Supraoptimal Root-zone Temperature Influences the Medium Solution and Growth of 'Helleri' Holly

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Abstract. Rooted cuttings of *Ilex crenata* Thunb. 'Helleri' were grown for 12 weeks in pine bark with two root-zone temperature treatments (unheated or heated to 40C for 6 hours-day⁻¹), two rates of limestone addition (0 or 6 kg-m⁻³), and three weekly N application rates (200, 400, or 600 mg-liter⁻¹ as urea ammonium nitrate) in a factorial combination. Decreases in shoot and root dry weights due to root-zone heating (69% and 75%, respectively) or limestone addition (41% and 42%, respectively) were not influenced by N application rate. Effects of root-zone heating on medium solution characteristics, which differed in response to limestone addition, were similar for all N application levels. In unlimed pine bark at 400 mg N/liter, the pH and the NH₄-N : NO₃-N ratio were higher in the heated medium (5.5 and 1.15, respectively) than in the unheated medium (3.9 and 0.64, respectively) after 80 days, suggesting that 6 hours of daily exposure to 40C inhibited nitrification. The higher medium solution pH due to root-zone heating resulted in lower medium solution and shoot tissue Mn concentrations.

The growth and nutrient composition of woody plants (Chrusic and Wright, 1983; Niemiera and Wright, 1986a; Walden and Epelman, 1988), as with plants in general (Barker and Mill, 1980), can be significantly influenced by the ionic form of N in the medium solution. When ammoniacal N is applied to a pine bark medium, the predominant form of N in the medium solution is largely determined by the nitrification rate (Niemiera and Wright, 1987b). Nitrification is the biological conversion of NH₄⁺ to NO₃⁻ and as such is influenced by several environmental factors, including medium temperature and pH (Alexander, 1977).

Medium temperatures in containers exposed to direct solar radiation can exceed 40C for ≤6 h-day⁻¹ in southern U.S. nurseries (Ingram, 1981; Martin and Ingram, 1992). In a pine bark medium supplied with NH₄-N and subjected to constant treatment temperature, having the medium at 40C inhibited nitrifica-

tion, resulting in a higher NH₄-N concentration in the medium solution at 40C than at 20 or 30C (Niemiera and Wright, 1987a). Southern U.S. nurseries often produce container-grown plants in pine bark media using fertilizers with an N source that is predominantly NH₄-N. During the summer months, heat-induced inhibition of nitrification may increase the NH₄-N : NO₃-N ratio in the medium solution of nursery containers, thereby influencing plant growth and nutrition.

Chemical inhibition of nitrification in a pine bark medium amended with nitrapyrin lowered the level of Mn in several species of woody plants (Niemiera and Wright, 1986a). Other researchers have found similar effects

on the Mn concentration in plants grown with fertilizer regimes high in NH₄-N (Edwards and Horton, 1982; Elamin and Wilcox, 1986). Reduced Mn concentrations were found in chlorotic tissue of apparently heat-stressed plants in Virginia nurseries (Walden et al., 1989), especially when urea ammonium nitrate was the principle N source. Heat-induced inhibition of nitrification may be a factor contributing to this chlorosis. In addition to medium temperature, rates of limestone addition and N application have influenced nitrification in a pine bark medium (Niemiera and Wright, 1986b, 1987b).

Our objective was to determine the effect of supraoptimal root-zone temperature (RZT) on the medium solution, growth, and nutrient composition of *Ilex crenata* grown in a pine bark medium. To achieve this objective, plants were grown in heated or unheated media at two levels of limestone addition and three N application levels from a predominantly ammoniacal N source.

Materials and Methods

Plant material and medium preparation. A milled pine bark medium was amended with 0 or 6 kg dolomitic limestone/m³ and placed in 3.8-liter polyethylene containers. To stimulate nitrification, the containers were irrigated biweekly with a solution containing (in mg-liter⁻¹) 100 N as (NH₄)₂SO₄, 20 P as KH₂PO₄, and 50 K as KH₂PO₄ and KCl. After 10 weeks, 10-cm rooted cuttings of 'Helleri' holly were transplanted on 1 Feb. into 1-liter containers filled with either the unamended or limestone-amended pine bark and placed in a glasshouse with a 26C day/16C night cycle. Incandescent light interrupted the dark period from 2300 to 0200 HR each day throughout the experiment. For 3 weeks before treatment initiation, plants were irrigated three times weekly with 200 ml of nutrient solution with 5 mg Fe/liter as FeEDTA and micronutrients added according to Hoagland and Arnon (1950).

RZT modification chambers. Eight RZT modification chambers, heated or unheated, were constructed from aluminum-faced foam insulation board. Air in the heated chambers

Table 1. Analysis of variance for the effects of root-zone temperature (RZT) treatment, limestone addition (LA), and weekly N application rate (NAR) on 'Helleri' holly dry weight (in grams) after 84 days and medium solution pH and Mn concentration (in milligrams per liter) after 80 days.

Source	df	Mean squares			
		Shoot dry wt	Root dry wt	pH	Mn concn
Replication (R)	3	4.74	0.10	1.52	0.15
RZT	1	131.45***	3.53**	12.81***	1.27**
Error A (RZT × R)	3	0.82	0.04	0.06	0.01
LA	1	35.19***	0.65***	17.52***	0.23**
RZT × LA	1	12.03***	0.20***	2.80***	0.70***
NAR	2				
Linear (L)	1	0.04	0.09**	3.38***	0.55***
Quadratic (Q)	1	0.21	0.02	0.04	0.00
RZT × NAR _L	1	0.04	0.01	0.40*	0.04
RZT × NAR _Q	1	0.02	0.00	0.03	0.01
LA × NAR _L	1	0.14	0.05	2.53***	0.15*
LA × NAR _Q	1	0.11	0.00	0.05	0.07
RZT × LA × NAR	2	0.56	0.01	0.08	0.02
Error B	30	0.34	0.01	0.08	0.03

***, ***, Significant F test at $P \leq 0.05$, 0.01, or 0.001, respectively.

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was warmed by thermostatically activated heat mats and distributed by a small fan. One-liter polyethylene containers filled with pine bark were suspended from openings in the top of each chamber. The surface of the medium in each container was covered with a white disk of closed-cell, polyethylene-foam, insulating material to reduce vertical temperature gradients in the container. The top of each chamber was painted white to lower the intensity of light reflected from the aluminum surface that could increase leaf temperatures.

The diurnal cycle of container medium temperatures in a heated chamber was determined over 5 days in a glasshouse. These temperatures were monitored with a copper-constantan thermocouple thermometer (Wescor, Logan, Utah). Thermocouples were placed in the container medium 2.5 cm from the container sidewall at three depths from the top of the container: surface (2.5 cm), middle (5.7 cm), and bottom (8.8 cm). Temperatures were recorded hourly from the start of a heating cycle at 0600 HR until 2000 HR each day. Heat mats were deactivated each day at 1600 HR. The medium moisture content was at container capacity at the start of each heating cycle.

Over 4 h, temperatures in the container medium gradually increased from the ambient glasshouse temperature to $40.6 \pm 0.4^\circ\text{C}$ ($\pm\text{SE}$) (middle) and remained there ≈ 6 h each day. There was a vertical temperature gradient from $41.3 \pm 0.6^\circ\text{C}$ (bottom) to $39.8 \pm 0.6^\circ\text{C}$ (surface). This same diurnal heating cycle was used during the experiment.

Experimental procedures. RZT treatments were initiated on 21 Feb. after we had harvested 12 plants to determine initial shoot and root dry weights. Nine containers with plants at each limestone amendment rate were suspended in each RZT modification chamber in a glasshouse. The insulating disk covering the surface of each container was slit through the center to accommodate the plant stem.

During the experiment, medium temperatures of three containers per heated chamber were monitored at 2-h intervals, beginning at 0800 HR, until heating units were deactivated each day. Medium temperatures in unheated chambers were monitored on selected days. Thermocouples were placed in the container medium 2.5 cm from the container sidewall at a depth of 5.7 cm from the top of the container. For unheated chambers, medium temperatures remained below ambient temperature until ≈ 1500 HR on most days and never exceeded ambient temperature. The glasshouse varied from a night minimum of 16°C to a day maximum of 35°C .

The initial N treatment application coincided with the start of RZT treatments. Containers were irrigated weekly with 200 ml of nutrient solution containing 200, 400, or 600 mg N/liter as urea ammonium nitrate. Other nutrients in the solutions were as previously described. The tap water used for the nutrient solutions supplied 20 and 5 mg of Ca and Mg/liter, respectively. All containers were irrigated with 200 ml of tap water once or twice between weekly N treatment applications,

Fig. 1. Influence of root-zone temperature and limestone addition on dry weight of *Ilex crenata*. Values are averaged over three N application rates. "T" represents the least significant difference (LSD) bar at $P \leq 0.05$ for comparison between root-zone temperature treatments when the limestone addition rate is fixed. "L" represents the LSD bar at $P \leq 0.05$ for comparison between limestone addition rates when the root-zone temperature treatment is fixed. Initial shoot and root dry weights were 0.86 and 0.12 g, respectively.

Fig. 2. Influence of root-zone temperature, limestone addition, and N application rate of (○) 200, (●) 400, or (▲) 600 mg·liter⁻¹ on medium solution pH. Vertical bars represent the SE of the mean ($n = 4$). Missing bars are smaller than symbols.

depending on plant need. All irrigations were applied at 1600 HR.

Treatments were arranged in randomized complete blocks with a split-plot design. The two RZT treatments comprised the main plots. A factorial combination of the two limestone addition rates and three N application rates (NAR) comprised the subplots. There were three plants per subplot in each of four blocks.

Medium solution extracts were obtained after the initial fertilizer treatment application and every 2 weeks thereafter. Medium solutions were extracted by the pour-through procedure (Wright, 1986) 16 h after the fertilizer solutions had been applied. Distilled water (75 ml) was applied to the surface of the medium, and the resulting leachate was collected. One container per treatment per block was sampled. The pH of the medium solution extracts was determined before freezing the solutions for later analysis. Medium solution concentrations of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were determined for all extraction dates using specific ion electrodes. Extracts taken on day 40 and day 80 were analyzed for P by the ammonium molybdate–ascorbic acid colorimetric method (Donohue, 1983) and for K, Ca, Mg, Zn, Fe, Mn, and Cu by atomic absorption spectroscopy.

After 12 weeks, plants were harvested to determine shoot and root dry weights. Shoot tissue was analyzed for N using a micro-Kjeldahl technique (Peterson and Chesters, 1964) and after dry-ashing for P, K, Ca, Mg, Zn, Fe, Mn, and Cu as previously described.

Statistical analysis. Data were subjected to an analysis of variance using SAS's general linear model procedure (SAS Institute, 1985). Regression analysis conducted to test for significant linear and quadratic effects of NAR and interactions of NAR with RZT and limestone addition were based on single-degree-of-freedom orthogonal comparisons.

Results and Discussion

Plant growth. Final shoot and root dry weights were decreased by root-zone heating and adding limestone (Table 1 and Fig. 1). The RZT $\times$ limestone addition interaction was due to the smaller growth reductions induced by root-zone heating when growth also was reduced by limestone addition. For example, the decrease in shoot dry weight due to root-zone heating was greater for the unlimed medium (4.3 g) than for the limed medium (2.3 g).

Reduced growth of *I. crenata* in limed media is consistent with the findings of Chrusic and Wright (1983), who attributed this effect to a lower medium solution $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio resulting from higher nitrification rates at higher medium pH. Several other woody plant species have demonstrated a positive response to $\text{NH}_4\text{-N}$ nutrition (Cain, 1952; Colgrove and Roberts, 1956; Greidanus et al., 1972). Reduced growth in the heated medium was likely the result of indirect heat injury because the diurnal medium thermoperiod we used was not sufficient for direct injury to root cell membranes of Japanese holly (Ingram, 1986). Shoot and root growth of several woody plant species has been decreased by exposing roots

for 6 h-day⁻¹ to 40°C compared to growth at lower root temperature (Harrison et al., 1988; Ingram et al., 1986; Johnson and Ingram, 1984; Yeager et al., 1991).

Final shoot dry weight was not influenced by NAR (Table 1). Averaged over RZT and limestone addition rate, final root dry weight decreased from 0.52 to 0.41 g as NAR increased from 200 to 600 mg N/liter. There were no significant NAR $\times$ RZT interactions on plant growth. This result concurs with that of Yeager et al. (1991) who found that increased N application rates did not alleviate growth reductions due to supraoptimal RZT for *I. crenata* 'Rotundifolia'.

Medium solution characteristics. In the unlimed medium, pH increased from 4.5 on the initial extraction date to a maximum pH on day 40 for both RZT treatments (Fig. 2). This increase in pH was greater at higher NAR. In the limed medium, there was no increase from an initial pH of 6.9 and little difference in pH due to NAR during the first 40 days for both RZT treatments. Medium solution pH gradually declined thereafter but remained higher in the heated medium regardless of limestone addition. The pH decline in the limed medium was greater at higher NAR. By day 80, a RZT $\times$ limestone addition interaction affected medium solution pH (Table 1 and Fig. 2). At each

Fig. 3. Influence of root-zone temperature treatment and limestone addition on medium solution concentration of (●, ○) $\text{NH}_4\text{-N}$ and (▲, △) $\text{NO}_3\text{-N}$ at N application rate of 400 mg-liter⁻¹. Open symbols = -limestone; solid symbols = +limestone. Vertical bars represent the SE of the mean (n = 4). Missing bars are smaller than symbols.

NAR, the increase in medium solution pH due to heating was greater in the unlimed medium than in the limed medium.

The influence of RZT and limestone addition on medium solution concentrations of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ was similar over all N application levels; thus, we show data for only $400 \text{ mg}\cdot\text{liter}^{-1}$ (Fig. 3). Limestone addition lowered the medium solution $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio for both RZTs. After day 40, the $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio was higher for the heated-unlimed treatment than for the unheated-unlimed treatment. This difference was due to higher $\text{NO}_3\text{-N}$ levels for the unheated-unlimed treatment and higher $\text{NH}_4\text{-N}$ than $\text{NO}_3\text{-N}$ levels for the heated-unlimed treatment.

The influence of RZT on the characteristics of the medium solution, especially medium solution pH, results from its dynamic interaction with other factors known to influence medium solution characteristics, such as N source, nitrification rate, plant growth, and N absorption. The nature of these interactions is best illustrated by focusing on pH changes over time in the unlimed medium (Fig. 2).

Urea ammonium nitrate, the N source used in this experiment, provides 50% of its N as urea. Urea applied to a cropped medium containing pine bark can be completely hydrolyzed within 24 h (Elliot, 1986). In acid soils, the resulting ammonium increases pH (Alexander, 1977). The initial increase in the pH of the unlimed medium was likely due to application of urea and its subsequent hydrolysis. Consistent with this hypothesis, the maximum pH attained in the unlimed medium increased as NAR increased (Fig. 2).

The initial pH of 4.5 in the unlimed medium would severely limit nitrification in pine bark (Niemiera and Wright, 1986b). However, by day 12, following urea application, the pH had increased to levels favorable for nitrifier development. Niemiera and Wright (1986b) first detected nitrification 41 days after amending pine bark with limestone. The decrease in medium solution pH after 40 days can be attributed to the acidifying effects of nitrification (oxidation of NH_4^+ to NO_3^-) and plant absorption of $\text{NH}_4\text{-N}$. Niemiera et al. (unpublished data) found that 'Helleri' holly absorbs $\text{NH}_4\text{-N}$ in preference to $\text{NO}_3\text{-N}$ at an approximate 3:1 ratio from a nutrient solution of NH_4NO_3 . Ammonium absorption tends to decrease medium solution pH (Kirkby and Mengel, 1967).

The decrease in pH was greater in the unheated-unlimed medium than in the heated-unlimed medium (Fig. 2). This difference is due in part to differences in plant growth. The larger plants that resulted from the unheated-unlimed treatment would absorb more $\text{NH}_4\text{-N}$ from the medium solution than the smaller plants that resulted from the heated-unlimed treatment (Fig. 1).

Differences in medium solution pH between these treatments also may be attributed to less nitrification at supraoptimal medium temperature. Nitrification rates have declined in mineral soil at temperatures above the optimum of 26°C (Beck, 1983). As medium solution pH decreased in the unheated-unlimed

medium (Fig. 2), there was a concomitant increase in the concentration of medium solution $\text{NO}_3\text{-N}$ after 40 days (Fig. 3), an indication that nitrification was proceeding. There were only slight increases in $\text{NO}_3\text{-N}$ in the medium solution extracted from the heated-unlimed medium during this period. Less nitrification took place in the heated-unlimed medium, resulting in a higher medium solution $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio compared to that in the unheated-unlimed medium (Fig. 3).

These results indicate that exposing the container medium to 40°C or higher daily, for durations such as those commonly observed in midsummer in nurseries of the southern United States, can decrease nitrification rates in a pine bark medium, thereby altering the $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio in the medium solution. When the fertilizer N source applied to containers consists of predominantly $\text{NH}_4\text{-N}$ under such conditions, the higher medium solution $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio that ensues may reduce the growth of species with a positive response to $\text{NO}_3\text{-N}$. Additionally, plants that assimilate $\text{NH}_4\text{-N}$ efficiently at moderate RZT may do so less efficiently at high RZT due to the lower carbohydrate content of roots grown at high temperature, resulting in ammonium toxicity (Ganmore-Neumann and Kafkafi, 1983).

In the limed medium, the initial hydrolysis

of urea did not increase the pH of the medium solution. The gradual decrease in medium solution pH after 12 days (Fig. 2) can be attributed to nitrification. The decline in medium solution pH was more rapid at the higher N application rates, reflecting increased nitrification due to greater availability of substrate N (Niemiera and Wright, 1987b). The higher pH by day 80 in the heated-limed medium (Fig. 2) compared to that in the unheated-limed medium at highest NAR suggests that nitrification may have been limited by high medium temperature at the highest substrate N level. However, medium solution $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratios at NAR of 600 ppm in the limed medium were similar, regardless of RZT treatment (data not shown).

When limestone was added to the medium, RZT had no appreciable effect on nitrification, as shown by the medium solution $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratios for heated and unheated media (Fig. 3). Growth and metabolism of a nitrifying population are pH-dependent (Sarithchandra, 1978). Adding limestone raised the initial pH of the pine bark medium from 4.5 to 6.9 (Fig. 2). In soils, nitrification rates increase from a minimum at pH 4 to 4.5 (Broadbent et al., 1957; Webber and Gainey, 1962) to a maximum at pH 7 to 8 (Focht and Verstraete, 1977). The limed medium likely

Fig. 4. Relationship between medium solution pH and medium solution Mn concentration on day 80. Symbols: (○) unheated-unlimed, (Δ) unheated-limed, (●) heated-unlimed, (▲) heated-limed. $y = 4.04 - 1.20x + 0.09x^2$, $R^2 = 0.76$.

had a higher nitrifier population throughout the experiment because the medium was at a pH favorable for nitrification for a longer period than the unlimed medium. Nitrification in the heated-limed medium may have been sufficient during daily periods of lower, more optimal, temperature to oxidize amounts of applied $\text{NH}_4\text{-N}$ that were equivalent to that oxidized in the unheated-limed medium during the 7 days between $\text{NH}_4\text{-N}$ applications. Evidently, substrate N did not exceed the oxidative capacity of the nitrifiers over this period in the limed medium for either RZT treatment.

In this experiment, heating the container medium to 40°C for 6 h·day⁻¹ proved sufficient to increase the medium solution $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio by decreasing nitrification in the unlimed medium. The $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio in the limed medium was lower than that in the unlimed medium, regardless of RZT treatment. That is, adding limestone to a pine bark medium promoted nitrification, even at supraoptimal medium temperature. Thus, adding sufficient limestone to encourage nitrification under conditions of high RZT may be an important cultural practice in nurseries in hot climates, where container medium temperatures are >40°C during the production of plants that prefer low $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratios.

Apart from $\text{NH}_4\text{-N}$ or $\text{NO}_3\text{-N}$, RZT had no influence on the concentrations of any nutrients in the medium solution extracted on day 40 and only minor influences (data not shown) on all but the Mn concentration on day 80. RZT influenced the medium solution Mn concentration primarily through its effect on medium solution pH. Generally, the solubility of micronutrient cations is decreased by increasing medium pH (Tisdale et al., 1985). Accordingly, medium solution pH and medium solution Mn concentration were highly correlated on day 80 (Fig. 4). Manganese concentration decreased as the medium solution pH increased. Like medium solution pH, medium solution Mn concentration was influenced by a RZT × limestone addition interaction (Table 1). For the unlimed medium, Mn concentrations were generally lower when the medium was heated than when it was unheated (Fig. 4). RZT treatment, however, had little influence on Mn concentrations in the limed medium.

Tissue nutrient content. Results of tissue analysis are presented for Mn only because the effects of RZT or interactions of RZT and NAR or limestone addition on other tissue nutrient concentrations were minor. A linear effect of NAR on shoot tissue Mn concentration differed between heated and unheated media ($P \leq 0.001$). Final shoot tissue Mn concentration doubled from the lowest to the highest NAR at moderate RZT but did not vary as NAR increased at high RZT (Fig. 5). As previously discussed, the influence of RZT and NAR on medium solution pH by day 80 (Fig. 2) and the subsequent influence of pH on the Mn concentration in the medium solution (Fig. 4) could account for much of the interaction of RZT and NAR on Mn levels in the plant. Final shoot tissue Mn concentration was highly correlated with medium solution Mn concentration on day 80 ($r = 0.78$).

These results suggest that when N is supplied as urea, medium temperature can influence plant absorption of Mn through its direct effect on nitrification and subsequent effect on medium solution pH. The increase in pH due to urea hydrolysis or limestone addition was counteracted to a lesser extent in the heated medium by the acidity generated by nitrification or plant $\text{NH}_4\text{-N}$ absorption than were corresponding pH increases in the unheated medium. Higher medium pH resulted in lower medium solution Mn concentrations and subsequently lower tissue Mn levels when the medium was heated. These effects could account for the lower Mn levels frequently observed in the tissue of container-grown nursery plants that are apparently heat-stressed and fertilized with N sources that contain significant amounts of urea-N. Additionally, higher $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratios in a container medium where high RZT has decreased nitrification may reduce plant Mn absorption further because Mn content in plant tissue has decreased as the $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$ ratio increases in nutrient solution (Edwards and Horton, 1982; Elamin and Wilcox, 1986). Using fertilizers with an N source containing no urea and ≤50% $\text{NH}_4\text{-N}$ for production of container-grown woody plants in nurseries in

hot climates may reduce the incidence of chlorosis due to Mn deficiency or ammonium toxicity induced by high RZT.

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Fig. 5. Shoot tissue Mn concentration as influenced by root-zone temperature treatment and N application rate. Values are averaged over limestone addition rates. Regression equations: unheated: $y = 136 + 0.76x$, $r^2 = 0.99$; heated: $y = 299 + 0.04x$, $r^2 = 0.54$. SE for within and between root-zone temperature comparisons are 52 and 60 mg·kg⁻¹, respectively.

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