6. Marini, R.P. 1987. Growth and cropping of 'Redhaven' peach trees following soil application of paclobutrazol. J. Amer. Soc. Hort. Sci. 112:18–21.

7. Norusis, M.J. 1988. SPSS/PC+ V2.0 Base Manual. SPSS Inc. Chicago, IL.

8. Steffens, G.L., J.K. Byun and S.Y. Wang. 1985. Controlling plant growth via the gibberellin biosynthesis system—I. Growth parameter alterations in apple seedlings. Physiol. Plant. 63:163–168.

9. Sterrett, J.P. and T.J. Tworkoski. 1987. Response of shade trees to root collar drenches of inhibitors Flurprimidol and paclobutrazol. J. Plant Growth Regul. 5:163–167.

10. Swietlik, D. and S.S. Miller. 1983. The effect of paclobutrazol on growth and response to water stress of apple seedlings. J. Amer. Soc. Hort. Sci. 108:1076–1080.

11. Wang, S.Y., J.K. Byun and G.L. Steffens. 1985. Controlling plant growth via the gibberellin biosynthesis system—II. Biochemical and physiological alterations in apple seedlings. Physiol. Plant. 63:169–175.

12. Wang, S.Y., G.L. Steffens and M. Faust. 1986. Effect of paclobutrazol on accumulation of carbohydrates in apple wood. HortScience 21:1419–1421.

13. Webster, A.D., J.D. Quinlan and P.J. Richardson. 1986. The influence of paclobutrazol on the growth and cropping of sweet cherry cultivars. I. The effect of annual soil treatments on the growth and cropping of cv. Early Rivers. J. Hort. Sci. 61:471–478.

14. Wieland, W.F. and R.L. Wample. 1985. Effects of paclobutrazol on growth, photosynthesis and carbohydrate content of 'Delicious' apples. Scientia Hortic. 26:139–147.

15. Williamson, J.G., D.C. Coston and L.W. Grimes. 1986. Growth responses of peach roots and shoots to soil and foliar-applied paclobutrazol. HortScience 21:1001–1003.

16. Wood, B.W. 1984. Influence of paclobutrazol on selected growth and chemical characteristics of young pecan seedlings. HortScience 19:837–839.

17. Zobel, B.J. and J.T. Talbert. 1984. Applied Forest Tree Improvement. John Wiley and Sons, New York, N.Y. pp505.

Influence of Root-zone Temperature on Growth of *Ailanthus altissima* (Mill.) Swingle[1]

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Abstract

Growth of tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) seedlings was evaluated during a 28-day exposure to constant root-zone temperatures of 18°, 24°, 30°, and 36°C (64°, 75°, 86°, and 97°F). Leaf area, stem length, root-to-shoot ratio, and shoot and root dry weights were greatest among plants with 24°C (75°F) root zones. Diminished growth among plants at high root-zone temperatures was associated with reduced leaf conductance. After 14 days of treatment, leaf diffusive resistance of plants in the 36°C (97°F) regime was eight times greater than that of plants with 24°C (75°F) root zones. Regulation of leaf gas exchange among plants with 36°C (97°F) root zones probably contributed to the maintenance of moderate leaf water potentials but limited the fixation of carbon necessary to sustain growth.

Index words: urban horticulture, root temperature stress

Introduction

Trees physically and aesthetically enhance the habitability of urban areas. Unfortunately, many city trees are plagued by symptoms of stress that decrease their visual quality and longevity. An increased heat load is characteristic of many urban mesoclimates and may contribute to the decline of urban trees. Commonly called the heat-island effect, mean annual air temperatures in metropolitan centers typically exceed those in surrounding areas by 1°C to 4°C (2°F to 7°F) (2, 10, 15). Within cities, diverse physical characteristics of different planting sites probably result in temperature regimes unique to the microclimate of each tree. For example, during the same 24-hr period in New York City, maximum air temperature near tree canopies in Central Park was 32°C (90°F), while canopy temperatures in Manhattan were as high as 41°C (106°F) (17).

Although urban atmospheric temperatures have been studied for many years, the relationship between urbanization and below-surface temperature has received little attention. Recently, root-zone temperatures 5 to 50 cm (2 to 20 in) beneath the surface at street tree planting sites in downtown Lafayette, Indiana, were reported to average 7°C (13°F) higher than those in a nearby wooded area (6). Temperatures exceeding 30°C (86°F) were common in urban Lafayette root zones where direct solar radiation was incident on soil surfaces covered with concrete and asphalt (4). Given the prevalence of these surface materials in most urban areas

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and the build-up of atmospheric heat shown in many cities, elevated root-zone temperatures may be a component of many street tree microclimates. Consequently, information concerning root-zone temperature responses of urban trees may aid in selection of species appropriate for a given environment.

Tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) colonizes urban sites where other species have not survived, and has been considered extremely stress tolerant (3, 12). However, responses of this species to environmental conditions associated with urban microclimates have not been studied under controlled conditions. The purpose of this experiment was to characterize the growth and water status of tree-of-heaven exposed to root-zone temperatures in the range observed at city planting sites.

Materials and Methods

Two-hundred untreated tree-of-heaven seeds were germinated under intermittent mist in a greenhouse. Four weeks after sowing seeds, 40 uniform seedlings were transplanted to 1-l (0.26-gal) plastic containers filled with ground, baked calcined clay. Plants were maintained in a greenhouse and irrigated daily with tap water. After 20 days, 32 visually similar plants were moved to a controlled-environment chamber with 16-hr photoperiods supplied by cool-white fluorescent and incandescent lamps. Photon flux at apices was 410 ($\pm$50) μmol m^{-2} sec^{-1} (400–700 nm), with 90% of the total flux supplied by the fluorescent lamps. Air temperature during photoperiod and nonphotoperiod hours was 24°C (75°F) and 21°C (70°F) ($\pm$2°C), respectively. Relative humidity during the middle of the photoperiod was 60% ($\pm$6%). Plants were irrigated to container capacity once daily with deionized water until treatments were applied 6 days later.

Eight replicates were assigned randomly to each of four constant root-zone temperatures, 18° (64°F), 24° (75°F), 30° (86°F), and 36°C (97°F). These temperatures were maintained within $\pm$1°C (2°F) by circulating temperature-controlled water around each pot in a system described previously (5). Single-strength Hoagland's solution #1 (8), used for daily irrigations beginning the day treatments were applied, was heated or cooled before each application such that root-zone temperatures were maintained during irrigations.

Shoot length from the stem apex to the medium surface was recorded at the time treatments were applied (day 0) and at 7-day intervals until treatments terminated on day 28.

Transpiration rate and stomatal diffusive resistance of the terminal leaflet on the first fully expanded leaf on each plant were measured on day 14 with a LI-COR 1600 Steady-state Porometer fitted with a 2 cm^2 (0.31 in^2) sampling chamber. Measurements began 7.5 hr after the beginning of the photoperiod, 2.5 hr after plants were irrigated. The order in which plants were sampled was randomized and independent of root-zone temperature treatments. All measurements were completed within 1 hr.

Xylem water potential of the youngest fully expanded leaf on each plant was measured 4 hr after the beginning of the photoperiod on day 28 as described previously (13) with a pressure chamber. Remaining leaves then were removed, and total leaf surface area of each plant was measured with a LI-COR 3000 Leaf Area Meter. Root systems were rinsed with deionized water to remove calcined clay. Root and shoot dry weight of each plant was determined after desiccating tissue in a forced-air oven at 65°C (149°F) for 48 hr and letting them cool at room temperature for 1 hr.

Shoot length data were analyzed by analysis of variance. Because the treatment-by-time interaction was significant, an overall least significant difference value was calculated (14). All other data were regressed against temperature, and the significance of linear and quadratic effects was tested. Diffusive resistance and transpiration rate data were analyzed after they were transformed to their natural logs and square roots, respectively, because the assumption of homogeneity of variances for the nontransformed data was rejected by Hartley's F-max test (16).

Results and Discussion

Shoot length of plants grown with root-zone temperatures of 18°C (64°F), 24°C (75°F), and 30°C (86°F) increased throughout the study at similar rates (Fig. 1). However, after 14 days of exposure, mean shoot length of plants with roots at 36°C (97°F) was significantly less than that for plants in the other treatments (Fig. 1). The distance between nodes was reduced greatly among plants in the 36°C (97°F) treatment, giving them a stunted, rosette-like form.

Shoot dry weight, root dry weight, and leaf area also were less for plants grown in 36°C (97°F) medium than for those grown at the other temperatures (Table 1). Plants in the 24°C (75°F) treatment had the greatest mean root and shoot biomass and leaf area, but for each of these variables differences between plants grown at 24°C (75°F) and plants grown at 30°C (86°F) were minor (Table 1). Plants grown at 18°C (64°F) and 24°C (75°F) had similar root-to-shoot ratios (Table 1). However, mean root-to-shoot ratios of plants grown with 30°C (86°F) and 36°C (97°F) root-zone temperature were 14% and 67% less, respectively, than that of plants in the 24°C (75°F) treatment (Table 1). Thus, relative to plants with 24°C (75°F) root medium, the 18°C (64°F) treatment reduced growth of roots and shoots to a similar extent, but growth reductions were greater for roots than for shoots at root-zone temperatures above 24°C (75°F). Leaves of plants in all treatments appeared turgid throughout the study, and there was no leaf abscission. Roots grown at all temperatures were white and appeared healthy.

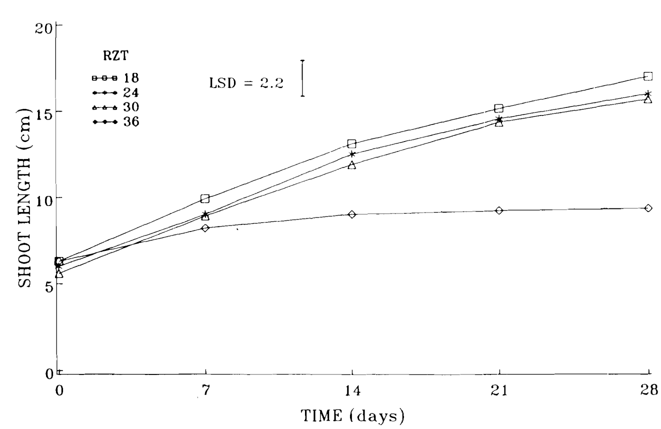

Fig. 1. Shoot length of tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) plants grown with constant root-zone temperatures of 18°C (64°F), 24°C (75°F), 30°C (86°F), and 36°C (97°F). Each point represents the mean of 8 replicates. Vertical bar represents least significant difference (LSD, $P \leq 0.05$).

Table 1. Growth and physiological responses of tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) plants to root-zone temperature. Values are means of 8 replicates and (SE).

	Root-zone temperature (°C)				Significance[z]	
Dependent variable	18	24	30	36	linear	quadratic
Root dry weight (g)	9.9(1.2)	11.8(0.5)	9.4(0.7)	2.1(0.2)	***	***
Shoot dry weight (g)	14.4(1.3)	16.6(0.6)	15.2(1.2)	8.8(0.5)	**	***
Root-to-shoot ratio	0.70(0.08)	0.72(0.04)	0.62(0.03)	0.24(0.02)	***	***
Leaf area (cm^2)	1710(144)	2015(69)	1859(167)	827(54)	***	***
Transpiration rate ($mg\ cm^{-2}\ sec^{-1}$)	2.7(0.4)	5.6(0.8)	4.9(0.9)	1.4(0.2)	NS	***
Diffusive resistance ($sec\ cm^{-1}$)	4.4(0.7)	2.2(0.5)	3.1(1.0)	18.2(10.7)	*	***
Leaf water potential (MPa)	−0.48(0.02)	−0.51(0.02)	−0.54(0.03)	−0.48(0.02)	NS	NS

[z]NS denotes not significant; *, **, and *** denote significance at $P \leq 0.05$, 0.01, and 0.001, respectively.

Tree-of-heaven plants in this experiment were irrigated to container capacity daily, yet some responses to high root-zone temperatures were typical of drought-stressed plants. For example, the stocky, rosette-like form of plants with 36°C (97°F) root zones may have contributed to water conservation by shading lower leaves. Also, tree-of-heaven plants with the least root and shoot growth were those showing strong resistance to the exchange of gasses between leaves and the atmosphere (Table 1). As a result, leaves with the greatest diffusive resistance had the lowest transpiration rates (Table 1), and the capacity for foliar exchange of other gasses, including carbon dioxide, probably also was reduced. Increased leaf resistance may have contributed to moderate leaf water potentials among plants with high root-zone temperature through the conservation of leaf water, but reduced carbon dioxide fixation may have limited growth by decreasing net assimilation.

Tree-of-heaven water status upon exposure to high root-zone temperature probably was not controlled solely by plant form and leaf resistance. Shoot turgor and growth are dependent on the capacity for roots to collect and transport water. The low mean root dry weight of 36°C (97°F) grown plants (Table 1) indicates roots did not penetrate the entire root zone. Correspondingly, during daily irrigations to container capacity, we noted that these plants required less than half the volume of solution necessary to irrigate 24°C (75°F) grown plants. The degree to which 36°C (97°F) grown root systems extracted soil water probably was limited by their size, but, in addition, resistance to water transport may have increased among roots at high temperatures. Axial resistance to water flow through xylem elements decreases with increasing vessel diameter (18), and observations of the xylem in tree-of-heaven roots indicated high temperature favored formation of relatively narrow vessel elements (4). Further, root suberization or changes in root cell membrane lipid composition may have increased resistance in the radial path between the root surface and the xylem (11). Any increased root resistance at high growth temperature was accompanied by large increases in leaf resistance that decreased the volume of root water uptake required to maintain shoot hydration (Table 1). Thus, changes in resistance to leaf water loss and root water uptake may have acted in concert to sustain moderate water potentials among leaves of tree-of-heaven plants with high root-zone temperature.

These responses to high root-zone temperature contrast those observed for other tree species. Reduced shoot and root growth of *Acer rubrum* L. (red maple) exposed to high temperature have been reported, but decreased growth was accompanied by decreased shoot water potential (7). Compared with tree-of-heaven, control over stomatal water vapor loss may have been less effective for red maple leaves, or the capacity for red maple roots to collect water may have been impaired to a greater extent when grown at high temperature. *Gleditsia triacanthos inermis* Willd. (thornless honey locust) grown with 34°C (93°F) root-zone temperature had greater transpiration rates, lower leaf water potentials, and underwent greater shoot growth than those grown at 24°C (75°F) (4). Stomata of this speices might be less responsive to prevailing leaf water potentials than those of tree-of-heaven.

Prolonged exposure to root-zone temperatures between 30°C (86°F) and 36°C (97°F) may limit growth of tree-of-heaven in urban microclimates where temperatures in this range have been observed (4, 6). However, the effects of root-zone temperature on trees in cities may differ from those observed in this experiment for several reasons. First, urban root-zone temperatures probably vary diurnally, and it is likely that the extent of heat injury to root tissue depends on the length of high-temperature exposure (9). Further research designed to determine effects of repeated, short-term episodes of supraoptimal root-zone temperatures is warranted. Second, the variable nature of urban root-zone temperature regimes (6) may allow most tree roots to avoid extreme heat near soil surfaces. Species such as tree-of-heaven, for which tenacious growth in urban areas has been attributed to vigorous lateral roots (12), may have a great capacity to explore portions of the root zone where conditions are favorable for growth. Third, other root-zone factors such as water supply, soil compaction, and salt content probably interact with temperature effects in cities, but characterization of these relationships awaits further study.

Significance to the Nursery Industry

City tree managers regard drought, air pollutants, nutrient deficiencies, and soil compaction as environmental constraints common to many urban tree microclimates (1), but the potential effects of other factors, including elevated root-zone temperature, often are overlooked. This study has shown that the growth and leaf conductance of tree-of-heaven, a species perceived tolerant of urban stresses, are affected adversely by root-zone temperatures of 30°C (86°F) and 36°C (97°F). These temperatures are in a range documented at city planting sites (4, 6). We must recognize root-zone temperature as a potential stress on urban trees, and cultural techniques to prevent the build-up of root-zone heat should be considered. The capacity for tree-of-heaven to maintain high leaf water potentials appears important for its survival at high root-zone temperatures. Further research to quantify such responses to high temperature and other environmental constraints among other species will benefit the horticultural industries by facilitating wise selection, production, installation, and maintenance practices.

Literature Cited

1. Beatty, R.A. and C.T. Heckman. 1981. Survey of urban tree programs in the United States. Urban Ecol. 5:81–102.

2. Bornstein, R.D. 1968. Observations of the urban heat island effect in New York City. J. Applied Met. 7:575–582.

3. Flint, H.L. 1985. Plants showing tolerance of urban stresses. J. Environ. Hort. 3:85–89.

4. Graves, W.R. 1988. Urban root-zone temperatures and their impact on tree hydrology and growth. Ph.D. Dissertation. Purdue University, West Lafayette, Indiana.

5. Graves, W.R. and M.N. Dana. 1987. A system to control root-zone temperature. HortScience 22:957–958.

6. Graves, W.R. and M.N. Dana. 1987. Root-zone temperature monitored at urban sites. HortScience 22:613–614.

7. Graves, W.R., M.N. Dana, and R.J. Joly. 1989. Root-zone temperature affects water status and growth of red maple. J. Amer. Soc. Hort. Sci. 114:(*in press*).

8. Hoagland, D.R. and D.I. Arnon. 1950. The water-culture method for growing plants without soil. California (Berkeley) Agr. Expt. Sta. Cir. 347.

9. Ingram, D.L. 1985. Modeling high temperature and exposure time interactions on *Pittosporum tobira* root cell membrane thermostability. J. Amer. Soc. Hort. Sci. 110:470–473.

10. Martin, F.P. and G.L. Powell. 1977. The urban heat island in Akron, Ohio. USDA For. Ser. Gen. Tech. Rpt. NE-25:109–114.

11. Oosterhuis, D.M. 1983. Resistances to water flow through the soil–plant system. S. Afr. J. Sci. 79:459–465.

12. Pan. E. and N. Bassuk. 1986. Establishment and distribution of *Ailanthus altissima* in the urban environment. J. Environ. Hort. 4:1–4.

13. Scholander, P.F., H.T. Hammel, D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148:339–346.

14. Steel, R.G.D. and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill, New York.

15. Viskanta, R., R.O. Johnson, and R.W. Bergstrom, Jr. 1977. Effect of urbanization on the thermal structure in the atmosphere. USDA For. Ser. Gen. Tech. Rpt. NE-25:62–76.

16. Weiner, B.J. 1971. Statistical Principles in Experimental Design. McGraw-Hill, New York.

17. Whitlow, T.H. and N.L. Bassuk. 1988. Ecophysiology of urban trees and their management—the North American experience. HortScience 23:542–546.