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High Soil Temperature and Water Relations of Endomycorrhizal Nursery Crops[1,2]

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Abstract

High root-zone temperatures can stress plants and reduce nursery productivity of container-grown crops. Predawn shoot water potential was initially increased (less water strain) by root-zone temperatures from 40° to 45 °C (104° to 113 °F) and then subsequently declined after 3 days. Stomatal conductance (SC) was reduced at similar root-zone temperatures. Hydraulic root conductance (Lp) increased linearly in response to increasing root-zone temperatures for high temperature tolerant species, and quadratically for susceptible species. Endomycorrhizal fungi colonization enhanced high root-zone temperature stress tolerance at moderate temperatures from 35° to 40°C (95° to 104°F).

Index words: *Berberis thunbergii* 'Atropurpurea,' *Buxus microphylla japonica, Pittosporum tobira* 'Wheeler,' root stress

Introduction

Mycorrhizal fungi are important to plant growth in low fertility soils (28). Mycorrhizal associations increase mineral uptake of plants on poorly managed, heavily cropped agricultural soils, drastically disturbed landscapes, and mine spoil reclamation sites (28, 30, 31, 39). Endo- and ectomycorrhizal fungi are capable of increasing phosphorus (P) uptake (3, 4, 12, 15, 18, 28, 47). The mechanism of P uptake is not fully understood (28). Increased P uptake may be caused by greater mineral solubilization, higher rates of translocation to the plant via mycelium, greater root surface to volume ratios, and increased hyphal exploration of soil regions (28).

Mycorrhizal fungi improve water uptake of root systems (4, 26, 28, 39, 42, 48). Safir et al. (42), demonstrated that mycorrhizal colonization reduced resistance to water transport in *Glycine max* (L.) Merrill (soybean). They postulated that this decrease in resistance may have been due to external hyphae increasing the effective surface area of the root, hyphal penetration of the cortex resulting in a lower resistance pathway, enhanced nutrient uptake, or a larger root system due to enhanced growth.

Mycorrhizal colonized plants grown in containers exhaust their water supply more rapidly than non-mycorrhizal plants (16) which is most likely due to increased biomass demands of mycorrhizal plants. Cytokinin activity increased in leaves of mycorrhizal plants (1, 9) and may alter the water status of mycorrhizal plants by keeping stomata open at lower potentials.

Phosphorus and nitrogen (N) nutrition have been implicated in improved hydraulic root conductance due to mycorrhizal fungi colonization. Water transport was reduced in non-mycorrhizal plants grown at low fertility levels compared to mycorrhizal plants (26, 41, 42, 44). Non-mycorrhizal plants grown at high fertility levels have similar hydraulic root conductance levels compared to colonized plants (14, 32, 43). Hydraulic root conductance for mycorrhizal plants was lower than non-mycorrhizal plants at moderately high P levels, as demonstrated by Sweatt and Davies (48).

High soil temperatures [>35 °C (>95 °F)] are common in southern container nurseries (11, 20, 50, 51, 53). Similar root-zone temperatures occur in mine spoils (34). Root damage occurs in a container nursery during mid-summer with the southern and western exposures of container beds most severely affected (11, 20, 33, 50, 51, 53). Root-zone temperatures as high as 50°C (122°F) have been reported (11, 33, 50, 51, 53). Roots either die or become weak on the exposed surfaces and plant vigor, survival, and quality declines (52). This is confounded after scheduled spacing if the original orientation of the container is not maintained.

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Marx and Bryan (29) reported that *Pinus taeda* L. (loblolly pine) seedlings colonized with *Pisolithus tinctorius* (Pers.) Coker and Couch (common puffball) maintained good plant growth and survival at soil temperatures of 34°C (93°F) compared to non-colonized control plants. Acceptable plant growth occurred with *Glycine max* (L.) Merrill (soybean) colonized with *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe (vesicular-arbuscular mycorrhiza) at root-zone temperatures of 36°C (97°F) (45). The increased tolerance to high soil temperatures has been postulated to be due to increased metabolites supplied by the fungal symbiont (29).

Discussion

Water Relations Studies. Berberis thunbergii 'Atropurpurea' D.C., *Buxus microphylla* var. *japonica* Seibold and Zucc., and *Pittosporum tobira* 'Wheeler' (Thunb.) Ait., non-mycorrhizal and mycorrhizal with a blend of *Glomus etunicatus* Baker and Gerd. and *Glomus fasiculatum* (Thax. *sensu* Gerd.) Gerd. and Trappe (endomycorrhizal fungi) in 3.8 L (#1) polyethylene containers containing by volume 3:1 composted pine bark and sand were grown in a glasshouse. The plants were subjected to root-zone temperatures of 25° (ambient glasshouse temperature), 35°, 40°, and 45°C (77°, 95°, 104°, and 113°F) for 5 days. During this period, predawn shoot water potential was measured with a pressure bomb and stomatal conductance (SC) was measured with a steady-state porometer.

Predawn shoot water potential at 40° and 45°C (104° and 113°F) was increased (less water strain) for all test species, mycorrhizal and non-mycorrhizal, compared to no increase at 25°C and 35°C (77°F and 95°F) (33). This illustrated that water uptake was not restricted at the temperatures 25° to 45°C (77° to 113°F). Syvertsen (49), demonstrated that hydraulic root conductance of *Citrus* rootstocks increased linearly with soil temperature.

Predawn shoot water potential, assuming stomata were closed and the atmospheric humidity was at or near saturation, should reflect water potential of the soil (40), and deviation from this would be in direct response to treatment differences. The increased shoot water potential observed in all species, and the increased hydration observed in only *B. microphylla* leaves indicated that the xylem was under pressure exceeding that of the soil. The soil water potential was at or near zero since the soil had been watered the previous evening to saturation and allowed to drain.

Soil temperature gradients induce water transport in soils. A change in temperature from 19° to 20°C (66° to 68°F) in soils results in a net vapor pressure change of 1.47 x 10^{-4} MPa (17). This potential moves water from warm parts of the soil to cool parts of soil. Thus, assuming 23°C (73°F) leaf temperature and 40° and 45°C (104° and 113°F) soil temperatures, the net osmotic pressure gradients from the soil to the leaf due to temperature differences alone were 5.88 x 10^{-3} MPa for 40°C (104°F) and 7.84 x 10^{-3} MPa for 45°C (113°F). Assuming that the stomata were effectively closed under predawn conditions, predawn shoot water potential approached zero (less water strain) because there was increased root pressure at high root-zone temperatures.

The 3 species responded differently to initial high soil temperature exposed that was reflected in root resistance. The predawn shoot water potential for *P. tobira* increased about 42% and 61% from 25° to 40° and 45°C (77° to 104° and 113°F), respectively; for *B. microphylla,* 31% and 50%; and for *B. thunbergii,* 33% and 42%. Colonization with mycorrhizal fungi did influence this parameter. Mycorrhizal fungi colonization mediated the effects of high soil temperature by maintaining lower predawn shoot water potential (less water strain) at 45°C (113°F) for *B. thunbergii* and *P. tobira* after initial exposure. Mycorrhizal fungi may have enhanced membrane thermostability or increased nutrient uptake thereby preventing some damage at those temperatures. A lower predawn shoot water potential was not detected for mycorrhizal *B. microphylla,* indicating that either colonization was insufficient or may not provide any protection and that *B. microphylla* was more tolerant to high temperature root stress than *B. thunbergii* or *P. tobira.*

Graham and Syvertsen (14), Nelson and Safir (32), and Safir, et al. (41), reported that enhanced water transport of mycorrhizal fungi mycorrhizal roots was due to improved P nutrition of the plants. Phosphorus is a major constituent of cell membranes (36, 46). Nitrogen and P deficiencies decrease hydraulic conductance of roots (37, 38), and P turnover rates are important in temperature acclimation of root cell membranes (22, 36); therefore, it is likely that enhanced nutritional status and overall plant vigor due to colonization were responsible for the added membrane integrity illustrated by lower predawn shoot water potential after initial exposure to high soil temperatures.

There was increased predawn shoot water potential for 2 days in all mycorrhizal and non-mycorrhizal test species, followed by a decline approaching initial potentials. Thus xylem vessels may have become occluded or that there was increased resistance to water within the symplast due to membrane damage.

All species, mycorrhizal and non-mycorrhizal, responded to increased high soil temperatures within the first day of exposure by reductions in SC (33). Two days' exposure to 45°C (113°F) reduced SC for *B. microphylla,* while 2 days' exposure to either 40° and 45°C (104° and 113°F) reduced SC for both *B. thunbergii* and *P. tobira.* Reduced SC was observed through day 5 for all 3 species.

Recall that 1 to 2 days' exposure to high soil temperature increased predawn shoot water potential due to enhanced water conductance, therefore, reduced SC was not due to lack of water transport. Kramer (23) reported that root systems killed by heat were able to conduct water. Reductions in transpiration and leaf death were due to the release of previously compartmentalized materials from disrupted root cells that occluded vessels and were toxic to leaves (24).

Mycorrhizal fungi colonization affected *B. microphylla* stomatal relations (33). Colonization increased SC at ambient soil temperatures, confirming results reported by Allen et al. (2), Dixon (8), Hardie and Leyton (16), Huang, et al. (19), Levy and Krikun (25), and Nelson and Safir (32). SC at 45°C (113°F) was substantially reduced, however colonization maintained higher

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SC levels for only *B. microphylla.*

Hydraulic Root Conductance Studies. Glasshouse grown *B. thunbergii* and *B. microphylla,* non-mycorrhizal and mycorrhizal with a blend of *G. etunicatus* and *G. fasiculatum* in 350 ml (12 oz) aluminum cans containing by volume 3:1 composted pine bark and sand; plants were subjected to root-zone temperatures of 25°, 35°, 40°, and 45°C (77°, 95°, 104°, and 113°F) for 48 hrs and hydraulic root conductance (Lp) was then measured according to Sweatt and Davies (48).

High soil temperatures increased Lp linearly from 25° to 40°C (77° to 104°F) (443% increase) for *B. thunbergii* and from 25° to 45°C (77° to 113°F) (606% increase) for *B. microphylla* (33). The near exponential increase in conductance from 25° to 45°C (77° to 113°F) (1,008% increase) for *B. thunbergii* indicated that between 40° and 45°C (104° and 113°F), biologically controlled resistances to water uptake had been reduced.

The endodermis, a single cell layer separating the root cortex from the vascular stele, is generally considered to be the main point of resistance to water transport in young roots (35). The young endodermal cell walls in the region of water absorption are impregnated with suberin completely encircling the radial and transverse walls of each cell (35). The totality and hydrophobic nature of the endodermal bands constitutes the Casparian strip (10). The Casparian strip blocks apoplastic water flux (intercellular water flow), hence, water that is to enter the vascular stele must enter by symplastic pathways (intracellular water flow). At high temperatures, membrane lipids become more fluid (36). Therefore, temperatures from 40° to 45°C (104° to 113°F) may have been sufficiently high to liquify membrane lipids of *B. thunbergii* roots, thus allowing greater Lp. Histological analysis of high temperatures stressed and unstressed *Citrus* root tissues (21) supports this hypothesis.

Membrane fluidity, at low temperatures, is altered by adaptive increases in unsaturated fatty acids (5, 7). Chloroplast membranes undergo adaptive changes in fatty acyl lipid residues with non-lethal exposures to high temperatures (13). *Anacystic nidulans,* a thermophyllic blue-green alga, adjusts to temperatures below 40°C (104°F) by an increase in unsaturated fatty acids and to temperatures above 40°C (104°F) by an increase in saturated fatty acids (27). Therefore, it is possible that the increased tolerance of *B. microphylla* exhibited by lower Lp at 45°C (113°F) was due to a higher level of saturated fatty acids.

Mycorrhizal fungi colonization, at a more moderate temperature of 35°C (95°F), appeared to mediate root damage by maintaining lower Lp. Enhanced P nutrition by mycorrhizal fungi has been postulated to alter Lp (14, 32, 41, 43). Kinney, et al. (22) demonstrated that warm and cool season grown *Secale cereale* L. (rye) roots had increased lipid-phosphorus metabolism with hardening at low (cool season) temperatures. This does not result in a net increase of P in the membranes, but increased turnover rates with a subsequent increase in lipid unsaturation (6, 7, 22). Presumably, with the increased availability of P due to mycorrhizal fungi, a degree of heat hardening had developed, possibly increasing the level of fatty acid saturation, and subsequently reduced Lp rates.

Mycorrhizal Fungi Selection. Improvements in high root-zone temperature tolerance in this study due to mycorrhizal fungi were limited to temperatures ranging from 35° to 40°C (95° to 104°F). These results concur with previously cited results of Marx and Bryan (29) and Schenck and Smith (45). Temperatures greater than 40°C (104°F) may have exceeded limits for plant improvement by the fungal symbiont due to ecotypic variation. The fungi for this study were from a temperate climate and perhaps not adapted to high soil temperatures. Better results may have been obtained at temperatures greater than 40°C (104°F) with the use of a fungal ecotype better adapted to high soil temperatures.

Significance to the Nursery Industry

Mycorrhizal fungi colonization has demonstrated potential for improving plant growth under container nursery conditions (33). Colonization does improve plant growth under conditions of water stress, low fertility, plant pathogens, and moderately high soil temperatures (28). All of these conditions may exist in a nursery and any means that a grower may use to reduce stress is beneficial. However, colonization of plants with mycorrhizal fungi does not reduce high root-zone temperature plant stress to a level significant enough to justify the efforts required for fungal colonization in a container production nursery compared to standard management practices. Future work on ecotypic selection of mycorrhizal fungi adapted to nursery conditions will be important in the overall feasibility of the commercial use of mycorrhizal fungi.

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