

Heat Tolerance of Selected Provenances of Atlantic White Cedar

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ABSTRACT. Seedlings of six provenances of Atlantic white cedar [*Chamaecyparis thyoides* (L.) B.S.P.] (Escambia Co., Ala., Santa Rosa Co., Fla., Wayne Co., N.C., Burlington Co., N.J., New London Co., Conn., and Barnstable Co., Mass.) were grown in controlled-environment chambers for 12 weeks under 16-hour photoperiods with 16-hour days/8-hour nights of 22/18 °C, 26/22 °C, 30/26 °C, 34/30 °C or 38/34 °C. Considerable variation in height, foliage color, and overall plant size was observed among plants from the various provenances. Seedlings from the two most northern provenances (Massachusetts and Connecticut) were most heat sensitive as indicated by decreasing growth rates at temperature regimes >22/18 °C. In contrast, plants from New Jersey and the three southern provenances (North Carolina, Florida, and Alabama) exhibited greater heat tolerance as indicated by steady or increasing growth rates and greater top and root dry weights as temperature regimes increased above 22/18 °C. Growth rates of seedlings from the four aforementioned provenances decreased rapidly at temperature regimes >30/26 °C suggesting low species tolerance to high temperatures. There were no significant differences in seedling dry matter production among provenances when temperature regimes were ≥34/30 °C. Net shoot photosynthesis and dark respiration of plants did not vary by provenance; however, net photosynthesis was temperature sensitive and decreased at temperature regimes >26/22 °C. Foliar respiration rates increased as temperature increased from 22/18 °C to 26/22 °C, but then remained relatively constant or decreased at higher temperature regimes. Plants at temperatures ≥34/30 °C exhibited severe stunting, chlorosis, and necrosis on branch tips. However, tissue concentrations of N, P, K, Ca, Mg, Fe, Zn, Cu, and Mn generally increased with temperature regimes >30/26 °C indicating that mineral nutrient concentration was not a limiting factor at high temperatures.

Atlantic white cedar [*Chamaecyparis thyoides* (L.) B. S. P.], also known as southern white cedar, has a wide distribution. This evergreen tree is native to freshwater swamps and bogs along a narrow coastal belt, 80 to 209 km wide from the southern coast of Maine to South Carolina, with isolated stands in Georgia and eastern Florida (Korstian and Brush, 1931; Little and Garrett, 1990). It also occurs from the panhandle of Florida to Mississippi, where some regard it as a separate botanical variety, *Chamaecyparis thyoides* var. *henryae* (Li) Little (Little, Jr., 1966). Because of the wide distribution of Atlantic white cedar, it would be beneficial to study variation in heat tolerance among plants from different provenances to understand the environmental tolerance of this species. In turn, these data would aid nurserymen and foresters in selecting superior provenances based on a designated area's climatic conditions.

Temperature is one of the most significant determinants of geographical distribution of plants. In addition, spatial distribution of a plant species is limited by the range of climatic conditions to which the species can adapt. High temperatures can also occur during nursery stock production in greenhouses or nursery beds where high soil temperatures are common. Seedlings are especially susceptible to high temperature stress (Colombo et al.,

1992; Colombo and Timmer, 1992).

Variation in thermotolerance of photosynthesis and respiratory systems can be principal factors in differential growth under high temperatures. Whole plant net photosynthesis, in particular, is one of the most heat-sensitive processes influencing plant growth (Björkman et al., 1980). The potential for photosynthetic acclimation and tolerance to high temperatures is variable among species and often reflects the temperature regime of a species' native habitat (Berry and Björkman, 1980). Large differences can also exist in photosynthetic capacity among plants from different provenances of the same species, particularly in conifers (Kozłowski and Pallardy, 1997).

Foresters are aware of the importance of selecting seed for plantation establishment from the most suitable provenances available. For many conifers, differences in productivity up to 100% have been attributed to seed source (Thulin, 1957). Often, less variation occurs among species than among provenances of a single species that inhabits widely differing environments (Zobel and Talbert, 1984). For example, seedlings of Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] from different geographic origins differ in growth even under common environmental conditions (Sorensen, 1967). Such growth differences could result from changes in seasonal duration of active growth, CO₂ exchange rates or distribution of assimilates (Sorensen and Ferrell, 1973). Provenances of certain species might also respond differently when grown in widely separated geographic areas, in different soils, or when managed differently (Jaynes et al., 1984).

The ability to absorb nutrients is also an important component of plant adaptation. Clonal and provenance variations in absorption of mineral nutrients can occur and are correlated with differences in growth rates (Kozłowski and Pallardy, 1997). For example, accumulation of N, P, Mg, Na, and B varied among 45 provenances of Scots pine (*Pinus sylvestris* L.) (Steinbeck, 1966). Plants have an ideal temperature range for optimum absorption of various mineral nutrients (Pisek et al., 1973). With regard to heat

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stress, Bakanova (1970) reported that Ca can increase heat tolerance of terrestrial plants. The effect of high temperature on mineral nutrient concentration of Atlantic white cedar has not been studied.

Optimal seedling growth of Atlantic white cedar from North Carolina was achieved by a day/night cycle of 30/22 °C and long days (9-h days with a 3-h night interruption) (Jull, 1998). Whether other provenances of Atlantic white cedar respond similarly to temperature is currently unknown. In addition, there are no published reports comparing effects of high temperature on seedling growth of different provenances of Atlantic white cedar. Therefore, the objective of this study was to evaluate selected provenances of Atlantic white cedar for heat tolerance by comparing growth, net photosynthesis, dark respiration, and tissue mineral nutrient concentration.

Materials and Methods

PLANT MATERIAL AND EXPERIMENTAL CONDITIONS. Mature cones of six provenances of Atlantic white cedar (Escambia Co., Ala., Santa Rosa Co., Fla., Wayne Co., N.C., Burlington Co., N.J., New London Co., Conn., and Barnstable Co., Mass.) were harvested from native stands of open pollinated trees during Fall 1994 (Alabama, North Carolina, New Jersey, and Connecticut), Winter 1995 (Massachusetts), or Fall 1995 (Florida). Seed extraction, cleaning, and germination followed procedures described by Jull et al. (1998).

Following germination, seedlings were planted 6.2 mm deep in flats containing a medium of 1 peat : 1 perlite : 1 coarse vermiculite (by vol.) in Jan. 1997. The flats were placed under natural irradiance on a greenhouse bench supplied with intermittent mist that operated daily for 6 s every 10 min from 7:00 AM to sunset. Day/night greenhouse temperatures were 24/18 ± 4 °C. After 2 weeks, flats were transferred to the Southeastern Plant Environment Laboratory (Phytotron). The seedlings were grown for 7 weeks in a greenhouse maintained at a 9/15-h thermoperiod of 26/22 ± 3 °C with natural irradiance. Seedlings received a 3-h night interruption from 11:00 PM to 2:00 AM daily from incandescent bulbs that provided a photosynthetic photon flux (*PPF*) (400 to 700 nm) of 11 to 12 μmol·m⁻²·s⁻¹, as measured at the top of the flats with a cosine corrected quantum-radiometer-photometer (LI-185; LI-COR, Lincoln, Neb.). Plants were fertilized weekly for 3 weeks with the standard Phytotron nutrient solution (Downs and Thomas, 1991) and later, twice weekly, for the last 4 weeks in the greenhouse. Deionized water was used on remaining days.

On 1 Apr. 1997, seedlings were transplanted individually into 0.95-L (#100) nursery containers using a medium of 1 peat : 1 perlite : 1 coarse vermiculite (by volume). The following day, plants were transferred to controlled environment, Phytotron B-chambers (Downs and Thomas, 1991) maintained at 16/8-h thermoperiods of 26/22 °C with a 16-h photoperiod.

On 16 Apr. 1997, uniform seedlings of each provenance were selected and placed into B-chambers maintained at varying temperature regimes. At treatment initiation, 10 plants from each provenance were harvested to determine plant height, and top, stem, and root dry weights (dried at 70 °C for 72 h).

Seedlings were arranged as a 5 × 6 factorial in a split-plot design with temperature regimes as the main plots and provenances as the subplots using 14 single-plant replications per treatment. Within each chamber, plants were arranged in a randomized complete block design. The main plots were five, 16-h day/8-h night temperature regimes of 22/18 °C, 26/22 °C, 30/26

°C, 34/30 °C or 38/34 °C each with a 16-h photoperiod of 550 to 600 μmol·m⁻²·s⁻¹ [photosynthetically active radiation (*PAR*)]. Temperatures were maintained within ±0.25 °C of the set point.

Relative humidity was >70% and CO₂ concentration was 300 to 400 μmol·m⁻²·s⁻¹. Seedlings were fertilized twice weekly with standard Phytotron nutrient solution and watered with deionized water on remaining days.

On 10 June 1997, a soil temperature recorder was inserted into two randomly selected pots per chamber for 24 h to monitor root zone temperatures (Omega Temperature Recorder, Omega Engineering, Inc., Stamford, Conn.). Thermocouples were inserted on the side of each pot ≈5 cm deep. Root zone temperatures ranged from -2.3 to 4.3 °C from ambient chamber temperatures.

SHOOT GAS EXCHANGE. On 8 July 1997, shoot gas exchange was measured with a portable infrared gas exchange system (LI-6200). *PAR*, air and shoot temperatures, and relative humidity inside a 0.25-L leaf chamber were measured concurrently with gas exchange for 30 s. Data were recorded on five plants per provenance at each temperature regime, except at 38/34 °C due to death of plants. Measurements were taken from lateral branches located ≈10 to 15 cm from the apex of the terminal portion of the plant.

Dark respiration was measured the following day using the same procedures as those for the photosynthesis measurements, with one variation. The 0.25-L leaf chamber was enclosed completely in aluminum foil to exclude light. Dark respiration and net photosynthesis of shoots were expressed on a leaf area basis, and leaf areas were determined using a Monochrome Agvision System 286 Image Analyzer (Decagon Devices, Inc., Pullman, Wash.). Different branches were sampled for gas exchange in the light and dark.

On 11 July 1997, 12 weeks after treatment initiation, plant heights were recorded. However, plants in the 38/34 °C chamber were harvested after 8.5 weeks due to death of plants. Roots were washed free of medium and seedlings were separated into foliage, stems (lower, woody portion), and roots. All tissue was dried at 70 °C for 72 h and weighed. Data were used to calculate the following: total plant dry weight (foliage + root + stem dry weight), growth rate [(final total plant dry weight - initial total plant dry weight)/duration of experiment in weeks], and root : shoot ratio (root dry weight/top dry weight).

TISSUE ANALYSES. Plants at the higher temperature regimes (34/30 °C and 38/34 °C) developed chlorotic shoot tips after 4 weeks. Decreased tissue nutrient concentrations at higher temperatures were suspected. Therefore, tops of five plants per provenance per temperature regime were sampled for tissue nutrient analyses the day before plants were harvested. After drying, tops of plants were ground in a Wiley mill to pass a 40-mesh (0.425-mm) screen. Tissue samples, (1.25 g) were combusted at 490 °C for 6 h. The resulting ash was dissolved in 10 mL 6 N HCl and adjusted to 50 mL with deionized, distilled water. Phosphorus, K, Ca, Mg, Cu, Fe, Mn, and Zn concentrations were determined by inductively coupled plasma emission spectroscopy. Nitrogen was determined using 10-mg samples in a CHN elemental analyzer (model 2400; Perkin Elmer Corp., Norwalk, Conn.). All nutrient analyses were conducted at the Analytical Service Laboratory, Department of Soil Science, North Carolina State University.

DATA ANALYSES. Data were subjected to analysis of variance (ANOVA) procedures (SAS Inst., 1990). Correlations among specified variables were examined. Means of provenances were compared by least significant difference (LSD) procedures at *P* =

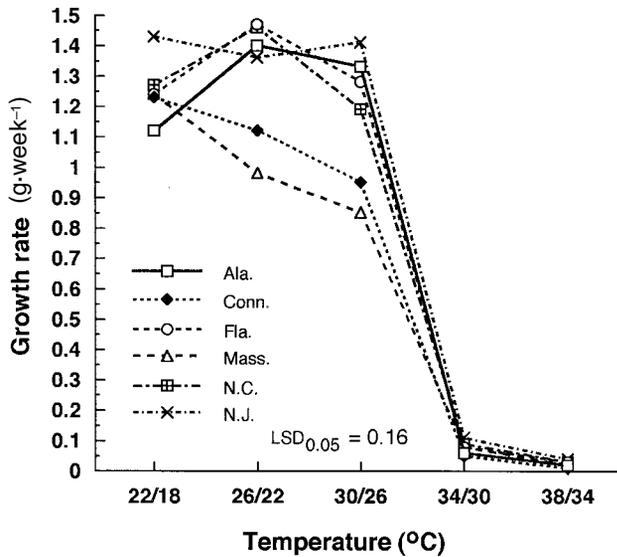


Fig. 1. Effects of temperature regimes (16-h days/8-h nights) and provenance on growth rate of seedlings of Atlantic white cedar. Each symbol is the mean of 14 observations.

0.05. Simple linear or polynomial curves were fitted to the temperature data when significant trends were identified in separate regression analyses. Growth data from plants at 38/34 °C were omitted from the regression analyses, except for mineral nutrient data, since the plants at this temperature regime were dead at 8.5 weeks. Average daily temperatures [(day temperature × 16 h) + (night temperature × 8 h)/24 h] were calculated for each temperature regime for the growth rate data. The average daily temperature for each temperature regime is as follows: 22/18 °C (20.7 °C), 26/22 °C (24.7 °C), 30/26 °C (28.7 °C), 34/30 °C (32.7 °C), 38/34 °C (36.7 °C). The growth rate temperature optimum for each provenance was estimated by calculating the temperature at which the first-order derivative of the average daily temperature response of growth rate was equal to zero.

Results and Discussion

Growth rates (increases in total plant dry weight/time) were a function of an interaction between provenance and temperature regime ($P = 0.0001$) (Fig. 1). The two most northern provenances (Massachusetts and Connecticut), were very heat sensitive as indicated by decreasing growth rates at temperature regimes >22/18 °C. In contrast, the New Jersey and three southern provenances (North Carolina, Florida, and Alabama), were more heat tolerant as indicated by steady or increasing growth rates as temperature regimes increased above 22/18 °C. Similarly, the most vigorous provenances of eastern white pine (*Pinus strobus* L.) are from the southern part of its native range; the least vigorous from the north (Matheson, 1977). Growth rate results for average daily temperatures were similar to the temperature regime data (data not presented).

Regression analyses revealed significant quadratic responses ($P = 0.0001$) for growth rate for each provenance over average daily temperatures of 20.7 to 32.7 °C (data not presented). Temperature optima for Massachusetts, Connecticut, New Jersey, North Carolina, Florida, and Alabama provenances were 21.1, 22.9, 24.2, 24.3, 24.6, and 25.0 °C, respectively. The temperature optima was calculated from the derivative of individual provenance regression equations for growth rate at the

average daily temperature [Massachusetts ($y = -231.42 + 33.37x - 0.79x^2$), Connecticut ($y = -520.67 + 56.47x - 1.23x^2$), New Jersey ($y = -961.57 + 92.74x - 1.92x^2$), North Carolina ($y = -1039.04 + 97.89x - 2.01x^2$), Florida ($y = -1190.87 + 109.34x - 2.22x^2$), and Alabama ($y = -1363.62 + 121.16x - 2.42x^2$)]. Growth rates decreased rapidly for all provenances when average daily temperatures exceeded 28.7 °C, suggesting Atlantic white cedar exhibits relatively low tolerance to high temperatures. Dry matter production was uniformly poor among the provenances when average daily temperatures were ≥ 32.7 °C and plants grown at 36.7 °C were dead 8.5 weeks after treatment initiation. Similarly, a 35 °C day in combination with 23 or 27 °C nights resulted in death of seedlings of redwood [*Sequoia sempervirens* (D. Don) Endl.] (Hellmers, 1966).

Temperature response of top and root dry weight for seedlings varied according to provenance, as indicated by significant provenance by temperature interactions ($P < 0.05$) (Fig. 2). Plants from the three southern provenances, in addition to the New

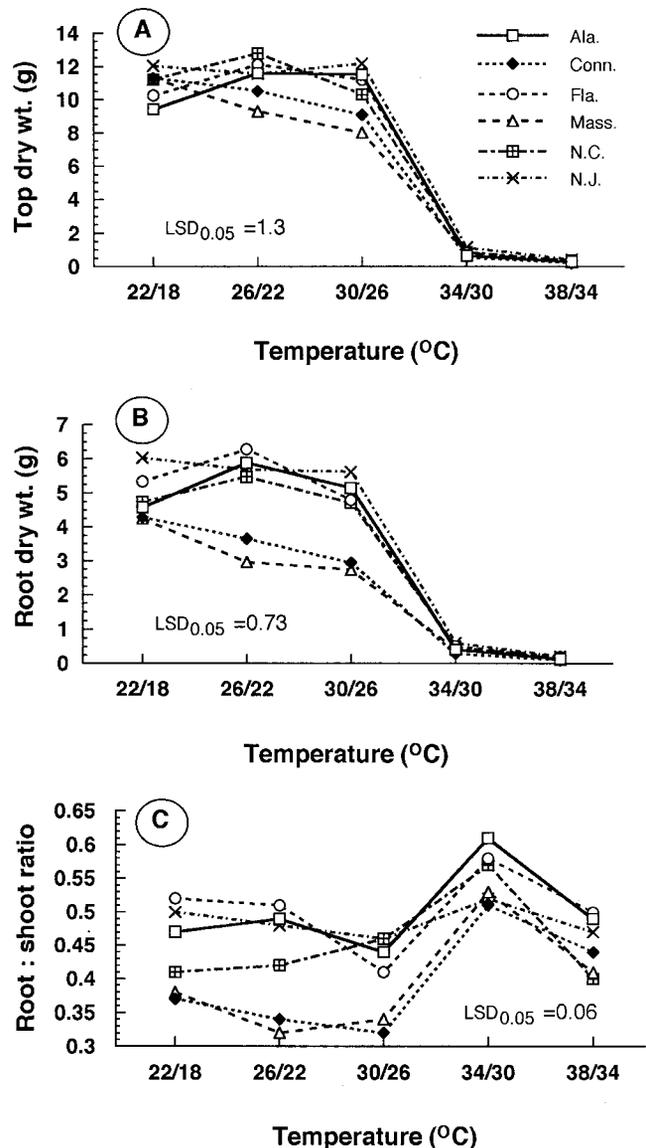


Fig. 2. Effects of temperature regimes (16-h days/8-h nights) and provenance on seedling growth of Atlantic white cedar: (A) top dry weight, (B) root dry weight, and (C) root:shoot ratio. Legend in A applies to all figures. In A–C, each symbol is the mean of 14 observations.

Jersey provenance, exhibited increasing top dry weight when temperature regimes increased from 22/18 °C to 26/22 °C. However, similar to growth rate, temperature regimes >30/26 °C severely inhibited top and root dry weights of all plants (Fig. 2A and B). Top and root dry weights of seedlings from Massachusetts and Connecticut decreased at temperature regimes >22/18 °C. Root growth appeared to be more temperature sensitive than top growth as temperature regimes increased from 22/18 to 30/26 °C. Significant quadratic responses ($P < 0.05$) were detected for top and root dry weights for all plants over the temperature regime range of 22/18 to 34/30 °C. Jull (1998) reported maximum top growth of seedlings of Atlantic white cedar from North Carolina at days/nights of 26/22 °C.

At lower temperature regimes (22/18 to 30/26 °C), plants from the two most northern provenances (Massachusetts and Connecticut) had lower root : shoot ratios than the New Jersey, Florida, and Alabama provenances (Fig. 2C). The root : shoot ratio for the North Carolina provenance was not significantly different from the two northern provenances at 22/18 °C. Root : shoot ratio increased for all plants between 30/26 °C and 34/30 °C then decreased at temperature regimes >34/30 °C. Similarly, Jull (1998) reported increased root : shoot ratios for North Carolina seedlings of Atlantic white cedar with increasing temperatures from 18/22 to 30/26 °C. At temperature regimes of 22/18 to 34/30 °C, seedlings from the Alabama, Florida, Connecticut, and Massachusetts provenances exhibited a quadratic response ($P < 0.01$) for root : shoot ratio. The root : shoot ratio of North Carolina seedlings responded linearly to temperature ($P < 0.001$) whereas the root : shoot ratio of New Jersey seedlings was not influenced by temperature.

Net photosynthesis of all plants was not affected by provenance. However, there was a significant temperature main effect ($P = 0.0001$) (Fig. 3A). Similarly, northern and southern provenances of pitch pine (*Pinus radiata* D. Don) originating from areas with very different thermal regimes had the same pattern of photosynthetic temperature response (Ledig et al., 1977). In the present study across all provenances, seedlings exhibited a quadratic response with increasing temperature regimes ($P = 0.0001$; $y = -54.48 + 4.78x + -0.09x^2$; $R^2 = 0.75$). Net photosynthesis was temperature sensitive and decreased at temperature regimes >26/22 °C. In comparison, net photosynthesis was maximized at 20 °C for seedlings of Hinoki false cypress [*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.] (Negisi and Satoo, 1961). Similarly, a rapid decrease in CO₂ uptake occurred at a constant 30 °C for trees of red spruce (*Picea rubens* Sarg.) with zero or negative carbon uptake at constant temperature regimes between 35 and 40 °C (Vann et al., 1994).

Decreases in gas exchange and dry matter accumulation at temperature regimes >30/26 °C for all provenances, in particular the southern provenances, is intriguing. Neilson et al. (1972) suggested that conifers may compensate for low net assimilation rates during the growing season by photosynthesizing throughout the year. Net photosynthesis of seedlings of loblolly pine (*Pinus taeda* L.), measured over the course of a year, peaked in late October. Seedlings of a Florida provenance of loblolly pine had greater photosynthetic rates averaged over the entire growing season compared to those from other sources (Boltz et al., 1986). Photosynthetic measurements in the field have also shown that winter carbon assimilation can be significant in regions where winter climates are mild, such as the southeastern United States, with trees from colder regions lacking this characteristic (Bourdeau, 1959; Kozlowski and Pallardy, 1997; Ludlow and

Jarvis, 1971). Measurements of seasonal photosynthetic rates of provenances of Atlantic white cedar may explain how southern provenances cope with temperature extremes intrinsic to its native habitat.

Dark respiration of plants also was not affected by provenance; however, temperature had a significant effect ($P = 0.0001$) (Fig. 3B). In comparison, no provenance differences were observed in shoot respiration rates of jack pine and eastern white pine (Bourdeau, 1963; Lavigne, 1996). In this study, seedlings exhibited a quadratic response to temperature ($P = 0.0001$; $y = -35.48 + 2.28x + -0.04x^2$; $R^2 = 0.22$). Foliar respiration rates increased from 22/18 °C to 26/22 °C, but then remained relatively constant or decreased at higher temperature regimes. This decrease in dark respiration could have been due to physiological and morphological changes at higher temperature regimes which resulted in lower respiration per unit leaf area.

Considerable variation in height, foliage color, and overall plant size was observed among the various provenances. In general, foliage of the northern provenances (Massachusetts and

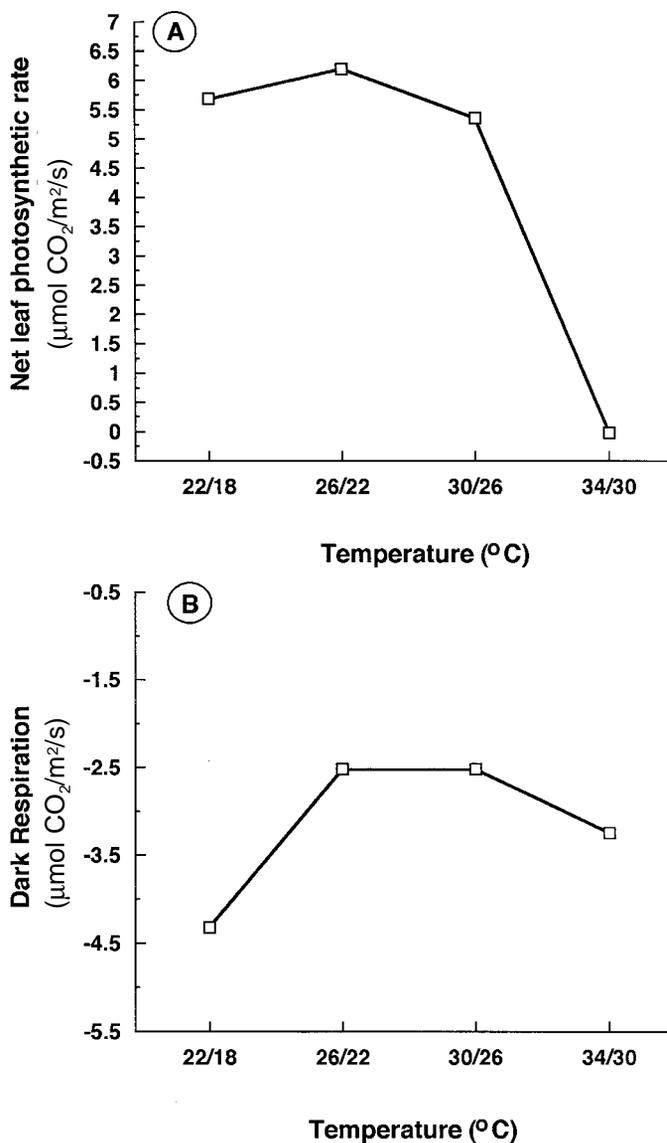


Fig. 3. Effect of temperature regimes (16-h days/8-h nights) on seedling growth of Atlantic white cedar: (A) net photosynthesis, and (B) dark respiration. In both, each symbol is the mean of 30 observations.

Connecticut), exhibited a blue-green to bluish color with waxy, glaucous markings on predominately scalelike leaves. Foliage of the southern provenances (Alabama and Florida), exhibited a mixture of scale and awl-like leaves, with a yellow-green to lime-green color. The North Carolina and New Jersey provenances had intermediate characteristics, but more closely resembled the extreme southern provenances. Variation in foliage color and leaf morphology agreed with observations of Durr (1997). Large differences have also been reported in overall plant size, form, height, and foliage color among provenances of jack pine (*Pinus banksiana* Lamb.), eastern white pine (*Pinus strobus* L.), blue spruce (*Picea pungens* Engelm.), and Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco.] (Jaynes et al., 1984; Matheson, 1977; Schantz-Hansen and Jensen, 1952; Townsend and Douglass, 1990).

Plants at temperature regimes $\geq 34/30$ °C exhibited severe stunting, chlorosis, and necrosis on branch tips. Temperature had a significant effect on tissue N, Mg, and Mn concentrations.

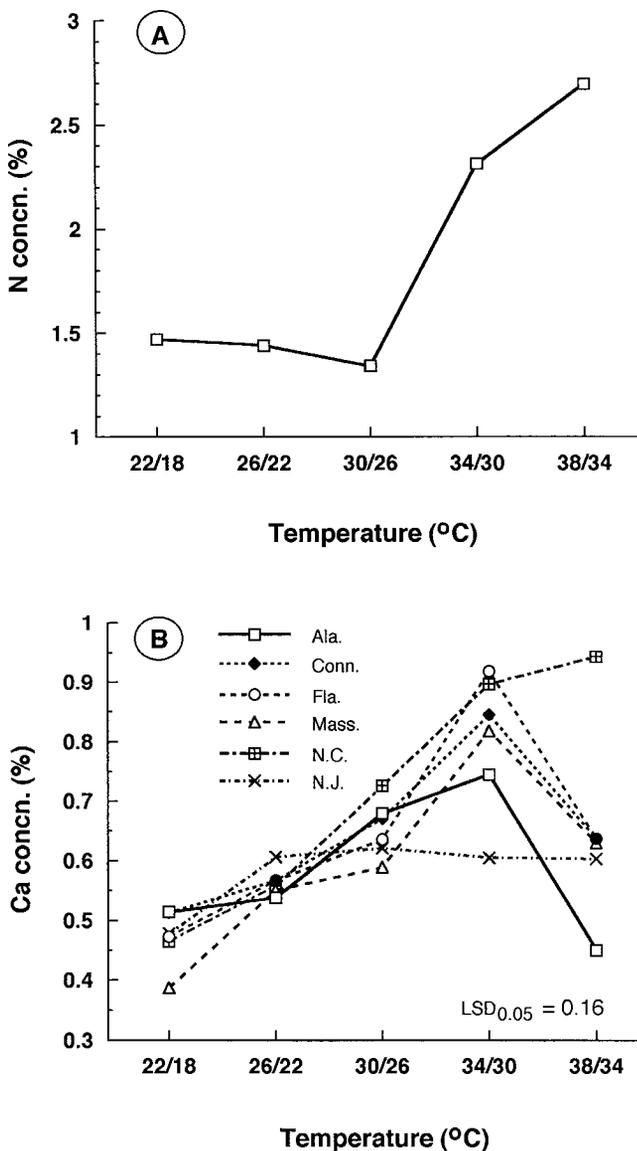


Fig. 4. Effects of temperature regimes (16-h days/8-h nights) on seedling growth of Atlantic white cedar: (A) N concentration combined over all provenances. Each symbol is the mean of 30 observations; (B) Ca concentration of each provenance. Each symbol is the mean of 5 observations.

Response of N concentration to all temperature regimes was quadratic ($P = 0.0001$; $y = 6.48 + -0.41x + 0.01x^2$; $R^2 = 0.74$) with maximum tissue concentrations at $38/34$ °C (Fig. 4A). Magnesium and Mn showed similar responses (data not presented). There were significant interactions between temperature and provenance for P, K, Ca, Cu, Fe, and Zn. However, concentrations of these nutrients generally increased with temperature indicating that tissue nutrient concentration was not a limiting factor at high temperature regimes.

With the exception of the New Jersey and North Carolina provenances, Ca was the only mineral nutrient that decreased at temperature regimes above $34/30$ °C (Fig. 4B). Regression analysis revealed significant quadratic responses ($P < 0.05$) for Ca concentration for seedlings from Alabama, Florida, and Connecticut provenances, whereas Massachusetts and North Carolina seedlings exhibited linear responses ($P < 0.001$) to temperature regime. New Jersey seedlings were not influenced by temperature. Dry matter production, particularly root growth, was limited severely at high temperatures (Fig. 2B). Calcium is absorbed by young root tips. Factors which prevent growth of new roots, such as temperature extremes, might reduce Ca uptake and thus induce Ca deficiency (Mengel and Kirkby, 1987). However, root growth was limited more severely at lower temperature regimes (between $30/26$ to $34/30$ °C) than that at which Ca concentration decreased, suggesting it was not a primary limiting factor.

Since tissue mineral nutrient concentrations were not limited at high temperature regimes, the chlorotic shoot tips may have been due to high temperature inhibition of other metabolic processes in addition to anatomical changes within the leaves (Smith and Silen, 1963). Mostowska (1997) reported that a decrease in the rate of photosynthesis is often accompanied by ultrastructural changes to the chloroplasts. Loss of chlorophyll between 32 and 40 °C in needles of red spruce was due to breakdown of chloroplast membranes (Vann et al., 1994). In comparison to lower temperature regimes, plants of rye (*Secale cereale* L.) grown at temperature regimes above 32 °C were deficient in chlorophyll and chloroplastic rRNA (Feierabend, 1977).

In summary, results indicate that plants from different provenances of Atlantic white cedar vary in heat tolerance. The northern provenances of Massachusetts and Connecticut were the most heat-sensitive as indicated by a low temperature optima for growth. The New Jersey and southern provenances (North Carolina, Florida, and Alabama) had greater heat tolerance and differential growth as indicated by their higher temperature optima. Heat tolerance at these moderately high temperature regimes, however, did not appear to result from differences in net photosynthesis, dark respiration, or mineral nutrient concentration. A temperature regime $\geq 34/30$ °C severely inhibited growth of all provenances suggesting Atlantic white cedar exhibits low relative tolerance to higher temperatures.

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