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REVIEW

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Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis

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Abstract Vesicular-arbuscular mycorrhizal fungi can affect the water balance of both amply watered and droughted host plants. This review summarizes these effects and possible causal mechanisms. Also discussed are host drought resistance and the influence of soil drying on the fungi.

Keywords Arbuscular · Mycorrhiza · Review · Stress · Vesicular-arbuscular · Water relations

Overview

Vesicular-arbuscular mycorrhizal (VAM) symbiosis often results in altered rates of water movement into, through and out of host plants, with consequent effects on tissue hydration and leaf physiology. This review summarizes published results and suggests underlying mechanisms. For previous reviews, see Reid (1979), Fitter (1985), Read and Boyd (1986), Nelsen (1987), Gupta (1991), Koide (1993), Sánchez-Díaz and Honrubia (1994), Smith and Read (1997), Augé (2000).

In the earliest work on the subject, Safir et al. (1971, 1972)[1] concluded that VAM symbiosis probably affected the water relations of soybean plants indirectly through improved P nutrition. The notion that VAM effects on water relations were mainly nutritional in nature was prevalent for several years, i.e. the behavior of VAM and non-mycorrhizal (NM) plants differed because plants differed in size or tissue P concentrations. Others subsequently demonstrated that water relations and gas exchange of soybean could be affected by VAM symbiosis independently of P nutrition (Harris et al. 1985; Brown and Bethlenfalvay 1987; Bethlenfalvay et al. 1988a, b). By the early 1980s, a few studies had shown important VAM effects on stomatal conductance, water potential (Ψ)[2], etc. of hosts other than soybean. Not all of these works compared VAM and NM plants of similar size and/or nutrition and so mycorrhizal effects related and unrelated to nutrition could not always be distinguished. However, these studies suggested ideas about mycorrhizal mechanisms of influence that are still being tested today: hormonal involvement (e.g. Allen et al. 1980, 1982; Levy and Krikun 1980), more effective scavenging of soil water (e.g. Hardie and Leyton 1981; Sieverding 1981), possibly through improved soil/root contact (e.g. Reid 1979), stimulation of gas exchange through increased sink strength (e.g. Allen et al. 1981; Johnson et al. 1982; Kucey and Paul 1982; Snellgrove et al. 1982) with possible effects on osmotic adjustment (Allen and

Dedicated to Dr. Robert Linderman and Dr. Gabor Bethlenfalvay, two scientists who taught me a lot about perspective

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[1] Abstracts for mycorrhizal water relations reports cited in this review can be viewed online at http://mycorrhiza.ag.utk.edu/

[2] Water potential is a useful but sometimes confusing concept used to quantify the water status of plants, soils and fungi. Derived from the field of irreversible thermodynamics (chemical potential, water activity), Ψ is by definition always negative in biological systems: the lower or more negative the Ψ value, the drier or more water-stressed is the sample being measured. The total Ψ of a tissue sample is composed primarily of two components: $\Psi = \Psi_\pi + \Psi_p$. Osmotic potential (Ψ_π) is a measure of the solute concentration of a solution: the lower the number, the higher the solute concentration. If a solution has any solutes whatsoever, its Ψ_π is negative (Ψ_π of pure water = 0). Hence, Ψ_π of cytoplasm, xylem fluid or soil water is always negative. Turgor potential (also termed pressure potential, Ψ_p) represents hydrostatic pressure. Ψ_p is positive in a turgid, living tissue. It can decline to zero if a tissue dehydrates sufficiently and it is negative in xylem of transpiring plants (negative pressure is termed tension). Intact membranes bounded by cell walls are required for positive turgors to develop. In soils, total Ψ is typically defined as $\Psi_m + \Psi_\pi$: matric potential plus osmotic potential. Matric potential is a somewhat controversial but nevertheless widely used term describing the strength with which soil particles bind water. Like Ψ_π, Ψ_m is measured in negative numbers; lower (more negative) Ψ_m numbers mean soil is more dry

Boosalis 1983), and contributions of soil hyphae to water absorption (Hardie and Leyton 1981; Allen 1982). Many works of the 1980s with carefully produced VAM and comparable control NM plants (e.g. Graham and Syvertsen 1984; Koide 1985; Fitter 1988) tended to confirm the conclusions of Safir et al. (1971, 1972). However, the results of several experiments indicated that VAM plants can exhibit water relations different to those of NM plants, even when size and P nutrition of VAM and NM plants are similar (e.g. Levy and Krikun 1980; Allen and Boosalis 1983; Levy et al. 1983b; Hardie 1985; Augé et al. 1986a, b, 1987a; Bethlenfalvay et al. 1988a, b). Two camps were apparent from the literature: those supporting strictly nutritional effects of VAM symbiosis on host water relations and those acknowledging that non-nutritional VAM effects may occur.

Considering further reports during the 1990s, many presenting more than one-time measurements of stomatal conductance or Ψ, it now seems incontrovertible that VAM fungi can modify host water relations, at least on some occasions and to some extent, in a way entirely unrelated to improved P acquisition. It seems also evident that VAM symbiosis, host phenology, P and carbon nutrition are usually so inextricably linked in nature that most field effects of VAM fungi on host water balance are probably at least partially related to modified plant size or developmental rates.

Effects

Tables 1, 2, 3, 4, 5, and 6 summarize published works[3] to date dealing with VAM symbioses and host water relations, shoot gas exchange and drought responses[4]. Table 1 shows reports of VAM effects related to enhanced host size or P nutrition, or in which size or P effects could not be readily excluded. Table 2 summarizes VAM effects probably not mediated through growth effects or P nutrition. Table 3 lists reports in which no differences were observed between VAM and NM plants in any parameter measured in the experiment or in at least one parameter. Tables 4 and 5 summarize reports of VAM-mediated changes in tissue nutrient concentrations other than P of plants exposed to drought. Table 6 lists papers dealing primarily with the influence of drought, aridity or soil-moisture gradients on VAM fungi themselves and also includes works cited in Tables 1, 2, 3, and 4 that report such effects. This review does not cover literature dealing with salinity stress.

Over 200 peer-reviewed articles have been published on the influence of VAM fungi on water relations, photosynthetic rates and drought responses of 90 host species representing 69 genera (Tables 1, 2, 3, 4; some papers are listed in more than one table). Five genera of mycorrhizal fungi, including 22 species of *Glomus*, have been studied, mostly with herbaceous host plants and mostly in controlled environments using potted plants and not in the field.

Stomatal conductance[5] and transpiration

As previous reviewers have noted (e.g. Read and Boyd 1986; Nelsen 1987; Smith and Gianinazzi-Pearson 1988; Gupta 1991; Koide 1993; Sánchez-Díaz and Honrubia 1994; Smith and Read 1997; Augé 2000), VAM and NM plants often display different transpiration rates and stomatal conductances to water vapor. Where these rates differ in VAM and NM plants, with few exceptions rates have been higher in VAM plants (Tables 1, 2). However, several investigators found no differences between VAM and NM plants in stomatal conductance or transpiration (Table 3). An experimenter can expect to find at least occasional differences in stomatal conductance among plants with different mycorrhizal treatments, especially if stomatal conductance is monitored several times in an experiment, if plants are exposed to a variety of environmental conditions (e.g. varied light or CO_2), or if VAM and NM plants differ in size. Yet we cannot predict with any certainty under which circumstances VAM and NM plants are most likely to differ in stomatal conductance[6].

VAM effects on stomatal conductance have been observed with similar frequency under amply watered and drought conditions. In several studies, differences between VAM and NM plants were observed only under drought, when stomatal conductance was measured under both non-stress and drought conditions (e.g. Bildusas et al. 1986; Bethlenfalvay et al. 1987; Henderson and Davies 1990; Ibrahim et al. 1990; Augé et al. 1992a, 1995; Awotoye et al. 1992; Davies et al. 1993). VAM symbiosis has also affected stomatal sensitivity to atmospheric water status (humidity) (Huang et al. 1985). VAM-induced increases in transpiration and stomatal

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[3] I attempted to locate every article published on this topic through 1999. My apologies to colleagues whose papers I have not listed

[4] Water relations physiologists sometimes distinguish between atmospheric drought and soil drought: dry air versus dry soil. In this review, drought refers to soil drought and is used synonymously with water deficit and water-deficit stress. Although water stress is often used to mean drought, strictly speaking it means any stress related to water, either too much (flooding) or too little

[5] Leaf conductance has two components: stomatal conductance (the ease with which water vapor moves through stomatal pores) and cuticular conductance (the ease with which water vapor moves through leaf cuticle). For most plant species, cuticular conductance is so small as to be negligible, making leaf conductance and stomatal conductance effectively synonymous. In this review, the term stomatal conductance is used in lieu of leaf conductance, as is common in the literature. Stomatal conductance (commonly abbreviated g_s) and its inverse, stomatal resistance (r_s or $1/g_s$), are quantitative measures of bulk stomatal openness. Numerical values of g_s increase (and numerical values of r_s decrease) as stomatal aperture increases. When most of the stomata in the leaf or piece of leaf being measured close, g_s approaches zero. The currently preferred unit for g_s is mmol (of water) m^{-2} s^{-1}; the unit often used in older literature is mm s^{-1} (or s mm^{-1} or s m^{-1} for r_s)

[6] There are several areas within the field of water relations for which it is not possible to generalize about mycorrhizal effects. Sometimes VAM and NM plants differ in a particular behavior, sometimes not. Often, we do not understand why the symbiosis altered behavior in one study but not in another

Table 1 Mycorrhizal effects on host gas exchange, water relations or drought resistance mediated by improved P nutrition (or for which modified P nutrition or plant size could not be ruled out as the cause). Unless noted, VAM effects on growth and biochemical parameters were associated with drought. Fungus genera are abbreviated as: *A. Acaulospora*, *E. Endogone*, *Ent. Entrophospora*, *G. Glomus*, *Gi. Gigaspora*, *S. Scutellospora* (*CER* carbon exchange rate: photosynthesis, *E* transpiration rate, g_s stomatal conductance, L_p root hydraulic conductivity, *X* plants were subjected to drought stress at some point in the experiments, *WUE* water use efficiency, Ψ water potential, Ψ_π osmotic potential, < > VAM symbiosis decreased or increased the parameter, respectively, Δ VAM symbiosis changed the parameter, variously decreasing and increasing it, *[ ]* concentration of a substance)

Host species	Fungus species	Parameter	Drought	Reference
Abutilon theophrasti	*G. etunicatum*	<WUE		Koide and Li (1991)
Abutilon theophrasti	*G. etunicatum*	>g_s, >CER		Koide and Schreiner (1994)
Acacia auriculiformis	*A.*, *G.*	>g_s, <leaf Ψ, <growth	X	Awotoye et al. (1992)
Acacia auriculiformis	*G.* spp.	>Growth	X	Mizoguchi (1992)
Acacia mangium	*G.* spp.	>Growth	X	Mizoguchi (1992)
Acacia nilotica	*G. etunicatum*, *G. mosseae*, *G. occultum*	>Growth	X	Michelson and Rosendahl (1990)
Acacia nilotica	*G. clarum*, or indigenous spp.	<Leaf Ψ, >growth, >leaf abscission	X	Osonubi et al. (1992)
Acacia tortilis	indigenous	>Survival, >growth	X	Wilson et al. (1991)
Agave desertii	*G. epigaeum*, *G. fasciculatum*, three other *G.* spp.	>WUE, >CER, >L_p		Cui and Nobel (1992)
Agropyron cristatum	Six *G.* spp.[a]	>WUE	X	Di and Allen (1991)
Agropyron desertorum	Six *G.* spp.[a]	>WUE	X	Di and Allen (1991)
Agropyron repens	*G. mosseae*	>E	X	George et al. (1992)
Agropyron smithii	*G. macrocarpum*, *G. microcarpum*	>g_s	X	Stahl and Smith (1984)
Agrostis palustris	*G. intraradices*	>Leaf Ψ, >recovery from wilting, >[chlorophyll], <[γ-amino-n-butyric acid]	X	Gemma et al. (1997)
Albizia lebbeck	*G.* spp., *A.* spp.	>Growth, >survival	X	Awotoye et al. (1992)
Albizia lebbeck	One *A.* sp., two *G.* spp.	<Leaf Ψ, >growth	X	Osonubi et al. (1991)
Allium cepa	*E.* sp.	Prevented leaf wilting	X	Mosse and Hayman (1971)
Allium cepa	*G. etunicatus*	>g_s, >E, >leaf Ψ, >L_p		Nelsen and Safir (1982a)
Allium cepa	*G. etunicatus*	>Growth	X	Nelsen and Safir (1982b)
Andropogon gerardii	*G. etunicatum*	>Growth	X	Hetrick et al. (1986, 1987)
Artemisia tridentata	Indigenous	>Survival	X	Stahl et al. (1998)
Baptisia australis	Four *G.* spp. [b]	>Growth	X	Zajicek et al. (1987)
Beilschmiedia pendula	Indigenous	>CER		Lovelock et al. (1997)
Berberis thunbergii	*G. etunicatus* + *G. fasciculatum*	>E, ΔL_p		Newman and Davies (1988)
Bouteloua gracilis	*G. fasciculatus*	>g_s and >E in stressed plants, >CER in non-stressed plants	X	Allen et al. (1981)
Bouteloua gracilis	*G. fasciculatus*	>g_s, >E, >L_p		Christensen and Allen (1979, 1980)
Buxus microphylla	*G. etunicatum* + *G. fasciculatum*	>g_s, <L_p		Newman and Davies (1987)
Buxus microphylla japonica	*G. etunicatus* + *G. fasciculatum*	>g_s, >E, ΔL_p		Newman and Davies (1988)
Capsicum annuum	*G. intraradices*	>g_s, >CER		Aguilera-Gomez et al. (1999)
Capsicum annuum	*G. aggregatum*	>Fruit yields	X	Waterer and Coltman (1989)
Cassia siamea	*G. deserticola*	>Soil water extraction		Okon et al. (1996)
Cenchrus ciliaris	*Gi. margarita*, *G. mosseae*, *G. fasciculatum*	>Growth	X	Tarafdar and Praveen-Kumar (1996)
Citrus aurantium	*G. intraradices*	>CER		Eissenstat et al. (1993)
Citrus aurantium	*G. intraradices*	>CER		Syvertsen and Graham (1999)
Citrus aurantium	*G. intraradices*	>E per unit root length, >L_p		Graham and Syvertsen (1984)
Citrus aurantium	*G. intraradices*	>CER		Nemec and Vu (1990)
Citrus sinensis	*G. intratardices*	>CER		Syvertsen and Graham (1999)
Citrus sinensis	*G. fasciculatus*	>g_s, >CER		Johnson et al. (1982)
Cucurbita pepo	*G. intraradices*	>E, >CER	X	Aboul-Nasr (1998)
Eupatorium odoratum	*G. macrocarpus*	>Growth, >WUE	X	Sieverding (1979, 1981, 1983)
Fraxinus pennsylvanica	*G. etunicatum*	<L_p per unit root [P]		Andersen et al. (1988)
Garcinia mangostana	*G. mosseae*, *S. calospora*	>g_s, >E, >CER		Masri et al. (1998)
Gliricidia sepium	*A.* spp., *G.* spp.	>g_s, >growth, >survival	X	Awotoye et al. (1992)
Gliricidia sepium	*G. deserticola*	>Soil water extraction		Okon et al. (1996)
Gliricidia sepium	One *A.* sp., two *G.* spp.	>Growth	X	Osonubi et al. (1991)
Glycine max	*G. mosseae*	>g_s, >E	X	Bethlenfalvay et al. (1987)
Glycine max	*G. mosseae*	>Growth	X	Bethlenfalvay et al. (1988a)
Glycine max	*G. mosseae*	>Photosynthetic P use efficiency		Brown and Bethlenfalvay (1987)
Glycine max	*G. fasciculatum*	<Predawn leaf Ψ, >seed weight, <pod abortion, >soil water extraction	X	Busse and Ellis (1985)

Table 1 Continued

Host species	Fungus species	Parameter	Drought	Reference
Glycine max	*E. mosseae*	<Resistance to water transport		Safir et al. (1971, 1972)
Glycine max	*G. mosseae*	>CER		Shabayev et al. (1995)
Glycine max	*G. mosseae*	>CER		Shabayev et al. (1996)
Glycine max	*Gi.* sp., *G.* sp.	>Growth	X	Barakah and Heggo (1998)
Guizotia abyssimica	*G. macrocarpus*	<WUE	X	Sieverding (1979)
Guizotia abyssimica	*G. mosseae*, *G. macrocarpum*	>Growth	X	Sieverding (1984)
Helianthus annuus	Unreported	>g_s, >E, <hydraulic resistance		Koide (1985)
Hevea brasiliensis	*G. mosseae*	>g_s, >E, >CER		Schwob et al. (1998)
Hippophae rhamnoides	*G. constrictum*, *G. geosporum*, *G. mosseae*	<Wilting coefficient	X	Tang and Chen (1999)
Lactuca sativa	*G. fasciculatum*, *G. mosseae*	>CER		Azcón et al. (1992)
Lactuca sativa	*G. fasciculatum*	>Nitrate reductase, >[proline]	X	Azcón et al. (1996)
Lactuca sativa	*G. mosseae*	>CER, >[proline]	X	Azcón et al. (1996)
Lactuca sativa	*G. deserticola*, *G. fasciculatum*	>g_s, >E, >CER of non-stressed plants, >Growth, >root water content, >WUE, <photosynthetic P use efficiency, >hyphal water transport	X	Ruiz-Lozano and Azcón (1995)
Lactuca sativa	*G. deserticola*, *G. mosseae*	>Shoot [protein], >root and shoot superoxide dismutase activity	X	Ruiz-Lozano et al. (1996b)
Lactuca sativa	Seven *G.* spp. [c]	>g_s, >E, >CER, >WUE, >growth, >[proline]	X	Ruiz-Lozano et al. (1995a, b)
Lactuca sativa	*G. mosseae*, *G. fasciculatum*	>Growth	X	Tobar et al. (1994b)
Lens esculenta	*G.*, *Gi.*	>Growth	X	Ishac et al. (1994)
Leucaena leucocephala	*A.* spp., *G.* spp.	>Growth, >survival	X	Awotoye et al. (1992)
Leucaena leucocephala	*Gi. margarita*, *G. deserticola*, *G. etunicatum*, *G. intraradices*	Non-stressed and stressed plants: >g_s, >CER, >leaf Ψ	X	Dixon et al. (1994)
Leucaena leucocephala	*G. fasciculatum*	>g_s, >E, >leaf Ψ, >leaf movements, >stomatal sensitivity to humidity	X	Huang et al. (1985)
Leucaena leucocephala	One *A.* sp., two *G.* spp.	>Growth	X	Osonubi et al. (1991)
Liatris aspera	Four *G.* spp. [b]	>Growth	X	Zajicek et al. (1987)
Linum usitatissimum	*G. intraradices*, others	>g_s, <[trigonelline]	X	von Reichenbach and Schönbeck (1995)
Liquidambar styraciflua	*G. fasciculatum*	>Root growth	X	Simmons and Pope (1988)
Lolium perenne	Unreported	<Growth	X	Jupp and Newman (1987)
Malus hupehensis	*G. versiforme*, *G. macrocarpum*	>g_s, >E, <leaf Ψ, >recovery rate	X	Runjin (1989)
Manihotis esculenta	Two *A.*, *Ent.*, three *G.*, *S.* [d]	>Growth	X	Sieverding and Toro (1988)
Musa sp.	*A. scrobiculata*, *G. clarum*, *G. etunicatum*	>g_s, >E		Yano-Melo et al. (1999)
Panicum coloratum	*Gi. margarita*	>g_s, >CER, >photosynthetic storage and export rates		Wang et al. (1989)
Parkia biglobosa	*G. deserticolum*	<Wilting, >g_s >E	X	Osundina (1995)
Pelargonium × *hortorum*	*G. mosseae*, *G. fasciculatus*	<Leaf Ψ, <L_p, >drought recovery	X	Sweatt and Davies (1984)
Phleum pratense	Four *G.*, *Gi.* [e]	>C assimilation		Clapperton and Reid (1992)
Phaseolus radiata	*G.*	>WUE	X	Honggang et al. (1989)
Phaseolus radiata	*G. fasciculatum*	>g_s, >E, >CER		Thakur and Panwar (1997)
Phaseolus vulgaris	*G. intraradices*	>g_s, Δ leaf Ψ, >CER	X	El-Tohamy et al. (1999)
Plantago lanceolata		<g_s	X	Whittingham (1980) (cited in Gupta 1991)
Poncirus trifoliata × *Citrus sinensis*	*G. intraradices*	>E per unit root length, >L_p		Graham and Syvertsen (1984)
Poncirus trifoliata × *Citrus unshiu*	Three *G.*, *Gi.* [f]	>E, occasional >CER, >Growth		Shrestha et al. (1995)
Prosopis juliflora	*G. macrocarpum*	>Growth	X	Dixon et al. (1997)
Prosopis juliflora	*Gi. margarita*, *G. mosseae*, *G. fasciculatum*	>Growth	X	Tarafdar and Praveen-Kumar (1996)
Prosopis juliflora	Indigenous	>Survival, >growth	X	Wilson et al. (1991)
Psidium guajava	*G. albidum*, *G, claroides*, *G. diaphanum*	>g_s, >CER		Estrada-Luna et al. (2000)
Schizachyrium scoparium	Indigenous [g]	<Growth	X	Cerligione et al. (1988)
Sorghum bicolor	*G. intraradices*	>g_s, >CER, >growth	X	Ibrahim et al. (1990)

Table 1 Continued

Host species	Fungus species	Parameter	Drought	Reference
Sorghum bicolor	*G. macrocarpus*	<WUE	X	Sieverding (1979)
Sorghum bicolor	*G. mosseae*, *G. macrocarpum*	>Growth	X	Sieverding (1984)
Sorghum bicolor	*G. macrocarpum*	>E, >growth	X	Sieverding (1986)
Terminalia brownii	Indigenous	>Survival, >growth	X	Wilson et al. (1991)
Terminalia prunioides	Indigenous	>Survival, >growth	X	Wilson et al. (1991)
Trifolium pratense	*G.* sp.	>g_s before stress	X	Fitter (1988)
Trifolium pratense	*G. mosseae*	>g_s, >E, <leaf Ψ, >L_p	X	Hardie and Leyton (1981)
Trifolium repens	*G. fasciculatum*	>Growth, >WUE	X	Puppi and Bras (1990)
Trifolium repens	*G. fasciculatum*	>Growth	X	Puppi and Bras (1990)
Trigonella foenumgraecum	*G. macrocarpus*	<WUE	X	Sieverding (1979)
Triticum aestivum	*G. etunicatum*	<Leaf necrosis	X	Bryla and Duniway (1997c)
Triticum aestivum	*G. deserticola*, *G. fasciculatum*	>g_s, >growth, >yield, <leaf drop, >soil water extraction	X	Ellis et al. (1985)
Triticum aestivum	*G. fasciculatum*	>CER		Panwar (1991)
Triticum aestivum	Unreported	>CER, >[chlorophyll], >nitrate reductase activity, >growth, >yield	X	Panwar (1992)
Triticum aestivum	*G.* spp.	>Leaf RWC, >[chlorophyll], >nitrate reductase activity, <leaf ion leakage	X	Panwar (1993)
Triticum aestivum	Indigenous	>g_s, >E, >CER		Trent et al. (1989)
Triticum durum	*G. mosseae*	>Growth	X	Al-Karaki and Al-Raddad (1997a)
Triticum durum	*G. mosseae*	>Growth	X	Al-Karaki and Al-Raddad (1997b)
Triticum durum	*G. monosporum*	>Growth, >WUE	X	Al-Karaki and Clark (1998)
Triticum durum	*G. monosporum*	>Growth	X	Al-Karaki (1998)
Vicia faba	*G.*, *Gi.*	>Growth	X	Ishac et al. (1994)
Vigna aconitifolia	*Gi. margarita*, *G. mosseae*, *G. fasciculatum*	>Growth	X	Tarafdar and Praveen-Kumar (1996)
Vigna radiata	*G.*	>WUE	X	Honggang et al. (1989)
Vigna sativa	*G. macrocarpum*	>Soil water extraction		Sharma and Srivastava (1991)
Vigna unguiculata	*G. intraradices*	<g_s, >growth	X	Ebel et al. (1996)
Vigna unguiculata	*G. clairodeum*	>E	X	Faber et al. (1991)
Zea mays	*G. fasciculatum*	Δ CER		Acosta-Avalos et al. (1996)
Zea mays	*G. etunicatum*	>Root growth, <leaf [proline]	X	Müller and Höfner (1991)
Zea mays	*G. caledonium*, indigenous	>[Proline]	Osmotic stress	Ramakrishnan et al. (1988a)
Zea mays	*G. caledonius*	>Photorespiration of non-stressed plants	Osmotic stress	Ramakrishnan et al. (1988b)
Zea mays	*G. intraradices*	>Leaf RWC, >glutamine synthatase activity	X	Subramanian and Charest (1999)
Zea mays	*G. intraradices*	>Growth, earlier emergence of tassels and silk	X	Subramanian and Charest (1997)
Zea mays	*G. intraradices*	>Leaf proteins, >[sugars], <[amino acids]	X	Subramanian and Charest (1995)
Zea mays	*G. intraradices*	Root and shoot: >N-assimilating enzymes, >[amino acids], >soluble [protein]	X	Subramanian and Charest (1998)
Zea mays	*G. intraradices*	>g_s, >E, >leaf Ψ, >green leaf area	X	Subramanian et al. (1995)
Zea mays	*G. intraradices*	>Leaf Ψ, >[sugars], >growth, <soil drying rate	X	Subramanian et al. (1997)
Zea mays	*G. etunicatum*	>Growth	X	Sylvia et al. (1993)
Ziziphus maritiana	*A.*, two *G.*, *Gi.*, *S.* [h]	<g_s, <E, >CER, >[leaf carbohydrate], >[chlorophyll], >[carotenoids]		Mathur and Vyas (1995)

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[a] *G. fasciculatum*, *G. macrocarpum*, *G. microcarpum*, *G. deserticola*, *G. occultum*, an unidentified *Glomus* sp.

[b] *G. etunicatum*, *G. mosseae*, *G. fasciculatum*, *G. deserticola*

[c] *G. etunicatum*, *G. intraradices*, *G. occultum*, *G. fasciculatum*, *G. deserticola*, *G. mosseae*, *G. caledonium*

[d] *A. longula*, *A. myriocarpa*, *Ent. colombiana*, *G. fasciculatus*, *G. manihotis*, *G. occultum*, *S. heterogama*

[e] *G. fasciculatum*, *G. macrocarpum*, *G. microcarpum*, *G. mosseae*, *Gi.* sp.

[f] *Gi. ramisporophora*, *G. ambisporum*, *G. fasciculatum*, *G. mosseae*

[g] *G. fuegianum*, *G. geosporum*, *G. mosseae*, *S. calospora*

[h] *A. morrowae*, *Gi. margarita*, *G. deserticola*, *G. fasciculatum*, *S. calospora*

Table 2 Mycorrhizal effects on host water relations or drought responses claimed to be not related to mycorrhizal effects on host size or P nutrition. Unless noted, VAM effects on growth and biochemical parameters were associated with drought. Fungus names are abbreviated as: *A. Acaulospora*, *G. Glomus*, *Gi. Gigaspora* (*CER* carbon exchange rate: photosynthesis, *E* transpiration rate, g_s stomatal conductance, L_p root hydraulic conductivity, *WUE* water use efficiency, *X* plants were subjected to drought stress at some point in the experiments, Ψ water potential, Ψ_π osmotic potential, Ψ_p turgor potential, < > VAM symbiosis decreased or increased the parameter, respectively, Δ VAM symbiosis changed the parameter, variously decreasing and increasing it, *[ ]* concentration of a substance)

Host species	Fungus species	Parameter	Drought	Reference
Acacia auriculiformis	One *A.* sp., two *G.* spp.	<Leaf Ψ, <leaf RWC, <soil water content, >growth relative to non-stressed plants	X	Osonubi et al. (1991)
Agropyron smithii	Indigenous	>g_s, >leaf Ψ	X	Allen and Allen (1986)
Allium cepa	*G. fasciculatum*	<Glutamine synthetase, >nitrate reductase	X	Azcón and Tobar (1998)
Allium porrum	*G. mosseae*	>E		Hardie (1985)
Allium porrum	*G. mosseae*	>Leaf hydration		Snellgrove et al. (1982)
Bouteloua gracilis	*G. fasciculatus*	>g_s, >E, <whole plant resistance, <soil-to-root resistance, <root-to-leaf resistance		Allen (1982)
Bromus inermis	*G. fasciculatum*	>g_s, >CER of non-stressed and stressed plants, >soil-plant liquid flow resistance	X	Bildusas et al. (1986)
Capsicum annuum	*G. deserticola*	>Leaf Ψ, >Ψ_p, >RWC, <wilting	X	Davies et al. (1992)
Capsicum annuum	*G. deserticola*	>g_s, >CER, >leaf Ψ_p, >osmotic adjustment	X	Davies et al. (1993)
Carthamus tinctorius	*G. etunicatum*	>g_s, >E of non-stressed plants; osmotic adjustment; >soil drying rate	X	Bryla and Duniway (1997a, 1998)
Carthamus tinctorius	Unreported	>g_s, <L_p		Safir and Nelsen (1981)
Citrus aurantium	*G. intraradices*	<L_p	X	Graham et al. (1987)
Citrus aurantium	*G. intraradices*	>CER		Nemec and Vu (1990)
Citrus jambhiri	Unclassified, probably *G. fasciculatus*	>g_s, >E, >CER	X	Levy and Krikun (1980)
Citrus jambhiri	*G. intraradices*	>E, <predawn leaf Ψ, <L_p	X	Levy et al. (1983b)
Citrus paradisi on *C. volkameriana*	*G. etunicatum*, *G. intraradices*	<Fine root mortality, <root/soil respiration	X	Espeleta et al. (1999)
Fragaria ananassa	*G. intraradices*	>Plantlet RWC		Hernández Sebastià et al. (1999)
Glycine max	*G. mosseae*	<Soil water content at permanent wilting, >growth, Ψ root and leaf [proline]	X	Bethlenfalvay et al. (1988a)
Glycine max	*G. macrocarpum*	<Soil water content at PWP, >access to bound water	X	Bethlenfalvay et al. (1988b)
Glycine max	*G. mosseae*	<Shoot water content relationships	X	Bethlenfalvay et al. (1990)
Glycine max	*G. mosseae*	>CER		Brown and Bethlenfalvay (1987)
Glycine max	*G. mosseae*	Altered soil water availability	X	Dakessian et al. (1986)
Glycine max	*G. mosseae*	<Nodule activity	X	Franson et al. (1991)
Glycine max	*G. fasciculatum*	>CER		Harris et al. (1985)
Glycine max	*G. mosseae*	>Nodule activity	X	Peña et al. (1988)
Helianthus annuus	*G. clairodeum*	>E, >hyphal water transport	X	Faber et al. (1991)
Hordeum vulgare	*G. mosseae*	Δ g_s, Δ CER		Fay et al. (1996)
Lactuca sativa	*G. fasciculatum*, *G. mosseae*	>CER, >[proline], >growth, >nitrate reductase	X	Azcón et al. (1996)
Lactuca sativa	*G. mosseae*, *G. fasciculatum*, *G. deserticola*	>Nitrate reductase activity	X	Ruiz-Lozano and Azcón (1996)
Lactuca sativa	*G. mosseae*, *G. fasciculatum*	<Growth, <proline accumulation	Osmotic stress	Ruiz-Lozano and Azcón (1997)
Leucaena leucocephala	*G. etunicatum*, *G. mosseae*, *G. occultum*	>Growth	X	Michelson and Rosendahl (1990)
Linum usitatissimum	*G.* spp.	>E, >CER		Drüge and Schönbeck (1992)
Medicago sativa	*G. mosseae*	>Growth, >nodulation	X	Azcón et al. (1988)
Medicago sativa	*G. fasciculatum*	>Free polyamines, >proline in leaves and roots	X	Goicoechea et al. (1998)

Table 2 Continued

Host species	Fungus species	Parameter	Drought	Reference
Medicago sativa	*G. fasciculatum*	<Leaf [cytokinins] before drought, delay leaf senescence with drought	X	Goicoechea et al. (1995)
Medicago sativa	*G. fasciculatum*	Non-stressed plants: <g_s, <E with drought: >CER, >leaf [ABA] without *Rhizobium*, <root [ABA], >root [cytokinins] with *Rhizobium*	X	Goicoechea et al. (1997a)
Medicago sativa	*G. fasciculatum*	>$\Psi_\pi{}^{100}$, $\Psi_p{}^{100}$ of non-stressed plants; >apoplastic water fraction, >elasticity	X	Goicoechea et at. (1997b)
Medicago sativa	*G. fasciculatum*	<Leaf Ψ, >nodule water content, >[cytokinin], >acid phosphatase activity	X	Goicoechea et al. (1996)
Medicago sativa	*G. mosseae*	>CER, >photosynthetic P use efficiency, >nodule activity, <internal [CO$_2$]	X	Sánchez-Díaz et al. (1990)
Nicotiana tabacum	*G. mosseae*	<Leaf hexoses, >root trehalose	X	Schellenbaum et al. (1999)
Plantago lanceolata	*G. mosseae*	>CER		Staddon et al. (1999)
Poncirus trifoliata × *Citrus sinensis*	*G. intraradices*	<L_p	X	Graham et al. (1987)
Prosopis alba	*G. intraradices*	<Growth	X	Martin and Stutz (1994)
Rosa hybrida	*G. intraradices*	<g_s	X	Augé and Duan (1991)
Rosa hybrida	*G. intraradices*, *G. deserticola*	>E	X	Augé (1989)
Rosa hybrida	*G. intraradices*	>Symplastic water fractions in roots	X	Augé and Stodola (1990)
Rosa hybrida	*G. deserticola*, *G. intraradices*	>g_s		Augé et al. (1986a)
Rosa hybrida	*G. deserticola*, *G. intraradices*	>g_s; >osmotic and turgor adjustment; <leaf and soil Ψ at stomatal closure; <leaf Ψ, RWC and Ψ_π at turgor loss; <symplastic water fractions in leaves	X	Augé et al. (1986b)
Rosa hybrida	*G. intraradices*, *G. deserticola*	>g_s, >leaf Ψ, >leaf Ψ_π, >[starch], <[soluble sugars], >[chlorophyll]	X	Augé et al. (1987a)
Rosa hybrida	*G. intraradices*, *G. deserticola*	>Leaf turgor, <leaf elasticity	X	Augé et al. (1987b)
Rosa hybrida	*G. intraradices*	<[Amino acids], <[root sucrose]	X	Augé et al. (1992b)
Rosa hybrida	*G. deserticola*, *G. intraradices*	>Root elastic modulus and >Ψ_p / leaf Ψ relations	X	Augé et al. (1987b)
Rosa hybrida	*G. deserticola*	>E	X	Davies et al. (1996)
Rosa hybrida	*G. intraradices*	>E	Fed ABA	Green et al. (1998)
Rosa hybrida	*G. deserticola*	>E, >leaf abscission, <leaf wax	X	Henderson and Davies (1990)
Rosa multiflora	*G. fasciculatum* + *G. mosseae*	<g_s, <E, leaf Ψ	X	Davies et al. (1987)
Solanum tuberosum	*G. intraradices*	>g_s, >CER, >plant water content		Louche-Tessandier et al. (1999)
Sorghum bicolor	*G. etunicatum*, *G. intraradices*	>g_s, >growth, <soil drying rate or no effect	X	Augé et al. (1995)
Sorghum bicolor	*G. intraradices*	>Growth, >soil drying rate	X	Ebel et al. (1994)
Sorghum bicolor	*A. dilatata*, two *G.* spp.	>Soil water extraction, maintenance of leaf Ψ to lower soil Ψ	X	Osonubi (1994)
Triticum aestivum	*G. etunicatum*	>Soil drying rate	X	Bryla and Duniway (1998)
Triticum aestivum	*G. fasciculatus*, *G. mosseae*	>g_s, >leaf osmotic adjustment, postponed stomatal closure and turgor loss	X	Allen and Boosalis (1983)
Trifolium pretense	*G. mosseae*	>E		Hardie (1985)
Trifolium repens	Unreported	>CER		Wright et al. (1998a, b)
Vicia faba	*G. mosseae*	>CER		Kucey and Paul (1982)
Vigna unguiculata	*G. intraradices*	>g_s	Osmotic stress	Augé et al. (1992a)

Table 2 Continued

Host species	Fungus species	Parameter	Drought	Reference
Vigna unguiculata	*G. intraradices*	>g_s, >E, >shoot Ψ, <xylem [ABA] per unit soil water content	X	Duan et al. (1996)
Vigna unguiculata	*G. intraradices*	<g_s, >soil drying rate	X	Ebel et al. (1996)
Vigna unguiculata	Cocktail: *G. mosseae*, *G. intraradices*, *Gi. margarita*, three isolates of *G. etunicatum*	>g_s, <xylem [ABA], at high soil water content, altered g_s/soil water content relation	X	Ebel et al. (1997)
Vigna unguiculata	*G. intraradices*	>g_s		Green et al. (1998)
Vigna unguiculata	*G. fasciculatum*	>Growth	X	Kwapata and Hall (1985)
Zea mays	*G. intraradices*	>Growth	X	Augé et al. (1994)
Zea mays	*G. mosseae*	>Leaf [imino acids], <[hexoses], >root [trehalose], <root acid invertase activity	X	Schellenbaum et al. (1998)

Table 3 **Upper part**: Reports indicating no effect of VAM symbiosis on any plant water relations parameter or drought growth response (papers not listed in Tables 1 or 2). **Lower part:** Reports indicating no effect of VAM symbiosis on particular plant water relations parameters or drought growth responses, in experiments in which VAM fungi did affect one or more other parameters (as indicated in Tables 1 or 2). Unless noted, VAM measurements on growth and biochemical parameters were associated with drought. Note: the lower part of this table does not include parameters listed in Table 1, in which observed differences between VAM and NM plants disappeared when NM plants were given sufficient P. Fungus names are abbreviated as: *A. Acaulospora*, *G. Glomus*, *Gi. Gigaspora* (*CER* carbon exchange rate: photosynthesis, *E* transpiration rate, g_s stomatal conductance, L_p root hydraulic conductivity, *WUE* water use efficiency, *X* plants were subjected to drought stress at some point in the experiments, Ψ water potential, Ψ_π osmotic potential, Ψ_p turgor potential, *[ ]* enclosing a substance signifies concentration)

Host species	Fungus species	Parameter	Drought	Reference
Reports indicating no effect of VAM symbiosis on any plant water relations parameter or drought growth response				
Agropyron repens	*G. mosseae*	Hyphal water transport	X	George et al. (1992)
Arachis hypogaea	*G. clarum*	Growth	X	Simpson and Daft (1991)
Carthamus tinctorius	*G. etunicatum*, *G. intraradices*	Soil drying rate, specific water uptake rate	X	Bryla and Duniway (1997b)
Citrus aurantium	*G. intraradices*	g_s, E, CER, L_p		Syvertsen and Graham (1990, Graham and Syvertsen (1985)
Citrus reshni	*G. intraradices*	E, CER, L_p		Graham and Syvertsen (1985)
Eucalytpus grandis	*G. etunicatum*	Growth	X	Fernandez et al. (1999)
Glycine max	*G. fasciculatum*	CER		Fredeen and Terry (1988)
Lactuca sativa	“VAM 510”	Growth, ferulic acid, caffeic acid, coumaric acid, cinnamic acid	X	Leinhos and Bergmann (1995)
Lolium perenne	Unreported	P uptake after drought	X	Jupp and Newman (1987)
Poncirus trifoliata × *Citrus sinensis*	*G. intraradices*	E, CER, L_p		Graham and Syvertsen (1985)
Poncirus trifoliata × *Citrus paradisi*	*G. intraradices*	E, CER, L_p		Graham and Syvertsen (1985)
Poncirus trifoliata	*G. intraradices*	E, CER, L_p		Graham and Syvertsen (1985)
Poncirus trifoliata × *Citrus sinensis*	*G. intraradices*	E	X	Johnson and Hummel (1985)
Sorghum bicolor	Two *A.*, four *G.*, indigenous [a]	Growth	X	Simpson and Daft (1990)
Trifolium repens	*G. mosseae*	Hyphal water transport	X	George et al. (1992)
Triticum aestivum	*G. etunicatum*, *G. intraradices*	Soil drying rate, specific water uptake rate	X	Bryla and Duniway (1997b)
Triticum aestivum	*G. mosseae*	E, hyphal water uptake		Tarafdar (1995)
Zea mays	*G. mosseae*	Growth	X	Hetrick et al. (1984)
Zea mays	*G. mosseae*	E		Kothari et al. (1990)
Zea mays	Two *A.*, four *G.*, indigenous [a]	Growth	X	Simpson and Daft (1990)
Reports indicating no effect of VAM symbiosis on particular plant water relations parameters or drought growth responses, in experiments in which VAM fungi did affect one or more other parameters				
Acacia melanoxylon	*G.* spp.	Growth	X	Mizoguchi (1992)
Agave deserti	Five *G.* spp. [b]	E		Cui and Nobel (1992)
Agropyron dasystachyum	Indigenous	g_s, leaf Ψ	X	Allen and Allen (1986)
Agropyron cristatum	Six *G.* spp.[c]	g_s, E, CER	X	Di and Allen (1991)
Agropyron desertorum	Six *G.* spp.[c]	g_s, E, CER	X	Di and Allen (1991)
Agropyron repens	*G. clarum*, indigenous spp.	Leaf Ψ of non-stressed plants	X	Osonubi et al. (1992)

Table 3 Continued

Host species	Fungus species	Parameter	Drought	Reference
Agropyron smithii	Indigenous spp.	g_s, leaf Ψ of non-stressed plants	X	Allen and Allen (1986)
Agropyron smithii	*G. microcarpum*, *G. macrocarpum*	Leaf Ψ		Stahl and Smith (1984)
Agrostis palutris	*G. intraradices*	Leaf Ψ of non-stressed plants	X	Gemma et al. (1997)
Albizia lebbeck	One *A.* sp., two *G.* spp.	Leaf Ψ of non-stressed plants	X	Osonubi et al. (1991)
Allium cepa	*G. etunicatus*	E, leaf Ψ	X	Nelsen and Safir (1982b)
Allium porrum	*G. mosseae*	CER		Snellgrove et al. (1982)
Andropogon gerardii	*G. deserticolum*	Growth	X	Hetrick et al. (1986)
Arachis hypogaea	*G. clarum*	Growth	X	Simpson and Daft (1991)
Bouteloua gracilis	*G. fasciculatus*	g_s and E of non-stressed plants, CER, leaf Ψ	X	Allen et al. (1981)
Buxus japonica microphylla	*G. etunicatus*, *G. fasciculatum*	Shoot Ψ		Newman and Davies (1988)
Capsicum annuum	*G. deserticola*	Non-stressed plants: g_s, CER, leaf Ψ, leaf Ψ_p	X	Davies et al. (1993)
Capsicum annuum	*G. aggregatum*	Growth in high P soil	X	Waterer and Coltman (1989)
Capsicum annuus	*G. deserticola*	E of unacclimated and stressed plants; leaf Ψ, Ψ_p, RWC of non-stressed plants	X	Davies et al. (1992)
Carthamus tinctorius	*G. etunicatum*	g_s, E, leaf Ψ_p	X	Bryla and Duniway (1997a)
Carthamus tinctorius	*G. etunicatum*	Leaf Ψ, leaf Ψ_π, leaf Ψ_p, daily water use, drought recovery, osmotic adjustment	X	Bryla and Duniway (1997c, (1998)
Citrus aurantium	*G. intraradices*	E, predawn and midday leaf Ψ of stressed and non-stressed plants, L_p of non-stressed plants	X	Graham et al. (1987)
Citrus jambhiri	Unclassified, probably *G. fasciculatus*	Leaf Ψ	X	Levy and Krikun (1980)
Citrus jambhiri	*G. intraradices*	Leaf Ψ in non-stressed plants		Levy et al. (1983b)
Faidherbia albida	*G. clarum*, indigenous spp.	Leaf Ψ of non-stressed plants	X	Osonubi et al. (1992)
Fragaria ananassa	*G. intraradices*	g_s, leaf and root Ψ_π, leaf RWC		Hernández Sebastià et al. (1999)
Fraxinus pennsylvanica	*G. etunicatum*	L_p per unit plant weight		Andersen et al. (1988)
Gliricidia sepium	One *A.* sp., two *G.* spp.	Leaf Ψ of non-stressed and droughted plants	X	Osonubi et al. (1991)
Glycine max	*G. mosseae*	g_s of non-stressed plants; CER; leaf Ψ, Ψ_π, Ψ_p, RWC	Osmotic stress	Augé et al. (1992a)
Glycine max	*G. mosseae*	g_s, E, CER, leaf Ψ, WUE		Bethlenfalvay et al. (1990)
Glycine max	*G. mosseae*	g_s of non-stressed plants	X	Bethlenfalvay et al. (1987)
Glycine max	*G. fasciculatum*	E	X	Busse and Ellis (1985)
Glycine max	*G. mosseae*	Nodule P use efficiency	X	Franson et al. (1991)
Glycine max	Unreported	Hyphal translocation of water	X	Safir and Nelsen (1981)
Guizotia abyssinica	*G. mosseae*, *G. macrocarpum*	E	X	Sieverding (1984)
Lactuca sativa	*G. mosseae*	CER		Azcón et al. (1992)
Leucaena leucocephala	One *A.* sp., two *G.* spp.	Leaf Ψ of non-stressed and droughted plants	X	Osonubi et al. (1991)
Linum usitatissimum	*G.* spp.	E, CER/E relation, shoot Ψ		Drüge and Schönbeck (1992)
Linum usitatissimum	Four *G.* isolates	E	X	von Reichenbach and Schönbeck (1995)
Liriodendron tulipifera	*G. fasciculatum*, *G. macrocarpum*	Root growth	X	Simmons and Pope (1988)
Medicago sativa	*G. fasciculatum*	Leaf Ψ of non-stressed or stressed plants	X	Goicoechea et al. (1998)
Medicago sativa	*G. fasciculatum*	Non-stressed plants: g_s, E, CER, leaf Ψ	X	Goicoechea et al. (1997a)
Medicago sativa	*G. fasciculatum*	Leaf Ψ_π, $\Psi_\pi{}^{100}$, $\Psi_p{}^{100}$, leaf Ψ of non-stressed plants	X	Goicoechea et at. (1997b)
Medicago sativa	*G. fasciculatum*	Leaf Ψ	X	Goicoechea et al. (1996)
Nicotiana tabacum	*G. mosseae*	CER of non-stressed and stressed plants	X	Schellenbaum et al. (1999)
Opuntia ficus-indica	Five *G.* spp. [b]	E, CER		Cui and Nobel (1992)
Pittosporum tobira	*G. etunicatus*, *G. fasciculatum*	g_s, E, shoot Ψ		Newman and Davies (1988)
Poncirus trifoliata × *Citrus sinensis*	*G. intraradices*	E; predawn and midday leaf Ψ of non-stressed and stressed plants; L_p of non-stressed plants	X X	Graham et al. (1987)

Table 3 Continued

Host species	Fungus species	Parameter	Drought	Reference
Rosa hybrida	*G. intraradices*	g_s; root full turgor Ψ_π, elasticity, RWC at turgor loss, symplastic water % of non-stressed roots		Augé and Stodola (1990)
Rosa hybrida	*G. intraradices*, *G. deserticola*	Leaf Ψ		Augé et al. (1986a)
Rosa hybrida	*G. intraradices*, *G. deserticola*	[sucrose], [total soluble carbohydrates]	X	Augé et al. (1987a)
Rosa hybrida	*G. intraradices*	Total [amino acids] and most individual [amino acids] in droughted roots	X	Augé et al. (1992b)
Rosa hybrida	*G. fasciculatum* + *G. mosseae*	Leaf Ψ	X	Davies et al. (1987)
Rosa hybrida	*G. deserticola*	E of non-stressed or acclimated plants, leaf Ψ, osmotic adjustment	X	Davies et al. (1996)
Rosa hybrida	*G. deserticola*	g_s, leaf Ψ (predawn, afternoon), leaf Ψ_π, leaf RWC, of non-stressed and stressed plants	X	Henderson and Davies (1990)
Solanum tuberosum	*G. intraradices*	g_s, CER, plant water content		Louche-Tessandier et al. (1999)
Sorghum bicolor	*G. intraradices*, *G. etunicatum*	g_s of non-stressed plants, leaf Ψ_π, leaf RWC		Augé et al. (1995)
Sorghum bicolor	*G. intraradices*	g_s, leaf Ψ		Ebel et al. (1994)
Sorghum bicolor	*G. intraradices*	g_s, E of non-stressed and highly stressed plants	X	Ibrahim et al. (1990)
Sorghum bicolor	*A. dilatata*, two *G.* spp.	Leaf Ψ of stressed and non-stressed plants	X	Osonubi (1994)
Sorghum bicolor	*G. mosseae*, *G. macrocarpum*	E	X	Sieverding (1984)
Sorghum vulgare	*G. etunicatum*	Growth	X	Hetrick et al. (1987)
Trifolium pratense	*G.* sp.	g_s	X	Fitter (1988)
Trifolium pratense	*G. mosseae*	g_s		Hardie (1985)
Trifolium repens	Unreported	CER		Wright et al. (1998a)
Triticum aestivum	*G. etunicatum*	g_s, E, leaf Ψ_p	X	Bryla and Duniway (1997a)
Triticum aestivum	*G. etunicatum*	Leaf Ψ, leaf Ψ_π, leaf Ψ_p, daily water use, drought recovery, osmotic adjustment	X	Bryla and Duniway (1997c)
Vigna unguiculata	*G. intraradices*	g_s/shoot Ψ and g_s/xylem [ABA] relations; xylem $[H^+]$, $[Ca^{++}]$, [cytokinin]; E of detached leaves	X	Duan et al. (1996)
Vigna unguiculata	*G. intraradices*	g_s		Ebel et al. (1996)
Vigna unguiculata	*G. intraradices*	Leaf Ψ_π, leaf RWC		Ebel et al. (1996)
Vigna unguiculata	Cocktail [d]	g_s, E, shoot Ψ, shoot RWC, xylem sap Ψ_π of stressed plants; g_s/xylem sap [ABA] relation	X	Ebel et al. (1997)
Vigna unguiculata	*G. clairodeum*	Leaf Ψ_π	X	Faber et al. (1991)
Vigna unguiculata	*G. intraradices*	E	Fed ABA	Green et al. (1998)
Zea mays	*G. intraradices*	g_s of non-stressed plants, leaf Ψ		Augé et al. (1994)
Zea mays	*G. etunicatum*	Growth	X	Hetrick et al. (1987)
Zea mays	*A. dilatata*, two *G.* spp.	Leaf Ψ of stressed and non-stressed plants	X	Osonubi (1994)
Zea mays	*G. caledonius*, indigenous	CER of stressed or non-stressed plants, leaf Ψ	Osmotic stress	Ramakrishnan (1988b)
Zea mays	*G. caledonium*, indigenous	Leaf Ψ at 0 to –1.0 MPa osmotic stress	Osmotic stress	Ramakrishnan et al. (1988a)
Zea mays	*G. mosseae*	g_s before and after drought	X	Schellenbaum et al. (1998)
Zea mays	*G. intraradices*	g_s of stressed plants, leaf RWC of non-stressed plants	X	Subramanian and Charest (1999)
Zea mays	*G. intraradices*	g_s, E, leaf Ψ of non-stressed plants	X	Subramanian et al. (1995)

[a] *A. morroweae*, *A.* sp., *G. clarum*, *G. constrictum*, *G. epigeum*, *G. monosporum*, indigenous mixture

[b] *G. epigaeam*, *G. fasciculatum*, three other *G.* spp.

[c] *G. fasciculatum*, *G. macrocarpum*, *G. microcarpum*, *G. deserticola*, *G. occultum*, an unidentified *Glomus* sp.

[d] *G. mosseae*, *G. intraradices*, *Gi. margarita*, three isolates of *G. etunicatum*

Table 4 Mycorrhizal papers reporting elemental concentrations (other than P), in various tissues of VAM and NM plants exposed to drought. Fungus names are abbreviated as: *A. Acaulospora*, *Ent. Entrophospora*, *G. Glomus*, *Gi. Gigaspora*, *S. Scutellospora.* Two plant size columns indicate whether VAM and NM plants were of similar size (=), or whether VAM plants were smaller (<) or larger (>) than NM plants, before or in the absence of drought (*watered*) or after drought (*droughted*). Papers reporting elemental contents but not providing corresponding plant or organ dry weights are not listed here. Absence of a symbol preceding an element signifies that the element was measured but VAM symbiosis did not alter its concentration (< > VAM symbiosis decreased or increased the concentration of that element in host tissues, respectively, Δ VAM symbiosis changed the concentration of the element, variously decreasing and increasing it, * data not reported)

Host species	Fungus species	Element	Length of drought (days)	Plant size (VAM/NM)		Reference
				Watered	Droughted	
Acacia auriculiformis	*A.*, *G.*	[a] Shoot: Ca, <K, Mg, N	84	<	<	Awotoye et al. (1992)
Acacia melanoxylon	*G.* spp.	Root: Ca, >Cu, <Fe, K, Mg, Mn, N, Na, <Zn shoot: Ca, >Cu, Fe, K, >Mg, Mn, >N, Na, Zn	~60	=	=	Mizoguchi (1992)
Acacia auriculiformis	*G.* spp.	Root: Ca, Cu, Fe, >K, Mg, Mn, N,>Na, Zn shoot: >Ca, Cu, Fe, K, Mg, Mn, >N, Na, Zn	~60	>	>	Mizoguchi (1992)
Acacia mangium	*G.* spp.	Root: Ca, Cu, Fe, K, Mg, Mn, >N, Na, Zn shoot: >Ca, >Cu, Fe, K, Mg, Mn, N, Na, Zn	~60	=	=	Mizoguchi (1992)
Agave deserti	[b] Five *Glomus* spp.	Root: B, Ca, Cu, Fe, K, Mg, Mn, Mo, N, Zn shoot: B, Ca, Cu, Fe, K, Mg, Mn, Mo, N, >Zn	~150	*	*	Cui and Nobel (1992)
Agropyron cvs.	[c] Six *G.* spp.	Plant N	~112	*	4=, 2<	Di and Allen (1991)
Agropyron repens	*G. mosseae*	Shoot: K, >N	5	*	=	George et al. (1992)
Albizia lebbeck	*A.*, *G.*	[a] Shoot: Ca, K, Mg, >N	84	>	>	Awotoye et al. (1992)
Bromus inermis	*G. fasciculatum*	Leaf: >Ca, Cu, K, >Mg, <Mn, N, Zn	126	<	<	Bildusas et al. (1986)
Capsicum annuum	*G. deserticola*	[d] Leaf: <Al, <B, <Ca, >Cu, <Fe, K,<Mg, <Mn, <Mo, <N, >Zn	[d] 4	=	=	Davies et al. (1992)
Carthamus tinctorius	*G. etunicatum*	<Leaf N	~20	=	=	Bryla and Duniway (1998)
Carthamus tinctorius	*G. etunicatum*	Leaf N, root N, floral N, <stem N	~6	=	=	Bryla and Duniway (1997a)
Carthamus tinctorius	*G. etunicatum*	Leaf: N, stem: N	6	=	=	Bryla and Duniway (1997b)
Cenchrus ciliaris	[e] Effect varied among three spp.	Shoot: >Cu, Fe, >K, Mn, N, >Zn	365	*	>	Tarafdar and Praveen-Kumar (1996)
Cucurbita pepo	*G. intraradices*	>Shoot K, >root N	14, 28	=	=	Aboul-Nasr (1998)
Eupatorium odoratum	*G. macrocarpus*	[f] Shoot: Ca, >K, >Mg, <N	~35–42	>	>	Sieverding (1983)
Ferocactus acanthodes	[b] Five *G.* spp.	Root: B, Ca, Cu, Fe, K, Mg, Mn, Mo, N, Zn shoot: B, Ca, Cu, Fe, K, Mg, Mn, Mo, N, >Zn	~150	*	*	Cui and Nobel (1992)
Gliricidia sepium	*A.*, *G.*	[a] Shoot: >Ca, >K, >Mg, >N	84	>	>	Awotoye et al. (1992)
Glycine max	*Gi.* sp., *G.* sp.	Shoot: Cu, Fe, >K, Mn, >N, Zn	60	>	>	Barakah and Heggo (1998)
Glycine max	*G. mosseae*	<Root N; leaf N	32	<	>	Bethlenfalvay et al. (1987)
Glycine max	*G. mosseae*	Leaf N	≤4	*	<	Bethlenfalvay et al. (1990)
Glycine max	*G. mosseae*	Plant N	≤4	*	<	Franson et al. (1991)
Hordeum vulgare	*G. mosseae*	Shoot: >Cu, >Mn, Zn	31	>	>	Al-Karaki and Clark (1999)
Lactuca sativa	*G. fasciculatum*, *G. mosseae*	[a,g] Leaf: Δ Ca, Δ K, >Mg, >N	~36	*	=, >	Azcón et al. (1996)
Lactuca sativa	*G deserticola*, *G. fasciculatum*	[h] Leaf: Ca, K, Mg, <N	≤72	>	>	Ruiz-Lozano and Azcón (1995)
Lactuca sativa	[i] Seven *G.* spp.	[a,j] Shoot (for all seven fungi): <Ca, <K, <Mg, <N	21	>	>	Ruiz-Lozano et al. (1995b)
Lactuca sativa	[k] Three *G.* spp.	Leaf: <N	42	<= >	>	Ruiz-Lozano and Azcón (1996)
Lactuca sativa	*G. fasciculatum*	[a] Shoot N, >root N	84	>	>	Tobar et al. (1994a)
Lactuca sativa	[l] *G deserticola*, *G. fasciculatum*	Plant: <N	91	≥	>	Tobar et al. (1994b)

Table 4 Continued

Host species	Fungus species	Element	Length of drought (days)	Plant size (VAM/NM)		Reference
				Watered	Droughted	
Leucaena leucocephala	*A.*, *G.*	[a] Shoot: >Ca, K, >Mg, >N	84	>	>	Awotoye et al. (1992)
Malus hupehensis	*G. versiforme*, *G. macrocarpum*	[m] Root: <B, >Ca, >Cu, Fe, K, Mg, >Mn, >Zn shoot: <B, Ca, <Cu, <Fe, K, Mg, <Mn, >Zn	Unreported	*	>	Runjin (1989)
Manihot esculenta	[n] Seven spp.	Shoot K, Δ N	75	Mostly>	Mostly>	Sieverding and Toro (1988)
Medicago sativa	*G. mosseae*	>Plant N	77	<	>	Azcón et al. (1988)
Opuntia ficus-indica	[b] Five *Glomus* spp.	Root: B, Ca, Cu, Fe, K, Mg, Mn, Mo, N, Zn shoot: B, Ca, Cu, Fe, K, Mg, Mn, Mo, N, Zn	~150	*	*	Cui and Nobel (1992)
Parkia biglobosa	*G. deserticola*	Leaf: >Ca, >K, >Mg, N	4, 8, 12	>	>	Osundina (1995)
Pelargonium × *hortorum*	*G. mosseae*, *G. fasciculatus*	>Plant N	~91	=	>	Sweatt and Davies (1984)
Prosopis juliflora	[e] Three spp.	Shoot: >Cu, Δ Fe, >K, <Mn, N, >Zn	365	*	>	Tarafdar and Praveen-Kumar (1996)
Rosa hybrida	*G. intraradices*	Root: B, >Ba, <Ca, Cu, <K, Mg, Sr, <Zn	21	=	=	Augé et al. (1992b)
Rosa hybrida	*G. deserticola*	Leaf: B, Ca, >Cu, Fe, K, Mg, Mn, Mo, N, Zn	4, 24	=	=	Henderson and Davies (1990)
Schizachyrium scoparium	[o] Indigenous	Shoot: >Al, <B, Ca, >Cu, >Fe, K, Mg, <Mn, >Na, S, >Zn	60	<	<	Cerligione et al. (1988)
Triticum aestivum	*G. etunicatum*	Leaf N, root N, floral N	~6	<	=	Bryla and Duniway (1997a)
Triticum aestivum	*G. etunicatum*	Leaf: N	6	=	=	Bryla and Duniway (1997b)
Triticum durum	*G. monosporum*	Shoot: >Cu, >Fe, Mn, >Zn	34	>	>	Al-Karaki et al. (1998)
Triticum durum	*G. mosseae*	Shoot: >Cu, >Fe, Mn, >Zn	34	>	>	Al-Karaki et al. (1998)
Triticum durum	*G. mosseae*	[a] Shoot: Cu, Fe, Mn, Zn	~60	>	>	Al-Karaki and Al-Raddad (1997a)
Triticum durum	*G. mosseae*	Shoot: Cu, Fe, Mn, Zn	54	>	>	Al-Karaki and Al-Raddad (1997b)
Triticum durum	*G. monosporum*	Shoot: Cu, Fe, Mn, Zn	~35	=	>	Al-Karaki and Clark (1998)
Vigna aconitifolia	[e] Three spp.	Shoot: Δ Cu, Δ K, >Zn	80	*	>	Tarafdar and Praveen-Kumar (1996)
Vigna unguiculata	*G. intraradices*	Xylem sap: Ca	2–8	=	=	Duan et al. (1996)
Vigna unguiculata	*G. fasciculatum*	Root: >Cu, >Zn shoot: Cu, Zn	39	=	<	Kwapata and Hall (1985)
Vigna unguiculata	*G. fasciculatum*	Plant and root: >^{45}Ca uptake	[p] 20/2.5	*	*	Pai et al. (1994)
Zea mays	*G. intraradices*	Root and shoot: >N	14	>	=	Subramanian and Charest (1999)
Zea mays	*G. intraradices*	Leaf: Ca, Mg, S	21	=	>	Augé et al. (1994)
Zea mays	*G. intraradices*	[a,q] Shoot: Ca, <Cu, <Fe, >K, Mg, <Mn, >N, S, Zn	21	=	≥	Subramanian and Charest (1997)
Zea mays	*G. etunicatum*	Shoot: <Ca, >Cu, K, Mg, <Mn, <Zn grain: <Ca, >Cu, K, Mg, Mn, <Zn	[r] 99, [s] 133	=	>	Sylvia et al. (1993)

[a] Element concentrations not reported by authors were computed from averages of whole plant dry weights and element contents. In these instances, < and > indicate when (VAM–NM)/NM values exceeded 0.3 (VAM and NM differed by more than 30%)

[b] *G. epigaeum*, *G. fasciculatum* and three other *Glomus* spp.

[c] *G. fasciculatum*, *G. macrocarpum*, *G. microcarpum*, *G. deserticola*, *G. occultum*, an unidentified *Glomus* sp.

[d] Results varied depending on whether or not plants were preacclimated to drought (four 4-day drought cycles) before exposure to subsequent drought

[e] *Gi. margarita*, *G. fasciculatum*, *G. mosseae*

[f] Based on pooled means for both non-stressed and droughted plants

[g] Varied with NO_3/NH_4 fertilization and with fungus

[h] Similar effects on each nutrient by *G. deserticola* and *G. fasciculatum*

[i] *G. etunicatum*, *G. intraradices*, *G. occultum*, *G. fasciculatum*, *G. deserticola*, *G. mosseae*, *G. caledonium*

[j] VAM shoots were ≥10-fold larger than NM shoots for six of the seven fungi

[k] *G. deserticola*, *G. fasciculatum*, *G. mosseae*

[l] *G. fasciculatum* and NM plants differed; *G. deserticola* and NM plants were similar

[m] Summarization of experiment 1 only

[n] *A. longula*, *A. myriocarpa*, *Ent. colombiana*, *G. fasciculatus*, *G. manihotis*, *G. occultum*, *S. heterogama*

[o] *G. fuegianum*, *G. geosporum*, *G. mosseae*, *S. calospora*

[p] 20 days withholding water, then ^{45}Ca added and assays done 60 h later

[q] For drought-resistant cultivar. For drought-sensitive, the only VAM versus NM difference was >Zn in VAM

[r] Element concentrations also reported for 28 and 52 days after planting

[s] Element concentrations also reported for 99 days after planting

Table 5 Number of reports cited in Table 4 in which VAM symbiosis decreased (<), increased (>) or had no effect (=) on shoot concentrations of the elements listed

VAM/NM	Element													
	Al	B	Ca	Cu	Fe	K	Mg	Mn	Mo	N	Na	S	Sr	Zn
<	1	3	4	2	3	3	2	7	1	8	0	0	0	1
=	0	4	12	10	12	15	13	14	4	18	3	2	1	12
>	1	0	7	11	3	7	6	1	0	12	1	0	0	10

Table 6 Effects of drought, aridity and soil moisture gradients on behavior of VAM fungi. The fungi are abbreviated as: *A. Acaulospora*, *E. Endogone*, *Ent. Entrophospora*, *G. Glomus*, *Gi. Gigaspora*, *S. Scutellospora*, *Scl. Sclerocystis*. Colonization was quantified as percent of root colonized, when abbreviations are followed by *%*. Numbers in parentheses are colonization percentages for droughted and non-stressed plants, respectively (*arb%* arbuscular colonization rates, *col%* total root colonization rates, *HA* hydroxyapatite, *hyp%* intraradical hyphal colonization rates, *intensity* intensity of colonization, *MCP* monocalcium phosphate, *spores* spore numbers, variously reported as spore abundance, spore density, spore production and sporulation, *ves%* vesicular colonization rates, < > soil drying decreased or increased parameters, respectively, *Δ* drying changed the parameter, variously decreasing and increasing it; absence of <, >or *Δ* before a parameter signifies that drought did not affect the parameter. ■ signifies information was not available in the abstract, in the two instances I was unable to obtain the full paper)

Fungus species	Host species	Parameter	Length of drought (days)	Reference
A. laevis	*Acacia saligna*	hyphal infectivity in dry soil (–21 MPa)	36	Jasper et al. (1989) °
A. laevis	*Acaia saligna*, *Trifolium subterraneum*	<col%, <entry points, >spores	21–189	Jasper et al. (1993) °
A. laevis	Clover and grass spp.	<spore germination, <hyphal length	21	Tommerup (1984) °
A. laevis	*Trifolium subterraneum*	>infectivity of pot culture, >infectivity of spores	~25–30	Braunberger et al. (1996) °
A. longula	Cassava	<col% (37, 64), <spores	75	Sieverding and Toro (1988)
A. longula	*Paspalum notatum*	spore germination	≤112	Douds and Schenck (1991) °
A. morroweae	*Zea mays*, *Sorghum bicolor*	col%, spores	28 *Zea*, 56 *Sorghum*	Simpson and Daft (1990)
A. myriocarpa	Cassava	col% (12, 8), <spores	75	Sieverding and Toro (1988)
A. sp.	*Zea mays*, *Sorghum bicolor*	col%, spores	28 *Zea*, 56 *Sorghum*	Simpson and Daft (1990)
E. sp.	*Khaya grandifolia*	>col% w/ least irrigation, *Δ* spores	210 of varied irrigation	Redhead (1975)
Ent. columbiana	Cassava	col% (66, 62), <spores	75	Sieverding and Toro (1988)
G. aggregatum	*Lythrum salicaria*	<arb% (10, 30), hyp% (22, 50), ves% (3, 3)	42	Stevens and Peterson (1996) °
G. caledonium	Clover and grass spp.	<spore germination, <hyphal length	14	Tommerup (1984) °
G. caledonium	*Lactuca sativa*	col% (27, 33)	21	Ruiz-Lozano et al. (1995a, b)
G. clarum	*Acacia nilotica*	<col% (30, 52) (34, 45) (27, 47)	84	Osonubi et al. (1992)
G. clarum	*Arachis hypogaea*	col%, *Δ* spores	23	Simpson and Daft (1991)
G. clarum	*Faidherbia albida*	<col% (19, 28) (16, 24) (19, 23)	70	Osonubi et al. (1992)
G. clarum	*Lythrum salicaria*	<arb% (1, 10), <hyp% (3, 19), ves% (1, 3)	42	Stevens and Peterson (1996) °
G. clarum	*Zea mays*, *Sorghum bicolor*	col%, spores	28 *Zea*, 56 *Sorghum*	Simpson and Daft (1990)
G. constrictum	*Zea mays*, *Sorghum bicolor*	col%, spores	28 *Zea*, 56 *Sorghum*	Simpson and Daft (1990)
G. deserticola	*Andropogon gerardii*	>col%, >intensity	unreported	Hetrick et al. (1986)
G. deserticola	*Baptisia australis*, *Liatris aspera*	col%, intensity (two P levels)	42	Zajicek et al. (1987)
G. deserticola	*Capsicum annuum*	col% (15, 10), spores, >extraradical hyphae	16	Davies et al. (1992)
G. deserticola	*Lactuca sativa*	col% (90, 93)	42	Ruiz-Lozano and Azcón (1996)
G. deserticola	*Lactuca sativa*	col% (76, 75)	21	Ruiz-Lozano et al. (1996a)
G. deserticola	*Lactuca sativa*	<col% (14, 73; experiment 2)	28	Ruiz-Lozano and Azcón (1995)

Table 6 Continued

Fungus species	Host species	Parameter	Length of drought (days)	Reference
G. deserticola	*Lactuca sativa*	col% (94, 92)	21	Ruiz-Lozano et al. (1995a, b)
G. deserticola	*Rosa hybrida*	>col% (76, 53)	17–20	Augé et al. (1986b)
G. deserticola	*Rosa hybrida*	col% (13, 9)	28	Davies et al. (1996)
G. deserticola	*Rosa hybrida*	>col% (13, 9)	24	Henderson and Davies (1990)
G. epigeum	*Zea mays*, *Sorghum bicolor*	col%, spores	28 *Zea*, 56 *Sorghum*	Simpson and Daft (1990)
G. etunicatum	*Allium cepa*	<spores (two P levels)	56	Nelsen (1987)
G. etunicatum	*Andropogon gerardii*	>col%, >intensity	unreported	Hetrick et al. (1986)
G. etunicatum	*Andropogon gerardii*	>col%, >intensity (two P levels)	77	Hetrick et al. (1987)
G. etunicatum	*Baptisia australis*, *Liatris aspera*	>col%, >intensity (three P levels)	42	Zajicek et al. (1987)
G. etunicatum	*Baptisia australis*, *Liatris aspera*	col%, intensity (two P levels)	42	Zajicek et al. (1987)
G. etunicatum	*Carthamus tinctorius*, *Triticum aestivum*	col% (five soil depths)	~6 or ~20	Bryla and Duniway (1997a, c; 1998)
G. etunicatum	*Eucalyptus grandis*	<col% (two P levels)	60	Fernandez et al. (1999)
G. etunicatum	*Lactuca sativa*	col% (66, 59)	21	Ruiz-Lozano et al. (1995a, b)
G. etunicatum	*Sorghum bicolor*	<arb%, <hyp%, ves%, (three P levels)	24	Augé et al. (1995)
G. etunicatum	*Sorghum vulgare*	col%, intensity (two P levels)	70	Hetrick et al. (1987)
G. etunicatum	*Zea mays*	<col%, intensity (two P levels)	42	Hetrick et al. (1987)
G. etunicatum	*Zea mays*	col%	84–91	Sylvia et al. (1993)
G. etunicatus	*Allium cepa*	>col%	91	Bolgiano et al. (1983) [o]
G. etunicatus	*Allium cepa*	<spores, intensity (two P levels)	56, 84	Nelson and Safir (1982b)
G. fasciculatum complex	*Agropyron desertorum*, *A. spicatum*	Δ col%, Δ spores (several dates)	≤730	Allen et al. (1989) [o]
G. fasciculatum	*Baptisia australis*, *Liatris aspera*	col%, intensity (two P levels)	42	Zajicek et al. (1987)
G. fasciculatum	*Bromus inermis*	>spores	123	Bildusas et al. (1986)
G. fasciculatum	Cassava	<col% (53, 73), spores	75	Sieverding and Toro (1988)
G. fasciculatum	*Glycine max*	<col% (28, 50)	9	Busse and Ellis (1985)
G. fasciculatum	*Lactuca sativa*	col% (63, 69)	21	Ruiz-Lozano et al. (1995a, b)
G. fasciculatum	*Lactuca sativa*	<col% (11, 75; experiment 2)	28	Ruiz-Lozano and Azcón (1995)
G. fasciculatum	*Lactuca sativa*	col% (80, 83)	42	Ruiz-Lozano and Azcón (1996)
G. fasciculatum	*Lactuca sativa*	>col% (76, 48)	84	Tobar et al. (1994b)
G. fasciculatum	*Lactuca sativa*	col% (74, 75)	84	Tobar et al. (1994a)
G. fasciculatum	*Lythrum salicaria*	arb% (20, 10), hyp% (31, 22), ves% (4, 3)	42	Stevens and Peterson (1996) [o]
G. fasciculatum	*Medicago sativa*	col% (26, 36), <col% (28, 47)	~10	Goicoechea et al. (1998)
G. fasciculatum	*Medicago sativa*	<col% (20, 44)	unreported	Goicoechea et al. (1996)
G. fasciculatum	*Medicago sativa*	<col% (18, 33) (15, 49)	~8	Goicoechea et al. (1995)
G. fasciculatum	*Medicago sativa*	<col% (26, 36) (28, 47)	~6–10	Goicoechea et al. (1997a)
G. fasciculatum	*Medicago sativa*	<col% (18, 33) (15, 49)	~8	Goicoechea et al. (1995)
G. fasciculatum	*Populus deltoides*, *Salix nigra*	Δ col%	natural H_2O gradients	Lodge (1989) [o]
G. fasciculatum	*Sorghum vulgare*, *Daucus carota*	<col%, <spores	≤1095 [a]	Safir et al. (1990) [o]
G. fasciculatum	*Trifolium repens*	Δ col% (four P levels)	~72	Puppi and Bras (1990)
G. fasciculatum	*Triticum aestivum*	col% (66, 59), <ves% (9, 20)	75	Allen and Boosalis (1983)
G. fasciculatum	*Vigna unguiculata*	<col% (51, 41)	39	Kwapata and Hall (1985)
G. fasciculatum complex	*Zea mays*	>col%, Δ propagule mortality	183–2190	Miller et al. (1985) [o]
G. fasciculatum (mostly); seven other spp. present [b]	Prairie communities	Δ col%, <spores	natural H_2O gradients	Dickman et al. (1984)
G. intraradices	*Cucurbita pepo*	>col% (26, 19)	14, 28	Aboul-Nasr (1998)
G. intraradices	*Lactuca sativa*	col% (87, 87)	21	Ruiz-Lozano et al. (1995a, b)

Table 6 Continued

Fungus species	Host species	Parameter	Length of drought (days)	Reference
G. intraradices	*Lythrum salicaria*	arb% (5, 20), hyp% (9, 34), ves% (1, 3)	42	Stevens and Peterson (1996) [o]
G. intraradices	*Paspalum notatum*	>spore germination	≤112	Douds and Schenck (1991) [o]
G. intraradices	*Poncirus trifoliata* × *Citrus sinensis*	col% (72, 65)	~135	Johnson and Hummel (1985)
G. intraradices	*Prosopis alba*	<col% (4, 30)	365	Martin and Stutz (1994)
G. intraradices	*Rosa hybrida*	<col% (24, 33)	21	Augé and Stodola (1990)
G. intraradices	*Rosa hybrida*	>col% (83, 66)	17–20	Augé et al. (1986b)
G. intraradices	*Sorghum bicolor*	arb%, hyp%, ves%, (three P levels)	24	Augé et al. (1995)
G. intraradices	*Sorghum bicolor*	arb%, hyp%, ves%	24	Ebel et al. (1994)
G. intraradices	*Zea mays*	col% (60, 47)	14	Subramanian and Charest (1999)
G. intraradices	*Zea mays*	col%	21	Subramanian and Charest (1997)
G. invermaium	*Trifolium subterraneum*	<infectivity of pot culture; <infectivity of root fragments; <infectivity of extraradical hyphae	~25–30	Braunberger et al. (1996) [o]
G. macrocarpum	*Eupatorium odoratum*	col% (84, 78) with MCP; col% (97, 91), arb%, >ves% with HA	~35–42	Sieverding (1981)
G. macrocarpum	*Glycine max*	<col%	unreported	Bethlenfalvay et al. (1988b)
G. macrocarpum	*Sorghum bicolor*	>col% (53, 30) with MCP; >col% (95, 59) >arb% >ves% with HA	~35–42	Sieverding (1981)
G. macrocarpus	*Eupatorium odoratum*	*Δ* col%, >hyp%, >arb%, <ves% [c]	unreported (<33)	Sieverding (1983)
G. macrocarpus	*Guizotia abyssinica*	col% (84, 82)	unreported	Sieverding (1984)
G. macrocarpus	*Sorghum bicolor*	>col% (53, 30) (95, 59) (96, 70) [d], >hyp, >arb, >ves	35–42	Sieverding (1979)
G. macrocarpus	*Sorghum bicolor*	>col% (73, 62)	unreported	Sieverding (1984)
G. manihotis	Cassava	>col% (98, 80), spores	75	Sieverding and Toro (1988)
G. monosporum	*Lythrum salicaria*	arb% (7, 20), hyp% (13, 34), ves% (1, 2)	42	Stevens and Peterson (1996) [o]
G. monosporum	*Trifolium subterranean*	>infectivity of spores	~25–30	Braunberger et al. (1996) [o]
G. monosporum	*Triticum durum*	<col% (29, 52) (24, 38)	~25	Al-Karaki (1998)
G. monosporum	*Triticum durum*	<col% (40, 12)	34	Al-Karaki et al. (1998)
G. monosporum	*Triticum durum*	<col% (28, 50) (22, 36)	35	Al-Karaki and Clark (1998)
G. monosporum	*Zea mays*, *Sorghum bicolor*	col%, spores	28 *Zea*, 56 *Sorghum*	Simpson and Daft (1990)
G. mosseae	*Baptisia australis*, *Liatris aspera*	col%, intensity (two P levels)	42	Zajicek et al. (1987)
G. mosseae mainly	*Citrus paradisii* on *Citrus aurantium*	<col% (several irrigation frequencies and soil depths)	unreported (>40)	Levy et al. (1983a)
G. mosseae	*Glycine max*	col% (40, 38)	32	Bethlenfalvay et al. (1987)
G. mosseae	*Glycine max*	col%, >biomass and length of extraradical hyphae	28	Bethlenfalvay et al. (1988a)
G. mosseae	*Guizotia abyssinica*	col% (62, 73)	unreported	Sieverding (1984)
G. mosseae	*Hordeum vulgare*	<col% (varied with rate of inoculum)	31	Al-Karaki and Clark (1999)
G. mosseae	*Lactuca sativa*	col% (63, 60)	21	Ruiz-Lozano et al. (1996a)
G. mosseae	*Lactuca sativa*	col% (80, 82)	42	Ruiz-Lozano and Azcón (1996)
G. mosseae	*Lactuca sativa*	>col% (79, 70)	21	Ruiz-Lozano et al. (1995a, b)
G. mosseae	*Lactuca sativa*	>col% (78, 68)	84	Tobar et al. (1994b)
G. mosseae	*Medicago sativa*	col%	77	Azcón et al. (1988)
G. mosseae	*Medicago sativa*	col% (40, 44)	30	Sánchez-Díaz et al. (1990)
G. mosseae (three isolates)	*Melilotus officianalis*	*Δ* col%, *Δ* spores	15–75	Stahl and Christensen (1991) [o]
G. mosseae	*Nicotiana tabacum*	<arb%, hyp%, <external mycelium	20	Schellenbaum et al. (1999)
G. mosseae	*Paspalum notatum*	spore germination	≤112	Douds and Schenck (1991) [o]

Table 6 Continued

Fungus species	Host species	Parameter	Length of drought (days)	Reference
G. mosseae	*Sorghum bicolor*	<col% (40, 52)	unreported	Sieverding (1984)
G. mosseae	*Sorghum vulgare*, *Daucus carota*	<col%, <spores	≤1095 [a]	Safir et al. (1990) [o]
G. mosseae	*Triticum aestivum*	col% (46, 43), <ves% (9, 17)	75	Allen and Boosalis (1983)
G. mosseae	*Triticum durum*	<col% (52, 18)	34	Al-Karaki et al. (1998)
G. mosseae	*Triticum durum*	<col% (20, 47)	54	Al-Karaki and Al-Raddad (1997b)
G. mosseae	*Triticum durum*	<col% (20, 47) (15, 33)	~60	Al-Karaki and Al-Raddad (1997a)
G. mosseae	*Zea mays*	>col% at lower P (27, 13) (19, 13) (13, 9) (8, 8) (4, 8)	~35	Hetrick et al. (1984)
G. mosseae	*Zea mays*	col% (88, 75) (81, 78), hyp% (29, 19) (20, 14), arb% (56, 50) (59, 58), ves% (6, 6) (2, 6)	12	Schellenbaum et al. (1998)
G. mosseae	None	<spore germination, <hyphal growth	3–21, osmotic stress	Estaun (1990) [o]
G. occultum	Cassava	col% (67, 78), spores	75	Sieverding and Toro (1988)
G. occultum	*Lactuca sativa*	<col% (32, 42)	21	Ruiz-Lozano et al. (1995a, b)
G. tenuis	Meadow, pasture grasses	>col%	natural H_2O gradient	Rabatin (1979)
G. versiforme	*Lythrum salicaria*	<arb% (4, 10), <hyp% (7, 20), ves% (1, 4)	42	Stevens and Peterson (1996) [o]
G. sp. FL904	*Citrus aurantium*	col%	42	Eissenstat et al. (1999)
G., various [e]	*Spartina pectinata*	<col%	51	Anderson et al. (1986) [o]
G. etunicatum, *G. mosseae*, *G. occultum* mixture	*Acacia nilotica*, *Leucaena leucocephala*	col%	21	Michelsen and Rosendahl (1990)
Gi. calospora	Clover and grass spp.	<spore germination, <hyphal length	14	Tommerup (1984) [o]
Gi. calospora	*Populus deltoides*, *Salix nigra*	*Δ* col%	natural H_2O gradients	Lodge (1989) [o]
Gi. margarita	*Paspalum notatum*	<spore germination, col%	≤133	Douds and Schenck (1991) [o]
Gi. margarita	*Populus deltoides*, *Salix nigra*	*Δ* col%	natural H_2O gradients	Lodge (1989) [o]
Five *G.* spp.	Six hosts [f]	<col%, *Δ* spores	natural H_2O gradient	Jacobson (1997) [o]
S. calospora	*Acaia saligna*, *Trifolium subterraneum*	col%, >spores	21–189	Jasper et al. (1993) [o]
S. calospora	*Trifolium subterranean*	infectivity of spores, >infectivity of root fragments	~25–30	Braunberger et al. (1996) [o]
S. heterogama	Cassava	col% (9, 8), spores	75	Sieverding and Toro (1988)
White reticulate	*Guizotia abyssinica*, *Sorghum bicolor*	<col% (53, 77), >col% (75, 57)	unreported	Sieverding (1984)
Yellow vacuolate	*Medicago trunculata*	*Δ* infections/unit root length	8	Reid and Bowen (1979) [o]
A. dilatata, two *G.* spp.	*Sorghum bicolor*, *Zea mays*	*Δ* col%	56	Osonubi (1994)
A. sp., *Gi.* spp., *G.* spp.	Six hosts [g]	>col%	unreported	Pande et al. (1999)
A. sp., two *G.* spp.	Four hosts [h]	<col% (39, 58) (35, 68) (34, 45) (23, 25)	84	Awotoye et al. (1992)
A. sp., two *G.* spp.	Four hosts [h]	<col%	84	Osonubi et al. (1991)
A. sp., *Gi.* sp., two *G.* spp., *Scl.* sp. [i]	*Acaia farnesiana*	>col%, >spores	seasonal changes	Udaiyan et al. (1996) [o]
A. sp., four *G.* spp. [j]	*Acaia planifrons*	>col%	seasonal changes	Udaiyan et al. (1996) [o]
A. sp., *G.* sp., *Gi.* sp., *S.* sp.	*Zea mays*	>inoculum potential (soil depth-moisture linked)	natural H_2O gradient	Al-Agely and Reeves (1995) [o]
Three *G.* spp., two *Gi.* spp. [k]	Twenty-three prairie spp.	<spores, <species richness, <species distribution	dry mesic vs. aquatic habitat	Anderson et al. (1984) [o]
One *A.* sp., three *G.* sp., one *Gi.* sp. [l]	Subterranean clover	hyphal survival of –50 MPa	~180	Tommerup and Abbott (1981) [o]
Fine endophytes	*Trifolium subterranean*	infectivity of pot culture	~25–30	Braunberger et al. (1996) [o]
Indigenous	Four hosts [m]	*Δ* col% (±water-retaining polymer in semi-arid habitat)	~210	Wilson et al. (1991)

Table 6 Continued

Fungus species	Host species	Parameter	Length of drought (days)	Reference
Indigenous	*Artemisia tridentata*	<arb%, hyp%, ves%, <hyphal lengths	<730	Trent et al. (1994)[o]
Indigenous	*Elytrigia dasystachym*, *E. trachycaulum*, *Sitanim hystrix*	<hyp%, <ves%, spores	92	White et al. (1992)[o]
Indigenous	*Genista hirsuta*	<col% (21, 32)	28	Lansac et al. (1993)
Indigenous	*Juglans nigra*	>col%	42–84	Ponder (1983)[o]
Indigenous	*Lavandula pedunculata*	<col% (39, 82)	28	Lansac et al. (1993)
Indigenous	*Lythrum salicaria*	>arb%, >hyp%, ves%	natural H_2O gradient	Stevens and Peterson (1996)[o]
Indigenous	*Thymus machtichina*	<col% (23, 73)	28	Lansac et al. (1993)
Indigenous	*Thymus zygis*	<col% (24, 58)	28	Lansac et al. (1993)
Indigenous	*Triticum*	<col% five times per year for 2 years	~150	Ryan and Ash (1996)[o]
Indigenous[n]	*Schizachyrium scoparium*	col%	60	Cerligione et al. (1988)
Indigenous	Pasture and prairie plants	>external hyphal length	~196	Miller et al. (1995)[o]
Indigenous	Prairie and wetland plants	>col%	natural H_2O gradient	Turner and Friese (1998)[o]
Unreported	*Brassica napus*	>col% (5, 2)	25	Mahmood and Iqbal (1982)[o]
Unreported	*Lens esculenta*	>col% (60, 40), >spores	~120	Ishac et al. (1994)
Unreported	*Triticum* sp.	>col%, >number of colonized plants	■	Khrushcheva (1955) (cited in Reid (1979)
Unreported	*Vicia faba*	>col% (64, 41), >spores	~120	Ishac et al. (1994)
■	*Hordeum*, *Triticum*, *Avena*	>col%, >spores	■	Iqbal and Tauqir (1982)[o]

[a] Wastewater irrigation versus no irrigation

[b] *A. laevis*, *G. fasciculatum*, *G. geosporum*, *G. mosseae*, *Gi. calospora*, *Gi. gigantea*, *Gi. heterogama*

[c] Colonization percentages varied with soil temperature and with fertilization. Effect of drought on mycelial, arbuscular and vesicular colonization was more pronounced at higher temperatures, with monocalcium phosphate. Drought effects on colonization were less consistent with hydroxyapatite.

[d] For most severely droughted plants given $Ca(H_2PO_4)\bullet H_2O$, $Ca_5(PO_4)_3OH$ and $FePO_4$, respectively

[e] *G. fasciculatum*, *G. geosporum*, *G. microcarpum*, *G. tenue*

[f] *Stipagrostis sabulicola*, *S. seelyae*, *S. lutescens*, *S. ciliata*, *Cladoraphis spinosa*, *Centropodia glauca*. Colonization percentages were given for species at several sites in 1990 and 1991

[g] *Acacia nilotica*, *Acacia tortilis*, *Azadirachta indica*, *Eucalyptus camaldulensis*, *Prosopis cineraria*, *Tecomella undulata*

[h] *Acacia auriculiformis*, *Albizia lebbeck*, *Gliricidia sepium*, *Leucaena leucocephala*

[i] *A. foveata*, *Gi. albida*, *G. fasciculatum*, *G. geosporum*, *Scl. sinuosa*

[j] *A. scrobiculata*, *G. fasciculatum*, *G. geosporum*, *G. microcarpum*, *G. pustulatum*

[k] *Gi. calospora*, *Gi. gigantea*, *G. caledonium*, *G. fasciculatum*, *G. geosporum*

[l] *A. laevis*, *G. caledonius*, *G. fasciculatus*, *G. monosporus*, *Gi. calospora*

[m] *Acacia tortilis*, *Prosopis juliflora*, *Terinalia brownii*, *T. prunioides*

[n] *G. geosporum*, *G. mosseae*, *S. calospora* and an undescribed *G.* sp. resembling *G. fuegianum*

[o] Drought effects on VAM fungi were the chief focus of these articles

conductance in non-stressed plants are often subtle but have been found to be three times that of P-limited NM controls (e.g. Ruiz-Lozano et al. 1995b).

VAM and NM plants sometimes show different critical points or thresholds of stomatal behavior during drought episodes: e.g. break point or intercept values of water status at which stomata first begin to close or close fully. Leaf Ψ was about 0.2 MPa lower in *Glomus fasciculatus*-colonized wheat plants than in similar-sized NM plants when stomata began to close (Allen and Boosalis 1983), and leaf Ψ at stomatal closure was about 0.7 MPa lower in roses colonized by *Glomus deserticola* or *Glomus intraradices* than in similar-sized NM roses (Augé et al. 1986b). Stomatal conductance in VAM plants has also remained unaffected by declines in available soil moisture longer than in NM plants (e.g. Osundina 1995; Duan et al. 1996).

Stomatal conductance and leaf Ψ are linked functionally: changes in one usually drive changes in the other. Thus, when VAM symbiosis hastens or postpones leaf dehydration, this would naturally be associated with altered stomatal behavior. The rates at which VAM and NM plants dry soil frequently differ and this typically occurs without altering the functional relationship between stomatal conductance and leaf Ψ. In some instances, however, stomatal parameters have been altered by VAM symbiosis without altering leaf hydration (Allen and Boosalis 1983; Stahl and Smith 1984; Allen and Allen 1986; Augé et al. 1986b; Sánchez-Díaz et al. 1990; Osundina 1995). When VAM and NM plants differ in stomatal conductance or transpiration at the same leaf Ψ (when the relationship between stomatal conductance and leaf Ψ has been modified) then the root symbiosis has resulted in a more fundamental change in leaf physiology, changes in intrinsic hydraulic or biochemical properties.

There are presently sufficient published data to allow trends to be identified regarding VAM effects on different hosts by different fungi (Tables 1, 2, 3). The stomatal conductance and transpiration of citrus taxa have usually not been changed by VAM colonization and sorghum has only sometimes been sensitive to VAM colonization. Blue grama, cowpea, lettuce, rose, safflower, soybean and wheat have each shown VAM-induced alterations of stomatal conductance or transpiration in three or more studies. Colonization by *Glomus fasciculatum* and *Glomus deserticola* has usually increased stomatal opening relative to uncolonized plants. Colonization by *Glomus intraradices*, *Glomus etunicatum* and *Glomus mosseae* has increased stomatal conductance or transpiration more often than not.

Investigators often generalize about VAM effects on host water relations, even though they are usually reporting observations on only one or two *Glomus* species. We do not have a good understanding of how VAM effects on stomatal behavior vary among VAM fungal genera or *Glomus* species, but we do know that they can differ (e.g. Stahl and Smith 1984; Dixon et al. 1994; Mathur and Vyas 1995; Ruiz-Lozano et al. 1995a, b). Dixon et al. (1994) reported that stomatal conductance differed both before and during drought among similar-sized *Leucaena leucocephala* colonized by four fungal species. Ruiz-Lozano et al. (1995a, b), comparing the influence of seven *Glomus* species on growth and gas exchange of lettuce plants, found that fungal influence on stomatal opening was closely linked to growth promotion, under both amply watered and droughted conditions. Gas exchange also varied considerably in non-stressed *Ziziphus mauritiana* colonized by five species of four VAM genera (Mathur and Vyas 1995). Association with different fungal partners resulted in a wide range of stomatal conductance and transpiration in both lettuce and *Ziziphus*, with the highest values (in *Glomus deserticola*-colonized lettuce and *Acaulospora morrowea*-colonized *Ziziphus*) about twice the lowest values (*Glomus occultum*-colonized lettuce and *Glomus fasciculatum*-colonized *Ziziphus*) (Mathur and Vyas 1995; Ruiz-Lozano et al. 1995a, b). Shrestha et al. (1995) observed that *Glomus mosseae*- and *Gigaspora ramisporophora*-colonized citrus trees tended to have higher transpiration rates than smaller *Glomus ambisporum*- or *Glomus fasciculatum*-colonized trees. Association with either of two *Glomus microcarpum* isolates allowed *Agropyron smithii* to maintain higher stomatal conductance as soil dried than association with either of two *Glomus macrocarpum* isolates (Stahl and Smith 1984).

Photosynthesis

VAM plants often show higher photosynthetic rates[7] than their experimental NM counterparts, which is consistent with VAM effects on stomatal conductance (Tables 1, 2). Like stomatal conductance and transpiration, photosynthesis is stimulated by VAM symbiosis about as frequently under non-stressed as under drought conditions. As with stomatal conductance, different VAM fungi have different effects on photosynthesis during drought, even when plants are of similar size (e.g. Dixon et al. 1994).

Most comparative studies of photosynthesis in VAM and NM plants report net carbon exchange rates, and a few studies provide more details. Increased photosynthesis in *Bouteloua gracilis* colonized by *Glomus fasciculatum* was related to sizeable reductions in both gas-phase and liquid-phase resistance to CO_2 transport in leaves (Allen et al. 1981). The authors suggested that VAM symbiosis may have increased the number of photosynthetic units. Internal CO_2 concentrations were lower in VAM than in NM *Medicago* plants (Sánchez-Díaz et al. 1990). Photosynthetic storage and export rates have been increased by VAM fungi (Wang et al. 1989). Photosynthesis per unit leaf P concentration was higher in droughted VAM than NM plants (Sánchez-Díaz et al. 1990; Davies et al. 1993). Ruiz-Lozano and Azcón (1995) found that VAM symbiosis with one *Glomus* species increased photosynthetic P-use efficiency relative to NM plants, while another *Glomus* decreased efficiency. This again illustrates the variable influence of mycobionts on host behavior. Koide (1993) has discussed photosynthetic capacity of VAM plants in relation to P nutrition and stomatal behavior.

Leaf hydration

Tissue hydration or water status is typically quantified by measuring Ψ or its components, or water content. Leaf Ψ of non-stressed plants has usually not been affected by VAM symbiosis (e.g. Allen et al. 1981; Allen 1982; Nelsen and Safir 1982a; Levy et al. 1983b; Augé et al. 1986a, 1994; Ramakrishnan et al. 1988b; Drüge and Schönbeck 1992; Osonubi et al. 1992; Davies et al. 1993; Ebel et al. 1994; Osonubi 1994; Goicoechea et al. 1996, 1997a, b, 1998; Bryla and Duniway 1997a, c). On some occasions, leaf Ψ has differed in non-stressed VAM and NM plants (Nelsen and Safir 1982a; Dixon et al. 1994; Gemma et al. 1997).

Because of their frequently different photosynthetic rates, leaves of non-stressed VAM and NM plants might be expected to develop dissimilar symplastic solute pools and consequently different leaf osmotic potentials, even when total leaf Ψ is similar (e.g. Goicoechea et al. 1997b). Lower full turgor osmotic potentials of non-stressed VAM plants have been observed in leaves of alfalfa (Goicoechea et al. 1997b) and rose (e.g. Augé et al. 1986b). However, leaf osmotic potential has generally not differed in VAM and NM plants when water is not limiting (Henderson and Davies 1990; Faber et al. 1991; Augé et al. 1992a, 1995; Davies et al. 1993; Ebel et al. 1996; Bryla and Duniway 1997c), nor has leaf turgor potential (Augé et al. 1992a; Davies et al. 1992, 1993; Bryla and Duniway 1997a, c).

VAM symbiosis has postponed declines in leaf Ψ during drought stress (Huang et al. 1985; Davies et al. 1992;

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[7] Usually quantified as net carbon exchange rate of leaves

Dixon et al. 1994; Subramanian et al. 1995, 1997; El-Tohamy et al. 1999), even at similar bulk soil moisture around VAM and NM roots (Allen and Allen 1986; Augé et al. 1987a for *Glomus deserticola*; Duan et al. 1996; Gemma et al. 1997) or when soil moisture was lower around mycorrhizae (Augé et al. 1987a for *Glomus intraradices*). Leaf Ψ has also been reported to return to control levels more quickly in VAM than NM plants after relief of drought (e.g. Subramanian et al. 1997). In several reports, leaf or shoot Ψ did not differ in VAM and NM plants during drought or during drought recovery (Levy and Krikun 1980; Nelsen and Safir 1982b; Davies et al. 1987, 1993; Graham and Syversten 1987; Ramakrishnan et al. 1988a; Osonubi et al. 1991; Osonubi 1994; Bryla and Duniway 1997c; Ebel et al. 1997; Goicoechea et al. 1997b, 1998), nor was the leaf Ψ/soil Ψ relation altered (e.g. Stahl and Smith 1984). Particularly when root systems were constrained to relatively small soil volumes, leaf Ψ declined more quickly in VAM than in NM plants with exposure to drought, most likely because VAM plants were larger and depleted soil moisture reserves more quickly (e.g. Hardie and Leyton 1981; Sweatt and Davies 1984; Busse and Ellis 1985; Runjin 1989; Osonubi et al. 1991, 1992; Goicoechea et al. 1996, 1997a). One exception was *Acacia auriculiformis*, in which leaf Ψ declined more in VAM than in NM plants, even though VAM plants were smaller (Awotoye et al. 1992).

Leaf osmotic potential may differ in VAM and NM plants during drought (Augé et al. 1986b, 1987a; Goicoechea et al. 1997b), but most investigators observed no VAM effects on leaf osmotic potential of droughted plants (Augé and Stodola 1990; Henderson and Davies 1990; Faber et al. 1991; Augé et al. 1992a; Bryla and Duniway 1997a, c; Goicoechea et al. 1997b) or osmotically stressed plants (Ramakrishnan et al. 1988b; Augé et al. 1992a). Not surprisingly, osmotic potential tends to be higher when total Ψ is higher in leaves of VAM than NM plants during drought, suggesting that VAM plants are not as strained[8] by the drought stress (e.g. Augé et al. 1987a; Davies et al. 1992). When drought-induced active accumulation of solutes (osmotic adjustment, changes in full turgor osmotic potential) has been compared in leaves of VAM and NM plants, VAM plants have sometimes shown more osmotic adjustment (Allen and Boosalis 1983; Augé et al. 1986b) and sometimes not (Davies et al. 1996; Bryla and Duniway 1997a, c, 1998; Goicoechea et al. 1997b). Larger osmotic adjustments in leaves resulted in higher leaf turgors in VAM plants during drought, when total Ψ was similar in leaves of VAM and NM plants (Davies et al. 1993). VAM colonization decreased osmotic potential of rose leaves at full turgor and at the turgor loss point (Augé et al. 1986b). VAM symbiosis did not affect the osmotic potential of xylem sap the one time it was measured (Ebel et al. 1997). Leaf turgor potential has been increased (Augé et al. 1986b; Davies et al. 1992, 1993; Osundina 1995) or not affected (Bryla and Duniway 1997a, c; Goicoechea et al. 1997b) by VAM symbiosis during drought.

Leaf water content or relative water content has been compared much less frequently in VAM and NM plants than has leaf Ψ. VAM symbiosis may postpone declines in leaf relative water content in droughted wheat (Panwar 1993), change shoot water content relationships (Bethlenfalvay et al. 1990), and allow leaves to maintain stomatal opening to lower leaf relative water content (Augé et al. 1986b). As might be expected, when leaf Ψ was unchanged by VAM symbiosis, leaf relative water content was also unchanged (e.g. Henderson and Davies 1990; Augé et al. 1992a, 1995; Davies et al. 1992; Ebel et al. 1996, 1997).

Some investigators have compared symplastic and apoplastic water fractions in leaves of VAM and NM plants, i.e. the amounts of water in the live portion (cytoplasm of cells still bound by membranes) versus the dead portion (xylem, cell walls). Symplastic water fractions were lower in leaves of alfalfa and rose plants after drought when plants were mycorrhizal (Augé et al. 1986b; Goicoechea et al. 1997b).

Root hydration

Root Ψ components and water contents are more difficult to measure than corresponding leaf parameters and root water relations of VAM and NM plants have seldom been compared. Nodule water content was higher in VAM than in NM alfalfa roots exposed to drought (Goicoechea et al. 1996). Symplastic water fractions were increased by VAM symbiosis in droughted rose roots, although root osmotic potential at full turgor and root relative water content at turgor loss were not affected (Augé and Stodola 1990). Symplastic water fractions of non-stressed roots were similar in VAM and NM roses in that study. Root Ψ was similar in roots of non-stressed plants of *Glomus fasciculatum*-colonized and NM *Bouteloua gracilis* (Allen 1982). Root water content was higher in VAM than in NM lettuce during drought (Ruiz-Lozano and Azcón 1995).

Hydraulic conductivity[9] and hyphal water transport

Root hydraulic conductivity is generally not improved by VAM symbiosis in the absence of VAM-induced growth or P effects (for discussion, see Koide 1993). In fact, hydraulic conductivity was lower in VA mycorrhi-

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[8] In the terminology of Levitt (1972, 1980), *strain* refers to a plant response, and *stress* refers to the external pressure stimulating the response

[9] Hydraulic conductance is a measure of the ease with which liquid water can be transported. Root hydraulic conductances normalized on the basis of root length have been referred to as root hydraulic conductivities (Koide et al. 1989). Conductance is the reciprocal of resistance and conductivity is the reciprocal of resistivity

zae than in NM roots when plants of similar size were examined (J.M. Duniway, personal communication, cited by Safir and Nelsen 1981; Levy et al. 1983b; Graham et al. 1987). In studies comparing VAM and NM plants of either dissimilar size or tissue P concentrations, hydraulic conductivity was usually higher in VAM than in NM roots (e.g. Hardie and Leyton 1981; Nelsen and Safir 1982b; Graham and Syvertsen 1984; Cui and Nobel 1992) but not always (Graham and Syvertsen 1985; Graham et al. 1987; Syvertsen and Graham 1990). Andersen et al. (1988) noted that VA mycorrhizae of *Fraxinus* had lower hydraulic conductivity per unit root P concentration than NM roots but similar hydraulic conductivity per unit plant weight. Where reported, specific water uptake rates[10] were not different in VAM and NM roots (Fitter 1988; Bryla and Duniway 1997b, 1998).

Other hydraulic conductances may be affected by VAM symbiosis. Colonization by *Glomus fasciculatum* increased whole plant, soil-to-root and root-to-leaf hydraulic conductances in *Bouteloua* (Allen et al. 1981; Allen 1982) and decreased soil-to-plant hydraulic conductance in *Bromus* (Bildusas et al. 1986) relative to similar-sized NM plants. Non-mycorrhizal soybean plants had lower whole plant and root conductances than larger *Endogone mosseae*-colonized soybeans, while stem-plus-leaf conductances were similar (Safir et al. 1972). VAM infection had no effect on the intrinsic hydraulic properties of the soil/plant system over a wide range of transpiration rates when VAM and NM sunflower plants of equivalent root length were compared (Koide 1985).

VAM hyphae were reported to enhance water uptake in sunflower and cowpea (Faber et al. 1991) and lettuce (Ruiz-Lozano and Azcón 1995) but not in clover or couchgrass (George et al. 1992) or wheat (Tarafdar 1995). Ruiz-Lozano and Azcón (1995) observed that hyphae of *Glomus deserticola* and *Glomus fasciculatum* differed in their influence on water uptake, despite similar intra- and extraradical hyphal extension. When calculated[11] rather than measured, hyphal water transport rates have generally been negligible (Graham and Syvertsen 1984; Fitter 1985; George et al. 1992; Koide 1993). Read and Boyd (1986) suggested that early experiments and computations may have involved unrealistically low numbers of hyphal entry points and that hyphal contributions to water uptake are may be significant.

Soil drying rates and moisture relations

VAM root systems can dry soil more quickly and thoroughly than NM root systems, signified by larger declines in soil water content or soil Ψ[12] over time. In many instances, this is probably because the shoots of the VAM plants were larger (more evaporative leaf surface area) or the root systems of VAM plants were larger or more finely divided (more water absorptive surface area) than those of the NM plants (e.g. Allen et al. 1981; Busse and Ellis 1985; Ellis et al. 1985; Huang et al. 1985; Sharma and Srivastava 1991; Osonubi et al. 1992; Osonubi 1994; Okon et al. 1996). Obviously, when large plants are constrained to the same restricted soil volume as small plants in potted experiments, the typically higher whole-plant transpiration rates of the larger plants will result in the limited soil volume drying more quickly (regardless of mycorrhizal symbiosis). For example, larger VAM soybeans dried soil more quickly than smaller NM plants (Bethlenfalvay et al. 1987) and larger NM soybeans dried soil more quickly than their smaller VAM counterparts (Bethlenfalvay et al. 1990). However, VAM root systems have also dried soils more quickly when VAM and NM plants were of similar size (e.g. Bryla and Duniway 1998).

Measurements of leaf Ψ near the end of a natural or growth-room dark period ("predawn leaf Ψ") are considered estimates of bulk rhizosphere Ψ, because Ψ has presumably equilibrated during the night within the non-transpiring plant and between roots and their surrounding soil. Predawn leaf Ψ did not differ between well-watered or droughted VAM and NM sour orange or Carrizo citrange (Graham et al. 1987) or rose (Henderson and Davies 1990). Predawn leaf Ψ was lower in VAM rough lemon (Levy et al. 1983b) and VAM soybean (Busse and Ellis 1985) than in NM plants, in accord with greater soil water extraction by VAM plants in those studies.

When comparing VAM and NM plants of similar leaf areas, soil drying rates would be expected to be higher in VAM plants if they are transpiring at higher rates. More rapid foliar water losses cause more rapid soil water losses (e.g. Faber et al. 1991). Because soil and plant water relations are interdependent, it may be difficult to isolate and compare single parameters in VAM and NM plants during a drought episode and interpret findings. In some split-root experiments, where leaf and soil water

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[10] ml water per cm root length per day

[11] Predicted rates of water uptake by hyphae have been calculated on the basis of hyphal entry points per unit of root length, hyphal cross-sectional areas and water potential gradients

[12] Both soil water content and Ψ (expressed as matric potential when the contribution of soil solutes to Ψ is not measured) are used to quantify soil moistness. Soil water content is the amount of water in a soil volume or mass. Soil Ψ is a measure of the free energy of soil water; it is a thermodynamic gauge of the availability of soil water to plant roots, how freely soil water can be expected to move into roots. Values for soil water content depend on soil type, whereas values for soil Ψ can be compared across soil types. The same holds true when considering Ψ and water content for plant tissues. Soil water content and soil Ψ are not linearly related. As soil water content declines when a soil dries, soil Ψ typically stays very high (near 0 MPa) and does not begin to decline appreciably until the soil loses half or more of the water it held at field capacity. The "breakpoint" varies with soil type. Once soil Ψ does begin to decline, it does so quite rapidly, i.e. relatively small decreases in water content then translate into relatively large decreases in soil Ψ. It is a negative exponential relationship (for examples of such curves, termed soil moisture characteristic curves or moisture release plots, see Kramer and Boyer 1995)

loss have been purposefully uncoupled, soils still dried more quickly with VAM than with similar-sized NM root systems (Ebel et al. 1994, 1996). This is an interesting experimental condition: one or more root compartments are watered while others remain unwatered, allowing measurement of soil drying rates in unwatered compartments of plants whose transpiration does not decline with soil drying (as inevitably happens when entire root systems are allowed to dry). In this situation, one in which the plant does not rely on water supply from the drying compartment or pot because the watered compartment satisfies shoot water requirements, VAM root systems dried soil more quickly than NM root systems of the same size, irrespective of whether about one-quarter, one-half or three-quarters of the root system remained unwatered (Ebel et al. 1994). However, VAM root systems were also reported to dry soil more slowly than NM root systems in split-pot experiments (Augé et al. 1994, 1995) or single pot experiments (Subramanian et al. 1997), even though the VAM plants were larger than NM plants in the latter work.

In about 75% of studies, VAM plants were observed to deplete soil water more thoroughly than NM plants before achieving a similar shoot response, a VAM effect only sometimes associated with growth enhancements. VAM legumes developed lower soil Ψ before wilting (Hardie and Leyton 1981) or at the permanent wilting point (Bethlenfalvay et al. 1988a, b) than NM plants. Soil Ψ at stomatal closure was 0.3 to 0.6 MPa lower in VAM roses than in similar-sized NM roses (Augé et al. 1986b). Soils of VAM cowpeas lost more water than soils of similar-sized NM plants before evoking similar stomatal conductance, shoot Ψ, transpiration and abscisic acid (ABA) concentration near stomatal closure (Duan et al. 1996). VAM sorghum was also able to maintain leaf Ψ to lower soil Ψ than similar-sized NM plants (Osonubi 1994). In contrast, VAM maize and sorghum wilted more quickly but at the same soil water content as NM plants (Simpson and Daft 1990) and association with *Glomus etunicatum* did not affect soil moistures at which wheat or safflower wilted (Bryla and Duniway 1997b).

Growth and nutrient uptake during drought

VAM symbiosis has usually increased host growth rates during drought by affecting nutrient acquisition and possibly hydration (Tables 1, 2, 3). VAM symbiosis has also typically increased water use efficiency[13] and colonization by different fungi has affected water use efficiency differently (Simpson and Daft 1990).

As soils first begin drying, shoot growth can be inhibited before any leaf dehydration occurs through a root-to-shoot non-hydraulic signaling mechanism (Davies and Zhang 1991; Davies et al. 1994; Thompson et al. 1997). In experiments designed to detect the influence of VAM symbiosis on such effects, growth of VAM plants was consistently less inhibited by non-hydraulic signals of soil drying than growth of NM plants (Augé et al. 1994, 1995; Ebel et al. 1994, 1996). The VAM effect was sometimes related to direct VAM influences on plant size and/or P fertilization (Ebel et al. 1996) but more often occurred independently of nutritional effects (Augé et al. 1994, 1995; Ebel et al. 1994). Plant and soil characters commonly affected by VAM symbioses can also markedly affect the degree to which leaf growth is inhibited by these non-hydraulic drought signals (Augé et al. 1995).

VAM effects on host growth during drought are often related to improved P acquisition (Table 1), as the availability of P in soils is reduced by soil drying (e.g. Viets 1972). Many investigators have reported different concentrations of elements other than P in organs of VAM and NM plants experimentally subjected to drought or naturally growing in arid conditions (Tables 4, 5). Some trends emerge from a composite view of the broad range of soils, fertilization and drought techniques used in the various studies. Copper and zinc concentrations were each higher in leaves of droughted VAM than NM plants in almost half of the studies (Tables 4, 5) (also noted in amply watered conditions: for reviews, see George et al. 1994; Marschner and Dell 1994; Sharma et al. 1994). Manganese concentrations were often lower in leaves of VAM than NM plants (Bethlenfalvay and Franson 1989; Lambert and Weidensaul 1991) and this also appears to occur often during drought. VAM plants also appear to absorb less boron than NM plants during drought. Shoot concentrations of nitrogen, potassium, calcium, magnesium, iron, sodium and molybdenum appear to be affected little by VAM symbiosis in drought conditions.

Metabolic effects during drought

When water relations measurements indicate that VAM plants respond more quickly or more slowly than NM plants to the onset of drought, this should be reflected in plant metabolism. A plant more strained by water stress would be expected to be more metabolically perturbed. Mycorrhizal drought studies have usually included one-time measurements of biochemical parameters and metabolic events. As in the case of stomatal conductance, a clear interpretation of data may be possible only by tracking plant behavior several times over the course of drought or recovery episodes. Some trends, however, do emerge from the literature on the subject.

Schellenbaum et al. (1998) observed that VAM symbiosis significantly affected tobacco plants during drought in terms of soluble carbohydrate accumulation and partitioning. Their VAM plants accumulated less glucose and fructose in leaves and roots than NM plants in drought conditions. Similar findings were reported for rose and pepper after drought (Augé et al. 1987a, 1992b;

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[13] The amount of water used per unit weight of plant produced or carbon assimilated

Davies et al. 1993). Schellenbaum et al. (1998) suggested that the fungus is a strong competitor for root-allocated carbon under conditions limiting photosynthesis. They also noted that the fungal disaccharide trehalose greatly increased in mycorrhizae during drought. It is also possible that higher sugar concentrations in NM than VAM tissues result when NM plants suffer greater drought strain. Cell growth is more sensitive to water stress than CO_2 assimilation and sugar accumulation (Hsiao 1973), so transient sugar build-ups could be observed in stressed leaves in which growth and translocation had declined more than photosynthetic rates.

Alternately, higher foliar concentrations of soluble sugars in VAM than in NM plants after drought, suggesting maintenance of greater photosynthetic capacity, has been attributed to greater drought resistance of VAM maize plants (Subramanian and Charest 1995; Subramanian et al. 1997). This interpretation was supported by the fact that VAM plants also showed less stress-induced accumulation of amino acids than NM plants and were able to sustain more normal nitrogen metabolism. Maintenance of greater photosynthetic capacity during drought in mycorrhizal plants has also been indicated by higher starch levels in leaves of VAM than in NM plants (Augé et al. 1987a; Davies et al. 1993). Again, VAM effects on single parameters must usually be assessed in association with other data from each study and the particular circumstances.

Concentrations of amino and imino acids in droughted plants have been reported to increase (Subramanian and Charest 1995; Schellenbaum et al. 1998) or decrease (Augé et al. 1992b; Subramanian and Charest 1995) with VAM symbiosis. Viewed in conjunction with other indicators in a study, investigators have usually suggested that the differences between VAM and NM plants reflect greater drought resistance in the VAM plants[14]. Lower accumulation of amino acids may indicate that plants more successfully avoided drought and so had less need to osmotically adjust symplasm or osmoprotect enzymes, or were showing less strain or injury. This interpretation would be supported if soil and/or leaf Ψ were correspondingly higher (less exposure to stress) in the VAM population. Greater accumulation of amino acids might also indicate plants more capably osmotically adjusted to the water stress. This interpretation would be supported if plants showing greater amino acid concentrations exhibited more normal (less strained) behavior at similar soil Ψ or water content than NM plants.

Levels of proline and other nitrogenous compounds have been compared in VAM and NM plants after drought, as a measure of acclimative capacity or injury[15]. Leaves of VAM plants have had lower concentrations of proline than NM plants following drought stress, attributable to greater drought resistance of VAM plants, i.e. less injury (e.g. Ramakrishnan 1988a; Müller and Höfner 1991; Ruiz-Lozano and Azcón 1997). Leaves of VAM plants also have had higher concentrations of proline than NM plants following drought stress, which was also attributed by the authors to greater drought resistance of VAM plants, i.e. more effective osmotic adjustment (Ruiz-Lozano et al. 1995b; Azcón et al. 1996). Higher free polyamine concentrations in leaves of VAM relative to NM alfalfa plants were attributed to enhanced resilience to drought stress (Goicoechea et al. 1998). Leaves of droughted VAM plants contained less γ-amino-n-butyric acid (Gemma et al. 1997) and trigonelline (von Reichenbach and Schönbeck 1995) than leaves of droughted NM plants; both compounds are considered to be indicators of drought injury.

The activities of several enzymes have been compared in VAM and NM plants during drought and found to be typically higher in VAM plants. Nitrate reductase activity in leaves and roots was increased by VAM symbiosis in numerous studies (Panwar 1992, 1993; Azcón et al. 1996; Ruiz-Lozano and Azcón 1996; Azcón and Tobar 1998; Subramanian and Charest 1998). VAM lettuce had higher root and shoot superoxide dismutase activity than NM lettuce (Ruiz-Lozano et al. 1996b) and VAM alfalfa higher acid phosphatase activity than NM alfalfa (Goicoechea et al. 1996). Glutamate-ammonia ligase activity was higher in VAM than in NM maize (Subramanian and Charest 1998). VAM symbiosis increased glutamine and glutamate synthase activity in leaves (Panwar 1992; Subramanian and Charest 1998) and increased nodule activity in soybean (Peña et al. 1988; Sánchez-Díaz et al. 1990). Acid invertase was lower and trehalase activity much higher in maize mycorrhizae than in NM roots during drought (Schellenbaum et al. 1998). Where reported, total protein concentrations have been consistently higher in VAM than NM plants during drought, considered by the authors to be a beneficial VAM effect (Subramanian and Charest 1995, 1998; Ruiz-Lozano et al. 1996b).

During drought, concentrations of ABA in xylem sap were reported to be lower in VAM than in NM plants (Duan et al. 1996) and lower in leaves and roots of VAM than in NM plants (Goicoechea et al. 1997a), suggesting that VAM plants were less strained. Cytokinin concentrations were similar in droughted VAM and NM plants, in leaves, roots and xylem sap (Goicoechea et al. 1995, 1996, 1997a; Duan et al. 1996).

Chlorophyll concentrations have often been higher in leaves of amply watered VAM than NM plants (e.g. Nemec and Vu 1990; Panwar 1991, Rao and Rao 1993; Ezz and Nawar 1994; Mathur and Vyas 1995; Bavaresco and Fogher 1996; Clark and Zeto 1996; Gemma et al. 1998). After drought, chlorophyll concentrations have also usually been higher in VAM than NM plants (e.g. Allen et al. 1981; Augé et al. 1987a; Davies et al. 1993; Mathur and Vyas 1995; Gemma et al. 1997). Higher

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[14] These are probably legitimate interpretations, but investigators seem to strain sometimes to paint a picture in which mycorrhizal symbiosis imparts greater stress resistance to host plants

[15] Proline enhancement during drought stress may be a beneficial, acclimative response, possibly related to membrane integrity (Larher et al. 1993; Van Rensburg et al. 1993), cytosolic enzymes and protein stability (Larher et al. 1993) and control of cellular pH (Venekamp 1989). Alternately, proline increases may be incidental changes associated with tissue injury (Hanson 1980; Radin 1983)

chlorophyll in VAM plants has sometimes been associated with higher rates of photosynthesis (e.g. Allen et al. 1981; Mathur and Vyas 1995).

Morphological effects during drought

VAM effects on plant water relations and metabolism during drought have been associated with morphological and phenological effects. VAM *Acacia* (Osonubi et al. 1992) and rose (Henderson and Davies 1990) showed more leaf abscission during drought than NM plants, while VAM wheat showed less leaf drop (Ellis et al. 1985) and less leaf necrosis (Bryla and Duniway 1997c). VAM maize had relatively more green leaf area than NM maize after drought (Subramanian et al. 1995) and VAM symbiosis delayed leaf senescence in droughted alfalfa (Goicoechea et al. 1997a). VAM soybeans had less drought-induced pod abortion than NM soybeans (Busse and Ellis 1985). Leaf movements were greater in VAM than in NM *Leucaena* (Huang et al. 1985). VAM rose leaves had less epicuticular wax and lower cuticle weight than NM leaves (Henderson and Davies 1990). VAM symbiosis both postponed (Mosse and Hayman 1971; Fitter 1988; Davies et al. 1992) and hastened (Hardie and Leyton 1981; Levy et al. 1983b; Sweatt and Davies 1984) wilting of leaves, depending on relative sizes of VAM and NM plants and the size of the soil water reservoir available to each. VAM plants have been reported to recover more quickly from wilting than NM plants upon relief of drought (e.g. Gemma et al. 1997).

When VAM and NM plants with similar leaf areas have been compared, VAM symbiosis has generally not affected stomatal density (number of stomata per leaf area: Allen et al. 1981; Henderson and Davies 1990) or guard cell size (e.g. Allen et al. 1981; Augé et al. 1986a; Henderson and Davies 1990; Drüge and Schönbeck 1992), even when transpiration or stomatal conductance differed.

Mechanisms

The ideas of early workers and reviewers about possible mechanisms of VAM influence are still quite applicable (e.g. Safir et al. 1972; Reid 1979). Perhaps because of the difficulty in consistently evoking or detecting VAM effects on host water balance, we have not improved our mechanistic understanding much in the intervening years. Further, in water relations work, cause and effect can be difficult to distinguish[16], which adds some ambiguity and overlap to the following discussion.

Mechanisms related to plant size

The best understood “mechanism” of VAM influence on host water balance involves VAM effects on plant size. The size of a plant can affect its water relations and drought responses and VAM symbiosis often affects plant size. Enhanced P acquisition is the most dramatic means by which VAM fungi affect overall plant biomass, but VAM effects on carbon and nitrogen relations and possibly other aspects of host biochemistry can also influence host size. VAM symbiosis also frequently changes the relative allocation of biomass within the plant. Both overall plant size and within-plant relationships, such as root-to-shoot ratios, can influence plant behavior, particularly when soil water becomes limiting.

Total biomass

Other things being equal, more water usually moves in the soil-plant-air continuum per unit time through large plants than small plants. When VAM plants have different soil drying or gas exchange rates than smaller NM plants, this is often similar to NM plants having different soil drying or gas exchange rates than smaller NM plants. VAM-induced changes in total plant size probably affect plant water relations and drought responses mostly through effects on tissue hydration: how quickly tissues lose water and how quickly they can replace it. Obviously, whole-plant transpiration rates will be higher in large than in small plants, even when transpiration rates per unit leaf area are equal. VAM plants constrained to the same soil volumes as smaller NM plants can thus be expected to deplete the available soil water more quickly than NM plants, eventually resulting in relatively lower tissue hydration and slowed foliar gas exchange in VAM plants. In experiments comparing VAM plants to smaller NM plants in relatively unrestricted soil volumes, e.g. experiments in the field or in large, non-rootbound pots, the reverse may occur. Drought-induced tissue dehydration may be allayed in VAM plants having deeper or more extensive root systems.

Within-plant size relationships

VAM colonization can change specific root length, root architecture and root/shoot ratio (e.g. Berta et al. 1993; Espeleta et al. 1999). Consequently, even in VAM and NM plants having similar shoot dry weights and leaf areas, differing ratios of root length/leaf area might alter shoot response to soil drying. When a relatively larger, more finely divided or more efficient root system improves access to soil water and enhances leaf hydration, the cascade of associated responses is likely to be affected: biophysical responses such as stomatal conductance, transpiration and to some extent photosynthesis, and biochemical responses such as compatible and total solute accumulation, enzyme activities, etc.

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[16] For instance, it is often assumed that leaf Ψ regulates stomatal conductance and rates of gas exchange. Yet in some situations or in some species, notably isohydric species (Meinzer and Grantz 1990; Jones 1998; Tardieu and Simonneau 1998), stomata may regulate leaf Ψ, opening and closing to maintain relatively constant leaf hydration (Jones 1990a, b)

It is often taken for granted that the root mass available for water absorption and supply to any given leaf area probably affects the rate of water loss by that leaf area when soil moisture is limiting. Examination of stomatal responses of the cowpea cultivar used by Augé et al. (1992a), however, revealed no dependence of stomatal conductance upon leaf area/root mass ratio. Others have also failed to detect a relationship between shoot/root ratio and rate of water loss per unit leaf area (Eavis and Taylor 1979), although such relationships can occur (Meinzer et al. 1991).

It has been suggested that extraradical hyphae may enhance the ratio of below-ground absorptive surface to leaf surface. Significant water uptake and transport by hyphae have been observed or computed in instances in which the VAM symbiosis has also affected stomatal behavior (Allen 1982; Faber et al. 1991; Ruiz-Lozano and Azcón 1995). When VAM-induced changes in stomatal conductance or transpiration of the host have been absent, hyphal contributions to water uptake have been negligible (Graham and Syvertsen 1984; Fitter 1985; George et al. 1992; Koide 1993; Tarafdar 1995).

Not all VAM-induced developmental changes that might affect water balance need do so by affecting tissue hydration. For instance, root/shoot ratios can affect stomatal conductance directly, even in amply watered soils in the absence of effects on leaf hydration (Meinzer et al. 1991). Within-plant size relationships may also influence stomatal behavior by affecting hormone relations and concentrations of xylem constituents (discussed below).

VAM symbiosis may alter host water relations wherever plant size and development rates affect water relations. Although simple and perhaps physiologically prosaic, this influence probably has profound ecological and agricultural consequences, by affecting plant establishment, vigor, productivity and survival in water-limiting conditions.

Mechanisms unrelated to plant size

Nutritional

Regardless of effects on overall plant or organ size, P concentrations themselves may also affect host water balance. For instance, stomatal conductance can be influenced by P starvation (Atkinson and Davison 1972; Bradbury and Malcolm 1977; Nagarajah and Ratnasuriya 1978; Radin and Eidenbach 1984). Koide (1993) suggested that increased stomatal conductance and transpiration in VAM plants may be due to P-mediated improvement in photosynthetic capacity. P concentrations in leaves may affect stomatal response to environmental perturbations, perhaps by affecting the energetics involved in guard cell osmotic parameters or wall stiffening governing stomatal movements (Weyers and Meidner 1990). ABA can exert a controlling influence on stomatal behavior and the amount of P in leaves can affect stomatal sensitivity to ABA (Radin 1984; Mansfield et al. 1990). There is apparently a close connection between the nutritional status of plants and the effectiveness of ABA as a root-to-shoot signal of soil drying (Schurr et al. 1992).

We commonly talk about similar nutrition when describing how we produce similar VAM and NM controls, when what we really mean is similar P nutrition. VAM symbiosis can alter uptake rates of nutrients other than P, nutrients that might alter gas exchange. Leaf nitrogen concentrations, for example, can affect stomatal behavior (e.g. Radin and Parker 1979; Radin 1990) and VAM symbiosis can modify N uptake and tissue concentrations (e.g. Azcón et al. 1996; for review, see Smith and Read 1997). Potassium and calcium are integrally involved in the physiology of stomatal opening and closing (Mansfield et al. 1990; Weyers and Meidner 1990) and VAM symbiosis may affect leaf concentrations of both (Tables 4, 5).

VAM influences on plant water balance and stomatal behavior might also occur via the influence of the symbiosis on the carbon dynamics of host leaves, apart from carbon-related VAM effects on plant size. Photosynthesis in VAM plants is probably at least partially sink-regulated and stimulated by mycorrhizal roots (e.g. Wright et al. 1998a, b). It is commonly suggested that 5–20% of all carbon assimilated by the VAM plant is eventually partitioned into fungal structures (e.g. Pang and Paul 1980; Kucey and Paul 1982; Snellgrove et al. 1982; Koch and Johnson 1984; Harris et al. 1985; Wang et al. 1989). VAM fungi, by requiring carbon assimilates and thus increasing the sink strength of root systems, may increase net movement of carbon out of leaves. If photosynthetic rates are not accelerated to meet the higher demand, this could result in constitutively lower carbon concentrations in leaf mesophyll. Stomatal opening is stimulated by lowered internal CO_2 concentrations and/or pools of carbon-fixing substrates (Mansfield et al. 1981; Jarvis and Davies 1998). VAM effects on leaf carbon concentrations, therefore, could directly affect stomatal behavior and plant water balance. VAM symbiosis, carbon economy and photosynthesis have been discussed by Eissenstat et al. (1993), Koide (1993), Graham and Eissenstat (1998), Staddon (1998), Wright et al. (1998a, b), and Douds and Pfeffer (2000).

Non-nutritional

It might be argued that a nutritional influence of VAM symbiosis on host water balance can never really be excluded from any experiment with complete confidence, given the integral effect of VAM fungi on P acquisition and plant growth. As often noted (e.g. Bethlenfalvay et al. 1988a) and demonstrated (e.g. Faber et al. 1991), P supplementation for producing proper controls is a conscious compromise, as P-supplemented NM plants do not conform to the desired criteria of root and leaf compatibility with VAM plants. It is very difficult, perhaps innately impossible with some host species, to produce

VAM and NM plants similar in every respect that might account for and control nutritional or size effects on host water relations.

Nonetheless, many experimenters who produced VAM and NM plants of similar size and with physiologically comparable P concentrations have still reported VAM-induced changes in host water relations or drought responses (Table 2). Almost half of the instances of VAM-induced increase in stomatal conductance or transpiration have involved similar-sized and nourished VAM and NM plants (Tables 1, 2). Moreover, in some VAM studies, P fertilization and leaf P concentration have been shown to have no effect on transpiration or the other leaf water relation parameters under study, and yet VAM and NM plants have differed in these parameters (e.g. Augé et al. 1987a; Augé 1989). Still others have observed higher rates of gas exchange by leaves of VAM plants, even when these leaves had significantly lower P concentrations than those from NM controls (e.g. Brown and Bethlenfalvay 1987). Larger plants, or plants having leaves with higher P concentration, do not always show higher gas exchange parameters than smaller plants or plants with lower P concentrations. For example, amply watered VAM *Bromus inermis* plants had higher photosynthetic rates than NM plants, even though the VAM plants were smaller (Bildusas et al. 1986). Amply watered *Glomus deserticola*-colonized rose plants, fed less P and having lower leaf and root P concentrations, had higher stomatal conductances than *Glomus intraradices*-colonized roses fed more P and with higher leaf and root P concentrations (Augé et al. 1986a). A strictly nutritional or size mechanism of VAM influence on host water balance does not appear to explain many of the published data.

Rates of water absorption and soil drying

As noted above, VAM effects on host gas exchange parameters (stomatal conductance, transpiration and photosynthesis) are probably often related to VAM effects on leaf hydration. When shoot size and nutritional effects are discounted, VAM colonization could affect leaf hydration by altering rates of water uptake and rates at which soil dehydrates.

Water uptake by entire root systems is determined by the amount of roots, the distribution of roots, and the rate of absorption per unit root. When total biomass is similar in VAM and NM root systems, differences in root distribution or specific water uptake rates may result in differing rates of water absorption.

Root systems explore soils by a combination of two processes: downward penetration of main vertical axes and proliferation of roots at any given depth by production of branches (Klepper 1990). Root diameter also affects water extraction from soils (Hamblin 1985). We know that VAM symbiosis can affect root branching and diameter, e.g. increased branching or fineness (Price et al. 1989; Kothari et al. 1990) and decreased root branching (Hetrick et al. 1991), as well as root length density, without affecting total root biomass.

Where reported, water uptake rates per unit root length (specific water uptake rates) did not differ between VAM and NM plants (Fitter 1988; Bryla and Duniway 1997b, 1998). In those studies, gas exchange and water balance were generally not affected by VAM symbiosis. Measurements of specific water uptake rates have not been included in studies reporting VAM-induced alterations of soil drying rate, leaf hydration or stomatal behavior.

Water absorption from soil to root has been modeled using an analogy to Ohm's law:

$$\text{Absorption} = \frac{\left(\Psi_{\text{soil}} - \Psi_{\text{root surface}}\right)}{R_{\text{soil}}} = \frac{\left(\Psi_{\text{root surface}} - \Psi_{\text{root xylem}}\right)}{R_{\text{root}}}$$

where R is the resistance to water movement and the subscripts soil, root surface and root xylem indicate positions in the soil-root system (e.g. Hamblin 1985; Klepper 1990; Kramer and Boyer 1995). Thus, the numerous factors affecting water absorption per unit root length can be classified into two groups: those that affect the resistance (conductance) to water movement through the soil and roots and those that affect the driving force or gradient in Ψ from soil to root.

Hydraulic conductances

Total conductance or resistance to liquid water flow has been divided into sequential steps: from the bulk soil to the soil near the root surface (pararhizal zone), across the soil-root interface (perirhizal zone), across the cortex to the xylem (radial), up the root xylem to the stem (axial or longitudinal), and up the shoot xylem to the leaf surface (Hamblin 1985). VAM symbiosis could conceivably affect any of these steps.

Resistance to water flow in root systems often accounts for the majority of the resistance to water flow through the plant (Boyer 1971; Black 1979; Nobel 1991). For years, investigators have suspected that root colonization by VAM fungi affects radial or axial resistance to water flow in roots (Safir et al. 1972; Reid 1979). As noted by Sands et al. (1982), if VAM colonization stimulates an increase in the total surface area of roots and fungus, then the conductance of the whole root system is increased[17]. Root resistances are not necessarily a constant, as implied in the Ohm's law model, but instead may decrease with increasing flow rates (Aston and Lawlor 1979; Meyer and Ritchie 1980) and even oscillate with stomatal oscillations (Kramer and Boyer 1995). Hence, whenever transpiration differs in VAM and NM plants, root resistances to water flow may also differ. Total plant resistance commonly increases as a

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[17] Some of the possible VAM influences mentioned in this section are at least partially related to plant size. I included them here so as to treat mechanisms related to hydraulic resistances and soil water relations in one place. I have noted where VAM influences may be linked to size effects

plant grows, which may reflect, in part, the increasing proportion of the root system that is suberized and nonabsorbing (Hamblin 1985). VAM symbiosis may, therefore, affect root system resistance through effects on plant growth and development. There are several other ways in which colonization of roots by VAM fungi might affect root axial or radial resistances.

Axial resistance is the resistance to flow in the xylem and it depends on the radius of the xylem, obstructions to xylary flow (e.g. tyloses, cavitation), viscosity of xylem sap and length of the root. Axial resistances are considered to be small, at least under most agronomic situations, but can become significant where the number or diameter of xylem vessels is altered or where anatomical restrictions occur (Klepper 1990). VAM symbioses can influence the size and quantity of stele tissue in roots (Daft and Okusanya 1973; Berta et al. 1990; Fusconi et al. 1994; Miller et al. 1997), which could alter axial resistance to water flow. Axial resistance can increase with root age (e.g. Ponsana 1975) and so could be affected by VAM symbiosis where the symbiosis changes developmental or turnover rates. Cavitation in root xylem can increase axial resistance (Byrne et al. 1977), so VAM symbiosis may affect axial resistance if cavitation is reduced in situations where VAM plants maintain more favorable water relations than NM plants under similar soil water deficit (e.g. Duan et al. 1996; Goicoechea et al. 1997a). Tyloses that block xylem vessels may preclude participation of those vessels in conduction; VAM effects on tyloses remain unstudied. Pressure differences across xylem walls can change vessel diameters (Greacen et al. 1976), so it is conceivable (but untested) that VAM fungi could cause at least transient changes in root axial resistance by modifying root turgor (e.g. Augé and Stodola 1990) and consequent pressure-induced changes in vessel diameter.

Radial root resistance to water flow arises because water, which may cross root tissues from epidermis to xylem in either cell walls (apoplast) or cytoplasm (symplast) up to the endodermis, is then forced to pass largely through cell membranes at the endodermal layer (Klepper 1990; Kramer and Boyer 1995). Transpiration rates can affect water flow through this less permeable part of the root system (Klepper 1990), so VAM effects on transpiration could affect radial resistance in this way. The relative abundance of newly expanded permeable root length available for uptake is a strong determinant of radial resistance (Klepper 1990). VAM effects on root development, architecture and fineness (e.g. Price et al. 1989; Kothari et al. 1990; Atkinson et al. 1994) would, thereby, likely affect the abundance of newly expanded permeable root lengths and thus radial resistance. VAM symbiosis can affect shoot Ψ (Table 2) and shoot Ψ can actually affect the presence of highly permeable new roots, through effects on root elongation rate (Bunce 1978). Root dehydration can also have a great impact on radial resistance to water flow (e.g. Kramer 1950; Nobel and Sanderson 1984) and, therefore, VAM symbiosis probably affects radial root resistance in those instances in which hydration differs in mycorrhizae and NM roots. Soil O_2 concentrations also affect root radial conductances (Holder and Brown 1980). Thus VAM symbiosis might affect radial conductances to water flow through the control the symbiosis exerts on soil microbes and soil aggregation and hence soil O_2. VAM effects on root conductances mediated by VAM effects on transpiration, root hydration or soil aeration would be indirect but nonetheless functionally significant.

Perirhizal resistances are of two general types: a draw-down resistance, diurnally imposed by the rapid loss of water from the soil immediately adjacent to the root, and a contact resistance, which increases as the surface of the root has less contact with rhizosphere water (Tinker 1976; Klepper 1990). Draw-down resistances result from drought-induced decreases in hydraulic conductivity of soil. When roots extract water rapidly from the adjacent soil, the rate of replacement of that water from bulk soil at a distance from the root depends on the conductivity of the rhizosphere soil for water. Significant draw-down resistances can develop when root length density is low (Cowan 1965) and VAM symbioses might reduce these resistances in those instances where they increase root length densities or root fineness. VAM fungi also likely affect rhizosphere conductivity through their effects on soil structure. Contact resistance increases as water retreats from large pores into smaller and smaller capillary areas in the soil and decreases the amount of root length actually wetted (Herkelrath et al. 1977). Root and soil shrinkage creates gaps between the root and the soil, which can decrease water absorption (e.g. Nobel and Cui 1992). Root hairs can help prevent air gaps at the soil-root interface, as they grow into very small pores and effectively "glue" themselves to soil particles with exuded mucilages (Klepper 1990). As has often been suggested (e.g. Reid 1979; Fitter 1985), it is easy to imagine that VAM soil hyphae serve this same function, perhaps even more effectively than root hairs because most hyphae can enter finer pores than can root hairs (Tisdall 1991). Those fungal species forming extensive extraradical mycelia or exuding copious amounts of glyco-proteins (Wright and Upadhyaya 1998; Wright et al. 1998) may especially function in this way.

Soil water relations

Whereas the water relations of VAM plants have been studied often, virtually nothing is known about the comparative water relations of soils colonized or uncolonized by VAM fungi. Soil Ψ and matric potential in mycorrhizal systems have been measured only in reference to host plant behavior, as a means of quantifying drought treatments imposed on plants or interpreting plant drought responses (e.g. Duan et al. 1996; Stahl et al. 1998) or characterizing rates at which root systems of VAM and nonmycorrhizal plants extract water from soils (e.g. Augé et al. 1994, 1995).

The relationship between soil water content and soil Ψ or matric potential has been termed the soil moisture characteristic, also called the moisture release plot or water retention curve (Klute 1986). It describes how the free energy of soil water changes as a soil dries and it is one of the material properties that most completely describes soil water relations (Hamblin 1985). The soil moisture characteristic is affected by soil structure and, therefore, is probably affected by VAM symbiosis through effects on soil structure. VAM hyphae grow into the soil matrix to create the skeletal structure holding primary soil particles together. They create conditions conducive to formation of microaggregates and they enmesh and stabilize microaggregates and small macroaggregates into macroaggregate structures (Gupta and Germida 1988; Miller and Jastrow 1990, 1992, 1994; Oades and Waters 1991; Tisdall 1991). Aggregate stability is correlated with root biomass and root length density and so VAM symbioses also indirectly affect soil structure when they stimulate root growth (Thomas et al. 1986).

We have demonstrated that colonization of a soil by *Glomus intraradices* for 7 months changed both the soil structure and its moisture characteristic curve, relative to non-mycorrhizal soils having similar root densities (Augé et al. 2001a). Well-structured soils contain more available water than poorly structured soils (e.g. Greacen and Williams 1983) and reductions in aggregate stability have been correlated with reduced soil water contents at particular soil Ψ (e.g. Fahad et al. 1982). Perhaps higher soil water content in VAM versus non-mycorrhizal soils at a particular low soil Ψ might explain how VAM plants sometimes wilted at lower soil Ψ (Hardie and Leyton 1981), maintained turgor to lower soil Ψ (Augé et al. 1986b), developed lower soil Ψ at the permanent wilting point (Bethlenfalvay et al. 1988a, b) or maintained higher shoot water status at a low soil water content (Duan et al. 1996) than NM plants. Dakessian et al. (1986), Bethlenfalvay et al. (1988b) and Franson et al. (1991) have provided evidence that better growth of VAM plants in drying soils may be related to improved exploitation of bound water, providing access to soil water below the permanent wilting Ψ of NM plants. These and other authors (e.g. Reid 1979) have suggested that VAM-mediated uptake of soil water of low Ψ is analogous to the uptake of P, where tapping supplies not available to the non-mycorrhizal plant results in a positive growth response.

Soil-root water potential gradients

We would expect stomatal conductance to differ between two groups of plants when soil moisture differed between them. Yet differences in stomatal conductance between VAM and NM plants have been reported even when the same amount of water was available to each (e.g. Augé et al. 1992a; Osundina 1995; Duan et al. 1996). As suggested by Hardie and Leyton (1981) and noted by Gupta (1991), even at similar bulk soil Ψ or bulk water content, soil Ψ could be higher in the rhizosphere of VAM plants if mycorrhizae more effectively ramify and dry out a particular volume of soil than do NM roots. Measurements indicating similar bulk soil Ψ or water content in VAM versus NM soils would not expose the possibility that, during a drying episode, soil may be drier around NM than VAM roots but wetter elsewhere in the NM than in the VAM soil volume. The untested but likely possibility of higher pararhizal or bulk conductivity of mycorrhizal soils would contribute further to relatively higher rhizosphere Ψ around VAM roots. If this does occur, VAM plants might also be expected to experience less of the commonly observed lag time between transpiration and absorption (Kramer 1937), but this remains unstudied.

Substantial hyphal contributions to water uptake and/or increased water uptake related to mycorrhizal changes in root morphology or soil structure could allow VAM plants in *drying* soil to sustain higher stomatal conductance, by depleting soil water more thoroughly from a larger percentage of the soil volume, relative to NM plants. However, when soil is flooded with osmoticum (e.g. Augé et al. 1992a), Ψ is lowered rapidly and evenly throughout the soil volume, both at the rhizoplane and in bulk soil, eliminating the possibility that shoots are provided access to an effectively larger reservoir of higher energy water by VAM than by NM roots. If stomatal conductance remains higher in VAM plants under these conditions, then the VAM root is either more capable of absorbing water at low Ψ than the NM root or the differences in stomatal behavior are a consequence of non-hydraulic rather than hydraulic differences between root systems (e.g. Augé and Duan 1991; Augé et al. 1994).

Water movement is not one-way (Kramer and Boyer 1995) and the possibility that VAM symbiosis affects water efflux (movement of water from roots to soil, e.g. hydraulic lift) remains mostly unstudied. Ebel et al. (1996) reported that VAM and NM root systems may differ in their conductance of water from wet to dry roots, hence in their ability to remoisten dry soil.

Plant water potential components

VAM symbiosis may result in changes in the relationship between stomatal conductance and leaf Ψ (Allen 1982; Allen and Boosalis 1983; Stahl and Smith 1984; Allen and Allen 1986; Augé et al. 1986b; Sánchez-Díaz et al. 1990; Osundina 1995). One way this might occur is by enhanced leaf solute accumulation (lowered osmotic potentials) in leaves of VAM plants, resulting in higher bulk leaf turgors at a particular total leaf Ψ. If higher photosynthetic rates sometimes associated with VAM symbiosis result in higher concentrations of soluble sugars and other photosynthetic byproducts in the leaf symplasm, this might manifest as higher cytoplastic osmolality in VAM than in NM plants. Adjustments in leaf osmotic potential and stomatal conductance are often related (e.g. Ludlow 1989) and VAM-induced alteration of leaf osmotic potential may explain VAM-induced promotion of stomatal conductance (e.g. Augé et al. 1986b).

Non-hydraulic root signals

With the exception of nutritional mechanisms unrelated to plant size, the mechanisms discussed so far have dealt primarily with direct hydraulic influences: mycorrhizal influences on one plant water status parameter brought about by mycorrhizal influence on another water status parameter. It is also plausible that VAM fungi could affect host water balance in some non-hydraulic way, perhaps by altering hormonal relations, as suggested by the work of Levy and Krikun (1980) and Christensen and Allen (1979, 1980). In fact, VAM alteration of stomatal conductance/leaf Ψ relationships (changed stomatal conductance in the absence of a change in tissue hydration) suggests that VAM symbioses probably do alter some non-hydraulic aspect of host drought physiology.

The traditional understanding of how soil drought affects leaf behavior is straightforward. When the rate of water loss from leaves exceeds the rate at which water can be replaced via absorption by roots, leaves begin to dehydrate. Continued leaf drying eventually leads to inhibition of stomatal closure and leaf growth (Kramer and Boyer 1995). However, partial drying of a root system can also lead to reduced stomatal conductance or leaf growth, even when enough roots remain in contact with moist soil to fully supply shoot water requirements. Some drought biologists have postulated that root dehydration can trigger or enhance the production and loading of a non-hydraulic, chemical signal into xylem (Davies et al. 1994). This signal moves via the transpiration stream to leaves, where it is received by guard cells, which respond by losing turgor to close stomata. Substantial stomatal inhibition (50% or more) can result from this non-hydraulic root-to-shoot communication of soil drying, i.e. before soil drought has affected root water absorption enough to perturb leaf water status (Zhang and Davies 1989a, b; Gowing et al. 1993).

ABA appears to be a primary candidate for the drought-induced, non-hydraulic root signal (Davies et al. 1994). It is an inhibitor of stomatal opening (e.g. Mittlehanser and Van Steveninck 1969; Jones and Mansfield 1970) and VAM fungi can affect host balances of ABA (Allen et al. 1982; Murakami-Mizukami et al. 1991; Danneberg et al. 1993; Duan et al. 1996; Goicoechea et al. 1997a). Furthermore, VAM hyphae apparently can produce ABA (Esch et al. 1994). Therefore, VAM influence on root-to-shoot movement of ABA may be a way for VAM fungi to affect stomatal behavior. VAM plants sometimes show stomatal conductances different from those of NM plants when only part of a root system dries and before leaf water relations are affected, suggesting a VAM effect on non-hydraulic root-to-shoot communication of soil drying (Augé et al. 1994, 1995). We also know that the rate of decline in stomatal conductance accompanying partial soil drying differs when VAM or NM roots are dried (Augé and Duan 1991). Two possibilities are that VAM symbiosis changes the movement of ABA from roots to shoots at a particular degree of drought, or the stomata of leaves of VAM and NM plants differ in sensitivity to ABA. In my lab, we tested these possibilities in cowpea plants and found that VAM symbiosis did not alter stomatal sensitivity to ABA, but that the amount of ABA moving in xylem as a function of soil water content around root systems was lower in VAM than in similar-sized NM plants in dry soil (Duan et al. 1996). Lower concentrations of ABA in VAM versus NM roots at similar soil water contents have also been observed in droughted alfalfa (Goicoechea et al. 1997a). VAM symbiosis can also change the relationship between xylem ABA concentration and soil water content at high water contents (Ebel et al. 1997).

Many investigators of plant water relations agree that both non-hydraulic and hydraulic factors probably act in concert to regulate leaf water relations and gas exchange, especially during drought (Tardieu et al. 1993; Davies et al. 1994; Saliendra et al. 1995). Even when stomata appear to close in response to declines in leaf water status (measurable as drops in leaf Ψ, turgor, or water content), the progression of events is thought to involve redistribution of ABA (Saliendra et al. 1995). Much ABA in leaves is sequestered within the cytoplasm in chloroplasts and it moves out of cells and into the apoplast as the leaf mesophyll dehydrates.

Cytokinins can also affect stomatal behavior, although most evidence does not implicate them in non-hydraulic root-to-shoot communication of soil drying (Davies et al. 1994). VAM fungi can change cytokinin concentrations in host tissues (e.g. Edriss et al. 1984; Drüge and Schönbeck 1992; Thiagarajan and Ahmad 1994). ABA/cytokinin balances have sometimes proven to be more physiologically important than absolute concentrations of ABA or cytokinin alone, and Goicoechea et al. (1997a) have suggested that ABA/cytokinin balance may have exerted control of gas exchange in droughted alfalfa. Duan et al. (1996) found no effect of VAM symbiosis on root-to-shoot movement of zeatin ribosides, the transported form of cytokinin, before or during drought. Mycorrhizal influences on host water relations related to mycorrhizal effects on hormone balance have been discussed by Sánchez-Díaz and Honrubia (1994).

VAM and NM plants might be expected to differ in root-to-shoot movement of other xylem sap constituents implicated in stomatal control, given the differing efficiencies of ion absorption of VAM and NM roots. This may be particularly evident when ion mobilities are reduced during soil drying. In the same way that stomatal conductance is much better correlated with current ABA flux from roots or with xylem concentrations of ABA than it is with bulk leaf concentrations of ABA (Davies and Zhang 1991; Jia et al. 1996), current supply of other xylem constituents may exert as much or more control of transpiration than bulk leaf contents of these constituents. This appears to be true of anion/cation supply and stomatal conductance (Gollan et al. 1992). Leaves having the same bulk P concentrations can have quite different responses to ABA when the P concentration of the transpiration stream is altered (R. Augé and C.L. Trejo, unpublished results). In a study of xylem sap composition of sunflower, stomatal conductance of drying plants showed the strongest correlation with P concentration in sap relative to several other anions and cations (Gollan et al. 1992). VAM and NM plants can differ in their ability to absorb P from drying soils, even when soil P and/or P fertilization rates are relatively high (Nelsen and Safir 1982b; Sylvia et al. 1993) and it is likely that xylem P concentrations also differ in VAM and NM plants during soil drying. Leaf Ca status of both cytoplasm and apoplasm also modulates stomatal response to ABA (De Silva et al. 1986; Atkinson et al. 1990; Ruiz et al. 1993; Thompson et al. 1997) and VAM infection may alter the Ca status of leaves (Tables 4, 5).

By changing the flux of both anions and cations moving in the transpiration stream to leaves, VAM symbiosis might modify xylem pH, another putative signal involved in non-hydraulic root-to-shoot communication of soil drying (Hartung and Slovik 1991; Jia and Zhang 1997; Wilkinson and Davies 1997). Small changes in the flux of H^+ to leaves via xylem can create large changes in apoplastic pH. The increased pH of leaf apoplast could in turn enhance the release of ABA from leaf mesophyll cells into the apoplast surrounding guard cells (Hartung et al. 1998). When transpiration rates of detached leaves exposed to solutions of varying pH were compared, mycorrhizae × pH interactions were significant for both rose and cowpea (Green et al. 1998). However, in at least one instance, VAM and NM cowpeas did not differ in xylem pH across a range of soil water contents, even when stomatal conductances did differ (Duan et al. 1996).

Drought resistance

Plants have evolved many physiological, morphological and phenological characteristics for responding to and resisting drought stress. Certain characteristics and responses to drought do not occur independently but appear to coincide, leading to the categorization of perennial plants as drought avoiders or drought tolerators (Fig. 1) (Levitt 1980; Ludlow et al. 1983). Drought avoiders have tissues that are very sensitive to dehydration. They tend to have characteristics allowing them to avoid tissue water deficits when soil moisture limitation occurs, e.g. deep roots to maximize water uptake, leaf movements or sensitive stomata to minimize leaf water loss. Drought tolerators have leaves that can tolerate dehydration and they tend to have poorly developed responses for avoiding dehydration. Tolerators rely on osmotic adjustment to survive drought (Ludlow et al. 1985). Ludlow (1989) has profiled the mechanistically linked characteristics that categorize these two drought-resistance strategies.

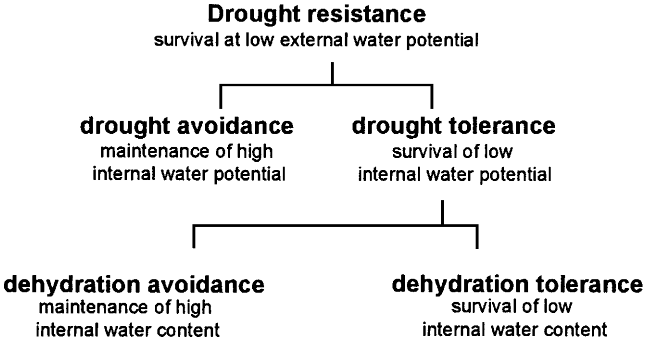

Fig. 1 Drought resistance can occur via drought avoidance (maintenance of high internal Ψ) or drought tolerance (survival of low internal Ψ). Drought tolerance can be further partitioned into dehydration avoidance (maintenance of high internal water content) or dehydration tolerance (survival of low internal water content). The figure, based on the nomenclature of Levitt (1972, 1980), defines drought resistance in terms of survival, but in the literature drought resistance is also used to characterize plant behavior or performance: a relatively more drought resistant plant would be one that exhibits behavior closer to that of amply watered controls

Physiological and morphological responses

Drought avoidance

In the first review of the subject, Reid (1979) noted that mycorrhizae appear to benefit the droughted plant primarily through direct drought avoidance. That assessment is still sound after an additional 20 years of research. There are a few reports of VAM-induced increases in drought tolerance, involving both increased dehydration avoidance and dehydration tolerance (Fig. 1). However, most experiments examining mycorrhizal effects on host drought resistance have demonstrated that when VAM symbiosis improves plant drought resistance, it does so by aiding drought avoidance. This improved drought avoidance has usually been associated with growth enhancement, probably linked to improved acquisition of P and possibly other nutrients.

Putative examples of VAM promotion of drought avoidance are numerous. Relative to NM controls, VAM plants have shown higher nitrogen assimilation and better nitrogen nutrition during development of and recovery from drought, characterized as higher soluble proteins, amino acids, nitrogenous enzymes and tissue N (Panwar 1992, 1993; Tobar et al. 1994a, b; Subramanian and Charest 1995, 1998; Azcón et al. 1996; Ruiz-Lozano and Azcón 1997; Azcón and Tobar 1998), higher activities of other enzymes (Goicoechea et al. 1996; Ruiz-Lozano et al. 1996b), decreased accumulation of proline and other nitrogenous indicators of drought injury (Runjin 1989; Müller and Höfner 1991; von Reichenbach and Schönbeck 1995; Gemma et al. 1997; Ruiz-Lozano and Azcón 1997), more normal carbohydrate metabolism (Augé et al. 1987a; Subramanian and Charest 1995; Subramanian et al. 1997), greater root growth (Osonubi et al. 1992), less wilting or leaf necrosis (Mosse and Hayman 1971; Fitter 1988; Osundina

1995; Subramanian et al. 1995; Bryla and Duniway 1997c; Gemma et al. 1997), increased protective leaf movements (e.g. Huang et al. 1985), both more (Osonubi et al. 1992) and less (Ellis et al. 1985) leaf abscission, increased soil water extraction (Busse and Ellis 1985; Ellis et al. 1985; Osonubi et al. 1992), more normal shoot water status during drought (e.g. Allen et al. 1981; Newman and Davies 1988; Dixon et al. 1994; Ruiz-Lozano et al. 1995a, b; Subramanian et al. 1995, 1997; Gemma et al. 1997) and quicker recovery of more normal status after drought (Sweatt and Davies 1984; Runjin 1989; Gemma et al. 1997). One of the most compelling cases for a VAM-mediated increase in drought resistance, likely via avoidance, was offered by Bethlenfalvay et al. (1988b), who demonstrated that the soil moisture content at permanent wilting of individual plants was closely inversely correlated with the extent of root colonization.

Drought tolerance

There are also instances in which differing drought resistance characteristics of VAM plants and NM plants are linked to differences in drought tolerance[18]: different survival or behavior at similar low tissue Ψ (Fig. 1). For instance, VAM colonization appears to have increased the drought tolerance of roses by increasing both their dehydration avoidance and dehydration tolerance capacities (Augé et al. 1986b, 1987a, b). Dehydration was avoided to a larger extent in VAM plants than in similar-sized NM plants through increased accumulation of solutes[19], which lowered bulk leaf symplastic osmotic potential. This allowed bulk leaf hydration and turgor to be sustained to lower leaf Ψ. Enhanced dehydration tolerance was also indicated by the tendency for VAM plants to sustain turgor and stomatal conductance at lower relative water content and lower relative osmotic water content than NM plants. Perhaps the single most important indicator of a drought resistance strategy is the dehydration tolerance of a species, i.e. its tissue capacity for withstanding desiccation. Dehydration tolerance has been operationally defined by Ludlow (1989) as the Ψ of the last surviving leaves (called the lethal Ψ) on a plant subjected to a slow, continuous soil drying episode. We have demonstrated that VAM symbiosis can change the lethal leaf Ψ of soybean (Augé et al. 2001b).

Higher capacity for osmotic adjustment is also a characteristic of higher drought tolerance. Therefore, VAM plants can be said to have been more physiologically tolerant of drought in those few instances in which they showed more osmotic adjustment in the face of similar drought pressure (e.g. Allen and Boosalis 1983; Augé et al. 1986b; Davies et al. 1993).

Productivity and survival

From ecological and agricultural perspectives, we are probably most interested in characterizing drought hardiness in terms of growth, yield and survival. VAM symbiosis appears to affect these mostly through drought avoidance, often associated with improved P nutrition. In about 80% of mycorrhizal studies reporting plant growth during drought, VAM plants were larger than NM plants (Tables 1, 2, 3), which seems to suggest an important role for VAM fungi in promoting the drought resistance of their hosts. However, in some of those studies, VAM plant growth also exceeded NM plant growth in the amply watered controls, indicating that the VAM influence occurred by relieving P stress rather than drought stress. Nevertheless, in many studies, VAM plants had higher yields in dry soils than more poorly nourished NM plants (e.g. Busse and Ellis 1985; Ellis et al. 1985; Kwapata and Hall 1985; Waterer and Coltman 1989; Subramanian and Charest 1997) and had higher survival rates in dry soils than more poorly nourished NM plants (Wilson et al. 1991; Awotoye et al. 1992; Stahl et al. 1998) through more effective drought avoidance. Stahl et al. (1998) reported that VAM *Artemisia tridentata* seedlings showed higher survival than NM seedlings as soil dried below soil Ψ values of –2.5 MPa to as dry as –3.8 MPa (i.e. VAM symbiosis decreased lethal soil Ψ). VAM-induced enhancements in transplant performance (e.g. Puthur et al. 1998; Subhan et al. 1998) almost certainly reflect enhanced drought resistance, as water limitation is usually the chief stress affecting survival and vigor of transplants in the field. Greater drought resistance was also suggested by VAM root systems showing lower fine root mortality than NM roots after 15 weeks exposure to dry surface soil (Espeleta et al. 1999). VAM-induced increases in drought resistance were not always observed (e.g. Hetrick et al. 1984, 1987; Jupp and Newman 1987; Simmons and Pope 1988; Simpson and Daft 1990, 1991; Mizoguchi 1992).

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[18] The terminology can be confusing. If one plant maintains higher leaf Ψ than another exposed to similar low soil water content (it remains more hydrated even though it is exposed to similar external stress), obviously that plant seems more tolerant of drought. However, in the terminology most common in the scientific literature (e.g. Levitt 1980; Ludlow 1989) (Fig. 1), that plant is not more drought *tolerant*; it is more drought *resistant* via better drought *avoidance*. If the plant has better performance (closer to that of non-stressed conditions) than a second plant at the same external drought pressure and both plants have similar and low internal Ψ, then the first plant is more drought *tolerant*. Cowpea, for example, is considered to be very drought resistant but quite intolerant of dehydration; it is an extreme drought avoider (Shackel and Hall 1983). Plants have been characterized as avoiders or tolerators according to absolute values of lethal Ψ (e.g. Ludlow 1989)

[19] During drought, if osmotic potential decreases more in VAM than in NM plants simply through the passive accumulation of solutes occurring when tissues lose water, then the VAM plant would probably show less stress resistance than its non-mycorrhizal counterpart. It has dehydrated more. If, however, a mycorrhizal plant actively accumulates more solutes than the non-mycorrhizal plant while maintaining hydration, e.g., the VAM and NM plants maintain similar total Ψ, then by definition turgor potential would be higher in the mycorrhizal plant. In this case, the mycorrhizal plant shows more stress resistance than the similarly challenged non-mycorrhizal plant. Higher or similar osmotic potentials in leaves of VAM relative to those of NM plants may also accompany higher total Ψ, an indication that VAM plants are less strained (less dehydrated)

VAM symbiosis has sometimes reduced injury from other environmental stresses physiologically related to water deficit stress, such as salinity (e.g. Pond et al. 1984; Rozema et al. 1986; Baker et al. 1995; Ruiz-Lozano et al. 1996a; Azcón and El-Atrach 1997), chilling (e.g. Charest et al. 1993; Paradis et al. 1995; El-Tohamy et al. 1999) and soil compaction (e.g. Yano et al. 1998).

Influence of soil drying on the fungi

Effects of soil drying on behavior of VAM fungal symbionts are summarized in Table 6. Drought affected levels of root colonization in about half of the reports providing such data, increasing root colonization more often than decreasing it. Most of the studies in Table 6 involved potted plants and were of relatively short duration; in such instances, duration of drought has not appeared to favor or discourage colonization. However, in field situations chronic drought may promote more extensive colonization. For example, of 43 flowering plants examined on a fallow agricultural site in Germany, 40 were heavily infected by VAM fungi in a low soil moisture habitat and 29 were heavily infected on a comparable but high soil moisture habitat (Kuhn 1991; Kuhn et al. 1991). As Bolgiano et al. (1983) noted, even if short-term soil water deficits decrease colonization in some associations, over longer periods the decreased P availability accompanying decreased soil water availability may override the more direct effect of soil water on colonization. Sustained decreases in soil moisture may increase colonization if plant P levels drop because of decreased soil P diffusion rates or lowered P uptake capacity.

The amount of soil water optimal for plant growth may also be optimal for VAM sporulation (e.g. Redhead 1975) and much less sporulation has occured at either extreme, i.e. chronically dry soils (Stahl and Christensen 1982; Cui and Nobel 1992; Stutz and Morton 1996) or flooded and permanently water-logged soils (Gerdemann 1974; Khan 1974). Both spore production and species richness of VAM fungi are reportedly lower in arid climates than in other ecosystems (Rose 1981; Pond et al. 1984) and decrease as aridity increases (Stahl and Christensen 1982). However, short-term, transient declines in soil moisture may promote spore production (Jacobson 1997). More sophisticated culture techniques have revealed that species richness in arid climes may be comparable to that of most other plant communities (Morton et al. 1995; Stutz and Morton 1996). A rapid, opportunistic growth response of mycelium to moisture and production of resilient spores in response to declining moisture may be characteristics allowing VAM fungal communities to function under especially arid conditions (Jacobson 1997). Spore germination was increased (Douds and Schenck 1991), decreased (Tommerup 1984; Estaun 1990; Douds and Schenck 1991) or unaffected (Douds and Schenck 1991) by soil drying, depending on the species. Hyphae of some VAM species may renew growth from roots stored at matric potentials of about –50 MPa for 6 months or longer (Tommerup and Abbott 1981)[20].

In addition to root colonization, spore production and spore germination, investigators have characterized the influence of soil drying on hyphal length, biomass and survival, the number of entry points and infections per unit root length, inoculum potential, pot culture infectivity, infectivity of hyphae and root fragments, propagule mortality and species distribution (Table 6).

Controls

Water relations and P nutrition are linked, and controlling for VAM effects on host P nutrition is a challenge. But the problem of producing proper or meaningful NM controls is not an insurmountable one. Some investigators have adjusted fertilization such that, if VAM and NM plants do not have statistically similar tissue phosphorus concentrations, NM plants have slightly higher values than VAM plants. The assumption is that P insufficiency of NM plants is usually the confounding factor. Other experiments have included several levels of P fertilization for either VAM or NM plants, attempting to bracket leaf P concentrations of one mycorrhizal treatment with those of another (e.g. Duan et al. 1996; Ebel et al. 1997). If NM plants with higher and lower leaf P concentrations than VAM plants show similar behavior, which differs from that of the VAM plants, it is a reasonable conclusion that the VAM influence on this behavior is not related to leaf P concentration. Another approach is to grow more plants of each mycorrhizal treatment than necessary and to visually select VAM and NM plants of similar size from this larger population at the start of drought experiments or water relations measurements (e.g. Green et al. 1998).

Finally, we may do away with NM controls altogether. Alastair Fitter echoed the sentiments of many when he suggested that we place undue emphasis on NM controls, because such plants are anomalous in nature (1st International Conference on Mycorrhizae, VAM Symbioses and Plant Stress Resistance Discussion Workshop, Berkeley, Calif., 1996). Instead of comparing VAM and NM plants, it may be more productive to examine the behavior of VAM plants in different soils, at different P levels, at different levels of intra- or extraradical colonization (e.g. Bethlenfalvay et al. 1988b; Al-Karaki and Clark 1999), in the presence or absence of soil grazers (Fitter 1985) or rhizobacteria commonly associated with VAM fungi (Linderman 1992), using one or more fungal species or geographical isolates (e.g. Stahl and Smith 1984), using single isolates versus cocktails, and using indigenous versus indigenous + exotic inocula (e.g. Ramakrishnan et al. 1988a; Osonubi et al. 1992), especially in field experiments.

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[20] Air of 69% relative humidity and 20 C has a Ψ of –50 MPa. Hyphae and spores of VAM fungi have also survived drying to water activities of 0.00025 and subsequent storage for 8 years (Tommerup 1988)

Conclusions

Mycorrhizal effects on plant water relations are not as dramatic and consistent as those on P acquisition and host growth and one would not expect them to be. Mycorrhizal influences on tissue hydration and foliar gas exchange are often subtle, transient, and probably circumstance and symbiont specific. Furthermore, we have yet to learn how to reliably reproduce these VAM effects. However, modest changes, if sustained, can have meaningful effects on plant fitness. Many VAM studies offer only momentary or short-term snapshots of leaf or root water relation behavior but, viewed as a whole, the literature suggests a substantive if only occasional VAM influence on host water relations and drought physiology.

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