

Mycorrhiza and Repeated Drought Exposure Affect Drought Resistance and Extraradical Hyphae Development of Pepper Plants Independent of Plant Size and Nutrient Content

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Summary

Pepper (*Capsicum annuum* L.) plants with and without VA-mycorrhiza (formed by the fungus *Glomus deserticola* Trappe, Bloss & Menge), VAM, and NVAM, respectively, were drought acclimated (DA) by four drought cycles or kept well watered (NDA). All plants were then subjected to an additional drought cycle. Similar shoot mass and leaf area were achieved in all treatments by giving more P fertilizer to NVAM than VAM plants. With few exceptions, leaf nutrient concentrations of 12 elements, including P, were either equal or higher in NVAM than VAM plants. During peak drought stress, plants with the combination of VAM-DA treatments had the greatest drought resistance, as indicated by the highest leaf water potential, turgor, relative water content and frequency of non-wilted plants. Some drought resistance, as indicated by intermediate frequency of wilting, occurred when VAM or DA were applied singly. Nutrition and plant size were not associated with this drought resistance. Extraradical hyphae development and soil aggregation of VAM plants were enhanced by drought acclimation, suggesting that these hyphae improved drought resistance by facilitating soil water uptake.

Key words: *Capsicum annuum*, drought acclimation, *Glomus deserticola*, phosphorus nutrition, vesicular-arbuscular mycorrhizal fungi, soil aggregates, water relations.

Abbreviations: DA = drought acclimation treatment; E = transpiration flux, (leaf area basis); LAR = leaf area ratio; LANS = Long Ashton nutrient solution; NVAM = non-mycorrhizal; NDA = non-drought acclimated; P = phosphorus; PPF = photosynthetic photon flux; RWC = relative water content; R/S ratio = root/shoot ratio; Ψ soil = soil water potential; Ψ leaf = leaf water potential; Ψ_s = leaf osmotic potential; Ψ_p = leaf turgor potential; VA-mycorrhiza = vesicular-arbuscular mycorrhiza; VAM = inoculated with the VA-mycorrhizal fungus *Glomus deserticola*.

Introduction

VA-mycorrhizae may increase drought resistance of plants by means of several mechanisms, including increased water uptake due to hyphal extraction of soil water (Hardie, 1985), increased stomatal sensitivity to leaf-air vapor pressure deficit (Huang et al., 1985), regulated stomatal conductance in response to hormonal signals (Allen et al., 1982), increased root hydraulic conductivity (Safir et al., 1972), or by lowered leaf osmotic potential for greater turgor maintenance (Augé

et al., 1986 a). The role of VA mycorrhizae in drought resistance is further complicated by an interaction of mycorrhizal fungi with prolonged or repeated drought (Augé et al., 1986 a).

VA-mycorrhizae effects on plant water status have also been associated with improved host nutrition, particularly P (Graham and Syvertsen, 1984; Nelsen and Safir, 1982; Fitter, 1988). However, others have reported that drought resistance of VA-mycorrhizal plants is independent of plant P concentration (Sweatt and Davies, 1984; Augé et al., 1986 a; Bethlenfalvay et al., 1988).

A major problem with many previous water relations studies has been that VA-mycorrhizal plants were larger with a larger transpirational surface and higher tissue P than non-inoculated plants. If plants are grown in containers of equal size, a plant size differential should lead to differential rates of soil water depletion. Also, plants with optimum P concentration should be more vigorous with higher photosynthetic rates and stomatal conductances than those with limiting P (Radin, 1984; Radin and Eidenbock, 1986), and might respond differently to drought. Few VA-mycorrhizal water relations studies have documented leaf tissue macro- and microelement levels, but VA-mycorrhizae could influence levels of elements other than P (Bildusas et al., 1986). To test for possible mechanisms of drought resistance in mycorrhizal plants, both mycorrhizal and non-mycorrhizal control plants should be equal in size and tissue elemental concentration, especially P concentration.

Our objective was to investigate mechanisms by which VA-mycorrhiza and repeated exposure to drought affect drought resistance of pepper (*Capsicum annuum* L.) plants. By higher P fertilization of non-mycorrhizal than mycorrhizal plants, we attempted to equalize growth and avoid higher P in mycorrhizal plants.

Materials and Methods

Plant inoculation and growing conditions

Inoculum of the mycorrhizal fungus *Glomus deserticola* (Trappe, Bloss and Menge) was obtained from NPI (Salt Lake City, UT) and quantified in order to make appropriate dilutions to have 20,000 spores per liter of container medium. A water suspension of mycorrhizal inoculum was sieved through an 11 μm mesh filter to remove VAM fungus propagules, and the filtrate was added to non-mycorrhizal controls to equalize the background microflora in all treatments. Inoculum was banded 4 cm below the surface in one-liter containers of steam pasteurized (60 °C for 30 min) river sand (texture of 91% sand and 13 mg kg⁻¹ P). Three-week-old seedlings of *Capsicum annuum* L. cv. Early Bountiful (seed germinated in flats) were then transplanted into the containers and grown in a glasshouse for 4 weeks (28/15 °C average day/night temperature with supplemental light for a 16-h photoperiod from high pressure sodium vapor lights having a PPF of 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Until drought treatments began, plants were fertilized weekly with 200 mL per container Long Ashton Nutrient Solution (LANS; Hewitt, 1966) per container. For mycorrhizal plants, LANS was modified to contain 22 instead of the normal 44 mg PL⁻¹ in an effort to equalize size and tissue P concentration between mycorrhizal and non-mycorrhizal plants. Plants were irrigated with water every 2 or 3 d to prevent wilting.

After the initial 4-week establishment period (plants were approximately 7 weeks old), half the plants were acclimated by four drought cycles (DA), each lasting 4 days and ending with irrigation to container capacity. LANS was applied during alternate irrigations. Immediately before irrigation of DA plants, predawn Ψ leaf reached ≈ -0.9 MPa [soil water potential (Ψ soil) ≈ -0.55 MPa]. Non-drought acclimated (NDA) plants were irrigated every other day, and predawn Ψ leaf of these plants was ≈ -0.2 MPa (Ψ soil ≈ -0.1 MPa). Predawn Ψ leaf was determined for each cycle, whereas predawn Ψ soil was determined during one cycle and a regression was used to equate predawn Ψ soil with predawn Ψ leaf. To determine Ψ soil, two soil psychrometers (Wescor PCT55) were permanently placed into the soil (upper and lower halves of pot) of two

containers per treatment, and the voltage was measured with a microvoltmeter (Wescor HR33T) in the dewpoint mode. Measurements of Ψ soil were made before dawn to allow equilibration of water in the soil matrix and to avoid possible thermal gradients between soil and air. All four treatments consisting of drought acclimated non-mycorrhizal and mycorrhizal plants (NVAM-DA, VAM-DA), and non-drought acclimated non-mycorrhizal and mycorrhizal plants (NVAM-NDA, VAM-NDA), were then subjected to a fifth (4-d) drought cycle.

Growth and physiological measurements

Before the drought acclimation cycles and at the end of the experiment, plants were evaluated for fruit and leaf number; leaf area; shoot, fruit and root dry mass; root/shoot (R/S) ratio; and leaf area ratio (LAR = total leaf area/total plant dry wt). At the end of the experiment, roots were cut into 1-cm segments and cleared and stained using the procedures of Phillips and Hayman (1970). Percent mycorrhizal colonization was determined by sampling 25 1-cm root segments from each of five plants ($n = 125$) and determining the percentage that contained mycorrhizal fungus arbuscules, vesicles, or hyphae. Extraradical hyphae development was estimated using the soil aggregation technique (Graham et al., 1982; Kough and Linderman, 1986). Soil in 10-mL aliquots was sampled from the four treatments, and spores were wet-sieved, recovered, and counted. Leaf tissue elemental analysis was done on an inductively coupled plasma atomic emission spectrophotometer (3510ICP, W.R. Grace & Co., Fogelsville, PA). Initial measurements were made immediately before DA treatment; final measurements were made at the end of the experiment.

Physiological parameters were measured during a low stress period (mid-morning, 9:00–11:00, day 2, cycle 5) and during peak stress (mid-afternoon, 13:00–15:00, day 4, cycle 5). A pressure chamber (Scholander et al., 1965) was used to measure leaf water potential (Ψ leaf) on newly matured leaves. Osmotic potential (Ψ_s) was determined by isopiestic psychrometry (Boyer and Knipling, 1965) on leaf discs (4.1 cm²) that were cut from leaves just after they were removed from the pressure chamber. These discs were sealed in parafilm envelopes immediately after cutting, frozen at -60 °C for a minimum of 2 h, and thawed for 15 min at 22 °C. Turgor (Ψ_p) was determined as the difference between Ψ leaf and Ψ_s . In preliminary studies, Ψ leaf determinations using the pressure chamber and isopiestic psychrometry were within 0.05 MPa over a range of Ψ leaf. Transpiration (E) was measured with a porometer/photosynthesis system (LI-COR 6000). Relative water content (RWC) was determined as $100\% \times \frac{\text{fm-dm}}{\text{sm-dm}}$, where sm = saturated mass, fm = fresh

mass, and dm = dry mass (Kramer, 1983). The fm was determined by immediately weighing 4.1 cm² discs cut from leaves adjacent to the leaves sampled for Ψ leaf immediately after the Ψ leaf measurements were made. Discs were then allowed to rehydrate for 2 h by floating them on water in a covered petri dish. The rehydrated discs were weighed to determine sm, and then the discs were dried at 70 °C for 24 h to determine dm. Plants were also visually evaluated for wilting response to drought late in the afternoon of day 4, cycle 5 using the following criteria: 1) non-wilted: leaves and petioles turgid, 2) moderately wilted: petioles horizontal, partial wilting of leaves, and 3) severely wilted: petioles with a 90° droop, severely wilted leaves curved under at margins and partial wilting of stem.

Experimental design

The 2 (\pm VAM) \times 2 (\pm DA) factorial experiment was in a completely randomized design with each plant as an experimental unit. For initial plant size, LAR and R/S ratio, $n = 5$ (plants per treatment). For final plant size at experiment termination, spore counts

Table 1: Effect of VAM combined with differential P fertilization on growth and development of *Capsicum annuum* L. prior to initiating drought acclimation treatments.

Mycorrhiza	Leaf no.	Leaf area (cm ²)	Shoot dry mass (g)	Root dry mass (g)	Root/shoot ratio	Leaf area ratio (m ² kg ⁻¹)
No	25a	357a	2.2a	1.0a	0.5a	11.2a
Yes	23a	313a	1.8a	1.1a	0.6a	10.9a

Means followed by same letters are not significantly different by Fisher's protected LSD test ($P \leq 0.05$); $n = 5$.

and extraradical hyphae determination, $n = 15$ (15 plants); for visual evaluation of water stress, $n = 40$. For determination of E, $n = 10$ (two leaves from each of five plants), and for % RWC, Ψ leaf and Ψ_p , $n = 6$ (two leaves from each of three plants); data were collected in random order from plants of the four treatments to preclude a time bias. For elemental analyses, all leaves of three plants were pooled for a single measurement. Initial measurements were made on three pooled samples per treatment ($n = 3$), while final measurements were made on five ($n = 5$).

Results

Prior to the initiation of drought acclimation cycles, both NVAM plants fertilized with P, 44 mg L⁻¹ (full strength LANS) and VAM plants fertilized with P, 22 mg L⁻¹, had

Table 2: Effect of VAM combined with differential P fertilization on leaf tissue macroelement and microelement concentration (dry weight basis) of *Capsicum annuum* L. prior to initiating drought acclimation treatments.

Mycorrhiza	Macro					Micro						
	N	P	K	Ca	Mg	Mn	Fe	Cu	B	Zn	Mo	Al
No	29a	3.3a	32a	12a	5a	41a	62b	4a	40a	19a	2a	16a
Yes	32a	2.2b	34a	13a	5a	43a	71a	4a	37a	19a	2a	24a

Means followed by the same letters are not significantly different by Fisher's protected LSD test ($P \leq 0.05$); $n = 3$.

comparable size (leaf number, leaf area, shoot and root dry weight, R/S ratio and LAR) (Table 1). Leaf tissue concentrations of macro and micro elements before drought acclimation were similar among treatments, except for P which was 50% higher in NVAM and Fe, which was slightly higher in VAM plants (Table 2).

Regardless of treatment, after the final drought, fruit number, leaf area, shoot and fruit dry weight and LAR were not significantly different (Table 3). However, VAM or DA alone or together lowered root weight and R/S ratio, with VAM-DA having the lowest R/S ratio.

Except for Cu, after the final drought, NVAM plants had either equal or higher leaf tissue elemental concentration

Table 3: Effect of VAM combined with differential P fertilization and drought acclimation treatment on growth and development of *Capsicum annuum* L. at experiment termination.

Mycorrhiza	Drought Acclimated	Fruit No.	Leaf No.	Leaf area (cm ²)	Shoot dry wt (g)	Fruit dry wt (g)	Shoot + Fruit dry wt (g)	Root dry wt (g)	Root/Shoot ratio	Leaf area ratio (m ² kg ⁻¹)
No	No	3.8a	46.5a	538a	4.4a	1.4a	5.8a	3.1a	.53a	6.1a
No	Yes	3.7a	44.1ab	490a	4.3a	1.4a	5.6a	2.6b	.46b	6.0a
Yes	No	3.1a	46.3a	518a	4.5a	1.2a	5.7a	2.6b	.46b	6.3a
Yes	Yes	3.7a	41.1b	508a	4.5a	1.5a	5.9a	2.4b	.41c	6.1a
Significance										
VAM		NS	NS	NS	NS	NS	NS	**	**	NS
DA		NS	**	NS	NS	NS	NS	**	**	NS
Interaction		NS	NS	NS	NS	NS	NS	NS	NS	NS

Means followed by common letter are not significantly different by Fisher's Protected LSD Test ($P \leq 0.05$); $n = 15$. Significance = NS, **; Nonsignificant or significant at 1% levels.

Table 4: Effect of VAM combined with differential P fertilization and drought acclimation treatment on leaf macroelement and microelement concentration (dry weight basis) of *Capsicum annuum* L. at experiment termination.

Mycorrhiza	Drought Acclimated	Macro							Micro				
		N	P	K	Ca	Mg	Mn	Fe	Cu	B	Zn	Mo	Al
No	No	20b	5.4a	34a	18a	6.4a	59a	52b	3a	53a	20a	6a	27a
No	Yes	23a	3.8b	34a	16b	5.7b	54b	55a	2b	52a	13c	3c	19b
Yes	No	20b	2.3c	33a	14b	4.8c	45c	46c	3a	48b	19ab	5b	19b
Yes	Yes	21b	1.7d	33a	15b	5.3bc	42c	47c	3a	48b	16bc	2d	19b
Significance													
VAM		*	*	NS	*	*	*	*	NS	*	NS	*	*
DA		*	*	NS	NS	NS	*	NS	*	NS	*	*	*
Interaction		NS	*	NS	*	*	NS	NS	*	NS	NS	NS	*

Means followed by common letter are not significantly different by Fisher's Protected LSD Test ($P \leq 0.05$); $n = 5$. Significance = NS, *; Nonsignificant or significant at 5% level.

Table 5: Effect of VAM combined with differential P fertilization and drought acclimation treatment on water relations of *Capsicum annuum* L. during low environmental stress (morning, day 2, cycle 5).

Mycorrhiza	Drought acclimated	E (H ₂ O, mmol m ⁻² s ⁻¹)	Ψ leaf (MPa)	Ψ p (MPa)	RWC (%)
No	No	2.5a	-0.20a	0.73a	96.1a
No	Yes	1.7b	-0.18a	0.74a	97.2a
Yes	No	2.6a	-0.19a	0.75a	96.6a
Yes	Yes	2.3a	-0.16a	0.78a	96.7a
Significance					
VAM		*	NS	NS	NS
DA		**	NS	NS	NS
Interaction		*	NS	NS	NS

Means followed by common letter are not significantly different by Fisher's Protected LSD Test ($P \leq 0.05$); $n = 10$ for E; $n = 6$ for Ψ leaf and RWC.

Significance = NS, *, **; Nonsignificant or significant at 5% or 1% levels, respectively.

than VAM plants with comparable DA treatments (Table 4). By itself, DA greatly reduced leaf P concentration of plants receiving comparable VAM treatment. The higher rate of fertilization of NVAM plants increased their P concentration twofold compared with VAM plants with comparable DA treatments. Iron was slightly higher in NVAM than

VAM plants, a reversal of Fe concentration prior to the drought acclimation cycles (Tables 2 and 4).

During the morning of day 2, cycle 5 when environmental stress was low, Ψ leaf, Ψ p and RWC were equal among treatments, but E was lowest in NVAM-DA plants (Table 5). On the afternoon of day 4, cycle 5 when environmental stress was greatest, E, Ψ leaf, Ψ p, RWC and % nonwilted plants were higher in VAM-DA than in nearly all other treatment/parameter combinations (Table 6). Plants with DA or VAM had less wilting than NVAM-NDA plants, and E values of both DA treatments were equally high (Table 6).

Drought acclimation had no effect on VAM root colonization levels or final *G. deserticola* spore concentration in the soil (Table 7). VAM-DA plants, however, had the greatest amount of extraradical hyphae attached to the root system as indicated by the soil aggregation assay (Table 7).

Discussion

The maintenance of several water relations parameters at relatively favorable levels in the VAM-DA plants under drought indicates that repeated drought in combination with VAM conferred drought resistance. To a lesser extent, VAM

Table 6: Effect of VAM combined with differential P fertilization and drought acclimation treatment on water relations of *Capsicum annuum* L. at the time of peak environmental stress (afternoon, 13:00–15:00, day 4, cycle 5).

Mycorrhiza	Drought acclimated	% Plants not wilted	% Plants moderately wilted	% Plants severely wilted	E (H ₂ O, mmol m ⁻² s ⁻¹)	Ψ leaf (MPa)	Ψ π (MPa)	RWC (%)
No	No	12c	5a	83a	0.7b	-1.04b	.16b	75.8b
No	Yes	43b	17a	40c	1.6a	-.99b	.23b	76.4b
Yes	No	28bc	10a	62b	0.8b	-.98b	.13b	83.2b
Yes	Yes	78a	7a	15d	1.8a	-.32a	.70a	96.1a
Significance								
VAM		*	NS	*	NS	*	*	*
DA		*	NS	*	*	*	*	NS
Interaction		NS	NS	NS	NS	*	*	NS

Means followed by common letter are not significantly different by Fisher's Protected LSD Test ($P \leq 0.05$); $n = 40$ for wilting; $n = 10$ for E; $n = 6$ for Ψ and RWC.

Significance: NS = Nonsignificant, * = significant at 5% level.

Table 7: Effect of drought acclimation treatment on VAM root colonization, soil aggregation and development of extraradical hyphae on *Capsicum annuum* L. at experiment termination.

Mycorrhiza	Drought Acclimated	% Root pieces with VAM	No. of spores recovered from soil (per 100 mL)	Root dry wt (g)	Soil aggregate (g)	Extraradical hyphae index ($\frac{\text{soil aggregate wt}}{\text{root dry wt}}$)
No	No	0b	0b	3.1a	4.8ab	1.6b
No	Yes	0b	0b	2.6bc	3.7b	1.5b
Yes	No	9.6a	926a	2.6bc	4.9ab	2.0b
Yes	Yes	15.2a	833a	2.4c	6.1a	2.6a
Significance						
VAM		*	*	**	*	**
DA		NS	NS	**	NS	NS
Interaction		NS	NS	NS	*	NS

Means followed by common letter are not significantly different by Fisher's Protected LSD Test ($P \leq 0.05$); $n = 15$.

Significance = NS, *, **; Nonsignificant or significant at 5% and 1% levels, respectively.

or DA applied singly also promoted resistance, and these results agree with Augé et al. (1986 a) for *G. deserticola*.

A major problem in interpreting most mycorrhizae-water relations studies is that mycorrhizal plants typically have greater mass than non-mycorrhizal plants (Fitter, 1988; Nelsen, 1987). With larger mass, mycorrhizal plants should have greater transpiring surfaces, and if their roots are confined in a container, such plants should desiccate more quickly and have lower Ψ leaf during drought compared to smaller controls (Hardie and Leyton, 1981; Levy et al., 1983; Sweatt and Davies, 1984). Our plants had equivalent leaf area, LAR, and shoot mass over all treatments before and after drought due to manipulation of P fertilization. Perhaps, drought resistance did not develop until too late in the experiment to significantly alter growth. Likewise, the duration of drought during DA apparently was too brief to affect accumulated growth. Alternatively, drought resistance could have compensated for drought treatment. Thus the greater drought resistance of VAM-DA plants was not confounded by differences in transpirational area, LAR, or shoot mass.

The greater root mass and R/S ratio of the NVAM-NDA plants probably was not due to higher P concentration in the NVAM-NDA plants, because plants in the other treatments had uniformly smaller root masses despite a twofold range in tissue P concentration among the other three treatments. The R/S ratio or root/leaf weight ratio may be increased (Bethlenfalvay et al., 1988; Graham et al., 1987), decreased (Hardie and Leyton, 1981), or unaffected (Augé et al., 1986 b) by mycorrhizae. A high R/S ratio is a frequent response to water stress (Kramer, 1983). In our study, R/S ratio decreased with either VAM or repeated drought, especially if they were combined, but greatest drought resistance occurred with a combination of VAM and DA indicating that a high R/S ratio is not necessarily associated with drought resistance.

The improved water relations of VAM-DA pepper plants cannot be attributed to P nutrition, a finding in agreement with Sweatt and Davies (1984), Augé et al. (1986 a), and Bethlenfalvay et al. (1988). Indeed, leaf tissue P of VAM plants was lower than that of NVAM plants. Also, the tissue concentrations of other essential elements were generally equal or higher in NVAM than VAM plants before and after drought acclimation treatments, indicating that VAM-DA treatments elicited improved water relations that were not mediated through these elements. The P levels of all treatments were in the range recommended for commercial production of pepper (Lorenz and Maynard, 1988). Contrary to our findings, Nelsen and Safir (1982), Graham and Syvertsen (1984), and Fitter (1988) attributed improved water relations of mycorrhizal plants to increased tissue nutrition, particularly P. Although mycorrhizae can promote P uptake, and P uptake is reduced under drought (Begg and Turner, 1976; Vietz, 1972), it is not clear how increased P could improve water relations or drought resistance.

Mycorrhizal colonization was reported to increase E and leaf P concentration (Hardie and Leyton, 1981), and in a non-mycorrhizal study, increasing leaf P increased E (Terry and Ulrich, 1973). However, data of Fitter (1988) indicate an increase in stomatal conductance (g) with increasing leaf P but only for non-mycorrhizal plants; g of mycorrhizal

plants, which had relatively high P concentration, did not change as leaf P increased. E and g should vary together. In our study, where leaf P varied widely, E did vary consistently with VAM or leaf P, and Graham et al. (1987) working with citrus, reported that mycorrhizae did not affect E. Also, data of Augé et al. (1986 b) indicate that g did not vary consistently with mycorrhizae or leaf P, but this study was complicated by P fertilization effects on colonization, and high colonization levels led to high g. Apparently, the relation between E or g, mycorrhizae, and leaf P is complex and controversial even for well watered plants.

Once a plant has been desiccated, stomatal conductance tends to remain low even after rehydration (Steuer et al., 1988), a probable cause for the reduced E of the NVAM-DA plants early in drought (day 2, cycle 5). Moderate E during periods of high soil moisture should conserve water and allow maintenance of moderately high E late in the drought cycle as we observed in NVAM-DA plants. The ability of the VAM-DA plants to maintain moderately high E late in a drought cycle, despite high E early in drought, suggests VAM improved the ability of these plants to extract water at low Ψ soil.

The visual wilting data during peak environmental stress show that within a treatment, our plants exhibited considerable variation in plant stress. This variation led to some inconsistency in the data that was most apparent with NVAM-DA plants that had relatively high E and the second highest % non-wilted plants, but similar Ψ leaf, Ψ_p and RWC to NDA plants. Variation could lead to this inconsistency because visual wilting and E were the means of 40 and 5 plants, respectively, per treatment, whereas Ψ leaf, Ψ_p and RWC were the means of only three plants per treatment. We have the greatest confidence in means based on the most plants. With the exception of NVAM-DA, the visual wilting data of the other three treatments corresponded to other water relations parameters and E values.

Drought resistance of the VAM-DA plants may have occurred because DA treatment promoted more extraradical hyphae that contributed to water uptake, a mechanism supported by the work of Allen (1982) and Hardie (1985). In a non-mycorrhizal study, McCoy et al. (1984) concluded that increasing root density created smaller root-to-soil water potential gradients and less negative root water potentials for a given daily transpiration loss. If mycorrhizal hyphae explore the soil volume in a manner analogous to increasing root density, then mycorrhizal roots could have higher water potentials than would occur in non-mycorrhizal roots, and this should promote higher Ψ leaf.

In addition to their role in exploring soil, hyphae could bridge gaps between soil and roots as well as bind soil particles to each other and to roots. Our data, as well as those of others (Sutton and Sheppard, 1976; Graham et al., 1982; Hardie, 1985; Fitter, 1985; Bronsten, 1988), indicate that hyphae bind soil or cause it to aggregate. This could be important as soil water decreased, causing soil shrinkage and creating gaps at the soil-root interface and between soil particles.

In conclusion, neither tissue nutrient concentrations nor plant transpirational surface accounted for the ability of DA and VAM to enhance water status of peppers under drought stress. Drought acclimation treatments enhanced drought re-

sistance and stimulated extraradical hyphae development and greater binding of soil particles to each other and to the roots of VAM plants. VAM-DA plants resisted stress and maintained relatively high Ψ leaf, Ψ_p , RWC, and E. A possible mechanism for improved drought resistance in VAM-DA plants was the greater development of extraradical hyphae that binds soil to roots, more thoroughly explores soil volume, and potentially helps maintain hydraulic contact between soil and root.

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