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INFLUENCE OF SOIL TEMPERATURE ON ECOPHYSIOLOGICAL TRAITS OF FOUR BOREAL TREE SPECIES

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ABSTRACT

Cheng, Song 1999. Influence of soil temperature on ecophysiological traits of four boreal tree species. 72 p. Supervisor: Dr. Dang, Qing-Lai.

Keywords: Soil temperature, photosynthesis, stomatal conductance, mesophyll conductance, transpiration, specific leaf area, xylem water potential, water use efficiency.

A new soil temperature control system was developed for greenhouse experiments. The system controlled soil temperature by circulating temperature-controlled water around seedling containers. The system was tested for 5, 20 and 30 °C soil temperatures. Tests showed that the system was very efficient in controlling soil temperature in the greenhouse. The coefficient of determination between water and soil temperatures was 0.99. Average soil temperatures of all 112 pots (13.5 cm deep, 11 cm top diameter) in each system were within ± 0.4 °C of the set values. The maximum vertical variation in soil temperature was less than 1 °C.

To investigate soil temperature effects on ecophysiological traits, a total 1568 (392 per species) of one-year old aspen, white spruce, black spruce and jack pine seedlings were grown at 5, 10, 15, 20, 25, 30 and 35 °C soil temperatures in two greenhouses. At the beginning of the third month, net photosynthesis, stomatal conductance, mesophyll conductance, transpiration, midday xylem water potential, water use efficiency and specific leaf area were measured. Soil temperature significantly affected all the traits in the four species. All the traits had a strong non-linear relationship with soil temperature modeled using a polynomial function. The derived model showed that the traits were the most sensitive to changes in soil temperature at 6.2, 8.9, 12.7 and 12.3 °C, and performed the best at 19.6, 21.8, 22.4 and 26.1 °C, respectively, for aspen, white spruce, black spruce and jack pine. All the aspen seedlings, about 40 % of jack pine, 20 % white and black spruce seedlings survived in the 35 °C treatment. In general, aspen was the most sensitive to low soil temperatures while black spruce was the most sensitive to high soil temperatures. Stepwise regression analysis showed that net photosynthesis of aspen was significantly correlated to mesophyll conductance, stomatal conductance and water use efficiency. In white spruce photosynthesis was significantly correlated to mesophyll conductance, stomatal conductance, transpiration and midday xylem water potential. For black spruce photosynthesis was significantly correlated to mesophyll conductance, stomatal conductance, transpiration and water use efficiency. In jack pine net photosynthesis was significantly correlated to mesophyll conductance, stomatal conductance and transpiration. Net photosynthesis had a strongly linear relationship with mesophyll conductance when data from all the species were combined.

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I was born in Chongqing city of China, which is located in a mountainous area and along the magnificent Yangtz River with few forests. In the summer, the temperature there is as high as 40 °C, due to the degraded ecological environrment. The city is one of the three places called "fire furnaces" in China.

My best years of childhood were spent there. My father was a journalist and poet. He often told me fairy stories about forests, where Snow White and the Seven Dwarfs live. At that time, a mysterious and beautiful forest was deeply impressed in my mind.

With the naive thirst and illusion of my childhood, I have chosen forestry as my profession and have devoted myself to forest-environment research.

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CHAPTER ONE: INTRODUCTION AND LITERATURE REVIEW

The boreal forest, as one of the largest terrestrial ecosystems in the world, occupies 11% of the earth's surface or about approximately 14.7 million km^2 (Bonan and Shugart 1989). The Canadian Forest Resource Data System (1991) reports that the boreal forest in Canada accounts for 74 % of the forested land, consisting of about 136.9 million hectares of softwood and 5,647 million m^3 or 80.5 million hectares of hardwood.

Wegley (1999) reported that the 20th century is the warmest of the millennium. The average surface temperature of the Earth has increased by 0.62 °C between 1901 to 1997, and the average surface temperature is now 14.0 °C annually (Wegley 1999). The CO_2 concentration in the atmosphere will likely double by 2070 at the present rate of CO_2 accumulation (Wegley 1999). Consequently the surface temperature could continue to increase in the future. Global warming has significant impacts on the ecophysiological processes of boreal ecosystems (Hall *et al.* 1993). The responses of the boreal forest to climate change will be of significance to the future climate conditions of the world, because boreal forests affect the fixation of atmospheric CO_2 and the production of O_2 (Ciais *et al.* 1995; Keeling *et al.* 1996), the exchange of water vapour between forests and the atmosphere (Dang *et al.* 1997), and the amount of carbon stored in the biosphere (Schlesinger 1991).

Soil temperature is one of the most important factors influencing the boreal forest ecosystem (Bonan and Shugart 1989). In natural stands, soil temperature depends on the energy balance and affects ecophysiological processes directly and indirectly. There are complicated relationships between ecophysiological traits and soil temperature. Understanding the effects of soil temperature on ecophysiological traits in different tree species may be critical for understanding the responses of boreal tree species to a changing environment. The information on tree soil temperature interactions may be also useful for formulating more effectively silvicultural treatments, such as site preparation, the natural regeneration of forests and plantation establishment.

Soil temperature and tree physiological processes

Soil temperatures directly influence ecophysiological processes (Lopushinsky and Kaufmann 1984). Tree species that are evolutionarily adapted to warm habitats are especially susceptible to low soil temperatures. Vesque (1878) (cited in Trottier 1989) and Clements and Martin (1934) (cited in Trottier 1989) found that water absorption by roots increased rapidly with increasing temperature from 10 to 15 °C. Low soil temperatures reduce water uptake and transpiration by plants (DeLucia 1987). Kramer (1940) reported that the rate of water movement through sunflower roots (*Helianthus* SPP.) at 0 and 40 °C was about 20 % and 160 % of the rate at 25 °C soil temperature, respectively. Similarly Evans (1975) found that the rate of water movement though the root system of Engelmann spruce (*Picea engelmann* Parry ex Engelm) at 7.5 °C was three times greater than at 0 °C soil temperature. Kramer (1940) attributed the decreased absorption of water by plants at low soil temperatures to the following factors:

1. a decrease in the rate of water movement from soil to the absorption surface of roots;
2. a retardation in the elongation of roots;

3. a decrease in cell permeability because the viscosity of protoplasm and the colloidal gels in the cell walls is much higher at low temperatures;
4. an increase in the viscosity of water, and
5. a reduction in physiological activity of the root cells.

However, the increased viscosity of water and decreased permeability of root cell membranes are primarily responsible for the low water absorption at low soil temperature (Kramer 1940). Root resistance of Monterey pine seedlings started to increase when soil temperatures decreased to between 12 and 13 °C (Kaufmann 1977). The root resistance of Engelmann spruce, on the other hand, did not increase until soil temperature decreased to 5 °C (Kaufmann 1975). At 0 °C soil temperature, root resistance in lodgepole pine seedlings (*Pinus contorta* Douglex Loud) was 93 % of the total plant resistance, while at 7 °C soil temperature, the root resistance was 33% of the total resistance (Running and Reid 1980). The root resistance of Pacific silver fir, in contrast, was unaffected by soil temperatures above 2 °C. The increased viscosity of the soil solution and root resistance can result in significant decreases in plant physiological activity (Elfring *et al.* 1972, Evans 1975, Lawrence and Oechel 1983).

Although low soil temperatures reduce transpiration, the response varies with plant species. Clements and Martin (1934) reported that the transpiration of some plants varied little at soil temperatures between 13 and 38 °C, but declined rapidly when soil temperature drops below 13 °C, particularly near 0·°C. The transpiration of Monterey pine (*Pinus radiata* Don) at 10 °C was only 27 % of the rate at 26.7 °C (Babalola *et al.* 1968). Sach (1875) (cited in Trottier 1989) and Kramer (1940) discovered that transpiration in some plants was low in cold, moist soils, that the plants wilted at 3-5 °C soil temperature, with that recovery of the transpiration recovered at 12–18 °C soil temperature. Transpiration for Douglas-fir (*Pseudotsuga menziesii* (Mirb) Frano) (Lopushinsky and Kaufmann 1984), Scotch pine and Norway spruce seedlings (Landis *et al.* 1993) increased with increasing soil temperature and they had different optimum soil temperatures, 34 °C for Douglas-fir and 22 °C for Scotch pine and Norway spruce. Kaufmann (1977) suggested that transpiration was reduced by low soil temperatures only when leaf water potential became low enough to close stomata. Clements and Martin (1934) observed that the stomata of *Helianthus annuus* did not close at soil temperatures about 4 °C, but almost completely closed at 3 °C. Meinzer *et al.* (1997) reported that low soil temperatures reduced the total transpiration of the plant by reducing the leaf area.

Low soil temperatures can also cause water stress in leaves and stomatal closure. Several species have been found to have lower tissue water potentials at lower soil temperatures. The water potential of scotch pine (*Pinus sylvestris* L.) and spruce (*Pices abies* Karst.) at 5 °C soil temperature was only 35% of that at 16 °C (Vapaavuori *et al.* 1992). The midday xylem pressure potential of Engelmann spruce growing in natural stands was as low as -20.4 bars at 0 to 5 °C soil temperatures as a result of deceased water uptake even though soil moisture was adequate (Kaufmann 1975). Stomatal conductance of Douglas-fir seedlings grown at 1.3 °C was 50% or less of that at soil temperature between 20 and 25 °C (Lopushinsky and Kaufmann 1984). Both Landhaausser *et al.* (1996) and Harper and Camm (1993) reported that stomatal conductance of black spruce increased linearly with soil temperature. Whereas, that of white spruce increased nonlinearly with soil warming from 3 and 15 °C and from 3 and 11 °C, respectively. The stimulate conductance of *Populus* species also decreased with decreasing soil temperature (Meinzer *et al.* 1997).

Soil temperatures affect the ecophysiological processes of leaves and their response to changes in environmental conditions. Soil temperatures are also likely to influence the response of leaf ecophysiological processes of boreal trees to changes in solar radiation (Chaisompongpan *et al.* 1990). For example, soil temperatures have shown to affect photosynthesis of *Populus tremuloides* and *Populus balsamifera* L. (Lawrence and Oechel 1983). Net photosynthesis of some trees is more sensitive to soil temperature than to air temperature, particularly in autumn and spring (Schwarz *et al.* 1997). DeLucia *et al.* (1987) observed that net photosynthesis of Engelmann spruce decreased with decreasing soil temperature from 12 to 0 °C. Landhaausser *et al.* (1996) reported that the net photosynthesis of black spruce and balsam poplar decreased with soil cooling from 11 to 3 °C. The net photosynthesis of black spruce peaked at 10 °C, while that of balsam poplar peaked at 15 °C. Lawrence and Oechel (1983) found that net photosynthesis of aspen decreased with soil cooling between 30 and 5 °C, with the maximum rate occurring at 25 °C. The decreased rate of photosynthesis at low soil temperatures resulted in decreases in the growth rates of *Pinus sylvestris*, *Picea abies* (Vapaavuori *et al.* 1992), and red spruce (Schwarz *et al.* 1997). Soil temperature also influenced leaf physiological processes through its effect on nutrient uptake. For example, lower soil temperatures reduced the nitrogen concentration of spruce needles (Vapaavuori *et al.* 1992, Chapin 1983).

Soil temperature and growth

Growth and development of roots are a function of temperature-dependent processes and the number of long roots and root system distribution are strongly dependent on soil temperature (Camm and Harper 1991). Low soil temperatures inhibit physiological activities and the development of root systems in boreal trees (Bonan and Shugart 1989). The seasonality of root growth in boreal trees is primarily determined by soil temperature , with low soil temperatures often limiting root system expansion and rooting depth of boreal species, such as trembling aspen, black spruce, white birch (*Betula papyrifera* var) and balsam poplar (*Populus basamifera*) (Tryon and Chapin III 1983). Barney (1951) has examined the root growth of Loblolly pine at soil temperatures from 5 to 35 °C and found that root growth increased with increasing soil temperature up to 25 °C and then decreased with further increases in soil temperature. Cooper (1973) found that the optimum soil temperature for the root growth of tomato plants was also 25 °C. Heninger and White (1974) found that the greatest root growth for white spruce (*Picea glauca* (Moench) Voss.) occurred at 19 °C soil temperature. Kaufmann (1977) reported that root extension was the greatest at 15 °C temperature for 2-year-old Monterey pine (*Pinus radiata* D. Don) and lower temperatures significantly reduced root growth. In addition, Nambiar *et al.* (1979) reported that soil temperature markedly affected the initiation of new root lateral primordia as well as the elongation, branching, diameter, weight and morphology of the root system in Monterey pine.

Grossnickle (1987) found that root growth of black and white spruces was slower at 10 °C soil temperature than at 20 °C. Poor performance in root growth of *Pinus contorta* was also attributed to inadequate soil temperature (Running and Reid 1980).

Soil temperature affects the characteristics of root systems. The number of root hairs decreased as soil temperature decreased (Cooper 1973). The colour of roots was white in cold soils, but brown in warmer soils. Low soil temperatures delayed root maturation (Bonan and Shugart 1989). The root angle relative to the horizontal plane was also sensitive to soil temperature. The two opposing geotropic processes that determine root angle responded differently to changes in soil temperature and their balance depended on the mean temperature at the root apex (Sheppard and Miller 1977). The root angle of some plants was typically 10 to 30° below the horizontal surface at 10 °C soil temperature but increased to 40 to 50 ° below the horizontal when soil temperature increases from 14 to 20 °C (Sheppard and Miller 1977). This indicates that cooler soil temperatures tended to cause more horizontal growth (Sheppard and Miller 1977). Roots can also sense soil temperature gradients and grow toward the region of more favourable temperature.

Soil temperature also influences the growth of other plant parts. Brand (1990) documented that height, basal area, and total biomass increased markedly with increasing soil temperatures in both white spruce and white pine (*Pinus strobus* L.). Vapaavuori *et al.* (1992) found that shoot weight growth of *Picea abies* increased with increasing soil temperature. Balisky and Burton (1997) and Fleming *et al.* (1998)

reported that root biomass, root-to-shoot ratio and root collar diameter increased with soil warming in both Engelmann spruce and lodgepole pine.

Soil temperature and mycorrhizae

The benefits of mycorrhizal infection to the growth and development of the host plant have been demonstrated for a wide array of plants. Mycorrhiza can increase nitrogen absorption by plants and promote plant growth (Barber 1984). The formation of mycorrhiza involves complex metabolic interactions between the fungus and the host plant. Soil temperature can influence the growth of fungal mycelium, or spore production, composition of root exudates, the growth and maturation of root tissue, and the degree of infection (Nambiar 1983). Soil temperature effects on mycorrhiza and the interaction between soil temperature and mycorrhiza were shown to affect the carbohydrate content of roots, the dry weight of shoots and roots as well as that of the whole plant (Ritag and Chaney 1987). The dry mass of leaves, stems, shoots, roots and the total dry mass of inoculated *Fraxinus pennsylvanica* seedlings increased much more with soil warming than that of the noninoculated seedlings (Ritag and Chaney 1987).

Soil temperature and nutrients

Soil temperature affected nutrient cycling in the forest (Jenkinson *et al.* 1991; Raich and Schlesinger 1992). The rate of nutrient cycling tended to increase with increasing soil temperature (MacDonald *et al.* 1992). Nitrogen enters the ecosystem as ammonium, nitrate and dissolved organic nitrogen in precipitation. Plant root systems and forest canopies both absorb N in soluble form as ammonia, but boreal tree canopies are lack of this capacity (D. Morris, personal communication). Annual N input from precipitation ranges from 1 to 5 kg ha^{-1} $year^{-1}$ in unpolluted regions, and from 10 to 40 kg ha^{-1} $year^{-1}$ in polluted areas where nitric acid rain occurs. Symbiotic N-fixing plants may add 100 kg N ha^{-1} $year^{-1}$ or more to an ecosystem. The total N content of most terrestrial ecosystems fell within the range of 1,500 to 15,000 kg ha^{-1} (Post *et al.* 1986). Over 98% of this nitrogen is stored in organic detritus and soil humus and becomes available to plants through microbial mineralization. Approximately 2-5% of soil organic nitrogen is released in inorganic forms as byproducts of microbial activity. The annual uptake of nitrogen in forest ecosystems falls within the range of 20-200 kg ha^{-1} $year^{-1}$. Soil temperature affects nitrogen cycling directly through its affect on root metabolism and indirectly by influencing soil microbes and mycorrhiza. Nitrogen absorption by plants increased with increasing soil temperature (Binkley and Richter 1986).

Phosphorus inputs from the atmosphere are usually small, commonly in the range of 0.1 to 0.5 kg ha^{-1} annually. Inputs from weathering vary greatly among ecosystems. Annual plant uptake is commonly 2 to 15 kg ha^{-1}. The amount of organic phosphate exceeds inorganic phosphate in most soils, and the turnover of organic P pools provides a large portion of phosphorus taken up by plants. The release of phosphate is often the direct result of the activity of enzymes produced by microbes and higher plants. Within a certain range, enzymative activity and thus phosphate release increased with increasing soil temperature (McGill and Cole 1981).

Sulfur inputs from the atmosphere in the form of sulfate (SO_4^{-2}) range from 1 to 10 kg ha^{-1} annually. In polluted regions, it can reach over 50 kg ha^{-1} $year^{-1}$. Sulfur is also released into soils by weathering of various minerals. SO_4^{-2} was the dominant form of S used by plants (Mengel and Kirkby 1983). Low soil temperatures reduced the rate of organic matter decomposition and restrict nutrient cycling (Bonan and Shugart 1989).

Boreal forest types with different soil temperatures are extremely different in the chemical composition of the forest floor. The differences reflected the rates of organic matter mineralization and tree growth (Flanagan and Van Cleve 1983). For example, cool. wet black spruce forests had the lowest N concentration while white spruce sites had increasingly higher N concentration with increasing soil temperature (Flanagan and Van Cleve. 1983). In general, increased forest floor temperature will raise the concentrations of extractable P and exchangeable NH_4^+ and NO_3^- in the forest humus. The concentrations of N, P and K in needles of black spruce seedlings increased from 0.76 to 1.05%, 0.099 to 0.136% and 0.56 to 0.80%, respectively, with an increase in soil temperature from 0 to 25 °C (Van Cleve *et al.* 1990).

Soil temperature and carbon storage in forest floor

Because of its vast distribution, the boreal forest is regarded as a major carbon sink along with tropical rainforests. In tropical rainforests, most carbon was stored in aboveground biomass, with forest floor detritus and soil carbon actively recycled due to the rapid decomposition of organic matter. In boreal ecosystems, in contrast, a much greater proportion of carbon is stored in the forest floor and soil profile, because of the slow decomposition of organic matter. Boreal forest ecosystems cumulatively represent one of the largest storage of soil carbon in the world (Peterson and Peterson 1992). The carbon storage in boreal forests had been estimated to be 179 Gt (Schlesinger 1991) to 286 Gt (Zinke *et al.* 1984). This pool represents 16 and 22%, respectively, of the estimated global soil carbon storage. This large carbon pool can have a great potential influence on the boreal ecosystem and the atmosphere (Schlesinger and Mitchell 1987). Soil temperature was an important determinant of soil carbon release (Peterson and Peterson 1992). The net carbon exchange between a terrestrial ecosystem and the atmosphere represents the balance between net carbon simulation by vegetation and carbon loss by the respiration of microorganisms and other heterotrophic organisms within the ecosystem. The respiratory carbon loss increased exponentially with increasing soil temperature (Schlesinger and Mitchell 1987). For example, in a black spruce forest, soil warming from 0 to 25 °C increased decomposition by 45% and carbon assimilation by trees by 65 % (Bonan and Van Cleve 1992).

Soil temperature and forest litter

In moist, shaded boreal forests, mosses replaced lichen as the dominant ground cover (Tamm 1950). A thick moss ground cover composed primarily of feathermosses (*Hyocomium splendens*, *Pleurozium schreberi*) or *Sphagnum* was common throughout the boreal forests of North America (Larson 1980). The depth of the moss layer averaged 20-30 cm in cold, wet black spruce stands, but may exceed 50 cm (Viereck and Dyrness 1979). In warmer, drier white spruce stands, the depth of the moss-organic mat was on the order of 0-10 cm.

The moss-organic layer influences forest structure and function. Mosses efficiently absorbed and immobilized nutrients from precipitation (Wein and Maclean 1983). On the other hand, cyanbacteria associated with green feathermosses were important nitrogen fixers (Viereck *et al.* 1986). Soil temperatures and the depth to the permafrost are directly related to the thickness of the forest floor organic layer. The moss-organic layer decreased soil temperature and thus reduced organic matter decomposition, immobilizing nutrients until the mosses died and were slowly decomposed (Weetman 1962). In forests with a thick moss layer, the forest floor often contained the largest pool of nutrients (Van Cleve and Yarie 1986). Due to their effects on soil temperature and nutrient cycling, mosses affect plant physiological activity. Soil warming reduced moss and litter accumulation and promoted nutrient cycling in boreal forest floor (Bonan and Shugart 1989).

Silvicultural treatments and soil temperature

The microsite conditions in the field were of crucial significance for the germination of seeds and the establishment and success of tree seedlings (Landhaausser *et al.* 1996). In natural forests, natural disturbances such as fire, soil erosion and anthropogenic activities can remove the insulating organic matter and result in higher soil temperature, facilitating the establishment of trees on these sites (Landhaausser and Wein 1993). Various silvicultural treatments can be used to raise soil temperatures, such as scarification, mounding and prescribed fire (McMinn 1982, Sutton 1984, and Brand 1990). Scarification is more effective in increasing soil temperature than other treatments (Brand 1990). Orlander (1987) suggested that mounding in northern ecosystem created positive biological effects, such as increased soil temperature. Fleming *et al.* (1998) documented that ripping (soil loosening) to a depth of 50 cm produced higher soil temperatures. Increased soil temperature can significantly increase soil-degree days, soil water content and survival for boreal tree seedlings (Fleming *et al.* 1998). Therefore, increasing soil temperature can be one of the key silvicultural objectives in boreal forests.

Despite the relatively extensive studies on soil temperature effects, the relationships between soil temperature and ecophysiological processes/traits of different boreal tree species are not well understood. This is partially because of the lack of equipment to control soil temperatures for greenhouse studies. The objectives of this thesis were 1) to develop a soil temperature control system for ecophysiological experiments in greenhouses and 2) to examine the effects of soil temperature on ecophysiological traits for aspen, white spruce, black spruce and jack pine seedlings.

CHAPTER TWO: DESIGN AND TEST OF A SOIL TEMPERATURE CONTROL SYSTEM

INTRODUCTION

Soil temperature is difficult to control independently of air temperature (Nielsen and Humphries 1996). Therefore, the effect of soil temperature on plant ecophysiological processes is often confounded with the effect of air temperature. Presently there are five ways used for controlling soil temperatures in ecophysiological research: (1) circulating temperature-controlled water or antifreeze solution through copper tubing that surrounds plant containers (Lawrence and Oechel 1983); (2) submerging plant containers in temperature controlled water or antifreeze solutions (Running and Reid 1980, Borges and Chaney 1989, Harper and Camm 1993, Lopushinsky and Max 1990, Landhaausser *et al.* 1996, Landhaausser and Lieffers 1998, Ziska 1998); (3) growing plants in temperature-controlled nutrient solutions (hydroponic system; Lorenzen *et al.* 1998); (4) controlling root temperatures through regulating air temperature (aeroponic system, or mist chambers); (5) using heating cables in the soil (Avanzato and Tamponi 1988, Christ *et al.* 1997). However, all the above systems have drawbacks for application in long-term, large greenhouse experiments in tree ecophysiological research.

The first method is very effective for long-term but small-scale experiments, but is not suitable for large experiments. Although copper tubing is relatively inexpensive, the resistance to water flow will increase as the length of tubing increases with increasing number of pots per treatment, if the pots are connected in series. This not only requires very high capacity water pumps, but also significantly increases the temperature difference between pots because of the cumulative heat exchange as water flows through the long path from the first to the last pot. Connecting the pots in parallel would reduce the temperature difference between pots, but the system would become very cumbersome as the number of pots increases. Additionally, the heat exchange between the soil and the copper tubing is generally not very efficient because of the relatively small contact surface between the pot and the tubing compared to the proportionally larger surface area exposed to the air or growing medium.

In the second method, the container must not contain drainage holes or containers with drainage holes must be placed in larger sealed containers to prevent antifreeze from contacting plant roots and fertilizers from leaking into the cooling water or antifreeze (Running and Reid 1980, Borges and Chaney 1989, Harper and Camm 1993, Lopushinsky and Max 1990, Landhaausser *et al.* 1996, Ziska 1998). The lack of drainage hole would cause salt accumulation and poor aeration in the growing medium, which are detrimental to plant ecophysiological processes (Landis *et al.* 1989). To solve this problem Landhaausser and Lieffers (1994, 1998) utilized a design where five pots with drainage holes were placed in a plywood box (69 × 63 × 21 cm) surrounded by plastic bags, with a tubular spacer between the bottom of the pot and the bag to permit drainage. After each watering, extra water was sucked out of the bag using a syringe. This process of excess water removal can become unmanageable for large experiments.

The third method, the hydroponic system, can be used for long-term and large experiments, but the root environment that the system creates is substantially different from that of soils. Consequently, the research results may not be as applicable to the field conditions. The same is true for the aeroponic system in mist boxes.

In the fifth method, it is very difficult to achieve uniform soil temperatures. For example, Verbury *et al.* (1999) reported that when soil was dry, soil temperature differences between pots increased with increasing distance from heating cables. Additionally, the heating cables can not be used to cool soils.

In this study, a new system was designed and tested to overcome the drawbacks of the above methods. This system has been proven to be suitable for conducting greenhouse experiments.

MATERIALS AND METHODS

Design

The system consisted of a large plywood box, polyethylene liner, polystyrene insulation, seedling pots, and a flow-through temperature controller (Figure 2.1). The internal dimensions of the plywood box were 112-cm wide, 196-cm long and 16-cm deep. Since the plywood used was not waterproof, heavy-duty polyethylene film (Emballagea Cascades Inc., Yamachiche, Quebec, Canada) was used to line the inner surface of the box. The top of the box was open. Food containers of 13.5-cm tall, 11-cm top diameter and 9.5-cm bottom diameter were used as the seedling container. One hundred and twelve containers were installed in each plywood box. A drain-hole (1.3-cm diameter) was drilled at the centre of the bottom of each container and through the bottom of the plywood box. To avoid water leakage from the container to the plywood

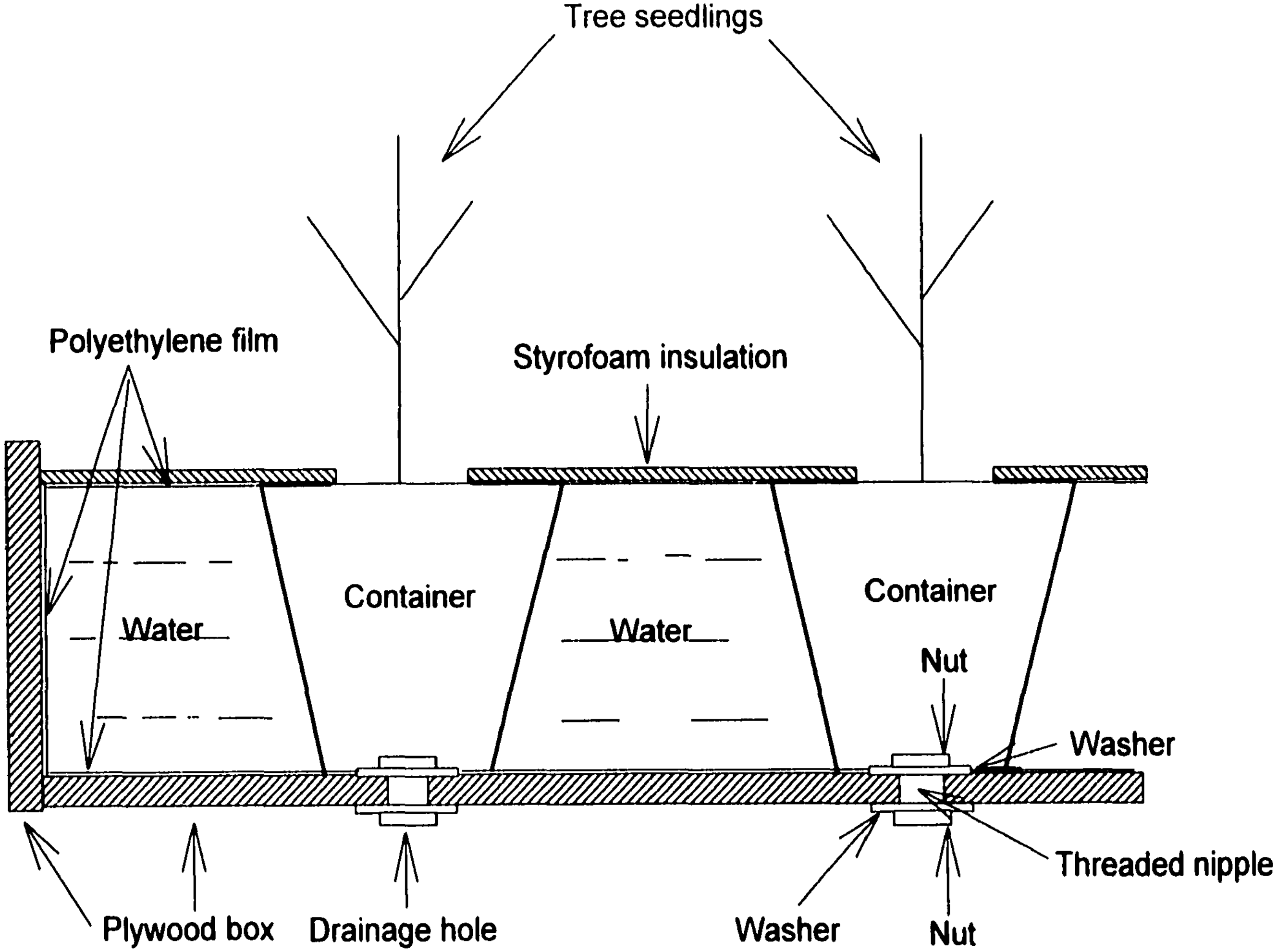

Figure 2.1. Partial cut-away view of the soil temperature control system.

box or from the plywood box, the containers were fixed to the plywood box using threaded nipples, stainless steel washers and nuts (3-mm thick, Figure 2.1). The containers were then filled with a peat-vermiculite growing medium.

The space between containers in the plywood box was filled with water and circulated through a flow-through heater (model 210) or cooler (model KR-30A, PolyScience, Nile, Illinois, USA), depending on the soil temperature desired. Three soil temperatures (5, 20 and 30 °C) were used in our tests. Because the flow-through cooler did not have a built-in temperature controller, a White-rodgers thermostat (Emerson Electric Co., Louis, MO., USA) was used to regulate the cooling unit. To prevent soil particles and the fertilizer solution from falling into the water and to minimize water evaporation from the box, the top of the plywood box was sealed with heavy-duty polyethylene film with holes (smaller than the opening of the container) cut for each container. To minimize the heat exchange between the water in the plywood box and the ambient air, the top of the plywood box was covered with polystyrene board insulation (Figure 2.1). A hole of 5-cm diameter was then cut through the polystyrene insulation around each seedling to facilitate irrigation, fertilization and the gas exchange between the growing medium and the ambient air. A water pump (model AC-2CP-MD, March Manufacturing, Inc., Glenview, Illinois, USA) was used to stir the water to ensure a uniform water temperature and thus a uniform soil temperature throughout the box. The inlet and outlet to the pump were installed at the two different ends of the plywood box to further improve the uniformity of water temperature and soil temperature.

Test

The following tests were conducted: (1) the relationship between soil temperature at the centre of the container and water temperature outside the container, (2) the homogeneity and distribution of soil temperature in all containers within the same plywood box. (3) variation of soil and water temperatures with depth to the surface, (4) diurnal variation of water and soil temperatures. Three soil temperatures were used in the tests: 5, 20 and 30 °C. Soil temperatures were measured at the centre of the container at a depth of 7 cm except the test for variation with depth. Soil and water temperatures were monitored using copper-constantan thermocouples connected to a SCXI-MS100 temperature monitoring system (National Instruments Corporation, Austin, Texas, USA) and a Pentium computer. Temperatures were logged every 10 minutes. To examine the homogeneity and distribution of soil temperature, the soil temperature of all 112 containers in the 30 °C treatment was measured.

The tests were conducted in the Lakehead University greenhouses. The ambient environmental conditions during the tests were set at 22/16 °C day/night temperature and a 16-hour photoperiod. However, the temperature in the greenhouse fluctuated around the setpoint. The daytime temperature was generally above the setpoint, particularly on sunny days. The relative humidity was not controlled and generally varied between 55 and 75 %. One-year old seedlings of aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea Mariana* (Mill.) B.S.P.) and white spruce (*Picea glauce* (Moench) Voss.) were planted at the beginning of the test. The seedlings were watered and fertilized every two days.

Statistical analysis

The relationship between water and soil temperature was analyzed using regression analysis together for all three-temperature treatments. Chi square test was used to examine the distribution of soil temperature among containers in the same plywood box:

$$\eta = \sum_{i=1}^{m} \{(V_i - n \times P_i)^2 / n \times P_i \}, \qquad [1]$$

where V_i is the actual number of samples having the same temperature value t; P_i is the probability for a normal distribution; $n \times P_i$ is the theoretical number of samples having temperature t; m is the total number of temperature values in the test. Analysis of variance was used to test the difference in the magnitude of diurnal temperature fluctuation among the three temperature treatments. Standard deviations were used as a measure of the magnitude of the diurnal fluctuation. Since ANOVA showed significant differences between the three temperature treatments, multiple-comparison (*q* test) was used to identify which temperature treatment was significantly different from which treatment (Fu 1979, Mason *et al.* 1989).

RESULTS AND DISCUSSION

Relationship between soil temperature and water temperature

Soil temperature (**T_{soil}**) was strongly correlated to water temperature (**T_{water}**) (Figure 2.2). T_{soil} increased linearly with T_{water} in all the temperature treatments (r^2 = 0.999, Table 2.1). The relationship was almost 1 to 1 (slope = 0.9914, Figure 2.2). However, the soil temperature was significantly greater than water temperature (intercept

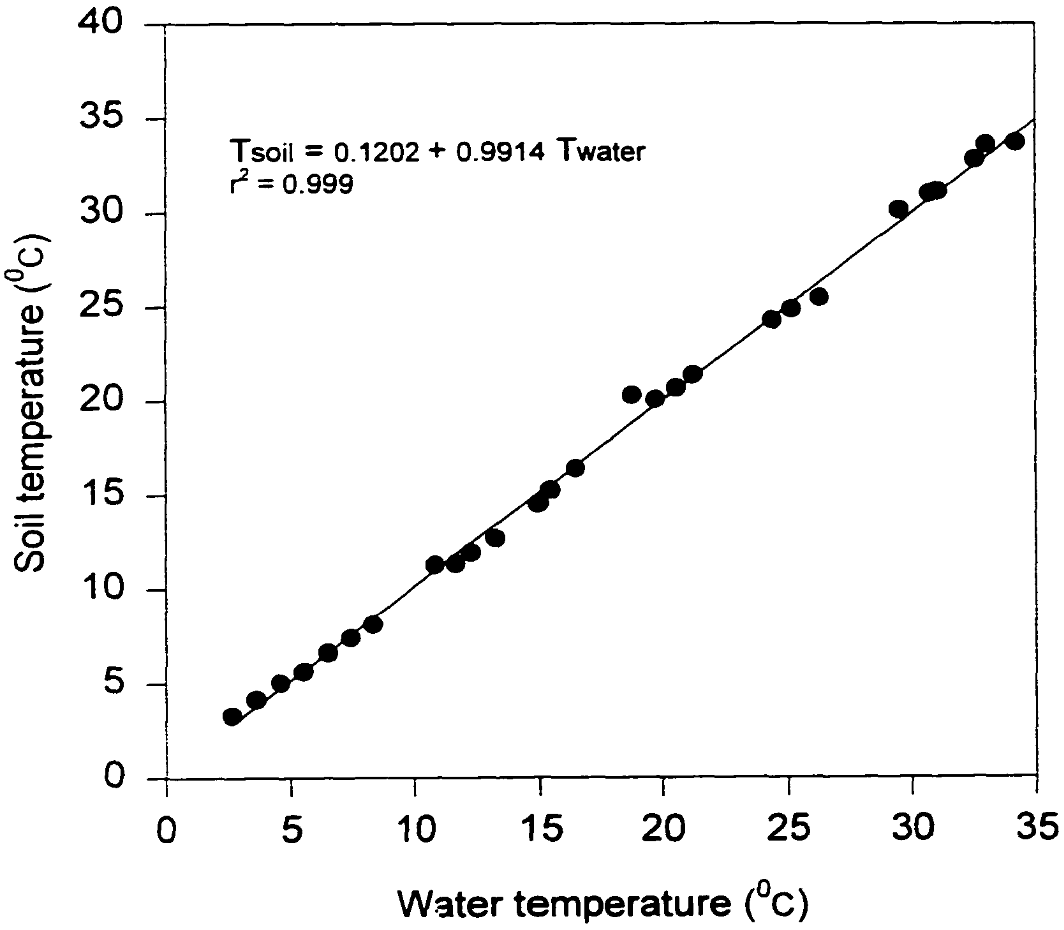

Figure 2.2. Linear regression between soil and water temperatures.

= 0.1202, Figure 2.2, Table 2.1). These results suggested that the heat exchange between the growing medium and the water outside the container was highly effective in the system. The precision of soil temperature control therefore depends solely on the precision of controlling the water temperature.

Table 2.1. Test of regression coefficients (β) and coefficient of determination (R^2) for the relationship between soil and water temperatures.

	Coefficient Test			
	β	S.E.	t	$t_{0.05}$
Slope	0.9989	0.0103	97.434*	2.064
Intercept	0.1203	0.0201	5.980*	2.064

	R^2 Test				
	d.f.	SS	MS	F ratio	$F_{0.05}$
Regression	1	2344.91	2344.91	9493.32*	4.28
Residual	24	5.93	0.25		

* = significant at 95 %.

Homogeneity and distribution of soil temperature (30 °C treatment only)

The soil temperature was very uniform throughout the box except a few containers at one end of the box where the soil temperature was higher than that in other containers (Figure 2.3). This was probably caused by the greenhouse heating system. The greenhouse was heated by steam heaters. The higher temperature in these containers was probably caused by the proximity of the radiator to these pots (end of plywood box).

The Chi square test showed that the soil temperature of all the containers within the box followed a normal distribution with a mean of 30.47 and a small standard deviation of 0.36 ($\eta = 5.107 < \chi^2_{0.05}(15) = 24.996$). This suggested that soil temperature measurements in a small number of pots can provide a reliable estimation of the average soil temperature for the treatment. For example, the temperatures of two pots provided an estimate of the average soil temperature in the 30 °C treatment with a 95% confidence level.

Variations of soil and water temperatures with depth from the surface

There was a gradient with depth from the surface in both water and soil temperatures (Figures 2.4, 2.5 and 2.6). The trend for the 30 °C treatment, however, was opposite of that for the 5 and 20 °C treatments. In the 5 and 20 °C treatments, both soil and water temperatures generally decreased from the top to the bottom of the container (Figures 2.4 and 2.5). In the 30 °C treatment, on the contrary, both soil and water temperatures increased as the depth to the surface increased (Figure 2.6). This temperature gradient suggested that there was still a fair amount of heat exchange between the ambient air and the surface of the growing medium and water despite the use of the polystyrene insulation. The opposite direction of the temperature gradient for the 30 °C treatment when compared to the other treatments suggests that the direction of the vertical temperature gradient was determined by the direction of heated exchange between the ambient air and the soil temperature control system. The soil and water temperatures in the 5 and 20 °C treatments were generally lower than ambient air temperature. Therefore, the growing medium and water gained heat from the air, resulting in higher temperatures at the surface than deeper levels.

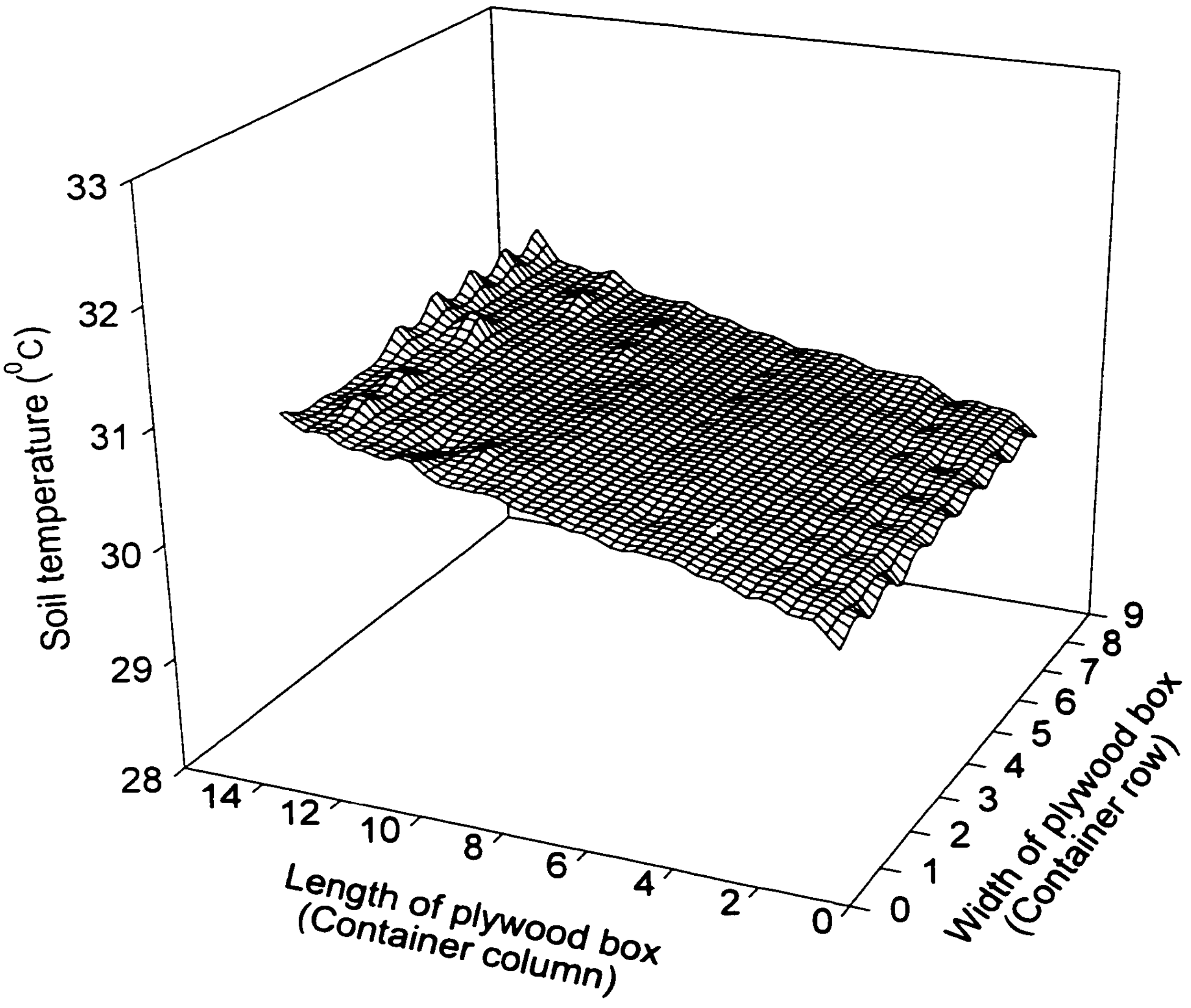

Figure 2.3. Horizontal distribution of soil temperature.

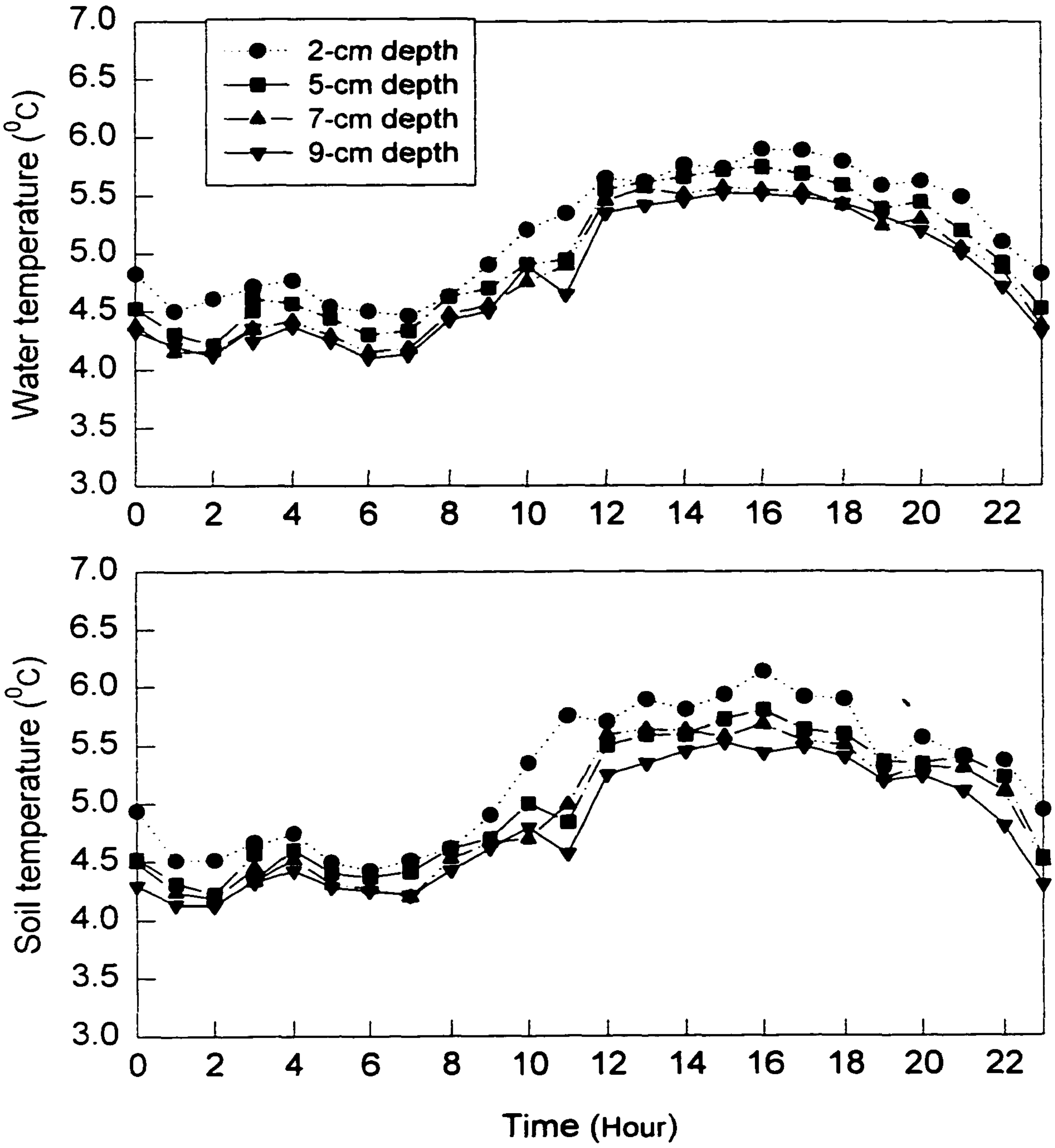

Figure 2.4. Diurnal variations of water and soil temperatures at different depths from the surface in the 5 ^{0}C treatment.

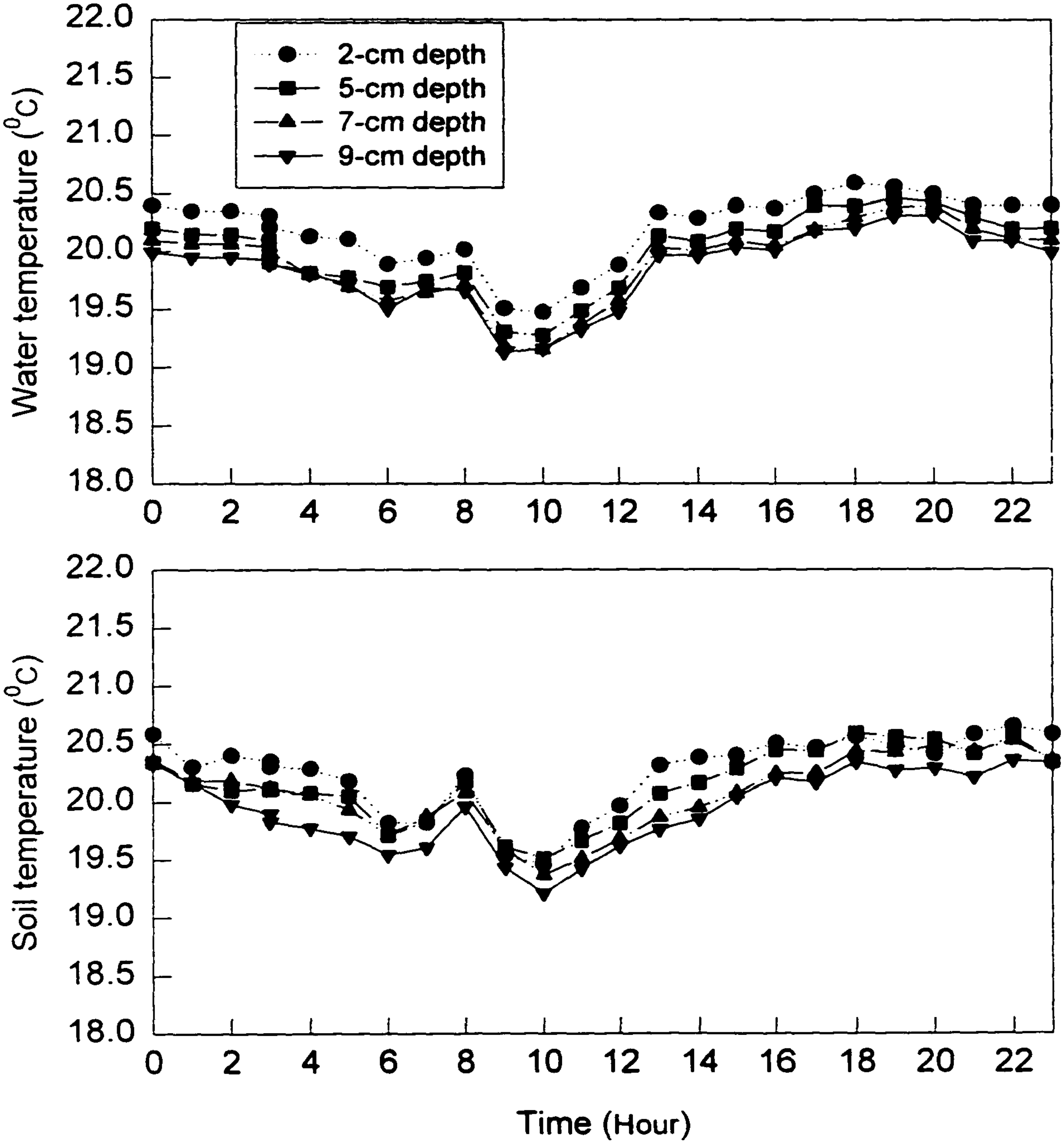

Figure 2.5. Diurnal variations of water and soil temperatures at different depths from the surface in the 20 ^{0}C treatment.

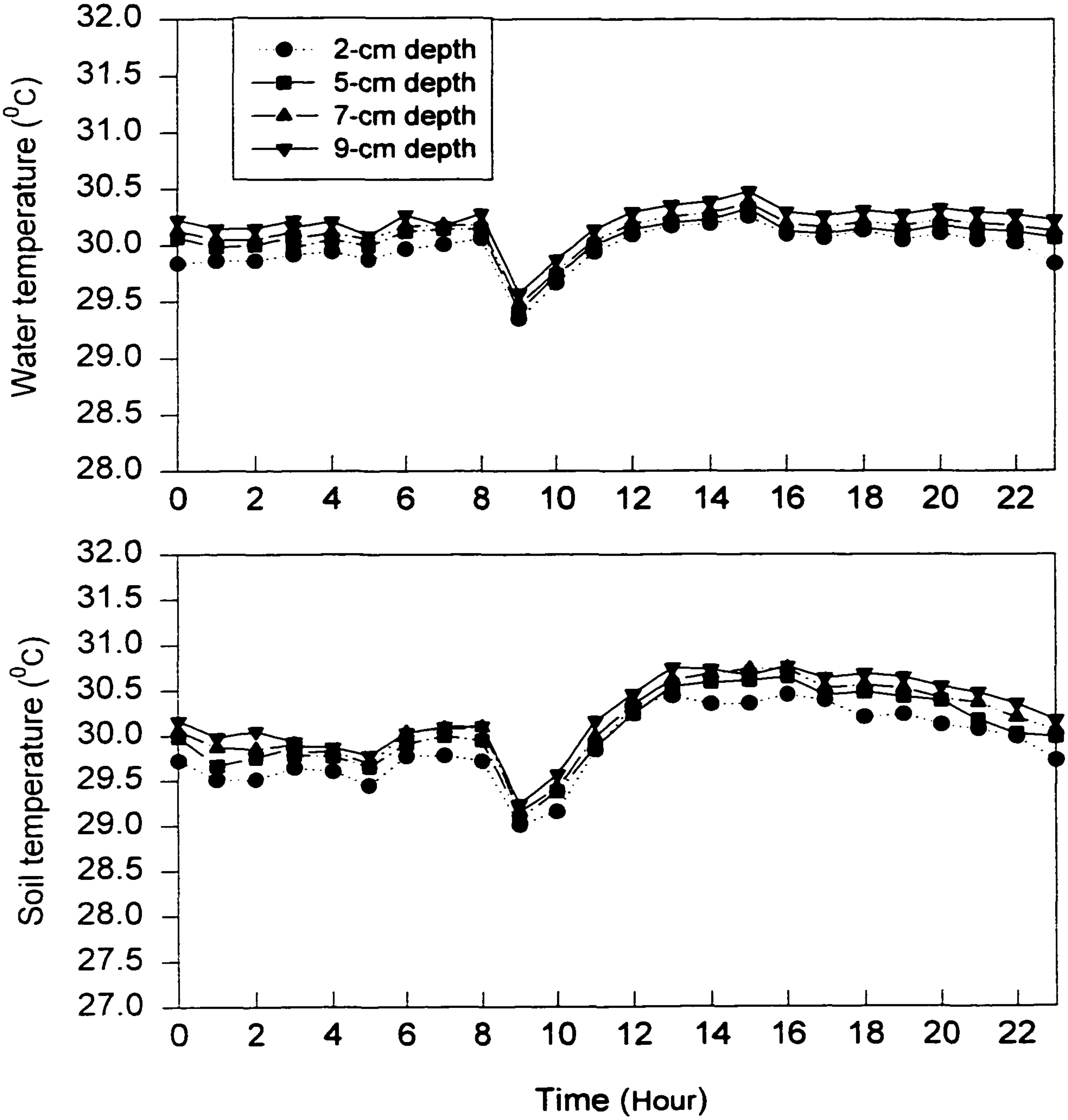

Figure 2.6. Diurnal variations of water and soil temperatures at different depths from the surface in the 30 ^{0}C treatment.

The soil temperature in the 30 °C treatment was generally higher than air temperature. The subsequent loss of heat resulted in lower temperatures at the surface. The temperature gradient, however, was very small (< 1 °C). If an even smaller gradient is required, the temperature gradient can be further reduced by a better mixing and stirring of the water and/or using better insulation, but better insulation may be less effective because reasonably large holes will have to be cut through the insulation to facilitate irrigation, fertilization and the aeration of the growing medium. Therefore the study recommend using a water pump with a higher flow rate or more than one pump to further reduce temperature gradient.

Diurnal variations of soil and water temperatures

Both water and soil temperatures decreased at night and increased during the day (Figures 2.4, 2.5 and 2.6). The soil temperature range (maximum - minimum) was 1.5, 0.8 and 1.0 °C, respectively, for 5, 20 and 30 °C treatments. Such a variation is most likely acceptable for most experiments. This diurnal variation was probably caused by a combination of light energy input into the system and heat exchange between the temperature control system and ambient air. Since the change in soil temperature followed the change of water temperature very closely (Figures 2.2 - 2.6), the diurnal variation in soil temperature can be further reduced by using temperature controllers of higher capacity.

The magnitude of the daily temperature fluctuation was significantly greater in the 5 °C treatment than in the 20 and 30 °C treatments (Tables 2.2 and 2.3). These of both the

20 and 30 °C treatments were statistically the same (Table 2.3). The averages of diurnal fluctuations were 0.69, 0.37 and 0.40 °C for 5, 20 and 30 °C in soil, and 0.61, 0.36 and 0.39 °C for 5, 20 and 30 °C in water (Table 2.3). The greater fluctuation in the 5 °C treatment was probably caused by the poor precision (± 1.5 °C) of the thermostat used to control the flow-through chiller. The temperature controlling device on the other two systems had better resolution (± 0.5 °C).

Table 2.2. ANOVA for differences in diurnal fluctuations in soil and water temperatures between the 5, 20 and 30 °C treatments.

	Soil				Water			
Source	d.f	SS	MS	F ratio	SS	MS	F ratio	$F_{0.05}$
Temperature	2	1.877	0.938	36.30*	2.581	1.291	50.06*	2.56
Error	21	0.543	0.026		0.541	0.026		

* = significant at 95 %.

It should be noted that the sudden drop in soil and water temperature in the morning (Figures 2.5 and 2.6) was not part of the normal diurnal variation. This drop was caused by the addition of the fertilization solution to the growing medium and the refill of water in the system. The temperature of the tap water was below 15 °C. Sudden addition of the cold water caused an immediate decline in water and soil temperatures. The system needed to be refilled with water every one to two weeks to replace the water loss through evaporation from the system. Recharging the system more often (thus adding a smaller amount of water each time) can minimize the sudden decrease in temperature. An automatic recharge device to keep the water level more constant should also minimize this effect.

Table 2.3. Multiple-comparison for the magnitude of diurnal fluctuation in soil and water temperatures between the 5, 10 and 30 °C treatments. $D = q_{0.05}(a, f) \times (S^2_w / m)^{0.5} = 0.1682$, where D is the critical value; "a" is the number of treatments (= 3); "f" is degree of freedom in the test (= 21); " $q_{0.05}(a, f)$" = 3.58 (from statistical q table); "m" is the number of samples within a temperature treatment (m = 8 in this experiment), S^2_w is the mean sum of squares of soil or water temperature (= 0.018 in this experiment).

Water temperature	T_i	$T_i - T_{30\,°C}$	$T_i - T_{20\,°C}$
5 °C	0.6132	0.2244*	0.2582*
20 °C	0.3550	0.0338	
30 °C	0.3888		
Soil temperature	T_i	$T_i - T_{30\,°C}$	$T_i - T_{20\,°C}$
5 °C	0.6891	0.2941*	0.3191*
20°C	0.3700	0.0250	
30 °C	0.3950		

* = significant at 95 %.

CONCLUSIONS

The evaluation tests show that the new soil temperature control system was efficient for large ecophysiological experiments in greenhouses. The average soil temperature was within ± 0.4 °C of the desired values (i.e., 5, 20 and 30 °C) in all the tests over a period of four months. The precision of soil temperature control using this system, however, does depend on the precision of the water temperature control by the water-bath, heater or cooler. The temperature of the growing medium in the seedling pot was almost equal to that of water. The soil temperature in the 112 pots installed in the system was very homogenous (STD = 0.34 °C). There was a small gradient (< 1 °C) in soil temperature from the top to the bottom of the pot. There was also a small diurnal fluctuation in soil temperature caused by the heat exchange between the system and the ambient air and input of light energy into the system during the day.

Most of the materials for constructing the system can be found in local stores, such as plywood, polystyrene board insulation, polyethelence film and food containers, and are inexpensive. The major expense is the cost of the temperature regulating mechanism (i.e., heater and coolers). Therefore, the system is affordable for large greenhouse experiments, particularly when water-baths are already available.

CHAPTER THREE: EFFECTS OF SOIL TEMPERATURE ON ECOPHYSIOLOGICAL TRAITS

INTRODUCTION

As noted in Chapter one, the boreal forest is one of the largest terrestrial ecosystems in the world. The boreal forest has a significant impact on the global climatic conditions (Ciais *et al.* 1995, Keeling *et al.* 1996). The boreal forest is also a critical land base for the production of forest products, the conservation of biodiversity, wildlife habitats, and recreation. The boreal forest accounts for 74 % of the 217,400,000 ha forested land of Canada. However, large amounts of boreal forest biomass are disturbed every year due to harvesting and natural disturbances, such as wildfires. The timely renewal of the boreal forest is critical for sustaining the above benefits.

Because of the large area and heterogeneous spatial patterns of the boreal forest, the environmental conditions of soils in the boreal forest are complex and highly variable. For example, soil moisture conditions range from water-logged to very dry; soil nutrient regimes range from very poor to rich; soil temperatures range from cold in wetlands to very warm on south facing slopes and newly burned sites (Bonan and Shugart 1989, OMNR 1997). Thus, a good understanding of how different tree species interact with the complex environmental conditions is essential for the successful renewal and management of the array of sites encountered in the boreal forest.

Soil temperature was one of the most important environmental factors in boreal forest (Bonan and Shugart 1989). Soil temperature directly and indirectly affected physiological processes of trees (Chaisompongpan *et al.* 1990), such as stomatal conductance (Day *et al.* 1989), transpiration, nutrient retranslocation, carbon dioxide uptake (DeLucia 1987), leaf resistance to heat (Chaisompongpan *et al.* 1990) and carbon allocation (Pereira 1990). Soil temperatures also indirectly influenced the physiological processes of plants through changing nutrient absorption and growth (Anderson and McNaughton 1973, Cooper 1973, McGill and Cole 1981, Chapin 1983, Camm and Harper 1991, Kaspar *et al.* 1992, Raich and Schlenger 1992, Ciais *et al.* 1995), and growth hormone production (Binkley and Richter 1986, Vapaavuori *et al.* 1991).

Despite the relatively large amount of information on soil temperature effects in the literature, comparative studies of the response of several species to a wide range of soil temperatures are rare. Comparative studies are particularly important for the management and renewal of mixed-species boreal forests and species/site selection in forest regeneration. Mixedwoods are the most productive type of the boreal forest, but are the most difficult to manage because of the complex interactions between different tree species and between trees and the environment (Papadopol 1995). Comparative studies can help us better understand those interactions. Furthermore, most studies exposed trees to a small range of soil temperatures, such as 3 to 15 °C for black spruce (Landhaauser *et al.* 1996) and 3 to 11 °C for white spruce (Harper and Camm 1993). Data on tree response to a wide range of soil temperatures are lacking. Additionally, the effect of soil temperature was often confounded with that of air temperature because of the technical difficulty in controlling soil temperature independently of air temperature (Nielsen and Humphries 1996). In this study, a new soil temperature control system was used to investigate the ecophysiological responses of four important boreal tree species: black spruce (*Picea mariana* (Mill) B.S.P.), white spruce (*Picea glauce* (Moench) Voss.), jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) to a wide range of soil temperatures (5 to 35 °C).

My hypotheses were: (1) Soil temperature would significantly influence the ecophysiological traits of all four species, (2) Trembling aspen would be the most sensitive to soil temperatures among the four species because its different leaf morphology, (3) There would be a low threshold and high threshold soil temperature in the response of ecophysiological performance.

MATERIALS AND METHODS

Plant materials

One-year old seedlings of black spruce, white spruce and jack pine were obtained from the A & R Container Tree Seedling Nursery in Dorion, Ontario. The seedlings were dormant and were placed in cold storage (-2 °C) before the start of the experiment. Trembling aspen seedlings were grown from seeds in the Lakehead University greenhouse. The dormancy of aspen seedlings was induced at the end of the fourth month by exposing them to 15/5 °C daytime/night temperatures and an 8-hour photoperiod. The aspen seedlings were also placed in cold storage before the initiation of the experiment.

Experimental design

The experiment was set up as a split-split plot design (Mason *et al.* 1989) with two greenhouses (main plots), seven soil temperatures (subplots) and four species (Table 3.1). Each greenhouse contained all seven soil temperatures: 5, 10, 15, 20, 25, 30 and 35 °C. The soil temperature plots were randomly assigned to each of the seven benches in each greenhouse. Soil temperatures were controlled by circulating temperature-controlled water around the seedling container (see chapter two for details). Eight rows of containers (14 in each row) were held in a plywood box with each species being randomly assigned to two rows. Soil temperatures were monitored continuously throughout the experiment using a National Instrumentation SCXI MS 100 temperature logging system (National Instruments Corporation, Austin, Texas, USA) and a Pentium computer. Figure 3.1 shows the diurnal pattern of the soil temperature regimes and the air temperature in the greenhouse.

Growing conditions

The day and night temperatures in both greenhouses were controlled at 22.5 ± 0.6 S.E. and 14.3 ± 0.3 S.E. °C, respectively. The daytime temperatures fluctuated more than the night temperatures and were generally above the setpoint on sunny days. The experiment started on February 6, 1999. High-pressure sodium lamps were used to extend the natural photoperiod to 16 hours in the early part of the experiment. The

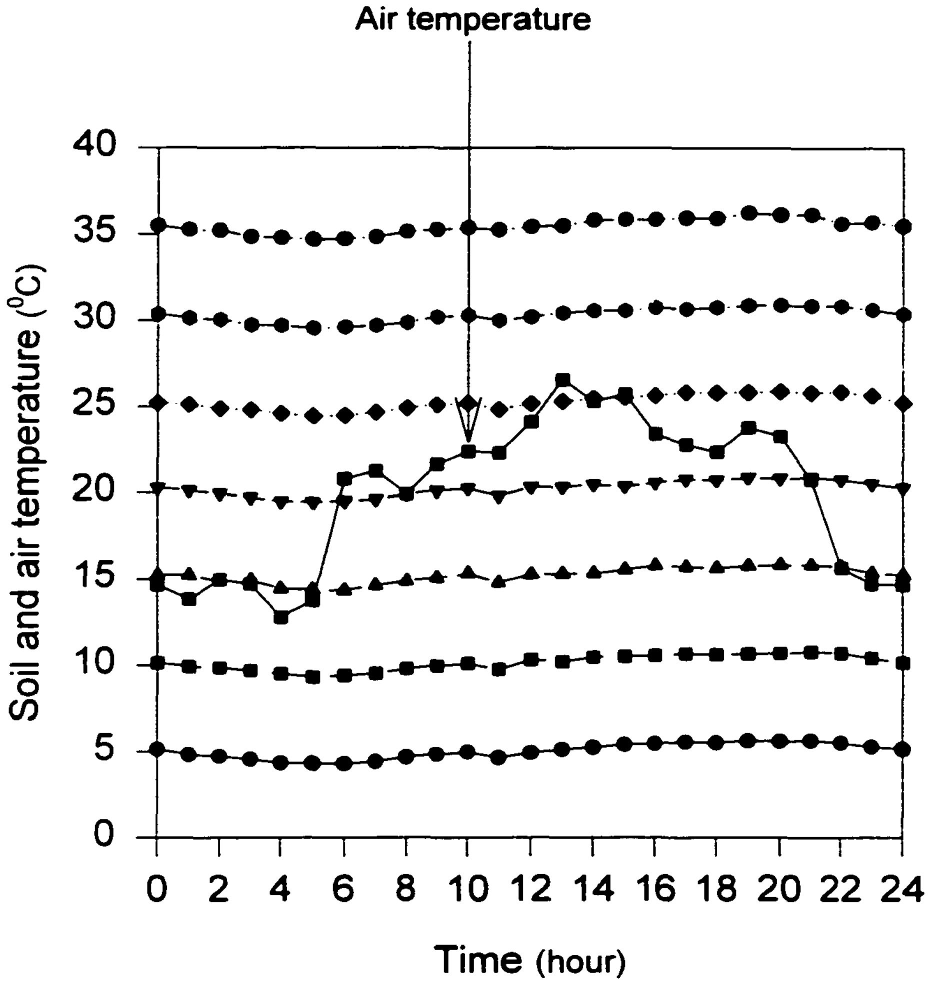

Figure 3.1. Diurnal patterns of soil temperatures in all seven treatments and the air temperature in greenhouse.

Table 3.1. General linear model and expected mean square table for the split-split-plot design. General linear model: $Y_{ijkl} = \mu + G_i + \sigma'_{(i)} + T_j + GT_{ij} + \sigma''_{(ij)} + S_k + GS_{ik} + ST_{jk} + GST_{ijk} + \varepsilon_{(ijk)l}$, where G is greenhouse, T is soil temperature treatment, S is species. i = 1, 2. j = 1, 2, 3, 4, 5, 6, 7. k = 1, 2, 3, 4. l (sample)= 1, 2, 3, 4.

Expected mean square table

Source	Degree of Freedom	2	7	4	4	Expected Mean Square
		F	F	F	R	
		i	j	k	l	
G_i	1	0	7	4	4	$\sigma^2 + 16\,\sigma^2_{\sigma''} + 112\,\sigma^2_{\sigma'} + 112\,\phi\,(G)$
$\sigma'_{(i)}$	0	1	7	4	4	$\sigma^2 + 16\,\sigma^2_{\sigma''} + 112\,\sigma^2_{\sigma'}$
T_j	6	2	0	4	4	$\sigma^2 + 16\,\sigma^2_{\sigma''} + 28\,\phi\,(T)$
GT_{ij}	6	0	0	4	4	$\sigma^2 + 16\,\sigma^2_{\sigma''} + 16\,\phi\,(GT)$
$\sigma''_{(ij)}$	0	1	1	4	4	$\sigma^2 + 16\,\sigma^2_{\sigma''}$
S_k	3	2	7	0	4	$\sigma^2 + 56\,\phi\,(S)$
SG_{ik}	3	0	7	0	4	$\sigma^2 + 28\,\phi\,(SG)$
ST_{jk}	18	2	0	0	4	$\sigma^2 + 8\,\phi\,(ST)$
SGT_{ijk}	18	0	0	0	4	$\sigma^2 + 4\,\phi\,(GST)$
$\varepsilon_{(ijk)l}$	56	1	1	1	1	σ^2

Tests of hypotheses for the experiment

Hypothesis	Test Statistic	F - Distribution
$\phi\,(G) = 0$	MS (G) / MS (σ') no test	F (1, 0)
$\phi\,(T) = 0$	MS (T) / MS (GS)	F (6, 6)*
$\phi\,(S) = 0$	MS (S) / MS (ε)	F (3, 56)
$\phi\,(SG) = 0$	MS (SG) / MS (ε)	F (3, 56)
$\phi\,(ST) = 0$	MS (ST) / MS (ε)	F (18, 56)
$\phi\,(GST) = 0$	MS (STG) / MS (ε)	F (18, 56)

* = Conservative test

growing medium used was a standard mixture of peat-moss and vermiculite (50%/50% volume/volume). Seedlings were watered and fertilized to saturation every two days using a fertilization solution of 126 ppm N, 44 ppm P, 83 ppm K, 40 ppm Mg, 52 ppm S, 30 ppm Ca, 2.5 ppm Fe, 0.67 ppm Mn, 0.4 ppm Zn, 0.3 ppm Cu, 0.12 ppm B, 0.003 ppm Mo (Table 3.2). The salinity and pH of the growing medium solution were measured at

Table 3.2. Formulation of fertilizer solution

Fertilizer 20-20-20® components

Nutrient	Content(%)
Total N	20
P_2O_5	20
K_2O	20
B	0.02
Chelated Cu	0.05
Chelated Fe	0.10
Chelated Mn	0.05
Mo	0.0005
Chelated Zn	0.05
EDTA	1.00

Maxmicro® fertilizer components

Nutrient	Content (%)
Fe	12
Mn	2.5
Zn	1.0
Cu	0.5
B	0.1
Mo	0.005
S	15.0

Fertilization solution concentration

Fertilizer	Weight (mg/L)
20-20-20®	500
Maxmicro®	17
$MgSO_4$	399
$Ca(NO_3)_2$.	176

the end of each month using an AGRITEST pH and EC/TDS meter (HANNA Instruments, Portugal). The largest value of electrical conductivity (EC) was 1.3 mS/cm, which is within the range (< 2.2 mS/cm) recommended by Landis *et al.* (1989). Soil pH was relatively stable throughout the experiment at approximately 5.9.

Measurements of ecophysiological traits

At the beginning of the third month of the experiment, two seedlings of each species were randomly selected from each of the two rows in each soil temperature treatment for the measurement of net photosynthesis (***A***), transpiration (***E***), stomatal conductance ($\boldsymbol{g_s}$) and midday xylem water potential (ψ). *A*, *E* and g_S were measured using a PP-Systems CIRAS-1 gas exchange system with Parkinson leaf cuvettes with automatic environment control (PP-Systems, Haverhill, MA., USA). The measurements were taken at 22 ± 0.1 °C air temperature, 360 ± 10 ppm CO_2, 800 μ mol m^{-2} s^{-1} photosynthetically active radiation, and 13.5 ± 0.22 mbar water vapour pressure. The xylem water potential was measured using a pressure chamber (PMS Instruments Co., Corvallis, Oregon, USA). Projected leaf area was measured using a Regent WinSEEDLE system (Regent Instruments Inc., Quebec City, Quebec, Canada). All the above measurements were made on the current year foliage. For aspen, all the measurements were made on the fifth leaf from the top. After the leaf area measurements, the foliage was dried at 70 °C for 48 hours for determining the dry mass and calculating specific leaf area (***SLA***). Photosynthetic water use efficiency (***WUE***) was calculated as *WUE* =A/E. Mesophyll conductance ($\boldsymbol{g_m}$) was calculated as $gm = (A/C_i) \times 1000$ (Teskey *et al.* 1986), where C_i is in the internal CO_2 concentration.

Data analysis

Analysis of variance (ANOVA) was used to test soil temperature effects on the ecophysiological traits and differences between species. For testing the responses of all the species, the soil temperature effect was tested against the interaction between soil temperature and greenhouse as a conservative test (Brown 1995), species effect and all the other interactions were tested against the experimental error (Table 3.1). When there was a significant effect of soil temperature on an ecophysiological trait for all species, further tests were performed for each individual species. For testing the response of each individual species, soil temperature was tested against its own experimental error. Stepwise regression analysis was used to determine the relationships between net photosynthesis and other ecophysiological variables. All dependent variables were graphically examined for the normality of their distribution using probability plots and for homogeneity of variance using scatter plots. All the data were found to satisfy the assumptions for ANOVA and regression analysis. Non-linear regression analysis of multivariate secant method was used to model the relationships between soil temperature and the ecophysiological variables as polynomial equation. The derivative functions of the models were used to express the sensitivity of each ecophysiological variable to changes in soil temperature. The larger the absolute value of the derivative function is, the more sensitive the variable is to soil temperature. The soil temperature at which the derivative function is a value of zero is defined as the optimal temperature. The soil temperature at which the ecophysiological variables change the fastest is defined as the sensitive temperature.

RESULTS

Net photosynthesis (*A*)

Soil temperature significantly affected net photosynthesis in all species (Tables 3.3 and 3.4). Net photosynthesis initially increased with increasing soil temperature and then decreased with a further increase in soil temperature (Figures 3.2 and 3.3). Among the seven soil temperatures, the maximum *A* of aspen, white spruce and black spruce occurred at 25 °C while the maximum *A* for jack pine occurred at 30 °C. However, the optimum soil temperature for *A* derived from the regression models (Table 3.5, Figure

Table 3.3. Analysis of variance for the effect of soil temperature on net photosynthesis (*A*), stomatal conductance (g_s), mesophyll conductance (g_m), transpiration (*E*), xylem water potential (ψ), water use efficiency (*WUE*) and specific leaf area (*SLA*) in four boreal tree species. The analyses were conducted separately for each species.

	Aspen		White spruce		Black spruce		Jack pine	
Trait	F-ratio	p	F-ratio	p	F-ratio	p	F-ratio	p
A	12.79**	0.000	3.69**	0.008	8.71**	0.000	27.83**	0.000
g_s	5.23**	0.001	4.65**	0.002	4.93**	0.001	5.11**	0.001
g_m	12.20**	0.000	3.22**	0.007	6.30**	0.000	12.84**	0.000
E	7.83**	0.000	1.45	0.233	4.14**	0.004	15.29**	0.000
ψ	5.80**	0.001	10.88**	0.000	14.83**	0.000	2.75*	0.032
WUE	1.27	0.302	2.55*	0.043	22.76**	0.000	1.92	0.113
SLA	4.24**	0.004	1.87	0.134	3.56*	0.010	9.60**	0.000

* = significant at 95%, ** = at 99%.

Table 3.4. Analysis of variance for the effect of soil temperature on net photosynthesis (*A*), stomatal conductance (g_s), mesophyll conductance (g_m), transpiration (*E*), xylem water potential (ψ), instantaneous photosynthetic water use efficiency (*WUE*) and specific leaf area (*SLA*). The analysis was done for all four species together.

		A		g_s		g_m		*E*	
Source	d.f.	MS	F	MS	F	MS	F	MS	F
Main plot									
Soil temperature (T)	6	139.3	15.6**	134861.7	6.2*	1570.5	13.1**	5.9	7.4*
Error A	6	8.9		21902.1		119.5		0.8	
Subplot									
Species (S)	3	103.9	14.4**	169758.6	12.7**	2595.8	27.6**	40.8	81.6**
Greenhouse (G) × S	3	16.0	2.1	53008.6	4.0*	659.8	7.0**	0.6	1.2
S × T	18	20.8	2.7**	487415.1	36.5**	3992.8	42.4**	23.1	46.2**
S × T × G	18	18.1	2.4**	670243.8	50.2**	3890.9	41.3**	15.6	31.2**
Error B	56	7.6		13350.5		94.1		0.5	
Total	110								

		ψ		*WUE*		*SLA*		*Critical Value*	
Source	d.f.	MS	F	MS	F	MS	F	$F_{0.05}$	$F_{0.01}$
Main plot									
Soil temperature (T)	6	0.6	6.0*	18.8	5.5*	12385.8	7.1*	4.28	8.47
Error A	6	0.1		3.4		1755.5			
Subplot									
Species (S)	3	0.8	8.0**	6.0	2.2	607420.4	989.9**	2.78	4.16
Greenhouse (G) × S	3	0.4	4.0*	7.2	2.6	5365.4	8.7**	2.78	4.16
S × T	18	2.5	25.0**	53.3	19.0**	25961.3	42.3**	1.80	2.28
S × T × G	18	2.3	23.0**	74.7	26.7**	24736.9	40.3**	1.80	2.28
Error B	56	0.1		2.8		613.6			
Total	110								

* = significant at 95 %; ** = strongly at 99%.

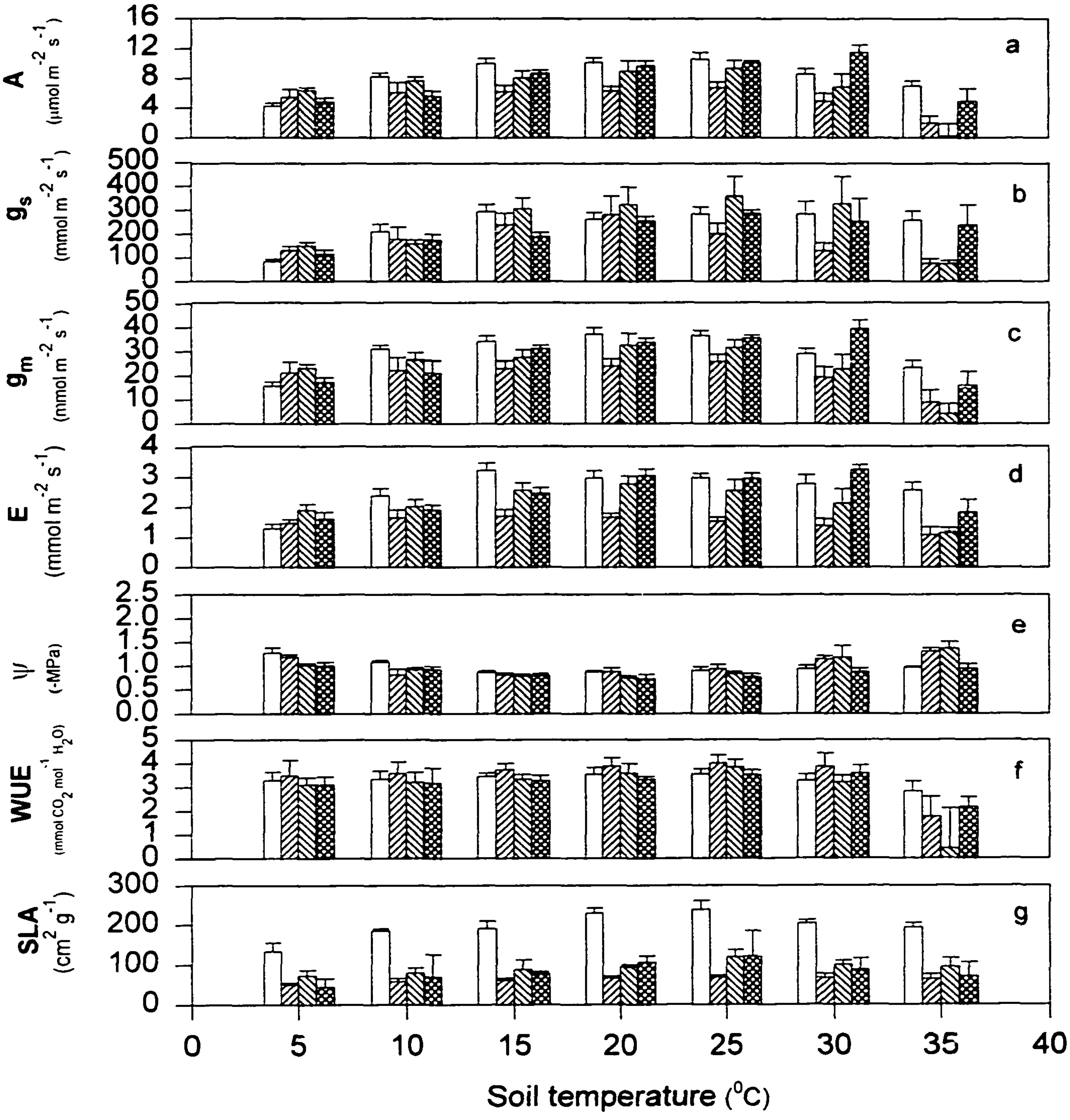

Figure 3.2. Soil temperature effects on a) Net photosynthesis (*A*), b) Stomatal conductance (g_s), c) Mesopyll conductance (g_m), d) Transpiration (*E*), e) Midday xylem water potential (ψ), f) Water use efficiency (*WUE*), and g) Specific leaf area (*SLA*) in aspen, white spruce, black spruce and jack pine (mean + SE, n=8).

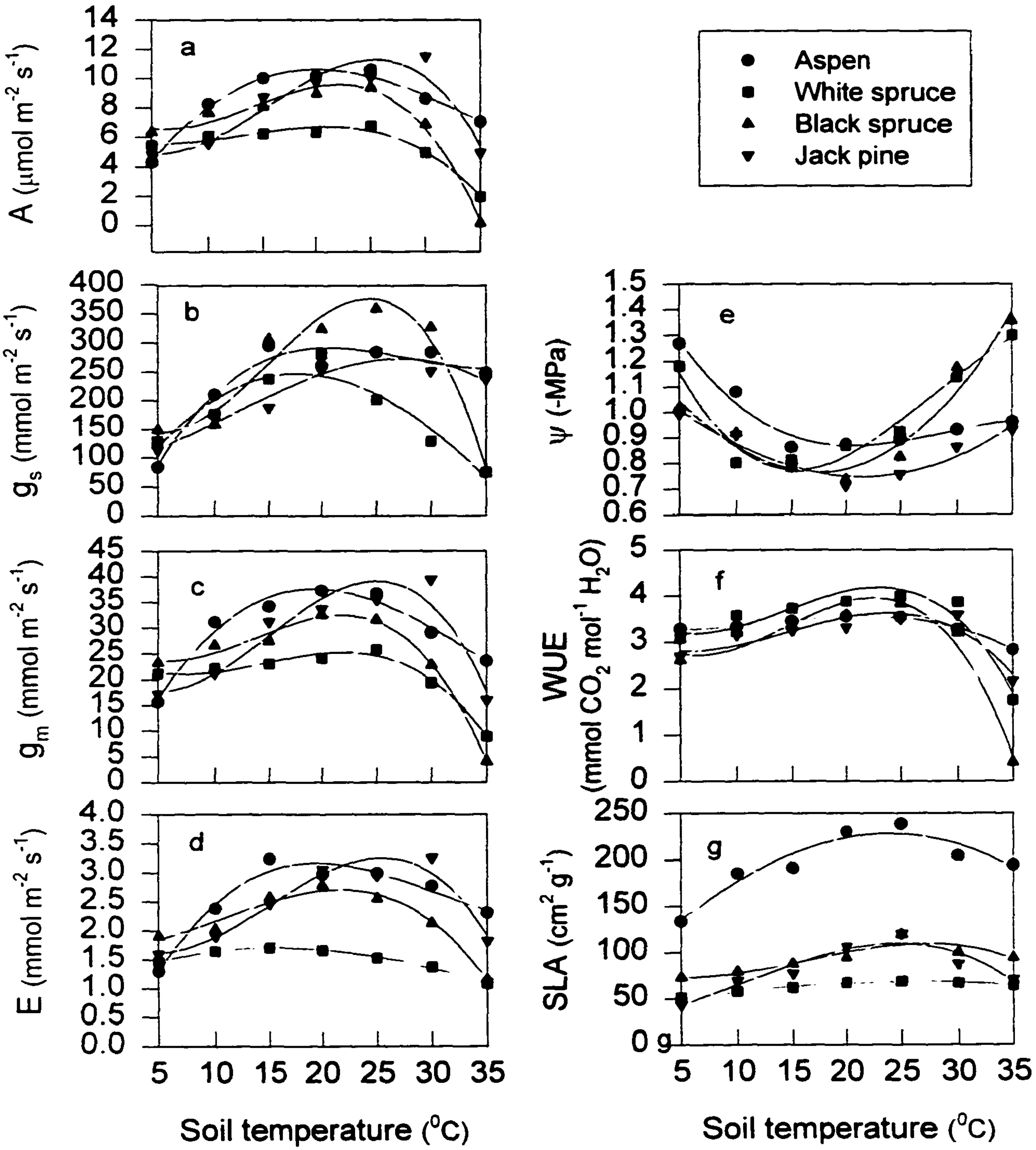

Figure 3.3. Nonlinear models for the relationships between soil temperature and *A*, g_s, g_m, *E*, *ψ*, *WUE* and *SLA* in aspen, white spruce, black spruce and jack pine. See Figure 3.2 for symbol definition.

3.3) varied with tree species: 21.8 °C for aspen, 19.6 °C for white spruce, 22.4 °C for black spruce and 26.1 °C for jack pine (Table 3.6). Aspen was the most sensitive to low soil temperatures among all four species while the other three species were similar in their sensitivity to low temperatures (Figure 3.4). However, black spruce was the most sensitive to high soil temperatures, followed by jack pine, white spruce and aspen (in decreasing sequence) (Figure 3.4). Aspen had the lowest rate of photosynthesis at 5 °C soil temperature but the highest A at other soil temperatures except 30 °C at which jack pine had the highest A. Black spruce generally had a higher A than did white spruce at all soil temperatures except 35 °C (Figure 3.2).

Table 3.5. Regression coefficients and coefficients of determination for relationships between ecophysiological traits and soil temperature. The model is: $Y = b_0 + b_1 T_{soil} + b_2 T_{soil}^2 + b_3 T_{soil}^3$ All the regressions are significantly at 95 % confidence level.

	Aspen					White spruce				
	b_0	b_1	b_2	b_3	r^2	b_0	b_1	b_2	b_3	r^2
A	-1.341	1.359	-0.046	0.000403	0.98	6.071	-0.217	0.025	-0.000636	0.98
g_s	-112.571	48.817	-1.880	0.022444	0.94	-13.883	31.512	-1.063	0.006495	0.91
E	-0.601	0.461	-0.017	0.000190	0.96	1.171	0.071	-0.003	0.000016	0.99
ψ	1.681	-0.097	0.004	-0.000042	0.97	1.701	-0.138	0.006	-0.000073	0.96
WUE	3.349	-0.033	0.004	-0.000107	0.99	3.677	-0.176	0.018	-0.000419	0.92
SLA	82.941	11.377	-0.189	-0.001398	0.91	44.330	1.375	-0.0003	-0.000667	0.99
g_m	-4.546	5.002	-0.178	0.001652	0.97	25.356	-1.311	0.119	-0.002716	0.98

	Black spruce					Jack pine				
	b_0	b_1	b_2	b_3	r^2	b_0	b_1	b_2	b_3	r^2
A	8.187	-0.596	0.063	-0.001490	0.98	6.473	-0.652	0.074	-0.001604	0.90
g_s	203.274	-24.643	2.897	-0.065479	0.95	81.749	5.237	0.368	-0.011783	0.95
E	1.694	0.006	0.006	-0.000187	0.98	1.877	-0.125	0.016	-0.000362	0.93
ψ	1.298	-0.058	0.001	0.000008	0.94	1.185	-0.039	0.0008	-0.000004	0.93
WUE	3.498	-0.264	0.026	-0.000601	0.96	3.075	-0.107	0.012	-0.000237	0.84
SLA	80.238	-2.928	0.333	-0.006838	0.84	28.933	1.984	0.236	-0.007470	0.90
g_m	27.858	-1.625	0.179	-0.004332	0.99	22.279	-1.971	- 0.238	-0.005310	0.93

Within the same species, the sensitivity of A to changes in soil temperature varied with the value of temperature. For example, A of jack pine was the most sensitive to soil temperature around 15.4 °C. Photosynthesis became less sensitive to changes in soil temperature as soil temperature approached the optimum from either side (Figure 3.4). As with the optimum temperature, the sensitive temperatures also varied with species. Aspen, white spruce and black spruce were the most sensitive to changes in soil temperatures at 5, 13.2 and 14.0 °C, respectively (Table 3.6).

Stomatal conductance (g_s)

Stomatal conductance significantly affected by soil temperature in all species (Tables 3.3 and 3.4). The maximum gs in aspen, white spruce, black spruce and jack pine occurred at 15, 20, 25 and 25 °C, respectively, among the seven treatments (Figure 3.2b). The optimum soil temperatures (derived from the models) for gs were: 20.5 °C for aspen, 17.7 °C for white spruce, 24.3 °C for black spruce and 27.3 °C for jack pine (Figures 3.3b and 3.2b, Table 3.6). gs was the most sensitive to changes in soil temperature at 5.0 °C for aspen and white spruce, 14.7 °C for black spruce, and 10.9 °C for jack pine (Figure 3.4b, Table 3.6). Black spruce was less sensitive to low temperatures but more sensitive to high soil temperatures than the other three species (Figure 3.4b). Aspen was the most sensitive to low soil temperatures followed by white spruce, jack pine and black spruce. Black spruce was the most sensitive to high temperatures followed by white spruce, jack pine and aspen (Figure 3.4b). In fact, g_S of aspen had little response to soil temperatures above 20 °C. Aspen and jack pine had the lowest g_s at 5 °C soil temperature while the two spruces had the lowest g_s at 35 °C. In general, black spruce had higher g_s than did white spruce (Figure 3.2b).

Mesophyll conductance (g_m)

Mesophyll conductance in all the species also changed significantly with changing soil temperature (Tables 3.3 and 3.4). The change in g_m with soil temperature followed a similar pattern as A (Figures 3.2c and 3.3c). The maximum g_m for aspen, white spruce and black spruce occurred at 20 °C while g_m of jack pine was the highest at 25 °C among the seven treatment temperatures (Figure 3.2c). The optimum soil temperatures for g_m (derived from the models) were 19.2 °C for aspen, 21.9 °C for white spruce, 21.7 °C for black spruce and 25.0 °C for jack pine (Figures 3.3c and 3.4c, Table 3.6). The sensitive soil temperatures of g_m were 5.0 °C for aspen, 14.6 °C for white spruce, 13.7 °C for black spruce, and 15.0 °C for jack pine (Table 3.6). Black spruce had higher g_m than white spruce at all treatment soil temperatures but 35 °C. Aspen was much more sensitive to low temperatures than the other three species while the sensitivity to low temperature was very similar between jack pine and the two spruces. Black spruce was the most sensitive to high temperatures followed by jack pine, white spruce and aspen (Figure 3.4c).

Transpiration (E)

Transpiration showed a similar response to soil temperature as photosynthesis did for aspen, black spruce and jack pine but the response of white spruce was not statistically significant (Figures 3.2a, 3.2d, 3.3a and 3.3d, Tables 3.3 and 3.4). The

Table 3.6. The sensitive and optimum soil temperatures for ecophysiological traits in the four boreal tree species. Average is the mean for all the ecophysiological traits in each species.

Trait	Aspen		White spruce		Black spruce		Jack pine	
	Sensitive T_{soil} (°C)	Optimum T_{soil} (°C)	Sensitive T_{soil} (°C)	Optimum T_{soil} (°C)	Sensitive T_{soil} (°C)	Optimum T_{soil} (°C)	Sensitive T_{soil} (°C)	Optimum T_{soil} (°C)
A	5.0	20.0	13.2	20.9	14.0	22.0	15.4	25.4
g_s	5.0	20.5	5.0	17.7	14.7	24.3	10.9	27.3
g_m	5.0	19.2	14.6	21.9	13.7	21.7	15.0	25.0
E	5.0	19.2	5.0	15.6	10.5	21.6	15.0	25.4
ψ	5.0	21.0	5.0	15.4	5.0	17.6	5.0	31.0
WUE	13.2	21.8	14.5	22.9	14.5	22.5	14.6	23.7
SLA	5.0	23.8	5.0	22.6	16.2	27.2	10.5	24.6
Average	6.2	21.8	8.9	19.6	12.7	22.4	12.3	26.1

maximum *E* in aspen, white spruce, black spruce and jack pine occurred at 15, 15, 20and 30 °C, respectively, among the seven treatments soil temperature (Figure 3.2d). Overall, white spruce had the lowest *E* among the four species. The optimum soil temperatures for *E* derived from the models were 19.2 °C for aspen, 15.6 °C for white spruce, 21.6 °C for black spruce and 25.4 °C for jack pine (Table 3.6, Figures 3.3E and 3.4E). The sensitive soil temperatures of *E* were 5.0 °C for aspen and white spruce, 10.5 °C for black spruce, and 15.0 °C for jack pine (Table 3.6). Aspen was the most sensitive to low soil temperatures followed by black spruce and jack pine. Jack pine was the most sensitive to high soil temperatures followed by black spruce and aspen (Figure 3.4d).

Midday xylem water potential (ψ)

Midday xylem water potential was significantly affected by soil temperature (Table 3.3). The models showed that the water potential was the highest (i.e., the least negative) at 15.4 °C soil temperature for white spruce, 17.6 °C for black spruce, 21.0 °C for aspen and 31.0 °C for jack pine (Figures 3.3e and 3.4e, Table 3.6). Among the seven treatment soil temperatures, ψ was the highest at 15 °C for aspen and white spruce but at 20 °C for black spruce and jack pine. ψ became increasingly more negative as soil temperature deviated from the optimum level (Figure 3.3e). White spruce was the most sensitive at low soil temperatures followed by aspen, black spruce and jack pine (in decreasing order). Black spruce was the most sensitive to high soil temperatures followed by white spruce, aspen and jack pine (Figure 3.4e). However, the difference in ψ between different soil temperatures was small (< -0.003 and -0.11 MPa, Figure 3.2e).

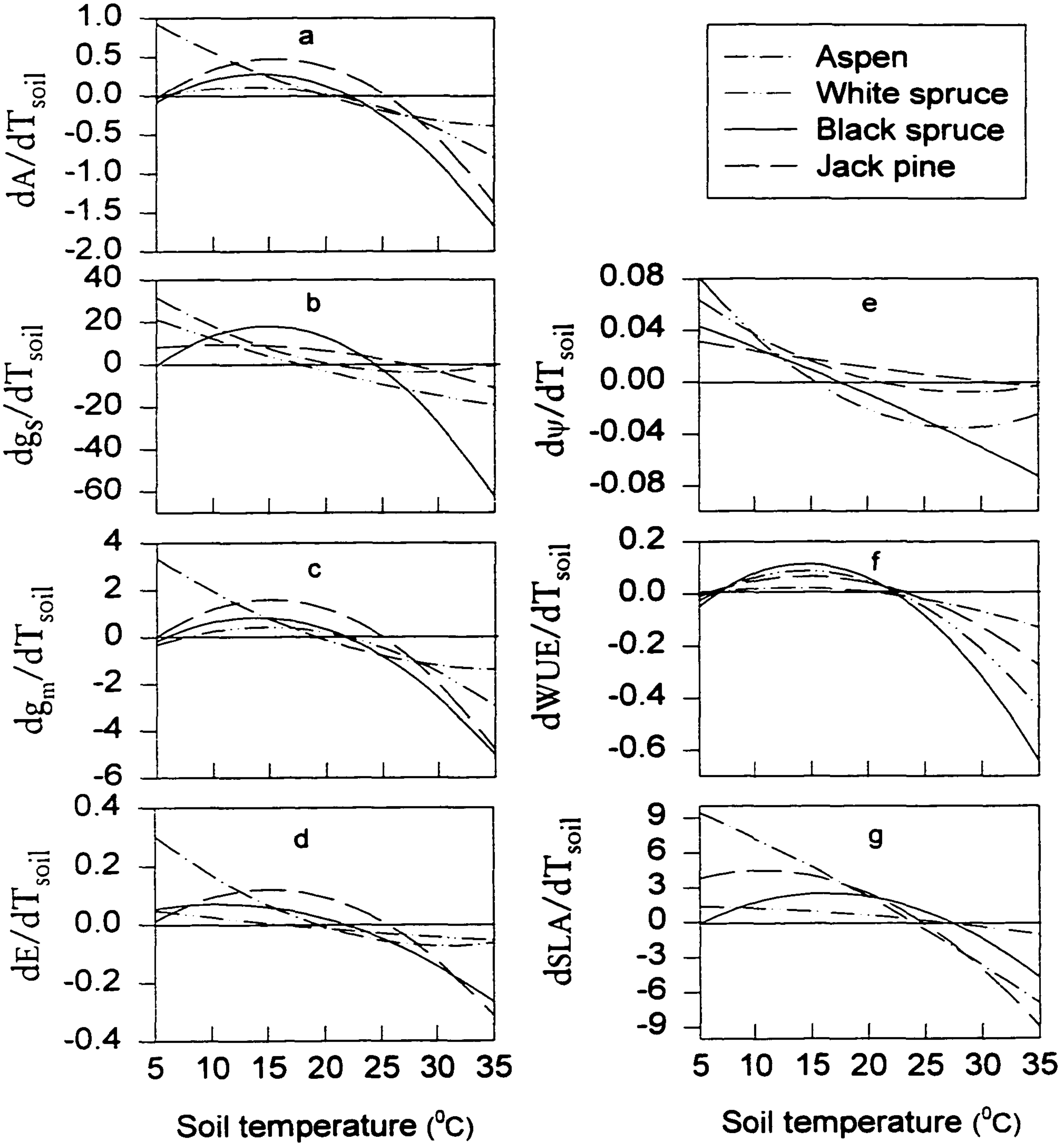

Figure 3.4. Derivative curves of the models presented in Figure 3.3. Derivative values represent the rate of change in ecophysiological variable as soil temperature changes.

Water use efficiency (*WUE*)

Soil temperature significantly influenced *WUE* (Tables 3.3 and 3.4). *WUE* at 35 °C soil temperature was lower than at all other temperatures but the difference in *WUE* between other soil temperatures was very small (< 0.18 mmol CO_2 mol^{-1} H_2O, Figure 3.2f). The soil temperature effect on *WUE* was statistically not significant in jack pine and aspen. The average *WUE* was not significantly different between species (Table 3.3). In general, the variation in *WUE* in the conifers was greater than in aspen (Figures 3.2f and 3.3f). The maximum *WUE* in both white spruce and black spruce occurred at 25 °C among the seven temperatures (Figure 3.2f). The derivative functions of models (Figure 3.4f) showed the optimum soil temperature for *WUE* was 22.9 °C for white spruce and 22.5 °C for black spruce. *WUE* of both spruces decreased as soil temperature deviated from the optimum but it was more sensitive to high soil temperatures than to low temperatures, particularly black spruce (Figures 3.3f and 3.4f). The sensitive soil temperatures of *WUE* were 14.5 °C for both white spruce and black spruce (Table 3.6).

Specific leaf area (*SLA*)

Specific leaf area was significantly affected by soil temperature in all the species but white spruce (Tables 3.3 and 3.4). The maximum *SLA* occurred at 25 °C soil temperature in all species (Figures 3.2g and 3.3g). The derivative function of the models suggests that the optimum soil temperatures for *SLA* were 23.8 °C for aspen, 24.6 °C for jack pine, 26.1 °C for white spruce and 27.2 °C for black spruce. *SLA* was the most sensitive to soil temperature at 5 °C for aspen, 10.5 °C for jack pine, 16.2 °C for black spruce (Figure 3.4g, Table 3.6). Aspen was the most sensitive to low soil temperatures followed by jack pine and black spruce, while jack pine was the most sensitive to high soil temperatures followed by aspen and black spruce (Figure 3.4g). *SLA* in aspen was much greater than that of conifers and *SLA* in jack pine and black spruce was generally greater than white spruce (Figures 3.2g and 3.3g).

Correlation between net photosynthesis and other variables

The variables that had significant correlation with *A* varied with species (Table 3.7). The photosynthesis of aspen was significantly correlated to $g_{m,}$ g_s and *WUE*. In white spruce, *A* was significantly correlated to $g_{m,}$ $g_{s,}$ *E* and ψ. For black spruce, A was significantly correlated to $g_{m,}$ $g_{s,}$ *E* and *WUE*. *A* of jack pine was significantly correlated to $g_{m,}$ g_s and *E*. Mesophyll conductance was the variable that was strongly correlated with *A* for all species combined but the relationship between *A* and g_s was weak (Figure 3.5).

DISCUSSION

This research demonstrates that each of the four species has its own sensitive soil temperature (Table 3.6). The average of sensitive soil temperatures for all the ecophysiological traits measured in each species is likely to be the low threshold soil temperature for the species to grow. Bassman (1989) stated that the low threshold soil temperature (at which ecophysiological traits decline sharply, such as, transpiration, plant water potential *etc.*) was between 2 and 10 °C for some boreal tree species, and between 12 and 13 °C for Monterey pine (Kaufmann 1977). The sensitive temperature of white spruce observed in this study (8.9 °C) was very similar to that (9 °C) reported

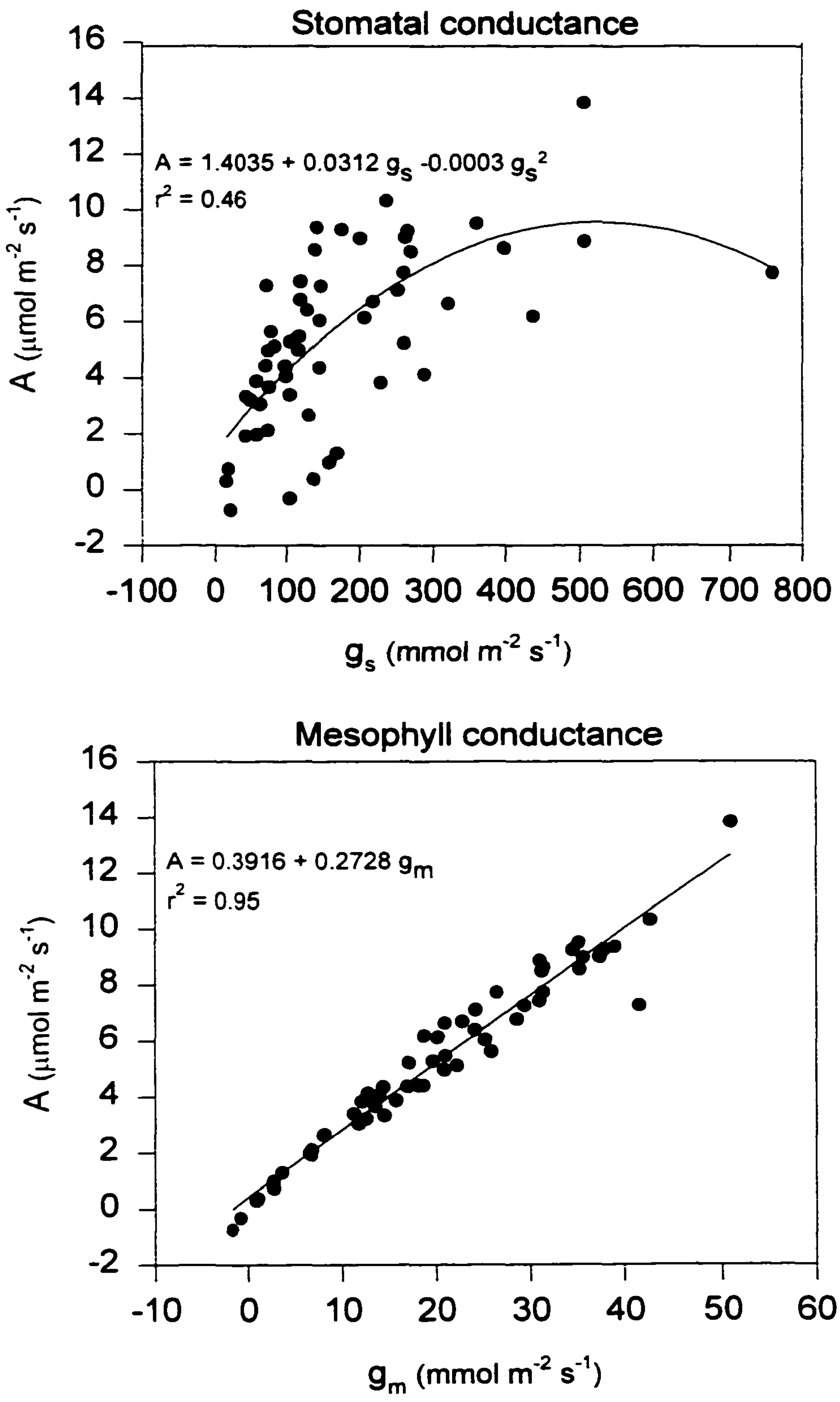

Figure 3.5. Relationships between net photosynthesis (*A*) and stomatal conductance (g_s), mesopyll conductance (g_m).

Table 3.7. Stepwise regression analysis for the relationships between net photosynthesis and stomatal conductance (g_s), mesophyll conductance (g_m), transpiration (E), xylem water potential (Ψ), specific leaf area (SLA) and instantaneous photosynthetic water use efficiency (WUE). β is coefficients of regression. T is the value of *t*-test. p is probability. r^2 is coefficients of determination.

Aspen					Jack pine				
Trait	β	T	p	r^2	Trait	β	T	p	r^2
Intercept	0.7174	2.235*	0.023	0.98	Intercept	-0.787	-3.19*	0.024	0.98
g_m	0.2455	25.49*	0.000		g_m	0.1990	21.11*	0.000	
g_s	0.0052	6.181*	0.000		E	1.0764	6.385*	0.000	
WUE	-0.226	-2.32*	0.024		g_s	0.0026	2.255*	0.028	

Black spruce					White spruce				
Trait	β	T	p	r^2	Trait	β	T	p	r^2
Intercept	-2.302	-10.6*	0.000	0.99	Intercept	0.5645	1.822	0.074	0.98
g_m	0.1670	12.77*	0.000		g_m	0.2132	36.51*	0.000	
E	1.5999	11.07*	0.000		g_s	0.0032	5.395*	0.000	
WUE	-0.526	9.503*	0.000		ψ	-0.611	-2.73*	0.009	
g_s	0.0024	3.635*	0.006		E	0.3122	2.174*	0.034	

*= significant at 95%.

by Goldstein *et al.* (1985), and the sensitive soil temperature for jack pine (12.3 °C) was similar to the low threshold soil temperature of Monterey pine (Kaufmann 1977). However, there are no reports on the low threshold soil temperatures for aspen, black spruce and jack pine. When the soil temperature was below the threshold low temperature, the ecophysiological performance of the trees declined sharply. The threshold soil temperature may have a significant impact on the range of distribution or performance of the species. Thus, if climate change elevates mean soil temperature, the northern boundary of distribution of each species will likely expand.

This study showed that the ecophysiological performance of black spruce was the least sensitive to low soil temperatures but the most sensitive to high soil temperatures among the four species. The low sensitivity to low temperature will allow this species to survive and grow on the cold and wet substrate. However, this study also showed that the optimum soil temperature for ecophysiological performance of black spruce was quite high (22.4 °C), higher than that for aspen (21.8 °C) and white spruce (19.6 °C). The result suggests that black spruce has the wider ecological amplitude and bimodal distribution. Black spruce can not only grow on wet and cold sites, but also on dry and warm sites, however, it will grow better on warmer sites than on wetlands. Given the high quality of black spruce wood for pulp and paper, this species can be planted on most boreal sites as far as soil temperature is concerned. The fact that the optimum soil temperatures for aspen, white spruce and black spruce are very close suggests that the three species may establish mixedwood stands. The results suggest that silvicultural treatments that increase soil temperatures, such as drainage of wetlands (Burns and Honkala 1990), scarification and plowing (Buse and Bell 1992), mounding and prescribed fires (McMinn 1992, Sutton 1984, Brand 1990), and ripping (Fleming *et al.* 1998), should enhance the ecophysiological performance of all three species. However, the fact that black spruce is the most sensitive to high temperature suggests that this species may not be suitable for regenerating high soil temperature sites above 25 °C. If climate change increases soil temperature, southern boundary of the spruces will be likely to diminish. It seems that 30 °C is the high threshold soil temperature for the survival of both black spruce and white spruce. Mortality of white spruce and black spruce were 49.3% and 62.5% at 30 °C, but the mortality of the spruces was nearly 80 % at 35 °C at the end of the experiment. Even though some ones were surviving, A of the spruce seedlings was near zero at 30 and 35 °C soil temperatures (Figures 3.2).

Jack pine had a much higher optimum soil temperature (26.1 °C) for ecophysiological performance than the other tree species. This may be related the adaptation of the species to fire disturbance. Soil temperatures on burned or opening sites (Hogg and Lieffers 1991) were generally close to the optimum found in this study during the summer months in the boreal forest region for the ecophysiological performance of jack pine. Thus, the soil temperature of newly burned sites should be very beneficial for the regeneration and growth of jack pine. Because of its serotinous cones, the natural regeneration of jack pine generally occurs after wildfires (Burns and Honkala 1990). The optimum soil temperature for ecophysiological performance found in this study was also similar to that for growth (27 °C) of the same species reported by Heninger and White (1974).

The ecophysiological performance of aspen was relatively insensitive to a wide range of soil temperatures (15 to 35 °C). This result suggests that aspen can survive and grow over a wide range of soil temperatures. In the study, the survival rate of aspen was 100 % across all soil temperature treatments. In contrast, only 20% of black and white spruce seedlings, and 80% of jack pine survived at in the 35 °C treatment.

WUE in black spruce was the most sensitive to soil temperature among the four species (Figure 3.4f). The synchronised changes in photosynthetic and transpiration rates in response to changes in soil temperature resulted in relatively constant *WUE* over a wide range of soil temperature in aspen, jack pine and white spruce. This result is in agreement with the study by Zwiazek and Black (1988), where no difference in *WUE* of black spruce was found between different soil temperatures. However, *WUE* of black spruce declined to a much greater extent as soil temperature deviated from the optimum. *WUE* is a measure of the coordination between mesophyll capacity to fix CO_2 and stomatal conductance for supplying CO_2. The fact that *WUE* of black spruce was more sensitive to soil temperature suggests that the coordination between mesophyll capacity and *gs* was poor in the acclimation to soil temperature. It is generally believed that soil temperature affects plant ecophysiological traits mainly by influencing the water absorption by roots (Evans 1975). For example, low soil temperature increases the viscosity of soil solution (Lawrence and Oechel 1983) and root resistance (Kaufmann 1977), and the absorbing activity of the root (Elfring *et al.* 1972). Consequently, water deficit is most likely to occur under unfavorable soil temperatures, which will in turn limit the ecophysiological activity of the foliage. However, in the study, the difference in ψ between treatments was very small (Figure 3.2) and ψ values were all above the thresholds for limiting photosynthesis (e.g., -2.4 MPa for black spruce, Dang *et al.* 1997). The average midday ψ was -1.17 MPa for black spruce. These results suggested that water was not a limiting factor for the ecophysiological traits. Thus, soil temperature must have affected the leaf ecophysiological traits through some other mechanisms.

The results of this study also suggest that mesophyll conductance was primarily responsible for changes in photosynthesis in response to changes in soil temperature, whereas stomatal conductance exerted little limitation. For all four species, mesophyll conductance was closely and linearly correlated to photosynthesis but the relationship between A and g_S is relatively poor (Figure 3.5). The stepwise regression analysis also indicated that mesophyll conductance was the most important variable affecting A in all species (Table 3.7). Similar results were found in the response of black spruce to changes in soil moisture (Dang *et al.* 1991). The mechanism of soil temperature effects on mesophyll activity is not known. Mesophyll conductance includes the conductance to the diffusion of CO_2 across the cell wall, membranes, and the cytoplasm to the carboxylation site, and various biochemical reactions (Bradford and Hsiao 1982, Edwards and Walker 1983). Any of these could have contributed to the decrease in mesophyll conductance.

The change in *SLA* with soil temperature was much greater in aspen than in the conifers (Figures 3.3g and 3.4g). The leaves were thinner and longer at the optimum soil temperature. Similar results were reported by Hall *et al.* (1993) and Meinzer *et al.* (1997). The result suggests broadleaf morphology is probably more adaptable to soil temperatures than is that of needles. This suggests that the trees tend to maximize their leaf area when soil temperature is more favorable. This may be related to the ease of water uptake and supply to leaves at different soil temperatures.

Boreal forest is characterized by its cold continental climate. For example, the average July soil temperature is about 15 °C in the boreal forest of Ontario (Stathers and

Spittlehouse 1990). Modeling research shows that global warming will likely increase the temperature of the Earth's surface from 1.9 in 1990 to 2.9 °C in 2100 (Wegley 1999). This research suggests that the four boreal species will likely respond to soil warming, i.e. optimum soil temperature for the ecophysiological traits was higher than 15 °C. Global warming will likely promote boreal tree growth and the fixation of atmospheric CO_2. The northern boundary may expand further north. If soil warming is above optimum temperature, the southern boundary of the boreal forest may also move northward. However, global change is likely to trigger a series of changes in other soil and atmospheric factors as well as soil temperature. For example, global warming will also result in soil drying and more fluctuating relative humidity, boost microbial activities and nutrient cycling in soil, and increase air temperature etc. Each of them can contribute to ecophysiological performance of plants. Therefore, the response of boreal trees will be much more complex than indicated by this research.

Ecophysiological traits are important indicators that reflect the ability of a species to regenerate, survive and grow. Except those examined in this study, other ecophysiological traits are also important, such as cold hardness, root resistance, carbon allocation, nitrogen allocation, nitrogen use efficiency, etc. The traits indicate the possible responses of plant growth and survival to environmental conditions in various ways. For example, the sensitive soil temperature of white spruce observed was 8.9 °C at which changes in ecophysiological traits was most sensitive to changes in soil temperature. Goldstein *et al.* (1985) documented that root resistance in white spruce increased sharply below 9 °C, which was low threshold soil temperature.

In this study, ecophysiological traits were measured only once in the third month of the experiment. At that time, foliage of the species was fully expanded and the seedlings were in rapid growth period. During this stage, ecophysiological traits are generally stable. After this phase, senescence will cause changes in ecophysiological traits. For example, when foliage senesces, the rate of photosynthesis will decline. Such declines may affect the conclusions.

For the experiment, fertilization concentration was controlled using conventional loading method. Soil temperature also influences soil nutrient cycling and nutrient uptake by the trees, resulting in changes in ecophysiological traits. In general, the concentrations of N, P and K in needles of plants increased with an increase in soil temperature from 0 to 25 °C (Binkley and Richter 1986, V an Cleve *et al.* 1990). Net photosynthesis decreased with decreasing foliage nitrogen content (Binkley and Richter 1986). In the experiment, optimum fertilization concentration was applied as recommendated by Landies *et al* (1989). Symptom of nutrient deficit on the seedlings foliage did not occur except in the 5 and 10 °C treatments where needles in the conifers became light yellow, indicating the occurrence of nutrient deficiency although there was sufficient nutrients in the growing medium.

Soil temperature in this study was almost constant throughout the experiment, but in nature, soil temperature varies daily and seasonally. Due to limitations in technique and facility, the daily fluctuation in soil temperature was not be simulated in the laboratory. Fluctuating soil temperatures might have produced a different result.

CONCLUSIONS

Soil temperature treatments significantly affected the ecophysiological traits of aspen, white spruce, black spruce and jack pine seedlings. Polynomial models of the relationships between soil temperature and ecophysiological traits (i.e. photosynthesis, stomatal conductance, mesophyll conductance, water use efficiency, transpiration, specific leaf area and midday water potential) showed that the optimum soil temperature varied with tree species: 19.6 °C for white spruce, 21.8 °C for aspen, 22.4 °C for black spruce and 26.1 °C for jack pine. The soil temperature that ecophysiological traits were the most sensitive to were also different for different tree species: 6.2 °C for aspen, 8.9 °C for white spruce, 12.3 °C for jack pine and 12.7 °C for black spruce. In general, aspen was the most sensitive to low temperatures, while black spruce was the most sensitive to high temperatures. 80% of black spruce and white spruce in the 35 °C soil temperature treatment died four months after the initiation of the treatment.

The study suggests that soil temperature must have affected the leaf ecophysiological traits through mechanisms other than water potential. The study demonstrated modifying soil temperatures through silvicultural measures can have a significant impact on the survival and improve the ecophysiological performance of tree seedlings. The study also suggests that southern and northern boundaries of boreal forest might move northward with further global warming.

The study also shows that the ecophysiological traits declined sharply at some threshold soil temperature above 28 °C (Figures 3.3, 3.4). Plants may die when soil temperature is above the high threshold soil temperature.

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