat, delta moraine that is underlain by gravel, cobble and stones. The soils throughout the area are generally fresh, well drained and fertile and are composed primarily of coarse sands, gravels and shales, with a smaller percentage of silt and small cobbles. The mixedwood stands that are supported by these soils are generally herb and shrub-rich, and tend to fall within the V6, V7, V9, V11 and V16 vegetation-types of the Forest Ecosystem Classification for Northwestern Ontario (Sims *et al.* 1989).

The Black Sturgeon research area supports a forest composition typical of the boreal mixedwood forests of northwest Ontario. The primary forests of the study area were horse-logged in the late 1930's and early 1940's. The second growth stand that followed was composed of trees that were present as advance regeneration at the time of the first harvest, as well as new seedlings that established in canopy openings after harvest.

At the time of the 1975 Forest Resources Inventory (FRI), stand compositions of the study area were approximated at 50% trembling aspen, 30% balsam fir, 10% black spruce and 10% white spruce, with localized mixtures of white birch and/or jack pine. By 1993, when harvesting of the research area took place, most of the balsam fir and white spruce in the upper canopy was either dead or declining due to past spruce budworm infestations. At this time, the average stand composition on a volume basis was estimated at 60% trembling aspen, 12% balsam fir, 11% white spruce, 9% white birch and 3% black spruce. Jack pine was still locally abundant, especially in the area of this particular study (Scarratt 2001).

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The study area was divided into 14, 315 x 320 m plots, to examine the effects of alternative harvesting methods on planted seedlings on a boreal mixedwood site. The research plots were harvested in the fall of 1993. The harvesting systems employed are shown in Figure 1.

In the summer of 1995, the area was Bräcke site-prepared. Prior to planting, in the spring of 1998, the 14 harvest plots were treated with the herbicide Vision® (5 %) using a backpack sprayer, and a brushsaw was used to remove competing vegetation. In late May 1998, jack pine, black spruce and white spruce container (styroblock®) seedlings were planted within each plot. Altogether, six rows of 40 seedlings were planted in each harvest plot. Seedlings were spaced 1 m apart within the rows, with approximately 1 m between rows. Two rows in each block were randomly assigned to each of the three species.

EXPERIMENTAL DESIGN

This particular study, as part of the BSBMRP, was established to study the effects of partial cut and clearcut silvicultural systems on planted jack pine, black spruce, white spruce and trembling aspen seedlings. The study was originally designed as a split plot experiment, with the 14 harvest plots as the whole plots and the rows of planted seedlings as the sub-plots. Unfortunately, in early May 1999 a severe fire swept through the area and burned over 50,000 ha of forest and cutover, including all but three of the harvest plots (Figure 1).

The fire damage almost eliminated the possibility of analyzing the experimental results to study silvicultural systems, since the three surviving

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whole plots provide only a single degree of freedom to estimate whole-plot error. While a test for clearcut vs. partial cut systems is technically possible, the test has almost no statistical power. To salvage what remained of the original experimental design, I decided to drop silvicultural system as a factor and to treat the surviving whole plots as blocks in a randomized complete block design. The reconceived experiment has 3 complete blocks with the surviving whole plots (*i.e.* 1, 2, 3) being reinterpreted as blocks.

Treatment history differed somewhat among the three surviving whole plots (henceforth, blocks). Block one was clearcut in 1993 with the use of a feller buncher and a grapple skidder. The block was manually cleaned in the summer of 1998, so that the height of the shrub canopy did not overtop the newly planted seedlings. Shrubs consisted of beaked hazel [*Corylus cornuta* Marsh.], pin cherry [*Prunus pensylvanica* L. fil], pussy willow [*Salix discolor* Muhl.], as well as some trembling aspen and white birch. The ground layer vegetation consisted of common strawberry [*Fragaria virginiana* Duchesne], low sweet blueberry [*Vaccinium angustifolium* Ait.], red raspberry [*Rubus idaeus* L.], fireweed [*Epilobium angustifolium* L.] and blue-joint grass [*Calamagrostis canadensis* (Michx.) Beauv.].

Block two was partially cut in 1993, using a feller buncher and a grapple skidder to remove approximately two-thirds of the merchantable volume in the block and retain a uniform residual canopy of good quality mature aspen stems. In the fall of 2002, the average post-cut diameter at breast height of the overstory aspen was 28.7 cm, and had a basal area of 13.7 m^2/ha. The shrub layer, consisting mainly of beaked hazel with some trembling aspen, was taller

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than in the clearcut block, as it was not cleaned in 1998. The ground layer contained red raspberry, low sweet blueberry, bunchberry [*Cornus canadensis* L.] and blue-joint grass.

The overstory of block three consisted mainly of mature trembling aspen, with a minor component of white birch and jack pine. It was also partially harvested in 1993, again using a feller buncher and a grapple skidder, with the same specifications as block two. In the fall of 200, post-cut, the average stem diameter was 21.3 cm, with a basal area of 15.8 m^2/ha (14.2 m^2/ha for trembling aspen, 1.57 m^2/ha for white birch and 1.36 m^2/ha for jack pine). The shrub layer consisted mainly of beaked hazel, and the ground vegetation layer was similar to block two. Photographs of all three blocks are presented in Appendix I.

FIELD/LAB PROCEDURE

General Site Information

Total height and root collar diameters of 10 seedlings per row were measured at the end of July 2001 (Table 1).

Table 1. Mean height and root collar diameter (with standard error) of planted seedlings by species and block (n=20).

Species	Block	Height (cm)	RCD (mm)
Jack pine	1	136.4 ± 6.6	21.55 ± 0.97
	2	97.9 ± 4.5	13.56 ± 0.82
	3	84.0 ± 6.1	11.15 ± 0.94
Black spruce	1	99.8 ± 4.3	13.78 ± 0.74
	2	93.1 ± 3.5	11.33 ± 0.57
	3	68.5 ± 2.7	8.45 ± 0.39
White spruce	1	54.2 ± 3.1	10.22 ± 0.53
	2	63.9 ± 4.0	9.52 ± 0.41
	3	52.9 ± 5.2	8.20 ± 0.36

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Soil pits revealed that the soils were generally similar across the three blocks (Figure 2).

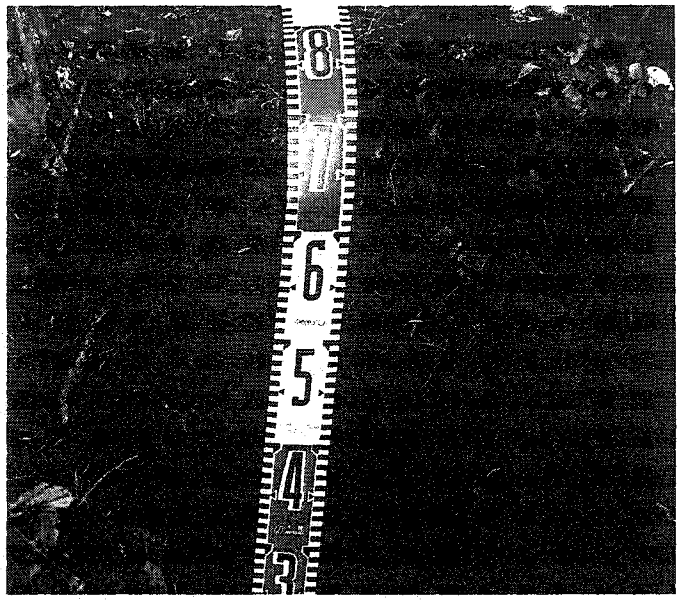

Figure 2. Soil profile from block 2 (Scale units are decimetres).

The C-horizon for all three sites had a coarse sand texture. The Bm_1 and Bm_2 horizons were also similar across the blocks, with sandy loam and medium sand textures, respectively. Blocks one and two had a clay loam textured Ah layer on top of the Bm_1 horizon, although this layer was thicker in block one. The Ah layer was absent in block three. All three pits had L, F and H layers at the top. The soil pits were dug until the C-horizon was reached, which was usually within 50 cm of the surface. There were significant amounts of coarse fragments in all soil horizons in all blocks, with the amount and size of these fragments decreasing with depth. The mode of deposition appeared to be glaciofluvial, as the rocks were rounded from water action and were sorted by size. The coarse fragments became more sorted from block one to block three.

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Physiological Measurements

Three seedlings per row were chosen at random for measurement of photosynthesis (A), stomatal conductance (g_s), and transpiration (E) during early, mid and late summer of the growing season of 2001. Gas exchange measurements were obtained using a portable photosynthesis system (CIRAS-1, PP Systems, Amesbury, MA). A Parkinson Leaf Cuvette (PLC) designed for conifer foliage was attached to the CIRAS-1. The cuvette was fitted with an external LED light unit to provide selected photosynthetic photon flux density (PPFD), or light levels during measurement. The light source was controlled by the CIRAS-1 console. Air temperature, humidity and CO_2 were set to specific levels in the cuvette for all gas exchange measurements (24°C, 50% RH [or 1.49 kPa] and 380 ppm, respectively), and controlled automatically by the cuvette with the use of peltier coolers.

Gas exchange measurements were made at seven levels of light intensity, or PPFD: 1000, 600, 400, 150, 100, 50 and 0 µmol (photons)/m^2/s to generate photosynthetic light response curves for the plant. A, g_s and E were measured on the current year's needles of a south-facing lateral branch, located at roughly half the height of the seedling. The measurements were taken from an approximately 3 cm long shoot segment located at the branch tip. To provide a good seal in the cuvette, needles were removed from the shoot along the rubber seal. The foliage was allowed to equilibrate to the cuvette environment for approximately three to five minutes before measurement at each light level was taken to allow steady-state gas exchange to occur.

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The early summer gas exchange measurements were collected on July 6, 9, 11, and 13, 2001. The shoot segments enclosed in the cuvette were excised and brought back to the lab for needle area determination, since the new foliage had not yet fully developed for that growing season. Gas exchange measurements for the second, or mid-summer sampling took place on July 26, 31, August 9 and 10. Three seedlings per row were chosen at random with no correlation to the seedlings chosen at the beginning of July. The needles were fully expanded at this sampling. The measured shoot was marked for future reference and sampled a second time for the late summer measurements (September 13-15). After the late summer measurements, the sampled branches were excised and brought back to the laboratory for needle area, weight and N determination.

In the laboratory, the needles from each measured shoot were removed and spread out on a scanner. The computer software WinSeedle (version 4.4, WinNeedle™, Regent Instruments Inc, Quebec, Canada) was used to determine projected needle area (cm^2). The foliage samples were then dried in a drying oven at 37°C[2] for 48 hours to determine dry weight. A relatively low drying temperature was used in order to preserve the foliar nitrogen. Specific leaf area (SLA) of tissue sampled was calculated using projected area and needle dry weight. Needle dry weight was also used to calculate A expressed on a mass basis. The samples were ground and then sent to the Science Instrumentation

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[2] Note that upon completion of the thesis, it was determined that oven drying temperature should have been higher (approximately 65 degrees Celsius). It is likely that a small amount of water still remained in the tissue and SLA and mass based A values presented are slightly underestimated.

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Laboratory at Lakehead University for total Kjeldahl N determination. The amount of tissue available was sufficient only for the determination of N content.

Total projected needle area of each shoot was used to estimate A on a unit area basis, using Equation 1, where A denotes the rate of CO_2 assimilation, or the difference in $[CO_2]$ of the input and output airstream from cuvette, in μmol $CO_2/m^2/s$. The value 10 represents the default leaf area value originally input in the CIRAS-1 to represent leaf area.

$$\text{actual } A = 10 \text{ (measured } A\text{)/ leaf area} \qquad \text{Eq. 1}$$

Analogous formulae were used for g_s and E, substituting these values for A in Eq. 1. Photosynthetic water use efficiency (WUE) was calculated as the ratio of A to E at light intensity = 1000 μmol/m^2/s for both A and E. (Lambers *et al.* 1998). Photosynthetic nitrogen use efficiency (NUE) was determined by dividing A (at 1000 μmol/m^2/s) by foliar nitrogen content (g/m^2) on a leaf area basis (Garnier *et al.* 1995).

DATA ANALYSIS

July-August Analysis of Variance

The July and August gas exchange and SLA data were compared and analyzed as a randomized complete block design using univariate (for each individual light level) and multivariate (for all seven light levels) analyses of variance (ANOVA and MANOVA, respectively). The statistical software Data Desk© 6.0.1 for Windows was used to perform the analysis. The data were first tested for normality within each treatment (block, species month) group and

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homogeneity of variance across the treatment groups. If the data did not meet these two criteria, they were transformed and re-tested. Based on these results, the original values for g_s and E required a logarithm transformation prior to analysis (Log (Y)). The sources of variation examined were block (B), species (S), month (M) of measure, and their second- and third-order interactions. Least significant difference (LSD) tests were also performed on the data. The raw data and the LSD test results are given in Appendices III and IV, respectively.

August-September Repeated Measures Analysis

The August and September data were compared and analyzed as a repeated measures experiment, using months as repeats on the same subjects (trees). Trees are nested within blocks and species (Appendix II). The data were again tested for normality and homogeneity of variance and, if found to be unacceptable, they were transformed as Log (Y).

Photosynthetic light response curves were created and visually compared for each species and for each month. From these graphical displays, the light compensation point (LCP) and light saturation point were determined by interpolation for each species. The relationships between foliar nitrogen concentration and area- and mass-based A were examined using linear regression. Photosynthesis values at A_{800} were estimated by linear interpolation in order to produce the figures. Finally, specific leaf area (SLA), WUE and NUE were calculated and analysed by means of univariate ANOVA.

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RESULTS

PHOTOSYNTHESIS

The multivariate A data were analyzed using two linear models. The July and August measurements used different subject trees on each sampling date, so that subset of data was analyzed as a randomized complete block design. The August and September measurements, on the other hand, used the same subject trees on both measurement occasions and so these data were analyzed as a repeated measures experiment. As a result, the August measurements are handled twice and this has implications for how some of the results are interpreted.

The MANOVA results from both analyses are summarized in Table 2. For both analyses (July/August and August/September), the main effects of species, month, and the block x month interaction were statistically significant.

Table 2. Wilks Lambda test statistic and MANOVA test results for treatment effects on A (at all light levels). Probabilities that are statistically significant at $\alpha = 0.05$ are presented in bold text.

	July/August RCBD MANOVA		August/September repeated measures MANOVA	
Source	Wilks Lambda	Prob. > λ	Wilks Lambda	Prob. > λ
Block (B)	No test	No test	No test	No test
Restriction error[1]	No test	No test	No test	No test
Species (S)	0.4325	**<0.001**	0.3961	**<0.001**
B*S	0.6653	0.15	0.4433	0.17
Tree w/in B*S	Not applicable[2]	Not applicable	0.0019	**0.01**
Month (M)	0.4681	**<0.001**	0.4331	**<0.001**
B*M	0.6541	**<0.001**	0.5015	**0.01**
S*M	0.8578	0.50	0.6035	0.10
B*S*M	0.6568	0.12	0.3738	**0.04**

[1] A restriction error is a random effect that denotes a restriction on randomization in the experimental design (Lorenzen and Anderson 1993).

[2] The term "trees within blocks and species" occurs only in the case of the repeated measures design.

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July-August

The MANOVA results for July and August, and details of the univariate ANOVA, are given in Table 3. When examining the block x month interaction closely (Figure 3), it appears that clearcut block one responds independently of the partial cut blocks.

Table 3. MANOVA and ANOVA results for treatment effects on A at individual light levels from July and August sampling periods. Multivariate and univariate results are the probabilities of a greater test statistic. Values in bold typeface are statistically significant at the $\alpha = 0.05$ level.

		Multi-Variate	Univariate results for photosynthesis at light level:[2]						
Source	df	results[1]	0	50	100	150	400	600	1000
Block (B)	2	no test	no test						
Restriction error	0	no test	no test						
Species (S)	2	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**0.01**	**0.02**	**<0.01**	**<0.01**
B*S	4	0.15	0.12	0.43	0.13	0.12	**0.01**	**<0.01**	**<0.01**
Month (M)	1	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
B*M	2	**<0.01**	0.69	0.22	0.17	**0.02**	**<0.01**	**<0.01**	**<0.01**
S*M	2	0.50	0.12	0.43	0.74	0.94	0.34	0.39	0.32
B*S*M	4	0.12	0.42	0.13	0.15	**0.01**	**0.04**	0.06	0.21

[1] Multivariate tests are based on Wilks λ statistics.
[2] Univariate tests are based on mean square ratios.

The light response curves sorted by species and month are of more interest than the main effect means for species when averaged over July and August. The photosynthetic light response curves are presented later in the thesis (Figures 8 and 9). The main effect means for sampling period are presented in Table 4.

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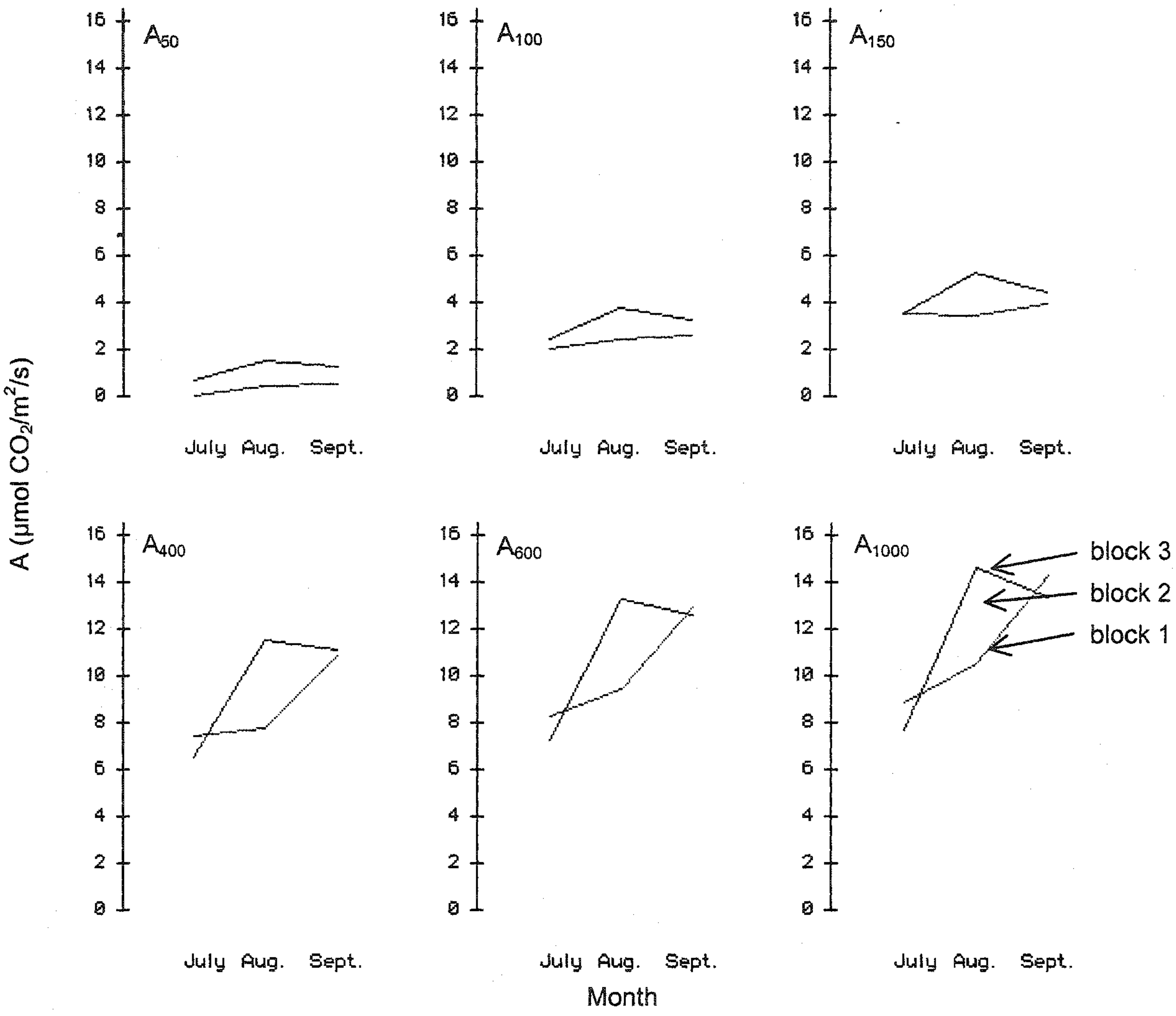

Figure 3. Block x month interaction cell means for A for all three months. The individual panels show the rate of photosynthesis at each of the following levels of light intensity: 50, 100, 150, 400, 600, and 1000. Blocks are labeled in the lower right panel.

Table 4. Mean rate of photosynthesis by month and light level.[1]

	Response variable in μmol $CO_2/m^2/s$						
Sampling Period	0	50	100	150	400	600	1000
	---------------------------- μmol $CO_2/m^2/s$ ----------------------------						
July	-2.08	0.32	2.28	3.61	7.21	8.07	8.74
August	-1.34	1.11	3.35	4.74	10.19	11.77	12.79
September	-1.06	0.91	2.92	4.17	11.11	12.92	14.00

[1] July and August means are statistically different at all incident light levels. The August and September means are different at incident light levels 0, 600, and 1000 μmol/m^2/s.

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August-September

The ANOVA and MANOVA results for the August and September analysis are given in Table 5. The block x month interaction cell means are presented in Figure 3. Results presented in tables 2 and 5 indicate that the block x species x month interaction is significant in the multivariate analysis. However, Table 5 shows that this 3-way interaction is not significant for any of the univariate ANOVAs, and there is little evidence of the 3-way interaction being meaningful in the July-August data subset.

Table 5. MANOVA and ANOVA results for treatment effects on A at individual light levels from August and September sampling periods. Multivariate and univariate results are the probabilities of a greater test statistic. Values in bold typeface are statistically significant at the $\alpha = 0.05$ level.

		Multi-Variate	Univariate results for photosynthesis at light level: [2]						
Source	df	results[1]	0	50	100	150	400	600	1000
Block (B)	2	no test	no test						
Restriction error	0	no test	no test						
Species (S)	2	**<0.01**	0.11	0.19	0.30	**0.01**	**0.03**	**<0.01**	**<0.01**
B*S	4	0.17	0.91	0.33	0.09	**0.02**	0.25	0.23	0.18
Tree	45	**0.01**	**0.04**	0.62	0.74	0.96	0.45	0.35	0.41
Month (M)	1	**<0.01**	**0.04**	0.35	0.15	0.17	0.07	**0.03**	**0.04**
B*M	2	**0.01**	0.52	0.64	0.24	0.14	**0.01**	**0.01**	**<0.01**
S*M	2	0.10	0.32	0.11	**0.04**	**0.03**	**0.02**	**0.03**	**0.03**
B*S*M	4	**0.04**	0.44	0.25	0.72	0.67	0.33	0.13	0.27

[1] Multivariate tests are based on Wilks λ statistics.
[2] Univariate tests are based on mean square ratios.

The light response curves sorted by species and month are presented in Figure 9, and show the means for each species for all three sampling periods. As noted above, the main effect means for months are presented in Table 4.

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STOMATAL CONDUCTANCE

As with the A data, the multivariate g_s data were analyzed under two linear models. The MANOVA results from are summarized in Table 6. On both sides of the analysis (July/August and August/September), the block x month and block x species interactions and the main effect of species are statistically significant.

Table 6. Wilks Lambda test statistic and MANOVA test results for r treatment effects on log (g_s) (at all light levels). Probabilities that are statistically significant at $\alpha = 0.05$ are presented in bold text.

	July/August RCBD MANOVA		August/September repeated measures MANOVA	
Source	Wilks Lambda	Prob. > λ	Wilks Lambda	Prob. > λ
Block (B)	No test	No test	No test	No test
Restriction error	No test	No test	No test	No test
Species (S)	0.5723	**<0.001**	0.5308	**0.02**
B*S	0.6085	**0.03**	0.3076	**0.01**
Tree w/in B*S	Not applicable[1]	Not applicable	0.0144	0.99
Month (M)	0.8656	0.09	0.3897	**<0.001**
B*M	0.6237	**<0.001**	0.5361	**0.03**
S*M	0.8196	0.25	0.5891	0.09
B*S*M	0.6507	0.11	0.6027	0.82

[1] The term "trees within blocks and species" occurs only in the case of the repeated measures design.

July-August

The MANOVA results for the July and August logarithm of g_s (log (g_s)), as well as the univariate ANOVA results, are presented in Table 7. The univariate ANOVA results show that the block x month and block x species interactions, as well as the main effects of month and species were statistically significant at all light levels (0 to 1000 μmol/m^2/s). The block x month interaction cell means are plotted in Figure 4 and the block x species interaction cell means are presented in Figure 5. In Figures 4 and 5, the measured units are plotted instead of the

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calculated log (g_s) values, as the actual values are of greater interest. The main effect means for months are presented in Table 8.

Table 7. MANOVA and ANOVA results for treatment effects on log (g_s) at individual light levels from July and August sampling periods. Multivariate and univariate results are the probabilities of a greater test statistic. Values in bold typeface are statistically significant at the $\alpha = 0.05$ level.

Source	df	Multi-Variate results[1]	Univariate results for log (g_s) at light level:[2]						
			0	50	100	150	400	600	1000
Block (B)	2	no test	no test						
Restriction error	0	no test	no test						
Species (S)	2	**<0.01**	**0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
B*S	4	**0.03**	**0.01**	**0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
Month (M)	1	0.09	**<0.01**	**0.01**	**0.02**	**0.02**	**0.03**	**0.02**	**0.01**
B*M	2	**<0.01**	**<0.01**	**<0.01**	**0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
S*M	2	0.25	0.06	**0.04**	**0.04**	0.06	0.31	0.39	0.52
B*S*M	4	0.11	0.10	**0.05**	**0.05**	0.20	0.12	0.10	**0.03**

[1] Multivariate tests are based on Wilks λ statistics.

[2] Univariate tests are based on mean square ratios.

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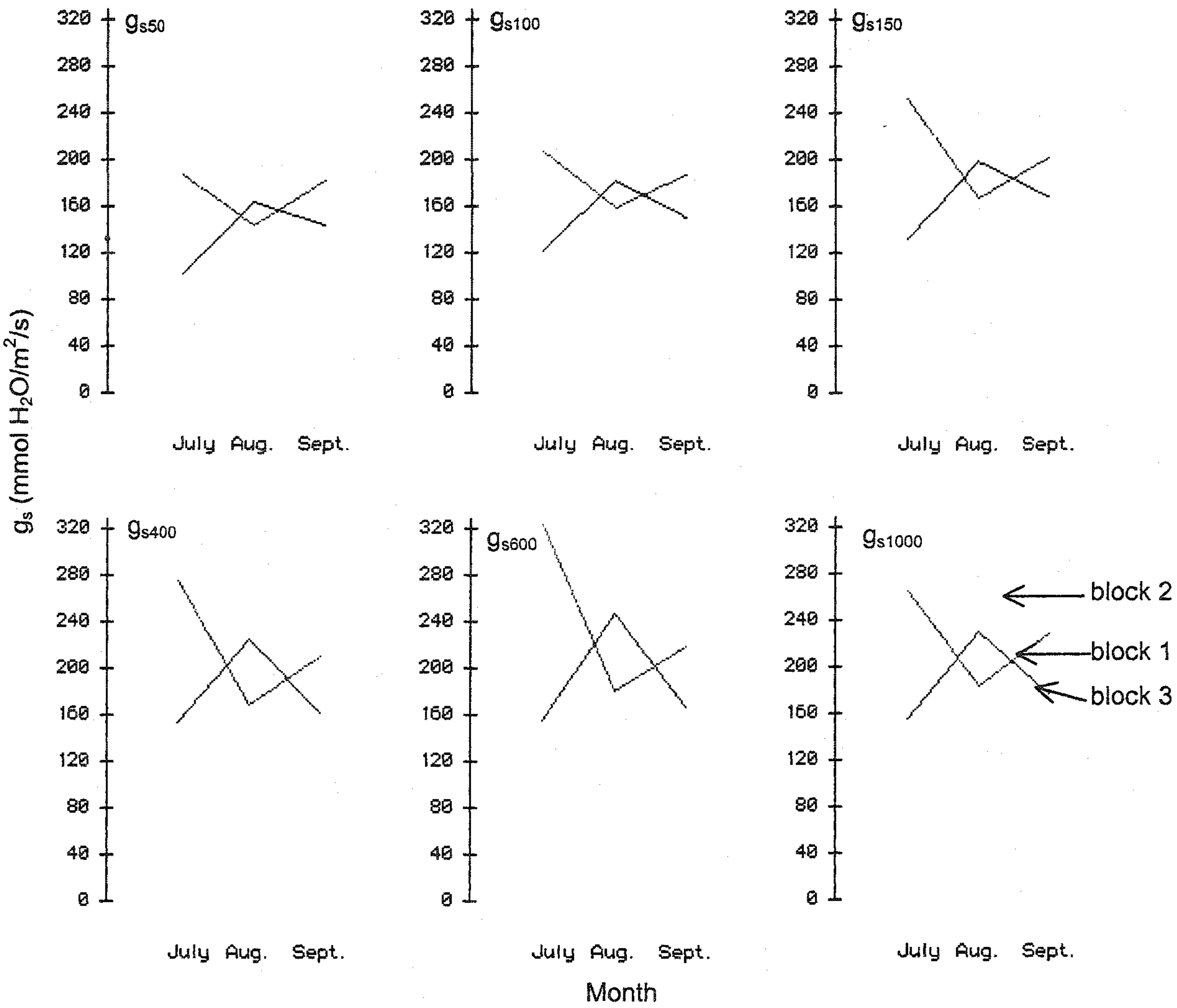

Figure 4. Block x month interaction cell means for g_s for all three months. The individual panels show the rate of stomatal conductance at each of the following levels of light intensity: 50, 100, 150, 400, 600, and 1000. Blocks are labeled in the lower-right panel.

Table 8. Mean rate of stomatal conductance by month and light level.[1]

Month	Light intensity (μmol photons/m²/s)						
	0	50	100	150	400	600	1000
	----------mmol $H_2O/m^2/s$----------						
July	131.7	153.7	180.4	200.9	221.6	234.9	218.2
August	156.0	168.7	183.7	197.8	217.8	239.0	231.9
September	197.2	173.3	180.1	192.1	192.8	195.4	203.9

[1] July and August means are statistically different at all incident light levels, but not in the MANOVA. The August and September means are different at incident light levels 0 and 600 μmol photons/m²/s in the MANOVA.

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August-September

The repeated measures MANOVA results for the logarithm of g_s, log (g_s), are given in Table 9. Block x species, block x month, species and month were significant in August and September. The interaction cell means for the measured values are plotted in Figure 4, since the real values are more relevant to the reader. The analysis was performed on the log re-expressed values and plots for log (g_s) values are presented in Appendix V.

Table 9. MANOVA and ANOVA results for treatment effects on log (g_s) at individual light levels from August and September sampling periods. Multivariate and univariate results are the probabilities of a greater test statistic. Values in bold typeface are statistically significant at the $\alpha = 0.05$ level.

Source	df	Multi-Variate results[1]	Univariate results for log (g_s) at light level:[2]						
			0	50	100	150	400	600	1000
Block (B)	2	no test	no test						
Restriction error	0	no test	no test						
Species (S)	2	**0.02**	0.61	0.78	0.99	0.72	0.35	0.07	**0.03**
B*S	4	**0.01**	0.11	0.16	0.06	**0.01**	0.10	0.22	0.18
Tree	45	0.99	0.81	0.88	0.92	0.97	0.87	0.87	0.77
Month (M)	1	**<0.01**	**0.04**	0.74	1.00	0.73	0.14	**0.02**	0.07
B*M	2	**0.03**	0.08	0.11	0.20	0.16	**0.02**	**0.01**	**0.01**
S*M	2	0.09	0.31	0.17	0.12	**0.02**	**<0.01**	**<0.01**	**<0.01**
B*S*M	4	0.82	0.21	0.18	0.10	0.10	0.08	0.06	0.10

[1] Multivariate tests are based on Wilks λ statistics.
[2] Univariate tests are based on mean square ratios.

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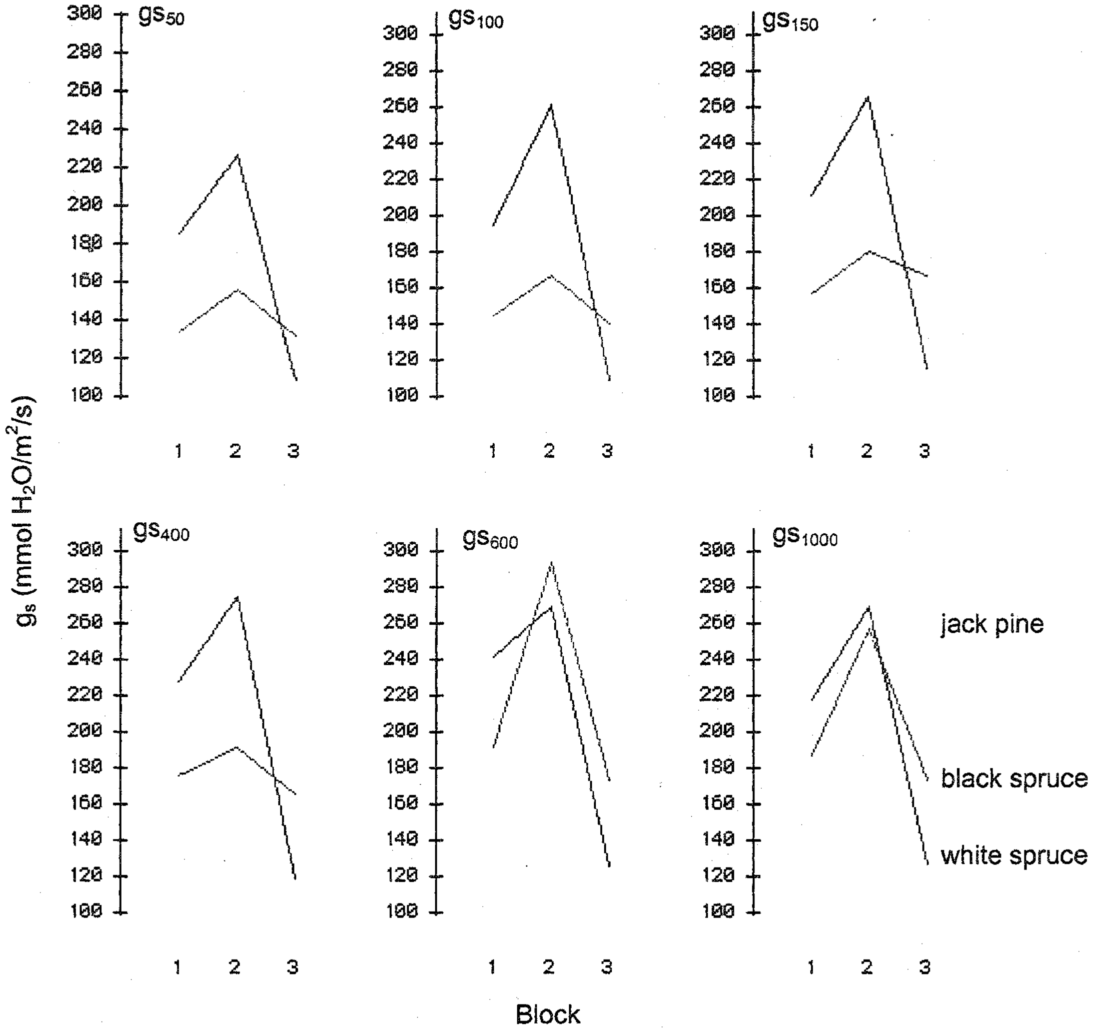

Figure 5. Block x species interaction cell means for g_s for all three months. The individual panels show the rate of stomatal conductance at each of the following levels of light intensity: 50, 100, 150, 400, 600, and 1000. Species are labeled in the lower-right panel.

TRANSPIRATION

The multivariate E data were once again analyzed under two linear models. The MANOVA results from both analyses are summarized in Table 10. On both sides of the analysis (July-August and August-September), the three-way interaction of block x species x month, the species x month interaction and the main effect for months are significant.

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Table 10. Wilks Lambda test statistic and MANOVA test results for treatment effects on log (E) (at all light levels). Probabilities that are statistically significant at $\alpha = 0.05$ are presented in bold text.

	July/August RCBD MANOVA		August/September repeated measures MANOVA	
Source	Wilks Lambda	Prob. > λ	Wilks Lambda	Prob. > λ
Block (B)	No test	No test	No test	No test
Restriction error	No test	No test	No test	No test
Species (S)	0.7574	**0.04**	0.6115	0.11
B*S	0.4883	**<0.001**	0.5083	0.41
Tree w/in B*S	Not applicable[1]	Not applicable	0.0484	0.36
Month (M)	0.7338	**<0.001**	0.4706	**<0.001**
B*M	0.7903	0.12	0.6650	0.15
S*M	0.6493	**<0.001**	0.4502	**<0.001**
B*S*M	0.6006	**0.02**	0.3629	**<0.001**

[1] The term "trees within blocks and species" occurs only in the case of the repeated measures design.

July-August

The MANOVA results for the July and August logarithm of E, log (E), as well as the ANOVA results, are presented in Table 11. The block x species interaction is significant only for July-August. The interaction cell means are presented in Figure 6, and the main effect means for months are presented in Table 12.

Table 11. MANOVA and ANOVA results for treatment effects on log (E) at individual light levels from July and August sampling periods. Multivariate and univariate results are the probabilities of a greater test statistic. Values in bold typeface are statistically significant at the $\alpha = 0.05$ level.

		Multi-Variate	Univariate results for log (E) at light level:[2]						
Source	df	results[1]	0	50	100	150	400	600	1000
Block (B)	2	no test	no test						
Restriction error	0	no test	no test						
Species (S)	2	**0.04**	0.90	0.74	0.90	0.59	0.21	0.07	0.07
B*S	4	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
Month (M)	1	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
B*M	2	0.12	0.21	**0.03**	0.08	**0.02**	**<0.01**	**0.01**	**<0.01**
S*M	2	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
B*S*M	4	**0.02**	0.16	**<0.01**	**0.01**	**0.02**	**0.01**	**0.01**	**0.01**

[1] Multivariate tests are based on Wilks λ statistics.
[2] Univariate tests are based on mean square ratios.

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Table 12. Mean rate of transpiration by month and light level.[1]

Month	Light intensity (μmol photons/m^2/s)						
	0	50	100	150	400	600	1000
	----mmol $H_2O/m^2/s$----						
July	1.85	2.06	2.18	2.36	2.54	2.70	2.83
August	2.45	2.51	2.60	2.77	2.90	3.14	3.19
September	3.30	3.27	3.27	3.37	3.46	3.55	3.50

[1] July and August means are statistically different at all incident light levels. The August and September means are different at all incident light levels except for 600, and 1000 μmol photons/m^2/s.

August-September

The MANOVA results for the August and September logarithm of E, log (E), along with details of the univariate ANOVA results, are given in Table 13.

Table 13. MANOVA and ANOVA results for treatment effects on log (E) at individual light levels from August and September sampling periods. Multivariate and univariate results are the probabilities of a greater test statistic. Values in bold typeface are statistically significant at the α = 0.05 level.

Source	df	Multi-Variate results[1]	Univariate results for log (E) at light level:[2]						
			0	50	100	150	400	600	1000
Block (B)	2	no test	no test						
Restriction error	0	no test	no test						
Species (S)	2	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
B*S	4	0.70	0.37	0.40	0.39	0.49	0.60	0.53	0.36
Tree	45	0.21	0.53	0.36	0.26	0.15	0.06	0.25	0.23
Month (M)	1	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**0.01**	0.39	0.75
B*M	2	0.76	0.46	0.20	0.15	0.19	0.17	0.27	0.22
S*M	2	**0.04**	0.62	0.72	0.69	0.70	0.07	**0.02**	**0.02**
B*S*M	4	**0.03**	0.17	0.11	**0.02**	**<0.01**	**0.02**	**0.03**	**0.01**

[1] Multivariate tests are based on Wilks λ statistics.

[2] Univariate tests are based on mean square ratios.

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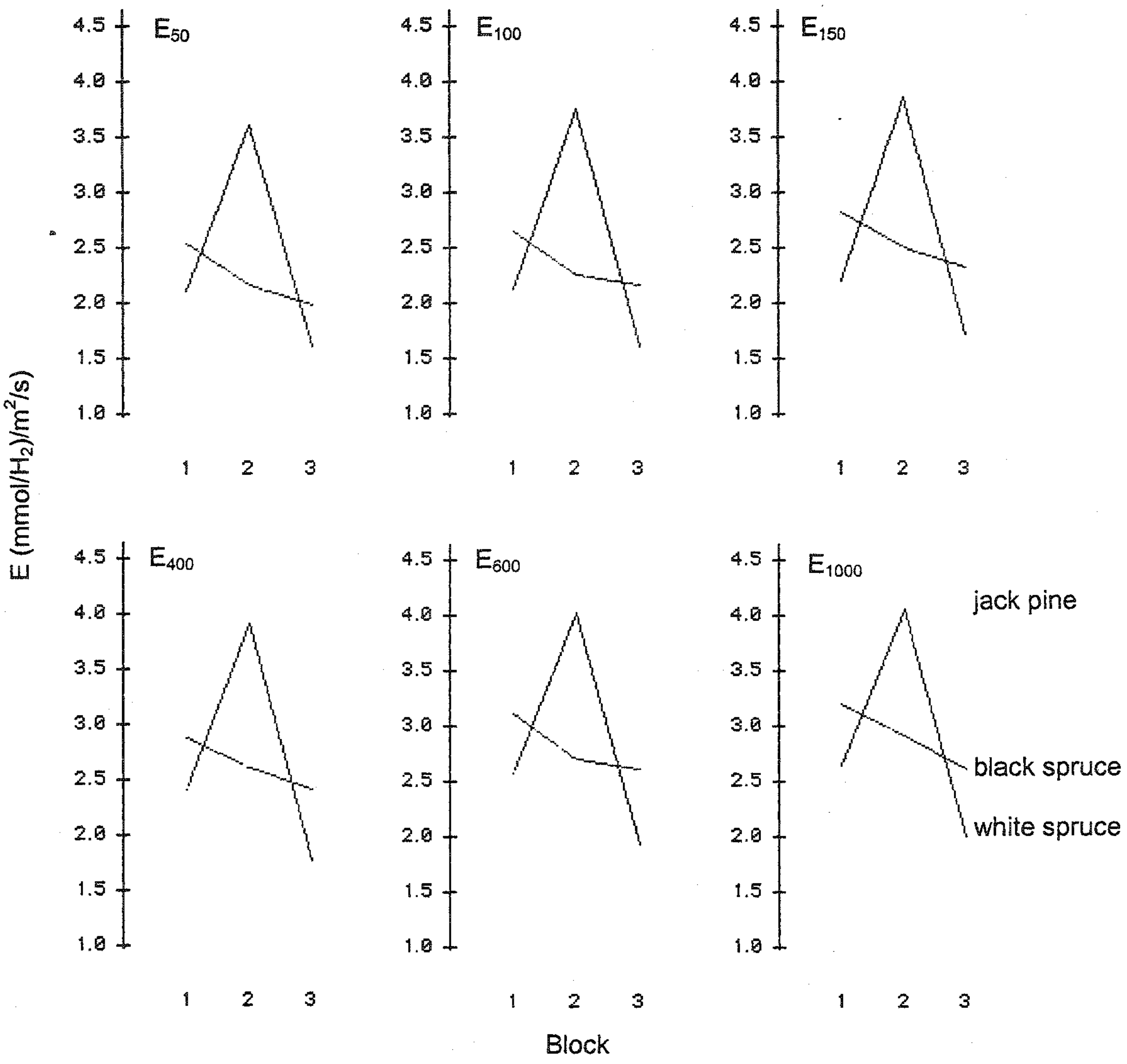

Figure 6. Block x species interaction cell means for E for July-August only. The individual panels show the rate of transpiration at each of the following levels of light intensity: 50, 100, 150, 400, 600, and 1000. Species are labeled in the lower-right panel.

The species x month interaction cell means for the actual measured values are presented graphically in Figure 7. Since the analysis was performed on the log re-expressed values, figures for log (E) values can be found in Appendix V.

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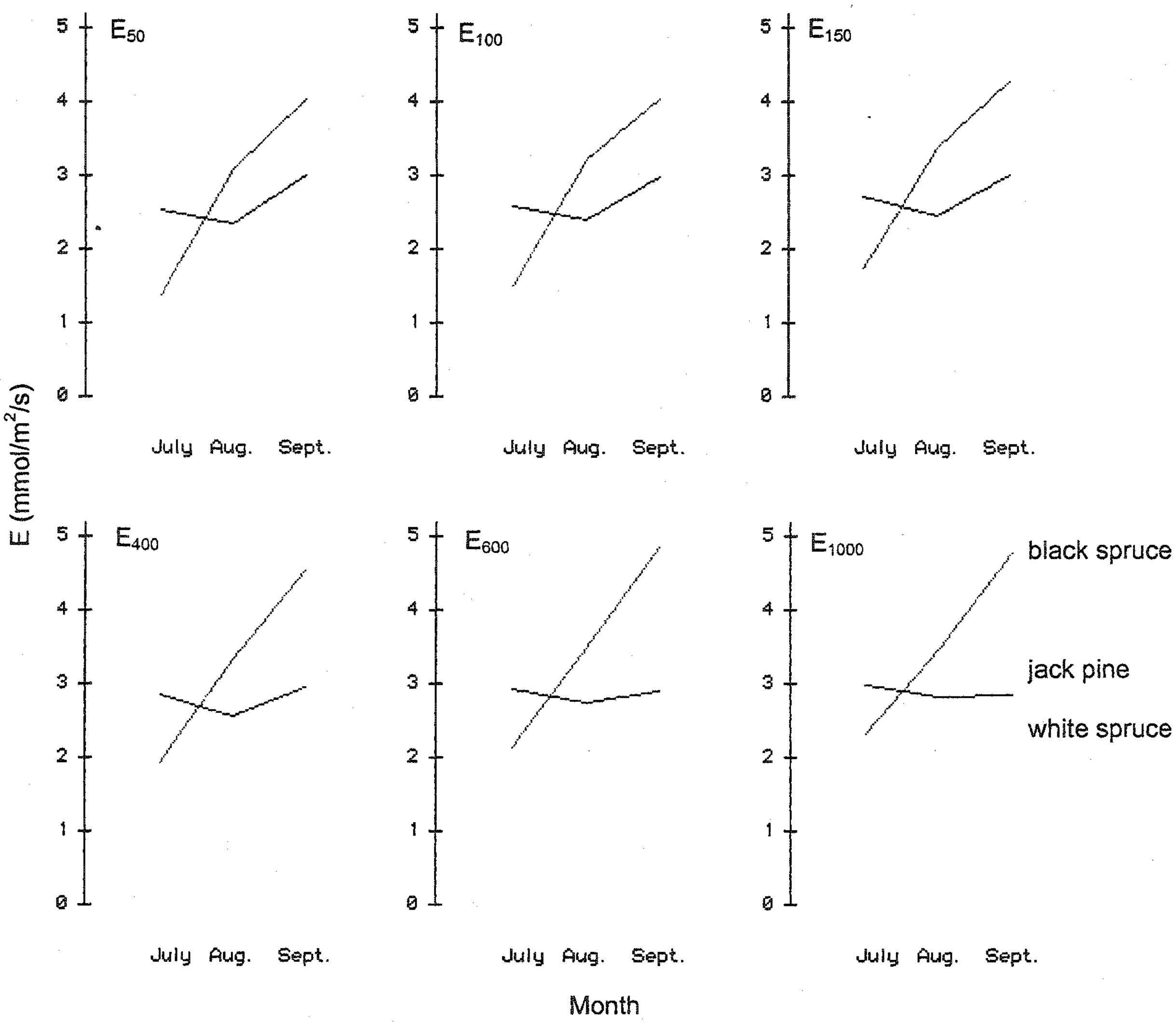

Figure 7. Species x month interaction cell means for E for all three months. The individual panels show the rate of transpiration at each of the following levels of light intensity: 50, 100, 150, 400, 600, and 1000. Species are labeled in the lower-right panel.

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PHOTOSYNTHETIC LIGHT RESPONSE CURVES

The light response curves for each species by sampling period are presented in Figure 8. Jack pine consistently had the highest rates of photosynthesis at the higher light levels (>300 μmol/m^2/s) of all three species. White spruce frequently had the second highest rates, except in September, and it often had the highest initial rate of A in the light-limited range of A.

When light response curves were compared among species (Figure 9), both jack pine and black spruce had higher rates of A in September, whereas white spruce had higher rates of A in August. The lowest photosynthetic rates for all species were observed in July. Light response curves for all three species were generally similar in August and September.

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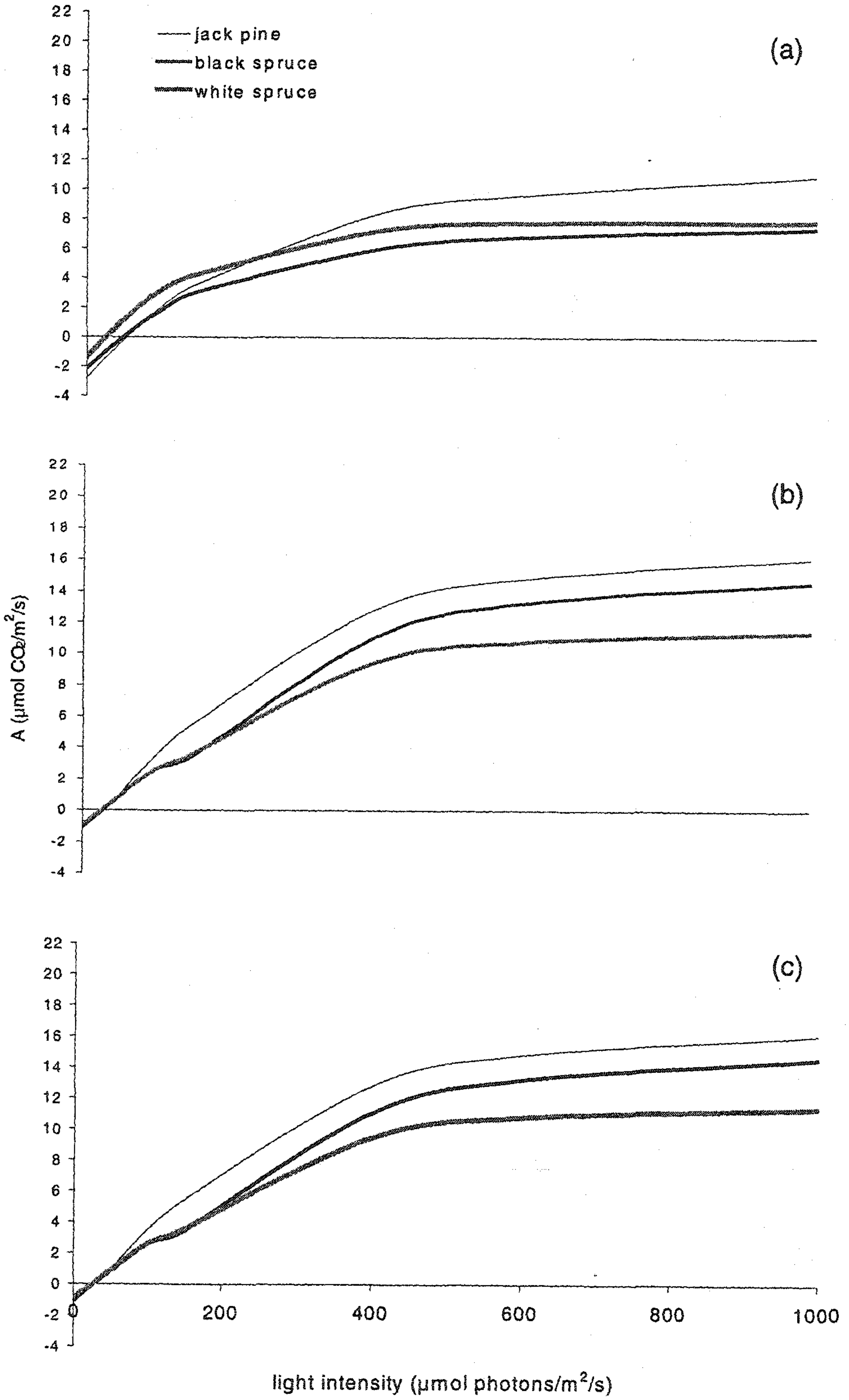

Figure 8. Species comparisons of photosynthetic light response curves for July (a), August (b) and September (c).

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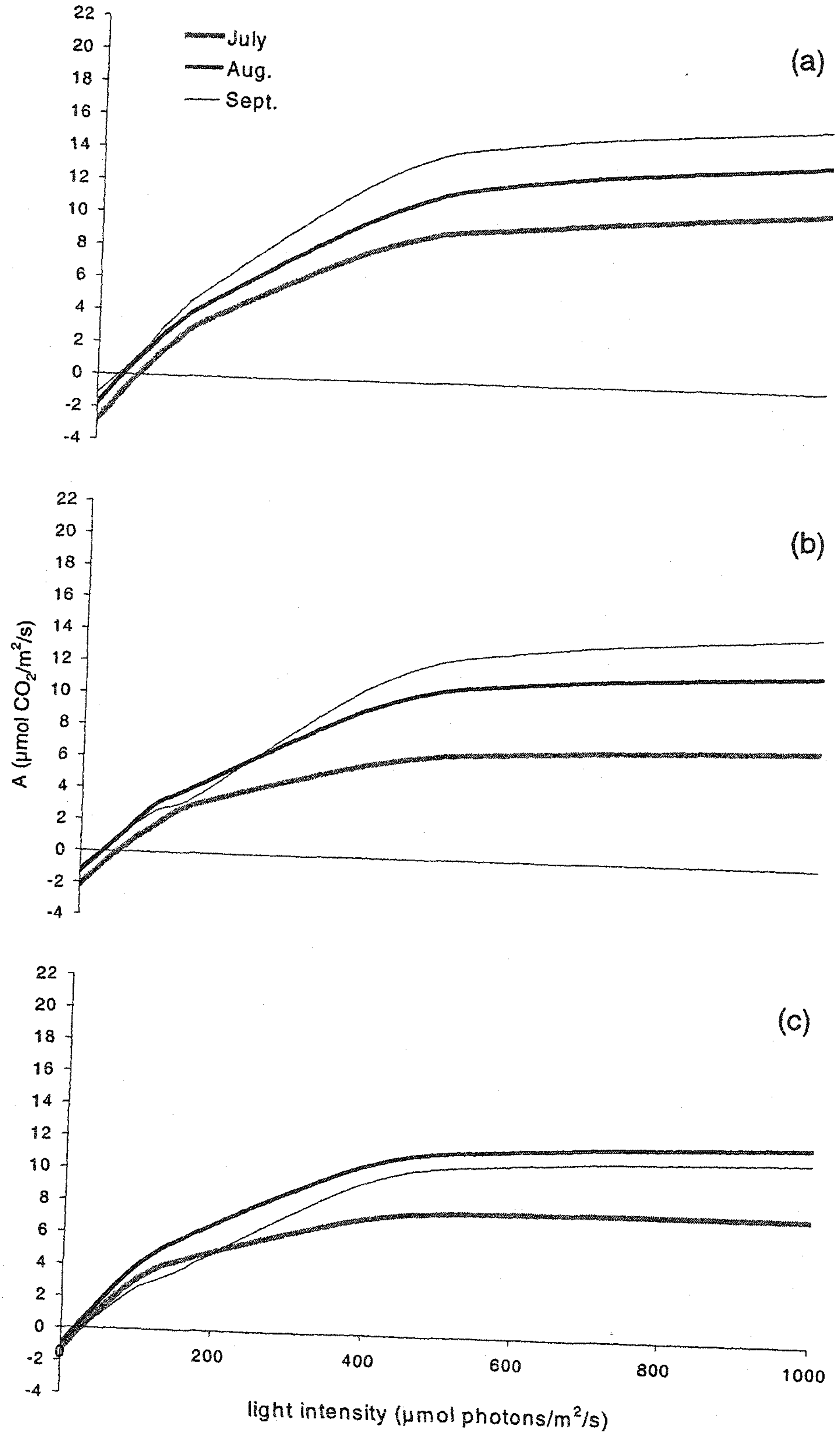

igure 9. Photosynthetic light response curves for jack pine (a), black spruce (b) and white spruce (c).

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LIGHT COMPENSATION POINTS

July-August

The LCP was calculated through interpolation for each tree in July and August. The ANOVA results for LCP are given in Table 14. White spruce had a significantly lower LCP than black spruce and jack pine, overall (Table 15).

Table 14. ANOVA table for July-August light compensation point comparison.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	8397.80	4198.90	no test	no test
Restriction error	0	no est.	no est.	no test	no test
Species (S)	2	13130.20	6565.12	15.90	**< 0.0001**
B*S	4	2052.87	513.22	1.24	0.2986
Month (M)	1	9296.33	9296.33	22.51	**< 0.0001**
B*M	2	286.72	143.36	0.35	0.7077
S*M	2	1218.39	609.19	1.48	0.2342
B*S*M	4	2485.39	621.35	1.50	0.2076
Error	90	37168.30	412.98		
Total	107	74036.10			

Table 15. Mean light compensation point values by species and month (in µmol photons/m^2/s).

		Species			Month Means
Month		jack pine	black spruce	white spruce	
July		59.1	55.9	28.6	47.9
August		40.2	29.3	18.4	29.3
September		36.6	24.3	24.6	28.5
Species Means	J/A	49.6	42.6	23.5	
	A/S	38.4	26.8	21.5	

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August-September

In the August-September analysis, species again had a significant effect on LCP, but the effect of month did not (Table 16).

Table 16. ANOVA for August-September light compensation point.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	9000.46	4500.23	no test	no test
Restriction error	0	no est.	no est.	no test	no test
Species (S)	2	5366.52	2683.26	7.00	**0.0023**
B*S	4	1582.26	395.57	1.03	0.4015
Tree	45	17259.80	383.55	1.72	**0.0366**
Month (M)	1	17.93	17.93	0.08	0.7783
B*M	2	109.80	54.90	0.25	0.7832
S*M	2	656.96	328.48	1.47	0.2408
B*S*M	4	1753.15	438.29	1.96	0.1167
Error	45	10056.20	223.47		
Total	107	45803.10			

FOLIAR NITROGEN

Foliar nitrogen concentration (%) and the rate of photosynthesis were not strongly correlated in this study (Figures 10 and 11). When the rate of photosynthesis was expressed on a mass basis, the correlation was no more apparent than when it was expressed on an area basis.

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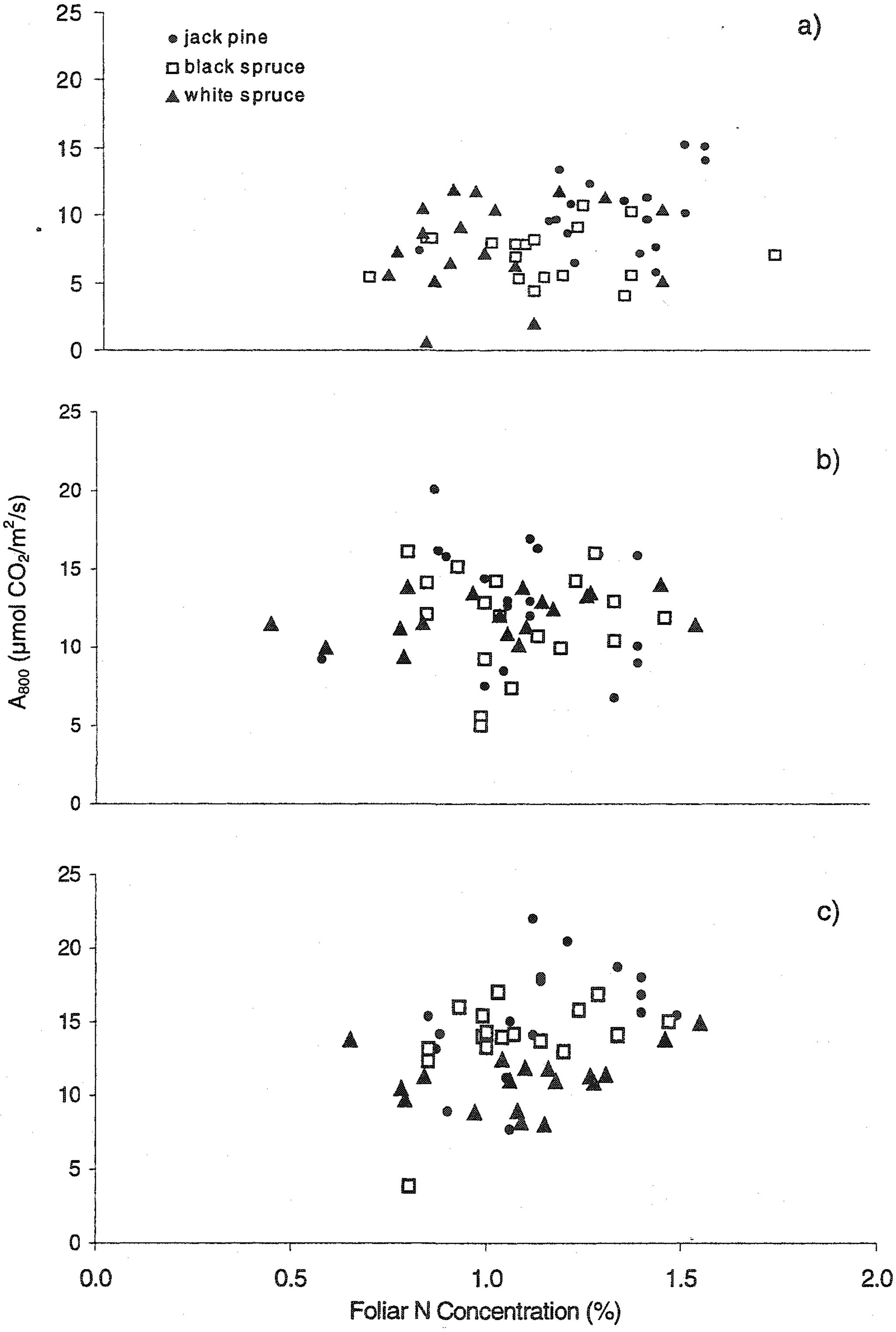

Figure 10. A_{max} (area) vs. foliar nitrogen concentration for July (a), August (b) and September (c). The plotted values are interpolated from measured values of A_{600} and A_{1000}. Regression lines have been omitted for ease of viewing, since no trend was apparent.

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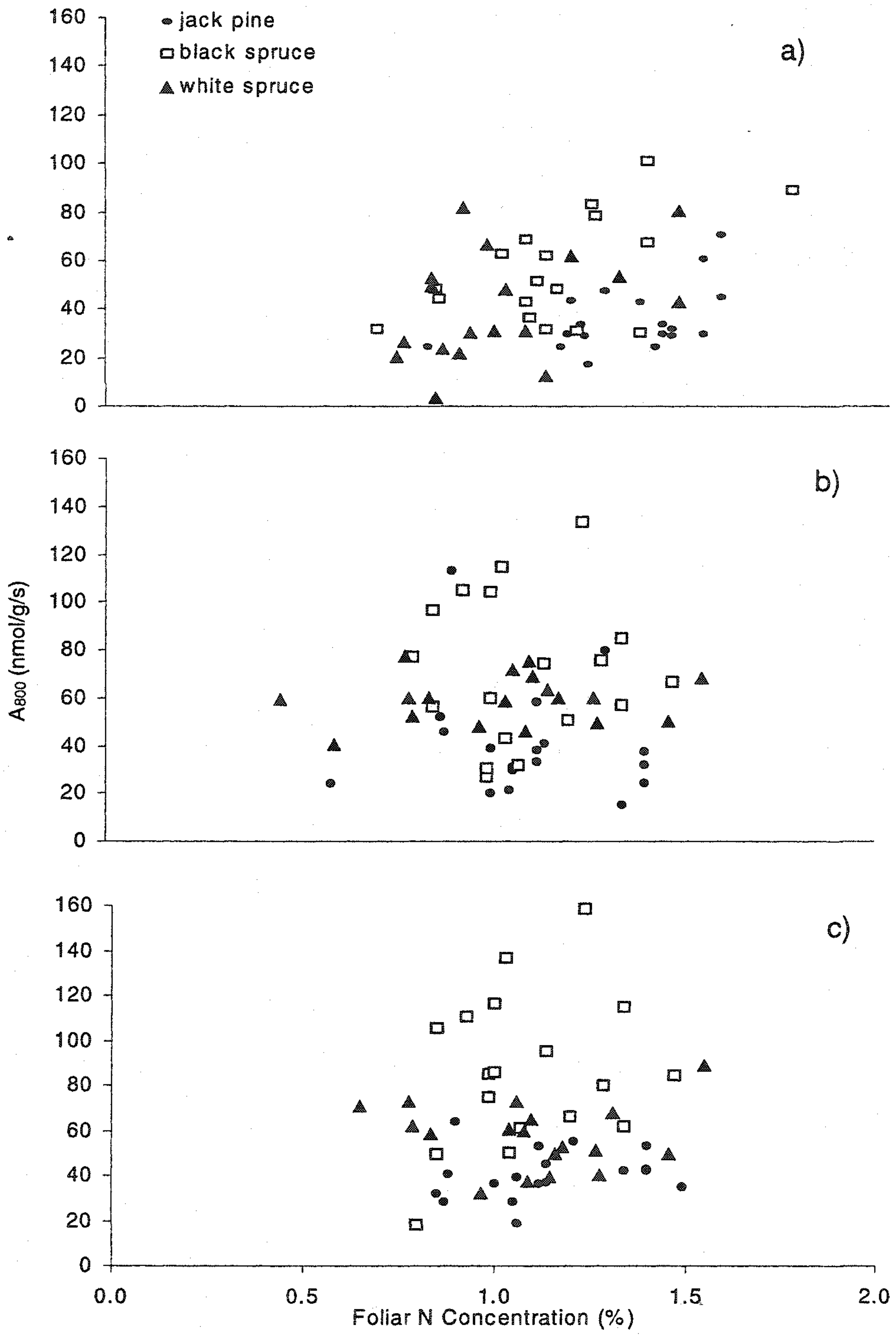

Figure 11. A_{max} (mass) vs. foliar nitrogen concentration for July (a), August (b) and September (c). The plotted values are interpolated from measured values of A_{600} and A_{1000}. Regression lines have been omitted for ease of viewing, since no trend was apparent.

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A significant positive relationship between foliar N and A was only found for the July mass-based A for jack pine and black spruce (Table 17). However, this relationship approached significance for jack pine (area-based) in September, for black spruce (area-based) in September and for white spruce (area and mass-based) for August and July, respectively.

Table 17. Results of linear regression analysis of A with foliar N for jack pine, black spruce and white spruce, by month. Coefficients of determination (r^2) and probability that $b_1 \neq 0$ (in parentheses) are presented.

		r^2 value		
Species	Photosynthesis	July	August	September
jack pine	area-based	0.16 (0.105)	0.04 (0.434)	0.19 (0.073)
	mass-based	0.24 (0.038)	0.02 (0.586)	0.04 (0.443)
black spruce	area-based	0.00 (0.934)	0.00 (0.957)	0.20 (0.063)
	mass-based	0.30 (0.020)	0.06 (0.770)	0.06 (0.318)
white spruce	area-based	0.03 (0.485)	0.18 (0.083)	0.04 (0.409)
	mass-based	0.18 (0.083)	0.01 (0.636)	0.06 (0.754)

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SPECIFIC LEAF AREA

July-August

Significant differences between SLA in July and August were found for species, month, block x species and species x month (Table 18). The expected cell means for the species x month interaction are presented in Table 19 and the results of the LSD test are presented graphically in Figure 12. The expected cell means for the block x species interaction are given in Table 20 and Figure 13.

Table 18. ANOVA table for July-August SLA comparison.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	5353.38	2676.69	no test	no test
Restriction error[1]	0	no est.	no est.	no test	no test
Species (S)	2	26079.80	13039.90	72.61	**< 0.0001**
B*S	4	3319.06	829.77	4.62	**0.0019**
Month (M)	1	1615.96	1615.96	9.00	**0.0035**
B*M	2	173.73	86.86	0.48	0.6181
S*M	2	1133.78	566.89	3.16	**0.0473**
B*S*M	4	646.49	161.62	0.90	0.4675
Error	90	16162.10	179.58		
Total	107	54484.30			

Table 19. Expected species x month interaction cell means for July-August SLA (cm^2/g).

Species	July	August
jack pine	34.95	30.69
black spruce	79.29	62.47
white spruce	52.17	50.04

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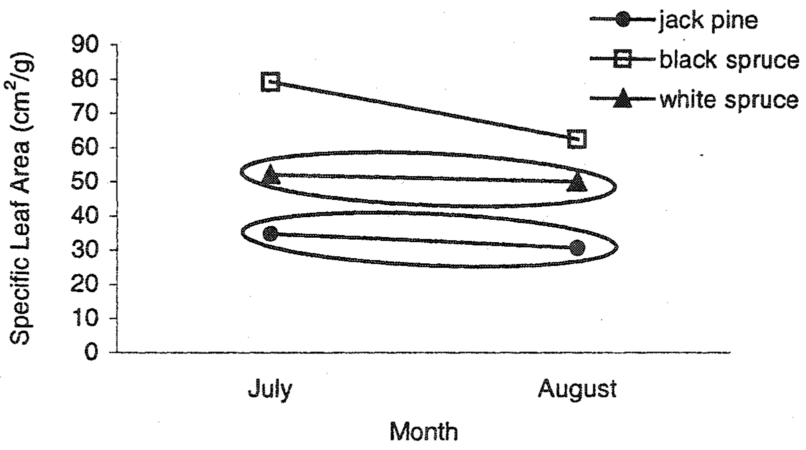

Figure 12. Mean values of SLA for jack pine, black spruce and white spruce for July-August. Points within the same ellipse are not significantly different under LSD post hoc comparisons.

Table 20. Expected block x species interaction cell means for July-August SLA (cm^2/s).

Species	Block 1	2	3
jack pine	31.27	29.54	37.67
black spruce	53.06	71.22	88.36
white spruce	44.64	54.01	54.68

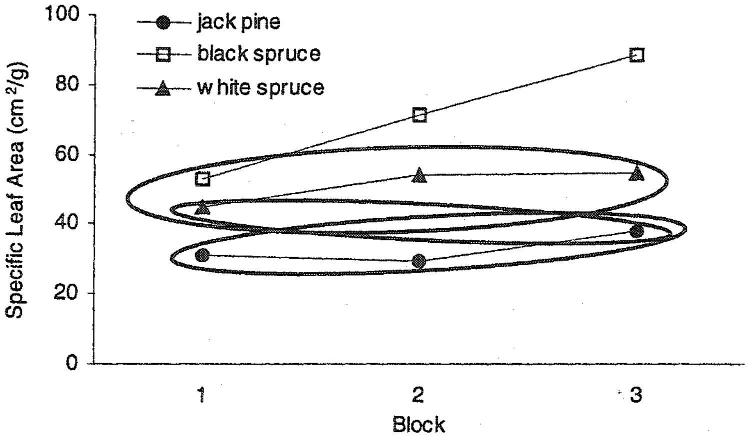

Figure 13. Mean values of SLA for jack pine, black spruce and white spruce for July-August. Points within the same ellipse are not significantly different under LSD post hoc comparisons.

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August-September

Species and tree within block and species were significant in the August-September ANOVA for SLA (Table 21). Differences between trees are not of critical importance in this study, as differences are likely a result of genetic variation between seedlings, varying amounts of competition in the blocks and general microsite effects not related to competition.

Table 21. ANOVA for August-September SLA comparison.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	3943.65	1971.82	no test	no test
Restriction error[1]	0	no est.	no est.	no test	no test
Species (S)	2	20649.30	10324.70	28.22	**< 0.0001**
B*S	4	3021.67	755.42	2.06	0.1013
Tree	45	16466.70	365.93	17.77	**< 0.0001**
Month (M)	1	7.66	7.66	0.37	0.5450
B*M	2	12.53	6.26	0.30	0.7392
S*M	2	105.79	52.89	2.57	0.0878
B*S*M	4	69.53	17.38	0.84	0.5045
Error	45	926.43	20.59		
Total	107	45203.30			

WATER USE EFFICIENCY

July-August

The July-August ANOVA for WUE showed that all treatment effects, except the block x month interaction were significant (Table 22). The expected cell means for the three-way interaction are given in Table 23 and Figure 14. The species x month interaction cell means are presented in Table 24 and Figure 15, while the block x species interaction cell means are presented in Table 25 and Figure 16.

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Table 22. ANOVA table for July-August WUE comparison. Significant values ($p < 0.05$) are denoted by bold text.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	1.71	0.86	no test	no test
Restriction error[1]	0	no est.	no est.	no test	no test
Species (S)	2	10.45	5.23	6.62	**0.0021**
B*S	4	13.81	3.45	4.37	**0.0028**
Month (M)	1	11.94	11.94	15.13	**0.0002**
B*M	2	2.12	1.06	1.34	0.2669
S*M	2	5.88	2.94	3.73	**0.0279**
B*S*M	4	7.92	1.98	2.51	**0.0475**
Error	90	71.05	0.79		
Total	107	124.88			

Table 23. Expected block x species x month interaction cell means for July-August WUE (mmol CO_2/mol H_2O).

Species	July			August		
	Block			Block		
	1	2	3	1	2	3
jack pine	4.59	3.48	3.00	4.03	4.81	4.28
black spruce	2.69	3.74	3.26	2.80	3.44	3.69
white spruce	2.84	2.40	4.06	4.13	4.21	4.64

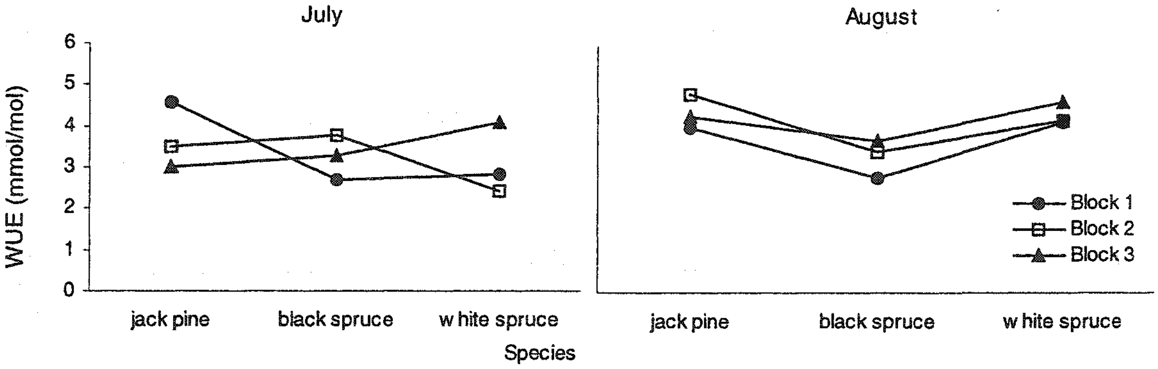

Figure 14. Plot of the block x species x month interaction cell means for July-August WUE. Ellipses have been omitted for ease of viewing, but LSD = 1.0 mmol CO_2/mol H_2O.

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Table 24. Expected species x month interaction cell means for July-August WUE (mmol CO_2/mol H_2O).

Species	July	August
jack pine	3.69	4.37
black spruce	3.23	3.31
white spruce	3.10	4.33

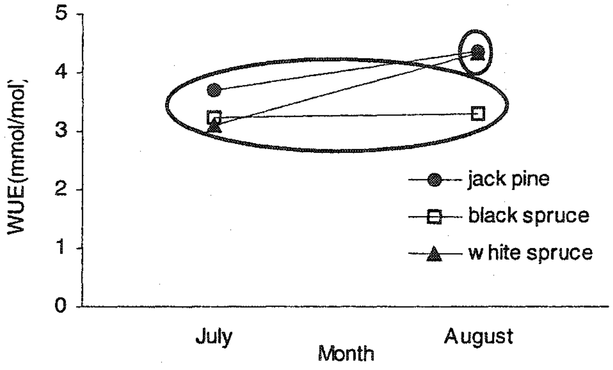

Figure 15. Plot of the species x month interaction cell means for July-August WUE. Points within the same ellipse are not significantly different under LSD post hoc comparisons.

Table 25. Expected block x species interaction cell means for July-August WUE (mmol CO_2/mol H_2O).

	Block		
Species	1	2	3
jack pine	4.31	4.14	3.64
black spruce	2.75	3.59	3.48
white spruce	3.48	3.30	4.35

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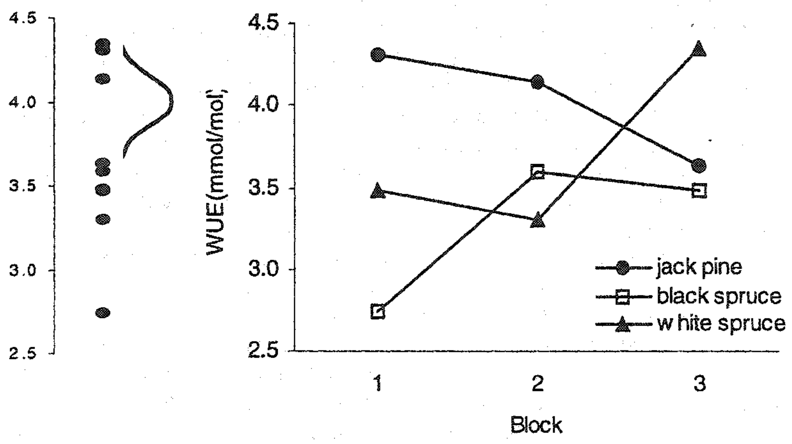

Figure 16. Plot of the block x species interaction cell means for July-August WUE. Points within the reference distribution shown on the left are not significantly different under LSD post hoc comparisons (Box *et al.* 1978).

August-September

In the August-September comparison, only species was found to have a significant effect on WUE (Table 26). The species means are presented in Table 27.

Table 26. ANOVA table for August-September WUE comparison.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	14.12	7.06	no test	no test
Restriction error[1]	0	no est.	no est.	no test	no test
Species (S)	2	72.59	36.29	11.64	**< 0.0001**
B*S	4	9.79	2.45	0.79	0.5409
Tree	45	140.26	3.12	0.87	0.6765
Month (M)	1	8.37	8.37	2.34	0.1331
B*M	2	1.79	0.90	0.25	0.7794
S*M	2	16.67	8.33	2.33	0.1089
B*S*M	4	25.42	6.36	1.78	0.1500
Error	45	160.92	3.58		
Total	107	449.92			

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Table 27. Expected cell means for species for August-September WUE (mmol CO_2/mol H_2O).

Species	August	September	Overall
jack pine	4.37	6.01	5.19
black spruce	3.31	3.09	3.20
white spruce	4.33	4.58	4.45

PHOTOSYNTHETIC NITROGEN USE EFFICIENCY

July-August

The species x month interaction was the only source of variation that did not have a significant effect on NUE in July-August (Table 28). Significant values (*i.e.* $p < 0.05$) are denoted by bold text.

Table 28. ANOVA table for July-August NUE comparison.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	53.03	26.51	no test	no test
Restriction error[1]	0	no est.	no est.	no test	no test
Species (S)	2	133.75	66.87	17.24	**< 0.0001**
B*S	4	52.66	13.16	3.39	**0.0124**
Month (M)	1	99.71	99.71	25.71	**< 0.0001**
B*M	2	93.90	46.95	12.11	**< 0.0001**
S*M	2	5.62	2.81	0.72	0.4874
B*S*M	4	52.85	13.21	3.41	**0.0121**
Error	90	349.03	3.88		
Total	107	840.54			

The expected cell means for the three-way interaction are given in Table 29 and Figure 17. The block x month interaction cell means are presented in Table 30 and Figure 18, while the block x species interaction cell means are presented in Table 31 and Figure 19.

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Table 29. Expected block x species x month interaction cell means for July-August NUE (μmol CO_2/gN).

Species	July			August		
	Block			Block		
	1	2	3	1	2	3
jack pine	2.95	2.26	3.37	3.03	3.50	5.93
black spruce	5.02	5.56	4.82	4.13	6.53	11.09
white spruce	3.13	6.60	2.47	6.41	5.59	7.28

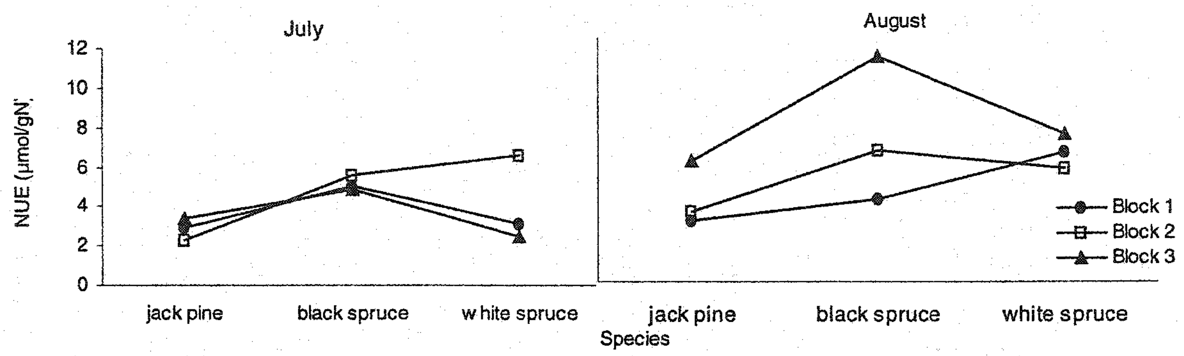

Figure 17. Plot of the block x species x month interaction cell means for July-August NUE. Ellipses have been omitted for ease of viewing, but LSD = 2.3 mmol CO_2/gN.

Table 30. Expected block x month interaction cell means for July-August NUE (μmol CO_2/gN).

Block	July	August
1	3.70	4.52
2	4.81	5.21
3	3.55	8.10

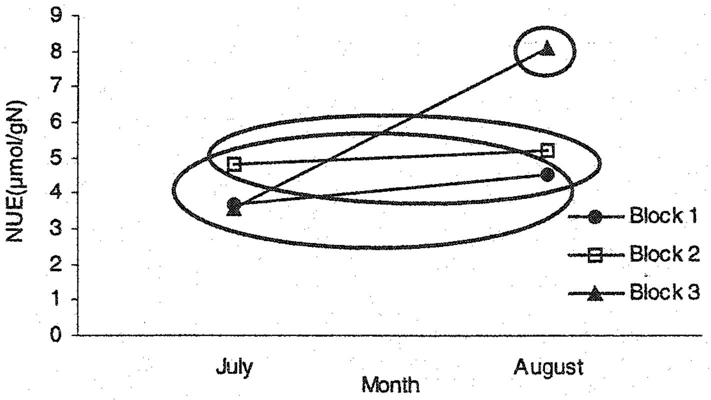

Figure 18. Plot of the block x month interaction cell means for July-August NUE. Points within the same ellipse are not significantly different under LSD post hoc comparisons.

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Table 31. Expected block x species interaction cell means for July-August NUE (in µmol/gN).

Species	Block 1	 2	 3
jack pine	2.99	2.88	4.65
black spruce	4.58	6.04	7.96
white spruce	4.77	6.10	4.88

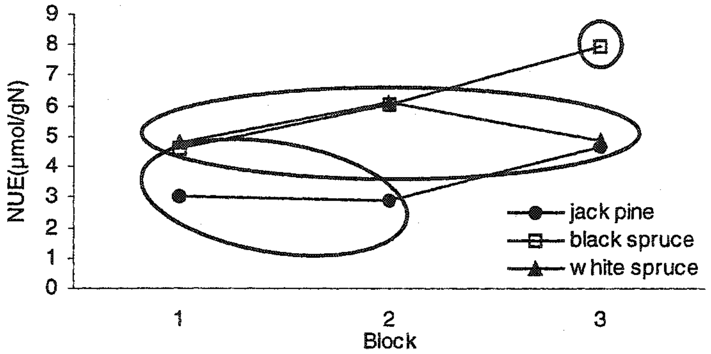

Figure 19. Plot of the block x species interaction cell means for July-August NUE. Points within the same ellipse are not significantly different under LSD post hoc comparisons.

August-September

The August-September ANOVA for NUE revealed that the interaction of species x month, as well as the main effects of species and tree (within block and species) had a significant effect (Table 32). The expected cell means for the species x month interaction (including July values for comparison) are presented in Table 33 and the results of the LSD test are presented graphically in Figure 20.

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Table 32. ANOVA table for August-September NUE comparison.

Source	df	Sums of Squares	Mean Square	F-ratio	Prob
Block (B)	2	158.28	79.14	no test	no test
Restriction error[1]	0	no est.	no est.	no test	no test
Species (S)	2	278.59	139.30	12.61	**< 0.0001**
B*S	4	93.23	23.31	2.11	0.0953
Tree	45	497.30	11.05	4.92	**< 0.0001**
Month (M)	1	0.61	0.61	0.27	0.6046
B*M	2	14.27	7.13	3.18	0.0512
S*M	2	18.26	9.13	4.07	**0.0238**
B*S*M	4	3.76	0.94	0.42	0.7942
Error	45	101.02	2.24		
Total	107	1165.32			

Table 33. Expected species x month interaction cell means for NUE for all three months (in µmol/gN).

Species	July	August	September
jack pine	2.86	3.81	4.15
black spruce	5.12	8.56	7.25
white spruce	4.07	5.91	6.43

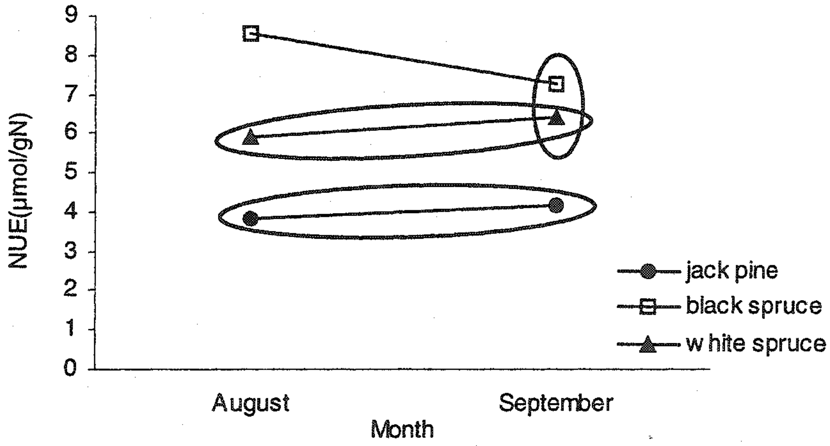

Figure 20. Plot of the species x month interaction cell means for August-September NUE. Points within the same ellipse are not significantly different under LSD post hoc comparisons.

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DISCUSSION

GAS EXCHANGE

Although gas exchange measurements were taken under steady-state conditions in the cuvette, the individual seedlings were acclimated to their growing environment, prior to measurement. Even though the environment inside the cuvette (temperature, CO_2, humidity) was controlled, only a small shoot of the seedling was placed inside the cuvette. The shoot was still attached to the rest of the seedling, which was exposed to the environmental conditions to which the seedling was acclimated.

Photosynthesis

In this and the succeeding sections, the discussion proceeds from the highest-order interactions that are statistically significant to lower-order interactions and on to main effects. Independently, a main effect may not be significant, but it may interact with another main effect to cause significant differences. When an interaction is significant, the corresponding main effects cease to have much meaning. The existence of a significant interaction means that the effect of one factor is strongly dependent on the level of the other. When the interaction is not significant, it may be assumed that the treatment effects operate independently, and conclusions based on the main effects may then be made (Davies 1956, Milliken and Johnson 1984).

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Block x Species x Month Interaction

The block x species x month interaction is significant in the multivariate sense for August and September (Tables 2 and 5). This three-way interaction is not significant for any of the univariate ANOVAs, nor is it meaningful in the July-August analysis. When the raw data were examined, two jack pine seedlings were found to be outliers in block three in August and September at the high light levels (400, 600 and 1000 µmol/m^2/s). The significant interaction seems to stem from these seedlings and thus may have little, if any, general interpretation. Gas exchange measurements of the pine were often problematic and only a small amount of foliage could be used. The jack pine needles were much larger than the spruce needles, especially when fully expanded in July and August. The gas exchange values for jack pine fluctuated greatly and took a longer time to level out than either of the spruces.

Block x Month Interaction

The block x month interaction is significant in the multivariate response for both July-August and August-September (Tables 2 and 6). One general feature of the response is that blocks 2 and 3 (both partial cut) tend to respond independently of block 1 (clearcut) over all light levels (Figure 3). The separation is most pronounced in August when the rate of CO_2 assimilation is higher in the partial cut blocks than in the clearcut block.

Although measurements of A were taken under steady-state conditions, the individual seedlings growing in these environments would have acclimated to their growing conditions. Measuring the seedlings in the partial cut at the high light conditions (*i.e.* 1000 µmol/m^2/s) after they had been growing in partially

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shaded conditions would not necessarily allow the seedlings enough time to adjust to the new light conditions. Zhang *et al.* (1996) found that it took more than seven days for loblolly pine to acclimate to higher light conditions.

Since the measured shoot was still attached to the seedling, the environment outside the cuvette would also affect seedlings. It is therefore not surprising that rates of A of seedlings in the clearcut block responded differently than seedlings in the partial cut blocks. The clearcut block had no residual overstory canopy, whereas the partial cut blocks both had a residual basal area of about 15 m^2/ha. The residual canopy contained a large proportion of trembling aspen, and thus the canopy density would have varied throughout the growing season as a result of aspen leaf flush, maturation and leaf drop in the fall. As a result, both the amount and quality of light transmitted to the understory seedlings must have differed greatly between the clearcut and partial cut blocks, and during the growing season on the partial cut blocks.

Seasonally, more light is transmitted through the canopies of deciduous stands in the leaf-off period during the spring and fall (Ross *et al.* 1986, Constabel and Lieffers 1996). Ross *et al.* (1986) studied seasonal variations in understory light quality and quantity, and found that it was affected seasonally by solar angle. They also found that the amount of photosynthetically active radiation (PAR) that reached the understory declined rapidly in May and June as a result of leaf expansion, but that it remained relatively stable during July and August. In September, PAR values gradually returned to those of early May, due to chlorophyll degradation and yellowing of the leaves, prior to leaf fall.

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Generally, the photosynthetic rates at imposed light levels for all three species were lowest in the clearcut block. These results are consistent with several other studies. Man and Lieffers (1997) observed a considerable decrease of net A in white spruce seedlings planted in the open, compared to seedlings planted under a forest canopy. Groot (1999) also stated that white spruce would benefit from shelter. Aspen stands with less than 35 m^2/ha basal area should provide suitable light levels for spruce growth, according to DeLong (1997). Shelterwoods moderate environmental conditions of the understory, and illuminate the extremes exhibited in a clearcut condition (Carlson and Groot 1997, Man and Lieffers 1999). The presence of a partial overstory reduces wind velocity and air and soil temperature. Carlson and Groot (1997) found that seasonal averages of daily maximum and minimum air temperatures in a clearcut were 3.8°C higher and 3.2°C lower, respectively, than under a forest canopy. Less extreme environmental conditions under a partial canopy and more rainfall in late summer interact to reduce overall water stress on the seedlings, which allows for higher rates of A (Man and Lieffers 1997).

Months Main Effect

The rate of A varied across the three months studied (Table 2). The rate was often highest in September and lowest in July (Table 4). Often unfavourable mid-summer weather conditions exist in July. Temperatures are usually warmer, and rainfall tends to be less than either earlier or later in the summer. These conditions tend to reduce water availability and increase plant water-stress. The high temperatures experienced in July may be greater than a tree's optimum temperature for A. When the seedlings were measured in July,

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they were likely water-stressed, which would have constrained A_{max}. Photorespiration often becomes proportionally more important and A will decline (Lambers *et al.* 1998). Grossnickle (2000) states that, in general, the optimum temperature range of A for spruce species is between 20°C and 25°C. Temperatures above this range are characteristic of the month of July.

Species Main Effect

The rate of A also varied among the three species (Table 2). At the higher light levels, jack pine consistently achieved higher rates than either black or white spruce, while at the lowest light levels, jack pine often achieved lower rates than the spruce species (Figure 9). White spruce had the highest rates of A out of the three species at the lower light levels (Figure 8).

These results are not unexpected, given the relative shade tolerance of each species. Jack pine is classified as shade intolerant, and once established on a site, it thrives in full sunlight. Full sunlight will greatly increase survival and early growth. Jack pine that must compete for light and nutrients in overstocked stands are often weak, with spindly stems that are susceptible to breakage (Rudolph and Laidly 1990). This was noted in the jack pine in areas under the partial canopy where there were an abundance of shrub species. Jack pine needles were also much larger than spruce needles, with a greater SLA, which would increase the photosynthetic capacity of the pine, as compared to the spruce. Jack pine is also one of the fastest growing conifers in its range, exceeded only by tamarack. Jack pine begins to flower at a very early age (Rudolph and Laidly 1990) and higher rates of A would produce the photosynthate required for greater growth rates and flower production.

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White spruce, on the other hand, is intermediate in its tolerance to shade, and is equally or less tolerant than black spruce. Juvenile white spruce growth is slower than its early successional associates and it can survive in the understory for up to 70 years (Nienstaedt and Zasada 1990). Although black spruce growth is much better in the open, it can develop in as little as 10 percent of full light intensity (Viereck and Johnston 1990). Lamhamedi and Bernier (1994) state that light is the dominant factor that influences the performance of outplanted black spruce seedlings under competitive stresses.

In the August-September analysis, tree (within blocks and species) was found to be a source of variance in the A measurements. However, these significant differences defy a simple interpretation, and are likely a result of genetic variation between seedlings, varying amounts of competition in the blocks, and general microsite effects not related to competition.

Stomatal Conductance

Effects that influenced A likely affected g_s (Table 6) because the two processes are highly correlated (Stewart *et al.* 1994, Dang *et al.* 1992, Brown *et al.* 1996, Man and Lieffers 1997, Sullivan *et al.* 1997). Stomatal conductance tends to increase or decrease in parallel with A, since the stomates control the entry of CO_2 into the leaf (Lamhamedi and Bernier 1994, Lambers *et al.* 1998).

Block x Month Interaction

Block x month probably had an effect on g_s, as temperatures were warmer and water more limiting earlier in the summer. High temperatures and limited water would cause the stomata to close, especially in the clearcut block where there was no shelter from extreme environmental conditions, resulting in reduced g_s (Figure 4). Although the environmental conditions in the cuvette were controlled, the remainder of the seedling was exposed to the drier environment. When soil water is not limiting, stomatal conductance is normally highest in fully expanded mature leaves. However, stomatal apertures begin to decline even with modest water limitations in the soil surface layers (Niinemets *et al.* 1999).

Block x Species Interaction

The significant block x species interaction is likely a result of the different amounts of residual vegetation in the blocks, and its influence on understory environmental conditions (Figure 5). The environmental conditions under a partial canopy are less harsh than a clearcut (Man and Lieffers 1997, Groot 1999), and often retain more soil moisture, as a result. In Figure 5, jack pine presumably responded independently of the spruce, as it is overall more tolerant of drought than both black and white spruce.

Transpiration

Block x Species x Month Interaction

The three-way interaction of block x species x month had a significant effect on E (Table 10). E was also consistently highest in September and lowest in July, as was A (Table 12).

The results from my study are not unusual. Man and Lieffers (1997) found seasonal trends of gas exchange for both white spruce and jack pine, and concluded that variability in gas exchange can be reduced by the presence of an

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overstory. They found that rates of A for both species dropped during periods of drought and hot days, but in the autumn, both species showed high photosynthetic capacities. Since the stomata of the needles must be open to allow CO_2 to enter the leaves for A, E is also affected. Man and Lieffers (1997) surmised that the existence of an overstory canopy could reduce gas exchange variability by improving environmental conditions and water relations.

Although the three-way interaction is significant for E, the explanation may not have a physiological cause. Transpiration for white spruce in block two in July was extremely high on average (Figure 6). It was not comparable to rates from the other partial cut. Several E values for white spruce in July in block two were double what they were for other seedlings, and the three-way interaction may be traceable to these particular measurements.

Block x Species Interaction

The block x species interaction (Figure 6) was also significant for E in the July-August analysis, likely for similar reasons as g_s (Figure 5). A general linear dependence of g_s on E is common (Whitehead 1998), and my data is in accord with this trend (Appendix VI).

Species x Month Interaction

Jack pine had elevated rates of E at the high light levels in July-August (Figure 7), which can be attributed to its fast growth rate and its intolerance to shade. This is also in accord with the higher photosynthetic rates of jack pine at the high light levels, as an increase in A is associated with greater g_s and therefore E. Sullivan *et al.* (1997) found E in a jack pine stand to be greater than those in a black spruce stand, which is in agreement with the July-August

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results. However, in the August-September analysis, black spruce consistently had the highest E values, even though it had only intermediate rates of A at the high light levels and the lowest rates of A at the lowest light levels. Transpiration for black spruce increased consistently over July, August and September, whereas E for jack pine and white spruce remained relatively constant. When the raw data were examined, several black spruce seedlings were found to be outliers in August and September. The consistent high averages seem to stem from these seedlings.

LIGHT RESPONSE CURVES

Since it is a shade intolerant species, and the most shade intolerant of the three species in my study, it is natural that it would have the highest rates of A at the higher light levels (Figure 8). White spruce had intermediate rates of A, except at the lower light levels, where it had the highest rates of A. This is again consistent with its relative shade tolerance. It is more shade tolerant than jack pine, yet equally, or less shade tolerant than black spruce (Nienstaedt and Zasada 1990).

Jack pine and black spruce had highest photosynthetic rates in September, whereas white spruce had highest photosynthetic rates in August (Figure 9). In all probability, this occurred because the trees were not water-stressed or nutrient-limited, and temperatures were still at or near an optimum level.

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LIGHT COMPENSATION POINTS

Months Main Effect

Light compensation points were consistently highest in July and lowest in September (Table 15). The needles were still expanding in July, so respiration rate was also higher at this time. Since the light compensation point is the point where photosynthetic CO_2 assimilation is balanced by CO_2 production in respiration, higher rates of respiration when the foliage is expanding would require higher rates of A to reach the light compensation point. Increased CO_2 assimilation could be produced with elevated light levels.

No interactions with block caused a significant difference in light compensation point, which is supported by a study done by Landhausser and Lieffers (2001). They found that light compensation point did not differ between trees grown under a canopy and plants grown in the open for six boreal tree species.

Species Main Effect

Jack pine had the highest light compensation point in July-August, but was not significantly different than black spruce (Table 15). Both were significantly different than white spruce. The average light compensation point for black spruce was extremely high in July, compared to what it was in August and September (Table 15). This is similar to a review by Lamhamedi and Bernier (1994) that states the light compensation point for black spruce is reached around 35-50 $\mu mol/m^2/s$, and may be as high as 100 $\mu mol/m^2/s$ under warm conditions. Grossnickle (2000) states that in spruce species, A rises

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rapidly up to 25-33% of full sunlight and then increases only gradually. Most spruce species should reach light saturation between 25 and 50% of full sunlight (Grossnickle 2000), although Kozlowski *et al.* (1991) stated that this point is closer to between 33% and 66% of full sunlight.

In August-September, jack pine had significantly higher light compensation points than both of the spruces, which were not significantly different from one another (Table 15). The spruces should have similar light compensation points, as they have similar shade tolerances and growth rates, both of which are much lower than jack pine. Differences in LCP among species might be due to their inherent growth rates. Jack pine tends to grow much faster than the spruce, and should therefore have a higher respiration rate, and thus, a higher LCP.

FOLIAR NITROGEN

The results of this study do not indicate a strong correlation between foliage N concentration and maximum rates of A (A_{max}). Weak, but significant relationships were only found for the mass-based July photosynthetic measurements for jack pine and black spruce (Table 17, Figures 10 and 11). This is in contrast to results of numerous studies of other tree species (Field *et al.* 1983, Johnsen 1983, Mitchell and Hinckley 1993, Reich and Walters 1994, Reich *et al.* 1994, Chandler and Dale 1995, Garnier *et al.* 1995, Sheriff and Mattay 1995). Foliar N concentrations are typically associated with net A, with A_{max} increasing linearly with leaf N concentration (Yin 1993, Lambers *et al.* 1998). Under N limitation, the entire photosynthetic process is down-regulated,

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with reduction in Rubisco and chlorophyll concentration, and g_s as a result (Lambers *et al.* 1998). Evans (1989) suggested that since N is such a valuable resource to a plant, it might be expected that the plant would optimize the partitioning of that N so that A is maximized.

Reich and Walters (1994) state that the slope of the linear relationship between A_{max} and N is usually higher when based on leaf mass rather than leaf area relationships. This was not the case in my study, although the slope was sometimes higher when A was expressed on a mass basis. Conversely, Field and Mooney (1986) state that the A-N relationship is little affected by the unit of expression of A, in agreement with the results of this study. However, it is important to note that the relationship between A and N is species-specific (Tan and Hogan 1995, Brown *et al.* 1996).

SPECIFIC LEAF AREA AND RESOURCE USE EFFICIENCIES

Specific Leaf Area

Species is the only effect that could show a significant effect in the August-September analysis, since the same area and weight measurements were used for both months.

Species x Month Interaction

From Figure 12, it appears that the SLA of black spruce decreases between July and August, whereas the SLA of the other two species remains more or less constant. In July, the current year's needles were not fully expanded, but when the measurements were taken in August, the needles had developed to their full size, which likely affected SLA. Dry weight continues to

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increase after area has stabilized. It is possible that since different trees were measured in July and August, that genetic variation could also have played a role.

Block x Species Interaction

The significant block x species interaction confirms suspicions that different species react differently to the environment (Figure 13). This is likely attributable to the different shade-tolerances of the three species, and also to the sun or shade leaves that would have been formed in full sunlight or low light environments. SLA is the leaf area per unit leaf mass (Lambers *et al.* 1998) and Kimmins (1997) states that shade leaves produced by shade-tolerant plants growing under low light intensities have high SLAs. The SLA of black spruce increased from blocks one to three, whereas the SLA of jack pine and white spruce remains more or less the same, although all three species have the highest values in block three. Of all three blocks, block three had the most shaded understory conditions, and because of these conditions, the seedlings probably produced more shade-adapted foliage (Kimmins 1997). Therefore, the area of the leaves would be greater, but the mass would be less, thereby increasing the SLA of the seedlings growing in the shaded conditions.

Species Main Effect

In this study, jack pine consistently had the lowest SLA values (Table 19). Black spruce had the highest values for SLA, followed by white spruce, although all were significantly different from one another (Figure 13). Lambers *et al.* (1998) suggest that plants with a higher SLA tend to have higher relative growth rates, and higher rates of mass-based A. My study is consistent with these

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findings, as species with high SLA also tended to have high mass-based A and vice-versa.

Water Use Efficiency

Block x Species x Month Interaction

The three-way interaction of block x species x month was significant for WUE, but only for the July-August analysis (Table 22). Different environmental conditions existed over the measurement period, as well as between blocks. The three species would react uniquely to the environmental conditions as a result of their different site requirements and silvical characteristics.

The three-way interaction of block x species x month (Figure 14) shows that there is interaction in more than one place, which makes the interpretation very complicated. The multiple interactions could be a result of different trees being measured in July and August, which could also help to explain why the three-way interaction was not significant in the August-September analysis, when the same trees were measured for both months.

Months Main Effect

Overall, July had the lowest WUE of all three months (Table 24). Wang *et al.* (1998) found that the highest values of WUE were not due to high rates of A, but rather to very low rates of g_s under severe water stress, which may help to explain why WUE was lowest in July, and highest in September. The results from this study are within the values given by Lambers *et al.* (1998) for water use efficiencies of woody C_3 plants. They give values of between 2 and 11 mmol/mol and the averages in this study were between 3.2 and 5.2 mmol/mol.

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Species Main Effect

The lowest WUE values often exist for black spruce (Tables 23, 24 and 25, Figure 7). Jack pine had the highest WUE average, although it was not different than white spruce for either the July-August or August-September comparisons.

A study done by Field *et al.* (1983) found that WUE was higher for species that grew naturally on drier sites, and lower for species that grew naturally in wetter areas. This may help to explain why jack pine often had higher WUE values than the spruce (Tables 23, 24 and 25). Black spruce, and to a lesser extent, white spruce, are capable of growing on wetter sites, whereas jack pine is predominantly found on drier sites and is generally more drought tolerant. Wang *et al.* (1998) state that high WUE is an adaptation to water limited environments. Since WUE was lowest in July (Tables 23 and 24), when temperatures were warmest and water the most limiting, it is likely that the trees in this study were not adapted to limited water, and that g_s was low due to the water stress.

It is also important to note that WUE, as well as NUE, are intended to provide a measure of potential resource-use efficiency under complex and varying natural conditions (Field *et al.* 1983), and that WUE, calculated from instantaneous measures of A and E apply only to that measurement period. A drought tolerant species may therefore show high and low WUE, dependent upon the environment at the time of measurement.

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Photosynthetic Nitrogen Use Efficiency

Block x Species x Month Interaction

Again, the three-way interaction had a significant effect in the July-August analysis of NUE (Table 28). The variable environmental conditions between blocks, as well as months, likely interacted with the specific silvical characteristics of the three species to produce significant differences in NUE. From Figure 17, it appears that NUE in August was highest for all species in block three. Block three was partially cut and had more residual stems per hectare than block two, providing the most shaded understory conditions of all three blocks. Photosynthesis was possibly highest overall in block three (Figure 3) because it had the most favorable environmental conditions for the seedlings in terms of soil water content. Different trees were measured in July and August, which could also have affected the results. The same trees were measured in August and September, and the three-way interaction was not significant for that analysis.

Species Main Effect

All species were significantly different from one another, but black spruce had the highest values (6.98 µmol CO_2/gN) and jack pine had the lowest values (3.61 µmol CO_2/gN) (Tables 29, 31 and 33). Values of NUE for this study were similar to those of Field *et al.* (1983) for five California evergreen species, although Field *et al.* (1983) reported that NUE varied more than two-fold between species in their study. Poorter and Evans (1998) state that a higher NUE may be caused by a relatively high absorption of light, which is related to

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SLA, or that some species invested more of their N in photosynthetic machinery. The results from this study support those of Poorter and Evans (1998), as black spruce had the highest NUE and SLA, whereas jack pine had the lowest NUE and SLA. Poorter and Evans (1998) also state that differences in NUE could be due to variation in activation of Rubisco or a variation in the amount of light needed to saturate A, both of which are species specific.

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SUMMARY AND CONCLUSIONS

The main objective of my study was to examine and compare the seasonal ecophysiological characteristics of three coniferous boreal tree species grown on a boreal mixedwood site. I hypothesized that jack pine would likely exhibit higher rates of A under high light conditions, as compared to the spruces, due to its shade intolerance and r-strategist tendencies. Jack pine did outperform both of the spruces in photosynthetic activity at the higher light levels. Although this difference was not as great in the August-September analysis, it was still significant. White spruce also performed as hypothesized, giving its poorest performance at high light levels, and its best performance at low light levels. Black spruce, predicted to be intermediate between jack pine and white spruce with respect to gas exchange, also performed as predicted.

Jack pine exhibited higher gas exchange activity in the clearcut block. In addition, it had the highest rates of A in the partial cut blocks at higher light intensities. However, the jack pine was generally small and spindly under the residual canopy, and it visually appeared as though its survival rate was much lower. Therefore, although physiological measurements may show that jack pine performs adequately under residual vegetation, visual assessment suggested otherwise.

It may be beneficial for all three species to have some form of overstory cover to control temperature ranges and RH, and to moderate the incidence and severity of night frosts. A partial overstory will also help to increase humidity

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levels, protect seedlings from the sun, and reduce E. A partial canopy may also help control more shade tolerant competing vegetation, while still permitting enough light through to allow crop trees to survive and grow. However, although residual overstory vegetation may increase physiological activity of all three species, it does not appear to aid morphological characteristics of jack pine. The jack pine persisted under the partial canopy, but there were large openings that likely allowed sufficient amounts of light through. Both of the spruce species survived and developed under the partial canopy, although from a visual assessment, it appeared as though the white spruce was heartier in the shade of a residual canopy than the black spruce. All three species were able to persist on the mixedwood site, but optimal site and environmental conditions are species specific.

Foliar N concentration and A were only weakly correlated in this study. Photosynthesis was likely limited by some other factor besides foliar N, such as soil water or nutrient availability.

Jack pine had a low SLA. Conversely, jack pine consistently had the highest WUE, although it was not significantly different than white spruce. Overall, July had the lowest WUE of all three months, probably due to very low rates of A under severe water stress. Averages in this study were between 3.2 and 5.2 mmol/mol for all species. Jack pine also had the lowest nutrient use efficiency (NUE) values, whereas black spruce had the highest NUE values, which may be related to specific leaf are (SLA).

All three species had the highest photosynthetic rates in September, indicating that conditions earlier in the summer may have been unfavourable.

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For example, the temperatures may have been much warmer than optimal. In September, the highest photosynthetic rates for jack pine were in the clearcut block, but the averages were quite similar to rates under the partial canopy. Although this phenomenon is probably caused by the more favourable environmental conditions in September, as opposed to the warmer summer months, Ross *et al.* (1986) also conclude that more light is transmitted through aspen canopies in September than during the summer months. It is possible that both of these factors have a positive effect on A.

All three species appeared to perform best and have their highest rates of A in September, when environmental conditions were most favorable, and perform least well in July, when temperatures were highest. It may be beneficial for forest managers to consider scheduling the majority of their regeneration efforts (*i.e.* tree planting) in the fall, rather than early in the summer. This would allow seedlings to establish themselves once the unfavorable mid-summer environmental conditions have passed, and not be exposed to them soon after their establishment. However, it is important to consider the fact that late summer or fall artificial regeneration efforts only allow a limited period of time for seedling root growth and reestablishment of the root system with the soil before cold temperatures arrive.

Both black and white spruce performed well under the partial canopies, which may be an indication that partial cutting systems are a feasible option to manage Ontario boreal mixedwood forests. Since the focus of my study was not on silvicultural systems, however, more research needs to be done to determine

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the optimal amount of residual vegetation needed to achieve the conditions for the understory trees.

HINDSIGHT

A major part of this project has been my own learning process. I gained an extensive amount of knowledge about experimental design and implementation during the progression of this thesis. If this project could be started again, I would make several changes to improve the flow and integrity of the thesis.

In hindsight, it would have been better to measure the same seedlings on all three measurement occasions. This would have allowed the whole experiment to be analysed as a repeated measures experiment, instead of breaking it up into two analyses. Or, if different seedlings had been measured every month, then the experiment could have been analysed as a straight RCBD, which would have also simplified the analysis of the data.

It also would have been helpful, in a mixedwood study, to examine trembling aspen, in addition to the three species studied. Although the small trembling aspen saplings on site were suckers from the previous stand, and not planted seedlings like the conifers, examining them would give a more complete comparison of ecophysiology of dominant species of northwestern Ontario mixedwood sites. This would have required the use of a different cuvette for the gas-exchange equipment. Although the same cuvette was used for both the pine and spruce, gas exchange measurements of the pine were often difficult and only a small amount of foliage could be used (~10 needles). A new cuvette

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for long-needle pines is now available, which would likely make the study of longer needle conifers easier, and possibly more accurate. New equipment (*e.g.* LI-6400 System from Li-Cor Biosciences, Lincoln, NE) is also available, which makes the collection of gas exchange data much easier and more accurate.

The objective of the original experimental design was to examine the effects of silvicultural systems on the growth of planted seedlings. When the fire destroyed much of the study area, a large part of that experiment was lost. It was decided at a later date to shift the focus of the study to species and seasonal effects, and away from silvicultural system effects. Obviously, with more control over the circumstances, it would have been better to have a broader range of conditions and treatments (*e.g.* clearcut – 0% residual, partial canopies – 30%, 60% residual and full canopy – 100% residual). The addition of more blocks would also have served to strengthen the experimental design.

Measuring ambient light levels for each measured seedling in the understory would have allowed for an improved study of seedling response to varying light conditions, which could have helped to better tie in the study of silvicultural system.

Through some miscommunication, when the foliage was oven dried, it was not dried at a high enough temperature. Since such a low temperature (37 °C, as opposed to 65 °C) was used to dry the foliage, it is likely that there was still water in the tissue and the weight of the foliage was not the true oven dry weight. Obviously, if I could start again, I would dry the foliage at a higher temperature.

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APPENDICES

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APPENDIX I
BLOCK PHOTOS

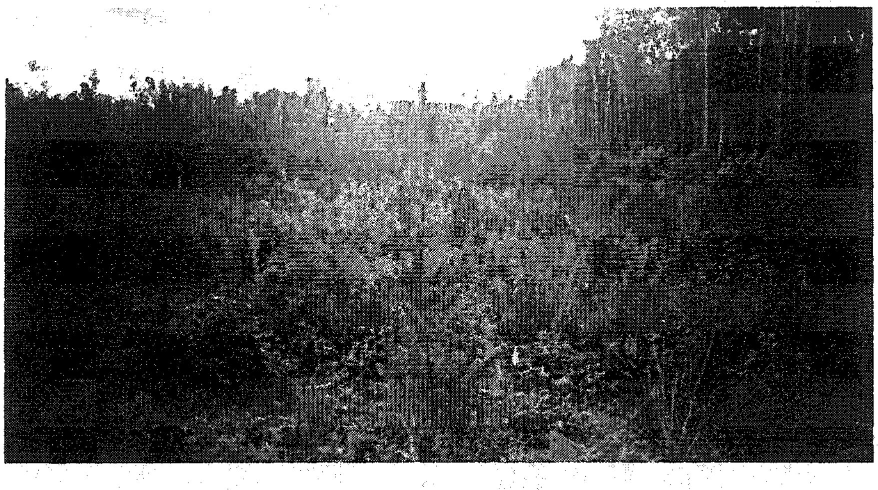

Figure I.1. General view of clearcut block one (July 14, 2001).

Figure I.2. General view of partially harvested block two (July 14, 2001).

Figure I.3. General view of partially harvested block three (July 14, 2001).

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APPENDIX II – LINEAR MODELS AND EMS TABLES

Linear model and EMS table for July-August:

$$Y_{ijklm} = \mu + B_i + \delta_{(l)j} + S_k + BS_{ik} + M_l + BM_{il} + SM_{kl} + BSM_{ikl} + \varepsilon_{(ijkl)m}$$

$$i = 1,2,3 \quad j = 1 \quad k = 1,2,3 \quad l = 1,2 \quad m = 1,2,3,4,5,6$$

	3	1	3	2	6		
	F	R	F	F	R		
	l	j	k	l	m	EMS	df
B_l	0	1	3	2	6	$\sigma^2 + 36\sigma^2_\delta + 36\phi$ (B)	2
Restriction error$_{(l)j}$[1]	1	1	3	2	6	$\sigma^2 + 36\sigma^2_\delta$	0
S_k	3	1	0	2	6	$\sigma^2 + 36\phi$ (S)	2
BS_{ik}	0	1	0	2	6	$\sigma^2 + 12\phi$ (BS)	4
M_l	3	1	3	0	6	$\sigma^2 + 54\phi$ (M)	1
BM_{il}	0	1	3	0	6	$\sigma^2 + 18\phi$ (BM)	2
SM_{kl}	3	1	0	0	6	$\sigma^2 + 18\phi$ (SM)	2
BSM_{ikl}	0	1	0	0	6	$\sigma^2 + 6\phi$ (BSM)	4
$\varepsilon_{(ijkl)m}$	1	1	1	1	1	σ^2	90

Linear model and EMS table for August-September:

$$Y_{ijklmn} = \mu + B_i + \delta_{(l)j} + S_k + BS_{ik} + T_{(ijk)l} + M_m + BM_{im} + SM_{km} + BSM_{ikm} + \varepsilon_{(ijklm)n}$$

$$i = 1,2,3 \quad j = 1 \quad k = 1,2,3 \quad l = 1,2,3,4,5,6 \quad m = 1,2 \quad n = 1$$

	3	1	3	6	2	1		
	F	R	F	R	F	R		
	l	j	k	l	m	n	EMS	df
B_i	0	1	3	6	2	1	$\sigma^2 + 36\sigma^2_\delta + 36\phi$ (B)	2
Restriction error$_{(l)j}$[1]	1	1	3	6	2	1	$\sigma^2 + 36\sigma^2_\delta$	0
S_k	3	1	0	6	2	1	$\sigma^2 + 36\phi$ (S)	2
BS_{ik}	0	1	0	6	2	1	$\sigma^2 + 12\phi$ (BS)	4
$T_{(ijk)l}$	1	1	1	0	2	1	$\sigma^2 + 2\phi$ (T)	45
M_m	3	1	3	6	0	1	$\sigma^2 + 54\phi$ (M)	1
Bm_{im}	0	1	3	6	0	1	$\sigma^2 + 18\phi$ (BM)	2
SM_{km}	3	1	0	6	0	1	$\sigma^2 + 18\phi$ (SM)	2
BSM_{ikm}	0	1	0	6	0	1	$\sigma^2 + 6\phi$ (BSM)	4
$TM_{(ijk)lm}$[2]	1	1	1	0	0	1	$\sigma^2 + \sigma^2_{TM}$	45
$\varepsilon_{(ijklm)n}$	1	1	1	1	1	1	σ^2	0

---

[1] A restriction error is a random effect that denotes a restriction on randomization in the experimental design (Lorenzen and Anderson 1993).

[2] Note that the T x M interaction was used in place of ε as the denominator in the test statistics, as it had more df.

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APPENDIX III - SUMMARY OF MEANS BY SPECIES, MONTH AND BLOCK

Jack Pine Summary

Month	Block		Leaf N	SLA	WUE	PNUE	LCP	ODW	Needle Area	Photosynthesis (A)								
										1000	600	1000	600	400	150	100	50	0
			%	(cm^2/g)	(mmol/mol)	(umol/gN)	(umol/m^2/s)	g	(cm^2)	(nmol/g/s)		(μmol/m^2/s)						
July	1	Mean	1.23	32.37	4.59	2.95	67.7	0.59	18.7	35.9	32.2	11.2	10.0	9.2	4.2	2.0	-0.4	-3.4
		S.D.	0.26	4.52	1.19	0.64	34.6	0.14	3.3	9.2	8.6	3.1	2.9	3.1	2.4	2.0	1.4	0.5
	2	Mean	1.34	29.74	3.48	2.26	65.5	0.41	11.9	30.0	24.7	10.2	8.5	7.1	2.5	1.3	-0.6	-2.6
		S.D.	0.14	4.74	1.23	0.51	17.9	0.11	2.2	6.3	4.3	2.1	1.9	1.8	1.4	0.9	0.7	1.0
	3	Mean	1.43	42.76	3.00	3.37	44.0	0.24	9.7	48.5	43.9	11.4	10.4	8.9	3.9	2.6	0.3	-2.4
		S.D.	0.11	8.14	0.62	1.13	6.9	0.10	3.2	18.5	16.1	4.0	3.5	2.5	0.5	0.4	0.4	0.5
	Total	Mean	1.33	34.95	3.69	2.86	59.1	0.41	13.4	38.1	33.6	10.9	9.6	8.4	3.6	2.0	-0.2	-2.8
		S.D.	0.19	8.10	1.20	0.89	24.1	0.18	4.8	14.1	13.0	3.0	2.8	2.5	1.7	1.3	1.0	0.8
August	1	Mean	1.08	30.16	4.03	3.03	63.5	0.41	11.2	30.8	26.3	9.8	8.2	6.3	1.8	1.3	-0.2	-2.2
		S.D.	0.29	9.60	1.28	1.55	23.4	0.16	2.5	15.2	16.2	1.6	2.2	1.9	1.0	1.4	0.7	1.0
	2	Mean	1.20	29.34	4.81	3.50	27.7	0.39	10.3	41.7	39.1	13.9	13.0	11.6	6.0	3.8	1.2	-1.5
		S.D.	0.18	10.48	0.76	1.65	3.0	0.13	1.8	21.5	19.3	3.1	2.1	2.1	1.7	1.1	0.3	0.4
	3	Mean	1.01	32.58	4.28	5.93	29.3	0.30	8.1	56.8	51.2	17.9	16.1	13.5	6.0	3.9	1.3	-1.5
		S.D.	0.13	19.47	0.72	3.84	14.7	0.11	1.1	31.9	28.1	4.3	3.2	3.2	2.1	1.3	1.0	0.9
	Total	Mean	1.10	30.69	4.37	4.15	40.2	0.37	9.9	43.1	38.9	13.9	12.4	10.4	4.6	3.0	0.8	-1.7
		S.D.	0.22	13.15	0.96	2.75	22.7	0.14	2.3	25.0	23.0	4.5	4.1	3.9	2.5	1.7	1.0	0.8
Sept.	1	Mean	1.13	24.67	5.20	3.53	43.7	0.49	11.7	39.7	36.7	16.3	14.9	12.5	4.6	2.8	0.3	-1.6
		S.D.	0.21	4.15	0.88	0.42	12.9	0.09	1.8	8.5	9.3	3.3	2.5	2.2	1.3	1.0	0.8	0.4
	2	Mean	1.27	25.29	5.58	3.23	36.2	0.43	10.8	40.7	37.4	16.0	14.7	12.7	5.4	3.3	0.8	-1.4
		S.D.	0.19	1.78	0.68	1.00	27.9	0.06	1.5	12.1	12.0	4.3	4.4	3.8	2.4	1.6	1.2	0.9
	3	Mean	1.01	32.58	7.24	4.67	30.0	0.30	8.1	46.4	42.8	15.9	14.7	13.2	6.4	4.5	1.8	-0.5
		S.D.	0.13	19.47	3.83	1.52	20.4	0.11	1.1	13.6	11.9	5.2	4.8	4.7	4.4	3.6	2.8	2.0
	Total	Mean	1.14	27.52	6.01	3.81	36.6	0.40	10.2	42.3	39.0	16.1	14.8	12.8	5.5	3.5	1.0	-1.1
		S.D.	0.20	11.45	2.35	1.19	20.8	0.12	2.1	11.3	10.8	4.1	3.8	3.5	2.9	2.3	1.8	1.3
Total	1	Mean	1.15	29.07	4.61	3.17	58.3	0.50	13.9	35.5	31.8	12.4	11.0	9.3	3.5	2.0	-0.1	-2.4
		S.D.	0.25	7.02	1.17	0.97	26.0	0.14	4.3	11.3	12.0	3.9	3.8	3.5	2.0	1.5	1.0	1.0
	2	Mean	1.27	28.12	4.62	3.00	43.1	0.41	11.0	37.5	33.7	13.4	12.1	10.5	4.6	2.8	0.5	-1.8
		S.D.	0.17	6.64	1.24	1.21	24.6	0.10	1.9	14.8	14.2	4.0	3.9	3.5	2.3	1.6	1.1	0.9
	3	Mean	1.15	35.97	4.84	4.66	34.4	0.28	8.6	50.6	46.0	15.1	13.8	11.9	5.4	3.7	1.1	-1.5
		S.D.	0.24	16.34	2.81	2.56	15.7	0.11	2.1	21.8	19.1	5.1	4.5	4.0	2.9	2.2	1.7	1.4
	Total	Mean	1.19	31.05	4.69	3.61	45.3	0.40	11.1	41.2	37.2	13.6	12.3	10.5	4.5	2.8	0.5	-1.9
		S.D.	0.22	11.31	1.87	1.86	24.3	0.15	3.6	17.6	16.4	4.4	4.1	3.8	2.5	1.9	1.4	1.2

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Jack Pine Summary (cont'd)

			Stomtal Conductance (g_s)							Transpiration (E)						
Month	Block		1000	600	400	150	100	50	0	1000	600	400	150	100	50	0
						(mmol/m^2/s)						(mmol/m^2/s)				
July	1	Mean	359.1	438.6	363.4	355.3	274.4	240.3	182.6	2.4	2.4	2.4	2.2	2.1	1.9	1.8
		S.D.	160.5	230.8	214.7	210.1	180.6	135.1	80.2	0.4	0.3	0.2	0.4	0.2	0.2	0.2
	2	Mean	208.5	206.5	197.8	187.9	176.6	155.4	140.5	3.2	3.0	2.9	2.7	2.5	2.3	2.2
		S.D.	132.9	120.5	129.9	109.2	93.3	68.8	85.9	1.5	1.0	0.9	0.8	0.8	0.8	1.0
	3	Mean	302.5	303.1	314.4	261.4	244.0	190.8	157.1	3.8	3.6	3.2	2.9	2.7	2.5	2.3
		S.D.	181.4	177.7	250.2	172.3	173.2	140.4	115.4	1.1	1.1	1.2	1.2	1.2	1.1	1.1
	Total	Mean	286.0	308.8	287.6	263.1	229.1	192.9	158.7	3.2	3.0	2.8	2.6	2.5	2.2	2.1
		S.D.	162.1	192.2	203.6	169.7	148.4	115.9	91.5	1.2	1.0	0.9	0.9	0.8	0.8	0.9
August	1	Mean	224.8	211.3	188.6	189.7	171.8	153.2	138.3	2.6	2.8	2.4	2.1	1.8	1.7	1.7
		S.D.	53.4	57.1	59.1	73.4	87.2	86.0	80.3	0.7	0.6	0.6	0.5	0.6	0.6	0.7
	2	Mean	313.2	327.4	273.0	192.4	167.6	162.9	143.6	3.0	2.8	2.4	2.1	1.8	1.7	1.7
		S.D.	118.5	177.4	159.2	106.0	117.3	120.2	109.6	0.8	0.6	0.6	0.5	0.6	0.6	0.7
	3	Mean	340.8	382.7	335.7	269.6	255.3	209.6	175.7	4.2	4.0	3.5	3.2	2.9	2.8	2.6
		S.D.	178.3	212.8	216.1	159.2	176.6	117.4	116.1	0.9	0.9	0.9	1.1	1.0	1.1	1.2
	Total	Mean	292.9	307.1	265.8	217.2	198.2	175.2	152.5	3.3	3.2	2.8	2.5	2.2	2.1	2.0
		S.D.	130.0	170.1	161.5	117.5	131.1	105.5	98.4	1.0	0.9	0.8	0.9	0.9	0.9	1.0
Sept.	1	Mean	238.3	220.2	203.1	214.6	196.4	189.0	246.1	3.1	3.2	3.2	3.2	3.2	3.2	3.2
		S.D.	69.3	87.8	76.4	102.1	82.2	42.1	59.0	0.6	0.6	0.6	0.6	0.6	0.4	0.4
	2	Mean	228.5	223.6	233.7	227.5	227.1	214.8	211.7	2.9	2.9	2.9	2.7	2.7	2.7	2.7
		S.D.	118.4	120.4	141.2	141.5	149.8	122.2	96.3	0.9	0.8	0.8	0.6	0.7	0.7	0.7
	3	Mean	141.4	129.2	124.2	124.3	126.2	111.6	120.8	2.5	2.6	2.6	2.5	2.5	2.5	2.4
		S.D.	67.5	67.7	66.2	64.2	63.5	59.8	61.9	1.0	1.0	1.0	1.1	1.1	1.1	1.1
	Total	Mean	202.7	191.0	187.0	188.8	183.2	171.8	192.8	2.9	2.9	2.9	2.8	2.8	2.8	2.7
		S.D.	94.3	99.5	105.5	111.3	108.0	89.5	88.5	0.8	0.8	0.8	0.8	0.8	0.8	0.8
Total	1	Mean	269.1	281.3	245.1	247.2	210.7	191.5	189.4	2.7	2.8	2.7	2.5	2.4	2.3	2.2
		S.D.	111.6	166.5	143.8	145.8	120.7	93.4	83.1	0.6	0.6	0.6	0.7	0.8	0.8	0.9
	2	Mean	250.1	252.5	234.8	202.6	190.4	177.7	165.3	3.0	2.9	2.7	2.5	2.3	2.2	2.2
		S.D.	125.0	144.3	138.9	114.1	118.0	103.8	97.8	1.0	0.8	0.8	0.7	0.8	0.8	0.9
	3	Mean	261.6	271.7	258.1	218.4	208.5	170.7	151.2	3.5	3.4	3.1	2.9	2.7	2.6	2.4
		S.D.	168.2	189.3	207.4	148.6	151.0	113.2	97.8	1.2	1.1	1.1	1.1	1.1	1.1	1.1
	Total	Mean	260.1	268.2	246.0	222.3	203.0	179.7	168.2	3.1	3.0	2.8	2.6	2.5	2.4	2.3
		S.D.	135.1	164.9	163.8	135.5	128.7	102.3	92.9	1.0	0.9	0.8	0.9	0.9	0.9	0.9

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Black Spruce Summary

Month	Block		Leaf N	SLA	WUE	PNUE	LCP	ODW	Needle Area	Photosynthesis (A)								
			%	(cm^2/g)	(mmol/mol)	(umol/gN)	(umol/m^2/s)	g	(cm^2)	1000 (nmol/g/s)	600 (nmol/g/s)	1000 (μmol/m^2/s)	600	400	150	100	50	0
July	1	Mean	0.99	60.68	2.69	5.02	54.8	0.13	7.7	49.0	45.8	8.0	7.4	6.7	3.3	1.5	-0.1	-2.2
		S.D.	0.23	7.20	0.42	1.44	16.5	0.03	1.1	18.4	16.4	2.2	1.9	1.5	1.2	0.7	0.8	0.4
	2	Mean	1.11	78.05	3.74	5.56	61.3	0.12	9.3	61.6	55.5	7.8	7.0	5.8	3.0	1.8	0.0	-2.0
		S.D.	0.08	10.62	0.31	1.45	33.1	0.03	1.7	17.5	19.6	1.4	1.9	2.0	1.5	1.3	0.8	0.7
	3	Mean	1.37	99.14	3.26	4.82	51.7	0.08	7.7	67.2	61.9	6.5	6.0	5.4	2.9	1.9	0.2	-2.2
		S.D.	0.27	24.95	0.44	2.24	20.1	0.02	0.9	35.4	31.3	2.3	2.1	2.9	1.8	1.3	0.8	0.6
	Total	Mean	1.15	79.29	3.23	5.14	55.9	0.11	8.2	59.3	54.4	7.4	6.8	6.0	3.0	1.7	0.0	-2.1
		S.D.	0.25	22.21	0.58	1.67	23.2	0.03	1.4	24.9	23.0	2.0	1.9	2.2	1.4	1.1	0.7	0.6
August	1	Mean	1.05	45.45	2.80	4.13	35.7	0.12	5.2	42.7	39.2	9.9	9.1	7.3	3.5	2.6	0.3	-1.3
		S.D.	0.16	8.66	1.52	1.51	21.4	0.03	0.9	13.8	12.9	4.1	3.9	4.4	2.4	2.0	1.1	0.6
	2	Mean	1.25	64.38	3.44	6.53	39.2	0.07	4.3	78.7	77.0	12.4	12.0	10.7	4.3	3.0	0.6	-1.8
		S.D.	0.16	14.96	0.61	2.52	25.3	0.03	0.8	20.8	22.8	2.7	2.4	2.7	1.8	1.6	0.9	0.9
	3	Mean	0.97	77.58	3.69	11.09	13.2	0.07	4.8	109.2	96.6	14.1	12.5	10.8	4.7	3.6	1.7	-0.8
		S.D.	0.15	24.90	0.51	2.76	10.8	0.03	0.8	42.0	36.0	2.5	2.5	1.9	2.6	1.5	0.4	1.0
	Total	Mean	1.09	62.47	3.31	7.25	29.3	0.09	4.8	76.9	70.9	12.1	11.2	9.6	4.1	3.1	0.9	-1.3
		S.D.	0.19	21.32	1.01	3.69	22.3	0.03	0.8	38.5	34.4	3.5	3.2	3.4	2.2	1.6	1.0	0.9
Sept.	1	Mean	1.05	45.45	3.30	6.46	30.8	0.12	5.2	66.6	60.8	14.6	13.3	11.0	4.2	3.0	1.1	-1.6
		S.D.	0.16	8.66	0.84	1.65	12.6	0.03	0.9	14.9	13.3	1.0	1.0	1.0	1.0	0.8	0.9	0.9
	2	Mean	1.25	64.38	3.15	8.33	27.3	0.07	4.3	100.9	91.6	15.7	14.2	11.4	3.2	2.4	0.9	-1.1
		S.D.	0.16	14.96	1.33	3.00	25.7	0.03	0.8	25.9	25.7	1.6	1.8	1.3	1.1	0.9	0.9	1.2
	3	Mean	0.97	77.58	2.84	10.89	14.8	0.07	4.8	109.2	100.5	13.4	12.1	10.8	3.1	2.5	0.7	-0.6
		S.D.	0.15	24.90	1.31	4.56	16.5	0.03	0.8	54.5	58.1	4.5	4.6	4.2	2.3	1.2	1.5	0.8
	Total	Mean	1.09	62.47	3.09	8.56	24.3	0.09	4.8	92.3	84.3	14.5	13.2	11.1	3.5	2.6	0.9	-1.1
		S.D.	0.19	21.32	1.13	3.62	19.2	0.03	0.8	38.7	39.3	2.8	2.9	2.4	1.6	1.0	1.1	1.0
Total	1	Mean	1.03	50.53	2.93	5.20	40.4	0.12	6.0	52.8	48.6	10.8	9.9	8.4	3.6	2.4	0.5	-1.7
		S.D.	0.18	10.67	1.01	1.75	19.4	0.03	1.5	18.2	16.3	3.9	3.5	3.2	1.6	1.4	1.0	0.7
	2	Mean	1.20	68.94	3.45	6.81	42.6	0.09	6.0	80.4	74.7	12.0	11.1	9.3	3.5	2.4	0.5	-1.6
		S.D.	0.14	14.45	0.85	2.56	30.3	0.03	2.6	26.2	26.3	3.8	3.6	3.2	1.5	1.3	0.9	1.0
	3	Mean	1.10	84.76	3.26	8.94	26.6	0.07	5.7	95.2	86.3	11.3	10.2	9.0	3.5	2.7	0.9	-1.2
		S.D.	0.27	25.64	0.88	4.34	23.8	0.02	1.6	46.6	44.5	4.7	4.3	3.9	2.3	1.4	1.1	1.1
	Total	Mean	1.11	68.08	3.21	6.98	36.5	0.09	5.9	76.1	69.9	11.4	10.4	8.9	3.6	2.5	0.6	-1.5
		S.D.	0.21	22.67	0.92	3.39	25.5	0.03	2.0	36.6	34.6	4.1	3.8	3.4	1.8	1.3	1.0	1.0

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Black Spruce Summary (cont'd)

Month	Block		Stomtal Conductance (g_s)							Transpiration (E)						
			1000	600	400	150	100	50	0	1000	600	400	150	100	50	0
			(mmol/m^2/s)							(mmol/m^2/s)						
July	1	Mean	189.7	209.9	183.0	156.3	146.3	133.3	119.6	2.8	2.7	2.4	2.2	2.0	1.8	1.7
		S.D.	93.2	79.5	90.0	56.5	59.9	47.9	42.7	0.5	0.3	0.4	0.4	0.4	0.4	0.3
	2	Mean	122.4	106.6	105.2	89.3	66.5	58.9	59.9	2.2	1.9	1.8	1.6	1.2	1.1	1.2
		S.D.	25.2	43.9	47.3	48.4	42.5	39.7	33.8	0.2	0.6	0.5	0.6	0.6	0.6	0.6
	3	Mean	94.7	95.8	85.1	73.7	67.4	60.5	49.6	2.0	1.8	1.6	1.5	1.4	1.2	1.2
		S.D.	42.2	50.6	49.8	35.5	35.3	29.9	20.9	0.6	0.6	0.6	0.6	0.5	0.4	0.4
	Total	Mean	135.6	137.4	124.4	106.4	93.4	84.2	76.3	2.3	2.2	1.9	1.7	1.5	1.4	1.4
		S.D.	70.4	77.3	75.2	58.0	58.6	51.7	44.9	0.6	0.6	0.6	0.6	0.6	0.5	0.5
August	1	Mean	121.8	123.4	117.7	120.7	113.0	101.8	94.1	3.6	3.5	3.4	3.5	3.3	3.3	3.1
		S.D.	68.5	69.8	73.1	85.6	85.6	79.6	74.5	0.8	0.8	0.7	0.7	0.4	0.4	0.3
	2	Mean	230.8	224.7	215.0	214.0	205.4	195.0	196.1	3.6	3.5	3.4	3.5	3.3	3.3	3.1
		S.D.	35.2	27.2	30.0	31.7	36.2	45.4	42.6	0.8	0.8	0.7	0.7	0.4	0.4	0.3
	3	Mean	182.9	192.8	187.6	185.3	164.4	152.0	142.5	3.3	3.4	3.2	3.2	3.0	2.7	2.7
		S.D.	50.1	47.0	45.0	54.2	54.5	52.0	52.5	0.6	0.7	0.7	0.7	0.8	0.7	0.7
	Total	Mean	178.5	180.3	173.4	173.3	160.9	149.6	144.3	3.5	3.5	3.3	3.4	3.2	3.1	3.0
		S.D.	67.7	64.8	64.9	70.2	70.2	69.3	69.4	0.7	0.7	0.7	0.6	0.6	0.6	0.5
Sept.	1	Mean	248.9	242.4	229.0	193.9	175.5	168.7	188.1	4.3	4.4	4.5	3.9	3.9	3.9	3.6
		S.D.	162.8	146.6	130.9	54.9	38.0	34.2	31.5	2.0	1.9	1.8	0.7	0.7	0.6	0.5
	2	Mean	274.6	257.7	255.1	238.8	231.3	213.5	238.0	4.6	4.6	4.5	4.2	4.2	4.1	4.5
		S.D.	123.2	102.0	84.4	69.3	72.6	65.7	79.6	1.4	1.3	1.3	1.1	1.0	1.0	1.1
	3	Mean	242.9	232.9	225.9	242.3	189.1	184.1	195.8	4.4	4.5	4.7	4.7	4.1	4.1	4.0
		S.D.	70.2	61.8	51.1	61.5	89.5	93.1	102.4	1.1	1.1	1.1	1.1	1.8	2.1	2.1
	Total	Mean	255.5	244.4	236.7	225.0	198.6	188.8	207.3	4.5	4.5	4.5	4.3	4.0	4.0	4.0
		S.D.	117.9	103.0	89.9	62.7	70.2	67.3	75.8	1.5	1.4	1.4	1.0	1.2	1.3	1.4
Total	1	Mean	186.8	191.9	176.6	157.0	145.0	134.6	133.9	3.6	3.6	3.4	3.2	3.1	3.0	2.8
		S.D.	120.8	110.8	105.9	70.2	65.8	60.6	64.3	1.4	1.3	1.4	0.9	1.0	1.0	0.9
	2	Mean	209.2	196.3	191.7	180.7	167.7	155.8	164.7	3.5	3.3	3.2	3.1	2.9	2.8	3.0
		S.D.	96.7	91.1	85.3	83.2	89.5	85.9	94.1	1.4	1.4	1.4	1.4	1.5	1.5	1.5
	3	Mean	173.5	173.8	166.2	167.1	140.3	132.2	129.3	3.2	3.3	3.2	3.1	2.8	2.7	2.6
		S.D.	81.5	77.7	76.4	86.9	80.7	80.7	88.8	1.3	1.4	1.5	1.6	1.6	1.7	1.7
	Total	Mean	189.9	187.3	178.2	168.3	151.0	140.9	142.6	3.4	3.4	3.3	3.1	2.9	2.8	2.8
		S.D.	100.1	92.9	88.9	79.5	78.7	75.8	83.3	1.3	1.4	1.4	1.3	1.3	1.4	1.4

White Spruce Summary

Month	Block		Leaf N	SLA	WUE	PNUE	LCP	ODW	Needle Area	Photosynthesis (A)								
										1000	600	1000	600	400	150	100	50	0
			%	(cm^2/g)	(mmol/mol)	(umol/gN)	(umol/m^2/s)	g	(cm^2)	(nmol/g/s)		(μmol/m^2/s)						
July	1	Mean	0.93	42.21	2.84	3.13	45.5	0.23	9.3	30.6	30.1	7.4	7.3	6.6	3.3	2.5	0.7	-1.6
		S.D.	0.21	7.66	1.37	1.52	39.2	0.07	3.4	19.0	18.3	4.0	3.9	3.5	2.0	1.4	0.8	0.7
	2	Mean	1.03	60.54	2.40	6.60	23.8	0.16	9.0	66.4	64.2	11.0	10.6	9.9	5.7	4.0	1.3	-1.6
		S.D.	0.25	11.09	0.90	1.34	11.1	0.05	1.6	11.4	16.3	1.0	1.5	1.5	1.3	1.1	0.7	1.1
	3	Mean	1.07	53.77	4.06	2.47	16.5	0.18	8.4	26.0	28.4	5.2	5.5	5.2	3.8	2.9	1.5	-0.7
		S.D.	0.22	18.18	0.56	0.79	12.6	0.06	0.9	9.2	12.1	1.9	1.8	1.6	1.3	1.1	0.9	0.5
	Total	Mean	1.01	52.17	3.10	4.07	28.6	0.19	8.9	41.0	40.9	7.9	7.8	7.2	4.2	3.1	1.2	-1.3
		S.D.	0.22	14.54	1.18	2.21	26.3	0.07	2.1	22.7	22.5	3.5	3.3	3.0	1.8	1.3	0.8	0.9
August	1	Mean	1.02	47.07	4.13	6.41	26.7	0.15	6.7	55.5	52.2	11.8	11.2	9.7	5.0	3.4	1.3	-1.4
		S.D.	0.42	8.00	0.97	3.61	11.4	0.06	1.4	11.8	8.5	1.5	1.3	1.6	1.6	1.4	0.8	0.5
	2	Mean	1.14	47.47	4.21	5.59	18.8	0.16	7.1	62.5	58.7	13.3	12.5	11.6	6.2	4.7	2.0	-1.2
		S.D.	0.17	10.02	0.72	1.23	10.2	0.05	1.8	11.3	9.9	1.1	1.1	0.6	0.9	0.7	0.2	0.9
	3	Mean	0.92	55.59	4.64	7.28	9.8	0.15	8.0	65.0	61.7	12.0	11.4	10.2	5.3	3.8	1.7	-0.4
		S.D.	0.20	12.64	0.58	1.81	7.5	0.04	0.9	10.2	8.2	1.8	1.5	1.2	0.8	0.7	0.4	0.3
	Total	Mean	1.03	50.04	4.33	6.43	18.4	0.15	7.3	61.0	57.6	12.3	11.7	10.5	5.5	4.0	1.7	-1.0
		S.D.	0.28	10.56	0.76	2.40	11.7	0.05	1.4	11.3	9.3	1.6	1.4	1.4	1.2	1.1	0.6	0.7
Sept.	1	Mean	1.11	51.33	3.19	6.65	40.3	0.14	6.6	61.5	54.8	11.9	10.6	9.1	3.2	2.1	0.3	-1.6
		S.D.	0.36	10.46	0.76	4.92	18.0	0.06	1.5	21.7	17.8	3.0	2.5	1.5	0.8	0.8	0.8	0.8
	2	Mean	1.17	47.25	6.34	4.61	24.0	0.16	7.1	53.5	51.0	11.3	10.8	9.8	3.5	2.9	1.0	-0.8
		S.D.	0.18	9.68	5.58	1.27	17.8	0.05	1.8	14.4	14.8	2.1	2.3	1.9	1.2	0.9	0.7	0.5
	3	Mean	0.98	56.29	4.21	6.48	9.3	0.15	7.8	60.5	61.4	10.9	11.0	9.5	4.0	2.9	1.3	-0.3
		S.D.	0.21	11.53	0.97	1.98	9.6	0.03	1.1	8.9	11.2	0.9	0.6	1.3	0.8	0.9	0.4	0.3
	Total	Mean	1.09	51.62	4.58	5.91	24.6	0.15	7.2	58.5	55.7	11.4	10.8	9.5	3.6	2.6	0.9	-0.9
		S.D.	0.26	10.64	3.38	3.10	19.6	0.05	1.5	15.4	14.6	2.1	1.9	1.5	1.0	0.9	0.8	0.8
Total	1	Mean	1.02	46.87	3.38	5.40	37.5	0.17	7.5	49.2	45.7	10.4	9.7	8.5	3.8	2.7	0.8	-1.5
		S.D.	0.33	9.11	1.15	3.79	25.5	0.07	2.5	21.8	18.5	3.5	3.1	2.7	1.7	1.3	0.9	0.7
	2	Mean	1.11	51.75	4.32	5.60	22.2	0.16	7.7	60.8	58.0	11.9	11.3	10.4	5.1	3.9	1.4	-1.2
		S.D.	0.20	11.58	3.51	1.47	12.9	0.05	1.9	12.9	14.2	1.7	1.8	1.6	1.6	1.2	0.7	0.9
	3	Mean	0.99	55.22	4.30	5.41	11.9	0.16	8.1	50.5	50.5	9.3	9.3	8.3	4.4	3.2	1.5	-0.5
		S.D.	0.20	13.58	0.73	2.64	10.1	0.05	0.9	20.0	18.9	3.4	3.1	2.6	1.2	1.0	0.6	0.4
	Total	Mean	1.04	51.28	4.00	5.47	23.9	0.16	7.8	53.5	51.4	10.5	10.1	9.1	4.4	3.2	1.2	-1.1
		S.D.	0.25	11.86	2.17	2.75	20.2	0.06	1.9	19.0	17.8	3.1	2.8	2.5	1.6	1.2	0.8	0.8

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White Spruce Summary (cont'd)

Month	Block		Stomtal Conductance (g_s)							Transpiration (E)						
			1000	600	400	150	100	50	0	1000	600	400	150	100	50	0
						(mmol/m²/s)							(mmol/m²/s)			
July	1	Mean	249.8	322.4	282.8	245.2	203.5	189.9	173.5	2.4	2.4	2.2	2.0	1.8	1.8	1.6
		S.D.	236.1	365.3	277.1	207.9	142.7	123.4	125.7	0.9	0.9	0.8	0.8	0.7	0.4	0.4
	2	Mean	367.4	360.3	397.5	377.4	386.8	298.7	254.0	5.1	5.0	5.1	5.0	4.9	4.8	3.6
		S.D.	140.6	236.9	277.5	335.3	290.5	221.2	190.4	1.8	2.2	2.5	3.0	3.3	3.5	2.1
	3	Mean	69.8	70.7	65.2	62.0	58.3	55.7	48.3	1.5	1.4	1.2	1.2	1.1	1.0	1.0
		S.D.	38.6	33.6	26.2	24.0	23.2	23.7	19.5	0.7	0.5	0.4	0.4	0.3	0.4	0.3
	Total	Mean	229.0	251.2	248.5	228.2	216.2	181.4	158.6	3.0	2.9	2.9	2.7	2.6	2.5	2.1
		S.D.	196.2	271.3	256.0	252.3	223.8	171.7	151.7	1.9	2.1	2.2	2.4	2.5	2.5	1.6
August	1	Mean	206.4	208.8	201.5	194.5	191.4	179.6	164.8	2.9	2.8	2.6	2.4	2.4	2.4	2.5
		S.D.	24.0	26.5	22.6	25.5	20.6	13.8	24.7	0.4	0.4	0.3	0.2	0.2	0.2	0.3
	2	Mean	299.8	313.2	286.2	269.9	254.9	231.2	229.2	3.0	3.0	2.8	2.7	2.7	2.5	2.7
		S.D.	43.0	55.3	42.8	40.6	51.7	33.0	25.3	0.3	0.4	0.4	0.3	0.2	0.3	0.3
	3	Mean	166.3	166.5	155.2	143.9	130.0	133.0	119.7	2.5	2.5	2.3	2.2	2.2	2.2	2.0
		S.D.	31.5	32.6	29.7	24.8	29.4	20.1	29.3	0.4	0.4	0.5	0.5	0.6	0.5	0.5
	Total	Mean	224.2	229.5	214.3	202.8	192.1	181.2	171.2	2.8	2.8	2.6	2.5	2.4	2.4	2.4
		S.D.	65.7	73.8	63.7	60.8	62.6	46.9	52.5	0.4	0.5	0.4	0.4	0.4	0.4	0.5
Sept.	1	Mean	198.2	192.6	199.2	196.8	189.8	189.5	217.3	3.6	3.7	3.7	3.7	3.7	3.6	3.5
		S.D.	143.2	139.7	148.1	145.4	138.0	152.5	207.7	1.9	1.9	1.9	1.9	1.9	2.0	2.0
	2	Mean	140.9	135.1	142.1	152.4	143.6	150.4	195.4	2.3	2.3	2.4	2.5	2.5	2.6	3.0
		S.D.	61.7	59.5	52.9	40.4	38.2	36.7	100.5	1.0	1.0	0.9	0.8	0.8	0.7	1.0
	3	Mean	146.3	142.1	137.1	140.9	139.2	134.4	152.7	2.7	2.7	2.8	2.8	2.8	2.8	2.8
		S.D.	28.7	25.7	28.5	33.7	32.4	31.3	33.1	0.6	0.6	0.6	0.6	0.6	0.6	0.6
	Total	Mean	161.8	156.6	159.5	163.3	157.5	158.1	188.5	2.9	2.9	3.0	3.0	3.0	3.0	3.1
		S.D.	90.0	87.6	91.4	87.4	83.0	90.0	129.4	1.3	1.3	1.3	1.3	1.3	1.3	1.3
Total	1	Mean	218.1	241.3	227.8	212.1	194.9	186.3	185.2	3.0	2.9	2.9	2.7	2.7	2.6	2.6
		S.D.	152.1	220.7	175.5	140.3	108.4	106.8	134.5	1.2	1.3	1.3	1.4	1.4	1.3	1.4
	2	Mean	269.4	269.6	275.3	266.5	261.8	226.8	226.2	3.5	3.5	3.4	3.4	3.3	3.3	3.1
		S.D.	130.5	168.6	188.6	207.3	191.0	137.8	120.1	1.6	1.8	1.9	2.1	2.2	2.2	1.3
	3	Mean	127.4	126.4	119.2	115.6	109.1	107.7	106.9	2.2	2.2	2.1	2.1	2.0	2.0	1.9
		S.D.	53.0	50.9	47.9	47.0	45.9	44.8	51.9	0.8	0.8	0.8	0.8	0.9	0.9	0.9
	Total	Mean	205.0	212.4	207.4	198.1	188.6	173.6	172.8	2.9	2.9	2.8	2.7	2.7	2.6	2.5
		S.D.	131.5	171.7	162.4	157.4	141.9	113.5	117.4	1.3	1.4	1.5	1.6	1.6	1.6	1.3

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APPENDIX IV - LSD TEST RESULTS FOR SPECIES

Table IV.1. LSD post-hoc test results for between-species comparisons: probability that the mean difference is zero by species and light level for July-Aug. A.

Species Contrast	Light intensity (μmol photons/m2/s)						
	0	50	100	150	400	600	1000
	-------------------------------mmol CO2/m2/s-------------------------------						
jack pine - black spruce	**0.002**	0.381	0.792	0.239	**0.005**	**0.001**	**0.000**
white spruce - black spruce	**0.001**	**0.000**	**0.000**	**0.002**	0.060	0.210	0.601
white spruce - jack pine	**0.000**	**0.000**	**0.001**	**0.040**	0.339	**0.025**	**0.000**

Table IV.2. LSD post-hoc test results for between-species comparisons: probability that the mean difference is zero by species and light level for Aug.-Sept. A.

Species Contrast	Light intensity (μmol photons/m2/s)						
	0	50	100	150	400	600	1000
	-------------------------------mmol CO2/m2/s-------------------------------						
jack pine - black spruce	0.258	0.949	0.209	**0.003**	**0.044**	**0.038**	**0.028**
white spruce - black spruce	0.317	0.123	0.161	0.061	0.586	0.160	**0.046**
white spruce - jack pine	**0.036**	0.109	0.880	0.237	**0.012**	**0.001**	**0.000**

Table IV.3. LSD post-hoc test results for between-species comparisons: probability that the mean difference is zero by species and light level for July-Aug. log (g_s).

Species Contrast	Light intensity (μmol photons/m2/s)						
	0	50	100	150	400	600	1000
	-------------------------------mmol CO2/m2/s-------------------------------						
jack pine - black spruce	**0.007**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
white spruce - black spruce	**0.007**	**0.002**	**0.006**	**0.027**	**0.019**	**0.028**	**0.032**
white spruce - jack pine	0.961	0.553	0.329	0.082	**0.030**	**0.003**	**0.002**

Table IV.4. LSD post-hoc test results for between-species comparisons: probability that the mean difference is zero by species and light level for Aug.-Sept. log (g_s).

Species Contrast	Light intensity (μmol photons/m2/s)						
	0	50	100	150	400	600	1000
	-------------------------------mmol CO2/m2/s-------------------------------						
jack pine - black spruce	0.902	0.911	0.900	0.712	0.574	0.214	0.104
white spruce - black spruce	0.438	0.517	0.909	0.417	0.387	0.300	0.334
white spruce - jack pine	0.362	0.585	0.990	0.651	0.150	**0.023**	**0.010**

Table IV.5. LSD post-hoc test results for between-species comparisons: probability that the mean difference is zero by species and light level for July-Aug. log (E).

Species Contrast	Light intensity (μmol photons/m2/s)						
	0	50	100	150	400	600	1000
	-------------------------------mmol CO2/m2/s-------------------------------						
jack pine - black spruce	0.825	0.685	0.645	0.722	0.249	0.120	0.190
white spruce - black spruce	0.810	0.438	0.772	0.513	0.549	0.496	0.321
white spruce - jack pine	0.644	0.711	0.865	0.314	0.082	**0.027**	**0.023**

Table IV.6. LSD post-hoc test results for between-species comparisons: probability that the mean difference is zero by species and light level for Aug.-Sept. log (E).

Species Contrast	Light intensity (μmol photons/m2/s)						
	0	50	100	150	400	600	1000
	-------------------------------mmol CO2/m2/s-------------------------------						
Species	E_0	E_{50}	E_{100}	E_{150}	E_{400}	E_{600}	E_{1000}
jack pine - black spruce	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**
white spruce - black spruce	0.194	**0.002**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
white spruce - jack pine	**0.042**	0.114	0.148	0.576	0.678	0.322	0.324

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APPENDIX V - Interaction Graphs and LSD Statistics for MANOVAs on A, log(gs), and log(E)

To avoid clutter, least significant difference (LSD) ellipses are not shown in Figures 3, 4, 5, 6, and 7 in the main text or in Figures V.1, V.2, V.3, and V.4 in this Appendix. Instead, tables of LSD values are provided below.

To compare means in Figs. 4, 5, 6, and 7, use Tables V.2 through V.5 respectively with Figs. V.1 through V.4 respectively. Then transfer the results into Figs. 4 through 7 respectively. For example, to compare the block-by-month interaction means displayed in Fig. 4, use the LSD values given in Table V.2 with Fig. V.1, which displays the BxM interaction means in log(g_s) units. Once the means of interest have been declared significantly different, or not significantly different, in the units of analysis, that information may be applied to Fig. 4.

In any case, use Tables V.1 through V.5 as follows. Read the column that corresponds to the plot of interest. For example, to examine the A_{600} plot in Fig. 3, use the PAR = 600 column in Table V.1. Then, to compare means either within July or between July and August, use the LSD value reported in the July/Aug row – e.g., LSD = 1.63 in the PAR = 600 column of Table V.1. To compare means either within September or between August and September, use the LSD value reported in the Aug/Sept row – e.g., LSD = 1.73 in the PAR = 600 column of Table V.1.

Comparisons within August present a special case. The issue here is that August data were used twice – once with the July data in an RCBD analysis and again with the September data in a repeated measures analysis. The most conservative rule is to use greater of the values {LSD July/August, LSD August/September} for within August comparisons.

Table V.1. Least significant differences (LSDs) for rate of photosynthesis (A) comparisons in Fig. 3 by grouping criteria and level of light intensity. Mean differences that match or exceed the tabulated LSD value are significantly different at α = 0.05.

Grouping	Cell count	Light Intensity (μmol photons/m^2/s)					
		50	100	150	400	600	1000
		μmol CO_2/m^2/s					
July/Aug BxM	18	0.52	0.84	1.10	1.59	1.63	1.78
Aug/Sept BxM	18	0.72	1.01	1.44	1.73	1.80	1.98

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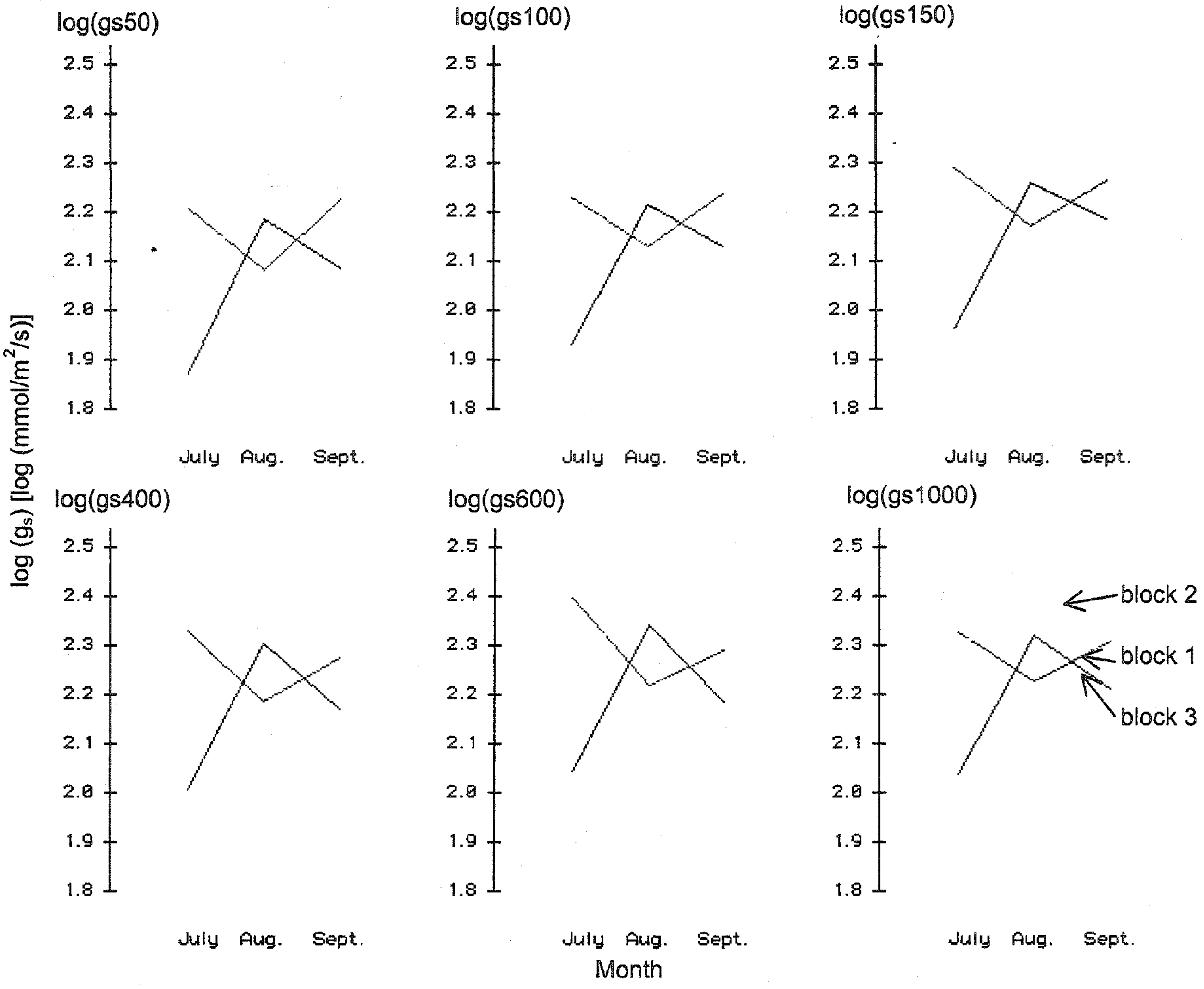

Figure V.1. Block x month interaction cell means for log (g_s).

Table V.2. Least significant differences (LSDs) for log(gs) comparisons in Fig. V.1 by grouping criteria and level of light intensity. Mean differences that match or exceed the tabulated LSD value are significantly different at α = 0.05.

Grouping	Cell count	Light Intensity (μmol photons/m²/s)					
		50	100	150	400	600	1000
		log(mmol/m²/s)					
July/Aug BxS	12	0.20	0.22	0.20	0.19	0.18	0.17
Aug/Sept BxS	12	0.19	0.18	0.16	0.15	0.17	0.15

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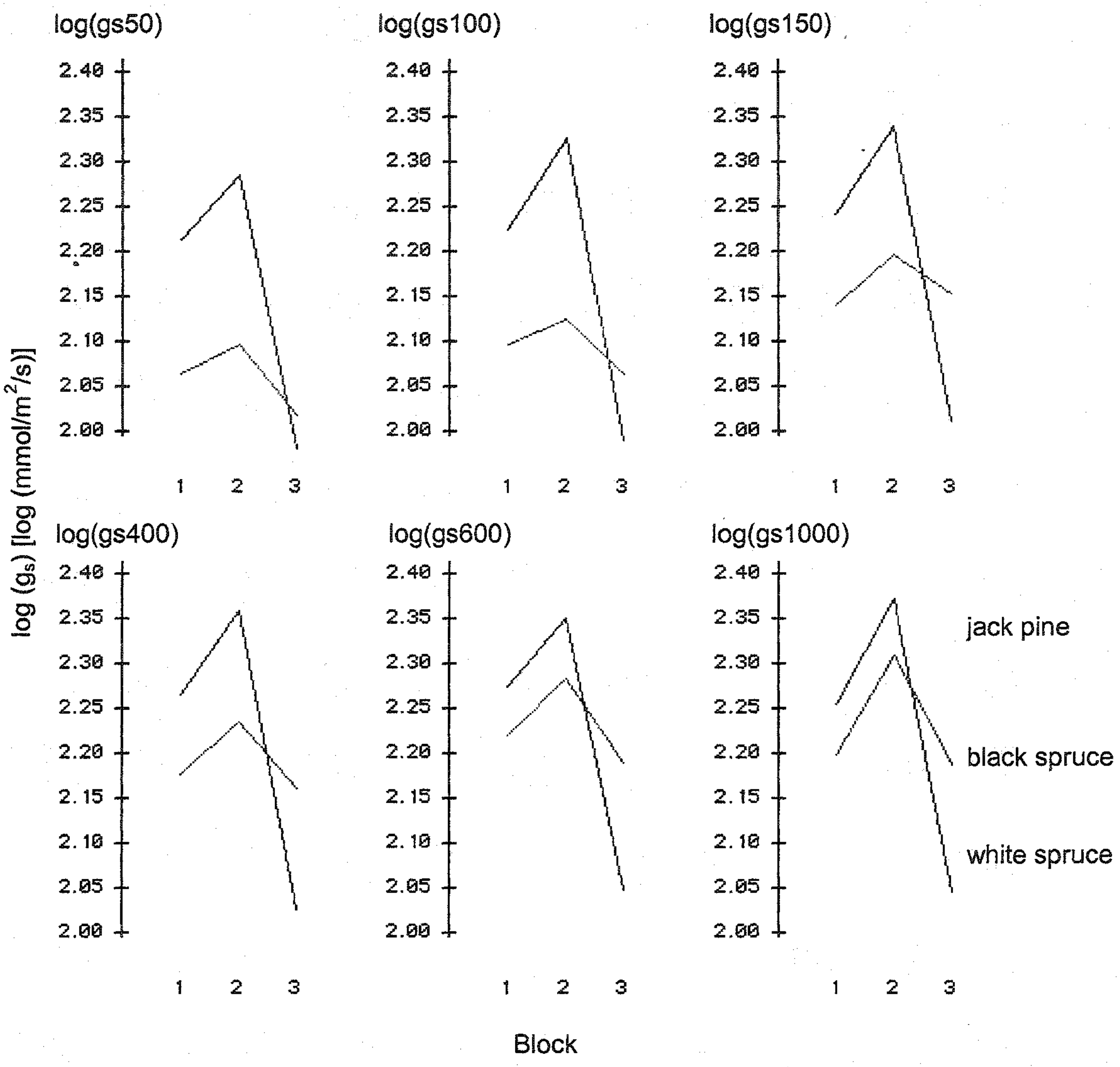

Figure V.2. Block x species interaction cell means for log (g_s).

Table V.3. Least significant differences (LSDs) for log(gs) comparisons in Fig. V.2 by grouping criteria and level light intensity. Mean differences that match or exceed the tabulated LSD value are significantly different at α = 0.05.

Grouping	Cell count	Light Intensity (μmol photons/m^2/s)					
		50	100	150	400	600	1000
		log(mmol/m^2/s)					
July/Aug BxM	18	0.16	0.18	0.16	0.16	0.15	0.14
Aug/Sept BxM	18	0.16	0.15	0.13	0.13	0.14	0.13

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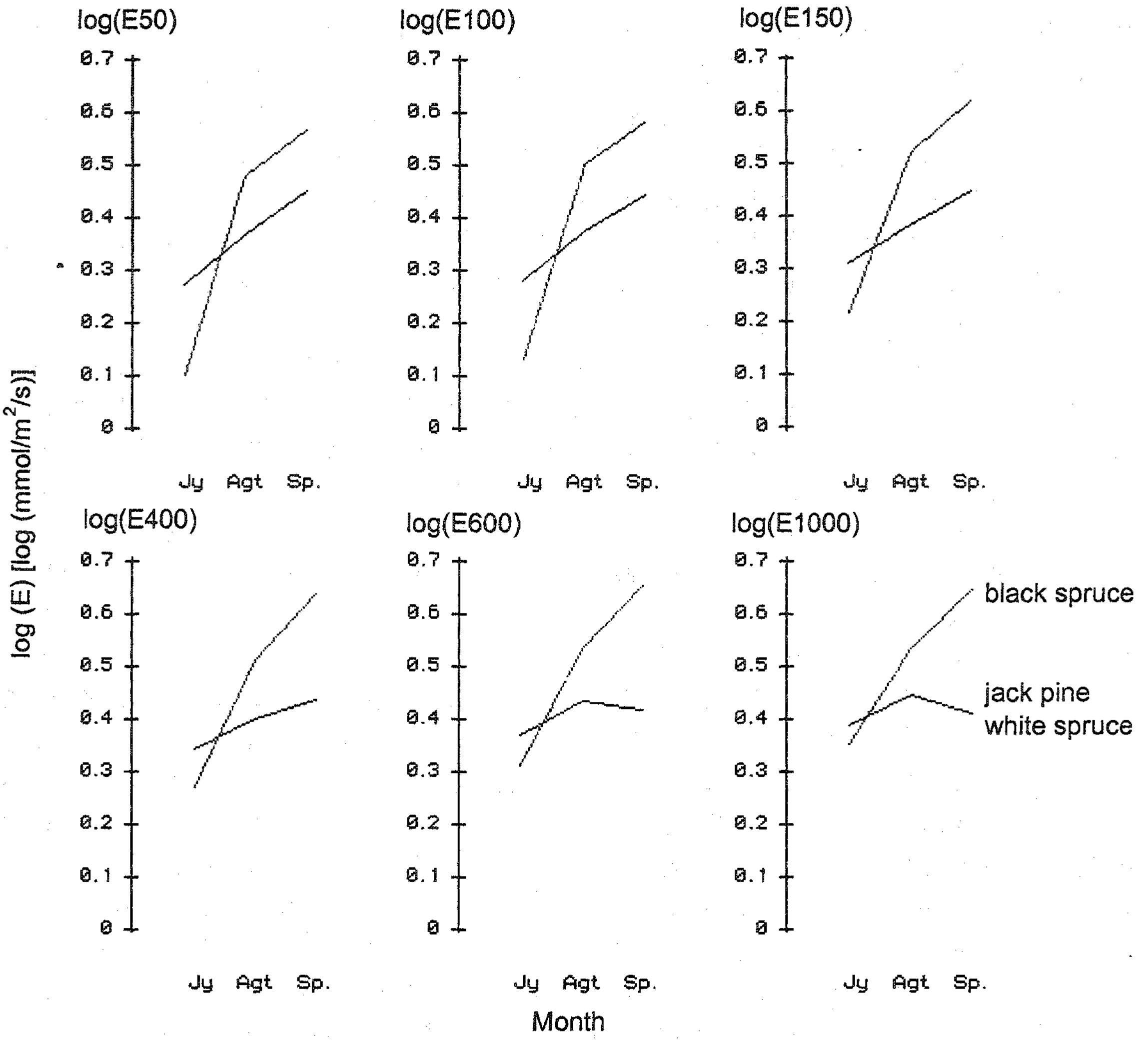

Figure V.3. Species x month interaction cell means for log (E).

Table V.4. Least significant differences (LSDs) for rate of log(E) comparisons in Fig. V.3 by grouping criteria and level of light intensity. Mean differences that match or exceed the tabulated LSD value are significantly different at α = 0.05.

Grouping	Cell count	Light Intensity (μmol photons/m^2/s)					
		50	100	150	400	600	1000
		log(mmol/m^2/s)					
July/Aug SxM	18	0.10	0.11	0.10	0.09	0.09	0.08
Aug/Sept SxM	18	0.09	0.08	0.07	0.07	0.09	0.09

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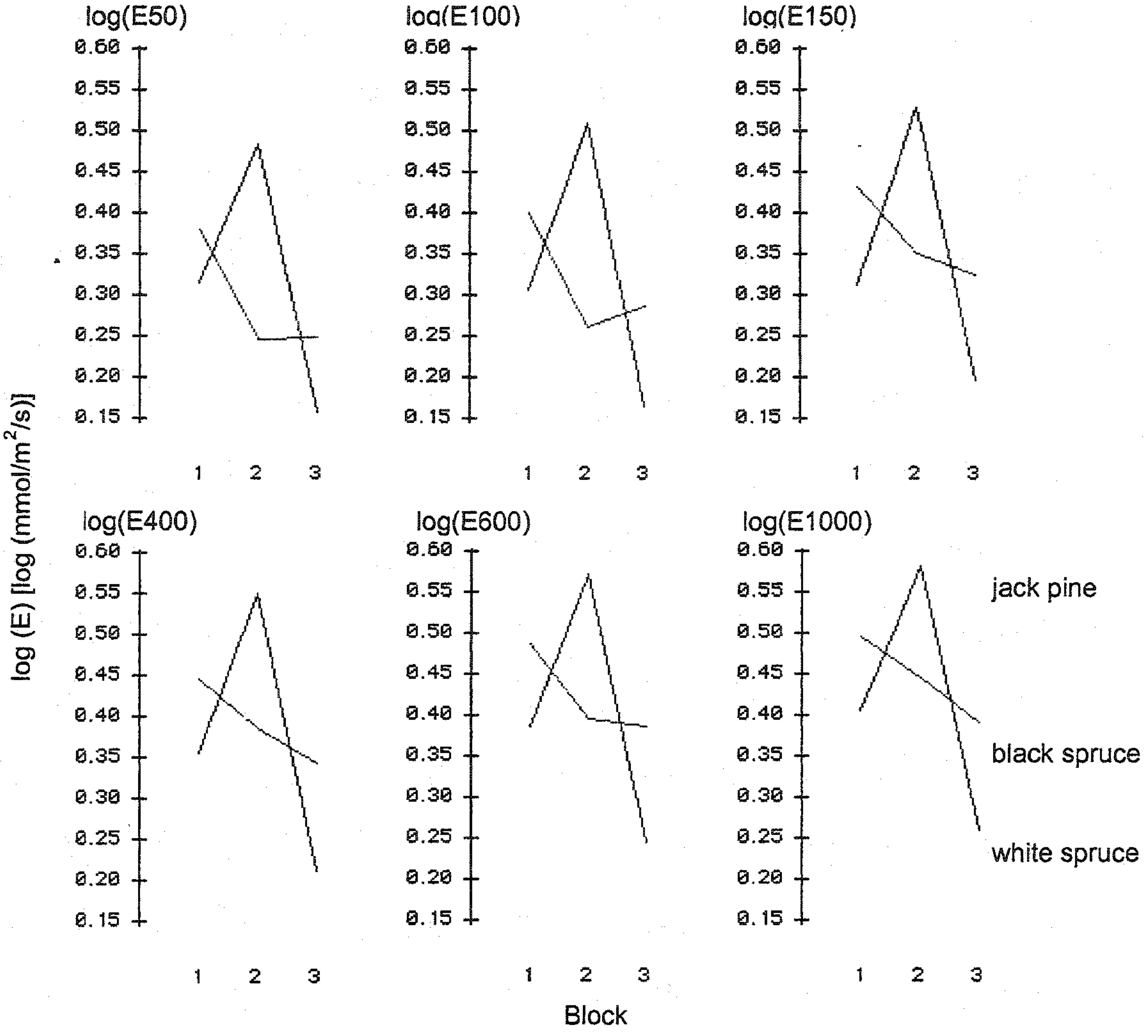

Figure V.4. Block x species interaction cell means for log (E), selected for July-August only.

Table V.5. Least significant differences (LSDs) for rate of log(E) comparisons in Fig. V.4 for July and August by level of light intensity. Mean differences that match or exceed the tabulated LSD value are significantly different at α = 0.05.

Grouping	Cell count	Light Intensity (μmol photons/m^2/s)					
		50	100	150	400	600	1000
		log(mmol/m^2/s)					
July/Aug BxS	12	0.12	0.13	0.12	0.11	0.11	0.10

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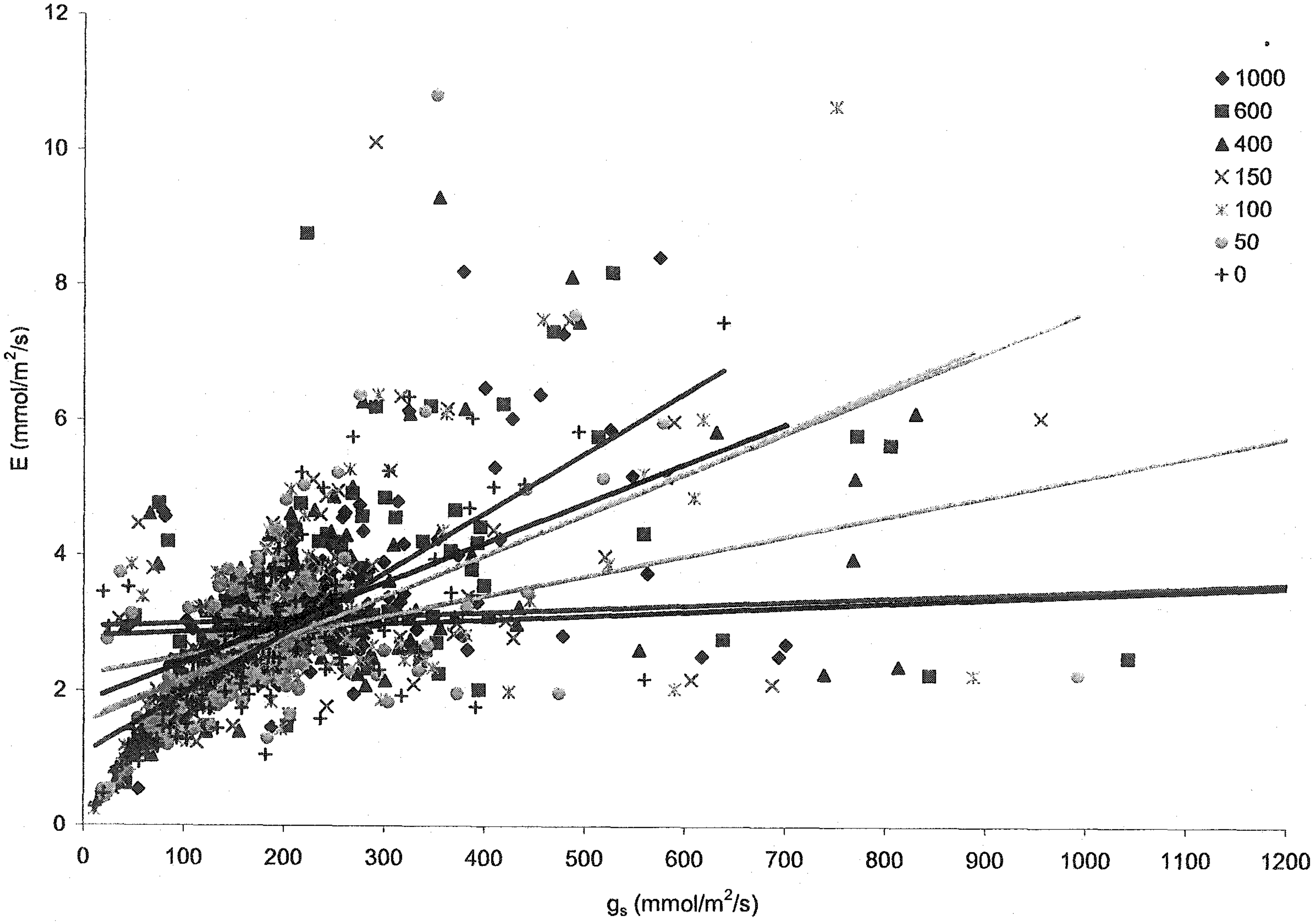
APPENDIX VI - SCATTERPLOT OF TRANSPIRATION AGAINST STOMATAL CONDUCTANCE



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APPENDIX VII - Individual tree values of A, g_s, and E in measured units.

Case No.	Treatment	Whole Plot	Block	Species	Row	Subjects	Month
1	clearcut	1	1	jack pine	1	1	July
2	clearcut	1	1	jack pine	1	2	July
3	clearcut	1	1	jack pine	1	3	July
4	clearcut	1	1	jack pine	2	1	July
5	clearcut	1	1	jack pine	2	2	July
6	clearcut	1	1	jack pine	2	3	July
7	clearcut	1	1	black spruce	1	1	July
8	clearcut	1	1	black spruce	1	2	July
9	clearcut	1	1	black spruce	1	3	July
10	clearcut	1	1	black spruce	2	1	July
11	clearcut	1	1	black spruce	2	2	July
12	clearcut	1	1	black spruce	2	3	July
13	clearcut	1	1	white spruce	1	1	July
14	clearcut	1	1	white spruce	1	2	July
15	clearcut	1	1	white spruce	1	3	July
16	clearcut	1	1	white spruce	2	1	July
17	clearcut	1	1	white spruce	2	2	July
18	clearcut	1	1	white spruce	2	3	July
19	partial cut	1	2	jack pine	1	1	July
20	partial cut	1	2	jack pine	1	2	July
21	partial cut	1	2	jack pine	1	3	July
22	partial cut	1	2	jack pine	2	1	July
23	partial cut	1	2	jack pine	2	2	July
24	partial cut	1	2	jack pine	2	3	July
25	partial cut	1	2	black spruce	1	1	July
26	partial cut	1	2	black spruce	1	2	July
27	partial cut	1	2	black spruce	1	3	July
28	partial cut	1	2	black spruce	2	1	July
29	partial cut	1	2	black spruce	2	2	July
30	partial cut	1	2	black spruce	2	3	July
31	partial cut	1	2	white spruce	1	1	July
32	partial cut	1	2	white spruce	1	2	July
33	partial cut	1	2	white spruce	1	3	July
34	partial cut	1	2	white spruce	2	1	July
35	partial cut	1	2	white spruce	2	2	July
36	partial cut	1	2	white spruce	2	3	July
37	partial cut	2	3	jack pine	1	1	July
38	partial cut	2	3	jack pine	1	2	July
39	partial cut	2	3	jack pine	1	3	July
40	partial cut	2	3	jack pine	2	1	July
41	partial cut	2	3	jack pine	2	2	July
42	partial cut	2	3	jack pine	2	3	July
43	partial cut	2	3	black spruce	1	1	July
44	partial cut	2	3	black spruce	1	2	July
45	partial cut	2	3	black spruce	1	3	July
46	partial cut	2	3	black spruce	2	1	July
47	partial cut	2	3	black spruce	2	2	July
48	partial cut	2	3	black spruce	2	3	July
49	partial cut	2	3	white spruce	1	1	July
50	partial cut	2	3	white spruce	1	2	July
51	partial cut	2	3	white spruce	1	3	July

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Case No.	Treatment	Whole Plot	Block	Species	Row	Subjects	Month
52	partial cut	2	3	white spruce	2	1	July
53	partial cut	2	3	white spruce	2	2	July
54	partial cut	2	3	white spruce	2	3	July
55	clearcut	1	1	jack pine	1	1	August
56	clearcut	1	1	jack pine	1	2	August
57	clearcut	1	1	jack pine	1	3	August
58	clearcut	1	1	jack pine	2	1	August
59	clearcut	1	1	jack pine	2	2	August
60	clearcut	1	1	jack pine	2	3	August
61	clearcut	1	1	black spruce	1	1	August
62	clearcut	1	1	black spruce	1	2	August
63	clearcut	1	1	black spruce	1	3	August
64	clearcut	1	1	black spruce	2	1	August
65	clearcut	1	1	black spruce	2	2	August
66	clearcut	1	1	black spruce	2	3	August
67	clearcut	1	1	white spruce	1	1	August
68	clearcut	1	1	white spruce	1	2	August
69	clearcut	1	1	white spruce	1	3	August
70	clearcut	1	1	white spruce	2	1	August
71	clearcut	1	1	white spruce	2	2	August
72	clearcut	1	1	white spruce	2	3	August
73	partial cut	1	2	jack pine	1	1	August
74	partial cut	1	2	jack pine	1	2	August
75	partial cut	1	2	jack pine	1	3	August
76	partial cut	1	2	jack pine	2	1	August
77	partial cut	1	2	jack pine	2	2	August
78	partial cut	1	2	jack pine	2	3	August
79	partial cut	1	2	black spruce	1	1	August
80	partial cut	1	2	black spruce	1	2	August
81	partial cut	1	2	black spruce	1	3	August
82	partial cut	1	2	black spruce	2	1	August
83	partial cut	1	2	black spruce	2	2	August
84	partial cut	1	2	black spruce	2	3	August
85	partial cut	1	2	white spruce	1	1	August
86	partial cut	1	2	white spruce	1	2	August
87	partial cut	1	2	white spruce	1	3	August
88	partial cut	1	2	white spruce	2	1	August
89	partial cut	1	2	white spruce	2	2	August
90	partial cut	1	2	white spruce	2	3	August
91	partial cut	2	3	jack pine	1	1	August
92	partial cut	2	3	jack pine	1	2	August
93	partial cut	2	3	jack pine	1	3	August
94	partial cut	2	3	jack pine	2	1	August
95	partial cut	2	3	jack pine	2	2	August
96	partial cut	2	3	jack pine	2	3	August
97	partial cut	2	3	black spruce	1	1	August
98	partial cut	2	3	black spruce	1	2	August
99	partial cut	2	3	black spruce	1	3	August
100	partial cut	2	3	black spruce	2	1	August
101	partial cut	2	3	black spruce	2	2	August
102	partial cut	2	3	black spruce	2	3	August

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Case No.	Treatment	Whole Plot	Block	Species	Row	Subjects	Month
103	partial cut	2	3	white spruce	1	1	August
104	partial cut	2	3	white spruce	1	2	August
105	partial cut	2	3	white spruce	1	3	August
106	partial cut	2	3	white spruce	2	1	August
107	partial cut	2	3	white spruce	2	2	August
108	partial cut	2	3	white spruce	2	3	August
109	clearcut	1	1	jack pine	1	1	Sept.
110	clearcut	1	1	jack pine	1	2	Sept.
111	clearcut	1	1	jack pine	1	3	Sept.
112	clearcut	1	1	jack pine	2	1	Sept.
113	clearcut	1	1	jack pine	2	2	Sept.
114	clearcut	1	1	jack pine	2	3	Sept.
115	clearcut	1	1	black spruce	1	1	Sept.
116	clearcut	1	1	black spruce	1	2	Sept.
117	clearcut	1	1	black spruce	1	3	Sept.
118	clearcut	1	1	black spruce	2	1	Sept.
119	clearcut	1	1	black spruce	2	2	Sept.
120	clearcut	1	1	black spruce	2	3	Sept.
121	clearcut	1	1	white spruce	1	1	Sept.
122	clearcut	1	1	white spruce	1	2	Sept.
123	clearcut	1	1	white spruce	1	3	Sept.
124	clearcut	1	1	white spruce	2	1	Sept.
125	clearcut	1	1	white spruce	2	2	Sept.
126	clearcut	1	1	white spruce	2	3	Sept.
127	partial cut	1	2	jack pine	1	1	Sept.
128	partial cut	1	2	jack pine	1	2	Sept.
129	partial cut	1	2	jack pine	1	3	Sept.
130	partial cut	1	2	jack pine	2	1	Sept.
131	partial cut	1	2	jack pine	2	2	Sept.
132	partial cut	1	2	jack pine	2	3	Sept.
133	partial cut	1	2	black spruce	1	1	Sept.
134	partial cut	1	2	black spruce	1	2	Sept.
135	partial cut	1	2	black spruce	1	3	Sept.
136	partial cut	1	2	black spruce	2	1	Sept.
137	partial cut	1	2	black spruce	2	2	Sept.
138	partial cut	1	2	black spruce	2	3	Sept.
139	partial cut	1	2	white spruce	1	1	Sept.
140	partial cut	1	2	white spruce	1	2	Sept.
141	partial cut	1	2	white spruce	1	3	Sept.
142	partial cut	1	2	white spruce	2	1	Sept.
143	partial cut	1	2	white spruce	2	2	Sept.
144	partial cut	1	2	white spruce	2	3	Sept.
145	partial cut	2	3	jack pine	1	1	Sept.
146	partial cut	2	3	jack pine	1	2	Sept.
147	partial cut	2	3	jack pine	1	3	Sept.
148	partial cut	2	3	jack pine	2	1	Sept.
149	partial cut	2	3	jack pine	2	2	Sept.
150	partial cut	2	3	jack pine	2	3	Sept.
151	partial cut	2	3	black spruce	1	1	Sept.
152	partial cut	2	3	black spruce	1	2	Sept.
153	partial cut	2	3	black spruce	1	3	Sept.

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Case No.	Treatment	Whole Plot	Block	Species	Row	Subjects	Month
154	partial cut	2	3	black spruce	2	1	Sept.
155	partial cut	2	3	black spruce	2	2	Sept.
156	partial cut	2	3	black spruce	2	3	Sept.
157	partial cut	2	3	white spruce	1	1	Sept.
158	partial cut	2	3	white spruce	1	2	Sept.
159	partial cut	2	3	white spruce	1	3	Sept.
160	partial cut	2	3	white spruce	2	1	Sept.
161	partial cut	2	3	white spruce	2	2	Sept.
162	partial cut	2	3	white spruce	2	3	Sept.

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Case No.	A1000	A600	A400	A150	A100	A50	A0
1	8.85	8.40	8.76	4.52	2.24	-0.05	-3.01
2	14.68	12.09	9.83	3.88	2.06	-0.05	-2.54
3	8.29	6.55	5.20	0.38	-0.68	-2.18	-3.77
4	15.53	14.69	14.69	7.80	5.40	1.98	-3.60
5	10.03	8.99	7.81	3.46	1.56	-1.14	-3.64
6	9.83	9.55	8.73	5.27	1.65	-1.04	-3.84
7	8.89	7.72	5.40	1.69	0.11	-0.15	-2.23
8	7.76	8.02	7.76	3.44	1.78	0.00	-2.25
9	11.22	10.28	9.19	5.30	1.87	0.00	-2.13
10	5.66	5.06	5.66	2.98	1.49	0.32	-1.40
11	8.90	7.71	7.00	2.97	2.02	0.87	-2.61
12	5.32	5.72	5.45	3.19	2.00	-1.44	-2.49
13	11.58	11.06	10.09	5.56	3.69	1.10	-1.29
14	10.53	10.11	7.82	2.19	1.88	0.52	-0.94
15	0.61	0.61	0.15	0.00	0.00	-0.91	-2.43
16	6.08	8.33	7.43	3.15	2.48	0.90	-0.79
17	9.21	8.88	8.78	4.98	4.01	1.30	-2.38
18	6.40	4.76	5.22	3.70	2.86	1.01	-2.02
19	11.74	7.64	6.80	1.21	0.28	-1.58	-2.70
20	11.15	9.05	7.39	2.53	1.16	-0.58	-2.32
21	8.50	6.60	5.59	1.45	1.01	0.00	-0.78
22	11.27	10.31	8.88	2.39	0.89	-1.23	-3.48
23	11.78	10.91	9.37	5.02	2.99	0.29	-2.99
24	6.61	6.21	4.80	2.67	1.42	-0.31	-3.22
25	8.19	7.65	6.36	2.91	2.05	0.32	-1.40
26	9.36	8.92	8.27	5.01	3.37	0.87	-2.61
27	6.95	6.95	6.04	2.49	1.44	-1.44	-2.49
28	8.30	7.28	5.23	3.07	2.05	0.45	-2.16
29	5.48	3.34	2.27	0.60	-0.48	-0.48	-0.95
30	8.40	7.92	6.80	3.92	2.08	0.00	-2.32
31	10.99	9.88	8.31	3.69	2.03	0.09	-2.22
32	10.02	10.80	10.69	7.01	5.23	1.89	-0.22
33	11.80	11.64	11.49	7.18	4.79	1.12	-3.35
34	9.56	7.78	7.90	4.78	3.78	2.00	-1.33
35	11.77	11.89	10.83	5.65	4.12	1.06	-1.41
36	12.01	11.44	10.00	5.67	4.13	1.63	-1.25
37	12.57	12.03	11.02	4.84	3.23	0.54	-2.82
38	16.30	14.21	11.30	3.84	2.33	-0.12	-2.68
39	14.74	13.28	10.35	3.76	2.93	0.42	-2.82
40	7.27	7.09	6.39	3.41	2.01	0.09	-1.66
41	6.15	5.30	5.47	3.59	2.56	1.03	-1.88
42	11.58	10.52	8.95	3.95	2.50	0.13	-2.37
43	7.34	6.75	3.67	1.30	1.42	0.24	-1.42
44	10.74	9.69	10.87	5.50	3.14	0.79	-2.36
45	5.15	5.74	5.97	4.33	3.51	1.17	-1.99
46	5.93	5.06	4.32	1.24	0.49	-0.86	-3.33
47	5.36	5.22	4.95	3.30	2.34	0.27	-2.34
48	4.41	3.60	2.62	1.47	0.65	-0.49	-1.96
49	5.35	4.82	4.71	2.57	1.82	0.54	-1.39
50	4.34	5.69	5.69	4.19	2.99	1.65	-0.15
51	6.45	6.45	6.10	3.87	2.82	0.94	-1.06

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Case No.	A1000	A600	A400	A150	A100	A50	A0
52	1.72	2.21	2.33	2.09	1.72	1.11	-0.49
53	7.02	7.24	7.13	5.68	4.68	3.01	-0.78
54	6.10	6.32	5.42	4.29	3.27	1.81	-0.34
55	10.18	8.29	6.40	1.80	1.35	-0.36	-1.89
56	10.99	9.14	6.90	3.01	1.65	0.29	-1.07
57	8.24	6.83	5.35	1.23	0.53	-0.09	-1.84
58	12.21	11.79	9.40	2.95	3.79	0.70	-3.93
59	8.00	5.54	3.72	0.95	0.00	-1.11	-2.38
60	9.40	7.57	5.75	0.74	0.41	-0.68	-2.03
61	12.24	11.72	11.46	5.47	4.43	1.04	-1.30
62	13.52	12.32	10.27	4.28	2.91	1.20	-0.68
63	14.72	13.48	11.53	6.74	5.32	1.42	-0.71
64	6.11	4.98	3.85	1.13	0.68	-0.45	-1.58
65	4.89	5.08	1.17	1.37	0.78	0.20	-1.56
66	7.89	6.90	5.59	1.81	1.48	-1.48	-2.14
67	13.67	13.23	12.57	7.94	5.73	2.65	-1.32
68	12.73	12.08	10.80	5.48	3.87	1.77	-0.64
69	9.57	10.33	8.81	3.95	3.65	1.52	-1.82
70	12.21	10.61	8.61	3.80	1.60	0.40	-1.80
71	11.82	11.14	9.28	5.06	3.04	1.18	-1.01
72	10.64	9.61	8.31	3.89	2.73	0.52	-1.82
73	16.50	15.34	14.45	7.80	5.11	1.66	-1.92
74	16.30	15.37	13.84	8.07	4.84	1.27	-1.95
75	8.14	9.85	9.69	4.88	3.74	1.46	-1.14
76	12.92	12.32	11.28	6.12	3.96	1.29	-1.72
77	15.47	13.32	10.35	4.20	2.66	0.92	-1.13
78	13.98	11.94	9.89	4.63	2.58	0.89	-1.34
79	11.68	12.03	11.34	6.10	3.66	1.05	-1.40
80	9.69	11.12	9.41	2.57	1.71	-0.86	-2.57
81	10.49	10.92	12.20	5.78	3.64	0.86	-2.35
82	16.63	15.39	12.66	3.97	4.71	1.24	-1.49
83	11.39	8.48	5.80	1.79	0.45	0.00	-2.46
84	14.65	13.82	12.71	5.53	3.87	1.38	-0.28
85	14.26	13.33	11.66	6.11	4.44	1.85	-2.59
86	11.94	12.05	10.96	5.64	4.45	2.06	-0.76
87	14.26	13.69	12.72	5.98	4.63	2.31	-1.54
88	11.86	10.68	11.36	7.80	4.92	1.86	-1.36
89	13.97	12.89	11.32	5.42	3.97	1.81	-0.12
90	13.42	12.35	11.76	6.53	5.94	2.14	-0.59
91	16.73	15.59	14.44	6.97	5.07	2.15	-1.14
92	18.19	15.62	12.50	2.79	2.12	0.00	-1.67
93	12.78	13.10	10.16	6.18	3.46	1.89	-0.94
94	17.44	15.17	11.95	4.78	2.75	0.24	-1.08
95	16.66	14.91	12.57	6.14	4.24	2.19	-1.02
96	25.75	22.39	19.32	8.93	5.56	1.32	-3.22
97	10.42	8.07	7.40	2.52	2.52	1.18	-0.50
98	15.42	13.01	11.57	5.30	4.82	2.41	0.00
99	12.75	11.47	9.94	2.29	3.06	1.53	-0.76
100	17.05	15.17	12.93	6.74	5.06	1.69	-0.19
101	12.96	12.74	11.65	8.57	4.61	1.76	-2.86
102	15.88	14.42	11.49	2.72	1.46	1.46	-0.42

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Case No.	A1000	A600	A400	A150	A100	A50	A0
103	11.75	10.61	9.20	3.82	2.69	0.99	-0.71
104	11.18	10.50	9.39	4.92	3.35	1.34	-0.67
105	13.64	12.90	11.41	6.20	4.46	1.98	-0.37
106	14.29	13.39	11.84	5.41	3.99	1.67	-0.26
107	11.69	11.37	10.71	5.79	4.26	1.97	-0.11
108	9.29	9.43	8.88	5.55	4.16	2.08	-0.14
109	15.89	14.84	12.37	3.90	1.90	-0.57	-1.71
110	16.53	17.11	15.36	6.61	4.38	1.85	-1.46
111	14.28	12.88	9.73	2.98	1.75	0.09	-1.14
112	19.27	16.31	13.26	4.96	3.05	-0.10	-2.19
113	20.27	17.18	14.01	5.15	3.17	0.08	-1.35
114	11.36	11.02	10.34	3.79	2.64	0.47	-1.49
115	14.32	13.54	11.72	5.47	4.17	1.82	-0.78
116	15.23	12.84	10.61	2.91	2.74	0.17	-0.86
117	12.95	11.71	10.64	4.43	3.02	0.53	-1.77
118	16.07	14.71	12.68	4.98	3.62	2.49	-1.13
119	14.67	13.30	10.36	3.72	2.54	1.37	-1.56
120	14.30	13.97	10.02	3.45	1.97	0.33	-3.29
121	11.36	10.36	9.37	4.08	2.76	0.55	-1.54
122	10.80	11.12	10.31	3.71	2.90	1.13	-0.64
123	8.93	8.93	6.83	2.63	1.23	-0.35	-2.63
124	16.61	13.21	10.01	2.20	1.40	-0.80	-2.60
125	14.35	13.17	10.47	4.05	2.87	1.01	-1.01
126	9.48	6.88	7.79	2.60	1.43	0.00	-1.17
127	15.44	15.44	14.43	6.65	4.06	1.01	-2.25
128	18.77	17.24	15.03	6.28	3.65	0.51	-1.19
129	16.44	14.81	12.53	5.21	3.26	0.98	-1.06
130	8.80	6.55	5.60	1.29	0.34	-0.86	-2.41
131	21.45	19.47	16.17	8.54	5.01	2.73	0.00
132	15.23	14.79	12.56	4.54	3.21	0.53	-1.43
133	15.69	14.30	13.25	2.96	3.14	1.22	-0.52
134	14.54	13.68	10.26	2.28	0.86	-0.57	-1.43
135	14.56	12.84	9.85	3.64	1.93	0.43	-3.21
136	17.58	16.13	12.41	3.97	2.48	0.74	-0.74
137	14.08	11.83	11.39	4.69	3.35	1.79	-0.45
138	17.69	16.30	11.33	1.66	2.49	1.66	0.00
139	11.85	11.85	11.29	2.22	3.15	1.48	0.00
140	12.92	11.94	10.96	4.45	3.80	1.52	-0.65
141	13.88	13.69	11.76	4.63	3.47	1.93	-0.77
142	11.66	11.14	9.98	4.66	3.16	0.67	-1.33
143	9.37	8.31	7.59	2.89	2.29	0.48	-0.84
144	8.34	7.72	7.24	2.14	1.43	0.00	-1.31
145	14.19	14.19	13.43	8.24	6.46	3.17	-1.27
146	24.22	22.99	21.43	14.62	10.94	6.92	3.46
147	15.30	12.89	10.16	4.30	2.62	0.52	-0.52
148	19.47	16.60	13.86	4.78	2.87	0.24	-1.55
149	9.36	8.48	7.45	3.07	1.46	0.00	-1.17
150	13.02	13.32	12.58	3.37	2.63	-0.15	-1.76
151	13.78	12.77	11.26	5.21	3.53	1.51	0.17
152	15.42	16.15	14.22	5.30	4.10	2.17	0.00
153	14.53	11.73	11.22	3.06	2.55	1.27	0.25

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Case No.	A1000	A600	A400	A150	A100	A50	A0
154	4.31	3.37	2.62	-0.75	1.12	-2.06	-1.87
155	15.38	13.18	13.40	1.54	1.32	0.66	-1.10
156	16.72	15.26	11.91	3.97	2.30	0.84	-0.84
157	10.33	10.61	10.19	4.67	3.68	1.42	-0.14
158	10.62	11.40	10.95	3.69	3.13	1.56	-0.22
159	11.41	11.16	7.19	3.60	2.85	0.74	-0.74
160	11.95	11.65	9.81	2.91	2.15	1.23	-0.61
161	11.37	11.15	9.29	5.25	1.53	1.09	0.00
162	9.57	9.85	9.29	4.16	3.88	1.80	-0.14

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Case No.	gs1000	gs600	gs400	gs150	gs100	gs50	gs0
1	617.08	843.93	738.95	687.37	589.70	474.22	316.76
2	700.69	4795.48	4795.48	1667.07	887.73	992.28	559.69
3	332.26	274.25	194.39	157.47	137.12	123.56	112.26
4	382.64	326.26	313.67	428.82	245.30	202.11	164.33
5	269.33	394.29	281.16	242.35	186.50	205.43	133.48
6	194.38	354.17	288.83	260.27	213.60	196.03	186.14
7	221.13	279.33	248.64	213.73	209.49	201.03	173.52
8	265.97	244.34	184.53	176.89	147.62	137.44	118.35
9	319.38	303.80	325.62	215.00	210.33	165.15	157.36
10	108.70	114.65	96.79	96.79	69.98	98.27	78.92
11	134.06	193.37	141.17	151.85	156.60	132.87	125.75
12	89.12	123.70	101.09	83.80	83.80	65.18	63.85
13	693.93	1042.52	812.93	606.63	424.25	372.51	390.62
14	278.41	283.63	300.31	329.51	296.14	303.44	235.66
15	41.01	36.45	30.38	28.86	36.45	77.47	62.28
16	195.78	226.16	212.66	219.41	185.65	166.53	157.52
17	222.11	248.11	236.20	214.53	202.61	153.85	140.85
18	67.34	97.64	104.37	72.39	75.75	65.65	53.87
19	427.43	310.62	207.19	218.67	267.42	223.63	194.74
20	312.13	389.62	434.52	372.24	287.51	219.43	183.95
21	135.29	176.65	203.49	197.90	181.13	145.35	43.60
22	91.54	94.95	87.44	94.27	90.85	115.44	131.15
23	172.82	179.58	181.51	182.47	180.54	184.41	251.02
24	111.69	87.31	72.36	62.14	51.91	44.05	38.54
25	97.00	79.76	88.38	91.61	82.99	74.37	61.44
26	157.78	163.22	193.69	178.46	138.20	130.58	117.52
27	108.90	103.65	86.60	81.35	59.04	53.79	52.48
28	108.03	109.17	78.46	54.58	45.49	25.02	53.45
29	112.08	40.54	63.19	39.35	10.73	26.23	11.92
30	150.31	143.12	120.73	90.35	62.36	43.18	62.36
31	547.63	771.12	829.70	954.77	558.72	518.08	439.58
32	525.48	513.23	631.24	588.94	617.88	577.80	493.19
33	378.34	221.90	354.30	290.31	750.17	351.47	303.08
34	237.96	146.78	121.21	72.28	76.73	64.49	52.26
35	270.68	281.27	275.38	227.13	216.54	213.01	187.12
36	244.11	227.78	172.99	130.71	100.91	67.28	49.01
37	562.59	559.23	767.59	520.24	523.60	442.94	366.32
38	409.93	370.33	308.61	287.65	251.55	213.12	158.38
39	373.30	399.44	370.17	369.12	340.89	188.22	164.17
40	105.93	116.44	98.05	88.42	78.79	70.91	55.16
41	102.52	95.68	80.30	64.93	59.80	49.55	46.13
42	260.46	277.56	261.78	238.10	209.16	180.22	152.59
43	93.55	93.55	76.97	67.50	52.10	49.74	42.63
44	174.17	195.12	183.33	142.74	136.19	116.55	86.43
45	71.46	71.46	70.29	70.29	70.29	67.95	59.75
46	102.51	88.92	72.87	60.52	50.64	39.52	32.11
47	66.00	70.12	66.00	61.87	57.75	55.00	45.37
48	60.48	55.58	40.87	39.23	37.60	34.33	31.06
49	54.59	56.73	49.23	48.16	41.74	37.46	33.18
50	40.40	50.87	68.83	74.81	64.34	70.32	61.35
51	96.19	95.02	79.77	69.21	62.17	61.00	46.92

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Case No.	gs1000	gs600	gs400	gs150	gs100	gs50	gs0
52	18.43	19.66	22.11	19.66	20.89	18.43	19.66
53	86.94	104.77	96.97	83.60	80.25	83.60	73.56
54	121.95	97.11	74.52	76.78	80.17	63.23	55.33
55	226.12	277.47	256.75	263.96	269.36	236.03	205.40
56	247.95	269.34	260.59	282.96	275.18	264.48	241.14
57	207.67	202.42	155.10	148.96	108.66	69.22	56.08
58	315.84	186.70	136.16	137.57	88.43	85.63	72.99
59	163.89	122.72	127.47	99.76	92.64	80.76	72.84
60	187.27	208.91	195.38	204.85	196.74	183.21	181.19
61	145.80	140.59	135.38	135.38	135.38	127.57	124.97
62	143.78	147.20	150.62	169.45	164.32	150.62	155.76
63	235.92	243.02	239.47	260.76	248.34	225.28	195.13
64	81.49	74.70	65.65	54.33	47.54	36.22	24.90
65	44.98	50.84	41.06	35.20	23.47	23.47	19.55
66	78.89	83.82	73.95	69.02	59.16	47.66	44.37
67	207.30	199.58	190.76	180.84	166.50	170.91	156.58
68	188.51	199.79	178.84	186.90	186.90	178.84	157.90
69	244.61	224.86	217.26	224.86	218.78	192.95	167.12
70	176.11	172.11	202.13	158.10	170.11	164.10	130.08
71	202.56	205.94	182.31	194.12	205.94	199.19	205.94
72	219.38	250.53	237.55	221.97	199.91	171.35	171.35
73	392.56	404.07	355.48	315.84	315.84	299.22	272.36
74	478.05	637.68	554.47	336.25	320.12	333.70	294.64
75	126.96	123.71	122.08	113.94	113.94	110.69	102.55
76	311.79	306.62	242.03	167.09	75.79	78.38	67.18
77	299.12	238.68	195.66	110.63	80.93	70.68	62.49
78	270.79	253.87	168.35	110.45	98.87	84.62	62.35
79	214.49	217.98	205.78	214.49	209.26	216.24	211.01
80	236.56	233.71	230.86	233.71	230.86	228.01	222.31
81	248.27	250.41	252.55	258.97	258.97	258.97	256.83
82	258.08	215.90	205.97	188.60	171.23	156.34	136.49
83	167.44	178.60	165.20	169.67	162.97	158.51	178.60
84	259.76	251.47	229.36	218.31	198.97	151.99	171.33
85	303.63	288.82	275.86	266.60	246.24	236.98	224.02
86	299.58	340.83	335.40	335.40	348.42	293.07	257.25
87	248.67	242.88	219.75	212.04	192.76	210.11	188.91
88	284.75	267.80	281.36	249.16	261.02	230.51	228.82
89	378.19	351.70	273.41	280.63	250.52	214.39	255.34
90	283.82	387.14	331.32	275.51	230.38	201.88	220.88
91	261.02	338.31	223.00	240.74	202.73	200.20	164.72
92	319.18	366.05	304.67	254.45	238.82	203.11	143.96
93	278.68	290.20	233.63	148.77	148.77	143.53	102.67
94	261.60	274.74	283.10	237.71	186.34	138.56	121.84
95	225.11	222.19	200.26	154.95	146.18	131.56	112.55
96	699.46	804.82	769.70	580.94	608.74	440.46	408.26
97	110.94	144.55	127.74	132.79	107.57	84.04	79.00
98	185.56	173.51	171.10	147.01	113.27	110.86	122.91
99	145.32	150.42	152.97	150.42	145.32	140.22	114.73
100	226.67	256.65	224.80	251.03	236.04	211.69	202.32
101	182.37	188.96	202.14	175.78	160.40	153.81	125.24
102	246.61	242.43	246.61	254.97	223.62	211.09	211.09

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Case No.	gs1000	gs600	gs400	gs150	gs100	gs50	gs0
103	174.07	172.65	157.09	168.41	168.41	162.75	148.59
104	162.04	157.57	154.22	144.16	135.22	148.63	153.10
105	171.11	164.91	166.15	145.07	123.99	115.31	102.91
106	206.00	212.43	182.82	136.47	103.00	109.44	86.26
107	174.87	179.25	172.69	168.32	156.29	134.44	134.44
108	109.56	112.33	98.46	101.24	92.92	127.59	92.92
109	192.18	166.50	150.32	125.59	136.05	133.20	168.40
110	165.30	200.31	163.36	160.44	159.47	168.22	224.61
111	229.58	165.61	184.89	178.76	160.36	183.14	242.72
112	352.99	395.92	354.90	409.28	358.71	260.45	350.13
113	285.03	209.02	200.31	238.32	201.11	202.69	250.19
114	204.85	183.89	164.96	175.10	162.93	186.59	240.68
115	158.82	153.61	156.21	164.02	151.01	135.38	140.59
116	152.33	148.91	166.03	147.20	147.20	135.22	160.89
117	172.07	152.55	134.81	136.59	133.04	143.68	189.80
118	574.96	527.42	486.68	228.63	205.99	201.46	217.31
119	195.55	209.23	195.55	207.28	185.77	189.68	201.41
120	239.94	262.95	235.01	279.38	230.08	207.07	218.58
121	92.62	102.55	109.16	109.16	99.24	84.90	109.16
122	153.07	141.79	127.29	120.84	116.01	104.73	116.01
123	126.05	119.04	134.80	141.80	124.30	131.30	133.05
124	478.30	468.29	494.31	484.30	458.28	490.30	638.40
125	214.38	204.25	202.56	207.63	217.75	200.87	178.93
126	124.62	119.42	127.21	116.83	123.32	124.62	128.51
127	151.05	156.68	151.05	157.81	147.67	161.19	182.61
128	193.60	168.12	157.09	151.14	144.35	153.69	184.26
129	190.45	192.89	190.45	183.12	174.98	183.94	221.37
130	96.54	82.69	84.41	68.04	68.90	64.60	56.85
131	415.25	392.80	387.10	383.69	445.17	382.55	325.62
132	324.24	348.29	432.02	421.33	381.24	342.94	299.29
133	455.15	418.53	380.16	362.72	360.98	340.05	387.14
134	1271.16	2106.25	324.92	253.66	219.46	196.66	190.96
135	156.89	158.38	162.66	166.94	162.66	158.38	267.53
136	192.89	198.53	203.49	205.97	191.08	193.56	193.56
137	245.87	234.41	265.67	250.04	265.67	221.02	212.09
138	196.35	190.68	193.44	193.44	187.91	171.33	176.86
139	137.00	157.37	161.07	170.33	164.78	164.78	175.88
140	226.86	207.32	210.57	189.95	184.52	183.44	195.38
141	181.20	165.78	165.78	173.49	159.99	154.21	163.85
142	54.65	41.58	68.19	113.09	103.11	157.99	384.17
143	92.14	89.13	90.33	90.33	89.13	78.29	81.90
144	153.72	149.63	156.75	176.94	160.32	163.88	171.01
145	77.29	69.69	67.15	70.96	124.17	79.83	88.70
146	119.41	84.82	77.00	83.70	68.08	69.19	87.05
147	104.77	96.38	97.43	112.10	99.53	94.29	107.91
148	248.46	224.57	213.82	224.57	220.98	199.48	212.62
149	97.94	93.55	86.24	73.09	62.86	54.08	49.70
150	200.47	206.33	203.40	181.45	181.45	172.67	178.52
151	168.08	154.64	146.23	156.32	149.59	144.55	178.17
152	274.73	267.50	267.50	306.06	265.09	253.04	216.89
153	323.78	290.64	277.89	316.13	293.19	275.34	323.78

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Case No.	gs1000	gs600	gs400	gs150	gs100	gs50	gs0
154	312.85	299.73	249.15	241.66	41.21	18.73	13.11
155	169.19	173.58	184.57	197.75	195.55	193.36	204.34
156	209.00	211.09	229.89	236.16	190.19	219.44	238.25
157	174.07	171.24	172.65	182.56	182.56	174.07	186.80
158	166.51	151.99	143.05	147.52	145.28	143.05	155.34
159	99.19	96.71	86.79	81.83	81.83	80.59	96.71
160	133.33	142.52	142.52	154.78	144.05	137.92	156.31
161	136.62	133.34	128.97	128.97	139.90	122.41	137.71
162	167.80	156.71	148.39	149.78	141.45	148.39	183.06

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Case No.	E1000	E600	E400	E150	E100	E50	E0
1	2.53	2.26	2.27	2.11	2.04	1.99	1.94
2	2.71	2.71	2.68	2.37	2.25	2.27	2.19
3	2.92	2.64	2.37	2.10	2.06	1.87	1.73
4	2.62	2.66	2.64	2.79	2.36	2.07	1.94
5	1.96	2.03	2.08	1.77	1.85	1.66	1.45
6	2.08	2.26	2.49	2.26	2.19	2.15	1.93
7	2.87	2.63	2.66	2.48	2.30	2.19	2.06
8	3.04	2.81	2.67	2.35	2.00	1.85	1.88
9	3.44	3.18	2.77	2.73	2.46	2.15	1.74
10	2.92	2.46	2.05	1.82	1.30	1.74	1.47
11	2.36	2.86	2.17	2.19	2.14	1.79	1.74
12	2.17	2.42	1.96	1.53	1.57	1.17	1.14
13	2.54	2.52	2.39	2.19	2.00	1.97	1.78
14	2.79	2.34	2.16	2.11	1.88	1.85	1.60
15	0.97	0.77	0.62	0.55	0.68	1.38	1.20
16	2.90	3.20	2.84	2.77	2.41	2.28	2.19
17	3.37	3.23	2.99	2.71	2.58	2.10	1.98
18	1.90	2.22	2.19	1.48	1.50	1.30	1.06
19	6.03	4.56	4.08	3.54	3.21	2.91	2.79
20	3.18	3.34	3.25	3.01	2.68	2.38	2.51
21	2.94	2.91	2.87	2.65	2.46	1.93	1.05
22	1.99	2.04	2.06	2.08	2.12	2.13	2.17
23	3.36	3.37	3.36	3.34	3.37	3.38	3.55
24	1.99	1.80	1.50	1.36	1.17	1.01	0.90
25	1.95	1.80	1.64	1.54	1.40	1.42	1.27
26	2.47	2.44	2.70	2.50	2.00	1.92	2.10
27	2.15	2.10	1.80	1.75	1.31	1.23	1.27
28	2.02	1.94	1.57	1.14	0.91	0.50	1.16
29	2.21	0.86	1.29	0.85	0.24	0.56	0.29
30	2.55	2.20	2.03	1.54	1.28	0.82	1.28
31	5.19	5.79	6.12	6.06	5.23	5.15	5.06
32	5.87	5.77	5.84	5.99	6.03	5.98	5.84
33	8.20	8.76	9.30	10.11	10.66	10.82	5.25
34	3.91	2.82	2.71	1.77	1.46	1.57	1.22
35	3.72	3.74	3.64	3.68	3.67	3.46	3.02
36	3.52	3.20	3.01	2.57	2.12	1.62	1.15
37	3.75	4.34	3.96	3.99	3.89	3.47	3.46
38	5.31	4.67	4.16	3.85	3.61	3.24	2.84
39	4.00	3.57	3.11	2.85	2.48	2.50	2.69
40	2.17	1.99	1.67	1.48	1.33	1.20	0.95
41	3.04	2.72	1.88	1.47	1.30	1.09	1.08
42	4.63	4.58	4.30	3.88	3.62	3.21	2.97
43	2.11	1.85	1.59	1.46	1.20	1.10	0.97
44	3.00	3.06	2.75	2.59	2.27	2.04	1.82
45	1.49	1.51	1.44	1.41	1.43	1.36	1.35
46	2.04	1.82	1.53	1.28	1.09	0.91	0.80
47	1.53	1.54	1.39	1.37	1.26	1.20	1.21
48	1.54	1.31	1.00	0.90	0.85	0.82	0.78
49	1.36	1.32	1.16	1.11	0.98	0.90	0.86
50	0.97	1.18	1.48	1.65	1.35	1.51	1.30
51	2.30	1.95	1.62	1.37	1.16	1.10	1.01

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Case No.	E1000	E600	E400	E150	E100	E50	E0
52	0.49	0.49	0.52	0.45	0.47	0.41	0.48
53	1.71	1.72	1.46	1.35	1.23	1.21	1.18
54	2.13	1.64	1.25	1.31	1.33	1.14	1.13
55	2.28	3.11	2.94	2.81	2.71	2.61	2.89
56	3.00	2.79	2.63	2.45	2.47	2.31	2.32
57	2.58	1.49	1.41	1.48	1.49	1.45	1.29
58	3.32	3.14	2.75	2.41	1.36	1.39	1.28
59	2.84	3.19	2.72	1.81	1.39	1.27	1.22
60	1.47	2.86	2.17	1.66	1.44	1.32	1.07
61	2.91	2.63	2.58	2.49	2.84	2.84	2.60
62	3.19	3.28	3.08	3.51	3.53	3.48	3.14
63	3.40	3.17	3.19	3.49	3.53	3.55	3.19
64	4.57	4.76	4.62	4.47	3.87	3.75	2.95
65	2.97	3.10	2.95	3.06	2.90	2.77	3.46
66	4.64	4.20	3.87	3.81	3.40	3.15	3.54
67	2.40	2.33	2.27	2.08	2.33	2.27	2.11
68	2.72	2.43	2.47	2.30	2.18	2.14	2.34
69	3.31	3.11	2.81	2.63	2.42	2.46	2.69
70	3.14	2.80	3.12	2.62	2.68	2.62	2.30
71	3.14	3.26	2.62	2.48	2.73	2.77	3.04
72	2.66	2.67	2.49	2.51	2.26	2.27	2.47
73	3.32	3.11	2.94	2.81	2.71	2.61	2.89
74	2.84	2.79	2.63	2.45	2.47	2.31	2.32
75	1.47	1.49	1.41	1.48	1.49	1.45	1.29
76	3.26	3.14	2.75	2.41	1.36	1.39	1.28
77	3.90	3.19	2.72	1.81	1.39	1.27	1.22
78	2.98	2.86	2.17	1.66	1.44	1.32	1.07
79	2.91	2.63	2.58	2.49	2.84	2.84	2.60
80	3.19	3.28	3.08	3.51	3.53	3.48	3.14
81	3.40	3.17	3.19	3.49	3.53	3.55	3.19
82	4.57	4.76	4.62	4.47	3.87	3.75	2.95
83	2.97	3.10	2.95	3.06	2.90	2.77	3.46
84	4.64	4.20	3.87	3.81	3.40	3.15	3.54
85	3.39	3.13	2.96	2.85	2.89	2.81	2.78
86	2.62	2.62	2.49	2.39	2.36	2.25	2.40
87	3.03	2.76	2.64	2.51	2.58	2.43	2.51
88	3.12	3.14	2.95	2.95	2.78	2.78	2.86
89	2.83	2.72	2.25	2.48	2.48	2.02	2.49
90	3.29	3.80	3.21	3.03	2.84	2.60	3.14
91	3.95	4.21	2.79	2.96	2.50	2.42	2.50
92	4.17	4.07	3.63	3.07	2.86	2.70	2.34
93	4.36	3.03	2.77	1.95	2.02	1.98	1.52
94	3.67	3.81	3.85	3.34	2.65	2.28	2.02
95	3.32	3.16	2.88	2.78	2.28	2.40	2.10
96	5.90	5.65	5.15	5.17	4.87	4.99	5.02
97	2.54	2.62	2.34	2.32	1.90	1.66	1.65
98	3.52	3.61	3.35	3.04	2.41	2.22	2.55
99	3.01	2.96	2.88	2.75	2.78	2.65	2.45
100	3.93	4.12	3.73	3.97	3.80	3.47	3.60
101	2.83	2.79	2.70	3.03	3.08	3.01	2.39
102	3.76	4.31	4.35	3.93	3.99	3.45	3.32

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Case No.	E1000	E600	E400	E150	E100	E50	E0
103	2.77	3.00	2.89	3.00	3.06	2.97	2.56
104	2.28	2.27	2.21	2.06	2.22	2.47	2.30
105	2.63	2.57	2.43	2.26	2.21	2.15	1.86
106	3.03	2.91	2.63	2.46	2.12	1.87	1.45
107	2.34	2.28	2.16	2.13	2.05	2.14	2.21
108	2.07	1.86	1.54	1.44	1.29	1.48	1.32
109	2.71	2.77	2.79	2.81	2.87	2.86	2.89
110	2.99	3.01	3.00	2.99	3.03	3.09	3.15
111	3.01	3.00	3.07	3.08	3.09	3.12	3.21
112	4.25	4.43	4.33	4.38	4.37	3.96	3.95
113	3.16	3.08	3.14	3.20	3.14	3.15	3.13
114	2.77	2.74	2.68	2.68	2.68	2.78	2.79
115	3.02	3.54	3.80	3.54	3.51	3.54	2.81
116	3.22	3.35	3.41	3.49	3.54	3.58	3.58
117	3.73	3.67	3.67	3.73	3.74	3.80	3.81
118	8.42	8.19	8.13	5.12	4.98	4.82	4.30
119	4.03	4.40	4.36	4.30	4.36	4.36	3.91
120	3.62	3.40	3.34	3.01	3.04	3.39	3.34
121	2.43	2.50	2.60	2.62	2.46	2.19	2.27
122	3.29	3.32	3.30	3.25	3.25	3.22	3.24
123	2.50	2.82	3.13	3.08	3.20	3.26	2.63
124	7.28	7.32	7.46	7.48	7.50	7.56	7.46
125	3.51	3.92	3.87	3.63	3.27	2.92	3.38
126	2.41	2.09	2.05	2.31	2.53	2.52	2.27
127	2.87	2.95	2.95	2.98	2.98	3.02	3.02
128	2.74	2.75	2.71	2.66	2.67	2.69	2.72
129	2.88	2.87	2.90	2.81	2.78	2.91	2.95
130	1.58	1.56	1.55	1.53	1.35	1.40	1.28
131	4.25	4.19	4.02	3.40	3.35	3.24	3.14
132	3.08	3.11	3.00	3.06	2.84	2.69	2.90
133	6.38	6.24	6.17	6.17	6.10	6.14	6.03
134	12.34	12.57	6.10	4.96	4.59	3.99	3.71
135	3.54	3.34	3.40	3.53	3.55	3.57	5.76
136	3.23	3.55	3.37	3.35	3.55	3.92	4.09
137	4.15	4.20	4.00	3.84	3.82	3.66	3.80
138	3.89	3.79	3.84	3.62	3.48	3.40	3.56
139	2.55	2.83	2.91	3.04	3.05	3.13	3.05
140	2.83	2.89	2.84	2.76	2.76	2.75	2.49
141	3.12	3.18	3.24	3.08	3.14	3.18	3.10
142	0.55	0.63	1.05	1.25	1.26	1.85	4.71
143	1.81	1.65	1.61	1.90	1.72	1.66	1.72
144	2.79	2.81	2.86	2.99	2.86	2.97	2.86
145	1.63	1.66	1.67	1.71	1.75	1.74	1.76
146	1.79	1.76	1.76	1.67	1.65	1.67	1.74
147	1.79	1.86	1.92	1.91	1.91	1.86	1.82
148	3.62	3.70	3.69	3.75	3.82	3.92	3.85
149	2.43	2.44	2.46	2.02	1.80	1.59	1.43
150	3.82	4.01	4.10	4.10	4.08	3.95	3.72
151	2.94	2.94	2.94	2.91	2.94	2.96	2.94
152	4.75	4.92	5.01	5.25	5.28	5.23	5.23
153	6.14	6.20	6.27	6.35	6.37	6.37	6.35

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Case No.	E1000	E600	E400	E150	E100	E50	E0
154	4.80	4.85	4.87	4.87	1.20	0.54	0.34
155	3.69	3.96	4.31	4.28	4.24	4.39	4.11
156	4.22	4.37	4.66	4.60	4.41	5.04	4.99
157	3.48	3.58	3.76	3.76	3.76	3.76	3.71
158	3.18	2.79	2.86	2.97	3.03	3.13	3.12
159	1.96	1.98	2.00	2.01	2.01	2.02	2.03
160	2.68	2.82	2.82	2.82	2.84	2.82	2.87
161	2.23	2.24	2.24	2.26	2.26	2.25	2.26
162	2.77	2.82	2.83	2.90	2.94	3.00	3.00

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