INFLUENCES OF SUPRAOPTIMAL ROOT-ZONE TEMPERATURE ON THE MEDIUM SOLUTION AND GROWTH OF WOODY NURSERY CROPS

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(ABSTRACT)

The effects of high medium temperatures on the growth and mineral nutrition of selected woody plants and on the composition of the medium solution were studied.

Medium temperature profiles were established for 3.8-liter black polyethylene containers exposed to solar radiation under Virginia nursery conditions. On clear days in mid-summer, maximum recorded medium temperatures on the southwest side of containers were as high as 45°C and could exceed 40°C for 4 to 5 hours. The high medium temperatures in exposed containers reduced the shoot relative growth rate and the specific rate of nitrogen uptake for *Ilex crenata* 'Convexa' in comparison to that of plants grown in containers insulated from solar radiation. Shoot dry weights of *I. crenata* 'Helleri', *Juniperus chinensis, Buxus microphylla,* and *Nandina domestica* were at least 20% lower in exposed containers than in insulated containers.

In a pine bark medium, growth response of *I. crenata, J. horizontalis*, or *N. domestica* to increased N application rate was similar when root-zones were at 40°C for 6 hrs/day or more optimal growth temperature. In unlimed pine bark, root-zone temperature of 40°C for 6 hrs/day resulted in higher medium solution pH and NH_4-N:NO_3-N ratio than at lower temperature. Limestone addition to the medium negated these effects and alleviated growth reductions due to high root-zone temperature for *N.*

domestica and *J. horizontalis*. The higher medium solution pH associated with heated root-zones resulted in lower medium solution and shoot tissue Mn concentrations for *I. crenata*.

A limed pine bark medium periodically fertilized with ammonium N was heated to temperatures of 28°, 34°, 40°, 46°, or 52°C for daily exposure duration of 1, 2, 4, 6, or 24 hours for 20 days. Treatment temperature of at least 40°C with a daily exposure duration of 24 hours resulted in an increase in medium solution NH_4-N concentration. Similar increase in NH_4-N was found for 2 hr/day exposure to 46°C, with further increases in NH_4-N at longer exposure times. The maximum level of NH_4-N occurred after 1 hr/day exposure to 52°C or 24 hr/day exposure to 46°C. Decreases in medium solution NO_3-N concentration generally coincided with the increases in NH_4-N. Results indicate that high container temperature may increase the ratio of NH_4-N:NO_3-N in the medium solution of plants fertilized with predominately ammoniacal N.

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CHAPTER I

INTRODUCTION

A large percentage of the plants produced in Virginia nurseries are grown in containers rather than in the field, utilizing pine bark as the major component of the growth medium. This intensive method of production results in more efficient land use, greater ease in handling, and greater control over production variables such as irrigation and fertilization. However, without the heat buffering capacity of a large soil mass, nursery container medium temperatures can exceed ambient temperature when container sidewalls are exposed to direct solar radiation (Fretz, 1971).

In Southern nurseries, container medium temperatures in excess of 40°C have been recorded for up to 6 hours a day in mid-summer (Ingram, 1981). Repeated exposure to root-zone temperatures as high as 40°C reduces the growth of woody nursery crops (Harrison et al., 1988; Johnson and Ingram, 1984; Yeager et al., 1991). In pine bark media, a constant medium temperature of 40°C dramatically inhibits nitrification compared to that at 20° or 30°C (Niemiera and Wright, 1987a). Nitrification is the biological process whereby ammonium nitrogen (NH_4-N) is converted to nitrate nitrogen (NO_3-N).

It is not known whether medium temperatures in nursery containers in Southern nurseries exceed 40°C for sufficient periods during mid-summer to inhibit nitrification. Many nurserymen use fertilizers high in NH_4-N or urea and unless nitrification occurs

NH_4-N will remain high in the medium solution. In Virginia, reduced growth, shoot chlorosis, and root injury of certain species of container-grown nursery crops often occurs during the hottest summer months of July and August, and in many instances renders these plants unsalable, resulting in considerable financial loss to the nurseryman.

Nursery Observations

In regard to this problem, the following observations were made in Virginia nurseries which seemed to implicate heat induced ammonia toxicity as a factor contributing to summer growth reductions.

Mid-summer injury of container-grown plants often became evident in the second growing season, not the first. First year plants are normally grown in a container-to-container arrangement, minimizing solar exposure of the container sidewall. Wider spacing of containers in the second year of production exposes containers to direct heating by the sun, potentially raising container medium temperatures to levels which are supraoptimal for both growth and nitrification. Shading from weeds growing next to containers, which would lower container temperature, often prevented chlorosis.

In exposed containers, species like Ilex often grew well adjacent to plants of Juniperus which were chlorotic, even though Ilex is considered to be more heat sensitive than Juniperus (Ingram and Buchanan, 1981). *Ilex* is known to prefer NH_4-N nutrition while *Juniperus* is thought to prefer lower medium solution ratios of NH_4-N:NO_3-N (Chrustic and Wright, 1983; Wright and Hinesly, 1991). Heat induced inhibition of

nitrification would favor growth of *Ilex* because NH_4-N would be the dominant N form in the container.

Heavy applications of dolomitic limestone sometimes helped to prevent or correct the chlorosis. Nitrification in pine bark media increases as pH increases with limestone addition (Niemiera and Wright, 1986b). Higher growth medium pH may encourage nitrification even during the hotter months of summer. Furthermore, some plant species susceptable to NH_4-N toxicity grow normally under NH_4-N nutrition, provided the pH of the growth medium is sufficiently high (Maynard and Barker, 1969; Walden and Epelman, 1988).

Foliar levels of Mn were always lower in chlorotic tissue of apparently heat-stressed plants. Plants grown in pine bark where nitrification was chemically inhibited also contained lower Mn levels in tissue (Niemiera and Wright, 1986a). Other researchers have found similar effects on the Mn concentration in plants grown with fertilizer regimes high in NH_4-N (Edwards and Horton, 1982; Elamin and Wilcox, 1986). If nitrification is inhibited by high medium temperature, higher levels of NH_4^+ would inhibit Mn uptake.

Plants often recovered from mid-summer chlorosis during the fall months. Cooler fall temperatures would increase nitrification rates, lowering the level of NH_4-N in containers. In support of this contention, leachates from containers in Virginia nurseries contained 50 ppm NH_4-N in August compared to 1-2 ppm NH_4-N in the cooler month of September (Walden et al., 1989).

Research Objectives

Based on these observations, research was initiated to examine the potential influence of high summer container medium temperatures on woody plant growth and nitrification in Virginia nurseries. These overall objectives were achieved by implementing studies with the following sub-objectives:

1) to determine the growth and nitrogen uptake response of *Ilex crenata* to high summer container medium temperatures which occur naturally under simulated Virginia nursery conditions (Chapter III);

2) to determine the growth response of four woody plant species to summer container temperature and limestone addition to pine bark media under simulated Virginia nursery conditions (Chapter IV);

3) to examine the influence of supraoptimal medium temperature, N application rate, and limestone amendment on medium solution composition, growth and nutrient content of three woody plant species (Chapter V);

4) determine the medium temperatures and durations of daily exposure to those temperatures which inhibit nitrification in pine bark (Chapter VI).

CHAPTER I

GENERAL LITERATURE REVIEW

Introduction

Temperature is an important environmental variable which influences the growth and development of plants. For each physiological process in the plant, there exists an optimum temperature range above and below which these processes decline (Larcher, 1980). The influence temperature exerts on the plant ranges from the molecular to the whole plant level and includes processes such as enzyme kinetics, solute solubilities, diffusion, osmotic potential, ion hydration, Gibbs free energy, membrane permeability, stomatal activity, respiration, photosynthesis, and transpiration (Voorhees et al., 1981).

Plant temperatures are influenced by net radiation, energy consumption, and heat exchange with the plant's surroundings but generally tend toward those of the immediate environment (Larcher, 1980). Shoot temperatures, therefore, tend toward assuming the temperature of the ambient air, while root temperatures tend toward that of the soil. In natural environments, root temperatures are usually lower and less variable during the growing season than shoot temperatures. As a result, roots are less adaptive to temperature extremes and optimum physiological temperatures for the plant are somewhat lower for roots than for the shoot (Nielsen, 1971). Optimum temperatures for root growth of many plant species are between 20°-30°C (Kramer, 1969)

The outstanding example of high temperature exposure to root systems is that of nursery crops growing in containers exposed to solar radiation. Absorption of solar radiation by container sidewalls and subsequent transfer of kinetic energy to the container medium can result in root-zone temperatures which exceed 40°C for 2 to 6 hours/day and commonly exceed 50°C on the western exposure (Ingram, 1981; Young and Hammet, 1980). Medium temperatures as high as 58°C have been recorded adjacent to the container sidewall (Martin and Ingram, 1988).

High Temperature Stress

At supraoptimal temperatures, plant stress occurs. High temperature stress is defined as the suppression or cessation of metabolic functions in response to high temperature. Levitt (1980) categorizes the injury which results from high temperature stress as either direct or indirect injury.

Direct heat injury. Direct heat injury occurs when plant tissue is exposed to extreme temperature for a brief period, such as heating beyond lethal limits for seconds to minutes, and is characterized by the speed of injury. Levitt (1980) lists protein denaturation and lipid liquification as primary mechanisms of direct heat injury. Plant membranes, which are composed of protein and lipids, are a major site for this type of injury. Daniell et al. (1969) reported disorganization of tonoplast, plasmalemma, and chloroplast membranes in *Glycine max* and *Elodea canadensis* at thermal death points. Soluble nitrogenous compounds which result from protein decomposition may translocate to unheated plant parts, accumulating to toxic concentrations (Larcher, 1980;

Levitt, 1980).

The temperature at which direct injury to roots occurs depends on the duration of exposure to that temperature (Levitt, 1980). Roots of 2 species of pine were killed by 2 hour exposure to 46°C or 5 hour exposure to 44°C (Shirley, 1936). Wong et al. (1971) reported that a 4 hour exposure to 50°C killed the roots of five woody plant species; exposure to 40°-45°C for 4 hours killed root tips.

Ingram (1985, 1986) and Ingram and Buchanan (1981, 1984) used an electrolyte leakage technique (Martineau et al., 1979) to determine critical temperature and exposure times which directly injured the root cell membranes of several woody plant species. The critical temperature, characterized by 50% electrolyte leakage, was reduced as exposure time increased, and increased as exposure time decreased. For example, *Pittosporum tobira* roots were directly injured by 30 minute exposure to 52.2°C or 300 minute exposure to 46.3°C (Ingram, 1985). The critical temperature for direct root cell membrane injury also varied with species. Direct injury occurred after 20 minute exposure to 50.5°, 48.5°, and 46.5°C for *Illicium anisatum, Juniperus chinensis,* and *Ilex cornuta*, respectively (Ingram and Buchanan, 1981).

Indirect heat injury. Indirect heat injury results from longer term exposure to supraoptimal but sublethal temperature. This type of injury is due to reversible metabolic strain (Levitt, 1980). A primary example of indirect heat injury is the gradual starvation of plants at high temperature as a consequence of the typically higher temperature optimum for respiration than for photosynthesis (Levitt, 1980). A net loss

of carbohydrates results when plant tissue temperature exceeds the temperature at which rates of photosynthesis and respiration are equal. Other mechanisms of indirect heat injury include toxicity and biochemical lesions due to disturbance of metabolic processes (Levitt, 1980).

The indirect injury due to supraoptimal root temperatures below a critical killing point has great influence on plant growth and physiology. For a number of woody plant species, shoot growth, root growth or both have been decreased by 6 hour/day exposure of roots to 40°C compared to growth at root-zone temperatures of 34°C or lower (Harrison et al., 1988; Ingram et al., 1986; Johnson and Ingram, 1984; Yeager et al., 1991). These growth effects likely result from several specific physiological responses to supraoptimal root temperatures which have been identified, including decreased rates of photosynthesis and increased rates of root respiration. Growth in terms of dry weight accumulation in the plant is the difference between CO_2 fixation via photosynthesis and the loss of CO_2 via respiration.

Leaf photosynthetic rates of *Pittosporum tobira* plants were lower after 7 months of 6 hour/day exposure of roots to 40°C than for plants at 32° and 27°C (Johnson and Ingram, 1984). Foster et al. (1991) observed decreased shoot carbon exchange rates in *Ilex crenata* in response to root-zone temperatures of 32°C or greater. Reduced photosynthesis was attributed to a non-stomatal inhibition since transpiration rates were unaffected by root temperature. The results of Martin et al. (1989) support this premise. They exposed roots of *Ilex x attenuata* to 28°, 35°, and 42°C for 6 hours/day

for 12 weeks. Leaf carbon exchange rate and stomatal conductance were reduced at 42°C after 4 weeks; however, carbon exchange rate recovery after 12 weeks exposure was much greater than the recovery of stomatal conductance. Reduced rates of photosynthesis for *I. crenata* at root temperature of 38° and 42°C compared to rates at 30° or 34°C were accompanied by reductions in leaf chlorophyll and carotenoid levels (Ruter and Ingram, 1992). Chlorophyll content of apple tree leaves decreased with increasing constant root-zone temperature from 22° to 36°C (Gur et al., 1976a).

Johnson and Ingram (1984) suggested that decreased biosynthesis of hormonal substances, such as cytokinins, may be responsible for decreased photosynthesis at supraoptimal root temperature. Cytokinin activity in roots of *Vitis vinifera* was lower at a root temperature of 30° than at 20°C (Skene and Kerridge, 1967). Supraoptimal root temperatures decreased the cytokinin levels in roots and leaves of apple with a concomitant decrease in leaf chlorophyll content (Gur et al, 1972). Exogenous application of kinetin to leaves of apple plants grown at 40°C root temperature restored leaf chlorophyll levels to those of plants grown at 25°C.

Respiration rates in actively growing plant tissue have been shown to increase as temperature increases up to temperatures as high as 45°C (Janes et al., 1988; Levitt, 1980). The increase in respiration with increasing temperature is particularly due to increased maintenance respiration which fuels energy requiring processes not resulting in dry matter accumulation (Gent and Enoch, 1983). Increasing the root temperature of *Helianthus annus* increased the maintenance portion of root respiration (Szaniawski

and Kielkiewicz, 1982). Root respiration of *I. crenata* increased as root temperature increased from 28° to 40°C after 7 days exposure (Foster et al., 1991). Ruter and Ingram (1991) found that respiration rates of *I. crenata* roots were similar when measured at temperatures from 30° to 42°C for roots grown for 3 weeks at the measurement temperature. For roots grown at 30°C, respiration was maximal at 34°C and decreased to a minimum at 46°C. Increased respiration of current photoassimilates was detected for *I. crenata* roots at 38°C compared to roots at cooler temperatures (Ruter and Ingram, 1990).

The distribution of soluble carbohydrates is responsive to the level of metabolic activity in sink tissue, which is greatly influenced by temperature (Wardlaw, 1968). An increase in sink temperature relative to that of the source can increase the import of assimilate into sink tissue (Harris and Jeffcoat, 1974). Thus, supraoptimal root-zone temperatures may alter the priority of assimilate distribution from shoot to root. That the distribution of carbohydrates between shoots and roots can be altered by supraoptimal root temperatures is evidenced by changes in shoot:root ratios, but the direction of change is species dependent (Ingram, 1981; Ingram et al., 1986; Johnson and Ingram, 1984).

Ruter and Ingram (1990) used a split-root technique to examine the effects of root temperature treatment combinations on photoassimilate partitioning in I. crenata. After 3 weeks exposure, they reported reduced shoot and root weight when root halves were at 34/34°, 38/38°, or 42/42°C for 6 hours daily, compared to growth at 30/30°C.

However, shoot weight and total root weight did not differ significantly when root halves were at 30/34° or 30/38°C compared to growth at 30/30°C. Shoot weight but not total root weight was reduced at 30/42°C. The authors suggest that a portion of the root system at cooler temperature may compensate for growth effects due to roots at supraoptimal temperature.

Supraoptimal root temperatures can influence the water status of plants. Barr and Pellett (1972) reported a trend toward reduced water content with increased root temperature for 7 woody plant species. Root water content increased and leaf water content decreased for apple as root temperature increased from 22° to 36°C (Gur et al., 1976a). Shoot water potential of several woody plant species decreased with increasing root-zone temperature (Graves, et al., 1989, 1991; Newman and Davies, 1988). Water flux through roots of two tree species was less for roots at 34°C than for roots at 24°C (Graves et al., 1991). Transpiration of four woody plant species was reduced as root temperature increased from 25° to 45°C (Newman and Davies, 1988). Leaf diffusive resistance of red maple seedlings grown at a root temperature of 36°C was five times greater than for plants with root zones at 30°C (Graves et al., 1989).

The mineral nutrient content of plants can also be altered in response to supraoptimal root-zone temperature. According to a review by Cooper (1973), the percent nutrient content will generally decrease with increasing root-zone temperature or increase to an optimal level, then decrease. For many woody plant species, percent P, K, Fe, and Zn in leaf tissue has generally been decreased by root temperatures

greater than 32°C, while percent N has increased (Barr and Pellett, 1972; Gur et al., 1976b; Harrison, et al., 1988; Johnson and Ingram, 1984; Young, 1980; Yusof et al., 1969). Yeager et al. (1991), however, reported a linear decrease in N accumulation for *Ilex crenata* as root-zone temperature increased from 28° to 40°C. The percent N in apple leaves was lower at root temperature of 35°C than that at 25°C (Gur et al., 1979). Cumbus and Nye (1985) reported that P inflow per unit root surface was greater at 35°C than at cooler temperatures, enabling plants at higher root temperature to maintain adequate tissue P levels despite lower root growth at high temperature.

Container Temperatures

Although dark colored containers have been shown to have higher root-zone temperatures than light colored containers (Fretz, 1971; Ingram, 1981; Verma, 1979), those made of rigid black polyethylene are preferred by most nurserymen because they are lightweight, durable, and relatively inexpensive. This material contains carbon-black, a substance which deters polymer breakdown due to UV-radiation which causes containers to become increasingly brittle. The use of colors other than black is not economical due to the cost of additional UV-inhibitors. Ingram (1981) reported increased growth and reduced medium temperatures when plants were grown in white polyethylene bags compared to those in conventional black nursery containers; however, the poly bags were too brittle to withstand rough handling after 6 months exposure to sunlight. In containers exposed to direct solar radiation, medium temperature varies within the container (Fretz, 1971; Ingram, 1981; Ingram et al., 1988). Those portions

of the root system within medium quadrants with southern or western exposure generally experience highest temperatures. In rigid, black containers in full sun, the mid-afternoon medium temperature in the western quadrant of the container was 46°C, while that in the eastern quadrant was 37°C (Ingram, 1981). Several reports indicate changes in the distribution of roots within exposed containers in response to medium temperature (Ingram et al., 1988; Martin et al., 1991; Newman, 1985). The biomass of roots exposed to highest temperatures is generally less than that exposed to more optimal temperatures, effectively restricting the viable volume available for root growth (Martin et al., 1991).

Influencing factors. The primary environmental factors influencing container medium temperatures are solar radiation, wind, air temperature, and absolute air humidity. Martin and Ingram (1990, 1991a, 1991b, 1992) developed models which simulated the thermal environment of a polyethylene container-root medium system to determine the relative influence of environmental factors and medium physical properties on container medium temperatures. The principle physical processes that affected temperature patterns in the medium were net radiation and convection. During daylight hours, the primary energy source to the medium was insolation and the primary energy sink from the medium was the surrounding atmosphere. That is, medium temperatures are largely determined by the balance between energy gained from solar radiation and energy lost to the surrounding air.

Container medium composition affects temperature dynamics in the container.

Thermal diffusivity of the container medium is influenced by differing thermal properties of media components (i.e., thermal conductivity, bulk density, specific heat capacity) as well as volumetric moisture content (VMC) (Martin and Ingram, 1991a). In the southern United States, milled pine bark and sand in various proportions make up the bulk of the growth medium used for container production of nursery crops. Adding sand to a pine bark medium reduced temperature gradients and caused higher overall temperatures in the container medium due to increased thermal diffusivity (Ingram and Martin, 1991a). Simulation modeling indicates that at low VMC, maximum medium temperatures in the center of the container were lower in a pine bark medium than in a pine bark medium supplemented with sand, but were similar for each medium at high VMC (Martin and Ingram, 1992). Generally, thermal diffusivity of the medium increases with increased VMC, resulting in media that warms faster, earlier in the day, but cools faster at night.

Container bed surface color can influence container medium temperatures. When containers are placed on lightly colored materials (white plastic, white shells, limestone rock) the resulting albedo increases medium temperatures in dark colored containers (Keever and Cobb, 1984; Newman, 1985; Whitcomb, 1980).

Container volume has an influence on container medium temperature. The maximum temperature in the center of 10, 27, and 57 L containers exposed to direct insolation was 42.3°, 40.8°, and 36.0°C, respectively (Martin et al., 1991). The medium in the largest container attained a maximum temperature later in the day than

the medium in the smaller containers due to the increased thermal capacity of a larger volume of media. This result agrees with predictions from computer simulation of volume effects on container medium temperatures (Martin and Ingram, 1991b).

Martin and Ingram (1991) evaluated the effects of irrigation volume and timing on container medium temperature dynamics. Midday irrigation will effectively lower medium temperatures provided the temperature of the irrigation water is cooler than the medium temperature and a sufficient volume of irrigation is applied. However, the volume of water that was required to physically disperse the thermal energy in the container was considered prohibitive in light of national water conservation efforts. When an inadequate volume of irrigation is applied, temperatures in the lower portions of the container can actually be increased by thermal energy flushed from the hotter medium surface (Martin and Ingram, 1991a).

The most effective means of lowering container medium temperatures involve strategies which minimize exposure of the container sidewall to direct solar radiation. Close spacing of containers, which promotes mutual shading of the container sidewall by plant canopies, decreases medium temperature and generally increases plant growth or quality (Brown, 1984; Ingram et al., 1988; Keever and Cobb, 1984; Laiche, 1985). Midday medium temperatures in 2.8 L containers arranged in a container-to-container spacing were 32°C compared to 39°C for containers spaced on 30 cm centers (Laiche, 1985). Whitcomb (1981) reported decreased container medium temperatures and increased root and shoot growth for 3 woody species when containers were shielded in

an insulated pallet.

Effects on nitrification. Temperature also influences the growth and metabolism of microorganisms in the growth medium (Alexander, 1977). In soils, nitrification is reportedly optimum at 26°C and minimal below 2°C or above 50°C (Beck, 1983). Nitrification is the process whereby ammonium nitrogen (NH_4-N) is biologically converted to nitrate nitrogen (NO_3-N). Niemiera and Wright (1987a) investigated the influence of temperature on nitrification in pine bark media. Nitrification was inhibited at constant 10° or 40°C compared to that at constant 20° or 30°C. The inhibition was greater at the higher temperature. High temperature inhibition of nitrification resulted in a higher medium solution ratio of NH_4-N:NO_3-N at 40°C.

Nitrogen Nutrition

It is well known that growth of many horticultural crops is influenced by the relative amounts of NH_4-N and NO_3-N supplied to the plant (Barker and Mills, 1980). Positive and negative responses to the ionic form of N have been well documented for woody plant species (Colgrove and Roberts, 1956; Dirr, 1975; Dirr et al., 1973; Edwards and Horton, 1982; Ingram and Joiner, 1982; McFee and Stone, 1968; Walden and Epelman, 1988). The growth response of some species of woody plant to limestone addition to a pine bark medium has been attributed to liming's influence on the medium solution NH_4-N:NO_3-N ratio (Chrustic and Wright, 1983; Wright and Hinesly, 1991; Walden and Epelman, 1988). Nitrification in pine bark increases as medium pH increases with limestone addition (Niemiera and Wright, 1986a).

Additionally, medium pH can influence plant response to the ionic form of N. *Phaseolus vulgaris*, a plant susceptible to ammonium toxicity, grew normally on NH_4-N nutrition when the pH of the nutrient solution was buffered by calcium carbonate (Barker et al., 1966). *Viburnum plicatum* was necrotic when NH_4-N was supplied at pH 3 or 4, but grew normally with NH_4-N at pH 7 or 8 (Dirr, 1975). When nitrification was chemically inhibited in a pine bark medium, shoot weight of *Buxus microphylla* supplied with N at an NH_4-N:NO_3-N ratio of 4:1 was increased nearly two fold by limestone addition to the media; limestone addition had no influence on growth at an NH_4-N:NO_3-N ratio of 1:4 (Walden and Epelman, 1988).

Growth reductions when NH_4-N is used as the principle N source have been attributed to increased acidification of the root-zone due to excess uptake of cations relative to anions as NH_4^+ is absorbed by the root (Kirkby and Mengel, 1967) and toxic accumulation of free NH_4^+ or ammonia in plant tissues (Puritch and Barker, 1967; Vines and Wedding, 1960). Tolley-Henry and Raper (1986) have proposed that ammonium toxicity results when absorption of NH_4^+ lowers pH in the immediate vicinity of the root to the extent that N absorption is impaired. Nitrogen stress within the plant then leads to a decline in photosynthetic rates, limiting carbohydrate reserves in the plant. Eventually, as carbohydrate reserves are depleted, soluble organic nitrogenous compounds are degraded to provide carbon skeletons in order to meet the demands of maintenance respiration. The resulting free NH_4^+ accumulates in leaf tissue. Thus, availability of carbohydrates can govern the occurrence of toxic effects

(Givan, 1979). High carbohydrate levels in the plant have also been shown to favor the uptake of NH_4-N (Kirkby and Hughes, 1970; Michael et al., 1970). Ammonium uptake by *Lolium perenne* resulted in greater depletion of soluble carbohydrates in the root than uptake of NO_3-N (Bowman and Paul, 1988).

Chemical inhibition of nitrification in pine bark influenced the composition of the medium solution, resulting in a higher ratio of NH_4-N:NO_3-N, higher pH, and lower concentration of Mn (Niemiera and Wright, 1986a). The lower medium solution concentration of Mn at higher pH was consistent with the inverse relationship between pH and the solubility of micronutrient cations (Tisdale et al., 1985). As a result, plants grown in the medium where nitrification was inhibited had lower tissue levels of Mn. When nitrification is not inhibited, medium pH declines as nitrification progresses, since 2 H^+ ions are produced for each molecule of NH_4^+ oxidized. The decrease in pH due to nitrification is higher at higher rates of NH_4-N application (Niemiera and Wright, 1987b). Thus, Ingram and Joiner (1982) reported a decrease in medium pH and an increase in leaf Mn content of *Quercus shumardii* in response to increased application of NH_4-N. There was a significant negative correlation of medium pH with Mn leaf content. In contrast, other studies have shown a decrease in tissue Mn content in response to increased levels of NH_4-N in nutrient solution or sand culture where nitrification was not a factor (Edwards and Horton, 1982; Elamin and Wilcox, 1986a, 1986b).

CHAPTER III

EFFECTS OF SUMMER CONTAINER TEMPERATURES ON NITROGEN ABSORPTION AND GROWTH OF *ILEX CRENATA* 'CONVEXA'

Introduction

Solar radiation incident on the sidewalls of dark colored nursery containers can elevate temperatures in the container medium to levels which are supraoptimal for plant growth. In Southern nurseries, container medium temperatures in excess of 40°C have been recorded for up to 6 hours a day in mid-summer (Ingram, 1981). Portions of the container medium can exceed 50°C for 2 hours while attaining maximum temperatures as high as 57°C (Martin and Ingram, 1988). Depending on the duration of exposure, medium temperatures of this magnitude can cause direct heat injury to the roots of woody plants, irreversibly damaging root cell membranes (Ingram, 1986; Ruter and Ingram, 1991). Indirect heat injury from exposure to sublethal, though supraoptimal, root-zone temperatures can decrease the growth and quality of container-grown plants in Southern nurseries (Ingram, 1981; Keever and Cobb, 1984; Newman, 1985).

Reduced growth of woody plants can result from various physiological responses to the stress of supraoptimal root-zone temperatures, including decreased rate of photosynthesis (Foster et al., 1991; Johnson and Ingram, 1984; Martin et al., 1989), increased rate of root respiration (Foster et al., 1991; Ruter and Ingram, 1991)) and alteration in the partitioning of photoassimilate between the shoot and roots (Ruter and

Ingram, 1990). The mineral nutrient content of plants can also be altered in response to supraoptimal root-zone temperature. According to a review by Cooper (1973), the percent nutrient content will generally decrease with increasing root-zone temperature or increase to an optimal level, then decrease. Nevertheless, most reports for woody plants indicate that the percent nitrogen in shoot or leaf tissue increases in response to increasing root-zone temperature (Harrison, et al., 1988; Johnson and Ingram, 1984; Young, 1980; Yusof et al., 1969). Yeager et al. (1991), however, reported a linear decrease in N accumulation for *Ilex crenata* as root-zone temperature increased from 28° to 40°C.

In most of the aforementioned studies, root-zone treatment temperatures were imposed on entire plant root systems. In containers exposed to direct solar radiation, medium temperature varies within the container (Fretz, 1971; Ingram, 1981; Ingram et al., 1988). Those portions of the root system within medium quadrants with southern or western exposure generally experience highest temperatures, the magnitude of which depends largely on the ambient temperature and the intensity and incident angle of solar radiation (Martin and Ingram, 1988). Under nursery conditions, temperature patterns differ between portions of the root system and those patterns may fluctuate on a daily basis, unlike the uniform root temperatures often used experimentally. Furthermore, several reports indicate changes in the distribution of roots within exposed containers in response to medium temperature (Martin et al., 1991; Newman, 1985). The biomass of roots exposed to highest temperatures is

generally less than that exposed to more optimal temperatures. Plant response to the variable temperature conditions in containers in the nursery may differ from that obtained when entire root systems are subjected to experimentally controlled temperature conditions. The purpose of this research was to determine the growth and nitrogen uptake response of *I. crenata* to supraoptimal root-zone temperatures which could occur under Virginia nursery conditions.

Materials and Methods

Rooted cuttings of *I. crenata* 'Convexa' were planted on May 20, 1987 in 3.8-liter black polyethylene containers in a medium of 4 parts pine bark:1 part sand (v:v). The medium was amended with dolomitic limestone at 2.4 $kg \cdot m^{-1}$ and Micromax (Sierra Chemical Co., Milpitas, CA), a micronutrient fertilizer, at 1 $kg \cdot m^{-1}$. Plants were separated into 5 blocks and grown in a container to container arrangement on an outdoor gravel nursery bed. Each container received a twice weekly application of 750 ml of a fertilizer solution containing 250 ppm N as urea ammonium nitrate, 50 ppm P as phosphoric acid and 125 ppm K as potassium chloride. Throughout the experimental period, on days when fertilizer was not applied, containers received 1.3 cm of water as overhead irrigation beginning at 0700 hours. On June 23, following an initial harvest of four plants per block, each block was divided into two container temperature (CT) treatments, insulated containers (IC) and uninsulated containers (UIC).

The IC treatment consisted of plants grown in 122 cm x 244 cm x 20 cm pallets, which were a modification of the design used by Whitcomb (1981). The top and sides

were made of 1.9 cm thick 'Tuff-R' insulation board (Celotex, Corp., R-value 5.4) with aluminum facing on both sides. Duct tape was used to fasten the corners and seal the edges. The open bottom of the pallet was placed on the gravel nursery bed. Circular holes 18.5 cm in diameter were cut into the top on 30.5 cm centers in a 4 x 8 arrangement. The diameter of this opening was slightly less than that of the uppermost rim of the polyethylene containers, so that containers placed in the openings were suspended from the top of the pallet and the openings were effectively sealed. The bottoms of the suspended containers just reached the gravel bed beneath the pallet. All but the upper surface of the container medium was enclosed within the pallet, completely shielding the container sidewall from solar radiation. The top of the pallet was supported by two boards which ran lengthwise beneath it, each of which was supported by two stakes driven into the gravel bed. The surface of the pallet top was painted to reduce the intensity of reflected light. The color closely matched the overall color of the gravel bed. There was one pallet for each of five blocks and 32 plants per pallet.

For the UIC treatment, 32 plants per block were grown on the gravel bed with containers at the same spacing as those in the pallet. A border row of containers with plants surrounded the treatment plants. This spacing and the east-west orientation of the rows allowed for maximum mid-afternoon exposure of the southwest container sidewall to solar radiation. The two CT treatments were considered to be representative of the maximum (spaced on a gravel bed) and minimum (insulated pallet) container

temperature regimes which might occur in Virginia nurseries. The experimental design was that of a randomized complete block with 5 replications.

After the initiation of treatments, plants were fertilized every 7 to 10 days with 750 ml of a solution which contained 400 ppm N, 80 ppm P, and 200 ppm K as previously described.

Differences in container medium temperature between the CT treatments were documented by recording the diurnal cycle of medium temperatures on selected clear days by means of soldered copper-constantan thermocouples and a thermocouple thermometer (Wescor model TH-65, Wescor, Inc., Logan, UT). Thermocouples were placed in the container media 2.5 cm from the container sidewall and 10 cm down from the top rim at the vertical center in two randomly selected containers per treatment per block. Insulated containers had one thermocouple on the southwest side. Uninsulated containers had an additional thermocouple on the northeast side of the container. Air temperatures in the plant canopy were also monitored by placing one thermocouple in the center of each group of treatment plants in each block at mid-canopy height. Temperatures were recorded every 2 hours beginning at 0800 hours (1 hr after irrigation) until 2000 hours and again at 0700 hours (prior to irrigation) the following day.

In addition to the initial harvest (June 23), four plants per treatment per block were randomly chosen for harvest at approximately 3 week intervals for a total of four growth periods, ending on 21 September. At each harvest, roots were separated from

the container media by washing the intact root ball in water and carefully removing any media particles from the roots. Shoots were then severed above the uppermost roots and roots and shoots were rinsed in distilled water. Dry weight and nitrogen content of the shoots and roots at each harvest was determined after oven drying for 48 hours at 70°C. After grinding in a Cyclotec mill (Tecator, Höganäs, Sweden), shoot and root tissue was analyzed for N using the micro-Kjeldahl technique (Peterson and Chesters, 1964).

Mean relative growth rates ($\bar{R}$) were calculated for the intervals between harvests from the relationship:

$$\bar{R} = \frac{\log_e W_2 - \log_e W_1}{T_2 - T_1}$$

where W is the dry weight of shoots or roots and T is time (Hunt, 1978). Nitrogen accumulated in the shoot and roots during the intervals between harvests was calculated as:

$$\text{N accumulated} = \frac{N_2 - N_1}{W_2 - W_1}$$

where N is the quantity of nitrogen in the shoot or roots and W is the dry weight of the shoot or roots. Mean specific absorption rates of nitrogen uptake ($\bar{S}_N$) were calculated from the relationship:

$$\bar{S}_N = \frac{N_2 - N_1}{W_2 - W_1} (\bar{R}_{roots})$$

where N is the quantity of nitrogen in the whole plant, W is the dry weight of roots, and $\bar{R}_{roots}$ is the mean relative growth rate of the roots over the interval (Welbank, 1962)

Following each harvest, the remaining plants in each treatment were consolidated to the original spacing to insure that all plants within a treatment continued to receive the same solar exposure. Openings in the pallet were closed by replacing the disc of insulation board originally removed to create the opening.

Statistical evaluation of the data was by analysis of variance.

Results and Discussion

Container medium temperatures. On 23 July, the mean temperature of the container medium rose from 25.8°C at 0800 hours to a maximum of 44.9°C at 1600 hours on the southwest side of uninsulated containers (Figure 3.1). This temperature differed significantly from the maximum of 39.2°C recorded at 1400 hours on the northeast side of the container. Medium temperature on the northeast side of the container continued to exceed 39°C at 1600 hours although the container sidewall was no longer exposed to direct solar radiation. Temperatures in the center of the container, although unrecorded, were probably between 39°C and 44°C during this time due to the thermal diffusivity of a pine bark:sand medium (Martin and Ingram, 1991).

For insulated containers, the maximum mean temperature of 33.0°C was recorded

at 1600 hours. Medium temperatures in insulated containers were significantly lower than canopy temperatures until 1600 hours. The mean maximum medium temperature in uninsulated containers exceeded that of the canopy by approximately 10°C.

Medium temperatures recorded on 18 August were very similar to those of July, although maximum canopy temperatures were higher on the August date (Figure 3.1). Due to the upright growth habit of *Ilex crenata* 'Convexa', shading of the exposed containers probably moderated temperatures in the container medium to some extent as plants increased in size. The mean maximum medium temperature in uninsulated containers recorded on this date was 45.3°C. The highest individual temperature observation recorded on this date was 48.4°C on the southwest side of an uninsulated container at 1600 hours.

The maximum air temperature (from a weather station within 200 meters) of 33.3°C on July 23 and 35.0°C on August 18 exceeded the normal daily maximum temperature by 2.5°C in July and 5.6°C in August (Donohue et al., 1984). Nevertheless, temperatures of this magnitude are not unusual for those months in Virginia.

The diurnal fluctuation of medium temperatures in uninsulated containers concurs with previously reported patterns of medium temperature in exposed containers (Ingram, 1981; Martin and Ingram, 1988). The maximum medium temperature was maintained for less than 1 hour, while temperatures in portions of the container exceeded 40°C for approximately 4 hours. Medium temperatures as high as 53°C have

been observed in 3.8-liter containers (Ingram et al., 1988). In Virginia nurseries, container medium temperatures higher than those recorded in the present study may occur since container medium temperatures are influenced by various factors including solar radiation, air temperature, relative humidity, wind speed, medium composition and moisture level, irrigation frequency, container size and spacing, and ground surface color (Ingram et al., 1988; Martin and Ingram, 1988, 1990, 1991, 1992; Newman, 1985).

The duration of root exposure to medium temperatures higher than 40°C was less than that required for direct injury to the roots of several woody plant species (Ingram and Buchanan, 1981; Ingram, 1985; Ingram, 1986). Nevertheless, medium temperatures in excess of 40°C recorded in this experiment are capable of indirect heat injury.

By mid-september, temperatures in the uninsulated containers had moderated considerably. On 15 September, the mean temperature of the container medium rose from 19.4°C at 0800 hours to a maximum of 33.9°C at 1400 hours on the southwest side of the uninsulated containers (Figure 3.1). This differed significantly from the maximum of 27.9°C recorded on the northeast side of the container at 1600 hours. The mean maximum container medium temperature of 26.2°C for insulated containers was also recorded at 1600 hours. The medium temperature in insulated containers did not exceed canopy temperature until 1600 hours and was still significantly higher at 0700 hours on 16 September. The maximum temperature in uninsulated containers

exceeded the maximum canopy temperature by approximately 7°C. The maximum air temperature on this date (27°C) was very similar to the 30 year norm (Donohue et al., 1984).

Optimum temperatures for root growth of many plant species are between 20°-30°C (Kramer, 1969). The insulated pallets utilized in this study were effective in maintaining container medium temperatures nearly within this optimum range and reduced the maximum container medium temperature more than 10°C compared to that in uninsulated containers on hot, clear days in mid-summer. Plant canopy temperatures for the two CT treatments differed by approximately 2°C for several hours in the late morning on the July recording date, and did not differ on the August recording date. It seems reasonable, therefore, to conclude that differences in plant response to treatment may be attributed to differences in root-zone temperature.

Growth analysis. CT treatment did not significantly influence root dry weight during the experimental period (Table 3.1). There was no significant difference in shoot dry weight due to treatment by the end of the first (June 23 to July 20) or second (July 21 to August 10) growth periods. Consequently, the shoot:root ratio for these growth periods did not differ between treatments. By the end of the third growth period (August 11 to September 2), shoot dry weight was significantly lower in the uninsulated containers, resulting in a lower shoot:root ratio compared to that of plants in the insulated containers. Shoot dry weight and the shoot:root ratio remained significantly greater in the insulated containers at the end of the fourth growth period

(September 3 to September 21).

Yeager et al. (1991) and Harrison et al. (1988) found reductions in shoot and root dry weight of *I. crenata* and *Photinia x fraseri*, respectively, when grown for 6 weeks at root-zone temperatures greater than 34°C for 6 hours a day. In the present study, no differences in dry weight response to container temperature treatment were observed after 4 weeks (growth period 1) or 7 weeks (end of growth period 2) of treatment, even though recorded root-zone temperatures appeared to be supraoptimal in the uninsulated containers on July 21 (Figure 3.1), midway between the first and second growth periods.

When plants were harvested at the conclusion of the first two growth periods, it was observed that the pattern of root growth differed between treatments. The roots in uninsulated containers were located mainly in the upper portion of the container medium, growing toward the center and northern regions of the container. Roots in the center and northern regions of containers in full sun would experience more moderate supraoptimal temperatures than those which were recorded on the southwest side of the container (Martin and Ingram, 1988). The majority of roots in insulated containers were observed to grow out across the upper portion of the container, close to the surface of the medium, and then down the perimeter of the container. When the container medium surface is exposed to solar radiation (the case for both container temperature treatments), medium temperatures near the upper surface of a pine bark:sand medium can approach 38°C (Martin and Ingram, 1991). During the first two

growth periods a considerable portion of the roots in insulated containers may have been exposed to supraoptimal temperature near the container medium surface. Subsequent shading of the container medium surface by larger plants in later growth periods probably lowered medium surface temperatures. These observations regarding the pattern of root growth during the first and second growth periods suggest that root temperatures may not have differed enough between CT treatments during these periods to effect a difference in growth response.

By the end of the third growth period, dry weight accumulation in the shoot was significantly influenced by CT treatment. The reduction in shoot dry weight at higher container temperature, with no concomitant reduction in root dry weight, conflicts with most published reports from similar studies. In those studies, root dry weight (Ingram et al., 1988; Ingram et al., 1986) or root and shoot dry weight (Harrison et al., 1988; Ingram, 1981; Johnson and Ingram, 1984; Yeager et al., 1991) decreased in response to increasing root-zone temperature. However, those experiments were done under controlled conditions where whole root systems were heated to supraoptimal temperatures, or under nursery conditions but at lower latitudes than the present study. In either case, plants in those studies may have experienced greater stress due to higher root-zone temperatures than the plants in this experiment.

When only a portion of the root system is at supraoptimal temperature, growth effects due to high root-zone temperature stress may vary from those obtained when the entire root system is submitted to high temperature. Ruter and Ingram (1990) used a

split-root technique to examine the effects of root temperature treatment combinations on photoassimilate partitioning in *I. crenata*. After 3 weeks exposure, they reported reduced shoot and root weight when root halves were at 34/34°, 38/38°, or 42/42°C for 6 hours daily, compared to growth at 30/30°C. However, shoot weight and total root weight did not differ significantly when root halves were at 30/34° or 30/38°C compared to growth at 30/30°C. Shoot weight but not total root weight was reduced at 30/42°C. Their results suggest that a portion of the root system at cooler temperature may compensate for growth effects due to roots at supraoptimal temperature. This compensation may be operative at medium temperatures which are sufficiently high to reduce shoot dry weight accumulation.

Dry weight accumulation in plants may be viewed in terms of a hierarchy of photosynthate partitioning (Thornley, 1976). Photosynthesis in the leaves supplies a soluble carbohydrate pool which is utilized for growth and respiration in the shoot and as the source for the carbohydrate pool in the roots. Soluble carbohydrates are distributed in descending priority to leaves, stems, and roots in response to the concentration of soluble carbohydrate in their respective pools. That is, excess carbohydrates not used for growth and respiration are distributed first from leaves to stems and then from stems to roots. According to this scheme of photoassimilate partitioning, any decrease in carbon fixation in the shoot (decrease in photosynthesis or increase in respiration) should first result in a decrease in assimilate partitioning to the roots. However, the distribution of soluble carbohydrates is also responsive to the level

of metabolic activity in sink tissue, which is greatly influenced by temperature (Wardlaw, 1968). An increase in sink temperature relative to that of the source can increase the import of assimilate into sink tissue (Harris and Jeffcoat, 1974). The rate of respiration in plants increases with increasing temperature, particularly maintenance respiration which fuels energy requiring processes not resulting in dry matter accumulation (Gent and Enoch, 1983). The maintenance portion of root respiration in *Helianthus annus* increased in response to increase in root-zone temperature (Szaniawski and Kielkiewicz, 1982). Root respiration in *I. crenata* has been shown to increase with increasing root-zone temperature (Foster et al., 1991; Ruter and Ingram, 1990). Thus, supraoptimal root-zone temperatures may alter the priority of assimilate distribution from shoot to root.

During the third growth period, less current assimilate may have been available for growth and respiration of plants in uninsulated containers compared with plants in insulated containers since decreased rates of photosynthesis have been reported in response to supraoptimal root-zone temperature (Gur et al., 1972; Johnson and Ingram, 1984; Foster *et al.*, 1991). Nevertheless, the requirements for assimilate may have been higher for roots in uninsulated containers due to higher root-zone temperature. Apparently, these requirements for root respiration and growth were adequately met since there was no difference in root dry weight between treatments. The increased root demand for assimilate from an already diminished pool would lower assimilate availability to the shoot in uninsulated containers, resulting in lower shoot dry weight,

compared to that in insulated containers (Table 3.1).

Relative growth rate (increase in plant material per unit of plant material per unit of time) is a measure of the efficiency of dry matter accumulation of the plant or individual plant components over a period of time (Evans, 1972; Hunt, 1978). As such, it is a more meaningful basis for comparison of the physiological performance of plants, particularly those of differing size, than absolute dry weight gain. Relative growth rates can vary over a wide range depending on plant age and species. The values recorded in this experiment (Table 3.1) were similar to those reported for other woody plant species (Hunt, 1978).

The $\bar{R}_{roots}$ did not differ between CT treatments during the experiment (Table 3.1). That is, higher root-zone temperatures did not alter the efficiency of dry matter accumulation in the roots. The $\bar{R}_{shoot}$ did not differ between CT treatments during the first two growth periods. During the third growth period, however, less assimilate per gram of shoot per day accumulated in the shoot in uninsulated containers, presumably due to alterations in carbon assimilation and partitioning as previously discussed. During the fourth growth period, $\bar{R}_{shoot}$ did not differ between treatments, although final shoot dry weights did differ. The apparent moderation of root-zone temperatures during the fourth growth period (Figure 3.1) may be responsible for the recovery of $\bar{R}_{shoot}$ in the uninsulated containers. These data suggest that, while the absolute loss of shoot dry weight due to high root-zone temperature was not recovered, the physiological effects of high root-zone temperature on dry matter accumulation in the

shoot were temporary and reversible under the conditions of this experiment.

Nitrogen uptake. The mean $\bar{S}_N$ (mg $N \cdot g^{-1}$ root dry $wt \cdot day^{1}$) was higher in uninsulated containers during the first growth period, and did not differ significantly between CT treatments over the second or fourth growth periods (Table 3.2). During the third growth period, however, there was a significant decrease in $\bar{S}_N$ in the uninsulated containers compared to that in the insulated containers.

The decrease in $\bar{S}_N$ at higher root-zone temperature was associated with a decrease in $\bar{R}_{shoot}$ during the same period (Table 3.1), underscoring the relationship between nitrogen absorption and shoot growth. Many woody plants exhibit episodic patterns of growth (Kramer and Kozlowski, 1979). Hershey and Paul (1983) demonstrated that nitrogen absorption can also be episodic, decreasing during shoot elongation of *Euonymus japonica*, and increasing after shoot elongation ceased. *I. crenata* responded to fertilizer applications which were timed to coincide with the period between episodes of shoot elongation (Gilliam and Wright, 1978). Growth of *I. crenata* has been shown to alternate between periods of root and shoot elongation (Mertens and Wright, 1978). Mertens and Wright (1978) theorized that plants which exhibit episodic growth absorb nutrients most readily during periods of root elongation, linking nutrient uptake to the availability of carbohydrates in the root.

Raper et al. (1978) have proposed a model, based on Thornley's scheme for carbohydrate partitioning, which describes nitrogen uptake by plants as a function of the balance between the demand for carbohydrates and nitrogen in the shoot and the

availability of nitrogen and carbohydrates in the root. The flux of nitrogen into the shoot influences photosynthesis, shoot growth, and, ultimately, the translocation of carbohydrates not utilized for shoot growth and maintenance to the root. The flux of carbohydrates into the root, which supports root growth and maintenance, is also necessary for absorption and assimilation of nitrogen (Henry and Raper, 1989; Kirkby and Hughes, 1970; Michael, et al., 1970), and ultimately influences the flux of nitrogen into the shoot.

Close correlation between the relative accumulation rate of nitrogen (an estimate of nitrogen assimilation in the plant with no implied dependence on physical characteristics of the root system) and the $\bar{R}_{roots}$ for several plant species (Raper et al., 1977, 1978) supports the premise that plant demand for nitrogen is proportional to the daily flow of carbohydrates from the shoot to the root. This interdependence of shoot growth and N uptake implies that a decrease in the availability of carbohydrates for nitrogen absorption and assimilation in the root, due to alterations in carbon assimilation and partitioning at high root-zone temperature, would decrease the apparent 'demand' for nitrogen in the shoot. The concomitant decreases in $\bar{S}_N$ and $\bar{R}_{shoot}$ for plants in uninsulated containers during the third growth period supports this hypothesis.

Because there were no differences in root dry weight between CT treatments during the experiment, the decrease in $\bar{S}_N$ during the third growth period indicates that less N was absorbed by plants grown in uninsulated containers. Nitrogen accumulated per gram of plant tissue, however, was higher than or similar to that accumulated in plants

grown in insulated containers during the same period (Table 3.2). This indicates that the decrease in N absorbed was proportionally smaller than the decrease in plant dry matter accumulated for plants in uninsulated containers. As a result, the higher root-zone temperatures in uninsulated containers did not lower the concentration of N in the plant, even though N absorption decreased. Total N content, however, would be lower for plants in uninsulated containers due to differences in shoot dry weight accumulation during the third and fourth growth periods.

In summary, summer container medium temperatures recorded in this study were sufficiently high to affect growth and mineral nutrition of *I. crenata*. Shoot growth, but not root growth, was reduced by container temperatures which could exceed 45°C in portions of the container on clear, hot days. These findings indicate that Virginia nurserymen should implement cultural practices which minimize container temperature such as gradual spacing of containers in order to maximize shading of container sidewalls by the plant canopy (Ingram et al., 1988).

The specific uptake of N for *I. crenata* was reduced by the higher root-zone temperatures in uninsulated containers. Nitrogen accumulation, however, was not reduced by high root-zone temperature. This suggests that increasing the level of N application to the container medium may not alleviate growth reductions due to high container temperature.

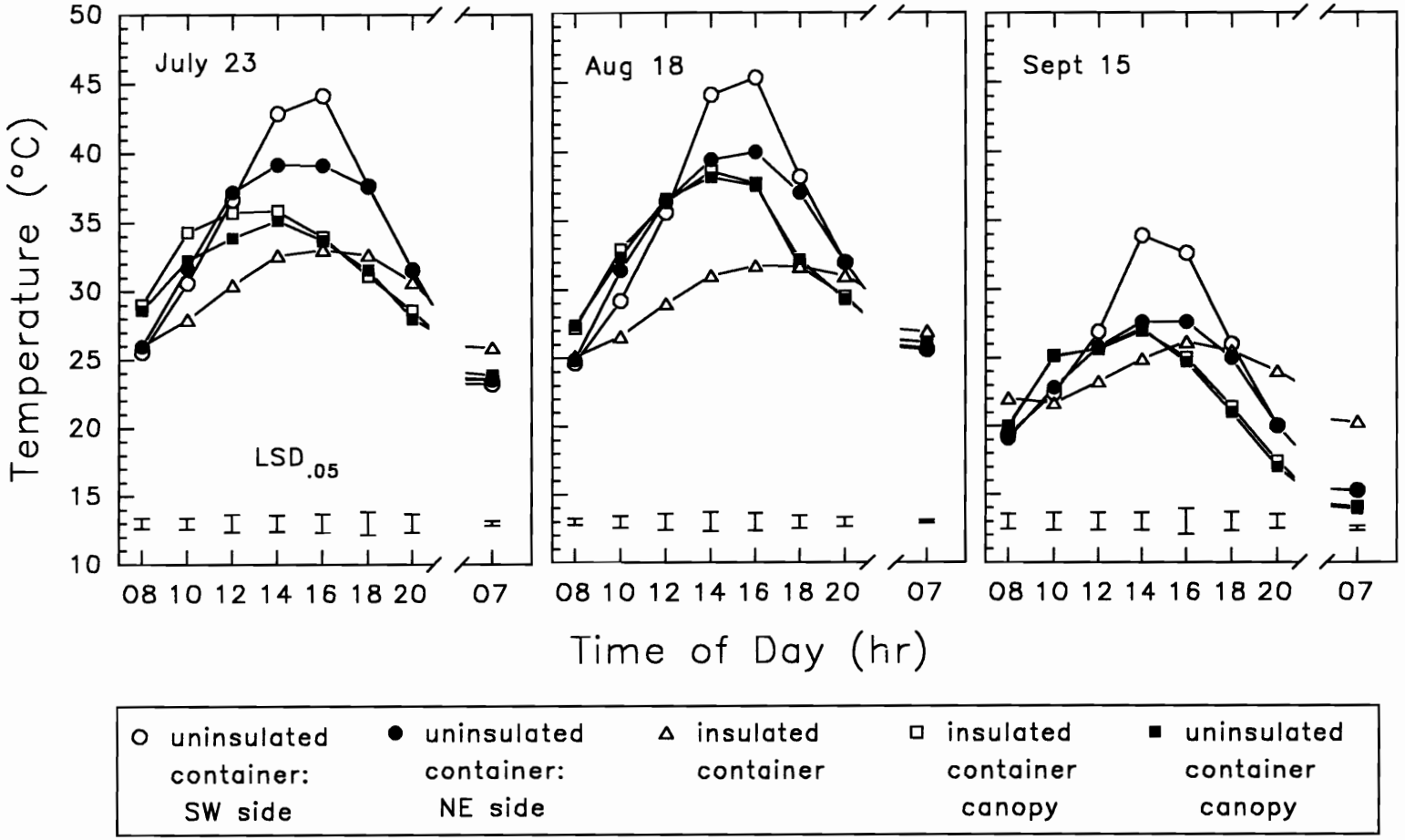

Figure 3.1. Diurnal container medium temperatures on selected clear days from 0800 hours to 2000 hours, and at 0700 hours the following day. Each point represents the mean of 10 containers.

Table 3.1. Influence of container temperature (CT) treatment (uninsulated vs insulated) on dry weight and mean relative growth rate ($\bar{R}$) of *Ilex crenata* 'Convexa' during 4 consecutive growth periods.

Growth period	CT treatment	Shoot wt	Root wt	Shoot:Root[z]	$\bar{R}_{shoot}$	$\bar{R}_{roots}$
		g			$mg \cdot g^{-1} \cdot day^{-1}$	
23Jun - 20Jul						
	uninsulated	3.8	0.9	4.4	25.5	15.9
	insulated	3.8	0.9	4.2	25.3	17.8
	Significance[y]	NS	NS	NS	NS	NS
21Jul - 10Aug						
	uninsulated	6.8	1.3	5.3	27.7	18.8
	insulated	6.9	1.3	5.2	28.7	18.4
	Significance	NS	NS	NS	NS	NS
11Aug - 2Sep						
	uninsulated	10.4	2.2	4.7	18.6	24.1
	insulated	12.9	2.4	5.4	27.4	25.6
	Significance	**	NS	*	**	NS
3Sep - 21Sep						
	uninsulated	16.5	3.8	4.4	24.5	27.9
	insulated	19.8	4.1	4.9	22.5	27.3
	Significance	*	NS	**	NS	NS

[z]Analyzed as square root-transformed values. Back-transformed means presented.
[y]Significance of F test: ** ≤ 0.01, * ≤ 0.05, NS >0.05

Table 3.2. Influence of container temperature treatment (uninsulated vs insulated) on mean specific absorption rate ($\bar{S}_N$) and accumulation of nitrogen (N) for *Ilex crenata* 'Convexa' during 4 consecutive growth periods.

Growth period	Container temperature treatment	$\bar{S}_N$	N accumulated	
			Shoot	Root
		mg N·g^{-1}root·day^{-1}	mg N·g^{-1} dry wt	
23Jun - 20Jul				
	uninsulated	3.76	32.3	38.4
	insulated	3.46	29.1	37.6
	Significance[z]	*	NS	NS
21Jul - 10Aug				
	uninsulated	2.85	17.7	22.1
	insulated	2.67	16.9	20.9
	Significance	NS	NS	NS
11Aug - 2Sep				
	uninsulated	2.69	22.8	23.0
	insulated	3.54	20.2	24.6
	Significance	**	*	NS
3Sep - 21Sep				
	uninsulated	2.81	20.1	21.4
	insulated	3.06	21.9	19.3
	Significance	NS	NS	NS

[z]Significance of F test: ** ≤ 0.01, * ≤ 0.05, NS >0.05

Chapter IV

EFFECTS OF SUMMER CONTAINER TEMPERATURES AND LIMESTONE ADDITION TO A PINE BARK MEDIUM ON GROWTH OF SELECTED CONTAINER-GROWN WOODY PLANTS

Introduction

Black polyethylene containers are widely used throughout the nursery industry for production of container-grown nursery crops. Exposure of the dark colored sidewalls of these containers to solar radiation can result in root-zone temperatures which exceed 40°C for up to 6 hours/day during summer (Ingram, 1981). Decreases in plant growth and quality due to supraoptimal root-zone temperatures have been well documented in container nurseries at lower latitudes where maximum air temperatures and the intensity of solar radiation generally exceed those in Virginia (Ingram, 1981; Keever and Cobb, 1984; Newman, 1985). Documentation of growth reductions due to high container medium temperatures under conditions which simulate those in Virginia nurseries may justify the cost of adjustments in cultural practices which lower container medium temperatures or alleviate growth reductions due to high root-zone temperature.

This experiment examined the growth response of several commonly grown woody plant species to supraoptimal container temperatures which might occur in Virginia nurseries, as well as their response to limestone addition (LA) to the container medium. Several nurserymen have reported that applications of dolomitic limestone have helped

prevent or correct chlorosis which appeared to be related to high container medium temperature (Walden et al., 1989).

Materials and Methods

Individual single-stem liners of *I. crenata* Thunb. 'Helleri', *Juniperus chinensis* 'Sea Green', *Buxus microphylla* var. *japonica* or *Nandina domestica* were planted on May 9, 1988 in 3.8 l black polyethylene containers in a medium of 5 bark:1 sand (v:v) amended with either 0 or 4 kg dolomitic limestone per m^3. Sixty-four plants of each species were grown on an outdoor gravel nursery bed with overhead irrigation. Plants were irrigated and fertilized at the frequency and rates described in Chapter III. The fertilizer solution was modified to supply 300 ppm NH_4-N as NH_4NO_3 and $(NH_4)_2SO_4$ and 100 ppm NO_3-N as NH_4NO_3 and KNO_3. Potassium was supplied as KNO_3. Micronutrients were supplied according to Hoagland and Arnon (1950) and 5 ppm Fe was supplied as FeNaEDTA. Additionally, 40 ppm Ca and 20 ppm Mg were supplied as $CaCl_2 \cdot 6H_2O$ and $MgCl_2 \cdot 2H_2O$ in a separate 750 ml irrigation of each container 2 days after irrigation with the N-P-K solution.

On June 25, limed and unlimed plants of each species were divided into insulated and uninsulated container temperature (CT) treatments, utilizing the pallet system described in Chapter III. Plants were arranged in randomized complete blocks with a split plot design. The main plots were comprised of the two container temperature regimes. Limestone amendment rates comprised the subplots. There were four plants per subplot per species in each of four blocks. Each plant species was treated as a

separate experiment.

Container medium temperatures were recorded on a clear day in August in *I. crenata* containers, following the procedure outlined in Chapter III, in order to verify temperature differences due to treatment. Medium solution extracts were obtained on August 8 from one container per treatment replication for *I. crenata* and *J. chinensis* by the pour-through procedure (Wright, 1987), 3 days after irrigation with the N-P-K solution. One-hundred fifty ml of distilled water was applied to the container medium surface two hours after irrigation and the resultant leachate was collected and analyzed for pH, NO_3^- and NH_4^+ using ion-selective electrodes (Orion, Cambridge, MA).

On September 26, roots and shoots were harvested for dry weight determination. Roots were separated from the container media by washing the intact root ball in water and carefully removing any media particles from the roots. Shoots were then severed above the uppermost roots. Dry weights of roots and shoots were determined after oven drying for 48 hours at 70°C. *Nandina domestica* plants were rated for chlorosis prior to harvesting on a scale of 1 to 5 (1=no chlorosis, 5=most chlorosis). Chlorosis was not evident in any other species. Leaf tissue of *N. domestica* was analyzed for N using the micro-kjeldahl technique (Peterson and Chesters, 1964), and after dry ashing, for P using a colorimetric procedure (Watanabe and Olsen, 1965). Determination of K, Ca, Mg, Zn, Fe, Mn, and Cu was by atomic absorption spectroscopy.

Statistical analysis of the data was by analysis of variance and linear regression.

Results and Discussion

Container medium temperature. Container medium temperatures recorded in August (data not shown) were similar in thermal period and range to those presented for August 1987 in Chapter III. The maximum medium temperature in uninsulated containers of 46°C was maintained for less than 1 hour, while temperatures in portions of the container exceeded 40°C for approximately 4 hours. A similar pattern of root-zone temperature in exposed containers reduced woody plant growth (Ingram, 1981). Medium temperatures in the insulated pallets did not exceed 32°C. Plant canopy temperatures for the two CT treatments did not differ.

Container medium extracts. The data from medium solution extracts obtained on August 8 for *I. crenata* and *J. chinensis* was similar for both genera (Table 4.1). Limestone addition increased medium solution pH to levels sufficiently high to stimulate nitrification (Niemiera and Wright, 1986b) and increase absorption of NH_4-N to the bark (Foster et al., 1983). Accordingly, the concentration of NH_4-N was lower and the concentration of NO_3-N higher in medium extracts from the limestone amended treatments. Container temperature also influenced the concentration of NH_4-N but not the concentration of NO_3-N. Higher levels of NH_4-N in the medium extract from uninsulated containers increased the NH_4:NO_3 ratio, especially in the unlimed medium.

Niemiera and Wright (1987a) found that nitrification rates in pine bark media decreased after 5 days constant exposure to 40°C compared to that at 34°C. At 40°C, the level of NH_4-N in media extracts increased, with a concomitant decrease in NO_3-N.

The effect on nitrification rate of daily exposure of a pine bark medium to temperatures higher than 40°C for shorter thermal periods has not been determined. Higher concentrations of NH_4-N were observed in leachates from a container nursery during August than during the cooler month of September (Walden et al., 1989).

In the present study, medium temperatures in uninsulated containers may have exceeded 40°C for a sufficient duration each day to inhibit nitrification. Reduced rates of nitrification due to higher medium temperature could account for the greater NH_4:NO_3 ratio in the medium solution of uninsulated containers. However, for both species, the ratio of NH_4:NO_3 is greatest in the unlimed medium where mean pH ranged from 3.8 - 4.2. Nitrification is generally negligible in mineral soils at this pH range, though acid-adapted strains of nitrifying organisms do exist (Alexander, 1977). Niemiera and Wright (1986) were unable to detect NO_3-N in unlimed pine bark at similar pH after 180 days of supplying NH_4-N as substrate. In the same study, nitrate accumulation was observed at pH 4.3, although this occurred 78 days after the pine bark had reached a maximum pH of 5.5 due to the addition of limestone. Furthermore, in the present study, there was no concomitant decrease in NO_3-N accompanying the increase in NH_4-N in uninsulated containers. It is not clear, then, to what extent nitrification can reasonably be expected to have taken place in the unlimed treatments, and, therefore, unclear as well whether high temperature induced inhibition of nitrification can account for the greater NH_4:NO_3 ratio in the medium solution of the uninsulated containers.

Limestone addition affected a low NH_4-N:NO_3-N ratio, regardless of container temperature (Table 4.1). This indicates that limestone addition to a pine bark medium may encourage nitrification even during periods of high container temperature.

Plant growth. *Ilex crenata* and *J. chinensis* responded similarly to CT treatment and LA (Table 4.2). Both shoot and root dry weights were lower in uninsulated containers than in insulated containers. Root dry weight, but not shoot dry weight, was reduced by LA. Other studies have demonstrated negative and positive growth response to limestone addition for *Ilex* and *Juniperus*, respectively (Chrustic and Wright, 1983; Wright and Hinesly, 1991). There were no significant interactions between CT treatment and LA for root or shoot dry weight for either species.

For *B. microphylla*, shoot and root dry weight decreased in the uninsulated containers and increased in response to LA (Table 4.2). The positive effect of liming on growth of *B. microphylla* concurs with previous work which indicated that *B. microphylla* prefers the lower medium solution NH_4-N:NO_3-N ratio which results from limestone addition to a pine bark medium (Walden and Epelman, 1988). There were no significant interactions of CT treatment and LA on growth of *B. microphylla*.

Shoot dry weight of *N. domestica* was influenced by an interaction of CT treatment and LA (Table 4.2). Shoot dry weight was reduced in uninsulated containers, but the magnitude of reduction was less when limestone was added to the medium. Limestone addition had no influence on shoot dry weight in insulated containers. Root dry weight exhibited a similar, though nonsignificant, trend.

The positive growth response of some woody plant species to limestone addition to soilless media has been attributed the lower ratio of NH_4-N:NO_3-N in the medium solution which results from increased nitrification at higher medium pH (Chrustic and Wright, 1983; Walden and Epelman, 1988; Wright and Hinesly, 1991). Chlorosis ratings (Table 4.3) suggest that *N. domestica* may be sensitive to the higher NH_4-N:NO_3-N ratio in unlimed than in limed media (Table 4.1).

Chlorosis ratings were positively correlated with leaf tissue Mn levels ($r=0.68^{**}$). That is, highest chlorosis ratings were associated with highest leaf tissue Mn levels. However, the relationship between these factors is probably not causal but arises from the fact that leaf tissue Mn concentrations were higher in unlimed treatments (data not shown). An inverse relationship between medium pH and tissue Mn levels has been demonstrated for plants grown in pine bark media (Ingram and Joiner, 1982; Niemiera and Wright, 1986a). Manganese concentrations in *N. domestica* leaf tissue ranged from 52 to 128 ppm. These levels are within the range considered sufficient for vigorous growth of woody nursery crops, and well below levels which may be associated with toxicity symptoms in certain species (Gilliam and Smith, 1980). There were no other significant correlations between chlorosis ratings and leaf tissue nutrient concentrations, discounting the possibility that the chlorosis was related to nutrient deficiency or toxicity .

The detrimental effects of a higher ratio of NH_4-N:NO_3-N in unlimed media may have influenced the physiology of *N. domestica* through a mechanism that was more

effective at supraoptimal medium temperatures, since the decrease in growth in uninsulated containers was greater in the unlimed medium. High container medium temperatures have been shown to lower carbohydrate levels in the plant (Foster et al., 1991; Johnson and Ingram, 1984; Ruter and Ingram; 1990). Reducing the level of carbohydrates in the plant is thought to reduce the effectiveness of NH_4-N as an N source since carbohydrates are necessary to detoxify free ammonium through incorporation into organic compounds (Givan, 1979). Thus, higher root-zone temperatures in the uninsulated containers may have enhanced the apparent toxicity of the higher NH_4-N:NO_3-N ratios in unlimed media.

In this experiment, growth was consistently reduced by the supraoptimal root-zone temperatures in uninsulated containers. Averaged over LA, shoot growth of *I. crenata* and *J. chinensis* in uninsulated containers was reduced by 21%, and that of *B. microphylla* by 29%, compared to that in the insulated containers. *Nandina domestica* demonstrated a requirement for limestone addition to the medium, especially when medium temperatures are supraoptimal for growth. Shoot growth of *N. domestica* in uninsulated containers was reduced by 29% when limed, and by 57% without the addition of limestone, compared to growth in insulated containers.

These results demonstrate the potential magnitude of growth reductions in Virginia nurseries due to high container temperature. Since nursery plants are sold on the basis of size, costs associated with cultural practices which reduce container medium temperatures (such as gradual spacing of containers to maximize shading of the

container sidewall by the plant canopy) may be offset by increased revenue from sale of larger plants.

Table 4.1. The influence of container temperature (CT) treatment (uninsulated or insulated) and limestone addition (LA) on medium solution pH and concentrations of NH_4-N and NO_3-N for *Ilex* and *Juniperus* on August 8.

Genus	CT treatment	LA	pH	NH_4-N	NO_3-N	NH_4-N:NO_3-N
				ppm		
Ilex	uninsulated	no lime	4.1	57	39	1.48
		lime[z]	5.2	15	85	0.18
	insulated	no lime	3.9	34	48	0.71
		lime	5.4	9	86	0.10
		CT	NS	**	NS	**
		LA	**	**	**	**
		CTxLA	NS	NS	NS	**
Juniperus	uninsulated	no lime	4.2	56	40	1.38
		lime	5.2	11	69	0.16
	insulated	no lime	3.8	30	43	0.70
		lime	5.4	5	62	0.08
		CT	NS	*	NS	**
		LA	**	**	**	**
		CTxLA	*	NS	NS	**

[z] 4 $kg \cdot m^{-3}$

NS,*,** Nonsignificant (NS) or significant at P = 0.05 or 0.01, respectively.

Table 4.2. Influence of container temperature (CT) treatment (insulated or uninsulated) and limestone addition (LA) on dry weight of *Ilex*, *Juniperus*, *Buxus, and Nandina*.

		Lime ($kg \cdot m^{-3}$)			
		0	4	0	4
Genus	CT treatment	Shoot wt		Root wt	
		g			
Ilex					
	uninsulated	26.8	26.7	5.1	4.5
	insulated	35.4	33.0	6.0	4.7
	CT	***		**	
	LA	NS		***	
	CTxLA	NS		NS	
Juniperus					
	uninsulated	20.9	21.6	3.1	2.2
	insulated	26.6	27.1	3.4	2.6
	CT	**		***	
	LA	NS		***	
	CTxLA	NS		NS	
Buxus					
	uninsulated	4.1	5.9	1.2	1.6
	insulated	6.1	7.7	2.3	2.4
	CT	***		***	
	LA	***		***	
	CTxLA	NS		NS	
Nandina					
	uninsulated	8.0	13.6	2.2	3.6
	insulated	19.5	19.0	4.7	4.6
	CT	**		***	
	LA	NS		NS	
	CTxLA	*		NS	

NS,*,**,***Nonsignificant (NS) or significant at P = 0.10, 0.05, or 0.01, respectively.

Table 4.3. Influence of container temperature (CT) treatment and limestone addition (LA) on chlorosis ratings for *Nandina domestica*.

	Chlorosis rating[z]	
	LA ($kg \cdot m^{-3}$)	
Ct treatment	0	4
uninsulated	2.9	1.1
insulated	2.2	1.1
CT	NS	
LA	***	
CTxLA	NS	

[z]Chlorosis rating: 1-5, 5=most chlorosis.
[NS,***]Nonsignificant (NS) or significant at P = 0.001.

CHAPTER V

EFFECTS OF ROOT-ZONE TEMPERATURE, LIMESTONE ADDITION, AND NITROGEN APPLICATION RATE ON THE MEDIUM SOLUTION AND GROWTH OF SELECTED CONTAINER-GROWN WOODY PLANTS

Introduction

In Virginia nurseries, reduced growth, chlorosis, and root injury of certain species of container-grown crops often occurs during the hottest summer months of July and August. *Nandina domestica* and certain cultivars of *Juniperus* are among those plants most susceptible to this problem. While direct effects of heat on physiological processes in the plant cannot be disregarded as a cause of these summer growth reductions, heat-induced ammonia toxicity has been proposed as one of the factors contributing to summer heat stress of container-grown plants (Walden et al., 1989).

In a pine bark medium supplied with NH_4-N and subjected to constant treatment temperature, a medium temperature of 40°C inhibited nitrification, resulting in a greater concentration of NH_4-N in the medium solution at 40°C than at 20° or 30°C (Niemiera and Wright, 1987a). Container medium temperatures in Southern nurseries can exceed 40°C for up to 6 hours a day during summer (Ingram, 1981). Producers of container-grown plants often use fertilizers with an N source that is primarily NH_4-N. During the hot summer months, high container temperatures could reduce nitrification and subsequently the growth of species which prefer NO_3-N. In support

of this theory, the level of NH_4-N in leachates from a container nursery was found to be considerably higher during August than during the cooler month of September (Walden et al., 1989). One objective of the following experiment was to examine the effect on nitrification of daily exposure of the container medium to 40°C for durations similar to medium temperature periods observed under nursery conditions.

Reduced concentrations of Mn have often been observed in the chlorotic tissue of apparently heat-stressed plants in Virginia nurseries (Walden et al., 1989). Woody plants grown in a pine bark medium where nitrification was chemically inhibited also contained lower levels of Mn (Niemiera and Wright, 1986a). Other researchers have found similar effects on the Mn concentration in plants grown with fertilizer regimes high in NH_4-N (Edwards and Horton, 1982; Elamin and Wilcox, 1986). Heat-induced inhibition of nitrification which results in low tissue levels of these nutrients could account for the observed summer chlorosis in Virginia nurseries.

Nitrification increases in a pine bark medium as medium pH increases with limestone amendment (Niemiera and Wright, 1986b). Virginia nurserymen have reported that additions of limestone to pine bark media helped to prevent or eliminate growth reductions and chlorosis in *Juniperus* (Walden et al., 1989). A second objective of this study was to examine the interactions of root-zone temperature, applied N rate from a predominantly ammoniacal N source, and limestone addition to a pine bark medium on the growth and Mn content of three species of woody plants commonly grown in Virginia nurseries.

Materials and Methods

Root-zone temperature modification chambers. Eight temperature control chambers were constructed from 1.9 cm thick 'Tuff-R' (Celotex Corp.) foam insulation board (R-value 5.4) with aluminum facing on both sides. The sides of each chamber were 55.9 cm wide, 297.2 cm long, and 14.0 cm high, with a top of corresponding dimension. Duct tape was used to fasten corners and seal edges. When the chambers were placed upon a greenhouse bench, a sheet of insulation board covering the bench served as the chamber bottom.

A series of holes 11.4 cm in diameter was cut into the top of each chamber on 15.2 cm centers, resulting in a 3 x 18 configuration of openings. Suspending media filled 1-liter nursery style polyethylene containers from these openings effectively sealed the top of the chamber. The outside surface of the top was painted white to reduce the intensity of reflected light.

A supporting frame was constructed to fit inside each chamber. This frame consisted of 1.2 cm thick plywood sides (running parallel to the long dimension of the chamber) joined together by plywood strips that ran just beneath the top between every third row of holes.

Four greenhouse benches were each covered with a 121.9 x 304.8 cm sheet of insulation board overlaid with 2 mil black polyethylene film. Each bench held two chambers, one heated and one unheated. Unheated chambers were placed directly on the polyethylene film. For heated chambers, two 'Agritape' electrical heating mats

(Ken-Bar, Inc., Reading, MA), each 27.9 cm wide x 304.8 cm long, were placed side by side on the polyethylene film. These mats were covered by a 58.4 x 304.8 cm 11 mil wire mesh aluminum grounding screen. Heated chambers were placed directly on this screen. A thermostat (Model T7075A-1024, Honeywell, Inc., Minneapolis, MN) with a remote temperature sensor (Honeywell Model 193987GA) suspended in the chamber air was used to control the heating mat. Two small circulating fans (Model 4M068, Dayton Electric Manufacturing Co., Chicago, IL) mixed the heated air in each chamber for a more uniform temperature. Thermostats were activated and deactivated each day by means of a time clock controller (Dayton Model 2E021).

The diurnal cycle of container medium temperatures in a heated chamber was determined over a 5 day period. One-liter containers, filled with milled pine bark which had been watered to container capacity, were suspended from the chamber openings. The bottoms of the suspended containers were 2.5 cm above the heat mats. The surface of the medium in each container was covered by a disk of 'Guilbond' (Guilford Packaging and Fiber, Inc., Highpoint, NC), a white closed-cell polyethylene foam insulating material, to reduce vertical temperature gradients in the container. Container medium temperatures were monitored with a thermocouple thermometer (Wescor Model TH-65, Wescor, Inc., Logan, UT) using soldered copper-constantan thermocouples. 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 monitored in eight

randomly chosen containers.

Temperatures were recorded hourly from the start of a heating cycle at 0600 hours until 2000 hours each day. Heat mats were deactivated at 1600 hours. The heated chambers gradually raised the root-zone temperature to 40.6°C ±0.4 (SE) (middle) over an approximate 4 hour period and maintained that temperature for about 6 hours each day. There was a vertical temperature gradient of 41.3°C ±0.6 (bottom) to 39.8°C ±0.6 (surface). Container medium temperatures cooled to ambient temperature before the start of the next heating cycle. This same diurnal heating cycle was used during the experimental period.

Plant material and media preparation. A milled pine bark medium was amended with 0 or 6 kg of dolomitic limestone per m^3 and placed in 3.8-liter black polyethylene containers. The containers were irrigated biweekly with a solution containing 100 ppm N as $(NH_4)_2SO_4$, 20 ppm P as KH_2PO_4, and 50 ppm K as KH_2PO_4 and KCl for 10 weeks in order to stimulate nitrification. On February 1, rooted cuttings of *Ilex crenata* Thunb. 'Helleri' and *Juniperus horizontalis* var. 'Prince of Wales' (an apparent heat-stress susceptible cultivar) or seedlings of *Nandina domestica* were transplanted into 1-liter containers filled with either the unamended or limestone amended pine bark and placed in a glasshouse with day/night temperatures of 26°/16°C. Plants were fertilized at each irrigation with 200 ml of a fertilizer solution containing 100 ppm N as NH_4NO_3, 20 ppm P as K_2HPO_4, 50 ppm K as K_2HPO_4 and KCl, 5 ppm Fe as FeEDTA, and micronutrients according to Hoagland and Arnon (1950) during the 3 weeks preceding

treatment initiation .

Experimental procedures. Root-zone temperature treatments were initiated on February 21. Nine containers of each species at each limestone amendment rate were suspended in each root-zone temperature modification chamber. A disk of 'Guilbond', which had been slit through the center to accommodate the plant stem, covered the surface of each container. There were four heated and four unheated chambers..

During the experimental period, medium temperatures of three containers per heated chamber were monitored at 2 hour intervals beginning at 0800 hours 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 about 1500 hours on most days, and were never observed to exceed ambient temperature during the experimental period. Temperatures in the greenhouse varied from a minimum nighttime temperature of 16°C to a maximum daytime temperature of 35°C during the experimental period.

The initial fertilizer treatment application coincided with the start of root-zone temperature treatments. Plants were irrigated weekly with 200 ml of a fertilizer solution containing 200, 400, or 600 ppm N as urea ammonium nitrate. Mid-summer injury to container grown nursery crops in Virginia has often been observed at nurseries using urea ammonium nitrate as the principle N source in a program of liquid

fertilization (R.D. Wright, personal communication). Other nutrients in the fertilizer solutions were as previously described. The irrigation water supplied 20 ppm Ca and 5 ppm Mg.

Depending on plant need, containers were irrigated with 200 ml of tap water once or twice between weekly irrigation with the fertilizer solutions. All irrigations were applied at 1600 hours. Medium solution extracts were obtained after the initial fertilizer treatment application and every two weeks thereafter. Medium solutions were extracted 16 hours after fertilizer solutions were applied, by pouring 75 ml distilled water on the surface of the medium and collecting the leachate. Medium solution extracts were obtained from *I. crenata* containers only. One container per treatment per block was sampled. The pH of the medium solution extracts was determined prior to freezing for later analysis. Medium solution concentrations of NH_4-N and NO_3-N were determined for all extraction dates using specific ion electrodes (Orion, Cambridge, MA). Medium solution extracts taken on day 40 and day 80 were analyzed for P using a colorimetric procedure (Watanabe and Olsen, 1965), and for K, Ca, Mg, Zn, Fe, Mn, and Cu by atomic absorption spectroscopy.

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

Experimental design. Treatments were arranged in randomized complete blocks

with a split plot design. The main plots were comprised of the two root-zone temperature regimes, while a factorial combination of the two limestone amendment rates and three N application rates comprised the subplots. There were three plants per subplot in each of four blocks. Each plant species was treated as a separate experiment.

Statistical Analysis. Data were subjected to an analysis of variance. Regression analysis conducted to test for significant linear and quadratic effects of nitrogen application rate (NAR) and interactions of NAR with root-zone temperature (RZT) and limestone addition (LA) were based on single degrees of freedom of orthogonal comparisons.

Results

Plant growth. Growth of each species was influenced by the interaction of RZT and LA (Table 5.1). Shoot and root dry weights of *I. crenata* were reduced by LA or high RZT ('heated'); however, the decrease in dry weights due to high RZT was greater when plants were grown in unlimed pine bark.

For *N. domestica*, shoot and root growth were increased by LA and reduced by high RZT (Table 5.1). The decrease in shoot dry weight due to high RZT was greater in the limed medium. Heated plants without limestone addition were totally necrotic within 4 weeks of the beginning of the experiment. Heated plants with limestone addition had a generalized chlorosis characterized by complete loss of pigmentation in the youngest leaves.

High RZT reduced shoot and root dry weights of *J. horizontalis*, but there were only slight differences in dry weights due to RZT in the limed medium (Table 5.1). The increase in shoot dry weight with limestone amendment was observed only at high RZT. Many of the heated/unlimed plants had an overall chlorosis characterized by a slight bronzing of the foliage.

An interaction of NAR and LA influenced the growth of *N. domestica* (Table 5.2). Shoot and root dry weights increased in response to increasing NAR in limed media, but showed no response to NAR in unlimed media. Growth of *I. crenata* or *J. horizontalis* was not influenced by any interactions of NAR with RZT or LA.

Tissue nutrient content. Tissue analysis results are presented for Mn only, since the effects of RZT or interactions of RZT and NAR or LA on other tissue nutrient levels were minor. The shoot tissue concentration of Mn in *I. crenata* was influenced by an interaction of RZT with NAR (Table 5.3). The concentration of Mn in shoots increased as NAR increased at moderate RZT, but was not affected by NAR at high RZT. For *N. domestica*, shoot tissue concentration of Mn showed a similar trend ($P \leq 0.10$) toward dependence on NAR and RZT. Tissue analysis for *N. domestica* are for limed treatments only, since heated/unlimed treatments yielded insufficient amounts of tissue for nutrient analysis. The concentration of Mn in shoots of *J. horizontalis* was decreased by high RZT but was not influenced by the interaction of RZT and NAR.

Medium solution composition. In unlimed media, pH increased from 4.5 on the initial extraction date to a maximum pH on day 40 (Figure 5.1). This increase in pH

was greater at higher NAR. In limed media, there was no increase from an initial pH of 6.9 and little difference in pH due to NAR during the first 40 days. Medium solution pH gradually declined thereafter, but remained higher in the heated media regardless of limestone addition. The rate of pH decline in limed media was greater at higher NAR.

Limestone addition resulted in a much lower medium solution ratio of NH_4-N:NO_3-N, whether heated or unheated (Figure 5.2). The influence of RZT and LA on concentrations of NH_4-N and NO_3-N was similar over all levels of nitrogen application, thus data for NAR of 400 ppm only are shown. After day 40, the ratio of NH_4-N:NO_3-N was significantly higher for the heated/unlimed treatment compared to the unheated/unlimed treatment. This difference was due to higher NO_3-N levels for the unheated/unlimed treatment and higher NH_4-N than NO_3-N for the heated/unlimed treatment.

Root-zone temperature had no influence on the concentrations of any other nutrients in the medium solution extracted on day 40, and only minor influences on all but the concentration of Mn on day 80. Root-zone temperature influenced the medium solution concentration of Mn 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, there was a significant linear relationship on day 80 between the pH of the medium solution and medium solution Mn concentration (Figure 5.3). Manganese concentration decreased as the medium solution pH increased. High

medium solution pH and low Mn concentrations were generally associated with heated treatments.

Discussion

High root temperature reduced the growth of all three species. Growth reductions were likely the result of indirect heat injury since critical temperatures for direct injury to root cell membranes of woody plants are higher than 40°C for 5 hour exposure (Ingram, 1985, 1986). For a number of woody plant species, shoot growth, root growth or both have been decreased by 6 hour/day exposure of roots to 40°C (Harrison et al., 1988; Ingram et al., 1986; Johnson and Ingram, 1984; Yeager et al., 1991). Reduced growth at supraoptimal root temperature can result from several specific physiological responses to supraoptimal root temperatures including decreased rates of photosynthesis, increased rates of respiration, and alterations in the partitioning of photoassimilate (Foster et al., 1991; Johnson and Ingram, 1984; Martin et al., 1989; Ruter and Ingram, 1990, 1991);

The interactive effect of RZT and LA on growth differed for each species. Reduced growth of *I. crenata* (Table 5.1) in limed media can be attributed to the lower medium solution NH_4-N:NO_3-N ratio (Figure 5.2). *Ilex crenata* and other woody plant species have demonstrated a preference for NH_4-N nutrition (Cain, 1952; Colgrove and Roberts, 1956; Chrustic and Wright, 1983; Greidanus, et al., 1972). The magnitude of growth reduction due to high root temperature was greater in the unlimed medium; however, the percent decrease in dry weight due to the interaction of RZT and LA was

similar. In the unlimed medium, shoot and root dry weights declined 69 and 74%, respectively, at high RZT. The decline in shoot and root weights due to high RZT was a similar 66 and 76%, respectively, in the limed medium. This suggests that, for *I. crenata*, the growth effects of physiological stress due to high RZT were independent of any growth effects due to LA (i.e., no synergism of RZT and LA).

Growth of *N. domestica* responded positively to limestone addition to the medium (Table 5.1). The magnitude of reduction in shoot growth due to high root temperature was greater in the limed medium. The percent decrease in dry weight due to the interaction of RZT and LA, however, was greater in the unlimed medium. High RZT reduced shoot dry weight by 55% in the limed medium and by 94% in the unlimed medium. Thus, there was an apparent synergism of the stress due to high RZT and whatever factors were present in the root environment of unlimed pine bark that were unfavorable for growth of *N. domestica*.

Growth of *N. domestica* may have been reduced by a higher ratio of NH_4-N:NO_3-N in unlimed pine bark, the effect of which was greater at high RZT. Although medium solution extracts were from *I. crenata* (Figure 5.2), liming effects on concentrations of NH_4-N and NO_3-N were likely similar for both species since the positive influence of limestone addition on nitrification and adsorption of NH_4^+ in pine bark media is well known (Chrustic and Wright, 1983; Foster et al., 1983; Niemiera and Wright, 1986b). Growth of *N. domestica* increased as NAR increased in limed media, but showed no response to NAR in unlimed media (Table 5.2), suggesting that this species prefers the

lower NH_4-N:NO_3-N ratio in limed media.

The utilization of ammonium as an N source is enhanced when carbohydrates are readily available within the plant (Mengel and Kirkby, 1982). In the root, carbohydrate availability influences the uptake of NH_4-N, since carbon skeletons and energy are necessary for rapid incorporation of NH_4^+ into amino acids for transport to the shoot (Kirkby and Hughes, 1970; Michael *et al.*, 1970). Carbohydrates in the shoot are necessary for detoxification of free ammonium through incorporation into organic compounds (Givan, 1979). It seems likely that any disruption in carbohydrate metabolism may lessen the effectiveness of ammonium as an N source.

In this experiment, it was observed that the initial growth of *N. domestica* in the unlimed medium was less vigorous than growth in the limed medium. Additionally, the majority of the previous year's leaves on *N. domestica* seedlings abscised during the initiation of shoot growth. This made growth of the new shoots dependent on stored carbohydrate reserves until new leaves made the transition from carbohydrate sink to carbohydrate source. The imposition of high root-zone temperature would have placed further demand on these stored carbohydrate reserves, since supraoptimal root temperatures have been shown to increase root respiration (Foster et al., 1991; Ruter and Ingram, 1991), as well as alter the distribution of carbohydrates between shoot and roots (Ruter and Ingram, 1990). Hence, the lower carbohydrate pool in plants subjected to high root temperature may have limited the ability of *N. domestica* to utilize the higher levels of NH_4-N in the unlimed medium or detoxify ammonium in the

plant. This was especially obvious early in the experiment. The initial shoot development of *N. domestica* grown in the unlimed medium was slower than that in the limed medium. Plants grown in the unlimed medium at high RZT never developed fully expanded leaves and were completely necrotic within 4 weeks from the start of the experiment. Growth of plants in the unheated, unlimed medium became more vigorous as the experiment progressed and the initial leaves matured.

Regardless of root-zone temperature, growth of *N. domestica* responded positively to limestone addition and the resulting lower NH_4-N:NO_3-N ratio present in the limed medium. In contrast, *Ilex crenata* demonstrated a positive growth response to no limestone addition and the higher NH_4-N:NO_3-N ratio which resulted.

The growth response of *J. horizontalis* to limestone addition was dependent on root-zone temperature. *Juniperus horizontalis* grew equally well in limed or unlimed pine bark at moderate RZT (Table 5.1). This result concurs with that of Cobb (1983) who found that growth of *Juniperus* was not influenced by limestone addition to a pine bark:sandy clay medium. Other studies have shown increased growth of *Juniperus* species in response to limestone addition to a pine bark:sand medium (Chrustic and Wright, 1983; Wright and Hinesly, 1991). Those authors speculated that *Juniperus* prefers the lower medium solution NH_4-N:NO_3-N ratio which results from limestone addition to media. In the present study, the NH_4-N:NO_3-N ratio did not appear to be critical for growth of *J. horizontalis* at optimal root-zone temperatures. At high RZT, there was a positive growth response to limestone addition, which may indicate that *J.*

horizontalis prefers an N regime of predominately NO_3-N when root temperatures are supraoptimal. Alterations in normal carbohydrate metabolism due to supraoptimal root temperature may have had less impact on plant utilization of NO_3-N than NH_4-N.

Alternatively, it can be argued that the growth increase due to limestone addition at high RZT was simply a direct result of lower acidity or increased calcium level in the limed medium. It is known that high concentrations of H^+ in the rhizosphere can influence root membrane stability, inducing leakage of root cell contents which can be counteracted by addition of Ca^{+2} (Mengel and Kirkby, 1982). Disruption of root cell membrane stability is considered one of the primary mechanisms by which heat stress of roots reduces the growth of container-grown plants (Ingram, 1986). Jacobson et al. (1957) demonstrated that an interaction of pH and root temperature can affect the stability of root cell membranes, thereby influencing the absorption of K by barley roots. At 40°C, there were similar net losses of K from barley roots at pH 3 or 4, due to K efflux from leaky root membranes, while there was a net influx of K into roots at pH 5. Addition of $CaCl_2$ to an incubation solution has decreased thermally induced leakage of betacyanin from beet root tissue at 45°C (Toprover and Glinka, 1976); however, this effect was observed at Ca concentrations (12.5 mM) significantly greater than those commonly observed in limed pine bark media (Wright and Hinesly, 1991).

Root-zone temperature influenced the composition of the *I. crenata* medium solution, especially medium solution pH. This influence results from the dynamic interaction of root-zone temperature with other factors known to affect medium solution

pH such as N source, nitrification rate, plant growth and absorption of N. The nature of these interactions is best illustrated by focusing on pH changes over time in the unlimed medium.

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 is completely hydrolyzed within 24 hours (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 unlimed media increased as NAR increased (Figure 5.1).

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 the development of a population of nitrifiers. 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 NH_4-N. Niemiera et al. (unpublished data) found that *I. crenata* 'Helleri' absorbs NH_4-N in preference to NO_3-N at a ratio of approximately 3:1 from a nutrient solution of NH_4NO_3. Ammonium nutrition 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 (Figure 5.1). This difference is due, in part, to differences in plant growth. The larger plants which resulted from the unheated/unlimed treatment would absorb more NH_4-N from the medium solution than the smaller plants which resulted from the heated/unlimed treatment (Table 5.1).

Differences in medium solution pH between these treatments may also be attributed to less nitrification at supraoptimal medium temperature. Rates of nitrification have been shown to decline in mineral soil at temperatures greater than an optimum of 26°C (Beck, 1983). As medium solution pH decreased in the unheated/unlimed medium (Figure 5.1), there was a concomitant increase in the concentration of medium solution NO_3-N after 40 days (Figure 5.2), an indication that nitrification was proceeding. There were only slight increases in NO_3-N in the medium solution extracted from the heated/unlimed medium during this period. Less nitrification took place in the unlimed medium at high RZT, resulting in a higher medium solution NH_4:NO_3 ratio in comparison to that in the unheated/unlimed medium (Figure 5.2).

These results indicate that daily exposures of the container medium to temperatures of 40°C or greater, for durations such as those commonly observed in mid-summer in Southern nurseries, can decrease rates of nitrification in a pine bark medium, thereby altering the NH_4:NO_3 ratio in the medium solution. Under conditions where the fertilizer N source consists of predominantly NH_4-N, a higher ratio of NH_4:NO_3 may reduce the growth of species which prefer NO_3-N.

In limed media, the initial hydrolysis of urea did not increase the pH of the medium

solution. The gradual decrease in medium solution pH after 12 days (Figure 5.1) can be attributed to nitrification. The decline in medium solution pH was more rapid at the higher rates of N application (Figure 5.1), 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 than in the unheated/limed medium at highest NAR suggests that nitrification may have been limited by high medium temperature at the highest substrate level, although medium solution ratios of NH_4-N:NO_3-N at NAR of 600 ppm in limed media were similar, regardless of RZT (data not shown).

When limestone was added to the medium, RZT had no appreciable effect on nitrification, as evidenced by the similar medium solution NH_4-N:NO_3-N ratios for heated or unheated/limed media (Figure 5.2). Limestone addition raised the initial pH of the pine bark medium from 4.5 to 6.9 (Figure 5.1). In soils, nitrification rates increase from a minimum at pH 4.0 - 4.5 (Broadbent, et al., 1957; Webber and Gainey, 1962) to a maximum at pH 7.0 - 8.0 (Focht and Verstraete, 1977). Growth and metabolism of a nitrifying population are pH-dependent (Sarathchandra, 1978). Over the 7 days between NH_4-N application, during daily periods of lower, more optimal temperature, nitrification in the heated/limed medium may have been sufficient to nitrify amounts of applied NH_4-N similar to that in the unheated/limed medium.

High RZT generally lowered the concentration of Mn in plants in this experiment. Direct effects of heat injury to roots on Mn uptake cannot be disregarded as possible cause for lower tissue levels of Mn; however, the influence of RZT on medium solution

pH could account for much of the influence of RZT on Mn levels in the plant. Tissue and medium solution data for *I. crenata* support this contention.

Final shoot tissue Mn concentration doubled from the lowest to the highest NAR at moderate RZT, but varied less with increasing NAR at high RZT (Table 5.3). The medium solution pH on day 80 was lower at higher NAR, but was generally higher at each level of NAR in the heated medium (Figure 5.1). Medium solution Mn concentrations on day 80 were lowest at highest pH; heated treatments were generally associated with high pH (Figure 5.3). Final shoot tissue Mn concentration decreased as medium solution Mn concentration on day 80 decreased (Figure 5.4).

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. In the heated medium, the pH increase due to urea hydrolysis or limestone addition was counteracted to a lesser extent by acidity due to nitrification or plant absorption of NH_4-N than similar pH increases in the unheated medium. The higher medium pH resulted in lower medium solution Mn concentrations and, subsequently, lower tissue levels of Mn, at high RZT. These effects could account for the lower Mn levels frequently observed in the tissue of apparently heat stressed container-grown plants fertilized with an N source high in urea-N. Additionally, higher ratios of NH_4-N:NO_3-N in container medium where high root-zone temperature has decreased nitrification may further reduce plant absorption of Mn, since manganese content in plant tissue has been shown to decrease as the NH_4-N:NO_3-N ratio increases

in nutrient solution (Edwards and Horton, 1982; Elamin and Wilcox, 1986). Use of fertilizers with an N source containing no urea and no more than 50% NH_4-N for production of container grown woody plants in Southern nurseries may help reduce the incidence of high root-zone temperature induced chlorosis due to Mn deficiency or ammonium toxicity.

In this experiment, heating of the container medium to 40°C for 6 hours/day proved sufficient to increase the medium solution NH_4-N:NO_3-N ratio by decreasing nitrification in unlimed media. The NH_4:NO_3 ratio in limed media was lower than that in unlimed media, regardless of RZT. That is, limestone addition to a pine bark medium promoted nitrification, even at supraoptimal medium temperature. Thus, addition of sufficient limestone to encourage nitrification under conditions of high root-zone temperature may be an important cultural practice in Southern nurseries where container medium temperatures exceed 40°C during the production of plants that prefer low ratios of NH_4-N:NO_3-N.

Table 5.1. Influence of root-zone temperature (RZT) and limestone addition (LA) on dry weight of *Ilex*, *Nandina*, and *Juniperus*.

		Lime ($kg \cdot m^{-3}$)			
		0	6	0	6
Genus	RZT	Shoot wt		Root wt	
		g			
Ilex					
	unheated	6.2	3.5	0.9	0.5
	heated	1.9	1.2	0.2	0.1
	RZT	***		**	
	LA	***		***	
	RZTxLA	***		***	
Nandina					
	unheated	3.3	8.2	0.8	1.9
	heated	0.2	3.7	0.2	0.6
	RZT	***		**	
	LA	***		***	
	RZTxLA	***		NS	
Juniperus					
	unheated	8.8	8.8	1.4	1.1
	heated	5.3	8.0	0.8	1.0
	RZT	**		*	
	LA	***		NS	
	RZTxLA	***		***	

NS,*,**,***Nonsignificant (NS) or significant at P = 0.05, 0.01, or 0.001, respectively.

Table 5.2. Influence of limestone addition (LA) and nitrogen application rate (NAR) on dry weight of *Nandina domestica*.

NAR (ppm)	LA ($kg \cdot m^{-3}$)			
	0	6	0	6
	Shoot wt		Root wt	
	g			
200	1.5	3.9	0.6	1.0
400	1.3	6.2	0.4	1.2
600	1.0	7.1	0.3	1.3
LA	***		***	
NAR_L	NS		NS	
NAR_Q	NS		NS	
$LAxNAR_L$	***		**	
$LAxNAR_Q$	NS		NS	

NS,**,***Nonsignificant (NS) or significant at P = 0.01 or 0.001, respectively.

Table 5.3. Influence of root-zone temperature (RZT) and nitrogen application rate (NAR) on shoot tissue Mn concentration.

Genus		RZT	
		unheated	heated
		Mn concentration	
		ppm	
Ilex			
	200	295	308
	400	430	312
	600	600	321
	RZT	NS	
	NAR_L	***	
	NAR_Q	NS	
	$RZTxNAR_L$	***	
	$RZTxNAR_Q$	NS	
Nandina[z]			
	200	17	18
	400	35	22
	600	70	40
	RZT	NS	
	NAR_L	***	
	NAR_Q	NS	
	$RZTxNAR_L$	NS	
	$RZTxNAR_Q$	NS	
Juniperus			
	200	164	106
	400	189	122
	600	224	148
	RZT	**	
	NAR_L	**	
	NAR_Q	NS	
	$RZTxNAR_L$	NS	
	$RZTxNAR_Q$	NS	

[z]Limestone amended treatments only.
[NS,**,***]Nonsignificant (NS) or significant at P = 0.01 or 0.001, respectively.

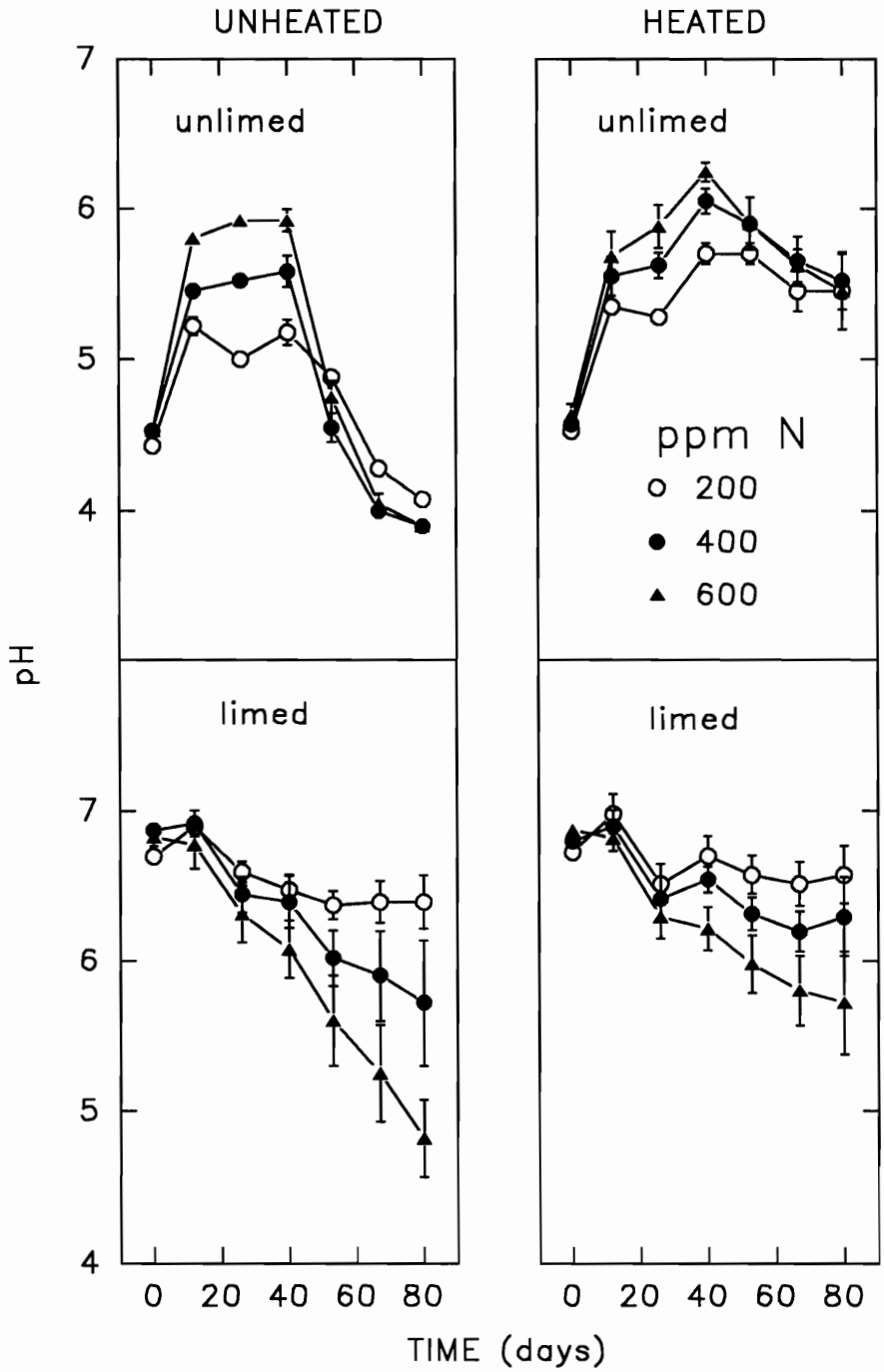

Figure 5.1. Influence of root-zone temperature, limestone addition, and nitrogen application rate on medium solution pH for *Ilex crenata*. Missing SE bars were smaller than symbols.

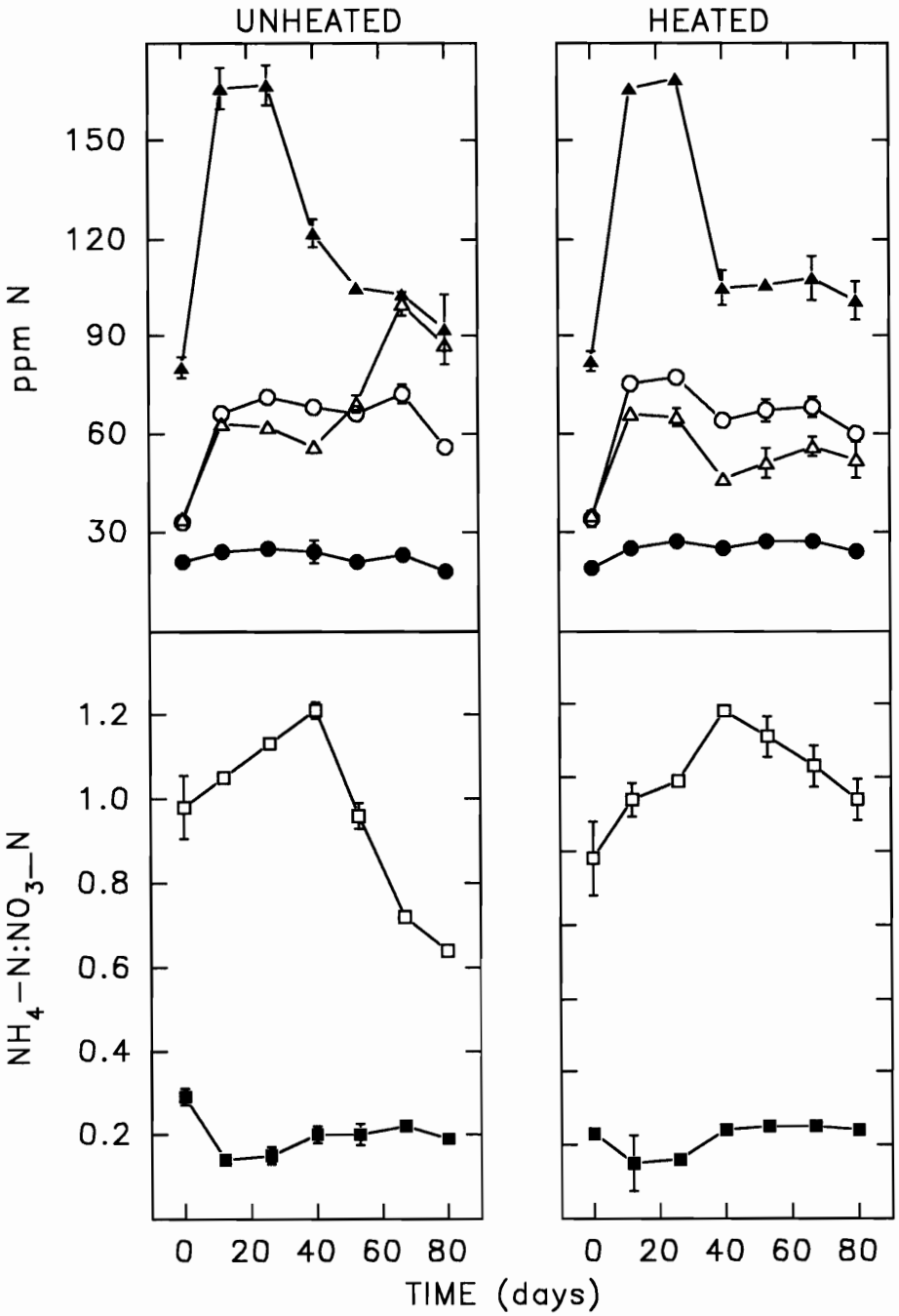

Figure 5.2. Influence of root-zone temperature and limestone addition on medium solution concentration of NH_4-N (○,●) and NO_3-N (△,▲) for *Ilex crenata* at nitrogen application rate of 400 ppm. Open symbols indicate no limestone addition. Solid symbols indicate limestone addition. Missing SE bars are smaller than symbols.

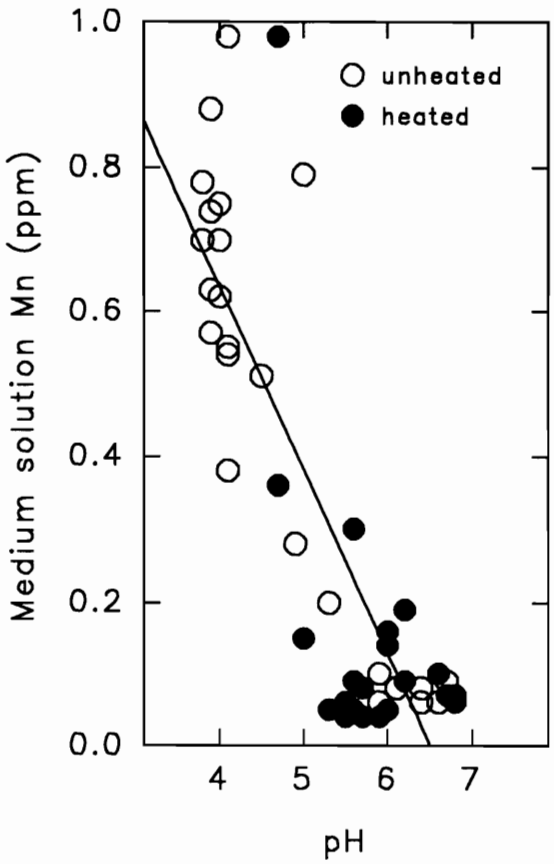

Figure 5.3. Relationship between medium solution pH and medium solution Mn concentration on day 80. $Y = 1.65 - 0.25X$, $r^2 = 0.71^{**}$.

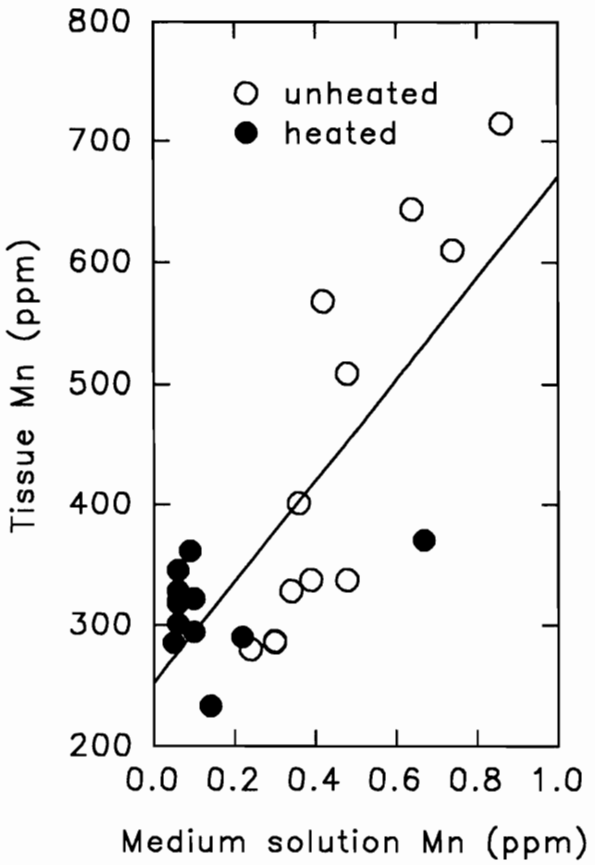

Figure 5.4. Relationship between medium solution Mn concentration on day 80 and final shoot tissue Mn concentration. $Y = 252 + 419X$, $r^2 = 0.61^{**}$.

CHAPTER VI

INFLUENCE OF HIGH TEMPERATURE AND EXPOSURE TIME ON NITRIFICATION IN A PINE BARK MEDIUM

Introduction

The growth and nutrient composition of container-grown woody plants can be significantly influenced by the ionic form of nitrogen in the container medium (Chrustic and Wright, 1983; Niemiera and Wright, 1986a; Walden and Epelman, 1988). When predominantly ammoniacal nitrogen sources are applied to a pine bark medium, the NH_4:NO_3 ratio in the medium solution is largely determined by the rate of nitrification (Niemiera and Wright, 1987b). Nitrification is the biological conversion of NH_4^+ to NO_3^- and, as such, is influenced by several environmental factors, including medium temperature (Alexander, 1977).

In Southern nurseries, the growth and quality of container-grown plants can be limited by the supraoptimal medium temperatures which result from heat gain due to solar radiation on the sidewalls of dark colored containers (Ingram, 1981; Keever and Cobb, 1984; Laiche, 1985). Medium temperatures can exceed 40°C for up to 6 hours a day, while portions of the container may exceed 50°C for as much as 2 hours (Ingram, 1981; Martin and Ingram, 1988). Temperatures this high may inhibit nitrification (Beck, 1983), potentially increasing the ratio of NH_4-N to NO_3-N in the medium solution of plants fertilized with ammoniacal nitrogen sources. Heat-induced

ammonia toxicity has been proposed as one of the factors contributing to summer heat stress of container-grown plants (Walden et al., 1989).

In a pine bark medium, a constant temperature of 20° or 30°C promoted rapid nitrification, while continuous exposure to 40°C significantly inhibited nitrification (Niemiera and Wright, 1987a). This response to medium temperature increased the concentration of NH_4-N relative to NO_3-N in medium solution extracts. In a previous experiment (Chapter V), where nitrogen was supplied largely in the ammoniacal form, a 6 hour/day exposure of the container medium to 40°C increased the medium solution NH_4:NO_3 ratio in comparison to that in media exposed to cooler temperatures. Higher concentrations of NH_4-N were observed in leachates from a container nursery during August than during the cooler month of September (Walden et al., 1989). This suggests that under nursery conditions, the container medium may reach temperatures sufficiently high for an adequate period of time to inhibit nitrification. The objective of this research was to determine the temperatures and the durations of daily exposure to those temperatures which inhibit nitrification in a pine bark medium. Knowledge of this interaction would help producers of container-grown plants adjust cultural practices for plants which may be sensitive to elevated levels of NH_4-N in the medium solution.

Materials and Methods

Preincubation procedure. One-hundred twenty 1-liter polyethylene containers were filled with a milled pine bark medium which had been amended with 6 kg dolomitic limestone per m^3. In order to stimulate nitrification, each container received

a twice weekly irrigation with 200 ml of a solution containing 200 ppm N as $(NH_4)_2SO_4$, as well as an occasional irrigation with plain tap water to avoid buildup of soluble salts in the medium. The containers were held for a 90 day preincubation period in a room whose temperature varied from 21° to 28°C. At the end of this period, the establishment of a population of nitrifiers was verified by the appearance of NO_3^- in the medium solution extracted by the pour-through procedure (Wright, 1987). Two hours after irrigation, distilled water (75 ml) was applied to the container medium surface, and the resultant leachate was collected and analyzed for NO_3-N and pH using ion-selective electrodes (Orion Research Inc., Boston, MA). The medium solution pH of a sampling from 10 containers was 5.9 $\pm$0.2 (SE). Although the optimum pH range for nitrification is 7 to 8 (Focht and Verstraete, 1977), nitrification readily occurs in a pine bark medium between pH 5 and 6 (Niemiera and Wright, 1986b).

Container temperature control chambers. The temperature control chambers used in this experiment were a modification of the heated chambers described in Chapter V. The modifications resulted in smaller chambers which completely enclosed containers for more precise control of container medium temperatures.

Five of the original chambers were partitioned into three sections by inserting two pieces of insulation board across the inside of a chamber. This created a smaller chamber in the midsection of the original chambers, 55.9 cm wide x 121.9 cm long x 14.0 cm high, with a 3 x 8 configuration of openings in the top. The two remaining

end sections of the original chamber, which were unused, were each covered by a piece of insulation board affixed with duct tape. The new chamber had two circulating fans and the same temperature control system previously described in Chapter V.

A removable cover of insulation board, with a foam gasket around the bottom edge, was fitted to the top of the chamber. This cover was placed over containers suspended in the openings, completely enclosing the containers in the chamber. The cover was then weighted down for a more efficient seal. Additionally, the surface of each container was covered by a disk of 'Guilbond' to provide further insulation and retard moisture loss from the container medium.

Experimental Design. On the morning following the preincubation period, 24 containers were placed in each of five temperature controlled chambers maintained at 28°, 34°, 40°, 46°, or 52°C. The containers in each chamber were gradually heated to their respective chamber temperature over a period of about 4 hours. Five containers were then randomly selected for removal from each chamber at intervals of 1, 2, 4, and 6 hours after reaching the chamber temperature. Container medium temperatures were monitored with a CR10 data acquisition system (Campbell Scientific Inc., Logan, UT) by means of soldered copper-constantan thermocouples placed in the center of the medium in the five containers which were the last to be removed from a chamber.

Following removal from a chamber, the containers were held in a room with a day/night temperature of 28°/22°C and allowed to equilibrate to the room temperature. This sequence was repeated every 24 hours using the same five containers, randomly

placed in a chamber, for each temperature and exposure time treatment combination. Four containers remained in each chamber for a 24 hour daily exposure to the chamber temperature.

The container medium attained the chamber temperature within 4 hours after placement into a chamber in all five chambers, with little variation in temperature during the exposure time (Figure 6.1). Following removal from a chamber, the containers equilibrated to room temperature over approximately 5 hours. This pattern of gradual heating and cooling of the container medium each day simulates temperature patterns observed in Southern nurseries during the summer months (Ingram, 1981; Ingram and Martin, 1988).

Prior to their initial placement in the chambers, containers were irrigated with 200 ml of a nutrient solution containing 200 ppm N as $(NH_4)_2SO_4$, 10 ppm P as H_3PO_4, and 25 ppm K as KCl. After 2 hours drainage, an initial weight was recorded for each container. All containers were brought back to this initial weight by the addition of distilled water at the beginning of each 24 hour period. This was intended to keep medium moisture levels above that which might inhibit nitrification.

Every 5 days, the medium solution of each container was extracted by the pour-through procedure, 2 hours after bringing containers back to their initial weight. Containers were then fertilized with 200 ml of the nutrient solution, drained for 1 hour, and returned to the temperature controlled chambers. This procedure was followed for 20 days, resulting in 4 extraction dates over the course of the experiment. There were

five replicate extracts for each temperature and exposure time treatment combination, with the exception of the 24 hour exposure, which had four replications. Medium solution extracts were analyzed for NH_4-N and NO_3-N using ion-selective electrodes (Orion Research Inc., Boston, MA).

Results and Discussion

The effects of temperature and daily exposure duration on the concentrations of NH_4-N in medium solution extracts were quite similar for all four extraction dates (Figure 6.2). Similar, low medium solution concentrations of NH_4-N were present at temperatures of 28° and 34°C for all daily exposure times and at 40°C for daily exposures of 6 hours or less. The low concentrations of NH_4-N in the medium solution, particularly after 15 and 20 days, indicate that, for these treatments, the availability of substrate (NH_4-N) did not exceed the oxidative capacity of the nitrifiers. Rates of nitrification have been shown to decline in mineral soil at temperatures greater than an optimum of 26°C (Beck, 1983). In a pine bark medium supplied with NH_4-N, nitrate accumulation rates were significantly lower at 40°C than at 30°C (Niemiera and Wright, 1987a). Presumably, in the present study, the container medium exposed to 40°C for 6 hours or less per day experienced lower, more optimum temperatures for sufficient periods of time during the 5 days between extractions to nitrify amounts of applied NH_4-N equivalent to that nitrified at 28° or 34°C. Alternatively, fluctuating medium temperatures may have stimulated nitrification, as has been observed in mineral soil (Campbell et al., 1973).

On all extraction dates, the concentration of NH_4-N in medium extracts from the 40°C treatments was higher for the 24 hour/day exposure than for shorter exposure times (Figure 6.2). This apparent inhibition of nitrification (increase in medium extract NH_4-N) caused by constant exposure to 40°C is in agreement with the results of Niemiera and Wright (1987a). On most days, there was a similar increase in NH_4-N for the 2 hour/day exposure to 46°C, with greater increases for longer exposures to this temperature. The further inhibition of nitrification at temperatures higher than 40°C indicates that nitrification was not completely inhibited at 40°C, even after 20 days of constant exposure to this temperature.

The maximum level of NH_4-N concentration in medium solution extracts was generally found after 24 hour/day exposure to 46°C, or after 1 hour/day exposure to 52°C, with no significant increases for longer exposures to 52°C. These results indicate that a short term (1 hour) daily exposure of the container medium to a temperature of 52°C completely inhibited nitrification, while the effect at 46°C varied with the duration of exposure. Beck (1983) found that nitrification ceased in mineral soil at an incubation temperature of 50°C. Ingram (1985) found very similar interactions of temperature and exposure duration on the root cell membrane thermostability of Pittosporum tobira. Using an electrolyte leakage model to describe these interactions, direct membrane injury was predicted for a 30 minute exposure to 52.2°C or a 5 hour exposure to 46.3°C. In the present study, 46°C appeared to be a critical temperature for nitrification in a pine bark medium since NH_4-N increased in

direct proportion to the duration of exposure.

Medium solution concentrations of NO_3-N decreased over time for all temperature and exposure time treatment combinations (Figure 6.2). The largest decreases in NO_3-N concentration generally corresponded to temperature related increases in NH_4-N concentration, consistent with an inhibition of nitrification. Although NO_3-N concentration was quite variable on the first two extraction dates, this relationship was strongly evident by day 15. At 46°C, the medium solution concentration of NO_3-N decreased for exposures greater than 2 hours/day. The lowest concentrations of NO_3-N were associated with 24 hour/day exposure to 46°C or any exposure of the medium to 52°C. It is noteworthy that by day 20, 1 hour/day exposure to 52°C resulted in a medium solution NH_4:NO_3 ratio approximately 70 times higher than that at a constant 28°C.

The concentration of NO_3-N for 6 hour/day exposure to 40°C was significantly less than that for the same exposure to 28° or 34°C on all four extraction dates. However, as previously noted, the low concentration of NH_4-N for 6 hour/day exposure to 40°C did not differ appreciably from that for the same exposure to lower temperature on any extraction date. The lack of a concomitant increase in NH_4-N with the decrease in NO_3-N makes uncertain the effect on nitrification of a 6 hour/day exposure to 40°C. The decrease in NO_3-N observed for a 6 hour/day exposure to 40°C is consistent, however, with the decrease in medium solution NO_3-N observed during a previous experiment (Chapter V) in unlimed pine bark.

Reasons for the lack of concomitant increase in NH_4-N with the decrease in NO_3-N are unclear. Because NO_3-N is anionic and, therefore, not adsorbed to the positively charged surface of pine bark particles, changes in the level of NO_3-N in a pine bark medium would be directly reflected in the concentration of NO_3-N in the medium solution. In contrast, NH_4-N is cationic and subject to adsorption to the surface of pine bark particles (Foster et al., 1986). For this reason, changes in the level of NH_4-N in a pine bark medium may not be as readily evident as those for NO_3-N in medium solution extracts obtained by a solution displacement procedure, such as the pour-through method.

The results of this experiment indicate that the patterns of container medium temperature often observed in Southern nurseries in mid-summer are capable of inhibiting nitrification and thereby influencing the ratio of NH_4-N to NO_3-N in the medium solution of plants fertilized with predominantly ammoniacal nitrogen. Medium temperature and exposure duration must be considered in defining conditions which are critical for nitrification.

In this experiment, a decrease in medium solution NO_3-N suggests that inhibition of nitrification begins after 6 hour/day exposure to 40°C. A medium temperature of 46°C had the greatest interaction with exposure time on nitrification, with little inhibition for a short term exposure (1 hour/day) and increasing inhibition for longer daily exposure times. Since nursery containers generally are at their maximum temperature for less than 1 hour per day (Ingram, 1981; Young and Hammet, 1980),

there likely will be no heat induced elevation of medium solution NH_4-N concentration if maximum container temperatures do not exceed 46°C. Furthermore, patterns of medium temperature in nursery containers observed in Chapter III and by others (Ingram, 19981; Martin and Ingram, 1992) indicate that when the maximum medium temperature does not exceed 46°C, medium temperatures will exceed 40°C for less than 6 hours. Nurserymen producing plants which might be sensitive to elevated ratios of NH_4-N:NO_3-N in the medium solution should adopt cultural practices which prevent maximum container medium temperatures from exceeding 46°C. However, it would be prudent for nurserymen to consider the many documented instances of negative growth response of woody plants to root-zone temperatures which exceed 40°C (Foster et al., 1991; Ingram et al., 1986; Johnson and Ingram, 1984; Newman and Davies, 1988; Ramcharan et al., 1991) when choosing a target maximum container medium temperature.

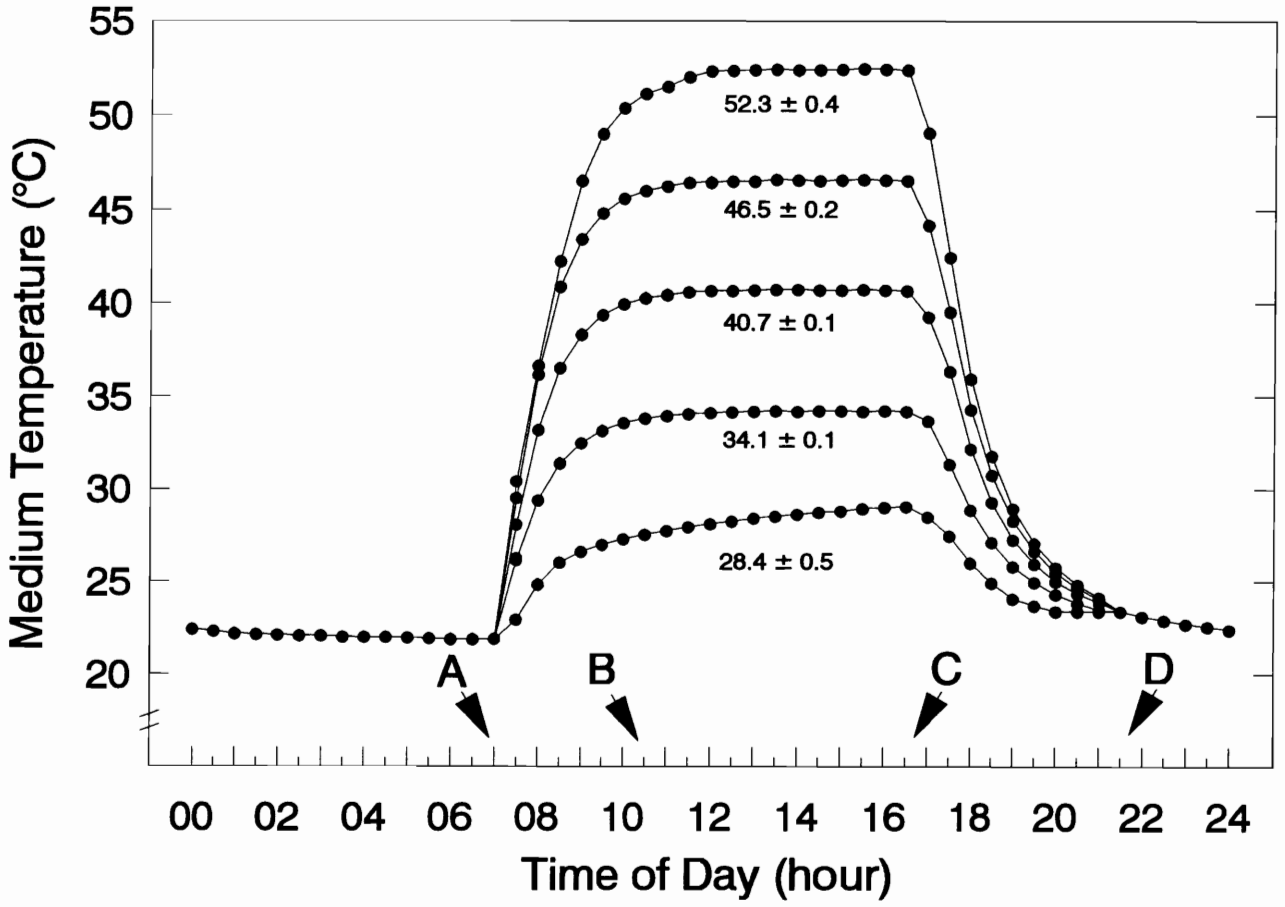

Figure 6.1. Diurnal temperatures of the container medium exposed to five chamber temperatures. Each point between placement of the containers into a chamber at 0700 hours (A) and equilibration to room temperature at 2100 hours (D) represents the mean of five containers. Mean container medium temperatures ± SE are shown for each chamber during a 6 hour exposure, beginning at 1030 hours, when the container medium reached the chamber temperature (B), and ending at 1630 hours, when the containers were removed from the chambers (C).

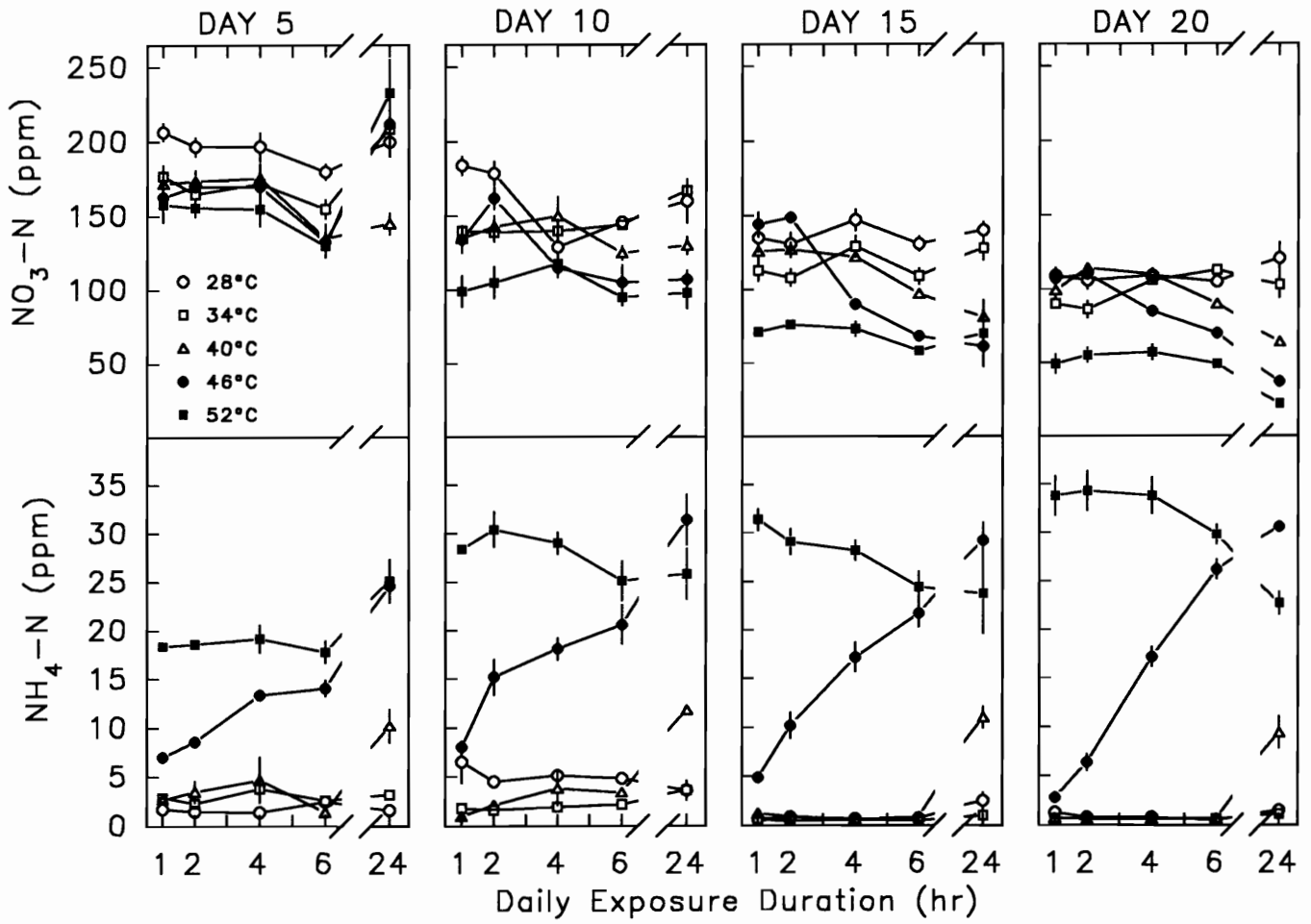

Figure 6.2. Influence of medium temperature and daily exposure duration on medium extract NH_4-N and NO_3-N concentrations over 20 days. Extracts on each date were obtained 5 days after fertilization. If bars are not indicated, the SE of NH_4-N and NO_3-N is less than 1.0 and 3.0 ppm, respectively.

CHAPTER VII

SUMMARY AND CONCLUSIONS

In Virginia nurseries, reduced growth, chlorosis, and root injury of certain species of container-grown crops often occurs during mid-summer when container medium temperatures are presumably high. Supraoptimal medium temperatures in nursery containers have been well documented in other regions of the United States (Fretz, 1971; Ingram, 1981; Whitcomb, 1980,1981; Young and Hammett, 1980). The overall objective of this research was to examine the potential influence of high medium temperatures on woody plant growth and nitrification in Virginia nurseries. This objective was met by implementing studies which: 1) established the pattern of container medium temperatures under simulated nursery conditions and determined the growth response of five woody plant species to these temperatures; 2) determined the influence of supraoptimal medium temperature, N application rate, and limestone amendment on medium solution composition, growth, and nutrient content of three woody plant species; and 3) determined the medium temperatures and durations of daily exposure to those temperatures which inhibit nitrification in pine bark.

Container medium temperatures. Plants were grown under simulated nursery conditions in insulated or uninsulated 3.8-liter black polyethylene containers. The highest container medium temperatures recorded in uninsulated containers on hot, clear days in July and August were near or slightly above 45°C on the southwest side of the

container at midafternoon. Corresponding medium temperatures on the northeast side of the container were near or slightly above 40°C. The highest medium temperatures on these days were maintained for less than 1 hour, while temperatures in portions of the container exceeded 40°C for 4-5 hours. Medium temperatures in insulated containers did not exceed 33°C on either date. In mid-September, the maximum medium temperature in uninsulated containers was below 33°C.

Plant growth. Growth of *I. crenata* 'Convexa' was influenced by container medium temperature. Shoot dry weight, but not root dry weight, was decreased by the higher medium temperatures in uninsulated containers. The lower shoot relative growth rate of *I. crenata* 'Convexa' in uninsulated containers during the month of August recovered when container medium temperatures modified during the latter part of the growing season, suggesting that the physiological effects of high root-zone temperature on growth were temporary.

Shoot and root dry weight of *I. crenata* 'Helleri' and *J. chinensis* was reduced by the high medium temperatures in uninsulated containers. Limestone amendment to the container medium decreased root dry weight but did not influence the shoot dry weight of either species. For *B. microphylla*, shoot and root dry weight decreased in uninsulated containers and increased in response to limestone amendment, regardless of container medium temperature.

Shoot dry weight of *N. domestica* was influenced by an interaction of container temperature treatment with limestone addition. The reduction in shoot dry weight in

the uninsulated containers was greater when limestone was omitted from the container medium. Limestone addition had no influence on shoot dry weight in insulated containers. Root dry weight exhibited similar trends. Plants grown in unlimed media had higher chlorosis ratings than those in limed media. Ammonium toxicity was postulated as the cause for chlorosis and growth reductions of *N. domestica* in unlimed media.

Plants were also grown in a greenhouse in root-zone temperature control chambers. Root zones were unheated or heated to 40°C for 6 hours/day. Shoot and root dry weights of *I. crenata 'Helleri'*, *N. domestica*, and *J. horizontalis* were reduced by high root-zone temperature (RZT) but there were interactions of RZT with limestone amendment. The percent reduction in shoot dry weight of *N. domestica* in response to high RZT was greater without limestone amendment. Shoot growth of *J. horizontalis* showed no response to limestone amendment when root-zones were unheated and a positive response to limestone amendment at high RZT.

For *I. crenata* 'Helleri' and *J. horizontalis*, the shoot dry weight response to N application rate (NAR) did not vary with RZT or limestone amendment rate. Shoot dry weight of *N. domestica* showed no response NAR in unlimed media but increased in response to N application in limed media.

Higher ratios of NH_4-N:NO_3-N in unlimed than in limed media, especially at high root-zone temperature, were postulated as the cause for the growth reductions in unlimed media. The influence of the ionic form of N on growth appeared to be greater

at high RZT for some species.

Nitrogen uptake. A decline in the specific uptake rate of N for *I. crenata* 'Convexa' in uninsulated containers corresponded to a decline in the relative growth rate of shoots. A decrease in N accumulation in the shoot accompanied the decline in specific uptake rate. The specific uptake rate and N accumulation recovered when container temperatures modified.

Tissue nutrient content. When root zones were unheated or heated to 40°C for 6 hours/day, RZT influenced the shoot tissue Mn concentration of the three species studied. The effects of RZT or interactions of RZT and NAR or limestone addition on other tissue nutrient levels were minor. The concentration of Mn in *I. crenata* increased as NAR increased at moderate RZT, but was not influenced by NAR at high RZT. The shoot tissue concentration of Mn in *N. domestica* showed a similar trend. The concentration of Mn in shoots of *J. horizontalis* was decreased by high RZT but was not influenced by the interaction of RZT and NAR.

Medium solution composition. Medium solution pH was influenced by an interaction of RZT with limestone amendment when the medium was unheated or heated to 40°C for 6 hours/day and N was supplied as urea ammonium nitrate. In unlimed pine bark media, solution pH increased as NAR increased and gradually declined thereafter. This decrease was greater at moderate RZT. Averaged over NAR, the mean pH in unlimed media on day 80 was 4.0 at moderate RZT and 5.4 at high RZT.

With limestone addition to the medium, solution pH gradually decreased over the experimental period as NAR increased. The decrease in pH was greater at moderate RZT. Averaged over NAR, the mean pH in limed media on day 80 was 5.6 at moderate RZT and 6.2 at high RZT.

Limestone addition resulted in a much lower medium solution ratio of NH_4-N:NO_3-N, whether heated or unheated. After day 40, the ratio of NH_4-N:NO_3-N was significantly higher in the heated/unlimed medium compared to the unheated/unlimed medium. This difference was due to higher NO_3-N levels in the unheated/unlimed medium and higher NH_4-N than NO_3-N in the heated/unlimed medium.

The initial increase in pH in the unlimed media was attributed to urea hydrolysis. The overall decline in pH was attributed to nitrification and plant absorption of N, which were reduced by high RZT in the unlimed media.

In the same experiment, RZT influenced the medium solution concentration of Mn primarily through its effect on medium solution pH. Manganese concentration decreased as the medium solution pH increased. High medium solution pH and low Mn concentrations were generally associated with heated treatments, accounting for reductions in tissue Mn levels at high RZT.

Combinations of temperature and exposure time which might limit nitrification in exposed containers were determined over 20 days. Similar, low medium solution concentrations of NH_4-N were present at temperatures of 28° and 34°C regardless of exposure time and at 40°C for daily exposures of 6 hours or less. The concentration

of NH_4-N in medium extracts from the 40°C treatments was greater at 24 hour/day exposure than for shorter exposure times. There was a similar increase in NH_4-N for a 2 hour/day exposure to 46°C, with greater increases for longer exposures to this temperature. The maximum level of NH_4-N concentration in medium solution extracts was generally found after 24 hour/day exposure to 46°C, or after 1 hour/day exposure to 52°C, with no significant increases for longer exposures to 52°C.

Decreases in medium solution NO_3-N concentration generally corresponded to temperature related increases in NH_4-N concentration. One hour/day exposure to 52°C resulted in a medium solution NH_4:NO_3 ratio approximately 70 times greater than that at a constant 28°C. The concentration of NO_3-N for 6 hour/day exposure to 40°C was significantly less than that for the same exposure to 28° or 34°C, although a concomitant increase in the concentration of NH_4-N was not observed for this treatment combination.

Conclusions. The maximum container medium temperatures recorded during this research under simulated nursery conditions were lower than those reported from nurseries in the deep South. Nevertheless, these temperatures proved supraoptimal for growth of several species of woody plants commonly produced in Virginia nurseries. The improved growth obtained through insulation of the container demonstrates that cultural practices which reduce container temperature would be beneficial in Virginia nurseries. Such practices would include 1) early establishment of plants in containers in order to provide sufficient plant canopy for shading of containers during the hottest

months of the growing season, 2) gradual spacing of containers to maintain shading from plant canopies on container sidewalls, and 3) overhead shading of the most heat-sensitive species.

The supraoptimal container medium temperatures recorded under nursery conditions had a negative influence on the specific uptake rate of N absorption; however, the dry weight response of plants to increasing levels of N application was similar when the medium was unheated or heated to 40°C for 6 hours/day. This result indicates that increasing the level of N application to the container medium will not alleviate growth reductions due to high root-zone temperature.

Daily exposures of the container medium to temperatures of 40°C or greater, for durations such as those commonly observed in mid-summer in Southern nurseries, can alter the NH_4:NO_3 ratio in a pine bark medium, presumably through heat-induced inhibition of nitrification . Under conditions where the fertilizer N source consists of predominantly NH_4-N, a higher ratio of NH_4:NO_3 may reduce the growth of species which prefer NO_3-N. Limestone addition to a pine bark medium promoted nitrification, even at supraoptimal medium temperature. Thus, addition of sufficient limestone to encourage nitrification under conditions of high root-zone temperature and use of fertilizers with a N source containing no more than 50% NH_4-N may be important cultural practices in Southern nurseries where container medium temperatures exceed 40°C during the production of plants that prefer low ratios of NH_4-N:NO_3-N. Additionally, the diurnal patterns of medium temperature in containers suggest that

cultural practices which prevent maximum container temperatures from exceeding 46°C should eliminate high medium solution NH_4-N:NO_3-N ratios which result from high temperature inhibition of nitrification.

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VITAE

Ronald Francis Walden was born in Boston, Massachusetts on April 9, 1950. He was employed in the greenhouse industry for several years before attending the University of Massachusetts. He graduated with a B.S. degree in 1979, majoring in Plant and Soil Science. After graduate work at Cornell University, he accepted a position at the Eastern Shore Agricultural Experiment Station in Painter, Virginia in 1981 as Agricultural Research Scientist, where he managed a soil testing laboratory and provided technical assistance to the Soil Scientist. In 1984, he accepted a similar position, working with turfgrass and nursery crop production, at the Hampton Roads Agricultural Experiment Station, Virginia Beach, Virginia, which later became a part of Virginia Tech. He was promoted to Research Associate in 1988.

Work was begun toward a Ph.D. in Horticulture in 1986. His doctoral research examined the influence of high container medium temperatures on growth and the medium solution of container-grown nursery crops. He is a member of several professional societies, including the American Society of Horticultural Science.