High Root-zone Temperature Causes Similar Changes in Water Relations and Growth of Silver Maples from 33° and 44°N Latitude

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ABSTRACT. Information on the heat resistance of silver maple (*Acer saccharinum* L.) could help develop stress-resistant Freeman maples (*Acer ×freemanii* E. Murray). Our first objective was to determine how 26, 30, 32, 34, and 36 °C in the root zone affect growth and water relations of plants from rooted cuttings of a silver maple clone indigenous to Mississippi (33.3 °N latitude). Fresh mass increased over time for plants at all temperatures and was highest for plants with root zones at 30 °C. Quadratic regression functions predicted maximal plant dry mass, leaf surface area, and stomatal conductance at 29, 29, and 28 °C, respectively. Stem xylem water potential (Ψ) during the photoperiod decreased linearly with increasing root-zone temperature from –0.83 MPa at 26 °C to –1.05 MPa at 36 °C. Our second objective was to compare six clones of silver maple from the Mississippi location with six clones from 44.4 °N latitude in Minnesota for effects of 35 °C in the root zone on plant growth, stomatal conductance, and stem Ψ . Provenance and temperature main effects were significant for most dependent variables, but there were no provenance $\times$ temperature interactions. Over both provenances, plant fresh and dry mass, leaf surface area, stomatal conductance, and stem Ψ during the photoperiod were higher at 29 than 35 °C. Over both temperatures, plants from Minnesota clones had higher fresh and dry mass and more leaf surface area than plants from Mississippi clones. The lack of temperature $\times$ provenance interactions suggests that ecotypic or clinal variation in heat resistance is minimal and will not be useful for identifying superior genotypes for use in interspecific crosses with red maple (*Acer rubrum* L.).

Heat islands develop in the atmospheres of cities (Viskanta et al., 1977). Concomitant increases in temperature of the upper 50 cm of urban soils are influenced by microclimatic factors such as solar radiation, underground utilities, and paving materials (Graves and Dana, 1987; Johnson et al., 1975). Root-zone temperatures in the range documented in cities can be supraoptimal for growth of woody plants, and variation in root-zone heat resistance exists among and within species. Dry mass of red maple (*Acer rubrum*) was not reduced by 30 °C (Graves et al., 1989) and 32 °C (Wilkins et al., 1995) in the root-zone, and 36 °C reduced dry mass similarly among plants of 'Franksred' (trademark, Red Sunset), 'October Glory', 'Schlesinger', and selections of red maple from Maine, Wisconsin, and Arkansas (Wilkins et al., 1995). 'Autumn Flame', 'Franksred', 'October Glory', and 'Schlesinger' red maple differed in the extent to which 34 °C in the root zone reduced transpiration rates, foliar chlorophyll, and root and shoot growth (Wilkins et al., 1995). These data demonstrate variation in heat resistance among red maples and show that exposure to root-zone temperatures between 32 and 36 °C results in expression of genotypic differences. Occurrence of soil temperatures in this range near urban trees (Graves and Dana, 1987) justifies selecting or developing maple cultivars with improved resistance to root-zone heat.

Hybridizing ornamentally superior red maples with tree genotypes that possess superior heat resistance could result in progeny with ornamental merit and improved resilience in stressful landscapes. Silver maple (*Acer saccharinum*) hybridizes with red maple in nature (Bachtell, 1989; Krahel et al., 1993), and controlled

crosses in which red maple was the female parent were first described by Freeman (1941). Several suspected or confirmed (Krahel et al., 1993) hybrids from nature (Santamour, 1993) are available commercially and are designated Freeman maples (*A. ×freemanii*). Because silver maples can survive in poor soils where other trees perish (Dirr, 1990), Freeman maples may be more resistant than red maples to environmental stress (Bachtell, 1989). Santamour (1993) has questioned whether such generalizations concerning stress resistance are valid, yet Freeman maples, unlike silver maples, are promoted as desirable for landscaping (Bachtell, 1989).

If the success of silver maples on poor soils is related to heat resistance, information on variation among silver maples in resistance to heat would be useful to tree breeders whose goal is to develop stress-tolerant Freeman maples with desirable landscape traits. Few data are available on variation in responses to environmental stresses among silver maples. The species is indigenous over a large area and occurs as far north as 46°N latitude in Quebec and as far south as 31°N latitude in Louisiana, Mississippi, Alabama, and Florida (Hightshoe, 1978). Ashby et al. (1991) reported that the time of chilling required to overcome dormancy of vegetative buds did not vary among silver maple genotypes from across the native range, but information on heat resistance is not available.

As an initial approach for assessing variation in root-zone heat resistance among silver maple genotypes, we tested the hypothesis that reduced growth and effects on plant water relations caused by high root-zone temperature would be more pronounced among genotypes from a northern provenance than among genotypes from a southern provenance. Our first objective was to determine how constant root-zone temperatures of 26 to 36 °C affect stomatal conductance, stem xylem water potential (Ψ), and plant dry mass of one clone of silver maple indigenous to 33.3°N latitude in Mississippi. Our second objective was to compare six clones of silver maple from the Mississippi location with plants of six clones from Minnesota (44.4°N latitude) for effects of 35 °C in the root zone on stomatal conductance, stem Ψ , and accrual of dry mass in roots and shoots.

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Table 1. Mean annual air temperature, frost-free days, heating and cooling degree days, and mean air temperature during July in Minnesota and Mississippi. Data were obtained from weather stations near the sites of origin of the silver maples used in this study. Minnesota data are from the Univ. of Minnesota Rosemount Experiment Station, Rosemount, Minn. Mississippi data are from the Mississippi State Univ. North Farm, Mississippi State, Miss.

Provenance	Mean annual				Mean air temp during July (°C)
	Air temp (°C)	Frost-free days	Heating degree days	Cooling degree days	
Minnesota	13.0	166	8235	535	26.6
Mississippi	16.9	241	2783	1883	26.7

Materials and Methods

PLANT MATERIALS AND EXPERIMENTAL DESIGN. John Preece, Southern Illinois Univ., provided stock plants of the 12 clones of silver maple designated by Preece et al. (1991) as no. 1-6 from provenances 01 and 19. Six clones were from Mississippi and had been obtained at 33.3°N latitude and 88.5°W longitude. The other six clones were from 44.4°N latitude and 93.1°W longitude in Minnesota (J. Preece, personal communication). Environmental characteristics of these provenances are summarized in Table 1. Individual stock plants were grown in containers with a top diameter and height of 16 cm, a bottom diameter of 11 cm, and a volume of 1840 cm³. A medium of 5 sphagnum peat : 3 coarse perlite : 2 soil (by volume) was used (pH = 6). Plants were irrigated with tap water periodically when the medium surface appeared dry. Tap water with N at 10.8 mol·m⁻³ from Peters Excel all-purpose 21N-2.2P-16.6K fertilizer (Scotts, Marietta, Ga.) was applied once weekly. The plants were grown in a greenhouse. Supplemental irradiation from incandescent lamps provided 15-h photoperiods from late August until late November. Stock plants were held in a dark cooler at 4 °C from late November until late February, when they were returned to the greenhouse.

Plants for all experiments were developed from single-node stem cuttings taken from the stock plants while their shoots were actively growing in the greenhouse. Cuttings were rooted in coarse perlite by using methods of Zhang and Graves (1995). The cuttings were subirrigated with N at 10.8 mol·m⁻³ from Peters Excel all-purpose 21N-2.2P-16.6K fertilizer in tap water. We allowed a shoot to develop from one of the two buds on each cutting. Plants with similar root and shoot development were transferred to individual 1.9-L stainless-steel vessels filled with aerated, half-strength Hoagland solution no. 1 (Hoagland and Arnon, 1950) with 50 µmol iron (Fe) supplied as Fe-EDDHA. Half-strength solution was replaced with full-strength solution on the day treatments began. Solutions were replaced on days 7 and 14 of treatment. Distilled water was added to vessels daily to maintain solution volume between replacements.

Individual vessels were housed within separate polyvinyl chloride jackets. Each jacket was connected by tubing to a water bath (RTE 111; Neslab, Newington, N.H.) that maintained prescribed root-zone temperatures to within ±0.5 °C by circulating temperature-controlled water inside the jacket and around the outside walls of the steel vessel. Randomized complete block designs were used. Plants were assigned to blocks based on a visual assessment of similarity in root and shoot development on the day treatments began. Vessels were held on greenhouse benches 1.2 m below 400-W high-pressure sodium lamps that supplemented solar radiation during 15-h photoperiods.

DATA COLLECTION. Photosynthetically active radiation (PAR), air temperature, and relative humidity (RH) adjacent to the plants

were determined at 1300 h central standard time during experiments by using a steady-state porometer (LI-1600; LI-COR, Lincoln, Neb.). Plant fresh mass was measured on days 0, 7, 14, and 21 of treatment. Destructive harvesting on day 21 began by using the porometer to measure stomatal conductance of the youngest fully expanded leaf of each plant. Stem Ψ was measured by using a pressure chamber (PMS Instruments, Corvallis, Ore.), and leaf surface area of each plant was determined using an area meter (LI-3100; LI-COR). Shoot and root tissues were weighed separately after they were dried at 67 °C for 48 h.

EXPERIMENT 1. Cuttings taken on 4 May 1994 from plants of clone no. 5 from Mississippi (Preece et al., 1991) were allowed to root for 42 d. Uniformly rooted cuttings were transferred to vessels connected to one of five water baths programmed to maintain constant root-zone temperatures of either 26, 30, 32, 34, or 36 °C. Treatments began 20 June (day 0), after plants had been acclimated in nutrient solutions at ambient greenhouse temperatures for 5 d. Plants were arranged in 15 blocks that each contained a single-plant replication of the five root-zone temperature treatments. PAR, air temperature, and RH ranged from 80 to 700 µmol·s⁻¹·m⁻², 21 to 26 °C, and 44 to 62%, respectively, between 1300 and 1500 hr on day 21. Mean PAR, air temperature, and RH were 327 µmol·s⁻¹·m⁻², 24 °C, and 50%, respectively. PAR data likely represent the range of PAR throughout treatments because day 21 was partly cloudy outdoors, and PAR values were obtained during both clear and overcast periods. Air temperature data from day 21 also should represent conditions throughout the experiment because the greenhouse was air conditioned and was programmed for uniform temperatures during the photoperiod and dark hours.

Data were analyzed by using the Statistical Analysis System (SAS Institute, Cary, N.C.). Analyses of variance (ANOVA) were performed by using the General Linear Model. Means of total fresh mass data were separated by using Fisher's LSD ($P = 0.05$). Significance of linear and quadratic effects of root-zone temperature on stomatal conductance, stem Ψ , total leaf area, and total dry mass were determined by using Procedure Reg.

EXPERIMENT 2. Cuttings of all 12 clones were taken on 22 May, 21 June, and 19 Aug. 1995, for the three times this experiment was conducted. Cuttings were allowed to root for 39 d. Plants selected for uniformity of root and shoot development were transferred singly to vessels and allowed to acclimatize for 3 d before treatments were initiated. PAR, air temperature, and RH were measured on two or three dates selected for maximal variation in outdoor weather conditions during each replication and ranged from 130 to 610 µmol·s⁻¹·m⁻², 17 to 28 °C, and 17% to 65%, respectively.

Root-zone treatments of continuous 29 and 35 °C for 21 d were initiated on 26 June, 26 July, and 25 Aug. during the three experiments. One single-plant replicate of the 24 treatment combinations (12 clones at each of two temperatures) was assigned to

each of two blocks during each experiment. Data were analyzed by using SAS. An ANOVA of treatment means from the three experiments was conducted with the General Linear Model. It partitioned variation due to clonal origin (provenance), clones within provenances, temperature, the provenance $\times$ temperature interaction, and the interaction of clone by temperature within provenances. Separation of means was done by using Fisher's LSD ($P = 0.05$).

Results

EXPERIMENT 1. Stomatal conductance varied with temperature quadratically, with a predicted maximal rate of $350 \text{ mmol} \cdot \text{cm}^{-2} \cdot \text{s}^{-1}$ at about 28°C and a 50% decrease in predicted stomatal conductance at 33.5°C (Fig. 1). Stem Ψ decreased linearly with increasing root-zone temperature from -0.83 MPa at 26°C to -1.05 MPa at 36°C (Fig. 1). Total fresh mass on day 21 was highest for plants at 30°C , which had 19% higher fresh mass than plants at 26 and 32°C (Fig. 2). Fresh mass of plants exposed to 34 and 36°C was 49% and 30%, respectively, of the fresh mass of plants at 30°C (Fig. 2). Total plant fresh mass increased by 469%, 500%, 483%, 194%, and 91% between days 0 and 21 for plants at 26 , 30 , 32 , 34 , and 36°C , respectively ($\text{LSD} = 34$). Relationships between root-zone temperature and leaf surface area and total plant dry mass were best described by quadratic regression functions that predict 29°C in the root-zone was optimal for these dependent variables (Fig. 3).

EXPERIMENT 2. Provenance and root-zone temperature affected all growth traits. The effect of clone within provenance, the provenance $\times$ temperature interaction, and the interaction of clone by temperature within provenances were not significant. Therefore, we determined means by provenance over both temperatures and means by temperature over both provenances. After 21 d, plants from Minnesota had 36% higher fresh mass and 43% more leaf surface area than plants from Mississippi (Table 2). Root and shoot dry mass were 35 and 59% higher, respectively, for plants from Minnesota than for plants from Mississippi over both temperatures (Table 2). Provenance did not affect midday stem Ψ and stomatal conductance (Table 2). Plant fresh mass after 21 days, leaf surface area, root dry mass, and shoot dry mass were 109%, 71%,

103%, and 47% greater, respectively, for plants grown with root zones at 29°C than for plants grown at 35°C (Table 2). Midday stem Ψ was 0.5 MPa more negative for plants at 35°C than for plants at 29°C , and stomatal conductance was 55% less for plants with root zones at 35°C than for those with root zones at 29°C (Table 2).

Discussion

Responses of silver maple to 26 to 36°C in the root zone were consistent with previously reported responses of red maple to this range of temperatures (Graves et al., 1989). Maintaining root zones at 36°C for 35 d decreased root and shoot dry mass of red maple indigenous to Florida by 68% and 57%, respectively, compared to the dry mass of plants grown with root zones at 30°C (Graves et al., 1989). Total dry mass of silver maple clone no. 5 from Mississippi was 59% less for plants exposed to 36°C than for plants at 30°C for 21 d (Fig. 3). Stem Ψ of red maples from Florida decreased linearly from -0.5 MPa to -1.0 MPa as root-zone temperature increased from 18 to 36°C , and foliar diffusive resistance was five times higher at 36°C than at 30°C (Graves et al., 1989). Likewise, silver maple clone no. 5 from Mississippi showed a linear decrease in stem Ψ as root-zone temperature increased (Fig. 1), and stem Ψ of plants from Minnesota and Mississippi was reduced to -1.20 MPa by 35°C during our second experiment (Table 2). Decreased stomatal conductance might reduce water use and sustain stem Ψ , but our data (Fig. 1, Table 2) and those of Graves et al. (1989) indicate these responses do not sustain stem Ψ characteristic of maples with root zones at temperatures that maximized growth.

Growth of plants from Minnesota exceeded the growth of plants from Mississippi (Table 2). We do not know if provenance differences in vigor exist in nature, but our findings for plants in the greenhouse are consistent with the growth of these clones in vitro. Preece et al. (1991) found that the mean shoot length and callus volume of the six clones from Minnesota were 18.9 mm and 1325 mm^3 , respectively. In contrast, mean length of shoots of the six clones from Mississippi was 13.7 mm , and their mean callus volume was 368 mm^3 . Although provenance affected plant vigor, the lack of provenance $\times$ temperature interactions provides no support for the hypothesis that growth reductions and effects on water relations caused by root-zone heat would be more pro-

Fig. 1. Influence of root-zone temperature on stomatal conductance (○) and stem xylem water potential (●) of plants of clone no. 5 of silver maple from 33.3°N latitude in Mississippi during Expt. 1. Data were collected after 21 d of treatment. Each point is the mean of one observation of 15 single-plant replications. Regression functions describing these relationships are as follows: stomatal conductance = $-3840 + 301(\text{temperature}) - 5.4(\text{temperature}^2)$, $r^2 = 0.81$, and water potential = $-0.006 - 0.03(\text{temperature})$, $r^2 = 0.80$.

Fig. 2. Increase in fresh mass of plants of clone no. 5 of silver maple from 33.3°N latitude in Mississippi during a 21-d exposure to root zones at 26 (●), 30 (○), 32 (■), 34 (▲), and 36 (▼) $^\circ\text{C}$ during Expt. 1. Each point is the mean of 15 single-plant replications. The vertical bar represents Fisher's LSD ($P = 0.05$).

Fig. 3. Influence of root-zone temperature on leaf surface area (○) and total dry mass (●) of plants of clone no. 5 of silver maple from 33.3°N latitude in Mississippi during Expt. 1. Data were collected after 21 d of treatment. Each point is the mean of one observation of 15 single-plant replications. Regression functions describing these relationships are as follows: leaf area = $-14440 + 1111(\text{temperature}) - 19.2(\text{temperature}^2)$, $r^2 = 0.99$, and dry mass = $-99.46 + 7.647(\text{temperature}) - 0.132(\text{temperature}^2)$, $r^2 = 0.96$.

nounced among genotypes from the Minnesota provenance than among the Mississippi genotypes. The similarity in the extent to which 35 °C reduced growth, stomatal conductance, and stem Ψ of plants from Minnesota and Mississippi might be related to temperature conditions in these provenances. Mean annual air temperature is 4 °C higher for Mississippi than for Minnesota, and the number of frost-free days and the heating and cooling degree days illustrate that the duration of relatively high temperatures is longer in Mississippi than in Minnesota (Table 1). But mean air temperature for the two provenances during July differs by only 0.1 °C (Table 1). Although the weather stations from which these data were obtained were unable to provide us with relevant soil temperature data, mean air temperatures during July suggest there may be little difference in the highest temperature to which trees indigenous at the two provenances are adapted. Provenance effects on heat resistance among silver maples have not been studied previously, but there is evidence that little variation in other temperature-related responses exists within this species. Time of chilling required to overcome dormancy of vegetative buds does not vary among silver maple genotypes from as far north as central Ontario to as far south as central Mississippi (Ashby et al., 1991). In contrast, red maples indigenous to Florida differ from those elsewhere in the native range by not having a chilling requirement

(Perry and Wang, 1960). The fact that genotypes of red maple also vary in responses to high root-zone temperatures (Wilkins et al., 1995) suggests that variation in temperature-dependent processes is greater among red maples than silver maples.

Similarities between the silver maple clones we studied and red maples from Florida studied by Graves et al. (1989) in percentage reductions in dry mass and decreases in stem Ψ resulting from high temperatures raise doubt about previous contentions that the heat resistance of silver maple exceeds that of red maple (Hightshoe, 1978). We are not the first to question the reputed stress resistance of silver maple. Santamour (1993) described the growth and survival of trees of silver maple, red maple, and crosses within and between these species that were developed in the 1930s and 1940s by the Northeastern Forest Experiment Station for the USDA Forest Service. More than 4000 of these trees were planted in 1946 near Beltsville, Md. Although statistical comparisons were not possible, Santamour (1993) stated that growth of silver maples was greater than growth of red maples and the hybrids during the first 6 years after planting. The silver maples had begun to decline by 1958, however, and were dead by 1974. Effects of growth rate, potential life span, and stress resistance on the performance of these trees could not be distinguished. But his observations led Santamour (1993) to question the idea that resistance to environmental stress is greater for silver maple than for red maple, and he concluded that Freeman maples cannot be presumed to have greater potential than red maples for use in urban landscapes.

Silver maple can grow at sites with poor soils where many other trees die (Dirr, 1990). This has generated speculation that Freeman maples are more resistant to urban conditions than red maples (Bachtell, 1989). Wilkins et al. (1995) grew plants of 'Autumn Flame', 'Franksred', 'October Glory', and 'Schlesinger' red maple and 'Indian Summer' and 'Jeffersred' (trademark, Autumn Blaze) Freeman maple with root zones at 28 and 34 °C. Stem length and plant dry mass were reduced by 34 °C for all cultivars except 'Autumn Flame' red maple and 'Jeffersred' Freeman maple. This indicates variation in heat resistance exists among cultivars of red maple and Freeman maple. Additionally, there is no indication from our data that genotypes of silver maple are generally more heat resistant than genotypes of red maple. Research with cultivars suggests the heat resistance of Freeman maples also does not differ uniformly from that of red maples (Wilkins et al., 1995). This is consistent with the conclusions of Santamour (1993) but contrasts with previous supposition about the stress resistance of Freeman maples (Bachtell, 1989). Our results do not rule out the possibility of identifying unusually heat-resistant genotypes of silver maple for use in Freeman maple breeding programs. The lack of provenance $\times$ temperature interactions in our second experiment,

Table 2. Plant fresh mass, leaf surface area, shoot and root dry mass, stem xylem water potential (Ψ), and stomatal conductance of silver maples from Minnesota (44.4°N latitude) and Mississippi (33.3°N latitude) grown with roots at 29 and 35 °C for 21 d. Twelve clones, six from both provenances, were studied in an experiment conducted three times. Main effects were significant for most dependent variables, and there were no latitude $\times$ temperature interactions, so means by both main effects are shown. Each value is the overall mean of treatment means from each experiment. Differences greater than the least significant difference (LSD) value are significant at ($P = 0.05$).

Dependent variable	Provenance (°N latitude of origin)		Root-zone temp (°C)		LSD
	33.3	44.4	29	35	
Plant fresh mass on day 21 (g)	16.8	22.9	27.0	12.9	3.7
Leaf surface area (cm ²)	414	594	639	374	103
Root dry mass (g)	0.40	0.54	0.63	0.31	0.09
Shoot dry mass (g)	1.97	3.13	3.05	2.08	0.60
Midday stem xylem Ψ (MPa)	-0.95	-0.98	-0.70	-1.20	0.05
Stomatal conductance (mmol·cm ⁻² ·s ⁻¹)	306	342	449	200	37

however, indicates that silver maples from southern provenances are not uniformly more resistant to high root-zone temperature than silver maples from northern provenances. Therefore, the success of silver maple at harsh planting sites must be attributed to factors other than root-zone heat resistance.

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