ABSTRACT

WRIGHT, AMY NOELLE. The Physiology of Landscape Establishment of *Kalmia latifolia*. (Under the direction of Drs. Stuart L. Warren and Frank A. Blazich)

Although native to the eastern United States, with a broad geographic range, mountain laurel (*Kalmia latifolia* L.) frequently does not survive transplanting from containers into the landscape and is generally regarded as a difficult-to-transplant species. In an effort to understand poor transplant success and to improve landscape establishment of the species, four experiments were conducted to describe some of the critical factors associated with transplanting mountain laurel. In some cases, research included comparison of mountain laurel to that of an easy-to-transplant species, Japanese holly (*Ilex crenata* Thunb.).

In the first study, root growth of mountain laurel was compared to that of Japanese holly over the course of 1 year. Root length and root surface area of mountain laurel increased in the fall but decreased in the spring, while root length and root surface area of Japanese holly increased linearly throughout the year. Root : shoot ratio increased linearly for Japanese holly but did not increase during the spring for mountain laurel.

The second study compared the effects of root-zone temperature on root growth of mountain laurel and Japanese holly. When mountain laurel and Japanese holly were grown hydroponically in the fall and the spring at 9 hour days/15 hour nights of 26/22C with root-zone temperatures of 16, 24, or 32C, percent increase in root length and root surface area were highest at 16C for mountain laurel and 24C for Japanese holly. At each root-zone temperature, percent survival was higher for Japanese holly than mountain

laurel. More root growth occurred in the fall than in the spring for both species. Root : shoot ratio of mountain laurel was higher in the fall than in the spring, whereas root : shoot ratio of Japanese holly was similar for both seasons.

A third investigation compared drought tolerance of mountain laurel to that of Japanese holly. In response to several drought treatments, shoot dry weight decreased more rapidly with increasing drought stress for mountain laurel than Japanese holly. Pre-dawn plant water potential decreased faster for mountain laurel than Japanese holly. Although both species appeared to osmotically adjust, mountain laurel was less drought tolerant than Japanese holly. Osmotic adjustment occurred only in more severely stressed plants.

The fourth experiment investigated the influence of root : shoot ratio on survival and subsequent growth of transplanted, container-grown mountain laurel. Landscape exposure and initial root : shoot ratio of transplanted mountain laurel influenced plant survival and growth over three growing seasons. Shoot growth (stems and leaves) and visual quality were highest for plants with largest initial root : shoot ratio. In general, plant growth, survival, and visual ratings were higher on north and east exposures than on south and west exposures.

The Physiology of Landscape Establishment of *Kalmia latifolia*

by

Amy Noelle Wright

A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the requirements for the Degree of

Doctor of Philosophy

Horticultural Science

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Approved by:

Udo Blum	Thomas G. Ranney
Stuart L. Warren (Co-chair)	Frank A. Blazich (Co-chair)

Dedication

The poet pointed where a flower

A simple daisy starred the sod…

“Proof of love and power

Behold, behold a smile of God!”

(From A Thought by William Cox Bennett)

Biography

Amy Noelle Wright grew up in Blacksburg, Virginia and graduated from Blacksburg High School in June 1992. Moving only as far as across town into a dormitory, in August 1992, Amy entered Virginia Tech as a freshman majoring in Chemistry. During her time as an undergraduate, Amy worked as a laboratory assistant in the Pesticide Residue Research Laboratory in the Department of Biochemistry and conducted undergraduate research in the Department of Food Science and Technology. In December 1996, Amy graduated from Virginia Tech, receiving a Bachelor of Science degree in Chemistry and a minor in Biochemistry. As exciting as her undergraduate program had been, it was time to switch directions, so in January 1997, Amy began her graduate work in the Department of Horticulture at Virginia Tech. By the time Amy graduated with a Master of Science degree in Horticulture in July 1998, she had enjoyed teaching class so much that she had decided to continue her education with the ultimate goal of teaching at a university (although secretly, she had always wanted to be a professor). In August 1998, Amy moved to Raleigh, North Carolina and entered the Ph.D. program in the Department of Horticultural Science at North Carolina State University. In September 2001, Amy moved one step closer towards reaching her goal of becoming a university professor when she accepted a position as Assistant Professor in the Department of Horticulture at Auburn University in Auburn, Alabama. Amy received the degree of Doctor of Philosophy in May 2002 after learning much about science and life in general. Amy's position at Auburn University began in the same month as her defense, adding some yet unknown, but hopefully interesting, lines to her biography.

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graduate school can be so much more difficult without it. My friends and family have always been important to me, and I continue to rely on them for friendship and support. Anthony, I have much heartfelt thanks for everything you've taught me about life and myself. I can't imagine my time in Raleigh without you. Finally, one truth remains constant and above all else. God's protection and guidance in my life will always send me in the right direction and are my ultimate source of support and love.

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Introduction

Mountain laurel (*Kalmia latifolia* L.) is a broadleaved evergreen shrub native to the eastern United States. A member of the Ericaceae (heath family), mountain laurel shares a family with genera such as *Arbutus* L. (madrone), *Enkianthus* Lour. (enkianthus), *Gaultheria* L. (wintergreen), *Leucothoe* D. Don (fetterbush), *Lyonia* Nutt. (staggerbush), *Oxydendrum* DC. (sourwood), *Pieris* D. Don (andromeda), *Rhododendon* L. (rhododendron and azalea), *Vaccinium* L. (blueberry), and *Zenobia* D. Don (dusty zenobia). The eastern portion of its geographic distribution extends from southern Maine into northern Florida, and the western part of this range is from central Ohio to southern Mississippi (Jaynes, 1997). Cold hardiness of this species includes USDA zones 4 to 9, although southern provenances may not be hardy in the North (Dirr, 1998). Although most commonly found growing in shady understory locations, the species also grows in full sun in cooler climates and at higher elevations. It is frequently found growing along high ridges, steep slopes, and even rocky mountain outcrops.

Depending on geographic location and elevation, mountain laurel produces an impressive floral display from May to July. Flowers are born in terminal clusters, with individual flowers having a unique broad-campanulate shape with stamens that reflex backwards and anthers that are held in small pockets within the corolla. Flower color ranges from pure white to deep pink, and flower bud color ranges from pure white to dark red. Corolla pigmentation may be solid or banded on the interior. Foliage size and color as well as growth form also vary widely within the species. As a result of these differences, much breeding and selection has been done for mountain laurel, and today, many unique cultivars are produced commercially in the United States. Although mountain laurel reproduces by seed in its native habitat, most cultivars and selections are propagated commercially by micropropagation (tissue culture) (Jaynes, 1997). Liners produced in this manner are grown in nurseries for at least three growing seasons before being sold for landscape use. Mountain laurel is frequently marketed in large, 19-L containers at an age (3 to 4 years) when full floral display is possible.

Because of the outstanding ornamental attributes of mountain laurel and its desireability as a native evergreen shrub, the species is prized by gardeners and horticulturists alike. Despite successful commercial production of numerous cultivars and selections of this species, mountain laurel frequently does not survive transplanting from containers into the landscape but often declines slowly and dies after one to three growing seasons.

There are many factors that may influence the ability of woody ornamental plants to survive transplanting from containers into the landscape and some of these have been studied extensively by various researchers. Of these factors, root growth into the surrounding soil appears to be most critical and is necessary if the plant is to obtain water and mineral nutrients needed for plant growth and development (Watson and Himelick, 1997). The time between transplanting and initiation of new root growth is important in predicting or describing transplant success, since initiation of new root growth shortly after transplanting has been correlated with successful transplant establishment (Woods, 1959). As might be expected, rate of root growth varies with species (Head, 1966;

Rogers and Head, 1969; Watson and Himelick, 1982b). Delay in new root growth following transplanting has been documented (Harris et al., 1996), and there is evidence that the time between transplanting and new root growth is longer for those species considered difficult-to-transplant (Struve et al., 1984).

Root growth rates and seasonal periodicity of root growth may also influence transplant survival. Alternating growth phases of roots and shoots were observed by Drew and Ledig (1980) in loblolly pine (*Pinus taeda* L.), where seasonal variation in dry matter allocation favored roots at certain times and shoots at others. Likewise, apple (*Malus* Mill. spp.) produced no root growth during periods of shoot growth in the spring; instead, roots grew during August through September after shoot growth had stopped (Rogers and Head, 1969). Root growth periodicity has application when choosing time of year for transplanting. Kozlowski and Davies (1975) suggested plants that exhibit seasonal growth periodicity should be transplanted during the time of the year when root growth rates are highest.

Plant response to environmental conditions also affects transplant survival. Soil temperature influences root growth and development, root morphology (elongation and branching), and root : shoot ratio (McMichael and Burke 1998; Spiers 1995). Supraoptimal root-zone temperatures can result in death of root cortical tissue (Beard and Daniel, 1965; Nightingale, 1935). Elevated root-zone temperatures have been correlated with higher rates of cell elongation, but shorter periods of elongation (Beauchamp and Lathwell, 1966; Burstrom 1956). As a result, maturation and differentiation of root tissue occurs closer to the root apex at higher temperatures (Beauchamp and Lathwell, 1966).

A decreased period of root elongation results in shorter roots overall. Exposure to high root-zone temperatures even during production may lengthen the landscape establishment period due to decreased root growth (Martin and Ingram, 1991).

Soil and plant water relations also determine survival of transplanted container-grown plants (Costello and Paul, 1975). Even when soil water is adequate to support plant growth, plant available water within the transplanted container root ball can be much lower (Costello and Paul, 1975). Not only is a perched water table not present in the landscape as it is in a container, but water may be drawn out of the root ball into the surrounding soil due to dissimilarity between physical properties of a coarse-textured container substrate such as pine bark and a fine-textured soil (Nelms and Spomer, 1983).

As mentioned previously, until roots of a transplanted container-grown plant extend into the surrounding soil, the plant will be unable to absorb water from the soil. As a result, plants must depend on water resources available within the original root ball, which are frequently insufficient due to limited irrigation and/or precipitation in the landscape. Root death may occur during rapid dehydration, while the root elongation zone and rate of root growth decrease in response to gradual drying (Dubrovsky et al., 1998). As a result, root growth into the surrounding soil is inhibited by lack of adequate water supply following transplanting (Witherspoon and Lumis, 1986).

Although transpiration and water use may decrease under extended periods of drought (Cremer, 1972; Pennypacker et al., 1990), leaf water deficits (or low plant water potentials) may still develop when water lost as a result of transpiration exceeds the amount taken up by the roots (Roberts and Knoerr, 1977). In response to low plant water potential, some plants accumulate solutes, a process known as osmotic adjustment (Blake and Bevilacqua, 1991; Ranney et al., 1991). This accumulation results in a decrease in osmotic potential which allows maintenance of turgor pressure at decreasing plant water potentials (Abrams, 1988). Although plant responses to drought vary for different species (Muller, 1991; Zhang and Archbold, 1993), osmotic adjustment has been documented for many species and appears to be most important under conditions of substantial drought stress (Meier et al., 1992; Ranney et al., 1991).

Similar to root growth rates, plant size and root : shoot ratio are important factors to consider when transplanting ornamentals (Harris, 1992). Personal observations by the author with mountain laurel indicate that smaller plants, with time, can surpass in growth larger plants planted at the same time. This has also been reported for other species (Watson 1985). Transplant size affects root : shoot ratio (Harris, 1992), and in the case of transplanted trees, smaller plants often have a higher root : shoot ratio (Watson, 1985). A larger root : shoot ratio is 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 (Kozlowski and Davies, 1975). Since root : shoot ratio can change with time, age, and production practices in the nursery, root : shoot ratios vary widely for transplanted ornamentals (Beeson, 1993; Keever and Cobb, 1987). It has been suggested that during nursery production, container-grown plants potted into larger containers in the fall may by spring have a higher root : shoot ratio due to continued root growth during the winter in mild to temperate climates (Harris, 1992). In contrast, plants potted in spring may by fall have a lower root : shoot ratio due to more shoot growth during summer months. Since a large, attractive plant canopy is typically the goal of commercial production, frequent watering and high fertility common during nursery production may result in more shoot growth than can be adequately supplied by the accompanying root ball following transplanting (Harris, 1992; Watson and Himelick, 1997).

Planting location with respect to exposure also affects transplant survival and may be particularly important for plants traditionally planted in full to partial shade (Andersen et al., 1991a, b). Differences in air and soil temperatures among exposures may account for differences in transplant survival and growth (Pair and Still, 1982). Exposure can also influence plant water relations (Pair, 1987) as well as root growth and distribution (Watson and Himelick, 1982a).

To improve survival of a species following transplanting, it is necessary to first determine and study those factors that influence its establishment in the landscape. It is clear that landscape establishment is a complicated process involving the interaction of many factors, none of which are totally independent. Many of these factors suggest the importance of appropriate post-transplant care for species which may be susceptible to environmental stress, as well as the need for production practices that result in plants more likely to survive transplanting. When a species is difficult-to-transplant, it may be helpful to compare its behavior to that of an easy-to-transplant species to determine what, if any, differences exist. Such an approach may be useful to understand poor trasplant survival of mountain laurel. Therefore, the following research was conducted in an effort to improve landscape establishment and survival of transplanted mountain laurel. Four experiments were conducted to describe some of the critical factors associated with transplanting mountain laurel. In some cases, research also included comparison of mountain laurel to an easy-to-transplant species, Japanese holly (*Ilex crenata* Thunb.). The four objectives of this research were to (1) determine rate and periodicity of root growth of mountain laurel and Japanese holly, (2) study the influence of root-zone temperature on root and shoot growth of mountain laurel and Japanese holly, (3) compare drought tolerance of mountain laurel and Japanese holly, and (4) study the effect of root : shoot ratio and landscape exposure on survival and growth of transplanted mountain laurel.

Literature Cited

Abrams, M.D. 1988. Sources of variation in osmotic potentials with special reference to North American tree species. For. Sci. 34:1030-1046.

Andersen, P.C., G.W. Knox, and J.G. Norcini. 1991a. Light intensity influences growth and leaf physiology of *Aucuba japonica* 'Variegata'. HortScience 26:1485-1488.

Andersen, P.C., J.G. Norcini, and G.W. Knox. 1991b. Influence of irradiance on leaf physiology and plant growth characteristics of *Rhododendron* x 'Pink Ruffles'. J. Amer. Soc. Hort. Sci. 116:881-887.

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.

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.

Beeson, R.C., Jr. 1993. Benefits of progressively increasing container size during nursery production depend on fertilizer regime and species. J. Amer. Soc. Hort. Sci. 118:752-756.

Blake, T.J. and E. Bevilacqua. 1991. Effects of repeated stress on turgor pressure and cell elasticity changes in black spruce seedlings. Can. J. For. Res. 21:1329-1333.

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

Costello, L. and J.L. Paul. 1975. Moisture relations in transplanted container plants. HortScience 10:371-372.

Cremer, K.W. 1972. Immediate resumption of growth by radiata pine after five months of minimal transpiration during drought. Austral. For. Res. 6:11-16.

Dirr, M.A. 1998. Manual of woody landscape plants: Their identification, ornamental characteristics, propagation and uses. 5th ed. Stipes Publishing, Champaign, Ill.

Drew, A.P. and F.T. Ledig. 1980. Episodic growth and relative shoot : root balance in loblolly pine seedlings. Ann. Bot. 45:143-148.

Dubrovsky, J.G., G.B. North, and P.S. Nobel. 1998. Root growth, developmental changes in the apex, and hydraulic conductivity for *Opuntia ficus-indica* during drought. New. Phytol. 138:75-82.

Harris, R.W. 1992. Arboriculture: Integrated management of landscape trees, shrubs, and vines. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Harris, J.R., P. Knight, and J. Fanelli. 1996. Fall transplanting improves establishment of balled and burlapped fringe tree (*Chionanthus virginicus* L.). HortScience 31:1143-1145.

Head, G.C. 1966. Estimating seasonal changes in the quantity of white unsuberized root on fruit trees. J. Hort. Sci. 41:197-206.

Jaynes, R.A. 1997. *Kalmia*: Mountain laurel and related species. Timber Press, Inc., Portland, Ore.

Keever, G.J. and G.S. Cobb. 1987. Effects of container volume and fertility rate on growth of two woody ornamentals. HortScience 22:891-893.

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

Martin, C.A. and D.L. Ingram. 1991. Root growth of southern magnolia following exposure to high root-zone temperature. HortScience 26:370-371.

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

Meier, C.E., R.J. Newton, J.D. Puryear, and S. Sen. 1992. Physiological responses of loblolly pine (*Pinus taeda* L.) to drought stress: Osmotic adjustment and tissue elasticity. J. Plant Physiol. 140:754-760.

Muller, R.N. 1991. Growing season water relations of *Rhododendron maximum* L. and *Kalmia latifolia* L. Bul. Torrey Bot. Club 118:123-127.

Nelms, L.R. and L.A. Spomer. 1983. Water retention of container soils transplanted into ground beds. HortScience 18:863-866.

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

Pair, J.C. 1987. Winter hardiness, leaf water potential, and heat tolerance of 'China Girl' holly as affected by landscape exposure. HortScience 22:268-270.

Pair, J.C. and S.M. Still. 1982. Growth, hardiness, and leaf-water potential of blue holly (*Ilex* x *meserveae*) cultivars as affected by exposure. HortScience 17:823-825.

Pennypacker, B.W., K.T. Leath, W.W. Stout, and R.R. Hill, Jr. 1990. Technique for simulating field drought stress in the greenhouse. Agron. J. 82:951-957.

Ranney, T.G., N.L. Bassuk, and T.H. Whitlow. 1991. Osmotic adjustment and solute constituents in leaves and roots of water-stressed cherry (*Prunus*) trees. J. Amer. Soc. Hort. Sci. 116:684-688.

Roberts, S.W. and K.R. Knoerr. 1977. Components of water potential estimated from xylem pressure measurements in five tree species. Oecologia 18:191-202.

Rogers, W.S. and G.C. Head. 1969. Factors affecting the distribution and growth of roots in perennial woody species, p. 280-295. In: W.J. Whittington (ed.). Root growth. Plenum Press, New York.

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

Struve, D.K., R.D. Kelly, and B.C. Moser. 1984. Promotion of root regeneration in difficult-to-transplant species. Proc. Intl. Plant Prop. Soc. 33:433-439.

Watson, G.W. 1985. Tree size affects root regeneration and top growth after transplanting. J. Arboricult. 11:37-40.

Watson, G.W. and E.B. Himelick. 1982a. Root distribution of nursery trees and its relationship to transplanting success. J. Arboricult. 8:225-229.

Watson, G.W. and E.B. Himelick. 1982b. Seasonal variation in root regeneration of transplanted trees. J. Arboricult. 8:305-310.

Watson, G.W. and E.B. Himelick. 1997. Principles and practice of planting trees and shrubs. Intl. Soc. Arboricult., Savoy, Ill.

Witherspoon, W.R. and G.P. Lumis. 1986. Root regeneration of *Tilia cordata* cultivars after transplanting in response to root exposure and soil moisture levels. J. Arboricult. 12:165-168.

Woods, F.W. 1959. Slash pine roots start growth soon after planting. J. For. 57:209.

Zhang, B. and D.D. Archbold. 1993. Water relations of a *Fragaria chiloensis* and a *F. virginiana* selection during and after water deficit stress. J. Amer. Soc. Hort. Sci. 188:274-279.

Chapter 1

Root Growth Periodicity of *Kalmia latifolia* 'Sarah' and *Ilex crenata* 'Compacta'

(In the format appropriate for submission to HortScience)

Subject Category: Crop Production: Nursery and Landscape Plants

Root Growth Periodicity of *Kalmia latifolia* 'Sarah' and *Ilex crenata* 'Compacta'

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Abstract. The length of time between transplanting and subsequent new root initiation, root growth rates, and root growth periodicity can influence the ability of woody ornamentals to survive transplanting into the landscape. Research was conducted to compare root growth of a difficult to transplant species, *Kalmia latifolia* L. (mountain laurel), to that of an easy to transplant species, *Ilex crenata* Thunb. (Japanese holly), over the course of 1 year. Micropropagated liners of 'Sarah' mountain laurel and rooted stem cuttings of 'Compacta' holly were potted in 3-L containers. Plants were grown in a greenhouse from May to September, at which time they were moved outside to a gravel pad where they remained until the following May. Destructive plant harvests were conducted every 2 to 4 weeks for 1 year. At each harvest leaf area, shoot DW (DW)(stems and leaves), root length, root area, and root DW were determined. Throughout the experiment, shoot DW and leaf area were similar for the two cultivars. New root growth of 'Compacta' holly and 'Sarah' mountain laurel was measurable 15 and 30 days after potting, respectively. Root length and root area of 'Sarah' mountain laurel increased during May through December but decreased during January through May. Root length and root area of 'Compacta' holly increased linearly throughout the course of the experiment. Final root:shoot ratio was nine times larger for 'Compacta' holly than 'Sarah' mountain laurel. Results suggest the poor transplant performance of mountain laurel in the landscape may be related to its slow rate of root growth.

When a plant is transplanted into the landscape from a container, many factors affect its survival. Of these, root growth into the surrounding soil appears to be one of the most critical (Watson and Himelick, 1997). Root growth following transplanting is necessary if the plant is to obtain water and mineral nutrients necessary for plant growth and development. The rate of root growth, as well as root growth periodicity, vary with species and environmental conditions (Head, 1966; Rogers and Head, 1969). Norway maple (*Acer platanoides* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and ginkgo (*Ginkgo biloba* L.) exhibited differences in root regeneration following transplanting and responded differently to the season of transplanting (Watson and Himelick, 1982). There is some evidence that the time between transplanting and new root growth is longer for those species considered difficult to transplant (Struve et al., 1984).

Traditionally, woody species considered difficult to transplant are those with tap root systems, whereas species with fibrous root systems are often considered easy to transplant (Pirone, 1978; Struve and Moser, 1984). However, many Ericaceous species, such as mountain laurel (*Kalmia latifolia*), which produce fibrous root systems, are often difficult to transplant (personal observations). Mountain laurel is an evergreen shrub native to the eastern United States with excellent ornamental attributes. Although mountain laurel produces a fibrous root system, it frequently does not survive transplanting from containers into the landscape, even in areas to which it is indigenous (Jaynes, 1997). Characterizing rate and periodicity of root growth of mountain laurel with subsequent comparison to root growth of an easy to transplant species, such as Japanese holly (*Ilex crenata* Thunb.), may provide insight into the difficulty associated with landscape establishment of this Ericaceous species. Therefore, the objective of this research was to compare rate and periodicity of root growth of mountain laurel and Japanese holly over the course of 1 year.

Materials and Methods

Six-month-old micropropagated liners of 'Sarah' mountain laurel and 1-year-old rooted stem cuttings of 'Compacta' holly were repotted into 3-L containers in May 1999. Plants were potted in arcillite, a calcined montmorillonite and illite clay (Turface-MVP™, Profile Products, Buffalo Grove, Ill.). Arcillite is a coarse-textured substrate that is removed easily to facilitate harvest of roots and is preferred over sand because of its mineral nutrient and water holding properties (Hiller and Koller, 1979). Prior to potting, roots of all plants were dyed by submerging each root system (substrate intact) in a solution of 0.5% (w/v) methylene blue for 10 s. This dye provides an effective way to distinguish between root tissue present at potting (blue) and new root tissue produced after potting (white) (Arnold and Young, 1990). Plants were potted with the original substrate intact to minimize injury to the root system and to simulate transplanting an undisturbed containerized rootball into the landscape. Upon potting, plants were immediately irrigated, effectively removing any excess dye that could possibly be transferred to new roots. Plants were grown in the Department of Horticultural Science Greenhouses, North Carolina State University, Raleigh, under natural photoperiod and irradiance with days/nights of 24/16C. In September 1999, plants were moved outdoors to a gravel pad at the Horticulture Field Laboratory, Raleigh, for the remainder of the study to allow the plants to experience seasonal changes in temperature. Plants were overwintered in a white polyethylene covered structure from December 1999 to February 2000.

While in the greenhouse, plants were fertilized three times weekly with a solution of Peters™ (Scotts Co., Marysville, Ohio) 20N-8.8P-16.6K water soluble fertilizer with trace elements at 100 $mg•L^{-1}$. Fertilizer solution also included Ca (as $CaCO_2H$)at 50 $mg•L^{-1}$ and Mg (as $MgSO_4$) at 25 $mg•L^{-1}$. Once per week plants received foliar application of iron chelate at 10 $mg•L^{-1}$, applied using a handheld mist sprayer. Foliage was sprayed until solution ran off the foliage. While outdoors, liquid fertilization was applied once weekly from September through November and from March through May (no fertilization during December through February). Foliar iron application was discontinued in September. Supplemental irrigation (tap water) was applied as needed throughout the experiment.

Experimental variables were cultivar and harvest date (days after potting, DAP) which were arranged in a randomized complete block design with five blocks. Each block contained 50 plants of each cultivar, arranged randomly. Destructive plant harvests were conducted every 2 to 4 weeks for 1 year (16 total harvests; Table 1) by randomly selecting one plant of each cultivar from each block. At all harvests, roots were carefully washed free of arcillite, and each plant was separated into shoots (aerial portion) and roots. Roots produced outside of the original root ball from the start of the experiment to a given harvest date (roots that were white and lacked blue dye) were removed from the original root ball, and total length and surface area of these roots were measured (hereafter referred to as root length and root area) using a Monochrome AgVision System

286 Image Analyzer (Decagon Devices, Inc., Pullman, Wash.). Any dead roots were present in such small amounts that these were not separated from living roots at harvest. Total leaf area was measured using a LI-COR 3000 leaf area meter (LI-COR, Inc., Lincoln, Nebr.). All tissue was dried at 70C (160F) for at least 72 h, and dry weights (DWs) of roots (those produced outside the original rootball from the start of the experiment to a given harvest date, hereafter referred to as root DW) and shoots (all stems and leaves) at each harvest were recorded. Effects of open spaces in a block created by repeatedly removing plants for harvest was eliminated by filling these spaces with excess plants that had been included in each block. As a result, plants harvested at the end of the study had similar container-to-container contact as those plants harvested at the beginning of the experiment.

Beginning in October 1999, root length and root area were determined by a subsampling technique, since growth of new root tissue had become too extensive for measurement of total new root length and root area. For each harvested plant, a subsample of the roots produced outside the original rootball from the start of the experiment to a given harvest was removed from the original rootball and length, area, and DW of the root subsample were determined. Total DW of all roots produced outside the original rootball from the start of the experiment to the given harvest was also determined. For each harvest, length and area of the root subsample were regressed on DW of the root subsample, and the resulting equation was used to calculate total root length or root area for a given total root DW value. All regressions had an $R^2 \geq 0.77$, with a majority ≥ 0.95. Regression equations were similar between harvests within cultivar. The equations root length = 2353x + 35.4 (R^2 = 0.98) and root area = 203x – 0.6 (R^2 = 0.94) were representative of those calculated for 'Sarah' mountain laurel. The equations root length = 978x +22.5 (R^2 = 0.92) and root area = 82x – 1.7 (R^2 = 0.94) were representative of those calculated for 'Compacta' holly. For all equations, x = DW of roots produced outside the original rootball from the start of the experiment to a given harvest. This method of determining root length and root area from a subsample was in agreement with the procedure employed by Thetford et al. (1995). As mentioned previously, root length and root area refer to length and area of roots produced outside the original rootball from the start of the experiment to a given harvest. Total leaf area and DW of shoots (all stems and leaves) were determined at each harvest as described previously.

Data were analyzed for significance of experimental variable main effects and interactions using a general linear models procedure (SAS Institute, Inc., 1988). Statistical analysis indicated a significant DAP x cultivar interaction (P<0.0001) for all measured variables, therefore regression analyses (SAS Institute, Inc., 1988) performed for all measurements plotted against DAP were separated by cultivar. Regression analysis for all root variables plotted over time included setting the y-intercept equal to zero, since at experiment initiation there was no new root tissue. This approach produced a regression fit that was consistent with the distribution of the data. Regression analyses were used only as descriptive rather than predictive tools.

Regression analysis was also used to describe several relationships between root and shoot measurements. To allometrically describe plant development, root DW was plotted against shoot DW, root area was plotted against leaf area, and root DW : shoot DW (root DW ÷ shoot DW) was plotted against total plant DW (Ledig et al., 1970). Change in root : shoot ratio over time was determined by plotting root DW : shoot DW and root area : leaf area (root area ÷ leaf area) against DAP (Brouwer, 1983; Wilson, 1988). Dry weight ratios (DWRs) were plotted against DAP to describe the relative distribution of dry matter between plant organs over time (Drew and Ledig, 1980). DWRs for stems, leaves, and roots were calculated as described by Thetford et al. (1995) and represented the percentage of the total plant DW comprised of stems, leaves, or roots, respectively.

Results

New root growth of 'Compacta' holly and 'Sarah' mountain laurel was measurable 15 and 30 DAP, respectively. Root DW increased linearly over time for both cultivars, and the slope of this increase was five times smaller for 'Sarah' mountain laurel than ‘Compacta’ holly (Table 2, Fig. 1A). Increase in root length and root area over time was best fit by linear regression for 'Compacta' holly and cubic regression for 'Sarah' mountain laurel (Table 2, Fig. 1B). The significant DAP x cultivar interaction for leaf area and shoot DW resulted from measurements for the two cultivars occasionally overlapping throughout the experiment (Fig. 2). However, the interaction appeared to be of little practical significance since both shoot DW and leaf area increased linearly over time for both cultivars, and there was no difference between cultivars in the rate (slope) of these increases (Fig. 2).

When root DW was plotted against shoot DW, the relationship was linear for both cultivars, and the slope of this relationship was seven times smaller for 'Sarah' mountain laurel than ‘Compacta’ holly (Fig. 3A). The relationship between root area and leaf area increased linearly for 'Compacta' holly but was best fit with a quadratic regression for 'Sarah' mountain laurel (Fig. 3B). The relationship between root DW : shoot DW and total plant DW was linear for 'Compacta' holly but followed a quadratic distribution for 'Sarah' mountain laurel (Fig. 4A). Plotting root DW : shoot DW over time produced similar results, with values increasing linearly for 'Compacta' holly while increasing and decreasing quadratically for 'Sarah' mountain laurel (Fig. 4B). Root area : leaf area increased linearly over time for 'Compacta' holly but was best fit with a cubic regression for 'Sarah' mountain laurel (Fig. 4C).

Graphs of DWRs indicated that throughout the experiment, both stems and leaves comprised a larger percentage of the total DW of 'Sarah' mountain laurel compared to the roots (Fig. 5A). In contrast, the root DWR of 'Compacta' holly surpassed that of both leaf and stem at 203 DAP (Fig. 5B) and remained larger through the remainder of the experiment.

Discussion

The regression fit of root length and root area plotted over time for 'Sarah' mountain laurel differed from that of root DW plotted over time (cubic vs. linear, respectively, Fig. 1). While one might expect root length and root area of a given species to follow similar patterns over time (root length and root area were highly correlated in the present investigation, $R^2 > 0.99$), they may differ dramatically from patterns for root

DW. An increase in root DW does not necessarily imply an increase in root length or root area. As perennial roots mature, they may lose their epidermis as well as cortical tissue and may also become lignified. Thus, as root diameter and root surface area decrease, root DW may actually increase as more structural tissue is laid down (Esau, 1965). When these changes in anatomy occur, root length and root area may provide more insight about root growth patterns and absorbing capabilities than root DW alone (Harris, 1992). While root DW is often considered by researchers to be related to root length and root area (personal observations), differences between changes in DW and changes in actual "exposed area" have been documented (Bruower, 1983). As a result, this exposed area is likely more biologically important than root DW. We do not attribute the decrease in root length and area to winter injury or predation by soil organisms since these events should also result in a decrease in root DW. Increased root length will increase exploration of surrounding soil following transplanting, and the associated larger root surface area will likely enhance water uptake (Kramer and Bullock, 1966). The difference in root length and root area between 'Compacta' holly and 'Sarah' mountain laurel may help explain their contrasting survival rates following transplanting.

The cubic fit of root length and root area over time for ‘Sarah’ mountain laurel exhibits the steepest slope during September to December (108 to 203 DAP) and a negative slope during January to May (249 to 374 DAP) (Fig. 1). This suggests that fall transplanting may improve transplant survival of mountain laurel due to more rapid increase in root length and root area. Benefits of fall transplanting have been reported for fringetree (*Chionanthus virginicus* L.), which exhibited more root and shoot growth after one growing season when transplanted in November compared to March (Harris et al., 1996). Based on those results, Harris et al. (1996) suggested that a longer period of recovery from post-transplant stress prior to spring budbreak is beneficial. The benefit of fall transplanting has also been shown when transplanting liners of woody nursery stock into larger containers (Laiche, 1991). Laiche (1991) reported "considerable root growth" was observed during the winter months when liners were potted in September. In addition to root growth during the winter, plants potted in September produced the most root and shoot growth after one growing season compared to plants potted in April or May. Kozlowski and Davies (1975) suggested plants that exhibit seasonal growth periodicity should be transplanted during the time of the year when root growth rates are highest. Our data suggest that time of transplanting may not be critical for Japanese holly as evidenced by 'Compacta' holly's consistent root growth year-round.

The decrease in root length and root area of 'Sarah' mountain laurel during January to May (249 to 374 DAP, Fig. 1A and B), in conjunction with an increase in shoot DW and leaf area during this time (Fig. 2A and B) suggest that mountain laurel exhibits seasonal patterns of root mortality and root and shoot growth. Thus, dry matter allocation appeared to favor roots from September through December and shoots from January through May. Despite decreased root length and root area of 'Sarah' mountain laurel in the spring, we would have expected a subsequent increase in root length and root area following spring shoot flushes had the experiment continued for another year (Drew and Ledig 1980). Cannell and Willett (1976) reported that increases in shoot growth are frequently compensated for by subsequent increases in root growth and thus suggested that feedback mechanisms exist such that temporary imbalances in the root : shoot ratio are ultimately corrected. Alternating growth phases were also observed by Drew and Ledig (1980) in loblolly pine (*Pinus taeda* L.), where seasonal variation in dry matter allocation favored roots at certain times and shoots at others. Likewise, apple (*Malus* Mill. sp.) produced no root growth during periods of shoot growth in the spring; instead, roots grew during August through September after shoot growth had stopped (Rogers and Head, 1969). In contrast to 'Sarah' mountain laurel, DWR for 'Compacta' holly indicated that root dry matter production of this cultivar continued to be favored over that of shoots, even during the spring (Fig. 5B). Since DWR for ‘Compacta’ holly appeared relatively constant from December (203 DAP) through the rest of the experiment, it is possible that 'Compacta' holly returned to its natural root : shoot ratio in December, and fluctuations in DWR previous to this time were the result of acclimation and adjustment following transplanting.

For a given increase in shoot DW, there was an eight times smaller proportional increase in root DW for 'Sarah' mountain laurel compared to ‘Compacta’ holly (Fig. 3A). There was nearly a 1:1 relationship between increases in root DW and shoot DW for 'Compacta' holly, suggesting a less consistent relationship between root and shoot biomass allocation in 'Sarah' mountain laurel than in ‘Compacta’ holly. Likewise, there was a much less consistent increase in root area per increase in leaf area for ‘Sara’ mountain laurel compared to ‘Compacta’ holly (Fig. 3B). As total plant DW increased, the rate of increase in the root DW : shoot DW was linear for 'Compacta' holly but quadratic for 'Sarah' mountain laurel (Fig. 4A). The quadratic nature of this plot for

'Sarah' mountain laurel (Fig. 4A) as well as the plots of root DW : shoot DW and root area : leaf area over time for 'Sarah' mountain laurel (Fig. 4B and C) suggest that shoot growth was favored over root growth from January to May (249 to 347 DAP) in 'Sarah' mountain laurel. Our data indicate that if root length and root area measurements are unavailable, plotting root DW : shoot DW over time provides a better interpretation of root growth than plotting root DW vs. shoot DW or plotting root DW alone over time. The graph of root DW : shoot DW over time was similar to the plots of root length and root area over time and thus gave a better indication of the patterns of root growth over time and in relation to plant size.

The larger proportional input into shoot biomass compared to root biomass by 'Sarah' mountain laurel may correspond with this plant being adapted to shade conditions (Ledig et al., 1970). In fact, slow root and shoot growth of eastern hemlock (*Tsuga canadensis* (L.) Carriere.) has been associated with adaptation to shade conditions, in which the plant's metabolic rates and physiology allows seedlings to survive in forest shade (Grime, 1965). A high root : shoot ratio would be more appropriate for a plant adapted to sun conditions, such as Japanese holly, that may experience higher transpiration rates (Ledig et al., 1970). In the case of tree of heaven (*Ailanthus altissima* (Mill.) Swingle), a faster growth rate allows this plant to avoid shade and rapidly exploit the soil in a full-sun environment (Grime, 1965).

A higher root : shoot ratio can mean larger quantities of water and mineral nutrients may be absorbed by the plant during acclimation, possibly alleviating some of the stress associated with transplanting. For mountain laurel transplanted into the landscape from different size containers, highest survival rates occurred for plants with the highest root : shoot ratio at the time of planting (Wright et al., 2001). Unfortunately, specific recommendations regarding root : shoot ratio are not known for many species (Andersen et al., 2000). Our research illustrates that root : shoot ratio can be linked to success of transplant establishment in the landscape, since the pattern of the root : shoot ratio over time and its relation to total plant biomass for 'Sarah' mountain laurel and 'Compacta' holly appear to correspond with their contrasting transplant survival rates in the landscape (personal observation).

There was a 30 DAP delay by 'Sarah' mountain laurel in production of new roots following potting. Delay in new root growth following transplanting has been documented in other species and demonstrates the importance of post-transplant irrigation (Harris et al., 1996). Time to initiation of new root growth is important in predicting or describing transplant success, since initiation of new root growth shortly after transplanting has been correlated with successful transplant establishment (Woods, 1959). Root growth may explain, at least in part, the difference in survival rates for different species (Harris et al., 1996; Struve and Moser, 1984). Data herein support the hypothesis that mountain laurel's poor transplant performance in the landscape is related to its remarkably slow rate of root growth.

Literature Cited

Andersen, L., H.N. Rasmussen, and P.E. Brander. 2000. Regrowth and dry matter allocation in *Quercus robur* L. seedlings root pruned prior to transplanting. New Forests 19:205-213.

Arnold, M.A. and E. Young. 1990. Use of dyes to facilitate measurement of new root growth of apple. HortScience 25:116-118.

Brouwer, R. 1983. Functional equilibrium: Sense or nonsense? Neth. J. Agr. Sci. 31:335-348.

Cannell, M.G.R. and S.C. Willett. 1976. Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of *Poplus trichocarpa*, *Picea sitchensis*, and *Pinus contorta* growing in Scotland. Silvae Genetica 25:49-59.

Drew, A.P. and F.T. Ledig. 1980. Episodic growth and relative shoot:root balance in loblolly pine seedlings. Ann. Bot. 45:143-148.

Esau, K. 1965. Plant anatomy. 2nd ed. Wiley, New York.

Grime, J.P. 1965. Comparative experiments as a key to the ecology of flowering plants. Ecology 46:513-515.

Harris, R.W. 1992. Arboriculture. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Harris, J.R., P. Knight, and J. Fanelli. 1996. Fall transplanting improves establishment of balled and burlapped fringe tree (*Chionanthus virginicus* L.). HortScience 31:1143-1145.

Head, G.C. 1966. Estimating seasonal changes in the quantity of white unsuberized root on fruit trees. J. Hort. Sci. 41:197-206.

Hiller, L.K. and D.C. Koller. 1979. Potato growth responses in arcillite and sand. HortScience 14:534-536.

Jaynes, R.A. 1997. *Kalmia*: Mountain laurel and related species. Timber Press, Inc., Portland, Ore.

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

Kramer, P.J. and H.C. Bullock. 1966. Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. Amer. J. Bot. 53:200-204.

Laiche, A.J., Jr. 1991. Time of transplanting liners and initial growing location affects growth of woody nursery plants. J. Environ. Hort. 9:145-148.

Ledig, F.T., F.H. Bormann, and K.F. Wenger. 1970. The distribution of dry matter growth between shoot and roots in loblolly pine. Bot. Gaz. 131:349-359.

Pirone, P.P. 1978. Tree maintenance. 5th ed. Oxford Univ. Press, New York.

Rogers, W.S. and G.C. Head. 1969. Factors affecting the distribution and growth of roots in perennial woody species, p. 280-295. In: W.J. Whittington (ed.). Root growth. Plenum Press, New York.

SAS Institute, Inc. 1988. SAS/STAT user's guide: Release 6.03 ed. SAS Institute, Inc., Cary, N.C.

Struve, D.K., R.D. Kelly, and B.C. Moser. 1984. Promotion of root regeneration in difficult-to-transplant species. Proc. Intl. Plant Prop. Soc. 33:433-439.

Struve, D.K. and B.C. Moser. 1984. Root system and root regeneration characteristics of pin and scarlet oak. HortScience 19:123-125.

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.

Watson, G.W. and E.B. Himelick. 1982. Seasonal variation in root regeneration of transplanted trees. J. Arboricult. 8:305-310.

Watson, G.W. and E.B. Himelick. 1997. Principles and practice of planting trees and shrubs. Intl. Soc. Arboricult., Savoy, Ill.

Wilson, J.B. 1988. A review of evidence on the control of shoot:root ratio, in relation to models. Ann. Bot. 61:433-449.

Woods, F.W. 1959. Slash pine roots start growth soon after planting. J. For. 57:209.

Wright, A.N., S.L. Warren, and F.A. Blazich. 2001. Exposure and plant size affect landscape establishment of *Kalmia latifolia*. Proc. SNA Res. Conf., 46th Annu. Rpt. p. 515-518.

Table 1. Harvest dates and corresponding days after potting (DAP).

Harvest	DAP	Date
--	0	17 May 1999
1	15	6 June 1999
2	30	16 June 1999
3	44	30 June 1999
4	64	20 July 1999
5	88	13 Aug. 1999
6	108	21 Sept. 1999
7	143	7 Oct. 1999
8	158	22 Oct. 1999
9	178	11 Nov. 1999
10	203	6 Dec. 1999
11	249	21 Jan. 2000
12	284	25 Feb. 2000
13	319	31 Mar. 2000
14	347	28 Apr. 2000
15	361	12 May 2000
16	374	25 May 2000

Table 2. Significance of the effects of days after potting (DAP), cultivar (CV), and their interaction on root length, root area, and root DW and regression analyses for root length, root area, and root DW of ‘Sarah’ mountain laurel (M) and ‘Compacta’ holly (H) as a function of time.

Factor	Root length		Root area		Root dry wt	
DAP	***		***		***	
CV	***		***		***	
DAP x CV	***		***		***	
	Root length		Root area		Root dry wt	
Regression analysis	M	H	M	H	M	H
Linear	***	***	***	***	***	***
Cubic	*	NS	*	NS	NS	NS

NS, *, *** Nonsignificant or significant at P<0.05 or 0.001, respectively.

Table 3. Significance of the effects of days after potting (DAP), cultivar (CV), and their interaction on leaf area and shoot DW and regression analyses for leaf area and shoot DW of ‘Sarah’ mountain laurel (M) and ‘Compacta’ holly (H).

Factor	Leaf area		Shoot dry wt	
DAP	***		***	
CV	**		**	
DAP x CV	***		*	
	Leaf area		Shoot dry wt	
Regression analysis	M	H	M	H
Linear	***	***	***	***

*, **, *** Significant at P<0.05, 0.01, or 0.001, respectively.

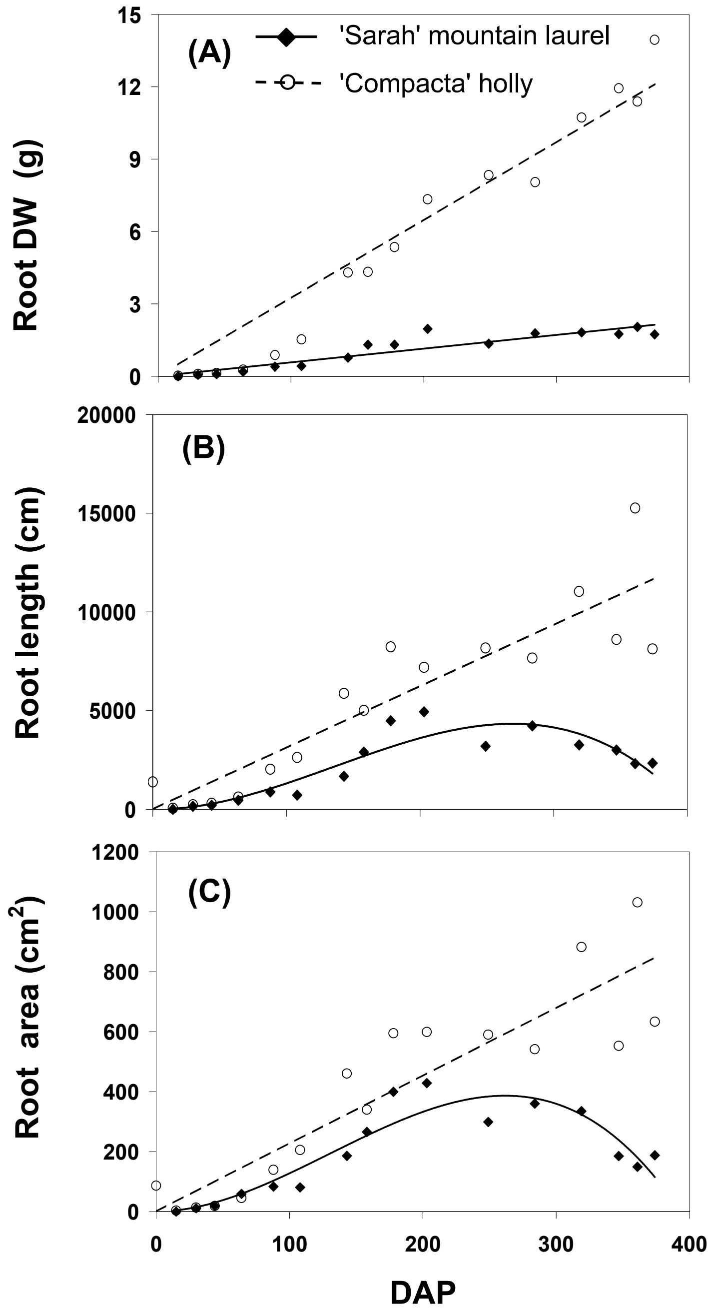

Fig. 1. (A) Root DW at each harvest for 'Sarah' mountain laurel ($y = 0.006x$, $R^2 = 0.85$) and 'Compacta' holly ($y = 0.03x$, $R^2 = 0.94$), (B) root length at each harvest for 'Sarah' mountain laurel ($y = -0.0005x^3 + 0.19x^2 - 0.89x$, $R^2 = 0.84$) and 'Compacta' holly ($y = 31.21x$, $R^2 = 0.83$), and (C) root area at each harvest for 'Sarah' mountain laurel ($y = -0.00004x^3 + 0.02x^2 + 0.04x$, $R^2 = 0.86$) and 'Compacta' holly ($y = 2.27x$, $R^2 = 0.82$). Harvest time is represented as days after potting (DAP). In all cases, slopes for the two cultivars are significantly different ($P<0.0001$). Symbols represent the mean of five observations. Values for root DW, root length, and root area represent measurements for roots produced outside the original root ball since the start of the experiment.

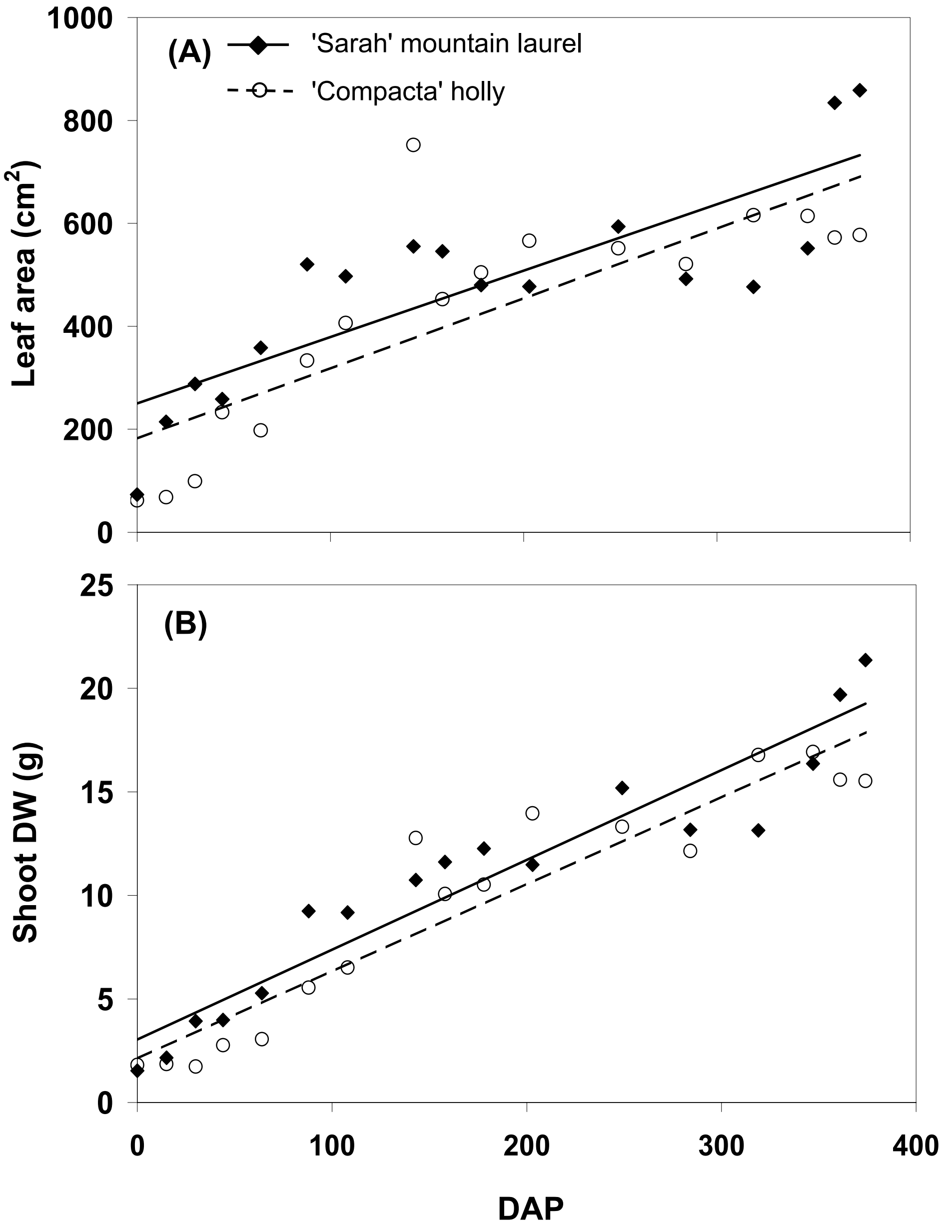

Fig. 2. (A) Leaf area at each harvest for 'Sarah' mountain laurel (y = 1.29x + 250.4, R^2 = 0.69) and 'Compacta' holly (y = 1.36x + 181.64, R^2 = 0.66) and (B) shoot DW at each harvest for 'Sarah' mountain laurel (y = 0.04x + 3.05, R^2 = 0.91) and 'Compacta' holly (y = 0.04x + 2.12, R^2 = 0.89). Harvest time is represented as days after potting (DAP). In all cases, slopes for the two cultivars were not significantly different (leaf area, P=0.56; shoot DW P=0.96). Symbols represent the mean of five observations.

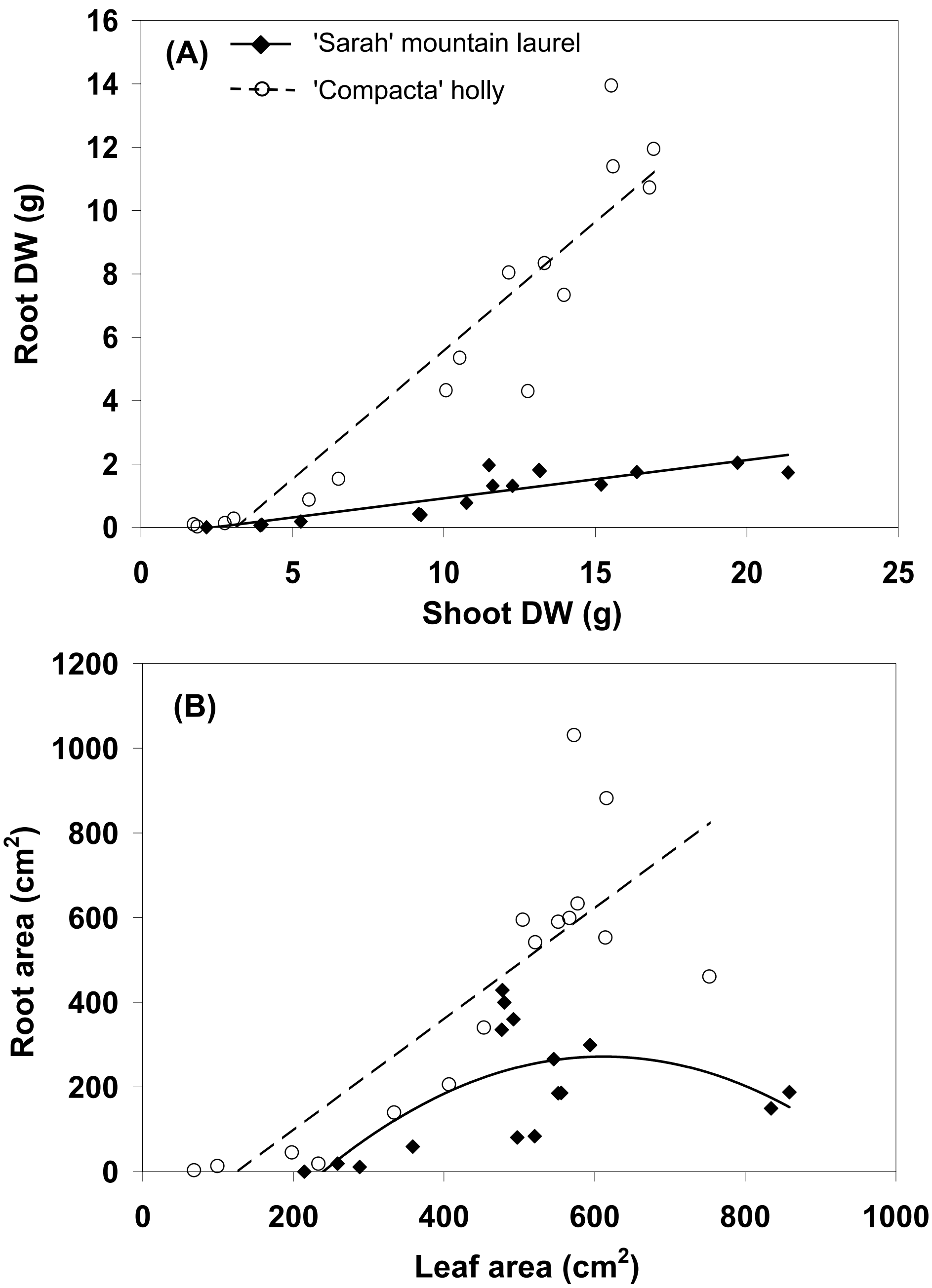

Fig. 3. (A) Root DW plotted against total shoot DW for 'Sarah' mountain laurel (y = 0.12x - 0.29, R^2 = 0.76) and 'Compacta' holly (y = 0.82x - 2.58, R^2 = 0.88) and (B) root area plotted against total leaf area for 'Sarah' mountain laurel (y = -0.002x^2 + 2.40x - 461.88, R^2 = 0.45) and 'Compacta' holly (y = 1.32x - 165.62, R^2 = 0.68). In all cases, slopes for the two cultivars are significantly different (P<0.0001). Symbols represent the mean of five observations.

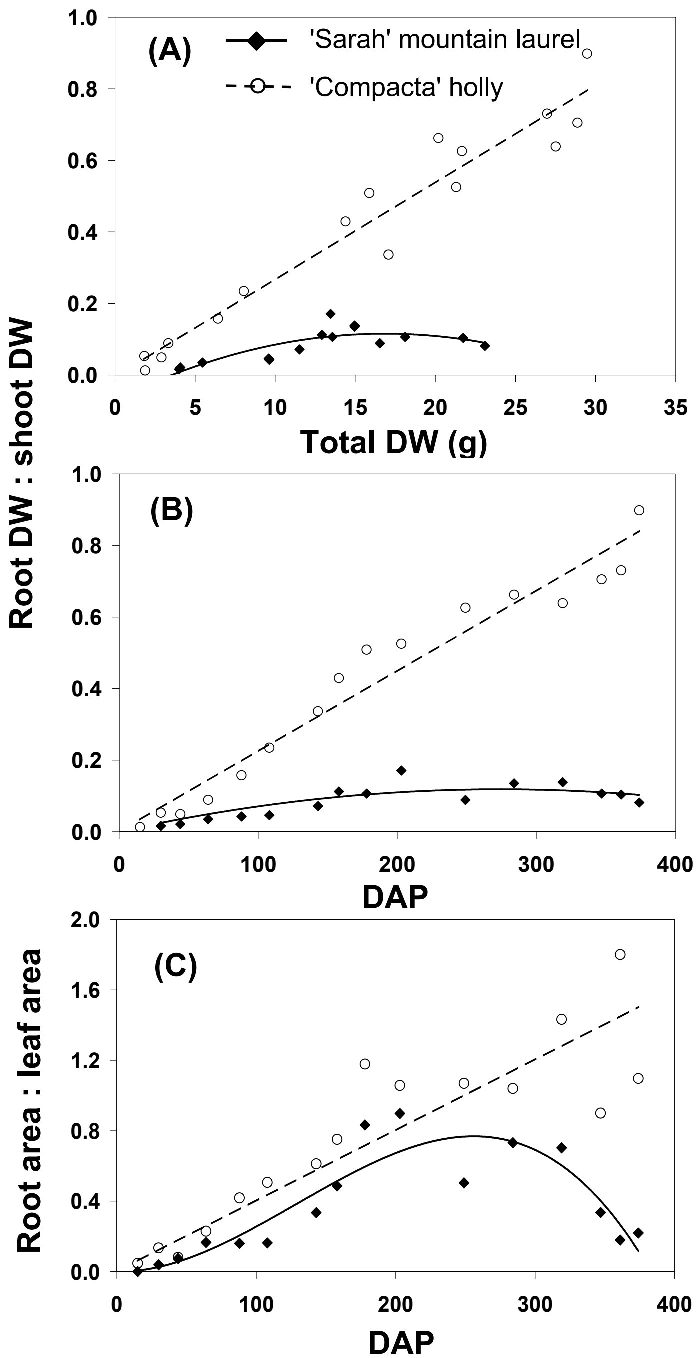

Fig. 4. (A) Root DW : shoot DW plotted against total plant DW for 'Sarah' mountain laurel (y = $-0.0007x^2 + 0.02x - 0.07$, $R^2 = 0.68$) and 'Compacta' holly (y = $0.03x - 0.06$, $R^2 = 0.94$), (B) root DW : shoot DW at each harvest for 'Sarah' mountain laurel (y = $-.000002x^2 + 0.0009x$, $R^2 = 0.73$) and 'Compacta' holly (y = $0.002x$, $R^2 = 0.95$), and (C) root area : leaf area at each harvest for 'Sarah' mountain laurel (y = $-9{\bullet}10^{-8}x^3 + 4{\bullet}10^{-5}x^2 - 0.0001x$, $R^2 = 0.81$) and 'Compacta' holly (y = $0.004x$, $R^2 = 0.78$). Time of harvest in (B) and (C) is represented as days after potting (DAP). In all cases, slopes of the two cultivars are significantly different ($P<0.0001$). Symbols represent the mean of five observations.

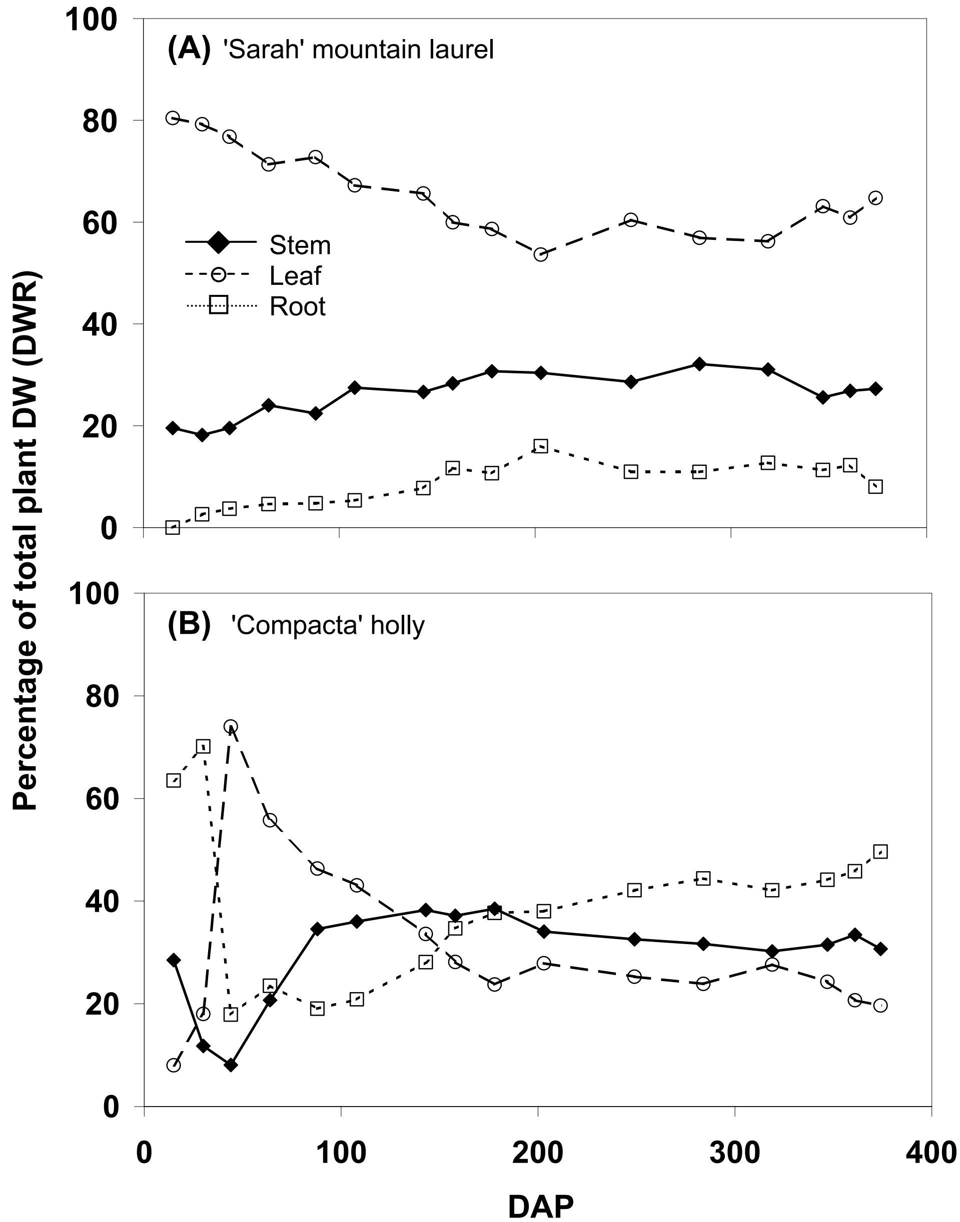

Fig. 5. Dry weight ratios (DWRs) at each harvest for (A) 'Sarah' mountain laurel and (B) 'Compacta' holly. DWR is the percentage of the total plant DW comprised of stems, leaves, or roots. Time of harvest is represented as days after potting (DAP). Symbols represent the mean of five observations.

Chapter 2

Root-zone Temperature Influences Root Growth of *Kalmia latifolia* Taxa and *Ilex crenata* 'Compacta'

(In the format appropriate for submission to Journal of Environmental Horticulture)

Root-zone Temperature Influences Root Growth of *Kalmia latifolia* Taxa and *Ilex crenata* 'Compacta'[1]

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Abstract

Root-zone temperature is an important environmental factor affecting transplant survival and landscape performance of woody ornamentals. Research was conducted to compare the effects of root-zone temperature on root growth 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 'Sarah' mountain laurel and rooted stem cuttings of 'Compacta' holly were grown hydroponically in controlled environment conditions under long days for 12 weeks at 9 hr days/15 hr nights of 26/22C (79/72F) with root-zone temperatures of 16, 24, or 32C (61, 75, or 90F). The study was conducted twice, once beginning October 2000 (fall) and once beginning March 2001 (spring). Plant material used in each experiment was grown prior to the studies under conditions of natural photoperiod, irradiance, and temperature, with the exception of mountain laurel seedlings used in the fall experiment which were greenhouse grown at days/nights of 24/16C (75/60F). Percentage increase in root dry weight, root length, and root area over the 12-week period were highest at 16C (61F) for mountain laurel and highest at 24C (75F) for 'Compacta' holly. In general, percentage increases for root dry weight, root length, and root area were higher for 'Compacta' holly than mountain laurel. More root growth occurred in the fall than in the spring for mountain laurel and 'Compacta' holly. Root : shoot ratio of mountain laurel was higher in the fall than in the spring, while root : shoot ratio of 'Compacta' holly was similar for both seasons. Results suggest that poor landscape performance of mountain laurel may be related to its sensitivity to high root-zone temperatures and that fall transplanting may

be preferable due to higher root:shoot ratio in the fall. Conversely, tolerance of high root-zone temperatures by 'Compacta' holly may explain the ease of transplanting associated with this cultivar and related taxa. Additionally, consistent root : shoot ratio of ‘Compacta’ holly in the fall and spring suggests that season of transplanting is not critical for this cultivar.

Index words. mountain laurel, Japanese holly, woody ornamentals, transplanting, relative growth rate, root : shoot ratio, root morphology.

Significance to the Nursery Industry

Mountain laurel (*Kalmia latifolia*) is an attractive woody ornamental species native to the eastern United States. Despite numerous commercially available cultivars, production remains limited since it frequently does not survive transplanting from containers into the landscape, even in areas to which it is indigenous. Improving transplant survival could encourage increased production by the nursery industry as well as improve appreciation of this attractive native species. Research herein compared the effect of root-zone temperature on root growth of mountain laurel and Japanese holly (*Ilex crenata*), a species which routinely survives transplanting. When grown at root-zone temperatures of 16, 24, or 32C (61, 75, or 90F), root relative growth rates were highest for mountain laurel at 16C (61F) and highest for Japanese holly at 24C (75F). Because root growth has been linked to landscape establishment by other authors, results herein suggest the need for mulch and/or shade when transplanting mountain laurel, particularly in areas with high soil temperatures.

Introduction

Mountain laurel, a member of the Ericaceae, is an ornamental, evergreen shrub native to the eastern United States. Even though its natural habitat extends from Maine to Florida, it frequently does not survive transplanting from containers into the landscape in the eastern United States (Jaynes, 1997). It has been suggested that planting location may dictate cultural requirements such as shade (Bir and Bilderback, 1989). The authors have often observed that mountain laurel grows in full sun in the northeastern United States and in the mountains of the Southeast, while frequently requiring shade in the warmer regions of the southeastern United States.

Soil temperature influences root growth and development, root morphology (elongation and branching) and root : shoot ratio (McMichael and Burke 1998). Exposure of container-grown ‘St. Mary’ southern magnolia (*Magnolia grandiflora* L. ‘St. Mary’) to high root-zone temperature influenced subsequent transplanting, with total root length and root and shoot dry weight decreasing as temperature increased (Martin and Ingram, 1991). This suggests that exposure to high root-zone temperatures during production may lengthen the landscape establishment period (due to decreased root growth). After transplanting southern highbush and rabbiteye blueberries (*Vaccinium corymbosum* L. and *V. ashei* Reade, respectively), also members of the Ericaceae, into the landscape, root-zone temperature had a greater influence on root growth than irrigation or incorporation of organic matter into the soil (Spiers 1995).

Research conducted to improve commercial production of mountain laurel has applications to its survival in the landscape following transplanting. Maximum root dry weight of 1-year-old mountain laurel seedlings occurred at day air temperatures of 22 and 26C (72 and 79F), whereas the least root dry weight resulted at day air temperature extremes of 18 and 30C (64 and 86F)(Malek et al., 1992). Similarly, in recent experiments, root and shoot growth of 1-year-old plants of mountain laurel were lower when grown at day air temperatures of 18 and 34C (64 and 86F) compared to 26C (79F) (Lasseigne, 2000, personal communication).

Even when grown at constant air temperatures, the temperature of the substrate and roots may be different from the air temperature. No work has been conducted to determine the effect of root-zone temperature, independent of shoot temperature, on root growth of mountain laurel or if the response to root temperature may be correlated to ease of landscape establishment. Comparison of the effects of root-zone temperature on root growth of mountain laurel and Japanese holly, a species which transplants readily into the landscape, may indicate their comparative tolerances to a range of root-zone temperatures. It is possible that the higher transplanting success rate of Japanese holly in the landscape is due to its ability to tolerate stressful root environments. Therefore, the objective of this research was to compare the effect of root-zone temperature on root growth of mountain laurel and Japanese holly.

Materials and Methods

Root-zone temperatures of 16, 24, or 32C (61, 75, or 90F) were produced by three large [200 L (211 qt)] continuous flow hydroponic units that allowed regulation of solution temperature to ± 0.5C and ensured uniformity of temperature throughout the root zone (Osmond et al., 1981). Hydroponic units were located in a controlled environment

A-chamber (Thomas and Downs, 1991) at the Southeastern Plant Environment Laboratory (Phytotron) at North Carolina State University, Raleigh. Air temperature in the chamber was maintained at 9 hr days/15 hr nights of 26/22C (79/72 F) (Malek et al., 1992). During the 9 hr high irradiance light period, cool-white fluorescent and incandescent lamps provided a photosynthetic photon flux (*PPF*) of 700 $\mu mol \bullet m^{-2} \bullet s^{-1}$ and photomorphogenic radiation (*PR*) of 12 $W \bullet m^{-2}$. Long day conditions were provided via a 3 hr night interruption from 11 p.m. to 2 a.m. by incandescent lamps providing a *PPF* of 70 $\mu mol \bullet m^{-2} \bullet s^{-1}$ and PR of 11 $W \bullet m^{-2}$. Atmospheric CO_2 concentration was maintained at 400 $\mu L \bullet L^{-1}$.

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 4.0 by manual additions of 5mM CaOH as needed. Each hydroponic unit included an upper 100-L (106 qt) root compartment and a lower 100-L (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' (‘Compacta’ holly) were placed in the hydroponic units October 20, 2000 (fall experiment). Prior to placement in the units, substrate was removed from the roots of each plant by gently submerging the root system in tap water. The mountain laurel seedlings had been grown in sand to facilitate substrate removal and minimize root system injury at time the experiment was initiated. The fall experiment was terminated January 10, 2001 (12 weeks after initiation). All living plants were harvested and separated into shoots (stems and leaves) and roots. Root length and root area were measured using a subsampling technique described by Thetford et al. (1995) and 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, NB). All tissue was dried at 70C (160F) for at least 72 h, and dry weights of leaves, stems, and roots were recorded. Root dry weight : shoot dry weight (root dry weight ÷ shoot dry weight) and root area : leaf area (root area ÷ leaf area) were calculated.

The experiment was repeated beginning March 16, 2001 (spring experiment) 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. The 'Sarah' mountain laurel liners were in a peat-based substrate, and to avoid serious injury to 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 (Lasseigne, personal communication), mountain laurel did not recover from injury to roots associated with vigorous washing of the root system. In contrast, 'Compacta' holly has a coarse root system, and substrate may be removed easily by submerging the root system in water.

Environmental conditions, growth chamber, hydroponic units, and nutrient solutions were the same as described for the fall experiment. The spring experiment was terminated June 7, 2001 (12 weeks after initiation), and plants were harvested as described above. At termination of the spring experiment, samples of individual roots were removed prior to harvesting. Five root samples, each consisting of the apical 2 cm (0.79 in) of an actively growing root were randomly collected from each taxa 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 (0.79 in) were recorded. If there were no lateral roots in the apical 2 cm (0.79 in), distance from the apex for 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 fall 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 experimental design was a split plot with treatments in a nested factorial combination of root-zone temperature and plant taxa within season (spring vs. fall). There was one hydroponic unit per root-zone temperature. Plant taxa were assigned in a randomized complete block design within each temperature. There were three blocks per temperature with two plants of each taxa per block for a total of six single plant replications per taxa per temperature per season. Experimental unit was a single plant. At the beginning of each experiment, six additional plants of each taxa were destructively harvested to determine initial shoot dry weight, leaf area, root dry weight, root area, and root length for each experiment. Plants used to determine initial measurements were uniform in size and represented the size of plants used in each experiment.

Since it was important to include plant death that occurred in response to treatments in the statistical analysis, percentage increases (PIs) in growth were calculated for the 12 week duration of both experiments. PI was calculated for shoot dry weight, leaf area, root dry weight, root length, and root area using the formula [(final – initial) ÷ initial]*100, in which initial plant measurements were those taken at the beginning of the experiment, and final plant measurements were those taken at experiment termination. For all dead plants, PI in growth was assumed to be zero. Except for root : shoot ratios, all data presented herein are PIs. All data were analyzed for significance of treatment main effects and interactions using a general linear models procedure (SAS Institute, Inc., 1988). Treatment and interaction means for percentage increases and root : shoot ratios were generated using LSMEANS, and their separation was performed using PDIFF procedure (P=0.05; SAS Institute, Inc., 1988). For the sake of simplicity, both *Kalmia* taxa will be referred to collectively as mountain laurel in the results and discussion.

Results

PIs in shoot dry weight and leaf area were similar for all root-zone temperatures for mountain laurel and higher at 24C (75F) than 16C (61F) for 'Compacta' holly (Table 2). In general, PIs in root dry weight, root length, and root area were highest at 16C (61F) for mountain laurel and 24C (75F) for 'Compacta' holly (Table 3). Plants of 'Compacta' holly were most attractive visually at 24C (75F), whereas plants of mountain laurel had the best visual appearance at 16C (61F). Neither taxa performed well at 32C (90F) (visual observations). Root dry weight : shoot dry weight (averaged across taxa) was higher at 16C (61F) than at 32C (90F) (Table 4).

At 24C (75F), PIs in root dry weight, root length, and root area were lower for mountain laurel than 'Compacta' holly while similar for both taxa at 16C (61F) and 32C

(90F) (Table 3). PIs in leaf area and shoot dry weight were lower for mountain laurel than 'Compacta' holly, except at 16C (61F) where there was no difference in shoot dry weight (Table 2). Death (averaged over temperature and season) was higher for mountain laurel (42%) than 'Compacta' holly (3%).

The statistically significant interaction of taxa x season for all variables was quantitative rather than qualitative (only the magnitude of the response to season by taxa changed, not the response itself), and thus was not biologically significant. PIs of all variables were higher in the fall than in the spring (data not presented). At the beginning of the spring experiment, there was an immediate shoot growth flush in both taxa (particularly mountain laurel). This response was not observed during the fall. Root dry weight : shoot dry weight and root area : leaf area were higher in the fall than in the spring for mountain laurel while similar in both seasons for ‘Compacta’ holly (Table 4).

At 32C (90F), roots of mountain laurel and 'Compacta' holly appeared brown, lacked turgor, and were stunted and stubby, whereas at 16C (61F) and 24C (75F), roots of both taxa were white, succulent, and vigorous (visual observations). Distance from root apex to the most recently emerged lateral root was shortest for roots grown at 32C (90F) and longest for roots grown at 16C (61F) (Table 5). In the root apical 2 cm (0.79 in), the highest number of lateral roots were produced at 32C (90F), and the least were produced at 16C (61F) (Table 5).

Discussion

Lower PIs in root dry weight, root length, and root area of mountain laurel and 'Compacta' holly at a root-zone temperature of 32C (90F) [compared to 16 and 24C (61 and 75F)] is similar to results reported for pittosporum (*Pittosporum tobira* Thunb.) which had lower root and shoot growth at 40C (104F) compared to 27C (81F) (Johnson and Ingram, 1984). Similarly, rose (*Rosa* L. sp.) and peach [*Prunus persica* (L.) Batsch. (Peach Group)] showed negative root growth response to root-zone temperatures >30C (86F) (Wong et al., 1971). Lower PI in root growth for mountain laurel compared to 'Compacta' holly at 24C (75F) is similar to results of a previous experiment in which mountain laurel produced less root growth than 'Compacta' holly over the course of 1 year (Wright et al., 2000). Despite low PI in root growth of 'Compacta' holly at 32C (90F), minimal death of this cultivar illustrates tolerance of stressful root environments. Conversely, death of mountain laurel across all temperatures may be attributed to sensitivity to root disturbance associated with transplanting. The vigorous root growth of mountain laurel at 16C (61F) in the present investigation suggests that in warmer climates such as Raleigh, NC, mulch and/or shade would be particularly important to reduce soil temperature. Daily soil temperatures [15-20 cm (6-8 in)] in Raleigh frequently average >30C (86F) during summer months (State Climate Office of North Carolina, North Carolina State University, 2000). The similarity of shoot growth of mountain laurel across root temperatures suggests that landscape performance of this species is related primarily to root growth. Also, lack of a significant interaction between temperature and season for root PIs indicates that the effects of root-zone temperature on root growth were consistent, regardless of time of year.

Despite this research being conducted in controlled environmental conditions, all taxa (mountain laurel and 'Compacta' holly) exhibited growth patterns consistent with the season in which the experiment was conducted. Seasonal growth patterns for mountain laurel in the current investigation were similar to those in a previous experiment in which highest rates of mountain laurel root growth occurred in the fall, while root growth decreased in the spring (Wright et al., 2000). Higher root dry weight : shoot dry weight and root area : leaf area of mountain laurel in the fall compared to the spring and lack of such a difference for ‘Compacta’ holly suggest that fall transplanting would benefit mountain laurel, while the season of transplanting is not critical for ‘Compacta’ holly. The higher root : shoot ratio (root dry weight : shoot dry weight) of both taxa at 16C (61F) compared to 32C (90F) reflects the negative root growth response of both taxa to high root-zone temperatures.

Visual appearance of roots at 32C (90F) (brown and lacking turgor) was due likely to death of root cortical tissue. In an experiment with apple (*Malus* Mill. sp.) and peach grown at root temperatures ranging from 7 to 35C (45 to 95F), cortex death was observed in roots grown at temperatures of 24C (75F) and higher, while no cortex death was observed in roots grown at 18C (64F) (Nightingale, 1935). The proliferation of white succulent roots at 16 and 24C (61 and 75F) in the present experiment are similar to results for bentgrass (*Agrostis palustris* Huds.), in which roots remained white and succulent through 45 days when grown at 16C (75F), but turned brown and shriveled after 35 days at 27C (81F) (Beard and Daniel, 1965).

There was substantially more branching of roots of mountain laurel and 'Compacta' holly at 32C (90F) compared to those at 24C (75F), and very little root branching occurred at 16C (61F). Influence of root-zone temperature on root architecture has been reported by other researchers. Root temperature affects the number of lateral roots and their distance from the root apex (Kasper and Bland, 1992). High root-zone temperatures have been correlated with higher rates of cell elongation, but shorter periods of elongation (Beauchamp and Lathwell, 1966; Burstrom 1956). As a result, maturation and differentiation of root tissue occurs closer to the root apex at higher temperatures (Beauchamp and Lathwell, 1966). When maturation occurs closer to the root apex, branching also occurs closer to the apex.

A decreased period of root elongation results in shorter roots overall. In the landscape, lack of root elongation and thus extension into the surrounding soil may hinder transplant establishment. Inhibition of root growth in mountain laurel by high root-zone temperatures may explain in part the poor landscape performance of this species. In contrast, the tolerance of 'Compacta' holly to a wide range of root-zone temperatures illustrates ability to survive stressful landscape situations. Results suggest the need for cultural practices that ensure lower root-zone temperature for mountain laurel in the landscape. Data herein also suggest that fall transplanting would be beneficial for mountain laurel, since root PIs were higher in the fall than in the spring, while season of transplanting is not critical for 'Compacta' holly.

Literature Cited

1. 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.
2. 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.
3. Bir, R.E. and T.E. Bilderback. 1989. Growing better mountain laurel in containers. Proc. Intl. Plant Prop. Soc. 39:442-447.
4. Burstrom, H. 1956. Temperature and root cell elongation. Physiol. Plant. 9:682-692.
5. Jaynes, R.A. 1997. *Kalmia*: Mountain Laurel and Related Species. Timber Press, Inc., Portland, OR.
6. Johnson, C.R. and D.L. Ingram. 1984. *Pittosporum tobira* response to container medium temperature. HortScience 19:524-525.
7. Kasper, T.C. and W.L. Bland. 1992. Soil temperature and root growth. Soil Sci. 154:290-299.
8. Lasseigne, F.T. (taxodium@mindspring.com). 2000. RE: *kalmia*. E-mail to A.N. Wright (amy_noelle@hotmail.com). [Apr. 26, 2000].
9. 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.
10. Martin, C.A. and D.L. Ingram. 1991. Root growth of southern magnolia following exposure to high root-zone temperature. HortScience 26:370-371.

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

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

13. 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.

14. SAS Inst., Inc. 1988. SAS/STAT User's Guide: Release 6.03 Edition. SAS Inst., Inc., Cary, NC.

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

16. State Climate Office of North Carolina at North Carolina State University. 2000. http://www.nc-climate.ncsu.edu/agnet/turf/2000/August/turf_082000.html. [Accessed Feb. 28, 2002].

17. 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.

18. Thomas, J.F. and R.J. Downs. 1991. Phytotron procedural manual for controlled environment research at the Southeastern Plant Environment Laboratory. N.C. Agr. Res. Serv. Tech. Bul. 244 (Revised).

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

20. Wright, A.N., S.L. Warren, and F.A. Blazich. 2000. Root growth of two woody ornamentals following transplanting. Proc. SNA. Res. Conf., 45th Annu. Rpt. p. 454-457.

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

Nutrient	Chemical source	Concentration ($mg \cdot L^{-1}$)	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	$CuSO_4 \cdot 5H_2O$	0.09	0.01
Zn	$ZnSO_4 \cdot H_2O$	0.30	0.005
B	H_3BO_3	0.21	0.02

Table 2. Effect of root-zone temperature on shoot relative growth rates of mountain laurel (M) and 'Compacta' holly (H) and significance of treatment main effects and interactions for relative growth rates.[z,y]

	Leaf area (cm^2•cm^{-2})		Shoot dry weight (g•g^{-1})	
	Taxa			
Temperature (C)	M	H	M	H
16	0.81 a[x]B[w]	3.40 bA	0.73 aA	1.55 bA
24	0.91 aB	6.90 aA	0.73 aB	3.49 aA
32	0.35 aB	3.00 bB	0.21 aB	2.74 aA
Significance				
Temperature	***		NS	
Taxa	***		***	
Season	***		*	
Temperature x taxa	***		NS	
Temperature x season	NS		**	
Taxa x season	***		***	
Temp x taxa x season	NS		NS	

[z]Relative growth rate = (final - initial) ÷ initial.
[y]Values represent the mean of six observations.
[x]Lowercase letters denote mean separation among temperatures within taxa by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
[w]Uppercase letters denote mean separation between taxa within temperature by PDIFF at $P<0.05$.
[NS, *, **, ***]Nonsignificant or significant at $P<$ 0.05, 0.01, or 0.001, respectively.

Table 3. Effect of root-zone temperature on root relative growth rates of mountain laurel (M) and 'Compacta' holly (H) and significance of treatment main effects and interactions for relative growth rates.[z,y]

	Root dry weight ($g \bullet g^{-1}$)		Root length ($cm \bullet cm^{-1}$)		Root area ($cm^2 \bullet cm^{-2}$)	
	Taxa					
Temperature (C)	M	H	M	H	M	H
16	0.36 a[x]A[w]	0.21 bA	2.21 aA	1.88 bA	2.72 aA	4.39 aA
24	0.01 bB	0.64 aA	0.62 abB	3.76 aA	0.86 abB	6.52 aA
32	-0.11 bA	-0.15 bA	0.04 bA	0.66 bA	0.27 bA	1.81 bA
Significance						
Temperature	*		**		***	
Taxa	NS		*		***	
Season	*		**		***	
Temperature x taxa	*		*		*	
Temperature x season	NS		NS		NS	
Taxa x season	***		*		**	
Temp x taxa x season	NS		NS		NS	

[z]Relative growth rate = (final - initial) ÷ initial.
[y]Values represent the mean of six observations.
[x]Lowercase letters denote mean separation among temperatures within taxa by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
[w]Uppercase letters denote mean separation between taxa within temperature by PDIFF at $P<0.05$.
[NS, *, **, ***]Nonsignificant or significant at $P< 0.05$, 0.01, or 0.001, respectively.

Table 4. Effect of season and root-zone temperature on root dry weight : shoot dry weight and root area : leaf area of mountain laurel (M) and 'Compacta' holly (H) and significance of treatment main effects and interactions for root dry weight : shoot dry weight and root area : leaf area.

	Root dry weight : shoot dry weight^z		Root area : leaf area^y	
Season	M	H	M	H
Fall	0.85 a^{x}A^w	0.23 aB	13.71 aA	1.05 aB
Spring	0.27 bA	0.22 aA	2.78 bA	1.53 aA
Temperature (C)				
16	0.59 a^v		8.39 a	
24	0.36 ab		3.95 ab	
32	0.22 b		1.97 b	
Significance				
Temperature	*		NS	
Taxa	**		**	
Season	*		*	
Temperature x taxa	NS		NS	
Temperature x season	NS		NS	
Taxa x season	*		*	
Temperature x taxa x season	NS		NS	

^{z}Root dry weight : shoot dry weight = root dry weight ÷ shoot dry weight.
^{y}Root area : leaf area = root area ÷ leaf area.

Table 4. (continued)

[x]Lowercase letters denote mean separation between seasons within taxa by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
[w]Uppercase letters denote mean separation between taxa within season by PDIFF at $P<0.05$.
[v]Lowercase letters denote mean separation between temperatures by PDIFF at $P<0.05$.
[NS, *, **]Nonsignificant or significant at $P<0.05$ or 0.01, respectively.

Table 5. Distance from root apex to most recently emerged lateral root [length > 1 mm (0.04 in)] and the number of lateral roots in the apical 2 cm (0.79 in) of a root sample as influenced by temperature for mountain laurel and 'Compacta' holly.[z]

Treatment	Distance (mm)	No. of lateral roots
Temperature (C)		
16	20.0 a[y]	0.4 c
24	14.8 b	4.5 b
32	2.9 c	13.0 a
Taxa		
Mountain laurel	10.7 b[x]	7.7 a
'Compacta' holly	14.4 a	4.2 b
Significance		
Temperature	***	***
Taxa	***	**
Temperature x taxa	NS	NS

[z]Values represent means of five observations.
[y]Mean separation among temperatures by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
[x]Mean separation between taxa by PDIFF at $P<0.05$.
[NS, **, ***]Nonsignificant or significant at $P<0.01$ or 0.001, respectively.

Chapter 3

Comparative Drought Tolerance of *Kalmia latifolia* 'Olympic Wedding' and *Ilex crenata* 'Compacta'

(In the format appropriate for submission to HortScience)

Subject Category: Crop Production: Nursery and Landscape Plants

Comparative Drought Tolerance of *Kalmia latifolia* 'Olympic Wedding' and *Ilex crenata* 'Compacta'

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Abstract. Container-grown ornamentals frequently experience drought following transplanting into the landscape. Research was conducted to compare drought tolerance of a difficult-to-transplant species, mountain laurel (*Kalmia latifolia* L.), to that of an easy-to-transplant species, Japanese holly (*Ilex crenata* Thunb.). Plants of 'Olympic Wedding' mountain laurel and ‘Compacta’ holly in 1-L containers were repotted on 25 Apr. 2001 into 19-L containers filled with a substrate of 4 pine bark : 2 peat : 1 perlite (by volume). Drought treatments, initiated on 28 June 2001, consisted of several dry-down cycles in which the container substrate was allowed to dry by withholding irrigation until pre-dawn plant water potential (PWP) reached -0.5, -1.0, or -1.5 MPa. Turgor loss point and osmotic potential at full and zero turgor were determined from pressure-volume curves constructed for both cultivars within each treatment. Plants were harvested 15 Sept. 2001, and shoot dry weight (DW) was determined. Shoot DW decreased linearly with increasing drought stress for both cultivars, and slope of this decrease was steeper for 'Olympic Wedding' mountain laurel than ‘Compacta’ holly. Partial death of shoot tissue was observed on some plants of 'Olympic Wedding' mountain laurel in -1.0 and -1.5 MPa treatments but was not observed for ‘Compacta’ holly. Although turgor loss occurred at a lower PWP for 'Olympic Wedding' mountain laurel compared to ‘Compacta’ holly, PWP decreased faster for 'Olympic Wedding' mountain laurel than ‘Compacta’ holly. Although both cultivars appeared to osmotically adjust, ‘Olympic Wedding’ mountain laurel was less drought tolerant than ‘Compacta’ holly. Osmotic potential at full turgor was lower (more negative) in -1.0 and -1.5 MPa treatments than in the -0.5 MPa treatment suggesting that osmotic adjustment occurred only in more

severely stressed plants. Results of this study indicate that poor performance of mountain laurel in the landscape is due in part to relatively low drought tolerance.

Water relations of container-grown ornamentals transplanted into the landscape may determine survival and affect establishment. Even when soil water is adequate to support plant growth, plant available water within the transplanted container root ball can be much lower (Costello and Paul, 1975). Not only is a perched water table not present in the landscape as it is in a container, but water may be drawn out of the root ball into the surrounding soil due to gradients in media matrix potentially resulting from different textures (Nelms and Spomer, 1983).

Until roots of a transplanted container-grown plant extend into the surrounding soil, the plant will be unable to absorb water from the soil. As a result, plants must depend on water resources available within the original rootball, which are frequently insufficient due to limited irrigation and/or precipitation in the landscape. Resulting drought conditions may induce leaf water deficits that develop when water lost through transpiration exceeds the amount taken up by the roots (Roberts and Knoerr, 1977).

Plant responses to drought vary for different species (Muller, 1991; Zhang and Archbold, 1993). Pressure-volume curve analysis may be used to describe water relations parameters such as osmotic potential and turgor loss point (Tyree and Hammel, 1972). This technique has also been used to compare water relations parameters for different species as well as different environments (Muller, 1991; Ranney et al., 1991a).

Mountain laurel (*Kalmia latifolia*) is an attractive flowering, broad-leaved evergreen shrub native to the eastern United States (Jaynes, 1997). Despite its broad geographic range (Maine to Florida), mountain laurel frequently does not survive transplanting from containers into the landscape. It is possible that low survival rate in the landscape following transplanting from containers is due to lack of drought tolerance. Comparison of drought tolerance of mountain laurel to that of an easy-to-transplant species, Japanese holly (*Ilex crenata*), may explain in part why mountain laurel often does not survive following transplanting from containers. Likewise, comparison of tissue water relations for the two species may provide specific details of the drought tolerance of these two woody ornamental landscape plants. Therefore, the objective of this research was to compare the effect of varying levels of drought on growth and plant water relations of mountain laurel and Japanese holly.

Materials and Methods

Plants of 'Olympic Wedding' mountain laurel and ‘Compacta’ holly in 1-L containers were repotted on 25 Apr. 2001 into 19-L containers filled with a substrate of 4 pine bark : 2 peat : 1 perlite (by volume). Large containers and a slow-drying substrate were used to produce a drying rate in the container that more closely simulated that of a landscape situation (Pennypacker et al., 1990). Substrate was preplant amended with 0.4 $kg{\bullet}m^{-3}$ dolomitic lime, 0.9 $kg{\bullet}m^{-3}$ 19N-2.6P-10K slow-release fertilizer (Osmocote™, 4-month formulation, Scotts-Sierra, Marysville, Ohio), and 0.9 $kg{\bullet}m^{-3}$ Micromax™ micronutrient fertilzer (Scotts-Sierra). Plants were grown in the Department of Horticultural Science Greenhouse, North Carolina State University, Raleigh, under natural photoperiod and irradiance with days/nights of 24/16 °C. All plants were hand watered with tap water until initiation of drought treatments 2 months after potting. Initiation of drought treatments did not occur immediately following transplanting to allow plants to acclimate and to allow for root growth into new substrate. Root systems were observed prior to imposing treatments to determine extent of root distribution in the container.

Three drought treatments were initiated on 28 June 2001, each consisting of several dry-down cycles (Zwack et al., 1999) in which the substrate was allowed to dry by withholding irrigation until pre-dawn plant water potential (PWP) reached -0.5, -1.0, or -1.5 MPa. A well-watered control was maintained for comparison. Drought treatments will be referred to hereafter by the corresponding target pre-dawn PWP. Pre-dawn PWP of five plants (replications) of each cultivar in each drought treatment was measured daily at 0500 HR using a Model 1000 Pressure Chamber Instrument (pressure-bomb, Plant Moisture Stress, Inc., Corvallis, Ore.). Since the small size (1 cm^2) of leaves of ‘Compacta’ holly prohibited individual leaf water potential measurements, measurements were taken using samples consisting of the apical 10 cm portion of a stem (included growing point) with leaves intact. Once the average of five replications equaled the target pre-dawn PWP, container substrate was returned to field capacity by hand watering to container saturation. To insure thorough rewetting of the substrate, rewatering was done gradually by applying water in small increments over the course of 2 d to avoid producing channels in the substrate. Substrate was then allowed to dry down again to generate the same pre-dawn PWP. The cycle of dry-down followed by hand watering to return the substrate to field capacity was repeated until experiment termination. Pre-dawn PWP was monitored separately for the two cultivars. Number of dry-down cycles and length of each cycle (days between rewatering) were recorded for each cultivar in each drought treatment.

Experimental design was a split-plot design with five blocks. Within each block, cultivar formed the main plot (to aid in ease of pre-dawn PWP measurements), and drought treatment formed the split-plot. Drought treatments were arranged randomly within each cultivar. Within each block, there were two single-container replications of each cultivar per treatment. One replication was used for PWP measurements, and the other was reserved for final plant harvest (due to the destructive nature of continually removing stem sections).

When a cultivar reached the end of the first dry-down cycle for each drought treatment (target pre-dawn PWP achieved), samples were collected for use in the preparation of a pressure-volume curve. Pressure-volume curves were constructed for each treatment within each cultivar. Each sample consisted of one apical stem section (containing growing point) at least 10 cm in length, removed prior to rewatering from each of four plants. All samples were recut under tap water and stored in the dark for 16 h with the cut end under water and the foliage covered with plastic (Zobel, 1996). Sample rehydration facilitates determination of true osmotic adjustment rather than simply a decrease in osmotic potential due to dehydration (Abrams, 1988). Following rehydration, stems were recut to 10 cm and the fresh (turgid) weight and initial balance pressure (BP) of each stem section was determined. Following initial BP determination, a chamber pressure of 0.3 MPa higher than that of the initial BP was applied (Muller, 1991) for 20 min. Sap expressed from the cut end of the stem as a result of applying this “overpressure” [pressures greater than the balance pressure (Roberts and Knoerr, 1977)] was collected by placing a tared vial containing tissue paper over the cut end of the stem (Ranney et al., 1991b). After 20 min, the pressure in the chamber was released, and the vial was weighed to determine the weight of the expressed sap. After a 5-min equilibration period following release of the chamber pressure, a new equilibrium balance pressure was determined. The pressure within the chamber was then increased to 0.3 MPa above the new equilibrium balance pressure and held constant for 20 min. The process of balance pressure determination, application of overpressure, sap collection, and equilibration was repeated to cover a range of equilibrium balance pressures from 0 to 3.5 MPa or until equilibrium BP appeared to reverse. An increase in BP sometimes accompanies exposure of foliage to pure nitrogen gas for >3 h (Cheung et al., 1975). Upon completion of each series of measurements, samples were dried overnight at 70 °C, and dry weights (DWs) were recorded.

Each series of measurements was used to construct a pressure-volume curve by plotting the inverse of balance pressure on the ordinate and water stress deficit (WSD) on the abscissa (Roberts and Knoerr, 1977). Water stress deficit represents the amount of water lost from the sample and was calculated as WSD = weight of expressed sap ÷ (turgid weight of rehydrated sample - DW of sample).

In some cases, data collected for pressure-volume analysis were insufficient to construct a meaningful curve and therefore were excluded from all subsequent analyses.

All pressure-volume curves were analyzed using segmented nonlinear regression analysis (SAS Institute, Inc., 1988) to estimate the curvilinear and linear portions of each curve and the joint point (x_0, point at which the shape of the curve changes from curvilinear to linear). The curvilinear and linear portions of each curve were approximated using equations of the form $y = a + b(x-x_0) + c(x-x_0)^2$ and $y = a + b(x-x_0)$, respectively. Values for a, b, c, and x_0 were estimated in the regression analysis for each pressure-volume curve. The curvilinear portion of the graph represents water potential as a function of both osmotic and pressure potentials ($\Psi w = \Psi\pi + \Psi p$). Pressure potential is referred to hereafter as turgor pressure. The joint point (x_0) was considered to be the water stress deficit at zero turgor (WSD_0), since the linear portion of the graph represents water potential as a function of osmotic potential only ($\Psi w = \Psi\pi$) (Abrams, 1988). The turgor loss point is the point at which cells lose turgor and incipient plasmolysis occurs (Abrams, 1988). Osmotic potential at full turgor ($\Psi\pi^{100}$) was calculated as the intersection of the ordinate by extrapolation of the linear portion of the curve, and osmotic potential at the turgor loss point ($\Psi\pi^0$) was calculated as the BP at x_0. Values from each curve for a, b, c, WSD_0, $\Psi\pi^{100}$, and $\Psi\pi^0$ were analyzed for significance of main effects and interaction of drought treatment and cultivar using a general linear models procedure (SAS Institute, Inc., 1988). Means for a, b, c, and x_0 were estimated using LSMEANS, were separated using PDIFF at $P<0.05$ (SAS Institute, Inc., 1988), and were used to construct a representative pressure volume curve for each drought treatment within each cultivar (Figs. 1). Data presented for WSD_0, $\Psi\pi^{100}$, and $\Psi\pi^0$ are the means of values calculated for individual curves.

On 15 Sept. 2001 shoots (stems and leaves) of the five nonsampled replications of each treatment within each cultivar were excised at the substrate level and dried for at least 72 h at 70 °C, and DWs of shoots were recorded. Root systems were evaluated visually to determine the extent of root exploration within the container during the course of the study. Values for shoot DW were analyzed for significance of main effects and interaction of drought treatment and cultivar using a general linear models procedure (SAS Institute, Inc., 1988). Statistical analysis indicated a significant drought treatment x cultivar interaction (P<0.001), therefore regression analysis was performed for shoot DW plotted against drought treatment for each cultivar (SAS Institute, Inc., 1988).

Results

Shoot DW decreased linearly with increasing drought stress for both cultivars, and the slope of this decrease was steeper for 'Olympic Wedding' mountain laurel than 'Compacta' holly (Fig. 2). Drought treatments affected root growth similarly to shoot growth (plants with the least amount of shoot growth also had the least amount of root growth, visual observations). Partial death of shoot tissue occurred on some plants of 'Olympic Wedding' mountain laurel in -1.0 and -1.5 MPa treatments, while no shoot tissue death was observed on plants of 'Compacta' holly (visual observations). The number of days in each dry down cycle was plotted to track the time it took for each cultivar to reach its target pre-dawn PWP (Fig. 3). In general, length of dry-down cycles (days between rewatering, as determined by the average of five pre-dawn PWP measurements) in all drought treatments increased over the course of the experiment for

'Olympic Wedding' mountain laurel, but was relatively constant for 'Compacta' holly (Fig. 3).

For parameters WSD_0, $\Psi\pi^{100}$, and $\Psi\pi^0$ estimated from representative pressure-volume curves, the drought treatment x cultivar interaction was nonsignificant, therefore data are presented for main effects of drought treatment and cultivar only (Table 1). Average WSD_0 was higher for 'Olympic Wedding' mountain laurel than 'Compacta' holly and was similar for all drought treatments (Table 1). Osmotic potential at full turgor ($\Psi\pi^{100}$) was lower (more negative) in the -1.0, and -1.5 MPa treatments than in the -0.5 MPa treatment and was similar for both cultivars (Table 1). Osmotic potential at turgor loss point ($\Psi\pi^0$) was lower (more negative) for 'Olympic Wedding' mountain laurel than 'Compacta' holly and was similar for drought treatments (Table 1).

Discussion

Larger decrease in shoot DW with increasing drought stress for ‘Olympic Wedding’ mountain laurel compared to ‘Compacta’ holly suggests that ‘Olympic Wedding’ mountain laurel is less drought tolerant than ‘Compacta’ holly. Likewise, visual differences in root growth among treatments corresponded to differences in shoot DW among treatments. Similar to shoot growth, root growth is also hindered by drought conditions and lack of water (Dubrovsky et al., 1998). Root death may occur during rapid dehydration, while the root elongation zone and the rate of root growth decrease in response to gradual drying (Dubrovsky et al., 1998). This would be of particular importance in the landscape with respect to root growth into the surrounding soil, since inhibition of root growth due to lack of adequate water supply following transplanting has been reported (Witherspoon and Lumis, 1986). Amount of plant tissue death that occurred in response to drought treatments was also indicative of the relative drought tolerance of these two cultivars. Low visual quality of 'Olympic Wedding' mountain laurel in -1.0 and -1.5 MPa treatments suggests that whole plant death would likely have occurred with time. In contrast, although 'Compacta' holly received no irrigation for 35 days in the -1.5 MPa treatment, no plant tissue death was observed. It is clear from these results that 'Compacta' holly would be able to withstand extended periods of drought in the landscape, while 'Olympic Wedding' mountain laurel would not.

While the number of cycles for each drought treatment was the same between cultivars, length of dry-down cycles was relatively constant for 'Compacta' holly but increased over time for 'Olympic Wedding' mountain laurel (Fig. 4). Since time of rewatering was determined in each drought treatment by plants reaching a target pre-dawn PWP, the length of a dry-down cycle is a representation of plant water relations and plant water use. Since pre-dawn PWP has been reported to be in equilibrium with and thus estimate soil water potential (Slatyer, 1967), the increase in length of dry-down cycles within a drought treatment indicates that plants of 'Olympic Wedding' mountain laurel began taking up less water from the container in response to repeated periods of drought. Decreased transpiration and water use by radiata pine (*Pinus radiata* D. Don) grown in containers was reported under extended periods of drought conditions (Cremer, 1972). Similarly, acclimatization by alfalfa (*Medicago sativa* L.) to drought conditions was apparent from lower transpiration rates (Pennypacker et al., 1990). Decreased root growth in response to drought would also result in less water taken up from the container substrate by ‘Olympic Wedding’ mountain laurel compared to ‘Compacta’ holly.

It is likely that plant water use was higher initially at the start of the experiment when irrigation was being applied regularly, and then decreased once drought treatments were imposed and water became less available. This adjustment period was expected since both cultivars had previously experienced conditions of unlimited water availability. The similarity in length of dry-down cycles within a drought treatment for 'Compacta' holly suggests that water use efficiency of this plant is perhaps more consistent over a broad range of drought conditions.

WSD_0 was higher for 'Olympic Wedding' mountain laurel than ‘Compacta’ holly (Table 1). Since the amount of water lost from a plant increases with increasing water stress defecit, it may appear as if ‘Compacta’ holly loses turgor sooner than 'Olympic Wedding' mountain laurel. However, because PWP decreased faster for 'Olympic Wedding' mountain laurel than ‘Compacta’ holly over the course of each dry-down cycle, a higher WSD_0 does not, in this case, imply greater drought tolerance of ‘Olympic Wedding’ mountain laurel compared to ‘Compacta’ holly. For example, water potential at the turgor loss point in the -0.5 MPa treatment was -1.5 and -1.2 MPa for ‘Olympic Wedding’ mountain laurel and ‘Compacta’ holly, respectively. Pre-dawn PWP of -1.5 MPa for ‘Olympic Wedding’ mountain laurel and -1.2 MPa for ‘Compacta’ holly occurred in our experiment after 18 and 30 d, respectively. So, although WSD_0 was higher for ‘Olympic Wedding’ mountain laurel, the time to reach the turgor loss point was longer for ‘Compacta’ holly.

$\Psi\pi^{100}$ was lower for 'Olympic Wedding' mountain laurel than for ‘Compacta’ holly, indicating that osmotic potential was a larger component of total PWP for mountain laurel than ‘Compacta’ holly (Table 1). This result suggests that solutes are concentrated at a greater rate with decreasing water potential in 'Olympic Wedding' mountain laurel compared to ‘Compacta’ holly. This difference is likely due to a higher tissue elasticity for ‘Olympic Wedding’ mountain laurel and ‘Compacta’ holly.

Since there was no significant difference between cultivars for $\Psi\pi^{0}$, decreasing $\Psi\pi^{0}$ with increasing drought stress suggests that both cultivars exhibited osmotic adjustment in response to drought stress. Despite this response to water-limiting conditions, osmotic adjustment may not prevent wilting or decreased growth (Abrams, 1988). Both wilting and substantial decrease in growth occurred for ‘Olympic Wedding’ mountain laurel, while no wilting was observed for ‘Compacta’ holly in this experiment.

Similar to results for cherry (*Prunus avium* L. x *P. pseudocerasus* Lindl. ‘Colt’ and *P. cerasus* L. ‘Meteor’) in which $\Psi\pi^{100}$ decreased in response to drought conditions (Ranney et al., 1991a), $\Psi\pi^{100}$ in our experiment was lower (more negative) in -1.0 and -1.5 MPa treatments than in -0.5 MPa treatments. A decrease in osmotic potential contributes to maintenance of turgor pressure at low PWP (Abrams, 1988) and may result from accumulation of solutes (osmotic adjustment) (Blake and Bevilacqua, 1991; Ranney et al., 1991a). Loblolly pine (*Pinus taeda* L.) exhibited significant osmotic adjustment at pre-dawn PWPs of -1.5 to -2.0 MPa (Meier et al., 1992). Lower $\Psi\pi^{100}$ in -1.0 and -1.5 MPa treatments in our experiment indicates that osmotic potential was a larger component of total PWP in these treatments compared to that of the more mild -0.5 MPa treatment. It has been suggested that osmotic adjustment is an important factor in plant water relations only in more severely stressed plants. In black spruce (*Picea mariana* Mill.), $\Psi\pi^{100}$ did not change during repeated short-term periods of drought (Blake and Bevilacqua, 1991). Our results suggest that osmotic adjustment may be less important to plant water relations at relatively low levels of drought stress and/or higher (less negative) PWP.

Plant growth, visual quality, and plant water relations parameters in this experiment indicate that poor performance of mountain laurel in the landscape may be due in part to lack of drought tolerance. In contrast, ‘Compacta’ holly was able to withstand a range of drought conditions that included extended periods of time with no irrigation. Results of this experiment illustrate the importance of adequate post-transplant irrigation of mountain laurel to ensure successful establishment in the landscape.

Literature Cited

Abrams, M.D. 1988. Sources of variation in osmotic potentials with special reference to North American tree species. For. Sci. 34:1030-1046.

Blake, T.J. and E. Bevilacqua. 1991. Effects of repeated stress on turgor pressure and cell elasticity changes in black spruce seedlings. Can. J. For. Res. 21:1329-1333.

Cheung, Y.N.S., M.T. Tyree, and J. Dainty. 1975. Water relations parameters on single leaves obtained in a pressure bomb and some ecological interpretations. Can. J. Bot. 53:1342-1346.

Costello, L. and J.L. Paul. 1975. Moisture relations in transplanted container plants. HortScience 10:371-372.

Cremer, K.W. 1972. Immediate resumption of growth by radiata pine after five months of minimal transpiration during drought. Austral. For. Res. 6:11-16.

Dubrovsky, J.G., G.B. North, and P.S. Nobel. 1998. Root growth, developmental changes in the apex, and hydraulic conductivity for *Opuntia ficus-indica* during drought. New. Phytol. 138:75-82.

Jaynes, R.A. 1997. *Kalmia*: Mountain laurel and related species. Timber Press, Inc., Portland, Ore.

Meier, C.E., R.J. Newton, J.D. Puryear, and S. Sen. 1992. Physiological responses of loblolly pine (*Pinus taeda* L.) to drought stress: Osmotic adjustment and tissue elasticity. J. Plant Physiol. 140:754-760.

Muller, R.N. 1991. Growing season water relations of *Rhododendron maximum* L. and *Kalmia latifolia* L. Bul. Torrey Bot. Club 118:123-127.

Nelms, L.R. and L.A. Spomer. 1983. Water retention of container soils transplanted into ground beds. HortScience 18:863-866.

Pennypacker, B.W., K.T. Leath, W.W. Stout, and R.R. Hill, Jr. 1990. Technique for simulating field drought stress in the greenhouse. Agron. J. 82:951-957.

Ranney, T.G., N.L. Bassuk, and T.H. Whitlow. 1991a. Osmotic adjustment and solute constituents in leaves and roots of water-stressed cherry (*Prunus*) trees. J. Amer. Soc. Hort. Sci. 116:684-688.

Ranney, T.G., N.L. Bassuk, and T.H. Whitlow. 1991b. Turgor maintenance in leaves and roots of ‘Colt’ cherry trees (*Prunus avium* x *pseudocerasus*) in response to water stress. J. Hort. Sci. 66:381-387.

Roberts, S.W. and K.R. Knoerr. 1977. Components of water potential estimated from xylem pressure measurements in five tree species. Oecologia 18:191-202.

SAS Inst., Inc. 1988. SAS/STAT user's guide: Release 6.03 edition. SAS Inst., Inc., Cary, N.C.

Slatyer, R.O. 1967. Plant-water relationships. Academic Press, New York.

Tyree, M.T. and H.T. Hammel. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. J. Expt. Bot. 23:267-282.

Witherspoon, W.R. and G.P. Lumis. 1986. Root regeneration of *Tilia cordata* cultivars after transplanting in response to root exposure and soil moisture levels. J. Arboricult. 12:165-168.

Zhang, B. and D.D. Archbold. 1993. Water relations of a *Fragaria chiloensis* and a *F. virginiana* selection during and after water deficit stress. J. Amer. Soc. Hort. Sci. 188:274-279.

Zobel, D.B. 1996. Variation of water relations parameters with extended rehydration time, leaf form, season, and proportion of leaf. Can. J. For. Res. 26:175-185.

Zwack, J.A., W.R. Graves, and A.M. Townsend. 1999. Variation among red and Freeman maples in response to drought and flooding. HortScience 34:664-668.

Table 1. Effect of drought treatment and cultivar on water stress deficit at the turgor loss point (WSD_0) and osmotic potential at full and zero turgor.[z]

Cultivar	WSD_0	Osmotic potential (-MPa) Full turgor ($\Psi\pi^{100}$)	Osmotic potential (-MPa) Zero turgor ($\Psi\pi^{0}$)
'Olympic Wedding' mountain laurel	0.10 a[y]	1.50 a	1.93 a
'Compacta' holly	0.05 b	1.38 a	1.50 b
Treatment (-MPa)			
0.5	0.08 a[x]	1.24 b	1.46 a
1.0	0.07 a	1.57 a	1.83 a
1.5	0.08 a	1.51 a	1.86 a
Significance			
Cultivar	*	NS	*
Treatment	NS	*	NS
Cultivar x treatment	NS	NS	NS

[z]WSD = weight of expressed sap ÷ (turgid weight of sample - DW of sample).
[y]Lowercase letters denote mean separation between cultivars by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
[x]Lowercase letters denote mean separation among drought treatments by PDIFF at $P<0.05$.
NS, * Nonsignificant or significant at $P<0.05$, respectively.

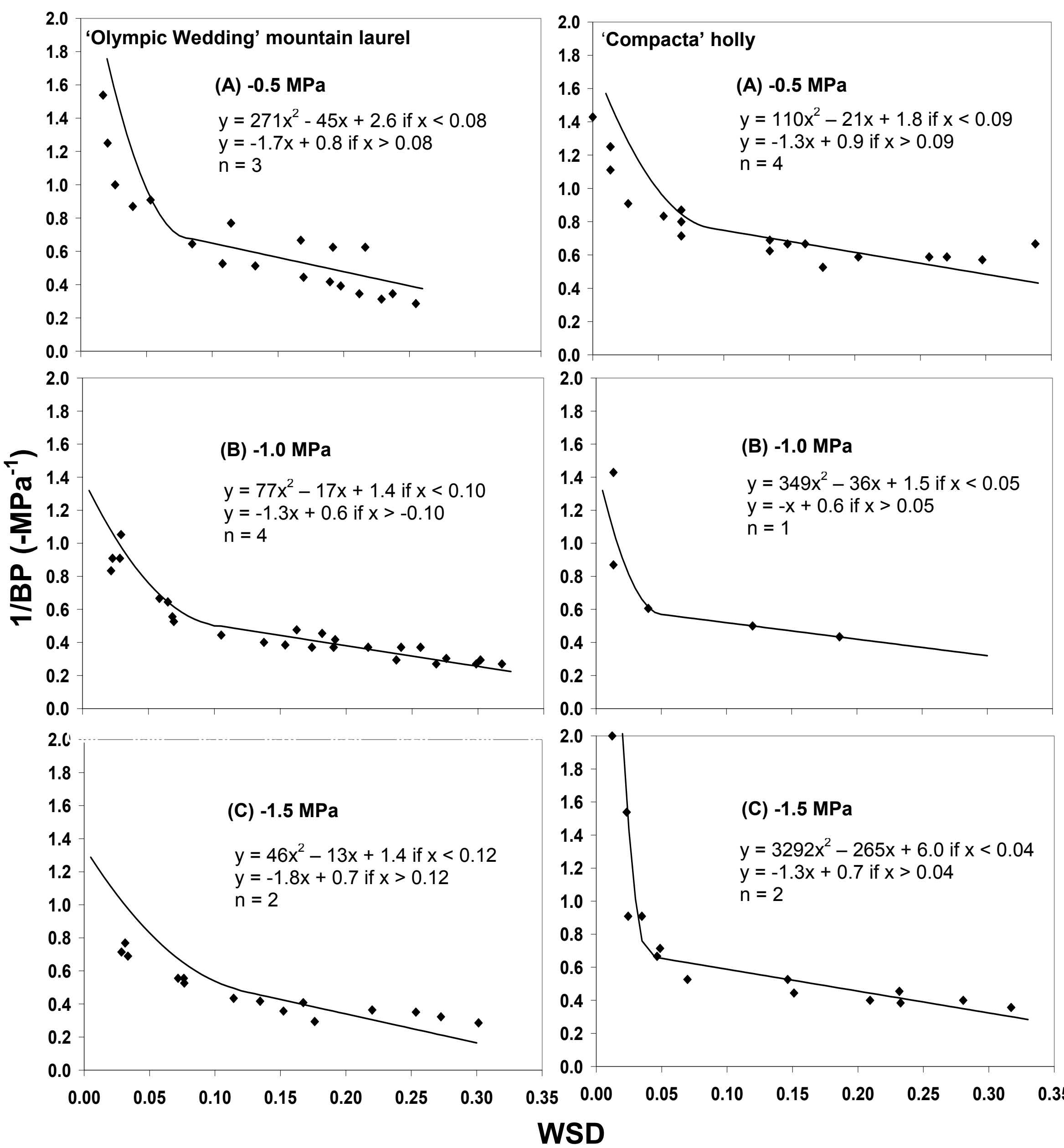

Fig. 1. Pressure-volume curves for 'Olympic Wedding' mountain laurel and 'Compacta' holly in (A) -0.5, (B) -1.0, and (C) -1.5 MPa drought treatments constructed by plotting the inverse of balance pressure (BP) against water stress deficit [WSD = weight of expressed sap ÷ (turgid weight of rehydrated sample - DW of sample)]. Symbols represent data collected for n pressure-volume curves. Line represents curve constructed using the average of n values for parameters a, b, c, and x_0 (joint point).

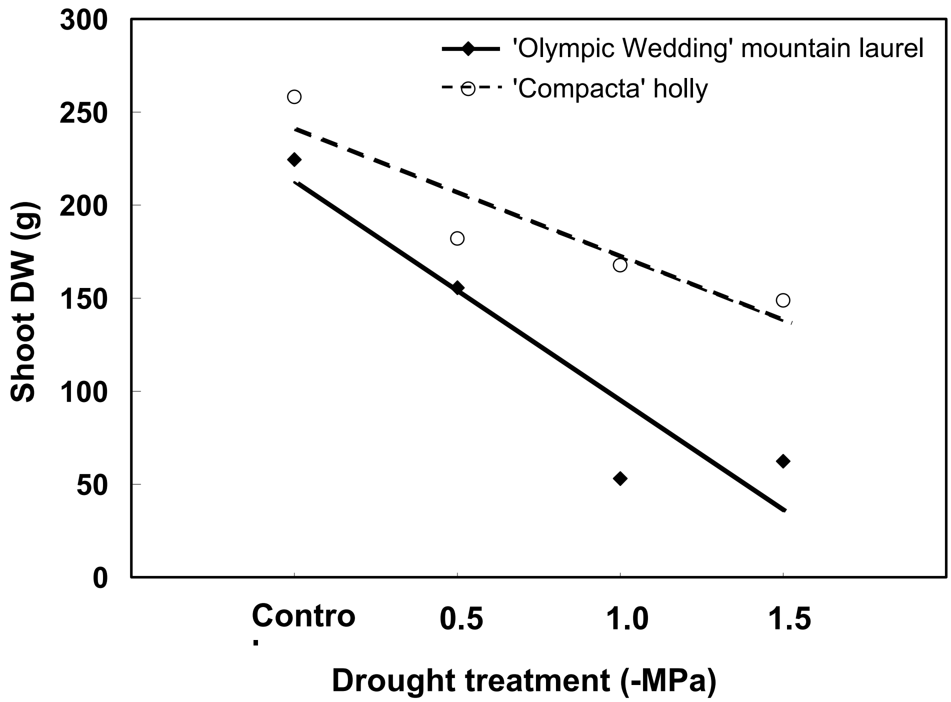

Fig. 2. Effect of drought treatment on shoot DW of 'Olympic Wedding' mountain laurel (y = -117.7x + 212.2; R^2 = 0.87) and 'Compacta' holly (y = -68.5x + 240.6; R^2 = 0.85). Slopes for the two cultivars are significantly different (P<0.001). Symbols represent the mean of five observations.

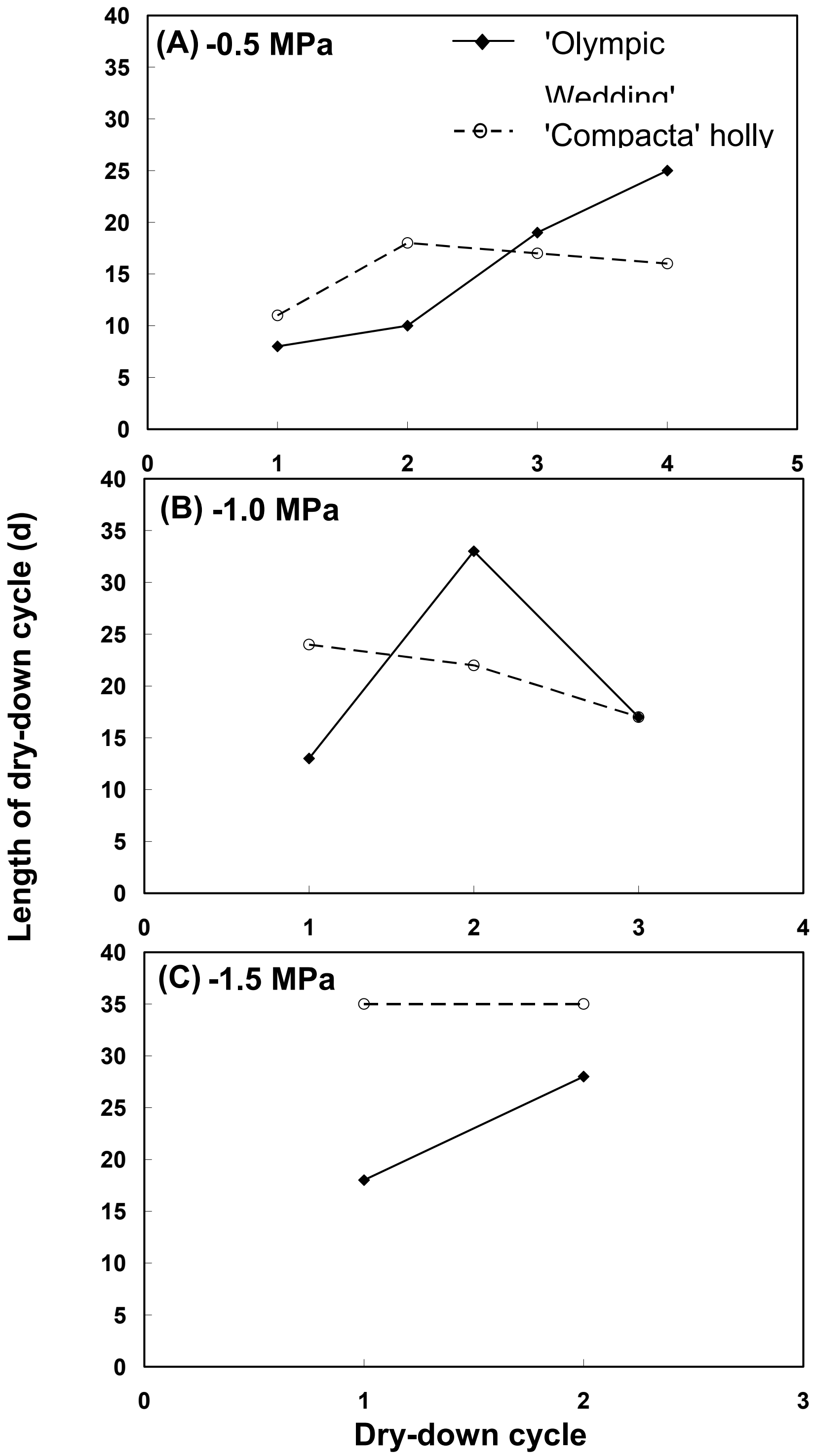

Fig. 3. Length of each dry-down cycle in (A) -0.5, (B) -1.0, and (C) -1.5 MPa drought treatments for 'Olympic Wedding' mountain laurel and 'Compacta' holly.

Chapter 4

Root : shoot Ratio and Landscape Exposure Affect Establishment of Transplanted *Kalmia latifolia* 'Olympic Wedding'

(In the format appropriate for submission to Journal of Environmental Horticulture)

Root : shoot Ratio and Landscape Exposure Affect Establishment of Transplanted *Kalmia latifolia* 'Olympic Wedding'[1]

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Abstract

Mountain laurel (*Kalmia latifolia* L.) is an attractive evergreen shrub that frequently does not survive transplanting from containers into the landscape. In an effort to improve survival of transplanted mountain laurel, research was conducted to determine the effect of root : shoot ratio and landscape exposure on survival and subsequent growth of transplanted container-grown mountain laurel. Plants of 'Olympic Wedding' mountain laurel with initial root : shoot ratios (root volume ÷ leaf area) of 0.002, 0.007, or 0.004 [1-, 7.5-, or 19-L (1-qt, 2-gal, or 5-gal) containers, respectively] were transplanted in Raleigh, NC in tilled beds amended with pine bark along four exposures (north, east, south, west). Plants were grown for three growing seasons. Plant death or survival, growth index, and visual ratings for leaf color, canopy fullness, and overall quality were recorded after each growing season. After three growing seasons, visual ratings were higher for plants with higher initial root : shoot ratio [7.5-L (2-gal)] than for plants with lower initial root : shoot ratio [1- or 19-L (1-qt or 5-gal)] and were higher on north exposures than on south and west exposures. Growth index increased throughout the experiment for 1- and 7.5-L (1-qt and 2-gal) plants, did not increase for 19-L (5-gal) plants, and in general was highest on the east exposure. Survival was highest on the east and north exposures and lowest on the west exposure. Results suggest that in climates similar to Raleigh, shaded exposures may improve survival of transplanted mountain laurel. Mountain laurel may also be marketed earlier in its production cycle, since 7.5-L (2-gal) plants had a higher root : shoot ratio and performed better than 19-L (5-gal) plants.

Index words: mountain laurel, woody ornamental, container-grown, plant size, Ericaceae

Significance to Nursery Industry

Mountain laurel (*Kalmia latifolia*), a broadleaved evergreen shrub with many ornamental attributes, frequently does not survive transplanting from containers into the landscape. Improving survival of transplanted mountain laurel may encourage increased commercial production and use of this native plant species. Research herein examined the effects of root : shoot ratio and landscape exposure on establishment of transplanted mountain laurel. Plant growth and visual quality were higher on north and east exposures than on south and west exposures, suggesting that in climates similar to Raleigh, NC, shaded exposures may increase survival of transplanted mountain laurel. Mountain laurel transplanted from 7.5-L (2-gal) containers had the highest intial root : shoot ratio and had higher visual ratings and a larger increase in growth than mountain laurel transplanted from 1- or 19-L (1-qt or 5-gal) containers. Growers may want to market mountain laurel earlier in its production cycle to improve landscape establishment.

Introduction

There are many factors that influence the ability of woody ornamental plants to survive transplanting from containers into the landscape, including plant size (Harris, 1992). Growth of smaller trees may eventually equal or surpass growth of larger trees transplanted at the same time (Watson 1985). Plant biomass of crape myrtle (*Lagerstroemia indica* L. x *Lagerstroemia fauriei* Koehne 'Tonto') was highest 16 weeks after transplanting for plants that had the smallest plant dry weight, canopy size, and leaf area (compared to other plants in the same experiment) at time of transplanting (Cabrera and Devereaux, 1999). Transplant size affects root : shoot ratio (Harris, 1992), and in the case of transplanted trees, smaller plants may have a higher root : shoot ratio (Watson, 1985). A larger root : shoot ratio is 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 (Kozlowski and Davies, 1975). Since a plant's root : shoot ratio can change with time, age, and production practices in the nursery, it is likely that root : shoot ratios may vary widely, depending on multiple factors (Beeson, 1993; Keever and Cobb, 1987).

Exposure in the landscape also affects transplant survival and may be particularly important for plants traditionally planted in full to partial shade. ‘Pink Ruffles’ azalea (*Rhododendron* L. x ‘Pink Ruffles’) had lower shoot and root dry weight when grown in full sun than when grown in shade (Andersen et al., 1991b), and Japanese aucuba (*Aucuba japonica* Thunb.) exhibited chlorosis, necrosis, and dieback when transplanted from shade into full sun (Andersen et al., 1991a). Differences in air and soil temperatures among exposures may account for differences in survival and growth. Blue holly (*Ilex* x *meserveae* S.Y. Hu) cultivars performed best when planted on northern exposures (compared to other exposures) where summer foliage temperatures were coolest (Pair and Still, 1982). Exposure can also influence plant water relations. ‘China Girl’ holly (*Ilex rugosa* Friedr. Schmidt. x *I. cornuta* Lindl. & Paxt.) had lowest leaf water potential at southern exposures (Pair, 1987). Root growth and distribution are also influenced by exposure. Roots of several transplanted tree species were concentrated on the north and east sides of the root ball (Watson and Himelick, 1982).

Mountain laurel is an attractive broadleaved evergreen shrub that produces an impressive floral display during late spring to early summer. Although most commonly found growing in shady understory locations, this species also grows in full sun in cooler climates and in the mountains of the southeastern United States (personal observations). Despite its extensive native range in the eastern United States (Maine to Florida), it frequently does not survive transplanting into the landscape even in areas to which it is indigenous (Dirr, 1998; Jaynes, 1997). Although frequently marketed commercially 3 years into the production cycle in 19-L (5-gal) containers, attractive plants of mountain laurel can also be produced in smaller containers after only 2 years in a nursery (personal observations). As a natural progression of plant growth during nursery production of mountain laurel, it appears as if the root : shoot ratio varies depending on the stage in its production (personal observation). By transplanting mountain laurel from different size containers at four exposures (north, east, south, and west) it may be possible to determine the effect of root : shoot ratio and landscape exposure on survival and subsequent growth of transplanted mountain laurel. Therefore, the objective of this research was to determine the effect of transplant size and landscape exposure on establishment of transplanted mountain laurel.

Materials and Methods

Research was conducted at the Horticulture Field Laboratory, North Carolina State University, Raleigh. Exposures in four directions (north, east, south, and west) were provided by square structures constructed from four panels of 1.8 m (6 ft) tall x 2.4 m (8 ft) wide spruce fencing material. Fencing panels consisted of twenty-three 10-cm (4 in) wide slats per panel with 0.6 cm (0.25 in) spacing between slats. Six structures were constructed, each representing one block (replication).

Tilled beds [1.2 m (4 ft) wide and 5 m (16 ft) long] were prepared adjacent to each side of a structure. Prior to planting, the Cecil clay soil (clayey Kaolinitic Thermic Typic Hapludult) was amended by incorporation with composted pine bark [5 cm (2 in)], and pH, phosphorus, and potassium were adjusted to recommended levels for mountain laurel in the landscape (Bir and Conner, 1991; Tucker and Rhodes, 1987). After planting and at the beginning of each growing season, beds received 0.03 kg/m^2 (0.6 lb/yd^2) 18N-6P_2O_5-12K_2O Osomcote™ slow release fertilizer (6-9 month formulation, Scotts-Sierra, Marysville, OH) and 2.5 cm (1 in) composted wood chip mulch.

Plants used in this study were 'Olympic Wedding' mountain laurel with initial root : shoot ratios of 0.002, 0.007, or 0.004 {in 1-, 7.5-, or 19-L [#sp-4, #2, or #5 (1-qt, 2-gal, or 5-gal)] containers, respectively}. Initial root : shoot ratio for each plant size was calculated as root volume ÷ leaf area. Since roots of each plant size filled the container, root volume used to calculate root : shoot ratio was equal to the container volume [1-, 7.5- or 19-L (1-qt, 2-gal, or 5-gal)]. To determine initial leaf area, two plants of each size (nonplanted) were harvested at experiment initiation, and leaf area was measured using a LI-COR 3000 leaf area meter (LI-COR, Inc., Lincoln, NB). For simplicity in description and presentation, plant root : shoot ratio will be referred to hereafter as plant size, and results will be presented in terms of container size. Plants in 1-, 7.5-, and 19-L (1-qt, 2-

gal, and 5-gal) containers were micropropagated liners (Brigg's Nursery, Olympia, WA) that had been container-grown (Historyland Nurseries, Inc., Montross, VA) for 1, 2, or 3 growing seasons, respectively. Because plants used in this study were not rootbound, the root : shoot ratio was that which occurred naturally during its nursery production and was not intentionally manipulated prior to transplanting.

In May 1999, plants were planted in the tilled beds surrounding each structure. Two rows of plants running lengthwise along each side of a structure were planted with one plant of each size per row (Fig. 1). Plants in the inside row were 0.2 m (8 in) from the structure and were evenly spaced 0.6 m (2 ft) from each other. The outside row was 0.5 m (20 in) from the inside row with similar spacing between plants. To minimize shading, plants in the outside row were offset from plants on the inside row by 0.15 m (6 in) towards the north or east on all sides. Plants were randomized by size within each row.

All plants were irrigated [2.5 cm (1 in) water] twice weekly during the first 30 d of the study. After 30 d, all plants were irrigated during the first growing season with 2.5 cm (1 in) of water when the average soil moisture tension reached -30 kPa (-30 cbar). Plants received no irrigation during subsequent growing seasons. Average annual precipitation in Raleigh is 107 cm (42 in) (State Climate Office of North Carolina at N.C. State University, 2000)]. Soil moisture at each exposure was measured three times weekly using Watermark Soil Moisture Sensors (-300 kPa capacity, Irrometer Co., Riverside, CA) installed in the soil [15 cm (6 in) depth] outside the root ball of one plant of each size per exposure (total of 12 sensors per block). Sensors were installed in this manner for two blocks (total of 24 sensors).

Leaf temperature in the horizontal and vertical center of the canopy of one plant of each size per exposure was measured by attaching a copper-constantan thermocouple to the underside of a leaf. Thermocouples were attached to the leaf using water resistant contact cement (Weldwood, DAP Inc., Dayton, OH). Soil temperature at each exposure was measured by inserting a similar thermocouple into the soil at a depth of 10 cm (4 in). Leaf and soil temperatures were measured every 15 min for three blocks, and hourly average, maximum, and minimum temperatures were recorded (23X Micrologger, Campbell Scientific Inc., Logan, Utah). Throughout the experiment, weed control was provided via handweeding in areas adjacent to mountain laurel plants and via chemical control (glyphosate) along the perimeter of the plots.

Plants were grown for three growing seasons. Plant death or survival was recorded for each plant after each growing season (Feb. 2000, Jan. 2001, and Nov. 2001). Nondestructive growth index (GI) measurements {plant height + [(maximum plant width + perpendicular width) ÷ 2]} were recorded for all plants at experiment initiation (May 1999) and for all living plants after each growing season (Feb. 2000, Jan. 2001, and Nov. 2001). Living plants were rated visually for leaf color, canopy fullness, and overall quality (Table 1) after each growing season (Feb. 2000, Jan. 2001, and Nov. 2001). Plants were harvested Nov. 2001. At harvest, shoots (aerial portions) of all plants were cut at the soil level and separated into stems and leaves. Leaf area for all living plants was determined as described previously. Stems and leaves were dried at 70C (160F) for at least 72 h, and dry weights of shoots were determined. Leaf area : shoot dry weight (leaf area ÷ shoot dry weight) was calculated to quantify canopy fullness. Rootballs of plants of each size on all exposures (two blocks) were excavated by hand digging, and root systems were observed visually for extent of root growth into soil (not quantified).

The experiment was a split plot design with six blocks. Within each block, exposure formed the main plot, and initial transplant size (hereafter referred to as plant size) formed the subplot (split-plot). In cases where repeated measurements were taken over time, measurement date was treated as a sub-subplot (split-split plot) factor. Data collected for plant growth and environmental conditions were analyzed for significance of treatment main effects and interactions using a general linear models procedures. Means were generated using LSMEANS and separated by PDIFF at P=0.05 (SAS Institute Inc., 1988). The effect of planting row was not significant, so all data presented are averaged over row.

Results

Effect of transplant size. Throughout the experiment, survival of ‘Olympic Wedding’ mountain laurel was lowest among 1-L (1-qt) plants, while no death occurred among 19-L (5-gal) plants (data presented for final rating, Table 2). The effect of plant size on visual ratings was similar throughout the course of the experiment (data not presented), so results are presented for final visual ratings only. In general, visual ratings for leaf color, canopy fullness, and overall quality were higher for 7.5-L (2-gal) plants than 1- or 19-L (1-qt or 5-gal) plants (Table 3).

Final leaf area and shoot dry weight were mandated by initial plant size, and thus were larger for 19-L (5-gal) plants than for 1- and 7.5-L (1-qt and 2-gal) plants (data not presented). Leaf area : shoot dry weight of 1- and 7.5-L (1-qt and 2-gal) plants was higher (0.27 and 0.28, respectively) than that of 19-L (5-gal) plants (0.17). Growth index (GI) increased 130% and 50% over time for 1- and 7.5-L (1-qt and 2-gal) plants, respectively, but did not increase for 19-L (5-gal) plants (Table 4). Plants transplanted from 7.5-L (2-gal) containers appeared to have the most root growth at the end of the experiment (visual observations).

Soil water potential (averaged over time) was higher when measured adjacent to 1-L (1-qt) plants than when measured adjacent to 7.5- or 19-L (2 or 5-gal) plants (Table 5). Leaf temperature was similar for all plant sizes (within exposure, data not presented).

Effect of exposure. Percentage survival was highest on the east and north exposures and lowest on the west exposure (Table 2). Visual ratings were, on average, 100% higher for plants grown on the north exposure than for plants grown on south and west exposures (Table 3). Leaf area, shoot dry weight, and leaf area : shoot dry weight were higher for plants grown on the east exposure compared to those grown on south and west exposures (Table 6). In general, GI was highest for 7.5- and 19-L (2 and 5-gal) plants on the east exposure, and was similar at all exposures for 1-L (1-qt) plants (Table 4).

Soil water potential was similar for all exposures (Table 5). Data for average hourly leaf and soil temperatures at each exposure are presented for August 29, 2000 as representative of the general trend and differences in temperatures between exposures throughout the year. In general, leaf and soil temperatures were higher on south and west exposures than north and east exposures (Fig. 2).

Discussion

Although, leaf area and shoot dry weight of 19-L (5-gal) plants were highest due to larger initial size at planting, GI of these plants was not different between May 1999 and Nov. 2001. This is in stark contrast with the change in GI measurements of 1- and 7.5-L (1-qt and 2-gal) plants, which increased over 100% and 50%, respectively for the same time period. Leaf area : shoot dry weight was lower for 19-L (5-gal) plants than other plant sizes, indicating that the amount of foliage per plant size was higher for 1- and 7.5-L (1-qt and 2-gal) plants. Loss of leaves on 19-L (5-gal) plants as a result of stem dieback was likely caused by plant water stress. In previous work, drought tolerance of ‘Olympic Wedding’ mountain laurel was much lower than that of ‘Compacta’ holly (Wright, 2002). Similarly, plants of 'Lodense' privet (*Ligustrum vulgare* L. 'Lodense) that received infrequent irrigation were more sparsely foliated than those that received irrigation every 5-6 days (Barnett, 1986). The higher leaf area : shoot dry weight of 7.5-L (2-gal) plants compared to 19-L (5-gal) plants is a quantitative reflection of the high visual quality of 7.5-L (2-gal) plants.

At final harvest, all 19-L (5-gal) plants were living, while 20% of the 1-L and 65% of the 7.5-L (1-qt and 2-gal) plants remained alive. Although surviving 1-L plants had large increases in GI, their extremely high mortality rate makes them unsuitable for transplanting. Despite no mortality of 19-L (5-gal) plants, their extremely low visual quality suggests that death of these plants may have commenced with time. We and other authors have observed that mountain laurel and other members of the Ericaceae, such as Japanese andromeda (*Pieris japonica* D. Don), frequently die several growing seasons after transplanting (Dirr, 1998).

In the present experiment 7.5-L (2-gal) plants performed best, and their superior visual quality and performance is attributed to their higher initial root : shoot ratio. Root : shoot ratio influences the relationship between water uptake via the roots and water loss via transpiration (Kozlowski and Davies, 1975), and it may be possible to manipulate this relationship during production (Beeson, 1993). It has been suggested that during nursery production, container-grown plants potted into larger containers in the fall may by spring have a higher root : shoot ratio due to continued root growth during the winter in mild to temperate climates (Harris, 1992). In contrast, plants potted in spring may by fall have a lower root : shoot ratio due to more shoot growth during summer months. Since a large, attractive plant canopy is typically the goal of commercial production, frequent watering and high fertility common during nursery production may also result in more shoot growth than can be adequately supplied by the accompanying rootball following transplanting (Harris, 1992; Watson and Himelick, 1997). Such a situation could likely increase the need for intensive post-transplant care and irrigation. Thus, we stress that the effect of plant size in this experiment with regard to landscape establishment is attributed more to the root : shoot ratio at planting rather than the container size. Additionally, because initial root : shoot ratios were not intentionally manipulated for this experiment prior to transplanting, it appears that it is possible within the normal production cycle for mountain laurel to produce plants with a root : shoot ratio favorable for transplanting.

In the current study, plants with the best visual quality and most shoot growth within each size also appeared to have the most root growth. Additionally, at experiment termination, size of root systems of 7.5-L (2-gal) plants equaled or surpassed that of 19-L (5-gal) plants (visual observations). Lack of extensive root growth in this study may have been due to soil texture. Although pine bark was incorporated into the soil prior to planting, heavy clay soils such as those in Raleigh may present a physical barrier to growth of roots of mountain laurel, which are very fine and fibrous (hair-like). Lack of root penetration into the surrounding soil due to dissimilarity in physical properties between container substrate and a mineral soil was reported for winged euonymus [*Euonymus alatus* (Thunb.) Siebold 'Compactus'] (Nicolosi and Fretz, 1980). In its natural environment, root distribution of mountain laurel is typically concentrated in the upper organic litter layer (personal observation). In our experiment, most root growth appeared to occur in the mulch layer, suggesting the importance of mulch for root growth and development of mountain laurel.

Rate and patterns of root growth of mountain laurel also likely affected plant performance in this experiment. Wright et al. (2000) found that mountain laurel has a low rate of root growth compared to *Ilex crenata* Thunb. 'Compacta'. Wright et al. (2000) also reported that fall transplanting may be best for mountain laurel due to more root growth by this species in the fall than in the spring. In the present study, plants were transplanted in the spring. Had they been transplanted in the fall, it is possible that overall survival rates may have been higher. Fall transplanting allows root growth and establishment to occur before spring shoot flush (Harris et al., 1996). Because mycorrhizal associations are common in the Ericaceae in the wild but not in production (Boyer et al., 1982; Largent et al., 1980), roots were examined for evidence of mycorrhizal infection. While the presence of mycorrhizal infection was observed in this experiment, its distribution was not quantified.

Higher (less negative) soil water potential measured adjacent to 1-L (1-qt) plants may have been due to smaller plants absorbing less water from the soil. Additionally, frequent death of 1-L (1-qt) plants meant no water uptake from soil in the vicinity of moisture sensors located outside the root balls of these (dead) plants. Although soil water potential in general appeared to be adequate, water content within the container ball can be much lower than that of the surrounding soil (Nelms and Spomer, 1983). Likewise, substrate water potential may decrease more rapidly in a transplanted root ball than in the surrounding soil (Costello and Paul, 1975). Measuring substrate water potential inside the root ball of a transplanted container-grown plant can be informative, particularly since many plants in this study had little root growth outside the original root ball, even after three full growing seasons. Lack of root growth outside the original root ball into the surrounding soil means that plants must depend primarily on water available from the interior of the original container root ball rather than water in the surrounding soil. Root growth of transplanted littleleaf linden (*Tilia cordata* Mill.) cultivars was higher when the root ball and surrounding soil were well watered (Witherspoon and Lumis, 1986). Root elongation rates have been shown to decease with decreasing soil moisture (Wraith and

Wright, 1998). Daily irrigation of transplanted live oak (*Quercus virginiana* Mill.) was required for over 30 weeks to minimize diurnal fluctuations in plant water potential and prevent transplant shock (Beeson, 1994). Percentage survival of plants in this experiment could possibly have been improved with increased irrigation, since it appeared as if visual decline of plants began once regular irrigation was discontinued.

Percentage survival was highest on north and east exposures and lowest on the west exposure. Similar impact of exposure on transplant survival rates has been reported by other researchers. In an experiment with several container-grown blue holly cultivars planted at different exposures, heat stress was the greatest factor affecting plant survival (Pair and Still, 1982). Similarly, survival of transplanted rhododendron and azalea (*Rhododendron* L. sp.) was highest on northern exposures (Pair, 1994). Flowering of rhododendron and azalea was also affected by exposure, and many plants died after one particularly hot summer (Pair, 1994). These results were similar to those in the current study in that plant death occurred during summer rather than winter months.

Higher visual ratings and more growth on north and east exposures were likely due to lower leaf and soil temperatures at these exposures. Similar to results in the current study, three cultivars of boxwood (*Buxus* L. sp.) had better visual quality and more growth when grown on north and east exposures than when grown on south exposures (LeDuc et al., 2000). In research conducted with transplanted blue hollies, although soil water supply was adequate at southern exposures, increased plant canopy temperatures associated with southern exposures negatively influenced plant growth (Pair and Still, 1982). In previous work, lack of tolerance of mountain laurel to high root-zone temperature was documented, and the optimum experimental root-zone temperature [16C (61F)] was substantially lower than summertime soil temperatures recorded in the current experiment (Wright, 2002). Although air and soil temperatures shown for August were among the highest temperatures of the year, temperature trends and differences between exposures for both leaf and soil were similar for other months. Additionally, soil temperatures observed in this study are representative of those that may actually be encountered in a landscape situation, since mulch was maintained throughout the experiment. Differences in temperature between exposures that occur during summer months are likely most important, since winters in Raleigh tend to be mild.

Although exposure did not affect soil water potential in this study, other researchers have reported variable effects of landscape exposure on plant water status. In research with rhododendron and azalea, plant water stress was similar for all exposures, although differences in plant growth and survival due to exposure were dramatic (Pair, 1994). In contrast, higher irradiance resulted in higher rates of sap flow and transpiration in wax leaf privet (*Ligustrum japonicum* Thunb.) (Heilman et al., 1989).

Results herein indicate that in climates similar to Raleigh, planting mountain laurel in shaded locations as well as regular irrigation throughout the first growing season may improve survival of this species following transplanting. Additionally, the importance of higher root : shoot ratio for transplant survival was documented, and it is suggested that growers market mountain laurel earlier in its production cycle to achieve a root : shoot ratio that would likely improve landscape establishment of this ornamental species.

Literature Cited

1. Andersen, P.C., G.W. Knox, and J.G. Norcini. 1991a. Light intensity influences growth and leaf physiology of *Aucuba japonica* 'Variegata'. HortScience 26:1485-1488.
2. Andersen, P.C., J.G. Norcini, and G.W. Knox. 1991b. Influence of irradiance on leaf physiology and plant growth characteristics of *Rhododendron* x 'Pink Ruffles'. J. Amer. Soc. Hort. Sci. 116:881-887.
3. Barnett, D. 1986. Root growth and water use by newly transplanted woody landscape plants. The public garden 1:23-25.
4. Beeson, R.C., Jr. 1993. Benefits of progressively increasing container size during nursery production depend on fertilizer regime and species. J. Amer. Soc. Hort. Sci. 118:752-756.
5. Beeson, R.C., Jr. 1994. Water relations of field-grown *Quercus virginiana* Mill. from preharvest through containerization and 1 year into a landscape. J. Amer. Soc. Hort. Sci. 119:169-174.
6. Bir, R.E. and J. Conner. 1991. *Kalmia* revisited. Amer. Nurseryman 174(1):56-63.
7. Boyer, E.P., J.R. Ballington, and C.M. Mainland. 1982. Endomycorrhizae of *Vaccinium corymbosum* L. in North Carolina. J. Amer. Soc. Hort. Sci. 107:751-754.
8. Cabrera, R.I. and D.R. Devereaux. 1999. Crape myrtle post-transplant growth as affected by nitrogen nutrition during nursery production. J. Amer. Soc. Hort. Sci. 124:94-98.

9. Costello, L. and J.L. Paul. 1975. Moisture relations in transplanted container plants. HortScience 10:371-372.

10. Dirr, M.A. 1998. Manual of Woody Landscape Plants: Their Identification, Ornamental Characteristics, Propagation and Uses. 5th ed. Stipes Publishing, Champaign, IL.

11. Harris, R.W. 1992. Arboriculture: Integrated Management of Landscape Trees, Shrubs, and Vines. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NJ.

12. Harris, J.R., P. Knight, and J. Fanelli. 1996. Fall transplanting improves establishment of balled and burlapped fringe tree (*Chionanthus virginicus* L.). HortScience 31:1143-1145.

13. Heilman, J.L., C.L Brittin, and J.M. Zajicek. 1989. Water use by shrubs as affected by energy exchange with building walls. Agr. For. Meteorol. 48:345-357.

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

15. Keever, G.J. and G.S. Cobb. 1987. Effects of container volulme and fertility rate on growth of two woody ornamentals. HortScience 22:891-893.

16. Kozlowski, T.T. and W.J. Davies. 1975. Control of water balance in transplanted trees. J. Arboticult. 1:1-10.

17. Largent, D.L., N. Sugihara, and C. Wishner. 1980. Occurrence of mycorrhizae on ericaceous and pyrolaceous plants in northern California. Can. J. Bot. 58:2274-2279.

18. Le Duc, A., L.R. Parsons, and J.C. Pair. 2000. Growth, survival, and aesthetic quality of boxwood cultivars as affected by landscape exposure. HortScience 35:205-208.

19. Nelms, L.R. and L.A. Spomer. 1983. Water retention of container soils transplanted into ground beds. HortScience 18:863-866.

20. Nicolosi, R.T. and T.A. Fretz. 1980. Evaluation of root growth in varying medium densities and through dissimilar soil surfaces. HortScience 15:642-644.

21. Pair, J.C. 1987. Winter hardiness, leaf water potential, and heat tolerance of 'China Girl' holly as affected by landscape exposure. HortScience 22:268-270.

22. Pair, J.C. 1994. Adaptability of evergreen rhododendrons to the great plains as influenced by landscape exposure. J. Amer. Rhododendron Soc. 48:69-72.

23. Pair, J.C. and S.M. Still. 1982. Growth, hardiness, and leaf-water potential of blue holly (*Ilex* x *meserveae*) cultivars as affected by exposure. HortScience 17:823-825.

24. SAS Institute, Inc. 1988. SAS/STAT User's Guide: Release 6.03 Edition. SAS Institute, Inc., Cary, NC.

25. State Climate Office of North Carolina at North Carolina State University. 2000. http://www.nc-climate.ncsu.edu/. [Accessed Mar. 28, 2002].

26. Tucker, M.R. and R. Rhodes. 1987. Crop fertilization based on N.C. soil tests. N.C. Dept. Agr. Circ. 1.

27. Watson, G.W. 1985. Tree size affects root regeneration and top growth after transplanting. J. Arboricult. 11:37-40.

28. Watson, G.W. and E.B. Himelick. 1982. Root distribution of nursery trees and its relationship to transplanting success. J. Arboricult. 8:225-229.

29. Watson, G.W. and E.B. Himelick. 1997. Principles and Practice of Planting Trees and Shrubs. Intl. Soc. Arboricult., Savoy, IL.

30. Witherspoon, W.R. and G.P. Lumis. 1986. Root regeneration of *Tilia cordata* cultivars after transplanting in response to root exposure and soil moisture levels. J. Arboricult. 12:165-168.

31. Wraith, J.M. and C.K. Wright. 1998. Soil water and root growth. HortScience 33:951-959.

32. Wright, A.N. 2002. The physiology of landscape establishment of *Kalmia latifolia*. Ph.D. Diss., North Carolina State Univ., Raleigh.

33. Wright, A.N., S.L. Warren, and F.A. Blazich. 2000. Root growth of two woody ornamentals following transplanting. Proc. SNA Res. Conf., 45th Annu. Rpt. p. 454-457.

Table 1. Visual rating scale used for evaluation of leaf color, canopy fullness, and overall plant quality of ‘Olympic Wedding’ mountain laurel.[z]

Rating	Leaf color	Canopy fullness	Overall quality
1	Yellow	Sparse	25% plant tissue living, substantial death
2	Light green	Some loss	26% to 50% of plant tissue living
3	Dark green	Full	51% to 75% plant tissue living
4	---	---	>75% plant tissue living
5	---	---	No death, vigorous growth

[z]Visual rating scale for leaf color and canopy fullness was 1-3 only.

Table 2. Effect of plant size and exposure on final survival of 'Olympic Wedding' mountain laurel and significance of main effects and interactions for survival.

Plant size	Survival (%)
1-L	21 c[z]
7.5-L	65 b
19-L	100 a
Exposure	
North	78 a[y]
East	83 a
South	72 b
West	56 c
Significance	
Size	***
Exposure	**
Size x exposure	NS

[z]Lowercase letters denote mean separation among plant size by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
[y]Lowercase letters denote mean separation among exposures by PDIFF at $P<0.05$.
NS,**, *** Nonsignificant or significant at $P<0.01$ or 0.001, respectively.

Table 3. Effect of plant size and exposure on final visual ratings of ‘Olympic Wedding’ mountain laurel and significance of main effects and interactions for visual ratings.

Plant size	Leaf color	Canopy fullness	Overall quality
1-L	1.5 b[z]	1.5 b	2.0 b
7.5-L	2.2 a	2.1 a	3.5 a
19-L	2.3 a	1.8 b	2.6 b
Exposure			
North	2.9 a[y]	2.4 a	4.0 a
East	2.2 b	2.2 a	3.4 a
South	1.4 c	1.4 b	1.8 b
West	1.5 c	1.2 b	1.8 b
Significance			
Size	*	**	**
Exposure	***	**	**
Size x exposure	NS	NS	NS

[z]Lowercase letters denote mean separation among plant sizes by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
[y]Lowercase letters denote mean separation among exposures by PDIFF at $P<0.05$.
NS,*, **, *** Nonsignificant or significant at $P<0.05$, 0.01, or 0.001, respectively.

Table 4. Effect of plant size and exposure on growth index, effect of plant size and date on growth index, and significance of main effects and interactions for growth index.[z]

	Growth index [y]		
	Plant size		
Exposure	1-L	7.5-L	19-L
North	30 a[x]	62 a	113 bc
East	28 a	61 a	121 a
South	25 a	51 b	111 c
West	34 a	46 b	118 ab
Date			
May 1999	16 c[w]	43 d	109 b
Feb. 2000	28 b	51 c	123 a
Jan. 2001	37 a	61 b	118 ab
Nov. 2001	35 a	65 a	114 b
Significance[v]			
Size		***	
Exposure		**	
Date		***	
Size x exposure		**	
Size x date		***	

[z]Plants were planted May 1999.
[y]Growth index = {plant height + [(maximum plant width + perpendicular width)/2]}.

Table 4. (continued)

[x]Lowercase letters denote mean separation among exposures within plant size by PDIFF at *P*<0.05 (SAS Institute, Inc., 1988).
[w]Lowercase letters denote mean separation among dates within plant size by PDIFF at *P*<0.05.
[v]Interactions not shown were nonsignificant at *P*<0.05.
, * Significant at P<0.01 or 0.001, respectively.

Table 5. Soil water potential measured adjacent to different size 'Olympic Wedding' mountain laurel and on four exposures.

	Soil Water Potential (-cbar)		
Size	Mean	Minimum	Maximum
1-L	5.5 ± 0.4^{z} a^{y}	0	28
7.5-L	8.8 ± 0.5 b	0	50
19-L	8.7 ± 0.5 b	0	33
Exposure			
North	6.6 ± 0.5^{x} a^{v}	0	28
East	7.1 ± 0.5 a	0	30
South	8.7 ± 0.6 a	0	33
West	8.3 ± 0.6 a	0	50
Significance			
Size	*		
Exposure	NS		
Size x exposure	NS		

^{z}Values represent the mean of 272 observations ± standard error.
^{y}Lowercase letters denote mean separation among plant size by LSD at P<0.05 (SAS Institute, Inc., 1988).
^{x}Values represent the mean of 204 observations ± standard error.
^{v}Lowercase letters denote mean separation among exposures by LSD at P<0.05.
NS, * Nonsignificant or significant at P<0.05

Table 6. Effect and significance of exposure on final leaf area, shoot dry weight, and leaf area : shoot dry weight of 'Olympic Wedding' mountain laurel.

Exposure	Leaf area (cm^2)	Shoot dry weight (g)	Leaf area : shoot dry weight [z]
North	1754 ab [x]	180 ab	0.25 b
East	2258 a	183 a	0.35 a
South	837 b	127 b	0.20 b
West	657 b	108 b	0.18 b
Significance			
Exposure	*	*	***

[z]Leaf area : shoot dry weight = leaf area ÷ shoot dry weight.
[x]Lowercase letters denote mean separation among exposures by PDIFF at $P<0.05$ (SAS Institute, Inc., 1988).
*, *** Significant at $P<0.05$ or 0.001, respectively.

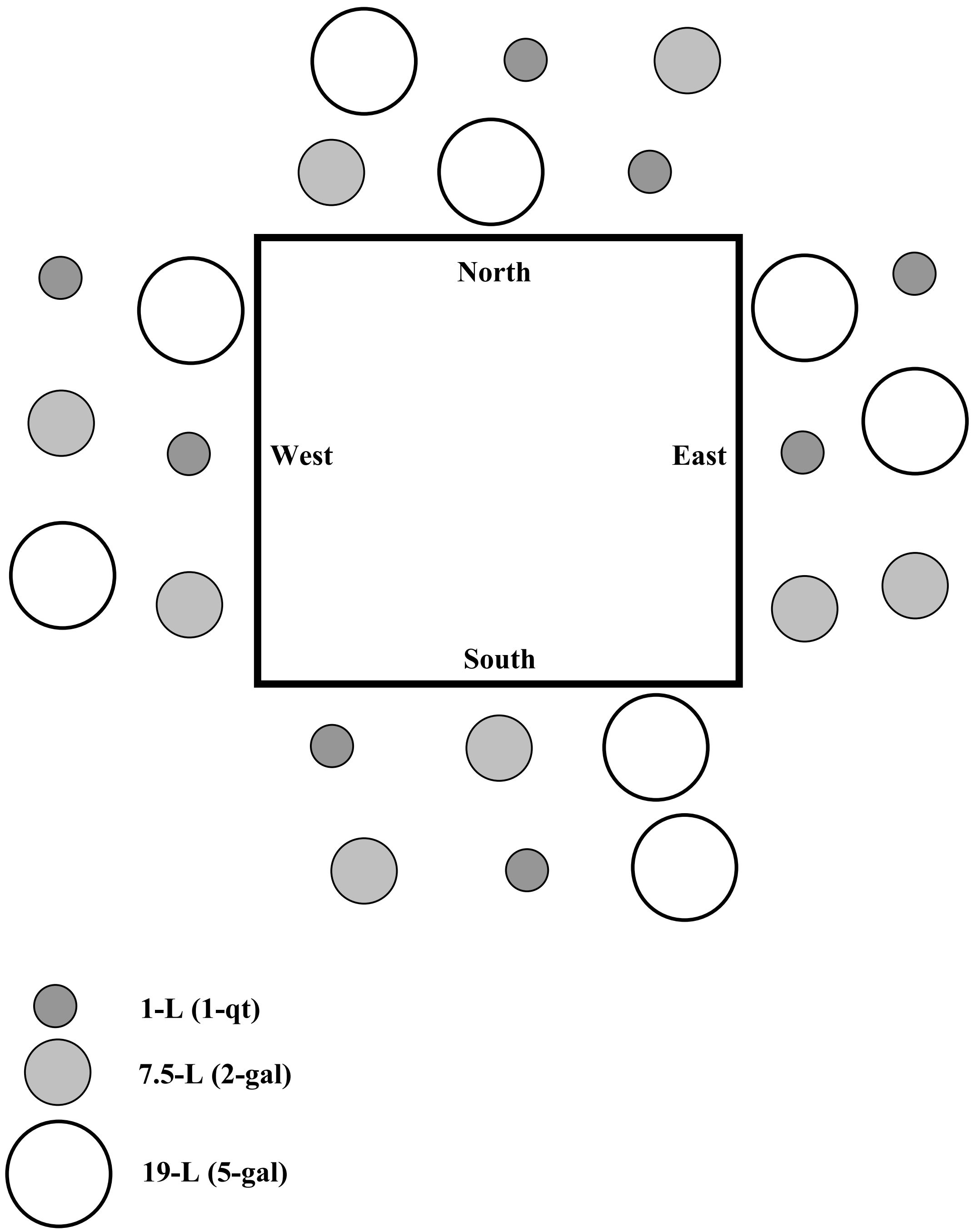

Fig. 1. Schematic of sample block showing two rows of plants per exposure and one plant of each size randomly arranged within each row.

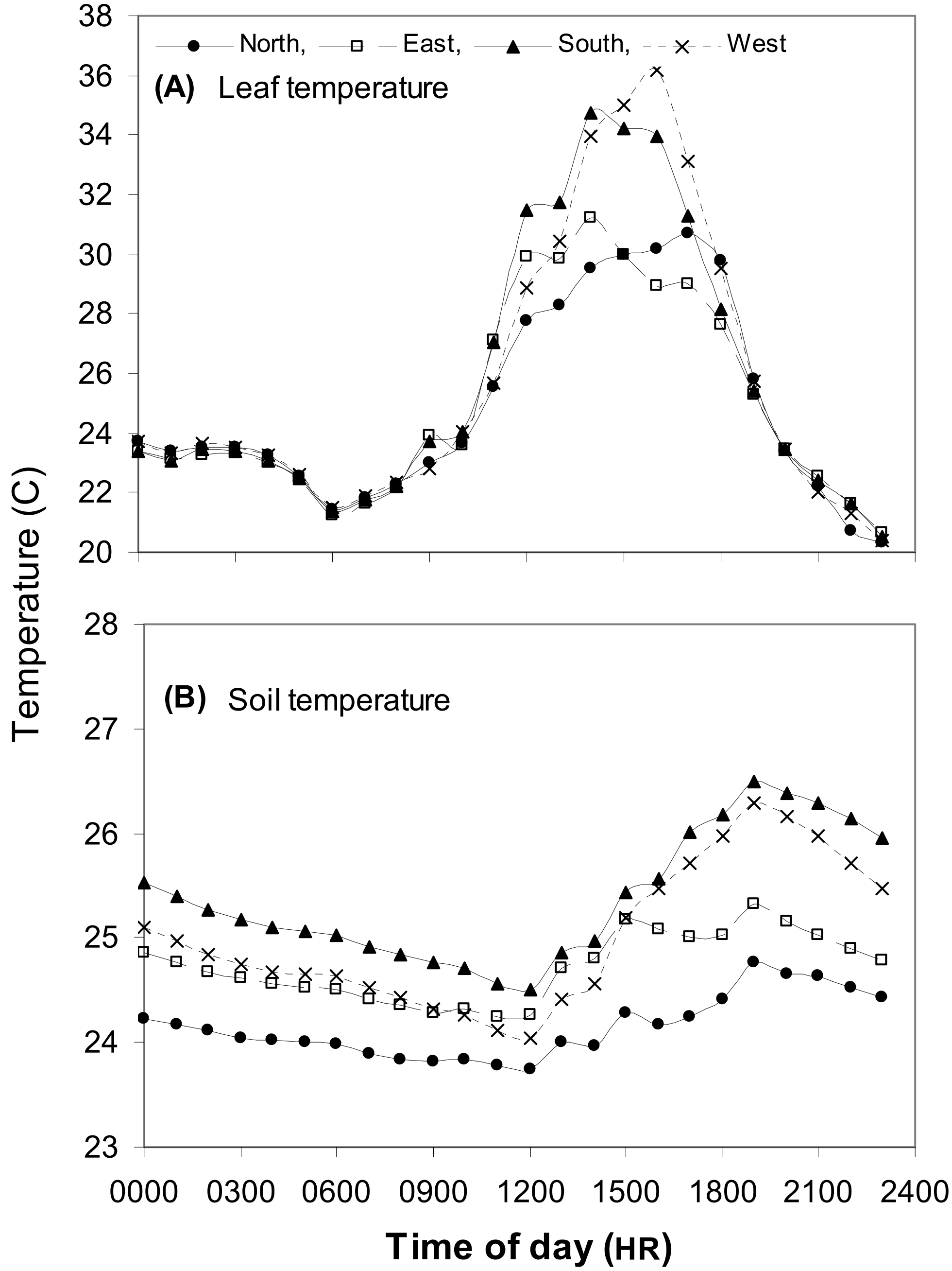

Fig. 2. Average hourly (A) leaf and (B) soil temperatures for Aug. 29, 2000. Symbols in (A) and (B) represent means of nine and three observations, respectively.