Water Use and Growth of Honey Locust and Tree-of-Heaven at High Root-zone Temperature

William R. Graves, Robert J. Joly, and Michael N. Dana

Department of Horticulture, Purdue University, West Lafayette, IN 47907

Abstract. Honey locust (Gleditsia triacanthos var. inermis, Ailanthus altissima, woody landscape plants, urban horticulture, root hydraulic conductivity, stress physiology, water relations

Elevated root-zone temperatures may contribute to premature senescence and high mortality rates of trees in urban microclimates. Graves and Dana (1987a) found that root-zone temperatures at urban tree planting sites averaged more than 7°C higher than those in a nearby temperate forest, and temperatures >30°C were observed frequently in soils at street-tree-planting sites.

Data on the responses of temperate trees found in urban landscapes to elevated root-zone temperature are limited, but the growth and water status of red maple (Acer rubrum L.) (Graves et al., 1989b) and tree-of-heaven (Graves et al., 1989a) are sensitive to high root-zone temperatures in the range documented at urban sites. In both species, stem elongation, leaf area, and root and shoot biomass were reduced with the root zone >30°C. Leaves of plants with roots at 36°C had high diffusive resistance, indicating that water transport was limited by stomatal closure or the capacity of the root system to extract water. Preliminary trials, however, indicated that seedling growth in honey locust was maintained at the temperatures that reduced growth in red maple and tree-of-heaven.

Therefore, the objective of this study was to test the hypothesis that seedlings of honey locust and tree-of-heaven differ in how elevated root-zone temperature affects growth, water relations, and root hydraulic properties. Shoot extension, leaf area, root : shoot ratio, and root dry weights were less for tree-of-heaven grown with the root zone at 34°C than for those with root zones at 24°C. Tree-of-heaven with roots at 34°C had a lower mean transpiration rate (E) than those grown at 24°C, but leaf water potential (ΨL) was similar at both temperatures. In contrast, shoot extension of seedlings of honey locust grown with roots at 34°C was greater than honey locust at 24°C, E was similar at both temperatures, and ΨL was reduced at 34°C. Hydraulic properties of root systems grown at both temperatures were determined during exposure to pressure in solution held at 24 or 34°C. For each species at both solution temperatures, water flux through root systems (Jx) grown at 34°C was less than for roots grown at 24°C. Roots of tree-of-heaven grown at 34°C had lower hydraulic conductivity coefficients (Ls) than those grown at 24°C, but Ls of roots of honey locust grown at the two temperatures was similar.

Table 1. Growth and shoot water relations of seedlings of honey locust and tree-of-heaven grown with root zones at 24 or 34°C. Values are means of eight replicates. SE of means are shown where least significant difference (LSD; α = 0.05) values are not applicable.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Root-zone temp (°C)</th>
<th>Honey locust</th>
<th>Tree-of-heaven</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>24</td>
<td>34</td>
<td>24</td>
</tr>
<tr>
<td>Root dry wt (g)</td>
<td>0.83</td>
<td>0.80</td>
<td>3.65</td>
</tr>
<tr>
<td>Shoot dry wt (g)</td>
<td>1.12</td>
<td>1.30</td>
<td>6.20</td>
</tr>
<tr>
<td>Root : shoot biomass ratio</td>
<td>0.74 (0.04)</td>
<td>0.67 (0.09)</td>
<td>0.59 (0.03)</td>
</tr>
<tr>
<td>Leaf area (cm²)</td>
<td>105.5</td>
<td>125.9</td>
<td>929.2</td>
</tr>
<tr>
<td>ΨL (MPa) before photoperiod</td>
<td>0.40 (0.03)</td>
<td>0.43 (0.02)</td>
<td>0.38 (0.03)</td>
</tr>
<tr>
<td>ΨL (MPa) during photoperiod</td>
<td>1.44 (0.10)</td>
<td>1.62 (0.04)</td>
<td>0.64 (0.04)</td>
</tr>
<tr>
<td>Transpiration rate (mmol·m⁻²·s⁻¹⁻¹)</td>
<td>1.31</td>
<td>1.54</td>
<td>1.56</td>
</tr>
</tbody>
</table>
Table 3. Significance of sources of variation in water flux ($J_v$) of root systems of honey locust and tree-of-heaven at 24 and 34°C. Each value is the mean of eight replicates. The vertical bar represents the LSD ($\alpha = 0.05$).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Honey locust (MPa)</th>
<th>Tree-of-heaven (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measurement temp (MT)</td>
<td>**</td>
<td>NS</td>
</tr>
<tr>
<td>Growth temp (GT)</td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td>Pressure</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Pressure (linear) $\times$ MT</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Pressure (quadratic)</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Pressure (quadratic) $\times$ MT</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Pressure (quadratic) $\times$ GT</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Pressure $\times$ MT $\times$ GT</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

NS, *Nonsignificant or significant at $\alpha = 0.05$, 0.01, and 0.001, respectively.

Dependent variables were analyzed by analysis of variance (ANOVA). A least significant difference (Steel and Torrie, 1980) was determined for variables with significant ($\alpha = 0.05$) interactions between time, species, or treatment.

Root conductance to water flow. Water conductance properties of root systems of honey locust and tree-of-heaven were analyzed in separate experiments using methods similar to those of Fiscus (1977). Seeds of honey locust were germinated as described for the previous experiment. Seedlings were planted in ground, calcined clay in l-liter plastic containers 21 days after seeds were sown. Plants were transferred to the growth chamber and grown with the environmental conditions described for the growth and shoot water relations study. Seven days after seedlings were moved to the growth chamber, eight uniform plants were assigned randomly to root zones at 24 or 34°C. Plants were irrigated once daily to container capacity with temperature-controlled Hoagland solution no. 1 such that root-zone temperatures were maintained during application. Two plants were selected at random from each treatment on day 56 of treatment. They were moved to a laboratory and irrigated to container capacity with deionized water. Root systems were gently separated from the growing medium, and stems were severed immediately below the scars where the cotyledons had been attached. Weight of leaves from each plant was determined after they were dehydrated as described for the previous experiment.

Tissues peripheral to the vascular cambium were peeled from the upper 5 cm of the stump of each root system to prevent axial water flow through cortical cells. Each stem was mounted singly in the lid of a stainless steel chamber filled with 50% Hoagland solution (no. 1, pH 5.7 to 5.9). Air was bubbled in the solution of the sealed chamber until pressure reached 0.345 MPa. Solution aeration was maintained by venting gas through the lid at the same rate it entered the solution, 0.8 cm$^3$·s$^{-1}$. One hour elapsed between severing shoots and attaining a vessel pressure of 0.345 MPa.

Root exudate was collected in tygon tubing fitted to each stump and was weighed on a balance every 3 min. Steady-state root water flux ($J_v$) was achieved within 3½ h and then was recorded for 1 hat each of four pressures (0.345, 0.414, 0.483, and 0.553 MPa) applied in ascending order, allowing five observations per system at each pressure. Root systems were held for 30 min at each new pressure to regain steady state before data were collected. $J_v$ was expressed on the basis of leaf dry weight. Compared with several other traits, using leaf dry weight to express data resulted in the least variation in $J_v$ among plants within treatments during a preliminary experiment.

A replication of this experiment consisted of $J_v$ determinations on two consecutive days. Four plants were analyzed each day, two from each growth temperature treatment. On the first day, temperature of the chamber solution was selected at random as 24 or 34°C ($\pm 1$C). Procedures were repeated with different plants during the same hours the 2nd day, but the alternate solution temperature was used. Four replications were performed. All data were combined for analysis.

Methods used for tree-of-heaven were identical to those for honey locust except for the following. Seedlings were potted in 2.5-liter containers 56 days after seeds were sown. Treatments were applied 14 days after seedlings were introduced to chamber conditions. Six plants were assigned to each of the two root-zone temperatures, and treatments lasted 28 days. $J_v$ was determined each minute for 40 min at each of the four pressures, allowing 10 observations per sample at each pressure. Root systems were held 60 min at each new pressure to allow $J_v$ to regain steady state before collecting data.

The root conductance experiments were analyzed as a split split-plot design with solution temperature as whole plots, growth temperature as subplots, and pressure as the sub-subplot treatment. ANOVA was performed for $J_v$ of each species using a generalized linear model procedure (SAS Institute, 1986). F-max tests showed the assumption of homogeneity of variances was violated for both species, and this could not be corrected by transforming data. Plots of predicted vs. residual values revealed irregular data points that exceeded predicted values by more than three standard deviations.
of the mean. J failed to attain steady state in root systems from which such data were generated. We assumed this was caused by physical damage to roots during preparation. These data, < 10% of the observations, were excluded as outliers, and the assumption of homogeneity of variances was no longer violated during ANOVA.

Within species and for all measurement and growth temperature combinations, I was fitted to regression models of the form \( J = b_0 + b_1(p) \). The hydraulic efficiency coefficient (\( L_0 \)) was determined as the slope of the linear regression of \( J \) on pressure (Fiscus, 1977).

**Growth and shoot water relations.** Stems elongated more in seedlings of honey locust with roots at 34°C than in those at 24°C, but the reverse was true for tree-of-heaven (Fig. 1). Seedlings of tree-of-heaven grown at 34°C also exhibited reduced root and shoot dry weights, smaller root : shoot biomass ratios and less leaf area than plants grown at 24°C (Table 1). Root-zone temperature did not affect these traits in seedlings of honey locust.

Before the beginning of the photoperiod on day 20, \( \psi_p \) ranged from 0.48 to 0.38 MPa for both species (Table 1). All plants had lowered \( \psi_p \) during the photoperiod, but the decrease was most evident among honey locust with roots at 34°C. Seedlings of tree-of-heaven grown at 34°C had a mean \( E = 46 \%) less than that at 24°C (Table 1). E of honey locust was similar at the two temperatures.

**Root conductance to water flow.** Roots of honey locust measured in solution at 34°C showed higher \( J \) than those measured at 24°C, and at both solution measurement temperatures, \( J \) was higher for systems grown with roots at 24°C than for those grown at 34°C (Tables 2 and 3). The pressure \( x \) measurement temperature and pressure \( x \) growth temperature interaction terms were not significant for honey locust (Table 3), indicating that \( L_0 \) at the two temperatures was not different (Table 2).

Measurement temperature did not affect the \( J \) through root systems of tree-of-heaven (Tables 2 and 3). Roots of tree-of-heaven grown at 24°C had higher \( J \) than those of root systems grown at 34°C (Tables 2 and 3). The interaction between pressure and growth temperature was significant (Table 3), indicating \( L_0 \) of systems grown at 24°C was higher than \( L_0 \) of roots grown at 34°C (Table 2).

These experiments support the hypothesis that high root-zone temperature affects root hydraulic properties, leaf water relations, and growth of seedlings of honey locust and tree-of-heaven differently. The capacity for seedlings of honey locust to collect, transport, and transpire water was not affected by continuous exposure of roots to 34°C. In contrast, the \( L_0 \) of roots of tree-of-heaven grown at 34°C was lower than the \( L_0 \) of roots of tree-of-heaven formed at 24°C. Assuming that the hydraulic properties of a whole root system are analogous to those of a single membrane (Fiscus, 1977), the \( L_0 \) of a root system defines the gradient in water potential within the hydraulic pathway (\( \Delta \psi \)) between root and shoot tissues at any given flow rate. Thus, the \( \Delta \psi \) required to sustain a given rate of water flow in tree-of-heaven grown with roots at 34°C likely was larger than that required for plants with root zones at 24°C. The relatively high \( \psi_p \) and relatively low \( E \) during the photoperiod suggest that seedlings of tree-of-heaven did not develop a \( \Delta \psi \) sufficient to override the increased resistance to flow in the roots, probably because of a transient decline in \( \psi_p \) that induced stomatal closure.

Because the driving force for water movement depends largely on \( E \), the magnitude of \( \Delta \psi \) would have decreased as stomata closed. Therefore, \( E \) may have decreased to a level governed principally by the rate of water absorption.

Unlike tree-of-heaven, root \( L_0 \) of honey locust was not reduced in plants grown with roots at 34°C relative to those grown at 24°C (Tables 2 and 3). Furthermore, the low \( \psi_p \) observed during the photoperiod indicates that a large \( \Delta \psi \) was maintained at high root-zone temperature (Table 1). \( E \) was unaffected by the higher growth temperature despite the decline in \( \psi_p \) (Table 1). Solute accumulation in leaves during exposure to high root-zone temperature may have enabled turgor and \( E \) to be maintained at low \( \psi_p \). Whether or not osmotic adjustment or some other mechanism to maintain turgor was involved, water transport to expanding tissues in seedlings of honey locust was not impaired at high root-zone temperature, and shoot and root growth were similar to that observed for plants with 24°C root zones (Table 1).

\( J \) was reduced among plants of both species grown with roots at 34°C (Tables 2 and 3). Others have found that roots formed at high temperatures are thinner than those produced at temperatures optimal for growth (Hellmers, 1963; Nielsen, 1974). Thus, high growth temperature may have reduced \( J \) by decreasing xylem vessel diameter, thereby increasing hydraulic resistance to water transport (Oosterhuis, 1983). Increased suberization or the deposition of secondary cell wall materials behind the zone of elongation where root water uptake is most rapid (Boyer, 1985) also may have reduced \( J \) at high temperature. Elevated root-zone temperature also might have influenced resistance by altering membrane structure and fatty acid composition. High temperature acclimation appears to involve changes in the degree of fatty acid unsaturation and fluidity of polar lipids (Berry and Bjorkman, 1980). Markhart et al. (1980) found that increased unsaturation in membrane fatty acids during temperature acclimation in soybean (Glycine max L.) was associated with increased resistance to root water uptake. Roots of honey locust grown at both temperatures showed greater \( J \) when measured at 34°C than when solution at 24°C was used (Tables 2 and 3). Although not significant at the \( \alpha = 0.05 \) level, the same trend was evident in tree-of-heaven, probably from the reduced viscosity of aqueous solutions at high temperature (Dainty et al., 1983).

Changes in \( \psi_p \), \( E \), and \( L_0 \) reported herein are consistent with numerous reports demonstrating that the root-zone environment can modify water transport characteristic of roots and alter \( \psi_p \) during transpiration. Water stress (Leyv et al., 1983; Oosterhuis and Wiebe, 1986; Ramos and Kaufmann, 1979), salinity (Shalhevet et al., 1976), and hypoxia (Kuper, 1964; Newman, 1976) are among the conditions affecting the capacity of roots to supply water to leaves. Each of these factors likely interacts with high temperature to influence growth-limiting hydraulic resistances of trees in urban microclimates.

Both species used in this study survived root zones constantly at 34°C, but they differed dramatically in the control over water use at high temperature. Our findings are consistent with a previous report that stomata of honey locust are relatively insensitive to low \( \psi_p \) (Potts and Herrington, 1982). The capacity for this species to maintain growth with roots at 34°C is unique when compared with tree-of-heaven and other temperate tree species subjected continuously to root-zone heat (Barney, 1951; Graves et al., 1989a, 1989b; Gur et al., 1976; Hellmers, 1963; Nightingale, 1935). Thus, honey locust appears unusually well adapted to microclimates with high soil temperature. How high temperature interacts with other environmental factors, such as drought, that may stress trees of this species is not clear. Graves and Wilkins (1991) found that growth of honey locust in solution culture was reduced when solution osmotic potential was reduced from \(-0.05 \) to \(-0.10 \) MPa by polyethylene glycol 8000 (PEG). In contrast to those at \(-0.05 \) MPa, growth of seedlings stressed with PEG was not reduced by 35°C root-zone temperature. Further studies are needed to determine whether these responses are consistent with those of honey locust grown in urban landscapes.

**Literature Cited**


Graves, W.R., R.J. Joly, and M.N. Dana. 1989b. Root-zone temperature affects water status and...


