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), 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

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1 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 the sample being measured. The total Ψ of a tissue sample is composed primarily of two components: Ψ = Ψ_π + Ψ_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 Ψ_π + Ψ_m: 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 \( \Psi \), 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 to date dealing with VAM symbioses and host water relations, shoot gas exchange and drought responses. 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, photo-

Stomatal conductance 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.

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.