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Osmotic Adjustment in Leaves of VA Mycorrhizal and Nonmycorrhizal Rose Plants in Response to Drought Stress[1]

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ABSTRACT

Osmotic adjustment in *Rosa hybrida* L. cv Samantha was characterized by the pressure-volume approach in drought-acclimated and unacclimated plants brought to the same level of drought strain, as assayed by stomatal closure. Plants were colonized by either of the vesicular-arbuscular mycorrhizal fungi *Glomus deserticola* Trappe, Bloss and Menge or *G. intraradices* Schenck and Smith, or were nonmycorrhizal. Both the acclimation and the mycorrhizal treatments decreased the osmotic potential (Ψ_π) of leaves at full turgor and at the turgor loss point, with a corresponding increase in pressure potential at full turgor. Mycorrhizae enabled plants to maintain leaf turgor and conductance at greater tissue water deficits, and lower leaf and soil water potentials, when compared with nonmycorrhizal plants. As indicated by the Ψ_π at the turgor loss point, the active Ψ_π depression which attended mycorrhizal colonization alone was 0.4 to 0.6 megapascals, and mycorrhizal colonization and acclimation in concert 0.6 to 0.9 megapascals, relative to unacclimated controls without mycorrhizae. Colonization levels and sporulation were higher in plants subjected to acclimation. In unacclimated hosts, leaf water potential, water saturation deficit, and soil water potential at a particular level of drought strain were affected most by *G. intraradices*. *G. deserticola* had the greater effect after drought preconditioning.

Recent evidence suggests that colonization of root systems by VA[2] mycorrhizal fungi affords host plants greater resistance to drought stress[3] (2, 22). Mycorrhizal plants may avoid drought to some extent through enhanced water uptake at low soil moisture levels (26). In onion the effect appears to be conferred through improved phosphorus nutrition (22), while in *Bromus* (6) and rose (RM Augé, KA Schekel, RL Wample, unpublished data) some other mechanism prevails. An influence on host osmotic potential has been observed in wheat (2); however, definitive studies on osmotic adjustment in mycorrhizal plants are lacking.

The influence of drought-acclimation and mycorrhizal colonization on tissue water relations and osmotic response in equally sized and adequately P-nourished rose plants is reported in this study. As drought may modify the partitioning of water into apoplastic and symplastic fractions (24), parameters for estimating these fractions were also calculated.

MATERIALS AND METHODS

Plant Culture, Inoculation Procedures and Growth Room Conditions. Rooted cuttings of *Rosa hybrida* L. cv Samantha were grown in calcined montmorillonite clay (Turface; IMCore, Mundelein, IL), initially in 13 cm pots, into which one of three VA mycorrhizal inocula had been incorporated at a rate of 1 inoculum:4 Turface (v/v). Inoculum of both *Glomus deserticola* Trappe, Bloss and Menge and *Glomus intraradices* Schenck and Smith consisted of fresh pot culture (soil and mycorrhizal root pieces) of soybean (*Glycine max* [L.] Merr.) cv Maple Amber and rose (*R. hybrida*) cv Sonia, growing in sand. The third inoculum was an autoclaved mixture (1:1, v/v) of the above two inocula, and served as a control. All plants received appropriate inoculum water extracts (final sieve = 25 μm) to establish the microflora associated with each inoculum.

Plants were grown in a greenhouse under natural light from January through September. At 7 months, plants were transplanted into 25 cm pots, and at 9 months plants of similar size were moved into a controlled environment growth room for drought acclimation and water relations studies. Growth room PPFD (400–700 nm) ranged from 290 to 350 μmol s^{-1} m^{-2}, with a 14 h photoperiod. Day/night temperature and RH were 22/17°C and 40/90%, respectively. Plants were watered daily throughout the experiment, and every other d received 10.4 and 3.1 mM N and K, respectively (as Peter's 15-0-15 soluble fertilizer). Uninoculated plants received 3.0 mM P and mycorrhizal plants 0.7 mM P as KH_2PO_4, weekly.

Drought Acclimation Procedure. For acclimation, plants were allowed to dry until the leaf conductance (g_L) declined to 1.1 (SE = 0.04) mm s^{-1}, and then were rewatered. Four such cycles were repeated on six replicates of each of the nonmycorrhizal and mycorrhizal treatments, for a total acclimation time of 17 to 20 d. Unacclimated treatments were watered daily, with g_L remaining above 5.6 mm s^{-1}. Fertilization was discontinued during the acclimation period.

Soil and Leaf Water Potential, Conductance and Water Saturation Deficit. A soil moisture characteristic curve was generated from thermocouple psychrometer (SC-10, Decagon Devices) measurements on a number of representative soil samples. Ψ_{soil} when g_L reached 1.1 mm s^{-1} was then calculated from the appropriate soil weights. Ψ_{leaf} and g_L were determined with a pressure chamber and porometer, respectively, as previously

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[2] Abbreviations: VA, vesicular-arbuscular; Ψ_π, leaf osmotic potential; PPFD, photosynthetic photon flux density; g_L, leaf conductance; Ψ_{soil}, soil water potential; Ψ_{leaf}, leaf water potential; WSD, leaf water saturation deficit; P-V, pressure-volume; Ψ_π^{100}, leaf osmotic potential at full turgor; Ψ_π^0, leaf osmotic potential at the turgor loss point; ROWC, leaf relative osmotic water content; RWC, leaf relative water content; RDW, leaf relative dry weight; A_p, apoplastic water percentage; Ψ_p^{100}, leaf pressure potential at full turgor; RWC^0, relative water content at the turgor loss point; $ROWC^0$, leaf relative osmotic water content at the turgor loss point.

[3] The terminology of Levitt (18) has been employed throughout this paper in distinguishing an environmental limitation ('stress') from the related plant response to the limitation ('strain).

described (4), on two to six subsamples per replicate. WSD was determined on four leaf discs per plant, rehydrated 5 h at 20°C, and calculated as (17):

$$WSD = 100(SW - FW)/(SW - DW) \quad (1)$$

where SW, FW, and DW were the saturated weight, intermediate fresh weight, and dry weight of discs after drying for 4 d at 65°C, respectively.

Pressure-Volume Relations. Following the four drought cycles, both unacclimated and acclimated plants were allowed to dry until g_L declined to approximately 1.1 (SE = 0.04) mm s^{-1} (this predetermined g_L denoted by g_L*). Then, between 0700 and 0900 h, Ψ_{soil}, Ψ_{leaf}, WSD and g_L were assayed, and leaves were excised for measurement of pressure-volume (P-V) relationships. P-V curves were generated using 'Method B' of Ritchie and Roden (28), on fully expanded leaves from similar heights in the canopy. Leaves were removed from the chamber between determinations, allowed to dry on the benchtop, and incremental water losses derived by weighing. Balance points were observed through a microscope mounted over the pressure chamber. N_2 pressure in the chamber was increased and released at a rate not higher than 0.02 MPa s^{-1} to avoid injury to the leaf cells which may occur at higher rates (16). Preliminary experiments comparing various pressurization and infiltration methods showed that rose leaves can be fully rehydrated (*i.e.* to Ψ_{leaf} above −0.02 MPa) simply by cutting petioles under water and keeping the ends in 40°C water in a humid chamber with an air temperature of 2 to 4°C, for 1 h. This technique was used in place of 'overnight' rehydration common in P-V work, to preclude changes in osmotic potential (Ψ_π) which can occur within several hours (13).

The inverse of the balance pressure ($-\Psi_{leaf}^{-1}$) (y axis) was plotted against the cumulative volume lost (V) (x axis) and a least-squares linear regression fitted to the linear segment of the curve (27, 34). The y intercept of this line ($-\Psi_\pi^{-1}$) gave the inverse of the leaf osmotic potential at full turgor (Ψ_π^{100}) and the x intercept gave the total volume of osmotic (symplastic) water in the leaf (V_{ref}) (15). ROWC was calculated as (15):

$$ROWC = 100(V_{ref} - V)/V_{ref} \quad (2)$$

and RWC as:

$$RWC = 100(V_{tot} - V)/V_{tot} \quad (3)$$

where V_{tot} is the total volume of water (symplastic plus apoplastic water). RDW of leaves used in P-V relations was calculated as (27):

$$RDW = 100(DW)/(SW - DW) \quad (4)$$

and A_p as:

$$A_p = 100(1 - [V_{ref}/V_{tot}]) \quad (5)$$

Colonization and Phosphorus Levels. Roots recovered from three soil cores from each plant were cleared in 10% NaOH (w/v), stained with chlorazol black E (7) and mycorrhizal colonization quantified as described earlier (4, 5). P content of lyophilized leaves was assayed immediately before and after the drought-acclimation cycles, by the vanadate-molybdate-yellow method, on samples (4–8 per treatment) dry-ashed with magnesium nitrate and digested in nitric acid (8).

Statistics. A 2 × 3 factorial, completely randomized design was used, with two preconditioning treatments (unacclimated or drought-acclimated) and three mycorrhizal treatments (*G. deserticola, G. intraradices*, or a nonmycorrhizal control). Ψ_{leaf}, Ψ_{soil}, g_L, WSD and P-V curves were determined for six plants per treatment. Univariate analyses of variance with specific linear contrasts were run on all data to partition the variance into main effects and the interaction between the two factors (30). Four contrasts, each involving more than two treatments, are listed in Tables I to IV. Standard error for each mean is also included in the tables.

RESULTS AND DISCUSSION

Plant Characteristics. Because VA mycorrhizae increase phosphorus uptake (9) and phosphorus fertility can sometimes alter plant response to water deficit stress (25), care was taken to produce nonmycorrhizal plants that had P contents similar to or greater than mycorrhizal plants (Table I). Plant P content was assayed prior to the acclimation cycles and again at the conclusion of the P-V work, since P uptake in nonmycorrhizal plants may be diminished in soils of low moisture content (20, 22). In this study P levels in the nonmycorrhizal controls were adequate throughout the experiment, and were higher than in plants with mycorrhizae (Table I). The 20-d drought treatment did not affect leaf P content.

Colonization levels by both *Glomus* species were somewhat higher in acclimated than in unacclimated roses (Table I), and sporulation by each mycobiont was much greater in the acclimated plants. Both effects have been observed before in other *Glomus* spp. in response to low soil moisture levels (3, 6, 22).

Drought Strain Imposition. Occurring in response to cellular water deficits and consequent Ψ_{leaf} depression, active osmotic adjustment allows turgor to be maintained at lower Ψ_{leaf} (14, 21, 33). As nonmycorrhizal and mycorrhizal plants may differ in drought avoidance capability and thus in degree of strain manifested at a particular low Ψ_{soil} (2, 19, 31), roses in this study were subjected to comparable drought strain, as assayed by stomatal closure. Cuticular conductance, measured on ab- and adaxial surfaces of excised leaves, was negligible, and it has been dem-

Table I. *Foliar Phosphorus (P) Content before and after Drought-Acclimation, and Level of Mycorrhizal Colonization in Rose*

P content of lyophilized rose leaves was assayed by the vanadate-molybdate-yellow method (8) on four to eight samples per treatment, immediately before and after the drought-acclimation cycles. Colonization levels in roots recovered from three soil cores from six plants per treatment were determined as described by Biermann and Linderman (5). Linear contrasts indicate nonsignificance (NS), or significance at the 1% (**) or 0.1% (***) level, and ± SE is listed beneath each mean.

Treatment	P Content		Colonization
	Before	After	
	mg g^{-1} dry wt		%
Nonmycorrhizal			
Unacclimated	3.1	2.7	0
	0.3	0.4	
Acclimated		2.9	0
		0.3	
G. deserticola			
Unacclimated	2.0	1.9	53
	0.3	0.2	
Acclimated		1.6	76
		0.4	
G. intraradices			
Unacclimated	2.7	2.2	66
	0.3	0.5	
Acclimated		1.9	83
		0.3	
Linear Contrasts			
Nonmycorrhizal *versus* mycorrhizal	***	***	
Unacclimated *versus* acclimated		NS	
G. deserticola versus G. intraradices	**	NS	
Mycorrhizae × acclimation		NS	

onstrated that stomatal density and size in rose leaves do not vary as a consequence of colonization by *Glomus* (4). Therefore, g_L was a direct measure of relative stomatal aperture, which in turn is a function of bulk leaf water status when ambient temperature, vapor pressure deficit, PPFD, and CO_2 concentrations do not limit stomatal opening. Bringing all plants to comparable low g_L thus allowed comparison of osmoregulatory response among plants experiencing similar internal water conditions, in terms of loss of guard cell turgor, regardless of the external soil water status leading to the response. In fact, plants colonized by either mycobiont were able to maintain g_L* to slightly lower Ψ_{soil} than nonmycorrhizal plants (Table II).

Leaf Water Status. In nonmycorrhizal plants, the drought-acclimation treatment produced greater solute concentrations relative to the unacclimated treatments (subjected to the final cycle only), as evidenced by lower Ψ_π's at full turgor (Ψ_π^{100}) and at the turgor loss point (Ψ_π^0) (Table III). Consequently, the pressure potential at full turgor (Ψ_p^{100}) was higher in the acclimated plants (Table III). Furthermore, both RWC and ROWC at the turgor loss point (RWC^0) and ($ROWC^0$) were lower in the nonmycorrhizal, acclimated plants than in the corresponding unacclimated plants (Table IV). On the other hand, plants colonized by either species of *Glomus* developed similar RWC^0 and $ROWC^0$ in response to drought strain, whether one or several drought cycles had been administered (Fig. 1; Table IV). Ψ_π^{100} and Ψ_π^0 tended to be lower in mycorrhizal plants, and Ψ_p^{100} higher, as a consequence of acclimation (Table III).

Regardless of stress history, Ψ_π^{100} and Ψ_π^0 were 0.2 to 0.6 MPa lower in the mycorrhizal than in the nonmycorrhizal plants, representing changes of 29 to 40% (Fig. 1; Table III). As a result, turgor pressures achieved by mycorrhizal plants at full saturation were higher than in nonmycorrhizal controls (Table III), and turgor was maintained in mycorrhizal plants to greater degrees of tissue dehydration, as indicated by RWC° and WSD (Fig. 1; Tables II and IV). The decrease in Ψ_π at any given RWC in mycorrhizal plants (Fig. 1) was correlated with higher turgor pressures in mycorrhizal plants throughout the range of Ψ_{leaf} (Fig. 2). The extent of these turgor differences ranged from 0.2 to 0.5 MPa. This relationship existed in both unacclimated and acclimated plants, and for both *Glomus* species (Figs. 1 and 2). Thus, the enhancement of osmotic adjustment associated with mycorrhizae afforded plants a greater drought avoidance capability, by maintaining greater turgor at a particular water potential. Moreover, mycorrhizae enabled rose plants to maintain stomatal opening at lower Ψ_{leaf} and Ψ_{soil}, and at greater WSD (Table II), effects associated with osmotic adjustment (33). As expected, the acclimation treatment also allowed g_L maintenance at generally lower Ψ_{leaf} and Ψ_{soil} (Table II), an effect reported for many potted and field plants (1, 23, 32). The difference between Ψ_{leaf} and Ψ_{soil} at g_L* was, on the whole, slightly greater in unacclimated treatments (0.32–0.57 MPa) than in acclimated treatments (0.20–0.29 MPa) (Table II).

In addition to osmotic adjustment in response to drought, the relative partitioning of water into apoplastic (or 'bound') and symplastic (or 'osmotically active') fractions may constitute a mechanism for turgor maintenance (24). Tissues may have equal water contents, but if the water is partitioned such that a particular tissue has a much greater apoplastic percentage (A_p), that tissue will experience more rapid concentration of solutes as RWC decreases (24). Changes in water partitioning may (10) or may not (11) accompany osmotic adjustment, and presently it is not clear whether this mechanism is much exploited by plants, or if a greater A_p value is indeed a general response to drought. The acclimation treatment in this study did not appear to affect

Table II. *Soil Water Potential (Ψ_{soil}), Leaf Water Potential (Ψ_{leaf}) and Leaf Water Saturation Deficit (WSD) of Rose Plants Subjected to a Predetermined Level of Drought Strain (g_L*)*

Plants of all treatments were allowed to dry out until leaf conductance had declined to 1.1 mm s^{-1} (g_L*). Values are the means of 6 to 12 replicates, assayed between 0700 and 0900 h, with ±SE listed beneath each mean. Linear contrasts indicate nonsignificance (NS), or significance at the 5% (*), 1% (**), or 0.1% (***) level.

Treatment	Ψ_{leaf}	Ψ_{soil}	WSD
	MPa		%
Nonmycorrhizal			
Unacclimated	−1.88	−1.56	17.6
	0.13	0.08	1.7
Acclimated	−2.10	−1.81	18.1
	0.12	0.15	1.6
G. deserticola			
Unacclimated	−2.07	−1.70	22.0
	0.03	0.09	1.5
Acclimated	−2.61	−2.41	22.2
	0.11	0.11	0.6
G. intraradices			
Unacclimated	−2.64	−2.07	24.0
	0.35	0.15	1.4
Acclimated	−2.32	−2.08	19.7
	0.07	0.15	1.4
Linear Contrasts			
Nonmycorrhizal *versus* mycorrhizal	**	***	**
Unacclimated *versus* acclimated	NS	***	NS
G. deserticola versus G. intraradices	NS	NS	NS
Mycorrhizae × acclimation	**	***	NS

Table III. *Component Water Potentials of Rose Leaves at Full Turgor, Ψ_π^{100} and Ψ_p^{100} (RWC and ROWC = 100%), and at the Turgor Loss Point, Ψ_π^0 (Ψ_p = 0)*

Plants of all treatments were allowed to dry out until leaf conductance had declined to 1.1 mm s^{-1}, and then leaves were excised (between 0900 and 0950 h) for pressure-volume P-V) determinations (see "Materials and Methods"). Values of Ψ_π^{100} were obtained by regressing the linear portion of the P-V curve and extrapolating to V = 0 (y intercept). Values of Ψ_π^0 were derived from the relationships between leaf turgor potential and leaf water potential for combined replicates. n = 6, ±SE listed beneath each mean. Linear contrasts indicate nonsignificance (NS), or significance at the 5% (*), 1% (**), or 0.1% (***) level.

Treatment	Ψ_π^{100}	Ψ_π^0	Ψ_p^{100}
		MPa	
Nonmycorrhizal			
Unacclimated	−1.12	−1.51	1.07
	0.05	0.06	0.04
Acclimated	−1.32	−1.86	1.28
	0.05	0.08	0.05
G. deserticola			
Unacclimated	−1.45	−2.12	1.32
	0.08	0.12	0.08
Acclimated	−1.58	−2.41	1.52
	0.08	0.09	0.09
G. intraradices			
Unacclimated	−1.38	−2.08	1.29
	0.07	0.14	0.07
Acclimated	−1.53	−2.29	1.47
	0.10	0.17	0.10
Linear Contrasts			
Nonmycorrhizal *versus* mycorrhizal	***	***	***
Unacclimated *versus* acclimated	*	*	**
G. deserticola versus G. intraradices	NS	NS	NS
Mycorrhizae × acclimation	NS	NS	NS

Table IV. *Relative Water Content (RWC^0) and Relative Osmotic Water Content (ROWC^0) at the Turgor Loss Point, Relative Dry Weight (RDW) and Apoplastic Water (A_p) in Rose Leaves*

Plants of all treatments were allowed to dry out until leaf conductance had declined to 1.1 mm s^{-1}, and then leaves were excised (between 0900 and 0950 h) for pressure-volume (P-V) determinations. Calculations for RWC, ROWC, and RDW are explained in "Materials and Methods." The apoplastic water percentage was obtained by regressing the linear portion of the P-V curve and extrapolating to $-\Psi_{leaf}^{-1} = \infty$ (x intercept). Values are means of six replicates, with ±SE listed beneath each mean. Linear contrasts indicate nonsignificance (NS), or significance at the 5% (*) or 1% (**) level.

Treatment	RWC^0	ROWC^0	RDW	A_p
		%		
Nonmycorrhizal				
Unacclimated	88.4	74.3	39.7	54.6
	0.7	1.0	2.0	2.8
Acclimated	86.0	71.5	44.7	50.6
	0.9	1.6	2.1	2.7
G. deserticola				
Unacclimated	81.4	68.8	42.6	41.0
	2.0	2.1	2.3	5.3
Acclimated	82.2	68.8	49.5	43.2
	1.1	1.0	2.2	3.2
G. intraradices				
Unacclimated	82.0	67.3	48.9	45.5
	2.0	2.7	3.0	3.1
Acclimated	83.0	67.5	58.2	47.3
	2.0	2.3	3.2	5.3
Linear Contrasts				
Nonmycorrhizal *versus* mycorrhizal	**	**	**	*
Unacclimated *versus* acclimated	NS	NS	**	NS
G. deserticola versus G. intraradices	NS	NS	**	NS
Mycorrhizae × acclimation	NS	NS	NS	NS

A_p, but mycorrhizal colonization actually promoted lower A_p values (Table IV). Richter *et al.* (27) have presented an alternate method for estimating the bound water fraction, based on relative dry weight (RDW). Unexpectedly, RDW was lowest in unacclimated plants without mycorrhizae, while A_p was highest in these same plants (Table IV).

Even though leaves of mycorrhizal plants had greater symplastic water percentages as estimated by P-V data (*i.e.* lower A_p), ROWC, which reflects symplastic volume only, was still lower at the turgor loss point in the *Glomus*-colonized roses (Table IV). This is another important indication that VA mycorrhizae enhanced the drought resistance of rose, in this case promoting drought tolerance by allowing turgor maintenance at lower protoplasmic water percentages. RWC^0 and ROWC^0 were lower in plants colonized by either *Glomus* species. In considering the pressure-volume data and Ψ of leaves and soil at g_L*, it is interesting and perhaps surprising to note that mycorrhizal colonization generally had a greater effect than drought-acclimation on water status parameters (Figs. 1 and 2; Table II, III, and IV).

When unacclimated roses were droughted, *G. intraradices* had the greater influence of the two fungi. Relative to nonmycorrhizal plants, the Ψ_{leaf} at g_L* of *G. intraradices*-colonized plants was decreased nearly 0.8 MPa, compared to 0.2 MPa in *G. deserticola*-colonized roses (Table II). This same trend was reflected in Ψ_{soil} and WSD values, and is consistent with other findings for these two fungi (RM Augé, KA Schekel, RL Wample, unpublished data). Note, however, that when subjected to the acclimation treatment, *G. deserticola* granted host plants the greater resilience to water deficit stress, decreasing Ψ_{leaf} 0.5 MPa and

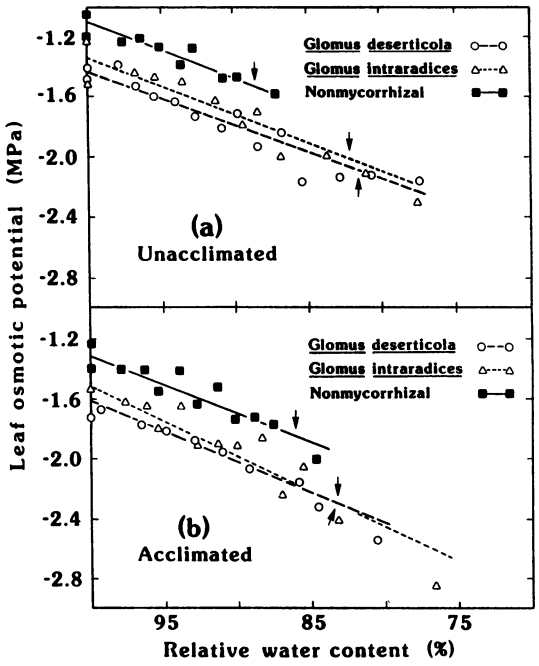

FIG. 1. Relationship between leaf osmotic potential ($\Psi\pi$) and relative water content (RWC) for (a) unacclimated and (b) acclimated rose plants that were nonmycorrhizal, or colonized by *G. deserticola* or *G. intraradices*. Arrows indicate bulk turgor loss point. Each point is the mean of three measurements. SE for Ψ_π ranged from 0.01 to 0.17 MPa, and for RWC from 0.0 to 1.6%. Lines are fitted linear regressions. Plots of Ψ_π as a function of ROWC depicted similar relationships.

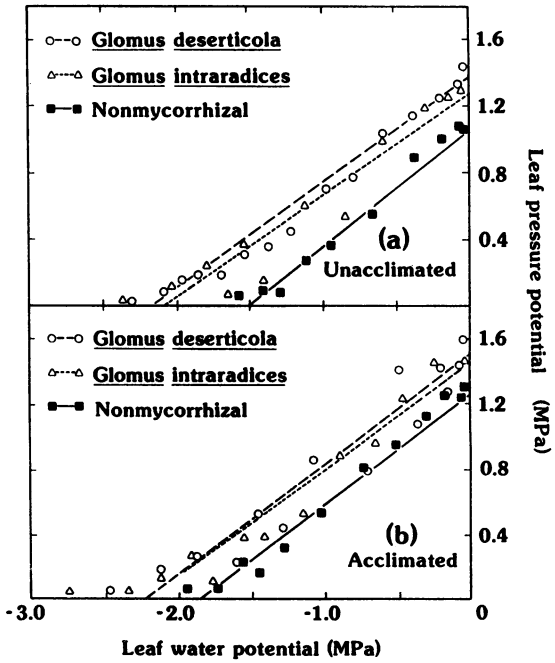

FIG. 2. Relationship between leaf pressure potential (Ψ_p) and leaf water potential (Ψ_{leaf}) for (a) unacclimated and (b) acclimated rose plants that were nonmycorrhizal, or colonized by *G. deserticola* or *G. intraradices*. Each point is the mean of three measurements. SE for Ψ_p ranged from 0.01 to 0.19 MPa, and for Ψ_{leaf} from 0.00 to 0.13 MPa. Lines are fitted linear regressions.

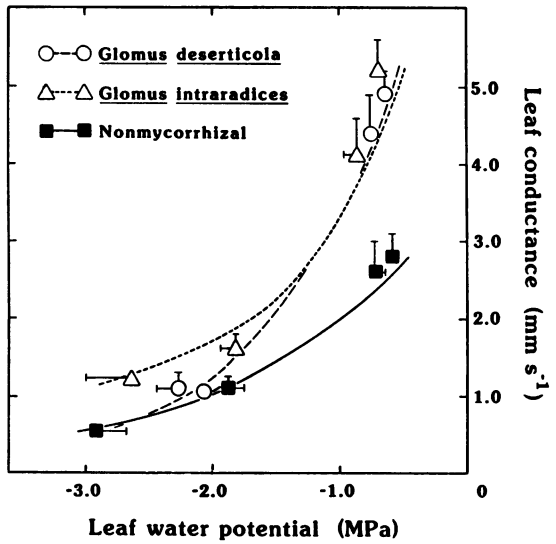

FIG. 3. Relationship between g_L and Ψ_{leaf} for unacclimated nonmycorrhizal and unacclimated mycorrhizal rose plants. Each point is the mean of six to eight measurements, summarizing four separate growth room experiments. Bars indicate ±SE (where absent, ±SE is included within the symbol). Curves were fitted to individual data points (30 per curve). *G. deserticola*, $g_L = \exp(1.1\ \Psi_{leaf})9.4$, $r = 0.87$. *G. intraradices*, $g_L = 10.0/(1+2.1\ \Psi_{leaf}^{1.23})$, $r = 0.75$. Nonmycorrhizal, $g_L = \exp(0.6\ \Psi_{leaf})3.7$, $r = 0.87$.

Ψ_{soil} 0.6 MPa beyond acclimated controls at g_L*. Though *G. intraradices*' influence on Ψ_{leaf} and Ψ_{soil} was sutained in acclimated plants, the acclimation treatment did not alter these parameters further (Table II). Overall, the two *Glomus* spp. produced a similar impact on parameters derived from P-V relationships (Tables III and IV).

Figure 3 summarizes data from the current and previous work on unacclimated rose plants under identical growth room conditions (4; RM Augé, KA Schekel, RL Wample, unpublished data). In mycorrhizal rose, g_L is higher at a particular Ψ_{leaf} than in nonmycorrhizal rose. In view of the present findings, this phenomenon might be explained in terms of lowered Ψ_π in mycorrhizal plants, even when preconditioning has not occurred.

In summary, both the drought acclimation and the mycorrhizal treatments furnished plants with higher solute levels (*i.e.* lower Ψ_π at full and zero turgor), compared with nonmycorrhizal plants having no drought preconditioning. The magnitude of this Ψ_π depression and the resultant effect on behavior of droughted roses was greatest in the mycorrhizal plants, regardless of stress history. As indicated by Ψ_π decreases at the turgor loss point (0.4–0.6 MPa below nonmycorrhizal plants), the capacity for solute accumulation which attended mycorrhizal colonization was similar to that reported for drought-induced osmotic adjustment in many plant species (24).

In the few mycorrhizal associations that have been examined, mycobiont influence on host water relations is often related to increased P uptake, particularly in well-watered soils (29). This is not always the case, however (4, 6, 12). Though investigated less frequently, it is possible and even quite likely that when soil moisture levels are low the activity of mycorrhizal fungi becomes more important for plant water uptake. Rose, commonly mycorrhizal under conditions of adequate P availability, clearly benefits by *Glomus* colonization during drought stress, in terms of osmotic adjustment and attendant turgor maintenance and leaf conductance at low soil and leaf water potentials. This influence is not accounted for by an enhancement of host phosphorus nutrition. Whether or not rose is typical or exceptional in this regard will be demonstrated as additional plant species are studied.

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LITERATURE CITED

1. ACKERSON RC 1980 Stomatal response of cotton to water stress and abscisic acid as affected by water stress history. Plant Physiol 65: 455–459
2. ALLEN MF, MG BOOSALIS 1983 Effects of two species of VA mycorrhizal fungi on drought tolerance of winter wheat. New Phytol 93: 67–76
3. ANDERSON RC, AE LIBERTA, LA DICKMAN 1984 Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil moisture-nutrient gradient. Oecologia 64: 111–117
4. AUGÉ RM, KA SCHEKEL, RL WAMPLE 1986 Greater leaf conductance of well-watered VA mycorrhizal rose plants is not related to phosphorus nutrition. New Phytol 103: 107–116
5. BIERMANN BJ, RG LINDERMAN 1981 Quantifying vesicular-arbuscular mycorrhizae: a proposed method toward standardization. New Phytol 87: 63–67
6. BILDUSAS IJ, RK DIXON, FL PFLEGER, EL STEWART 1986 Growth, nutrition and gas exchange of *Bromus inermis* inoculated with *Glomus fasciculatum*. New Phytol 102: 303–311
7. BRUNDRETT MC, Y PICHE, RL PETERSON 1984 A new method for observing the morphology of vesicular-arbuscular mycorrhizae. Can J Bot 62: 2128–2134
8. CHAPMAN HD, PF PRATT 1961 Methods of Analysis for Soils, Plants and Waters. University of California, Riverside, pp 161–174
9. COOPER KM 1984 Physiology of VA mycorrhizal associations. *In* CL Powell, DJ Bagyaraj, eds, VA Mycorrhiza. CRC Press, Inc, Boca Raton, FL, pp 157–165
10. CUTLER JM, DW RAINS 1978 Effects of water stress and hardening on internal water relations and osmotic constituents of cotton leaves. Physiol Plant 42: 261–268
11. FERERES E, E ACEVEDO, DW HENDERSON, TC HSIAO 1978 Seasonal changes in water potential and turgor maintenance in sorghum and maize under water stress. Physiol Plant 44: 261–267
12. HARDIE K 1985 The effect of removal of extraradical hyphae on water uptake by vesicular-arbuscular mycorrhizal plants. New Phytol 101: 677–684
13. HSIAO TC, E ACEVEDO, E FERERES, DW HENDERSON 1976 Stress metabolism. Phil Trans R Soc Lond B 273: 479–500
14. JONES HG, AN LAKSO, JP SYVERTSEN 1985 Physiological control of water status in temperate and subtropical fruit trees. Hortic Rev 7: 301–344
15. JONES MM, NC TURNER 1980 Osmotic adjustment in expanding and fully expanded leaves of sunflower in response to water deficits. Aust J Plant Physiol 7: 181–192
16. KIKUTA SB, E KYRIAKOPOULOUS, H RICHTER 1985 Leaf hygrometer *v.* pressure chamber: a comparison of pressure-volume curve data obtained on single leaves by alternating measurements. Plant Cell Environ 8: 363–367
17. KRAMER PJ 1983 Water Relations of Plants. Academic Press, New York, pp 376–379
18. LEVITT J 1980 Responses of Plants to Environmental Stresses. II. Water, Radiation, Salt, and Other Stresses. Academic Press, London, pp 3–53
19. LEVY Y, JP SYVERTSEN, S NEMEC 1983 Effect of drought stress and vesicular-arbuscular mycorrhiza on citrus transpiration and hydraulic conductivity of roots. New Phytol 93: 61–66
20. MACKAY AD, SA BARBER 1985 Soil moisture effects on root growth and phosphorus uptake by corn. Agron J 77: 519–523
21. MORGAN JM 1984 Osmoregulation and water stress in higher plants. Annu Rev Plant Physiol 35: 299–319
22. NELSEN CE, GR SAFIR 1982 Increased drought tolerance of mycorrhizal onion plants caused by improved phosphorus nutrition. Planta 154: 407–413
23. NILSEN ET, MR SHARIFI, PW RUNDEL 1984 Comparative water relations of phreatophytes in the Sonoran desert of California. Ecology 65: 767–778
24. RADIN JW 1983 Physiological consequences of cellular water deficits: osmotic adjustment. *In* HM Taylor, WR Jordan, TR Sinclair, eds, Limitations to Efficient Water Use in Crop Production. ASA-CSSA-SSSA, Madison, WI, pp 267–276
25. RADIN JW 1984 Stomatal responses to water stress and to abscisic acid in phosphorus-deficient cotton plants. Plant Physiol 76: 392–394
26. REID CPP 1978 Mycorrhizae and water stress. *In* A Reidecker, J Gagnaire-Michard, eds, Root Physiology and Symbiosis. IUFRO Proc, Nancy, France, pp 392–408
27. RICHTER H, F DUHME, G GLATZEL, TM HINCKLEY, H KARLIC 1979 Some limitations and applications of the pressure-volume curve technique in ecophysiological research. *In* J Grace, ED Ford, PG Jarvis, eds, Plants and Their Atmospheric Environment. Blackwell Scientific Publications, Boston, pp 263–272
28. RITCHIE GA, JR RODEN 1985 Comparison between two methods of generating pressure-volume curves. Plant Cell Environ 8: 49–53
29. SAFIR GR, CE NELSEN 1985 VA mycorrhizas: plant and fungal water relations. *In* R Molina, ed, Proceedings of the Sixth North American Conference on Mycorrhizae, Forest Research Laboratory, Corvallis, OR, pp 161–164

30. STEELE RGD, JH TORRIE 1980 Principles and Procedures of Statistics, Ed 2. McGraw-Hill, New York, pp 336–411
31. SWEATT MR, FT DAVIES JR 1984 Mycorrhizae, water relations, growth, and nutrient uptake of geranium grown under moderately high phosphorus regimes. J Am Soc Hortic Sci 109: 210–213
32. THOMAS JC, KW BROWN, WR JORDAN 1976 Stomatal response to leaf water potential as affected by preconditioning in the field. Agron J 68: 706–708
33. TURNER NC, MM JONES 1980 Turgor maintenance by osmotic adjustment: a review and evaluation. *In* NC Turner, PJ Kramer, eds, Adaptation of Plants to Water and High Temperature Stress. John Wiley and Sons, New York, pp 87–103
34. TYREE MT, HT HAMMEL 1972 The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. J Exp Bot 23: 267–282