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Ectomycorrhizal Effect on Host Plant Response to Drought Stress¹

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Abstract

Ectomycorrhizal symbiosis affects the water relations and drought resistance of woody landscape trees and shrubs in the families *Pinaceae*, *Fagaceae*, *Betulaceae*, and others. It has frequently been observed that host plants mycorrhizal with drought-adapted fungi exhibit improved growth and survival during drought and more rapid recovery after rewatering than non-mycorrhizal plants or plants mycorrhizal with fungi not adapted to dry sites. Relatively few studies have addressed the effect of mycorrhizae on the physiological response of host plants to drought stress. It is suggested that some fungi confer drought tolerance to their host, while others confer drought avoidance. Possible mechanisms by which mycorrhizae influence host water relations are discussed.

Index words: symbiosis, fungus, mycorrhiza, water relations, drought resistance

Introduction

Limitations to horticultural (27, 12) and forest (19, 20) productivity due to drought stress are well documented. Water deficiencies result in mortality of woody landscape plants during the critical post-transplant establishment stage and reduce the growth rates of established trees and shrubs.

Selection of drought-resistant germplasm is one promising method for minimizing these drought related limitations. Another which seems equally promising, but which has been little exploited to date, is selection of symbiotic rhizosphere microorganisms, specifically ectomycorrhizal fungi, capable of enhancing drought resistance of host trees. The importance of ectomycorrhizae in host water relations is generally accepted, though not well characterized or understood in terms of the mechanisms involved (30). The feasibility of selecting strains of ectomycorrhizal fungi adapted to stressful environmental conditions has been demonstrated by Marx and colleagues (23) in the case of *Pisolithus tinctorium* (Pers.) Coker and Couch. This fungus, isolated from drought stressed coal spoils, has been shown to improve survival and performance of seedlings planted under a range of stressful conditions. Naturally occurring mycorrhizal fungi found in seedling nurseries (e.g. *Thelephora terrestris* Ehrl. per Fr.), where drought stress is deliberately minimized, are not as well adapted to drought. Presumably such fungi do relatively little to ameliorate drought stress encountered by their hosts upon transplanting from optimal nursery conditions to harsher outplanting sites (36). The lack of a drought adapted fungal symbiont may reasonably be expected to contribute to high mortality on outplanting.

Mycorrhiza-Related Drought Resistance

A better understanding of the strategies involved in mycorrhiza-related plant drought resistance is critical if this phenomenon is to be manipulated to full advantage in landscape ecosystems. Observations in the literature and a limited amount of experimental evidence suggests that some fungi may confer drought tolerance to host trees while others confer drought avoidance. "Tolerance" and "avoidance" as we use these terms follow the definitions of Levitt (21). Tolerance refers to strategies such as osmoregulation which enable the plant to remain physiologically active at greater levels of internal strain (more negative water potential, Ψ). Drought avoidance, on the other hand, refers to strategies which minimize internal strain either by conservation of available water or adaptations which permit exploitation of water inaccessible to nonadapted plants. Conservation would include stomatal closure at relatively high Ψ , and increased water use efficiency (WUE = ratio of water transpired to CO₂ fixed). A frequently cited example of the drought avoidance based on access to otherwise unavailable water is a deep rooting habit. Short term avoidance mechanisms include increased root system absorptive surface area, and increased root system hydraulic conductivity.

The notion that mycorrhizae may have beneficial effects on host plant water relations during drought is supported by field observations which suggest that mycorrhizal plants often exhibit enhanced survival and better growth than their nonmycorrhizal counterparts during drought stress (24, 31, 34). In an experimental comparison of mycorrhizal Douglas fir seedlings with nonmycorrhizal seedlings, Parke et al. (29) reported no growth differences when seedlings were well watered throughout the experiment, but when subjected to cyclic drought, the mycorrhizal seedlings had significantly greater growth over a 12-week period.

Rapid Recovery from Drought

Several reports suggest that mycorrhizae facilitate more rapid recovery from drought after rewatering.

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Parke et al. (29), found that the rate of photosynthesis during a period of daily watering after a series of drought cycles was 10 fold higher in mycorrhizal plants than in nonmycorrhizal plants. Dixon et al. (7) found that upon rewatering after a period of drought, white oak seedlings inoculated with *P. tinctorius* recovered nonstress levels of xylem water potential sooner than uninoculated seedlings. Runov (31) reported that mycorrhizal oaks recovered from water stress more rapidly than non-mycorrhizal oaks. Similarly, Goss (10) found that a higher percentage of mycorrhizal than non-mycorrhizal ponderosa pine seedlings recovered from prolonged drought upon rewatering. Experimental verification of mycorrhizal effects on recovery from drought is complicated by a methodological problem related to the fact that plants given different mycorrhizal treatments may have dried down at different rates, and thus have different tissue water potentials (an indicator of the level of internal strain) at a given time at the end of a drying cycle. If all treatments are rewatered at the same time, as was the case in the experiments performed by Parke, et al. (29), and by Dixon et al. (7) they will be recovering from different levels of strain, and thus direct comparison of their recovery should be made cautiously.

Mycorrhizal Effects on Host Water Relations and Gas Exchange During Drought

Despite reports that certain mycorrhizal fungi confer an advantage in terms of growth, survival, and/or subsequent recovery to plants subjected to drought, there have been relatively few attempts to elucidate the actual effects of those fungi on the physiological responses of host plants. Limited experimental evidence summarized in Table 1 suggests that different species of ectomycorrhizal fungi differ in their effects on host plant response to drought. Walker et al. (36), compared the field performance on a droughty coal spoil of Virginia pine (*Pinus virginiana* Mill.) previously inoculated with either *P. tinctorius* or mycorrhizal with native nursery fungi (primarily *T. terrestris*). Seedlings with *P. tinctorius* mycorrhizae had less negative predawn and mid-day xylem pressure potentials (less internal strain) than the seedlings mycorrhizal with other fungi. In contrast

are several reports that mycorrhizal seedlings had greater levels of internal strain (lower Ψ) than non-mycorrhizal seedlings. Dixon et al. (7) reported that mycorrhizal white oaks inoculated with *P. tinctorius* had slightly lower leaf Ψ (greater strain) than non-mycorrhizal plants, but exhibited higher rates of root growth and were capable of more rapid recovery from drought stress upon rewatering. Sands and Theodorou (33) found that mycorrhizal Monterey pine seedlings inoculated with *P. tinctorius* had lower leaf Ψ than non-mycorrhizal seedlings, but that there were no differences in transpiration rates. Similarly, Parke et al. (29) found lower leaf Ψ (increased strain) during drought and yet more rapid photosynthetic rates in mycorrhizal Douglas fir than in non-mycorrhizal controls. These instances of mycorrhiza-associated depression of plant water potential (increased strain) in the absence of negative effects on growth, photosynthesis or transpiration are consistent with the interpretation that drought tolerance is conferred by these mycorrhizal associations. An additional experiment by Parke et al. (29), however suggests that not all fungi confer drought tolerance. In a comparison of Douglas fir seedlings inoculated with 4 species of fungi, they reported that while *P. tinctorius*-inoculated seedlings transpired and fixed CO_2 at higher rates than controls, at the start of an 8 day drying cycle, those mycorrhizal with *Rhizopogon vinicolor* (the one fungal species which did not stimulate growth) transpired at a rate well below the controls. Furthermore, transpiration rate of *Rhizopogon*-inoculated seedlings began to decline earlier in the drought cycle (day 3) than that of the *Pisolithus*-inoculated seedlings (day 5). The other 2 species of fungi tested fell between these 2 extremes. After rewatering (day 8) seedlings inoculated with the "conservative" fungus, *R. vinicolor*, recovered from drought more rapidly than checks or those inoculated with other fungi, as measured by the reinitiation of transpiration and photosynthesis. Thus, in the case of *R. vinicolor*, rapid recovery from drought seemed to be associated with early cessation of assimilation and transpiration during drought. This could be interpreted as a drought avoidance strategy if associated with maintenance of relatively high internal Ψ . Regrettably, plant Ψ during this experiment were not reported.

We have derived WUE values from the data of Parke

Table 1. Mycorrhizal effects on host plant water relations and gas exchange during and after drought.

Investigators	Host/Fungus ^y	Mycorrhizal effect ^z			
		Y	Trans.	PS	Recovery
Walker et al. (36)	Virginia Pine/P.t.	I	—	—	—
Dixon et al. (7)	White Oak/P.t.	D	I	—	I
Sands & Theodorou (33)	Monterey Pine/R.l.	D	O	—	—
Parke et al. (29)	Douglas Fir/NF	D	—	I	—
	Douglas Fir/P.t.	—	I	O	O
	Douglas Fir/R.v.	—	D	O	I
Diebolt & Mudge (unpublished)	Scots Pine/P.t., H.c., L.l.	O	O	—	—

^zI, D, O. denote stimulation, inhibition, and no effect, respectively.

^yAbbreviations: NF = native fungi; P.t. = *Pisolithus tinctorius*; R.l. = *Rhizopogon luteolus*; R.v. = *Rhizopogon vinicolor*; H.c. = *Hebeloma crustuliniformae*; L.l. = *Laccaria laccata*; Y = tissue water potential; Trans. = transpiration; PS = photosynthesis.

et al. (29) which indicate variation in WUE among plants inoculated with various fungal isolates from 2 to 5 fold (pre and post-stress, respectively). Thus mycorrhizal fungi appear to induce changes in host plant WUE which may exceed intraspecific (2) and interfamilial (13) differences found in the literature. *R. vinicolor*, which was the most conservative fungus with respect to effects on photosynthesis and transpiration during drought, was the one which conferred the greatest WUE.

In our own research with Scots pine (*Pinus sylvestris* L.) we compared the water relations (predawn xylem Ψ and transpiration) of uninoculated seedlings with those inoculated with *P. tinctorius*, *Hebeloma crustuliniforme* (Bull. ex St. Amans) Quel., or either of 2 isolates of *Laccaria laccata* (Scop. ex Fr.) Berk. & Br. In contrast to the results of the previous studies presented above, mycorrhizal treatment had no effect on host xylem Ψ during a 9 day dry down period (data not shown). With respect to measurement of transpiration, a troublesome problem frequently encountered in this and other mycorrhizal studies is that seedlings frequently vary in size due to mycorrhizal treatment or seedling (genetic) variation. As a result, transpiration expressed on a whole plant basis will also vary due to differences in plant size, independent of any direct effect of mycorrhizae. The normally simple solution of expressing transpiration on a leaf surface area basis is not so simple with pine needles and/or when the measurement must be made non-destructively as during a time course study. We have developed a non-destructive technique for estimating pine needle surface area which involves the use of a video camera coupled to an instrument which measures the surface area of a video image of the pine shoot. Regardless of whether this technique was used to normalize transpirational measurements or not, mycorrhizal treatment had no significant effect on seedling water loss at any stage during the drying cycle (data not shown). These experiments have been conducted using 2 different container sizes, and we are convinced that under some conditions mycorrhizae do not have the expected effects on host response to drought. We are presently attempting to better define the interaction between host, fungus and environment in this regard.

Mechanistic Hypotheses

The limited experimental evidence summarized above suggests that mycorrhizae differ in the extent and mechanisms by which they influence plant water relations. The work of Parke et al. (29) is the only published research which approaches a whole plant characterization of mycorrhizal effects on drought response. Nonetheless, the lack of information about the Ψ during these measurements, low frequency of measurements, and lack of simultaneous data in some cases makes it impossible to evaluate the role of various mechanisms. Indeed, many hypotheses have been suggested but little research has been conducted to elucidate the mechanism by which mycorrhizae confer their effects on host water relations (30).

The increase in rootsystem absorptive surface area resulting from a mantle and an extramatrical mycelium (fungal hyphae, strands, and rhizomorphs extending from the root into the surrounding soil) would suggest a

drought avoidance mechanism by which otherwise inaccessible soil moisture becomes available, resulting in reduced plant water stress. Transport of significant quantities of water across physiologically relevant distances from soil to plant root via mycorrhizal rhizomorphs has been demonstrated by Duddridge et al. (8), and Brownlee et al. (4). Their finding that the rate of water transport through rhizomorphs was comparable to that through xylem supports Reid's (30) suggestion that resistance to the flow of water may be less along extramatrical fungal structures than through bulk soil, although the latter has not been tested experimentally. Although it has frequently been noted that mycorrhizal fungi vary considerably in their tendency to form an extramatrical mycelium (30), this has not been quantified or correlated with effect on host plant water relations.

In addition to the increase in rootsystem surface area due to fungal biomass, there is convincing evidence that mycorrhizal symbiosis results in a stimulation of root growth *per se*. Promotive effects of mycorrhizal inoculation on lateral root formation (11), dichotomous branching of pine roots (16), and overall root biomass (1) has been demonstrated. When mycorrhizal stimulation of root growth exceeds that of shoots, i.e., increased root-shoot ratio (1), a beneficial effect on plant water relations is a reasonable expectation because of the increase in water absorbing surface (root) per unit of transpiring surface (shoot). However, stimulation of root growth is frequently offset by an even greater stimulation of shoot growth (35) i.e., a decrease in root-shoot ratio, resulting in an increase in transpirational demand on the root system, and possibly a net negative effect on plant water status. It has been suggested that the effective size of a mycorrhizal root system may be increased during drought since mycorrhizal roots have been observed to be more resistant to dessication than non-mycorrhizal roots, thus increasing the size of the functional portion of the root system (6, 15).

During drought periods, roots and soil peds are known to contract, resulting in decreased soil-root continuity. There is evidence that extramatrical hyphae of mycorrhizae may serve as an important pathway for transport of water and nutrients under these conditions (15) resulting in an increase in root plus soil hydraulic

Table 2. Possible mechanisms for ectomycorrhiza related effects on host plant water relations.

Mechanism	Relevant literature ²
I. Roots system absorptive surface area	
A. Fungal component	Brownlee et al., 1983; Duddridge et al., 1980
B. Plant component	Graham and Linderman, 1980; Hatch and Doak, 1933; Alexander, 1981
II. Hydraulic conductivity	Sands et al., 1982; Sands and Theodorou, 1978
III. Osmoregulation	
A. Fungal	Mudge (unpublished)
B. Plant	Pallardy et al., 1982
IV. Nutrition	Walker et al., 1982

²Either supports or refutes the possible mechanism.

conductivity. The presence of a Hartig net within the cortex of the mycorrhizal root, the mantle and the extramatrical mycelium extending from the root out into the surrounding soil are fungal structures which might be involved in a mechanism based on increased hydraulic conductivity (water movement). Alternatively, if a mycorrhizal fungus resulted in decreased root system hydraulic conductivity (compared to a non-mycorrhizal plant or one inoculated with another fungus), this might result indirectly in an increase in WUE, i.e., decreased hydraulic conductivity causes a decrease in plant Ψ (more strain) leading to partial stomatal closure. The latter has been associated with increased WUE due to greater reduction in water loss than in CO_2 uptake (9).

Despite the compelling logic of hypotheses related to hydraulic conductivity, estimates of the hydraulic conductivity of pine root systems by analysis of pressure volume curves has failed to demonstrate any relationship between the percentage of the root system which was mycorrhizal and hydraulic conductivity (32). On the contrary, Sands and Theodorou (33) found that mycorrhizal plants had higher root plus soil resistance to water flow than non-mycorrhizal plants. These authors qualify their findings by pointing out that the extramatrical mycelium was poorly developed. Thus, these results do not refute the hypothesis that mycorrhizae increase hydraulic conductivity when there is a well developed extramatrical mycelium.

The seemingly paradoxical observation that mycorrhizal plants frequently have more negative Y while continuing to grow (7), transpire (33) and/or fix carbon (29) at rates equivalent or higher than control plants suggest that osmoregulation might be involved in the response of mycorrhizal plants to drought. This would allow transpiration and assimilation to occur at lower soil Y , without loss of turgor. While there is evidence for plant osmoregulation in response to drought stress (5, 17) it is not obvious how this might be facilitated by mycorrhizal symbiosis. Ectomycorrhizal fungi are known to accumulate osmotically significant levels of polyols (22) which might result in maintenance of a more negative water potential by the fungus than in the surrounding soil. Our own preliminary results indicate that pure cultures of the ectomycorrhizal fungus *P. tinctorius* undergo an approximate ten-fold increase in the level of mannitol (a polyol) in response to an osmotic stress of 1 MPa (unpublished). Although fungal osmoregulation would facilitate water uptake from soil to fungus it is difficult to imagine how a favorable Y gradient from fungus to plant would be induced. Conceivably, high fungal metabolic activity during drought might act as a sink to stimulate plant photosynthesis and consequently increase the level of soluble carbohydrates in the plant, thus providing the necessary solutes for plant osmoregulation. Another mechanism by which a mycorrhizal fungus might influence host plant osmoregulation is suggested by a recent simulation by McCoy et al. (25) who found that increasing root density results in smaller potential differences and less negative Y at the root surface. These workers conclude that increasing root length density ultimately reduces the rate at which negative potentials develop at the root surface, thus allowing time for the plant to accumulate solutes (osmoregulate)

before becoming metabolically inactive due to the effects of the stress. Ectomycorrhizal fungi have been reported to increase root density, so it is possible that they might influence host osmoregulation in this manner. Despite conceptual difficulties with an hypothesis based on osmoregulation, Pallardy et al. (28) have investigated the possibility in shortleaf pine seedlings using pressure volume curves. They found no differences in either root or shoot osmotic potential between mycorrhizal and non-mycorrhizal seedlings.

The effects of mycorrhizae on host plant nitrogen (N) and phosphorus (P) nutrition are extremely well documented and it has been suggested that mycorrhiza-associated drought resistance might be simply a result of enhanced mineral nutrition. Diffusion-limited nutrient ions such as inorganic phosphate become increasingly unavailable in drier soils. Hu (18) has demonstrated that the extramatrical hyphae of ectomycorrhizae remain functional with respect to uptake of N, P, and potassium (K) at lower soil water potentials than uninfected roots. Evidence of Walker, et al. (36) suggests that improved nutrition alone could not account for an effect of *P. tinctorius* mycorrhizae on the Y of Virginia pine, because there was no effect of fertilization on the response.

Significance to the Nursery Industry

Drought stress is a major limiting factor in the transplant survival of woody landscape plants. Ectomycorrhizal symbiosis is an important but frequently overlooked component of the response of woody landscape trees and shrubs to drought. Because the mycorrhizal fungi which inhabit nurseries are not well adapted to drought, they contribute little to host plant drought resistance upon transplanting from optimal nursery conditions to more stressful landscape sites. On the other hand, drought adapted fungi have been selected from harsh sites, such as mine spoils, which apparently can, under certain conditions, significantly improve host plant drought resistance. Further research along these lines may result in the use of mycorrhizal inoculation as a management tool in the production and culture of woody landscape plants for adverse sites.

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