PHYSIOL. PLANTARUM 70: 175–182. Copenhagen 1987

Rose leaf elasticity changes in response to mycorrhizal colonization and drought acclimation

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Augé, R. M., Schekel, K. A. and Wample, R. L. 1987. Rose leaf elasticity changes in response to mycorrhizal colonization and drought acclimation. – Physiol. Plantarum 70: 175–182.

Tissue elasticity can affect plant response to drought, in terms of turgor maintenance and water uptake from drying soils. The purpose of this study was to determine the effect of mycorrhizal colonization and drought acclimation on rose (*Rosa hybrida* L. cv. Samantha) leaf elasticity. Bulk elasticity was characterized by the pressure-volume method using plots of the elastic modulus as a function of leaf turgor pressure, total water potential and relative water content. The treatments, arranged in a 2×3 factorial design, included acclimated and unacclimated plants, and either *Glomus intraradices* Schenck and Smith, *Glomus deserticola* Trappe, Bloss and Menge, or a non-mycorrhizal control. Plants with root mycorrhizal colonization showed reduced leaf elasticity (i.e. higher elastic moduli) over a broad range of leaf water potential and water content. Both mycorrhizal colonization and acclimation facilitated the maintenance of positive values of turgor and elasticity at lower leaf water potential and water content than in controls. Mycorrhizal infections may aid plants in acclimating to water deficits through effects on leaf tissue elasticity.

Additional key words – Elastic modulus, *Glomus*, mycorrhizae, pressure-volume, *Rosa hybrida*, turgor, water relations.

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Introduction

It is believed that cell turgor plays an important role in the transduction of cellular water status into physiological and biochemical terms (Zimmermann 1978). At a particular water potential or water content, the turgor pressure (pressure potential) in higher plant tissues depends upon the osmotic potential and tissue elasticity (Turner and Jones 1980; Radin 1983). Turgor pressure changes are coupled with volume changes by the elastic properties of the cell walls, described by the so-called volumetric elastic modulus, E (Zimmermann 1978). The bulk tissue elastic modulus is a useful parameter for relating overall tissue turgor pressure changes to changes in tissue water content.

Turgor maintenance in tissues subjected to water deficits is facilitated by osmotic adjustment (Turner and Jones 1980, Bowman and Roberts 1985). The fraction of total osmotic adjustment attributable to active solute accumulation varies with species and environmental conditions, and may be small (Fereres et al. 1979, Jones et al. 1985). The amount of passive osmotic adjustment due to tissue water loss depends on the elasticity of the cell walls (Jones et al. 1985). Therefore, wall elasticity may exert a substantial influence on total osmotic adjustment.

Mycorrhizae can alter host response to drought stress (Nelsen and Safir 1982, Allen and Boosalis 1983, Busse and Ellis 1985, Augé et al. 1986c, Bildusas et al. 1986). One mechanism for this alteration is an enhancement of osmotic adjustment in mycorrhizal plants (Augé et al. 1986b). A mycorrhizal effect on tissue elasticity could further aid drought acclimation. The present paper characterizes elasticity relationships in rose leaves, and

Received 18 August, 1986; revised 14 January, 1987

summarizes the effects of mycorrhizal colonization and drought acclimation on bulk elasticity in leaves from plants of similar size and phosphorus nutrition.

Abbreviations – DW, leaf dry weight; *E*, bulk leaf elastic modulus; E_m, the maximum value of *E*; E_i, *E* near full turgor; FW, leaf intermediate fresh weight; g, leaf conductance; *K*, slope of the linear portion of the E-Ψ_p relationship at low turgors; PPFD, photosynthetic photon flux density (400–700 nm); P-V, pressure-volume; RWC, relative leaf water content; RWC^0, the RWC at which *E* became 0; SW, leaf saturated weight; VA, vesicular-arbuscular; W_{ro}, relative osmotic water content; WSD, leaf water saturation deficit; Ψ_p, bulk leaf turgor pressure; $\Psi_p(E_m)$, Ψ_p at E_m; Ψ_{leaf}, bulk leaf water potential; $\Psi_{leaf}(E_m)$, Ψ_{leaf} at E_m; Ψ_π, bulk leaf osmotic potential; $\Psi_\pi(E_m)$, Ψ_π at E_m.

Materials and methods

Bulk elastic modulus derivation

Tissue elasticity was characterized with the pressure-volume (P-V) approach (Tyree and Hammel 1972, Richter et al. 1979), using the bench top drying procedure (Robichaux 1984, Ritchie and Roden 1985) on leaves sampled as described earlier (Augé et al. 1986b). Leaves were removed from the chamber between determinations, allowed to dry on the laboratory bench, and incremental water losses derived by weighing.

Balance points were observed through a microscope mounted above the pressure chamber (Soilmoisture Equip. Corp., Santa Barbara, CA), and appropriate P-V precautions observed (Kikuta et al. 1985). In computing P-V parameters, no attempt was made to correct for possible cavitations occurring during leaf dehydration.

The bulk tissue elastic modulus, *E*, was calculated as the slope of the relationship between bulk leaf turgor pressure (Ψ_p) and relative osmotic water fraction (W_{ro}) for every increment in tissue water loss (Zimmermann 1978, Jones and Turner 1980, Jones et al. 1985):

$$E = d\Psi_p/(dV/V_{ref}) \simeq \Delta\Psi_p/\Delta W_{ro} \qquad (1)$$

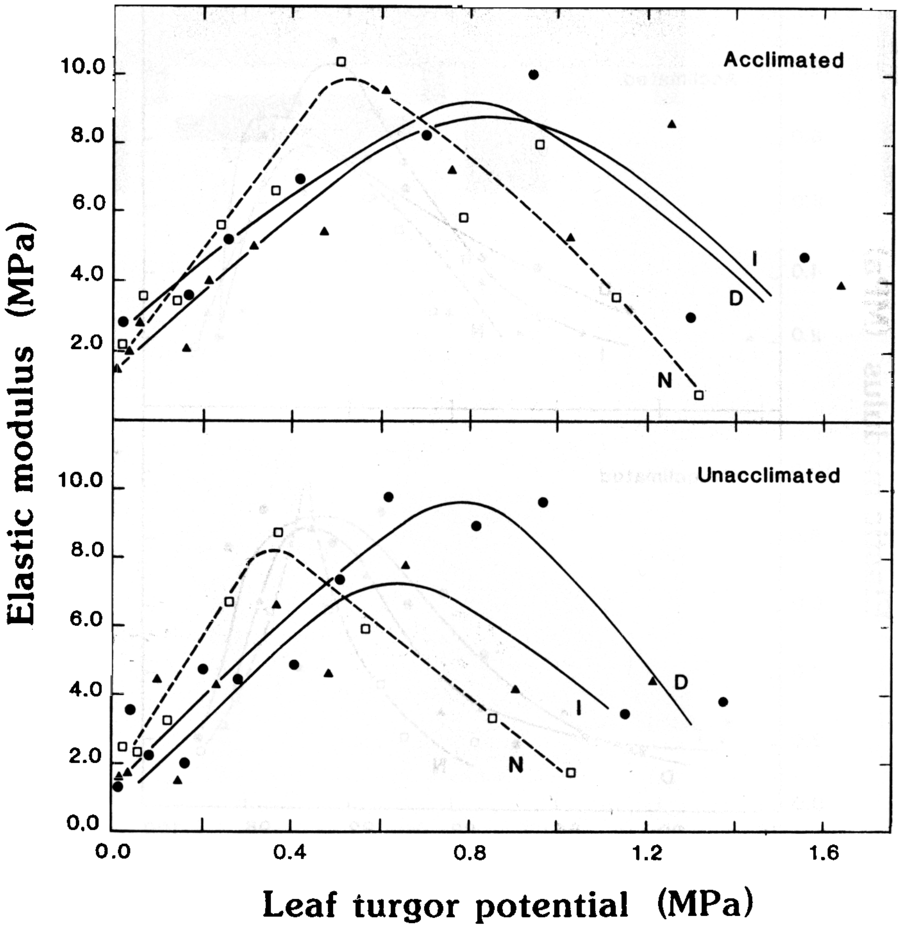
where V is the cumulative volume of water evaporated during the P-V determination, and V_{ref} represents the total volume of osmotic (symplastic) water in the leaf. Ψ_p was calculated from the measurements of leaf water potential and the osmotic potential obtained from the P-V regression. W_{ro} was calculated as:

$$W_{ro} = (V_{ref} - V)/V_{ref}. \qquad (2)$$

Tab. 1. Summary of the bulk leaf elasticity for non-mycorrhizal and mycorrhizal rose plants, which were unacclimated or acclimated to drought stress. Given for each treatment are: the initial slope *K* of the *E*-turgor pressure relationship; E_m, the maximum bulk elastic modulus; E_i, *E* near full turgor; $\Psi_p(E_m)$, the turgor pressure at E_m; $\Psi_\pi(E_m)$, the osmotic potential at E_m; $\Psi_{leaf}(E_m)$, the total leaf water potential at E_m; and RWC^0, the value of the RWC as *E* became zero (turgor loss point). Values are means of 6 replicates, with ± SE listed beneath each mean (except for *K*, in which regression coefficient is listed; see text for details). Linear contrast indicate non-significance (NS), or significance at the 5% (*), 1% (**) or 0.1% (***) level.

Treatment		*K*	E_m (MPa)	E_i (MPa)	$\Psi_p(E_m)$ (MPa)	$\Psi_\pi(E_m)$ (MPa)	$\Psi_{leaf}(E_m)$ (MPa)	RWC^0 (%)
Non-mycorrhizal	Unacclimated	19.5	8.0	2.2	0.35	–1.30	–0.96	88.4
		r = 0.98	1.2	0.6	0.02	0.05	0.05	0.7
	Acclimated	15.6	9.1	1.3	0.54	–1.56	–1.01	86.0
		r = 0.98	0.8	0.3	0.07	0.06	0.07	0.9
G. intraradices	Unacclimated	8.7	7.4	3.6	0.58	–1.60	–1.02	82.0
		r = 0.85	1.1	0.6	0.10	0.10	0.13	2.0
	Acclimated	9.1	9.1	2.9	0.69	–1.76	–1.07	83.0
		r = 0.91	1.6	0.5	0.11	0.11	0.09	2.0
G. deserticola	Unacclimated	10.0	10.7	3.2	0.74	–1.62	–0.87	81.4
		r = 0.93	1.1	1.0	0.08	0.10	0.05	2.0
	Acclimated	7.9	9.7	2.5	0.99	–1.90	–0.92	82.2
		r = 0.98	0.9	0.5	0.07	0.06	0.07	1.1
Linear contrasts								
Non-mycorrhizal vs mycorrhizal		–	NS	*	***	***	NS	**
Unacclimated vs acclimated		–	NS	NS	**	***	NS	NS
G. deserticola vs *G. intraradices*		–	NS	NS	**	NS	NS	NS
Mycorrhizae × acclimation		–	NS	NS	NS	NS	NS	NS

Fig. 1. Relationship between the leaf elastic modulus, E, and turgor pressure, Ψ_p, for unacclimated and acclimated rose plants. Each point is the mean of 3 measurements. SE for E ranged from 0.1 to 2.7 MPa, and for Ψ_p from 0.00 to 0.08 MPa. □, non-mycorrhizal plants (N); ▲, *Glomus intraradices*-colonized plants (I); ●, *Glomus deserticola*-colonized plants (D).



To determine V_{ref}, the inverse of the balance pressure (P^{-1}) (y axis) was plotted against V (x axis) and a least squares linear regression was fitted to the linear segment of the curve. This line represented the relationship between the inverse of the leaf osmotic potential and the volume expressed, V, with the x intercept indicating V_{ref}.

Leaf water saturation deficit (WSD) was calculated as (Kramer 1983):

$$\mathrm{WSD} = 100\,(\mathrm{SW} - \mathrm{FW})/(\mathrm{SW} - \mathrm{DW}) \qquad (3)$$

where SW, FW and DW were the saturated weight, intermediate fresh weight and dry weight, respectively, of leaves used in P-V relations. Leaf relative water content (RWC) = 100 − WSD.

As E is generally not constant at all leaf turgor pressures (Ψ_p), water potentials (Ψ_{leaf}) and relative water contents (RWC); (Cheung et al. 1976, Jones et al. 1985), E was characterized using plots of E as a function of each of these variables. In addition, the following parameters were recorded: K, the initial slope (at low turgors) of the E-Ψ_p relation (Roberts et al. 1981); E_m, the maximum value of E obtained from each replicate's P-V plot; E_i, the bulk elastic modulus near full turgor; $\Psi_p(E_m)$, $\Psi_\pi(E_m)$ and $\Psi_{leaf}(E_m)$, the turgor pressure, osmotic potential and bulk leaf water potential, respectively, at E_m; and RWC^0, the value of leaf RWC as E became 0 (the turgor loss point). K was derived by regressing the means in the linear portion of the E-Ψ_p plots in Fig. 1.

Plant culture, inoculation procedures and growth room conditions

Rosa hybrida L. cv. Samantha plants were grown in a greenhouse in calcined montmorillonite clay (Turface; IMCore, Mundelein, IL) with one of three vesicular-arbuscular (VA) mycorrhizal inocula originally 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 soil and mycorrhizal root pieces of *Glycine max* (L.) Merr cv. Maple Amber and *Rosa hybrida* L. cv. Sonia, grown in sand. The third inoculum, a control, was an autoclaved mixture (1:1, v/v) of the above two inocula. All plants received appropriate inoculum water extracts (final sieve 25 μm) to establish the microflora as-

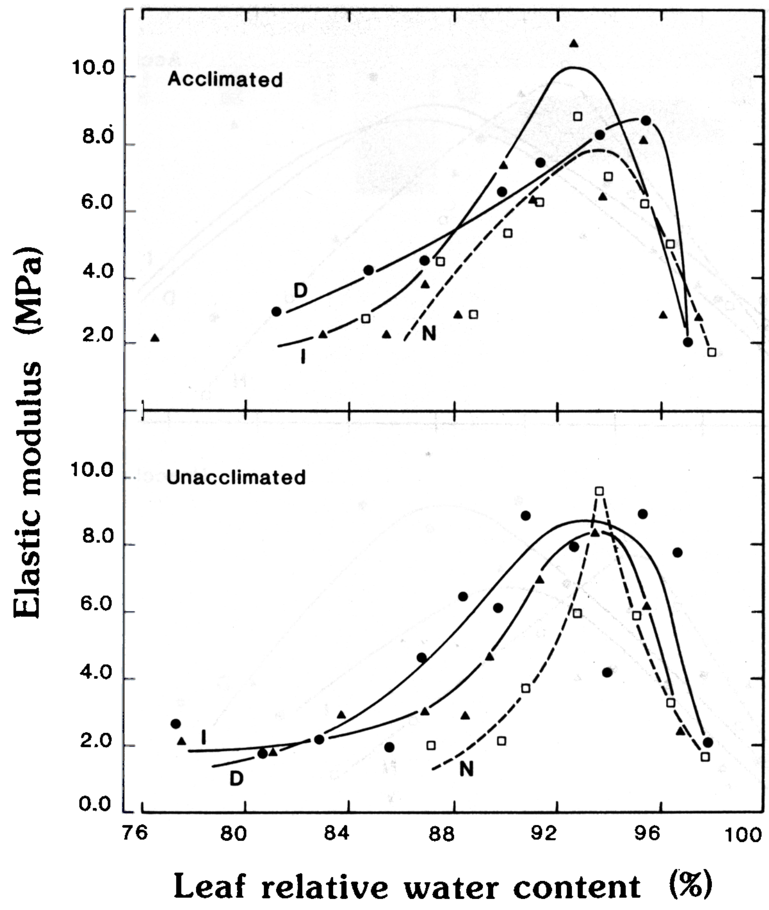


Fig. 2. Relationship between the leaf elastic modulus and relative water content, RWC, for unacclimated and acclimated rose plants. Each point is the mean of 3 measurements. SE for *E* ranged from 0.1 to 2.7 MPa, and for RWC from 0.1 to 1.6%. □, non-mycorrhizal plants (N); ▲, *Glomus intraradices*-colonized plants (I); ●, *Glomus deserticola*-colonized plants (D).

sociated with each inoculum (Linderman and Hendrix 1982).

At seven months, plants were transplanted into 25 cm pots, and at nine months plants of similar size were moved into a controlled environment growth room for drought acclimation and water relations studies. Growth room PPFD ranged from 290 to 350 μmol m^{-2} s^{-1}, with a 14 h photoperiod. Day/night temperature and relative humidity were 22/17°C and 40/90%, respectively. Plants were watered daily throughout the experiment, and every other day received 10.4 m*M* N and 3.1 m*M* K (as Peter's 15-0-15 soluble fertilizer; W. R. Grace & Co., Fogelsville, PA). Control and mycorrhizal plants received weekly 3.0 and 0.7 m*M* P, respectively, as KH_2PO_4.

Drought acclimation procedure

For acclimation, plants were allowed to dry until leaf conductance (g) declined to 1.0 mm s^{-1}, and then were rewatered. Four such cycles were repeated on 6 replicates of each of the non-mycorrhizal and mycorrhizal treatments, for a total acclimation time of 17–20 days. Unacclimated treatments were watered daily, with g remaining above 5.6 mm s^{-1}. Leaf conductance was determined with a porometer (Delta-T Devices, Cambridge, England) as previously described (Augé et al. 1986a). Fertilization was discontinued during the acclimation period.

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 (Brundrett et al. 1984) and mycorrhizal colonization quantified as described earlier (Biermann and Linderman 1981, Augé et al. 1986a). 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 (Chapman and Pratt 1961).

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 non-mycorrhizal control). P-V curves were determined for 6

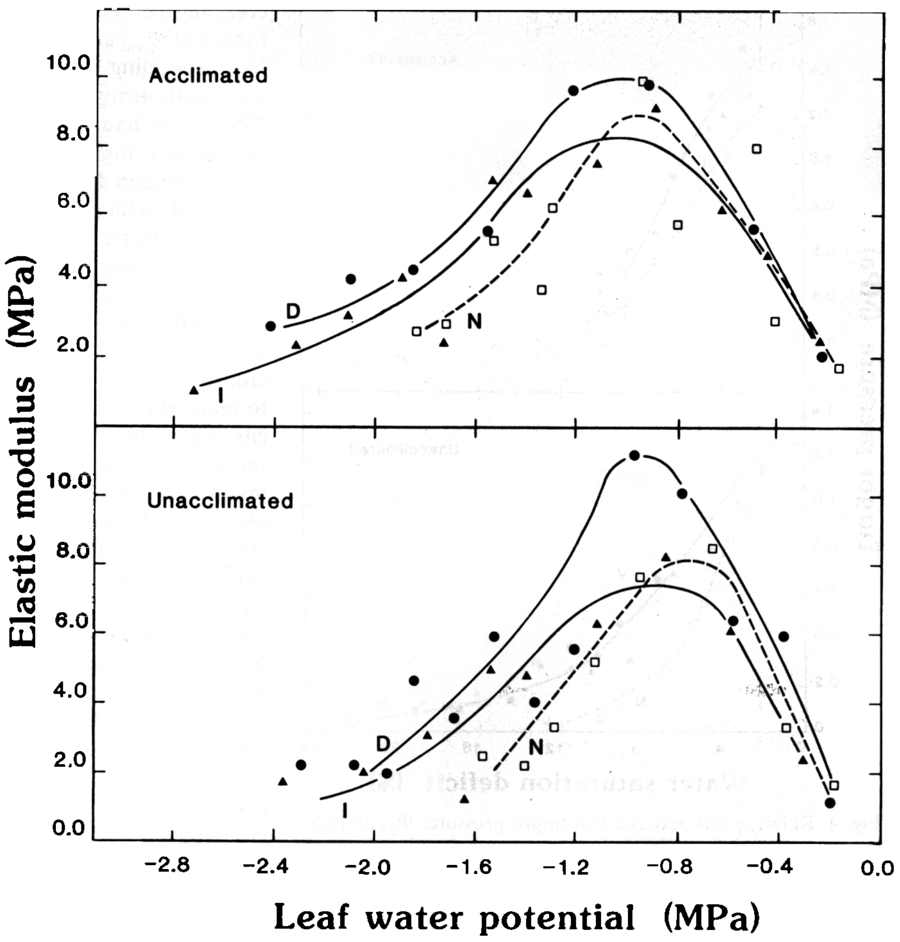


Fig. 3. Relationship between the leaf elastic modulus and total water potential, Ψ_{leaf}, for unacclimated and acclimated rose plants. Each point is the mean of 3 measurements. SE for E ranged from 0.0 to 2.1 MPa, and for Ψ_{leaf} from 0.00 to 0.08 MPa. □, non-mycorrhizal plants (N); ▲, *Glomus intraradices*-colonized plants (I); ●, *Glomus deserticola*-colonized plants (D).

plants per treatment. Univariate analyses of variance with specific linear contrasts were performed to partition the variance into the main effects and the interaction between the two factors (Steele and Torrie 1980). Four contrasts, each involving more than two treatments, are listed in Tab. 1, as are SE for each mean.

Results

The relationships between E and leaf Ψ_p, RWC and Ψ_{leaf} are shown in Figs 1, 2 and 3. Leaf E of mycorrhizal plants was greater than in non-mycorrhizal plants over much of the E-RWC and E-Ψ_{leaf} plots, particularly in the drought range (Figs 2 and 3). Below Ψ_{leaf} of −1.0 MPa and RWC of about 92%, E values were always highest for the mycorrhizal plants, in both the unacclimated and acclimated treatments. When plotted as a function of Ψ_p, E was greatest at higher turgors in the mycorrhizal plants (Fig. 1). Both mycorrhizal and acclimation treatments permitted the attainment of higher turgor pressures at full tissue saturation (Fig. 1).

Maximum values of E did not differ appreciably in magnitude among treatments (Tab. 1). E_m was developed in both mycorrhizal treatments at turgor pressures approximately 0.2 to 0.4 MPa greater than in non-mycorrhizal treatments, regardless of acclimation (Tab. 1, Fig. 1). As indicated by linear contrast, $\Psi_p(E_m)$ was greater in *G. deserticola*-colonized roses than in *G. intraradices*-colonized roses (Tab. 1). Acclimated plants also had significantly higher $\Psi_p(E_m)$ (Tab. 1). Treatment effects on $\Psi_\pi(E_m)$ corresponded to effects on $\Psi_\pi(E_m)$ (Tab. 1). Those plants with higher turgors at E_m were also plants with lower Ψ_π at E_m. The result was that $\Psi_{leaf}(E_m)$ remained relatively unaffected by acclimation or mycorrhizal colonization. E_m was attained at a Ψ_{leaf} of about −1.0 MPa and a RWC of about 93% in all treatments (Tab. 1, Figs 2 and 3).

E_i was increased by an average of 75% by mycorrhizal colonization (Tab. 1, Fig. 1), and K values in mycorrhizal plants were approximately half that of non-mycorrhizal plants (Tab. 1). RWC^0, unaffected by acclimation, was significantly affected by colonization by both fungi (Tab. 1). Overall, mycorrhizae decreased RWC^0

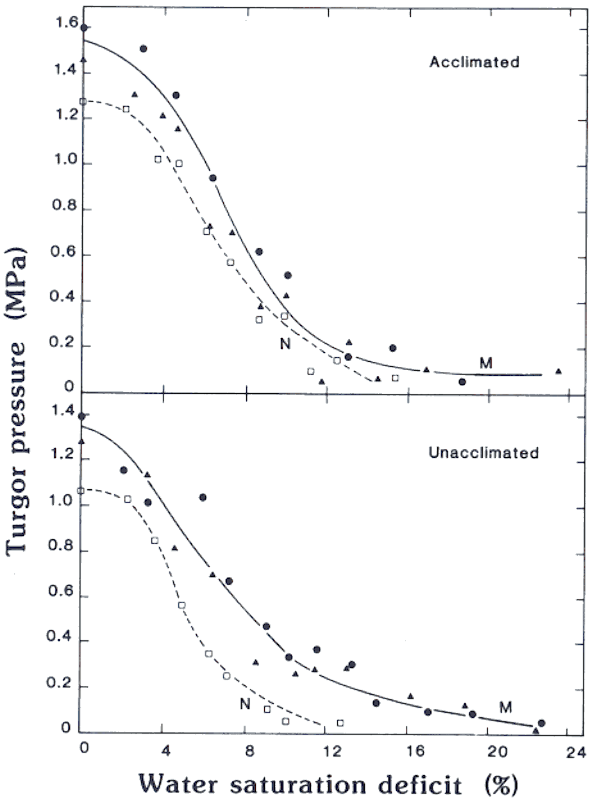


Fig. 4. Relationship between leaf turgor pressure, Ψ_p, and water saturation deficit, WSD, for unacclimated and acclimated rose plants. WSD = 100 − RWC. Each point is the mean of 3 measurements. SE for Ψ_p ranged from 0.00 to 0.24 MPa, and for WSD from 0.1 to 1.6%. □, non-mycorrhizal plants (N); ▲, *Glomus intraradices*-colonized plants; ●, *Glomus deserticola*-colonized plants. The curve for the mycorrhizal plants (M) was fitted to data points from both *Glomus* species.

(which also represents the turgor loss point) by 39%. Because turgor was maintained at lower RWC, positive values of *E* were also maintained at these lower RWC in mycorrhizal plants (Fig. 2). Regardless of acclimation, Ψ_π was greater at any particular level of WSD when plants were mycorrhizal (Fig. 4).

Generally, leaves from plants colonized by either *Glomus* species displayed similar values for elasticity parameters (Tab. 1, Figs 1 and 2). Colonization levels were 53 to 66% for unacclimated mycorrhizal plants, and 76 to 83% for acclimated mycorrhizal plants.

Plants from all treatments had adequate phosphorus levels. Leaves of non-mycorrhizal, *G. intraradices*-colonized and *G. deserticola*-colonized plants had 0.3, 0.2–0.3 and 0.2% P, respectively. Drought acclimation had no effect on leaf P content.

Discussion

Colonization of rose plants by both *Glomus* species affected leaves by generally decreasing elasticity (i.e. increasing the elastic modulus), particularly in the lower ranges of Ψ_{leaf} and RWC. Although low *E* and E_i values (corresponding to flexible cell walls) have been correlated with drought-adaptation in *Dubautia* (Robichaux 1984, Robichaux and Canfield 1985) and may provide cells with a high resistance to short-term water stress (Zimmermann 1978), a review of recent literature suggests that an increase in tissue rigidity often occurs in response to water deficit stress and may offer physiological and ecological advantages (Cheung et al. 1975, Jones and Turner 1978, Zimmermann 1978, Jones et al. 1980, Monson and Smith 1982, Bowman and Roberts 1985). Tissues with rigid cell walls undergo a greater decrease in Ψ_p per unit decrease in water content relative to more elastic walls. This can reduce tissue water deficits associated with decreases in plant Ψ_{leaf}, mostly through decreases in Ψ_p (Cheung et al. 1975, Zimmermann 1978, Monson and Smith 1982). This effect may also facilitate continued water uptake from drying soils (Bowman and Roberts 1985). Hence, in terms of an elasticity response, mycorrhizal colonization may offer an advantage to plants growing in dry soils. The above results for mycorrhizal plants are consistent with the observation that mycorrhizal hosts may have thicker cell walls than non-mycorrhizal plants, through increased lignification and production of other polysaccharides (Dehne and Schonbeck 1979).

Values of *E* varied with Ψ_p changes in all treatments (Fig. 1), an effect reported previously for many species (Cheung et al. 1976, Zimmermann 1978, Roberts et al. 1981, Robichaux 1984, Bowman and Roberts 1985, Jones et al. 1985). Roberts et al. (1981) have described four general response classes for the relationship between *E* and Ψ_p. Unacclimated, acclimated, mycorrhizal and non-mycorrhizal roses all displayed a "type III" response: an initial increase of *E* with increasing turgor, then a peak in *E* at some intermediate turgor, followed by a decrease in *E* with further increase in turgor (Fig. 1). These plots resemble those in a drought-adapted *Dubautia* species (Robichaux 1984, Robichaux and Canfield 1985). Similar plots exemplified the *E*-RWC and *E*-Ψ_{leaf} relationships, as well. As was the case for the type III response in *Acer rubrum* (Roberts et al. 1981) and in the dry-habitat *Dubautia* (Robichaux 1984, Robichaux and Canfield 1985), the initial increases in the *E*-Ψ_p plots for rose were linear. These initial slopes *(K)* showed that non-mycorrhizal leaves were twice as responsive in elasticity changes with changes in Ψ_p, in both unacclimated and acclimated plants (Tab. 1).

The significance of the different *E* response types can be illustrated by plots of turgor as a function of water saturation deficit (WSD); (Roberts et al. 1981, Robichaux and Canfield 1985). Figure 4, which shows a sigmoidal relation between Ψ_p and WSD in rose, closely resembles the type III response reported by Roberts et al.: a slow loss of turgor at low water deficits preceeds a break in the response with rapid loss of turgor at intermediate water deficits, and finally another break in the response to again a slow loss of turgor at the larger deficits. Turgor response patterns are important because of their effect on turgor-sensitive processes, and also because of the large contribution of the Ψ_p component to Ψ_{leaf}, which in turn regulates the water potential gradient responsible for water uptake (Roberts et al. 1981). At most WSD, turgor was greater in mycorrhizal plants than in non-mycorrhizal plants, again suggesting the acclimative value of mycorrhizal colonization, especially to short-term water deficits (Fig. 4, lower graph). Greater Ψ_p at a particular RWC has also been demonstrated to occur in response to drought in desert species (Monson and Smith 1982) and in the droughtadapted species *Dubautia ciliolata* and *D. menziesii* (Robichaux 1984, Robichaux and Canfield 1985).

Cheung et al. (1975) found that the difference between the Ψ_π at full and zero turgor for a given tissue tended to be smaller when cells have more rigid walls. The reverse was observed in mycorrhizal rose leaves. Plants colonized by both *Glomus* species had the greatest difference between, as well as the lowest values for, Ψ_π at full and zero turgor (Augé et al. 1986b). Mycorrhizal plants also tended to have stiffer walls (higher E values). As Bowman and Roberts (1985) note, this combination of characteristics, a high E and a low Ψ_Π, may allow decreases in Ψ_{leaf} to occur, facilitating water uptake and maintaining positive turgor at low soil moistures. Mycorrhizal roses have been shown, in fact, to maintain turgor at lower soil water potential than uncolonized roses (Augé et al. 1986b).

The functional dependency of the elastic properties of bulk tissue on tissue water status is complex (Roberts et al. 1981) and a decision as to the exact function of elasticity changes in the regulation of plant water relations cannot be made with any certainty at the present time (Zimmermann 1978). Nevertheless, mycorrhizal colonization of rose roots does influence the elasticity of leaves, and this influence, indicative of enhanced acclimation to drought stress, is in accord with previous studies on rose plant water relations and mycorrhizae (Augé et al. 1986a,b,c).

Acknowledgements – The senior author gratefully acknowledges the immense support of Ms. Kay Peterson. Scientific paper No. 7527, Agriculture Research Center, Washington State Univ.

References

Allen, M. F. & Boosalis, M. G. 1983. Effects of two species of VA mycorrhizal fungi on drought tolerance of winter wheat. – New Phytol. 93: 67–76.

Augé, R. M., Schekel, K. A. & Wample, R. L. 1986a. Greater leaf conductance of VA mycorrhizal rose plants is not related to phosphorus nutrition. – New Phytol. 103: 107–116.

– , Schekel, K. A. & Wample, R. L. 1986b. Osmotic adjustment in leaves of VA mycorrhizal and nonmycorrhizal rose plants in response to drought stress. – Plant Physiol. 82: 765–770.

– , Schekel, K. A. & Wample, R. L. 1986c. Leaf water and carbohydrate status of VA mycorrhizal rose exposed to drought stress. – Plant Soil (In press).

Biermann, B. J. & Linderman, R. G. 1981. Quantifying ves icular-arbuscular mycorrhizae: a proposed method toward standardization. – New Phytol. 87: 63–67.

Bildusas, I. J., Dixon, R. K., Pfleger, F. L. & Stewart, E. L. 1986. Growth, nutrition and gas exchange of *Bromus inermis* inoculated with *Glomus fasciculatum*. – New Phytol. 102: 303–311.

Bowman, W. D. & Roberts, S. W. 1985. Seasonal changes in tissue elasticity in chaparral shrubs. – Physiol. Plantarum 65: 233–236.

Brundrett, M. C., Piche, Y. & Peterson, R. L. 1984. A new method for observing the morphology of vesicular-arbuscular mycorrhizae. – Can. J. Bot. 62: 2128–2134.

Busse, M. D. & Ellis, J. R. 1985. Vesicular-arbuscular mycorrhizal *(Glomus fasciculatum)* influence on soybean drought tolerance in high phosphorus soil. – Can. J. Bot. 63: 2290–2294.

Chapman, H. D. & Pratt, P. F. 1961. Methods of Analysis for Soils, Plants and Waters. – Univ. of California, Riverside. pp. 161–174.

Cheung, Y. N. S., Tyree, M. T. & Dainty, J. 1975. Water relations parameters on single leaves obtained in a pressure bomb and some ecological interpretations. – Can. J. Bot. 53: 1342–1346.

– , Tyree, M. T. & Dainty, J. 1976. Some possible sources of error in determining bulk elastic moduli and other parameters from pressure-volume curves of shoots and leaves. – Can. J. Bot. 54: 758–765.

Dehne, H.-W. & Schonbeck, F. 1979. Untersuchungen zum Einfluss der endotrophen Mycorrhiza auf Pflanzenkrankheiten. II. Phenolstoffwechsel und Lignifizierung. – Phytopath. Z. 95: 210–216.

Fereres, E., Cruz-Romero, G., Hoffmann, G. J. & Rawlins, S. L. 1979. Recovery of orange trees following severe water stress. – J. Appl. Ecol. 16: 833–842.

Jones, H. G., Lakso, A. N. & Syvertsen, J. P. 1985. Physiological control of water status in temperate and subtropical fruit trees. – Hortic. Rev. 7: 301–344.

Jones, M. M. & Turner, N. C. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. – Plant Physiol. 61: 122–126.

– & Turner, N. C. 1980. Osmotic adjustment in expanding and fully expanded leaves of sunflower in response to water deficits. – Aust. J. Plant Physiol. 7: 181–192.

– , Turner, N. C. & Osmond, C. B. 1980. Mechanisms of drought resistance. – *In* The Physiology and Biochemistry of Drought Resistance (L. G. Paleg and D. Aspinall, eds), pp. 15–37. Academic Press, New York. ISBN 0-12-544380-3.

Kikuta, S. B., Kyriakopoulous, E. & Richter, H. 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.

Kramer, P. J. 1983. Water Relations of Plants. – Academic Press, New York, pp. 376–379. ISBN 0-12-425040-8.

Linderman, R. G. & Hendrix, J. W. 1982. Evaluation of plant response to colonization by vesicular-arbuscular mycorrhizal fungi. A. Host variables. – *In* Methods and Principles of Mycorrhizal Research (N. C. Schenck, ed.), pp. 69–76. American Phytopathological Society, St. Paul, MN. ISBN 0-89-054046-2.

Monson, R. K. & Smith, S. D. 1982. Seasonal water potential components of Sonoran Desert plants. – Ecology 63: 113–123.

Nelsen, C. E. & Safir, G. R. 1982. Increased drought tolerance of mycorrhizal onion plants caused by improved phosphorus nutrition. – Planta 154: 407–413.

Radin, J. W. 1983. Physiological consequences of cellular water deficits: osmotic adjustment. – *In* Limitations to Efficient Water Use in Crop Production (H. M. Taylor, W. R. Jordan and T. R. Sinclair, eds), pp. 267–276. ASA-CSSA-SSSA, Madison, WI. ISBN 0-89-118074-5.

Richter, H., Duhme, F., Glatzel, G., Hinckley, T. M. & Karlic, H. 1979. Some limitations and applications of the pressure-volume curve technique in ecophysiological research. – *In* Plants and their Atmospheric Environment (J. Grace, E. D. Ford and P. G. Jarvis, eds), pp. 263–272. Blackwell Scientific Publications, Boston, MA. ISBN 0-63-200525-4.

Ritchie, G. A. & Roden, J. R. 1985. Comparison between two methods of generating pressure-volume curves. – Plant Cell Environ. 8: 49–53.

Roberts, S. W., Strain, B. R. & Knoerr, K. R. 1981. Seasonal variation of leaf tissue elasticity in four forest tree species. – Physiol. Plantarum 52: 245–250.

Robichaux, R. H. 1984. Variation in the tissue water relations of two sympatric Hawaiian *Dubautia* species and their natural hybrid. – Oecologia (Berlin) 65: 75–81.

– & Canfield, J. E. 1985. Tissue elastic properties of eight Hawaiian *Dubautia* species that differ in habitat and diploid chromosome number. – Oecologia (Berlin) 66: 77–80.

Steele, R. G. D. & Torrie, J. H. 1980. Principles and Procedures of Statistics. – McGraw-Hill, New York. pp. 336–411. ISBN 0-07-060926-8.

Turner, N. C. & Jones, M. M. 1980. Turgor maintenance by osmotic adjustment: a review and evaluation. – *In* Adaptation of Plants to Water and High Temperature Stress (N. C. Turner and P. J. Kramer, eds), pp. 87–103. John Wiley & Sons, New York. ISBN 0-47-105372-4.

Tyree, M. T. & Hammel, H. T. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure technique. – J. Exp. Bot. 23: 267–282.

Zimmermann, U. 1978. Physics of turgor- and osmoregulation. – Annu. Rev. Plant Physiol. 29: 121–148.

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Edited by P. Nissen