Effect of Root-zone Temperature on Survival, Growth, and Root Morphology of *Kalmia latifolia* and *Ilex crenata* 'Compacta'[1]

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Abstract

Root-zone temperature (RZT) is an important environmental factor affecting growth and performance of woody ornamental plants in the landscape. Research was conducted to compare the effects of RZT on survival, growth, and root morphology of a difficult-to-transplant species, mountain laurel (*Kalmia latifolia* L.), and an easy to transplant species, Japanese holly (*Ilex crenata* Thunb.). Seedlings of mountain laurel or micropropagated liners of mountain laurel (*Kalmia latifolia* L. 'Sarah') and rooted stem cuttings of Japanese holly (*Ilex crenata* Thunb. 'Compacta') were grown hydroponically for 12 weeks in controlled environment conditions under long days at 9-hr days/15-hr nights of 26/22C (79/72F) with RZTs of 16, 24, or 32C (61, 75, or 90F). Compared to 16 and 24C (61 and 75F), percent survival of mountain laurel was reduced by a RZT of 32C (90F), whereas percent survival of Compacta holly was unaffected by RZT. Root dry weight of mountain laurel was reduced 72% at 32C (90F) while top dry weight was unaffected by RZT. Top and root dry weights of Compacta holly were unaffected by RZT. Root:top ratio of mountain laurel was reduced by increasing RZT, whereas root:top ratio of Compacta holly was unaffected by RZT. Root area of mountain laurel and Compacta holly were reduced 80 and 64%, respectively, at 32C (90F) compared with 16C (61F). Number of lateral roots in the apical 2 cm (0.8 in) of primary roots of both taxa increased with increasing RZT. Results of this research indicate that reducing RZT in the landscape may increase survival and root growth of transplanted mountain laurel.

Index words: mountain laurel, Japanese holly, woody ornamentals, transplanting, root:top ratio, root morphology, Ericaceae, Aquifoliaceae, root area.

Species used in this study: mountain laurel (*Kalmia latifolia* L. 'Sarah'), Japanese holly (*Ilex crenata* Thunb. 'Compacta').

Significance to the Nursery Industry

Mountain laurel (*Kalmia latifolia*) is an attractive woody landscape species native to the eastern United States. It frequently does not survive transplanting from containers into the landscape, even in areas where it is indigenous. Increasing transplant survival could encourage increased use in the landscape industry and appreciation of this attractive native species. Research herein compared the effects of root-zone temperature (RZT) on growth and survival of mountain laurel and Japanese holly (*Ilex crenata*), a species which routinely survives transplanting. When grown at RZTs of 16, 24, or 32C (61, 75, or 90F) for 12 weeks, root growth of mountain laurel decreased with increasing RZT while root growth of Compacta Japanese holly was unaffected by RZT. Results for root:top ratio (RTR) were similar, i.e., mountain laurel decreased with increasing RZT and Compacta holly was unaffected. Since maintaining a proper root:top balance and root growth are critical for landscape establishment at transplanting, this may explain why mountain laurel is difficult to transplant into warm soil. In areas with high soil temperatures, cultural practices to reduce soil temperature such as mulching or planting in shade or on northern/eastern exposures to accelerate root growth and maintain higher RTRs may increase survival of transplanted mountain laurel. Top growth of mountain laurel and Compacta Japanese holly were unaffected by RZTs indicating cultural practices encouraging root growth need not compromise top growth.

Introduction

Mountain laurel, a member of the Ericaceae, is an ornamental, evergreen shrub native to the eastern United States. Although its native habitat extends from Maine to Florida, it frequently does not survive transplanting from containers into the landscape (10). Wright et al. (29) studied root growth of mountain laurel and an easy-to-transplant species, Japanese holly, over the course of 1 year. Based on their data, they hypothesized that poor landscape performance of mountain laurel at transplanting was related to its slow rate of root growth. In addition, Wright et al. (30) reported planting aspect and root:top ratio (RTR, root dry weight ÷ top dry weight) at transplanting into the landscape affected survival and growth of container-grown Olympic Wedding mountain laurel. They reported survival was highest on east and north exposures, whereas survival was lowest on a western exposure. After 3 years, growth was greatest on an east exposure and lowest on south and west exposures suggesting soil temperatures may play a role in landscape performance of mountain laurel as soil temperatures were higher on the southern and western exposures compared to the eastern exposure.

Growth and morphological responses known to be influenced by RZT include root growth and development, root morphology (elongation and branching), top growth, and RTR (15). In general, top and root growth, and root elongation tend to increase with increasing RZT until an optimum is

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reached above which growth or elongation is reduced (17). Optimum RZTs range from > 35C (95F), 20 to 25C (68 to 77F), and 15 to 20C (59 to 68F) for subtropical, warm temperate, and cool temperate plants, respectively (5). In addition, RZTs frequently affect carbon balance in plants resulting in a marked decrease in RTR at both low and high RZTs (12). In contrast, Cooper (7) indicated the most common response was a higher RTR at low and high RZTs.

In previous research where tops and roots of mountain laurel were exposed to the same temperature, the optimal day temperature (air) for top growth of 1-year-old seedlings of mountain laurel was 26C (79F) but for root growth it was 22C (72F) (16). Malek et al. (16) reported root growth of mountain laurel was more sensitive to high day temperatures (air) as days of 18 or 30C (64 to 86F) produced similar top growth, but root dry weight was lower at 30C (86F) compared to 18C (64F) with a subsequent decrease in RTR.

It appears no research has been conducted to determine the effect of RZT, independent of top temperature (air), on survival and growth of mountain laurel. Comparison of the effects of RZT on survival and growth of mountain laurel and Japanese holly, a species which transplants readily into the landscape, may indicate whether RZT is a major factor in transplant performance of mountain laurel. After transplanting southern highbush and rabbiteye blueberries (*Vaccinium corymbosum* L. and *V. ashei* Reade, respectively), other members of the Ericaceae, into the landscape, RZT had a greater influence on root growth than irrigation or incorporation of organic matter into the soil (24). Therefore, the objective of this research was to compare the effects of RZT on survival, growth, and root morphology of mountain laurel and Japanese holly.

Materials and Methods

Root-zone temperatures of 16, 24, or 32C (61, 75, or 90F) were maintained in three 200-liter (211-qt) continuous flow hydroponic units that provided aeration and allowed regulation of solution temperature to ± 0.5C (0.9F) and ensured uniformity of temperature throughout the root zone (20). Hydroponic units were located in a controlled environment A-chamber (27) at the Southeastern Plant Environment Laboratory (NC State University Phytotron, Raleigh). Air temperature in the chamber was maintained at a 9-hr day/15-hr night thermoperiod of 26/22C (79/72 F) (16). During the 9-hr high irradiance light period, cool-white fluorescent lamps and incandescent bulbs provided a photosynthetic photon flux (*PPF*) of 700 µmol/m^2/s and photomorphogenic radiation (PR) of 12 W/m^2. Long day conditions were provided via a night interruption from 2300 to 0200 hr by incandescent bulbs providing a *PPF* of 70 µmol/m^2/s and PR of 11 W/m^2. Atmospheric CO_2 concentration was maintained at 400 µL/liter.

Hydroponic nutrient solution (hereafter referred to as nutrient solution) was prepared using deionized water and was replaced weekly (Table 1). The pH of the nutrient solution was maintained at 5.5 by manual additions of 5 mM CaOH as needed. Each hydroponic unit included an upper 100-liter (106-qt) root compartment and a lower 100-liter (106-qt) reservoir with continuous circulation of the nutrient solution between the two compartments.

Eight-month-old seedlings of mountain laurel (western North Carolina provenance) and 8-month-old rooted stem cuttings of Compacta holly were placed in the hydroponic units on October 20, 2000. To determine initial top and root dry weights, 10 plants of each taxa were harvested at treatment initiation and dried for 72 hr at 70C (160F). Top and root dry weights were 4.8 g ± 0.5 and 2.4 g ± 0.4, and 3.1 g ± 0.2 and 1.9 g ± 0.1 for mountain laurel and Compacta holly, respectively. Prior to placement in the units, substrate was removed from the roots of each plant by gently submerging the root system in tap water. Seedlings of mountain laurel had been grown previously in sand to facilitate substrate removal and minimize root system injury at experiment initiation. The experiment was terminated January 10, 2001 (12 weeks after initiation). Survival was recorded, and all living plants were harvested and separated into leaves, stems, and roots. Root length and root area were measured using a subsampling technique (26) utilizing a Monochrome AgVision System 286 Image Analyzer (Decagon Devices, Inc., Pullman, WA). Leaf area was measured using a LI-COR 3000 leaf area meter (LI-COR, Lincoln, NE). All plant tissues were dried at 70C (160F) for at least 72 h and weighed. Dry weights (g), leaf area (cm^2), root length (cm), and root area (cm^2) data were used to calculate top dry weight (stem + leaf), root:top ratio (RTR, root dry weight ÷ top dry weight), specific leaf weight (SLW, leaf dry weight ÷ leaf area), root area:root length ratio (RA:RL, root area ÷ root length), specific root weight (SRW, root dry weight ÷ root area), and estimated mean root diameter {ERD, [(root area ÷ root length) ÷ 3.1416]}.

The experiment was repeated beginning March 16, 2001, using 6-month-old micropropagated liners (Briggs Nursery, Inc., Olympia, WA) of Sarah mountain laurel and 1-year-old rooted stem cuttings of Compacta holly. Initial top and root dry weights were 0.6 and 0.3 g, and 2.9 and 1.9 g for mountain laurel and Compacta holly, respectively. The mountain laurel liners of Sarah were in a peat-based substrate, and to avoid injuring the root systems, substrate was not removed from the liners prior to installation. The fine root system of mountain laurel makes removal of organic substrates from the roots difficult. In past experiments, mountain laurel did not recover from injury to roots associated with vigorous washing of the root system (Todd Lasseigne, personal communication). To maintain consistency between the taxa, the substrate was also not removed from the Compacta holly for this second experiment.

Environmental conditions, growth chamber, hydroponic units, and nutrient solutions were the same as described previously for the first experiment. The second experiment was terminated June 7, 2001 (12 weeks after initiation), and plants were harvested as described for the first experiment. At termination of this experiment and prior to harvesting, five root samples, each consisting of the apical 2 cm (0.8 in) of an actively growing primary root, were randomly removed from

Table 1. Chemical source and concentration of mineral nutrients in the hydroponic nutrient solution.

Nutrient	Chemical source	Concentration (mg/L)	Concentration (mM)
NO_3	$CaNO_3$	31	0.5
NH_4	$(NH_4)_2SO_4$	18	1.0
P	KH_2PO_4	16	0.5
K	KH_2PO_4, K_2SO_4	40	1.0
Ca	$CaNO_3$	10	0.25
Mg	$MgSO_4$	12	0.5
Fe	Fe chelate (10%)	1.0	0.02
Mn	$MnCl_2$	0.32	0.006
Cu	$CuSO_4·5H_2O$	0.09	0.01
Zn	$ZnSO_4·H_2O$	0.30	0.005
B	H_3BO_3	0.21	0.02

each taxon at each temperature. The distance from the root apex to the first emerged lateral root [length >1 mm (0.04 in)] and the number of lateral roots in the apical 2 cm (0.8 in) were recorded. If there were no lateral roots in the apical 2 cm (0.8 in), distance from the apex to the first lateral root was recorded as 2.1 cm (0.83 in) for use in statistical analysis.

With the exception of the mountain laurel seedlings used in the first experiment [greenhouse grown under conditions of natural photoperiod, irradiance, and days/nights of 24/16C (75/60F)], all plants were brought into the Phytotron at experiment initiation from conditions of natural photoperiod, irradiance, and temperature. The experiments were a completely randomized design with treatments in a factorial combination of RZT and plant taxa. There was one hydroponic unit per RZT, and plant taxa were arranged randomly within each unit for a total of six single plant replications per taxon per temperature per experiment. Each experimental unit consisted of a single plant. All data were analyzed for significance of treatment main effects and interactions via analysis of variance (23). Prior to analysis, percent survival was arcsine transformed. Results for percent survival were similar for transformed and untransformed data so untransformed are presented. Treatment and interaction means were generated using LSMEANS, and their separation was performed using PDIFF procedure at P = 0.05 (23). For simplicity, both *Kalmia* taxa will be referred to collectively as mountain laurel in the results and discussion.

Results and Discussion

Although there were statistical differences between the two experiments, responses to RZT were consistent within each experiment (significance was not qualitative), so data were pooled. Survival of mountain laurel averaged 67% when grown at RZTs of 16 or 24C (61 or 75F) but survival decreased to 42% when grown at a RZT of 32C (90F) (Table 2). Similarly Wright et al. (29) reported decreased survival of Olympic Wedding mountain laurel when grown in the landscape on a west and south aspect compared to a northern aspect. They speculated elevated soil temperature on the west and north aspect was responsible for decreased survival. In contrast, survival (mean = 97%) of Compacta holly was unaffected by RZT.

Compared to root dry weight of mountain laurel grown at 16C (61F), root dry weight of mountain laurel grown at RZTs of 24 or 32C (75 or 90F) decreased 58 and 72% respectively, whereas top dry weight was unaffected by RZT (Table 2). Similar to data herein, root dry weight of dracaena (*Dracaena marginata* L.) decreased with increasing RZT from 28 to 40C (82 to 104F) but top dry weight was unaffected (9). However, top and root dry weights of Compacta holly were unaffected by RZT. This is supported by Ruter and Ingram (22) who reported RZTs < 38C (100F) did not reduce root growth of Rotundifolia holly (*Ilex crenata* 'Rotundifolia'). Even though Cooper (7) and others reported RZT affects top dry weight, top dry weight of both taxa in the present study were unaffected by RZT.

Carbon balance within mountain laurel was affected as the RTR of mountain laurel grown at RZTs of 24 or 32C (75 or 90F) decreased 48 and 65%, respectively, compared to the RTR of plants grown at 16C (61F) indicating top growth was favored over root growth at higher RZTs (Table 2). This is also supported by no statistical reduction in top dry weight while root dry weight decreased 72% with increasing RZTs. Likewise, Malek et al. (16) reported RTR decreased with increasing air temperature. Decreasing RTR could contribute to decreased survival and growth at transplanting as Wright et al. (30) reported Olympic Wedding mountain laurel with the highest RTR at transplanting had the best growth after 3 years in the landscape. Currently, there is no good quantitative theory on what determines distribution of assimilates between roots and tops at different RZT although various empirical models have been developed for distribution of assimilates (5).

In contrast, RTR of Compacta holly was unaffected by RZT indicating growth of tops and roots responded similarly to increasing RZT. Ruter and Ingram (22) also reported RTR of Rotundifolia holly was unaffected by increasing RZTs but it was a short-term experiment (21 days). Ingram et al. (8) reported root dry weight of Helleri holly (*Ilex crenata* Thunb. 'Helleri') decreased with increasing RZT which subsequently reduced RTR. Maintaining a consistent RTR may be particularly important for providing adequate water via the roots to replenish water lost via transpiration. Maintaining such a water balance within the plant is critical for transplant survival (13).

Similar to top dry weight, leaf area of mountain laurel was unaffected by RZT (data not presented); however, SLW of mountain laurel decreased from 0.014 g/cm^2 at 16C (61F) to 0.012 g/cm^2 at 32C (90F) indicating leaves were getting thinner with increasing RZT (Table 3). Even though SLW of Compacta holly was reduced 13% at 24C (75F) compared to 16C (61F), SLW at 32C (90F) was not different from 16C (61F). Thus, there was no apparent trend with increasing RZT.

Table 2. Effect of root-zone temperature on survival, top and root dry weights, and root:top ratio (RTR) of mountain laurel (M) and Compacta holly (H).

	Survival (%)		Top dry wt (g)		Root dry wt (g)		RTR[z]	
	Taxa							
Temperature (C)	M	H	M	H	M	H	M	H
16	75a[y]	92a	4.3a	11.8a	3.6a	2.9a	0.81a	0.25a
24	58a	100a	2.7a	10.3a	1.5b	2.6a	0.42b	0.28a
32	42b	100a	4.4a	11.6a	1.0b	1.6a	0.28b	0.14a
P-value								
Temperature	0.50		0.75		0.01		0.05	
Taxa	<0.0001		<0.001		0.44		0.007	
Temperature × taxa	0.16		0.99		0.15		0.12	

[z]Root top ratio (RTR) = root dry weight ÷ top dry weight.

[y]Lowercase letters denote mean separation among temperatures within taxa by PDIFF at $P \leq 0.05$.

The RA:RL ratio was unaffected by RZT for both taxa indicating root area and root length were affected similarly by RZT (data not presented). Therefore, only root area will be presented. Compared to mountain laurel grown at a RZT of 16C (61F), root area was reduced 45 and 80%, when grown at RZTs of 24 or 32C (75 or 90F), respectively (Table 3). The pattern of root area suppression was reflective of the 72% reduction in root dry weight from 16 to 32C (61 to 90F) (Table 2). Reduced root area in combination with increasing RTR with increasing RZT could reduce the potential for water and mineral nutrient uptake in the landscape by limiting the volume of soil that can be exploited resulting in poor landscape performance (21). Even though root dry weight of Compacta holly was unaffected by RZT (Table 2), root area was reduced 64%, as RZT increased from 16C (61F) to 32C (90F) (Table 3). Root area can be more sensitive to RZT above or below the optimum than root dry weight (14). Wright et al. (29) also reported root dry weight and root area do not always follow the same trend.

SRW increased for both taxa from 16C (61F) to 32C (90F) indicating thicker roots were produced at 32C (90F). However, estimated mean root diameter for mountain laurel [mean = 0.50 mm (0.02 in)] and Compacta holly [mean = 0.51 mm (0.02 in)] were unaffected by RZT and were surprisingly similar in size (Table 3). This is in contrast to Cooper (7) who reported root diameter is inversely related to RZT. This could be an artifact of growing in a hydroponic solution. However, Abbas Al-Ani and Hay (1) reported RZT from 5 to 25C (41 to 77F) had only a small impact on root diameter.

Lower root dry weight and root area for mountain laurel at a RZT of 32C (90F) [compared to 16 or 24C (61 and 75F)] were similar to results reported for pittosporum (*Pittosporum tobira* Thunb.) which had lower root and top growth at 40C (104F) compared to 27C (81F) (11). Similarly, rose (*Rosa* L. sp.) and peach [*Prunus persica* (L.) Batsch. (Peach Group)] had reduced root growth when RZTs were ≥ 30C (86F) (28). Vigorous root growth of mountain laurel at 16C (61F) in the present investigation suggests that in warmer climates such as Raleigh, NC, mulch or shade could be particularly important to reduce soil temperature. Wright et al. (30) offered similar recommendations based on landscape research with Olympic Wedding mountain laurel. Daily soil temperatures [depth of 15–20 cm (6–8 in)] in Raleigh (lat. 35°11' N, long. 80°25' W, ARS heat zone 4) frequently average > 30C (86F) during summer months (25). The similarity of top growth of mountain laurel across RZTs indicates poor landscape performance of this species may be related to reduced root growth at elevated soil temperatures.

Tops of Compacta holly were most attractive visually at a RZT of 24C (75F), whereas mountain laurel had the best visual appearance at a RZT of 16C (61F) (personal observations). At 32C (90F), roots of both taxa were brown, stunted, and stubby, whereas at 16 and 24C (61 and 75F), roots of both taxa were white, succulent, and vigorous (personal observations). Likewise, roots of bentgrass (*Agrostis palustris* Huds.) remained white and succulent when grown at 16C (75F), but turned brown and withered after 35 days at 27C (81F) (2). Visual appearance of roots at 32C (90F) (brown and lacking turgor) was likely due to death of root cortical tissue. In an experiment with apple (*Malus* Mill. sp.) and peach grown at RZTs ranging from 7 to 35C (45 to 95F), cortex death was observed in roots grown at RZTs ≥ 24C (75F), while no cortex death was observed in roots grown at ≤ 18C (64F) RZT (19). Most reports regarding root maturation and turnover in response to RZT is qualitative (5).

For both taxa, distance from the root apex of primary roots to the most recently emerged lateral root decreased with increasing RZT (Table 4). Similarly, Bowen (4) reported that for radiata pine (*Pinus radiata* D. Don) the most recently emerged lateral root was 108 mm (0.4 in) at 14C (57F) and 51 mm (0.2 in) at 25C (77F) from the apex.

In the present investigation, the number of lateral roots for both taxa in the apical 2 cm (0.8 in) of primary roots increased dramatically at 32C (90F). Influence of RZT on root architecture has been reported by other researchers with number of lateral roots increasing with increasing RZTs (5, 18) However, response of number of lateral roots to RZT differs dramatically among species and among genotypes with species (12). Bowen (5) suggested caution regarding generalized conclusions regarding the effect of RZT on lateral root production.

High RZTs have been correlated with higher rates of cell elongation, but shorter periods of elongation (3, 6). As a result, maturation and differentiation of root tissue occurs closer

Table 3. Effect of root-zone temperature on specific leaf weight, root area, specific root weight, and estimated root diameter of mountain laurel (M) and Compacta holly (H).

	Specific leaf weight[z] (g/cm^2)		Root area (cm^2)		Specific root weight[y] (g/cm^2)		Root diameter[x] (mm)	
	Taxa							
Temperature (C)	M	H	M	H	M	H	M	H
16	0.014a[w]	0.008a	2606a	1421a	0.001b	0.002b	0.48a	0.45a
24	0.013ab	0.007b	1432b	1170ab	0.001b	0.002b	0.53a	0.52a
32	0.012b	0.009a	512b	503b	0.002a	0.003a	0.51a	0.53a
P-value								
Temperature	0.11		0.002		0.01		0.07	
Taxa	<0.0001		0.14		0.0002		0.78	
Temperature × taxa	0.03		0.18		0.07		0.79	

[z]Specific leaf weight = leaf dry weight ÷ leaf area.

[y]Specific root weight = root dry weight ÷ root area.

[x]Estimated root diameter = [(root area ÷ root length) ÷ 3.1416].

[w]Lowercase letters denote mean separation among temperatures within taxa by PDIFF at $P \leq 0.05$.

Table 4. **Effect of root-zone temperature on distance from the root apex of primary roots to most recently emerged lateral root [length > 1 mm (0.04 in)] and the number of lateral roots in the apical 2 cm (0.8 in) of the primary roots of mountain laurel (M) and Compacta holly (H).**

	Distance from apex (mm)		No. of lateral roots	
Temperature (C)	**M**	**H**	**M**	**H**
16	19a[z]	21a	0.8c	0b
24	12b	18a	8b	1b
32	2c	4b	14a	12a
P-value				
Temperature	0.001		0.001	
Taxa	0.001		0.002	
Temperature × taxa	0.15		0.06	

[z]Lowercase letters denote mean separation among temperatures within taxa by PDIFF at $P \leq 0.05$.

to the root apex at higher RZTs (3). When maturation occurs closer to the root apex, branching also occurs closer to the apex. In addition, a decreased period of root elongation usually results in shorter roots overall. In the landscape, lack of root elongation and thus extension into the surrounding soil may hinder transplant establishment. For example, uptake of phosphorus (P) from soil is dominated by root length and reduced root growth was the primary reason for a 40% reduction in P uptake by corn (*Zea mays* L.) at 18C (64F) compared to 25C (77F) (15). Johnson and Ingram (11) reported reduced foliar K, Fe, and Zn content in pittosporum when exposed to a RZT of 40C (104F). Thus, increasing RZT may impact water and mineral nutrient uptake.

Inhibition of root growth and decreased RTR of mountain laurel by high RZTs may explain, in part, poor landscape performance of this species. Even though Compacta holly also experienced a decrease in root area, the ability to maintain similar RTR when grown in RZTs from 16 to 32C (61 to 90F) may be a survival mechanism during landscape establishment. Results of this research concur with conclusions of Wright et al. (30) that reducing RZT in the landscape via mulch, shade, and/or aspect may increase survival and growth of transplanted mountain laurel. In addition, top growth of mountain laurel was relatively unaffected by RZTs indicating cultural practices promoting root growth need not compromise top growth.

Literature Cited

1. Abbas Al-Ani, M.K. and R.K.M. Hay. 1983. The influence of growing temperature on the growth and morphology of cereal seedling root systems. J. Expt. Bot. 34:1720–1730.

2. Beard, J.B. and W.H. Daniel. 1965. The effect of temperature and cutting on the growth of creeping bentgrass (*Agrostis palustris* Huds.) roots. Agron. J. 57:249–250.

3. Beauchamp, E. and D.J. Lathwell. 1966. Root-zone temperature effects on the vascular development of adventitious roots in *Zea mays*. Bot. Gaz. 127:153–158.

4. Bowen, G.D. 1970. Effects of soil temperature on root growth and on phosphate uptake along *Pinus radiata* roots. Austral. J. Soil Res. 8:31–42.

5. Bowen, G.D. 1991. Soil temperature, root growth, and plant function. p. 309–330. *In*: Y. Waisel, A. Eshel, and U. Kafkafi (Editors). Plant Roots: The Hidden Half. Marcel Dekker, Inc., New York.

6. Burstrom, H. 1956. Temperature and root cell elongation. Physiol. Plant. 9:682–692.

7. Cooper, A.J. 1973. Root Temperature and Plant Growth. Commonwealth Agr. Bur., Slough, U.K.

8. Ingram, D.L., C. Martin, and B. Castro. 1988. Container spacing treatments influence temperature fluctuations and holly growth. Proc. Fla. State Hort. Soc. 101:328–331.

9. Ingram, D.L., C. Ramcharan, and T.A. Nell. 1986. Response of container-grown banana, ixora, citrus, and dracaena to elevated root temperatures. HortScience 21:254–255.

10. Jaynes, R.A. 1997. *Kalmia*: Mountain Laurel and Related Species. Timber Press, Inc., Portland, OR.

11. Johnson, C.R. and D.L. Ingram. 1984. *Pittosporum tobira* response to container medium temperature. HortScience 19:524–525.

12. Kasper, T.C. and W.L. Bland. 1992. Soil temperature and root growth. Soil Sci. 154:290–299.

13. Kozlowski, T.T. and W.J. Davies. 1975. Control of water balance in transplanted trees. J. Arboricult. 1:1–10.

14. Loffroy, O., C. Hubac, and J.B.V. da Silva. 1983. Effect of temperature on drought resistance and growth of cotton plants. Physiol. Plant. 59:297–301.

15. MacKay, A.D. and S.A. Barber. 1984. Soil temperature effects on root growth and phosphate uptake by corn. Soil Sci. Soc. Amer. J. 48:818–823.

16. Malek, A.A., F.A. Blazich, S.L. Warren, and J.E. Shelton. 1992. Initial growth of seedlings of mountain laurel as influenced by day/night temperature. J. Amer. Soc. Hort. Sci. 117:736–739.

17. McMichael, B.L. and J.J. Burke. 1998. Soil temperature and root growth. HortScience 33:947–951.

18. McMichael, B.L. and J.J. Burke. 2002. Temperature effects on root growth. p. 717–728. *In*: Y. Waisel, A. Eshel, and U. Kafkafi (Editors). Plant Roots: The Hidden Half. Marcel Dekker, Inc., New York.

19. Nightingale, G.T. 1935. Effects of temperature on growth, anatomy, and metabolism of apple and peach roots. Bot. Gaz. 96:581–639.

20. Osmond, D.L., E.K. York, and C.D. Raper. 1981. A system for independently controlled root and shoot temperatures for nutrient uptake studies. Tobacco Intl. 183:38–39.

21. Russell, R.S. 1977. Plant Root Systems. McGraw-Hill, London.

22. Ruter, J.M. and D.L. Ingram. 1990. ^{14}Carbon-labeled photosynthate partitioning in *Ilex crenata* 'Rotundifolia' at supraoptimal root-zone temperatures. J. Amer. Soc. Hort. Sci. 115:1008–1013.

23. SAS Inst., Inc. 2005. SAS/STAT User's Guide: Release 8.2 Ed. SAS Inst., Inc., Cary, NC.

24. Spiers, J.M. 1995. Substrate temperatures influence root and shoot growth of southern highbush and rabbiteye blueberries. HortScience 30:1029–1030.

25. State Climate Office of North Carolina at North Carolina State University. 2000. NCARS Weather and Climate Network: Turfgrass Field Lab. Accessed February 28, 2002. <http://www.nc-climate.ncsu.edu/agnet/turf/2000/Ausust/turf_08200.html>.

26. Thetford, M., S.L. Warren, and F.A. Blazich. 1995. Response of *Forsythia* x *intermedia* 'Spectabilis' to uniconazole. I. Growth; dry-matter distribution; and mineral nutrient content, concentration and partitioning. J. Amer. Soc. Hort. Sci. 120:977–982.

27. Thomas, J.F., R.J. Downs, and C.H. Saravitz. 2004. Phytotron procedural manual for controlled-environment research at the Southeastern Plant Environment Laboratory. N.C. Agr. Res. Serv. Tech. Bul. 244 (Revised). Accessed March 5, 2004. <http://www.ncsu.edu/phytotron/manual.pdf>.

28. Wong, T.L. R.W. Harris, and R.E. Fissel. 1971. Influence of high soil temperatures on five woody-plant species. J. Amer. Soc. Hort. Sci. 96:80–83.

29. Wright, A.N., S.L. Warren, F.A. Blazich, and U. Blum. 2004. Root and shoot growth periodicity of *Kalmia latifolia* 'Sarah' and *Ilex crenata* 'Compacta'. HortScience 39:243–247.

30. Wright, A.N., S.L. Warren, F.A. Blazich, J.R. Harris, and R.D. Wright. 2005. Initial plant size and landscape exposure affect establishment of transplanted *Kalmia latifolia* 'Olympic Wedding'. J. Environ. Hort. 23:91–96.