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Review

Vesicular-arbuscular mycorrhizas and soil salinity

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Abstract. This review discusses the growth and activity of vesicular-arbuscular (VA) mycorrhizal fungi in saline conditions. The review includes examination of the effects of high concentrations of salts on the occurrence of VA mycorrhizal fungi in field soils, and on spore germination, growth of hyphae, establishment of the symbiosis and production of spores in controlled conditions. Information on the growth and reproduction of VA mycorrhizal fungi under saline conditions is scarce and is often circumstantial. There is clear evidence that germination of spores and subsequent hyphal growth of some VA mycorrhizal fungi are reduced by increasing concentration of salts. However, in plant growth experiments, experimental designs and methodologies have generally not allowed the direct effects of salinity on fungal growth to be separated from plant-mediated effects. There is a need for controlled studies to investigate the responses of VA mycorrhizal fungi to soil salinity. Research is required which distinguishes between effects on different phases of the fungus lifecycle and which includes in its design the ability to separate direct effects from plant-mediated influences on fungal growth and reproduction.

Key words: Mycorrhiza – Arbuscular – Salinity

Introduction

Vesicular-arbuscular (VA) mycorrhizal fungi are present in most soils and are generally not considered to be host specific (Bowen 1987). However, population levels and species composition are highly variable and are influenced by plant characteristics and a number of environmental factors such as temperature, soil pH, soil moisture, phosphorus and nitrogen levels, heavy metal concentrations (Daniels and Trappe 1980), the presence of other microorganisms, application of fertilizers and pesticides and soil salinity (Barea and Azcon-Aguilar 1983). Species and strains of VA mycorrhizal fungi differ in their ranges of tolerance of physical and chemical properties of soil (Abbott and Robson 1991) and, therefore, differ also in their effectiveness in increasing plant growth in particular soils.

VA mycorrhizas have been shown to decrease yield losses of plants in saline soils (Hirrel and Gerdemann 1980; Ojala et al. 1983; Pond et al. 1984; Poss et al. 1985; Pfeiffer and Bloss 1988). This may be due to increased uptake of phosphorus leading to increased growth and subsequent dilution of toxic ion effects, to an ameliorative effect of mycorrhizas on water stress of plants, or to some combination of these effects.

There has been little investigation of the effects of salinity on the biology or ecology of VA mycorrhizal fungi. Most studies have concentrated on the effects of inoculation with VA mycorrhizal fungi on the growth of plants in saline soil, and information on the effects of salinity on growth of the fungi is scarce and is often circumstantial.

This review will discuss literature relating to the growth and activity of VA mycorrhizal fungi in saline conditions. The review will cover the effects of high concentrations of salts on the occurrence of VA mycorrhizal fungi in field soils, and also on spore germination, growth of hyphae, establishment of the symbiosis, and production of spores in controlled conditions. Included in the discussion will be a comparison of the effects of salinity and the closely related stress of low water potential.

Measurement and expression of soil salinity

Comparison of results of experiments on soil salinity is complicated by differences in methods of measuring soil salinity. Usually, all soluble salts are extracted and salinity is expressed as concentrations of specific ions or total soluble salts in dry soil (Bernstein 1975). However, salinity of the soil solution depends not only on the concentration of salts in the dry soil but also on the volume of water in the soil. Fine soils have up to five

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times the water-holding capacity of coarse soils; therefore, at a given salt content, the soil solution of a coarse soil will contain up to five times the salt concentration of a fine soil (Bernstein 1975).

Soil salinity is frequently expressed as the electrical conductivity (EC) of a soil extract. This may be measured with a conductivity meter or calculated from the known linear relationship between EC and total dissolved salts in a solution at a given temperature (Richards 1954). In the United States of America, the preferred scale for estimation of salinity is the EC of a saturated soil extract (EC_s) (Richards 1954). In Australia, the EC of a 1:5 soil water suspension ($EC_{1:5}$) is the scale most often used (George and Wren 1985). Conversions may be made between the two scales. However, the conversion factor is highly influenced by other physical and chemical soil characteristics such as texture and lime content of the soil and needs to be determined for each group of soils.

A soil is generally considered to be saline where the EC_s exceeds 4 dS m^{-1}. Alternatively, where a soil is described in terms of salt concentration, a saline soil is one in which the salt content exceeds 0.1% (Richards 1954).

Dissolved salts may directly affect soil organisms by the specific toxicity of high concentrations of ions such as sodium or chloride, or by the non-specific effect of solutes on osmotic potential and, therefore, on water potential. The lower (more negative) soil water potential becomes, the more difficult it is for organisms to take up water from the soil. The matric (capillary) potential is the most important determinant of water potential in most unsaturated soils. However, the osmotic potential is significant in saline soils and in some soils amended with organic wastes or fertilizer (Papendick and Campbell 1981). In solution culture, the water potential is determined by the osmotic potential.

The water potential of a soil may be estimated from a relationship between water potential and the relative humidity above single-salt solutions of particular concentration, if the salt concentration, temperature, water content and matric characteristics of the soil are known (Hillel 1971). Unfortunately, little of the literature on mycorrhizas and salinity includes sufficient information about the physical and chemical characteristics of the soil to enable these estimations to be made.

The occurrence of VA mycorrhizas in saline soils

Discussion of the ecology of VA mycorrhizal fungi in saline environments has been confused by the need to distinguish between biotic and abiotic effects on the distribution and relative abundance of the fungi.

VA mycorrhizal fungi have been shown by several workers to occur naturally in saline environments, (Khan, 1974; Allen and Cunningham 1983; Pond et al. 1984; Rozema et al. 1986; Ho 1987), despite the comparatively low mycorrhizal affinity of many halophytic plants (Brundrett 1991). Chenopods were not generally considered to form mycorrhizal associations (Gerdemann 1968); however, there is increasing evidence that some chenopods form mycorrhizas (Pond et al. 1984; Rozema et al. 1986; Sengupta and Chaudhuri 1990; Brown 1990).

Plant material and rhizosphere soil from 89 halophytes, xerophytes and hydrophytes growing in a wide range of environments and soil types in Pakistan were surveyed for the presence of VA mycorrhizal fungi (Khan 1974). Of the 21 halophytes included in the survey, 11 contained VA mycorrhizal infection in the root cortices and spores of VA mycorrhizal fungi in the rhizosphere. These plants were members of the Papilionaceae, Sapindaceae, Salvadoraceae, Apocynaceae, Solanaceae and the Gramineae. The noninfected plants represented all the members of the Chenopodiaceae, Tamiaraceae and Zygophyllaceae in the survey. Of these, seven contained spores of VA mycorrhizal fungi in the rhizosphere. Soil salinity was not measured at the collection sites, thus the relative importance of plant characteristics and soil salinity on the occurrence of VA mycorrhizal fungi could not be determined.

The relationship between soil salinity and the occurrence of mycorrhizas on halophytes has been investigated by several workers (Kim and Weber 1985; Pond et al. 1984; Allen and Cunningham 1983; Ho 1987). The roots of halophytes were surveyed for mycorrhizas along transects from the centres to the outer zones of Playa lakes in Utah, and spores were counted in the rhizosphere of the same plants. In a salt playa predominantly vegetated with *Distichlis spicata* (Gramineae), both percentage infection and spore number were negatively correlated with sodium content of the soil, over a range of 153–11 600 μg/g (Kim and Weber 1985). Mycorrhizas were not observed where soil sodium exceeded 3131 μg/g. In well-drained playas with relatively low soil sodium contents (10–32 μg/g and 275–622 μg/g) and diverse plant cover, spore numbers and infection levels were high (up to 80%) and were not correlated with soil sodium concentration (Kim and Weber 1985). In waterlogged playas vegetated with *Salicornia* spp. (Chenopodiaceae), spore numbers and infection levels were negligible at all sodium concentrations (Kim and Weber 1985). It was not determined whether this was primarily due to an effect of waterlogging or to mycorrhizal nonaffinity of the predominant plant species.

A wide-ranging survey of saline soils in California and Nevada found mycorrhizal plant roots and spores of VA mycorrhizal fungi in a range of habitats and levels of soil salinity up to 185 dS m^{-1} (Pond et al. 1984). No attempt was made to correlate the amount of infection or spore numbers with soil parameters. However, subsequent inoculation of tomato plants with field-collected material gave negative correlations between infection and sodium concentration, EC_s and osmotic potential of the field soils (Pond et al. 1984). These correlations may indicate that either the number of propagules or the infectivity of fungal isolates decreased with increasing salt.

A survey of alkaline desert soils ranging in salinity

between 1.26 and 13.0 dS m^{-1} found VA mycorrhizal colonization of the roots of salt-tolerant grasses such as *Festuca idahoensis* and *Distichlis stricta.* The numbers of spores of VA mycorrhizal fungi were inversely highly correlated with sodium concentration of the soils but were not related to any other measured parameter, including pH, conductivity and concentration of a range of other cations (Ho 1987).

In most of the above studies, no attempt was made to determine the viability of spores extracted from the soils and it is not known whether spores collected from highly saline soils were formed in situ or were transported to the centre of the playa by wind, water or animal activity. Several workers reported species identification of the VA mycorrhizal fungi occurring at the saline sites they surveyed. Positive identification of VA mycorrhizal fungi to species is a difficult and highly specialized procedure and may be impossible when the material is collected from field soil. Limited numbers of spores, lack of knowledge about their age, and spore damage due to decomposition or parasitism can easily lead to misidentification or even erroneous descriptions of "new species" (J. B. Morton 1991, personal communication; C. Walker 1991, personal communication). Only Pond et al. (1984) reported the establishment of field-collected fungi in pot culture prior to identification. The VA mycorrhizal fungi most commonly observed in saline soils are *Glomus* spp. (Allen and Cunningham 1983; Pond et al. 1984; Ho 1987).

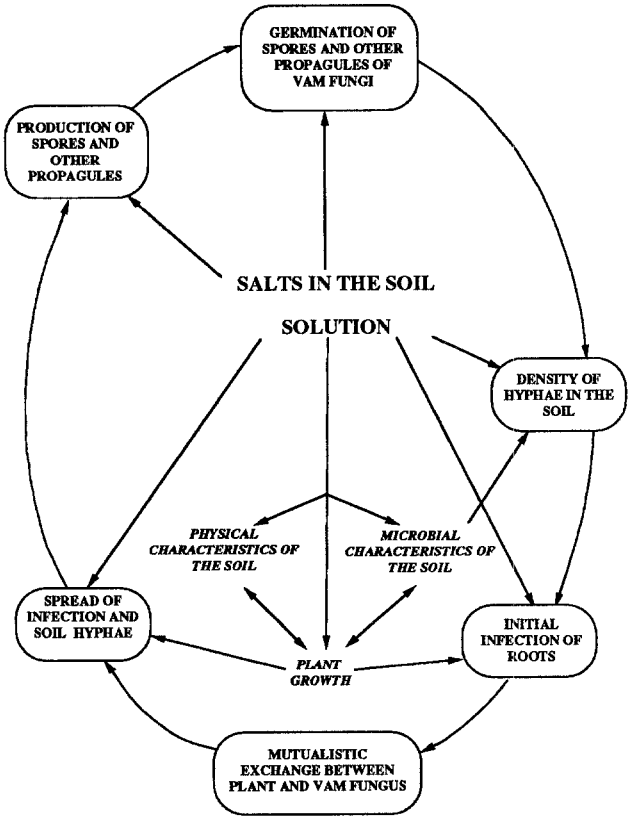

Fig. 1. Schematic summary of pathways by which the activity of VA mycorrhizal fungi may be affected by soil salinity

The effect of soil salinity on VA mycorrhizal fungi under controlled conditions

Soil salinity may influence the growth and activity of VA mycorrhizal fungi via several mechanisms, either discretely or interactively (Fig. 1).

VA mycorrhizal fungi are obligate biotrophs; therefore, any environmental factor which affects the physiology of a host plant is likely to affect its fungal symbiont. Since it has not so far been possible to maintain VA mycorrhizal fungi in axenic culture, it is extremely difficult to distinguish between direct and plant-mediated effects on their biology.

The single phase of the VA mycorrhizal fungus life cycle which can be studied in isolation from complex interactions with plant growth is spore germination, since this is independent of the presence of a plant (Daniels and Graham 1976; Hepper 1979; Daniels and Trappe 1980).

The effect of soil salinity on spore germination

Germination of spores of a VA mycorrhizal fungus can be described as consisting of four phases: hydration, activation, germ tube emergence, and growth of hyphae (Tommerup 1984). Firstly, water enters the spore, the components of which become hydrated. After hydration of some or all organelles and macromolecules is complete, ribonucleic acid and enzymes become active, leading to increased metabolic activity. Two to 10 days after the spore is activated, a germ tube appears, and is followed by hyphal growth (Tommerup 1984). Delay or prevention of all or any of the phases of spore germination by dissolved salts in the soil solution would delay or prevent growth of hyphae and, therefore, colonization of plant roots and establishment of the symbiosis.

There is very little published information about the effects of salinity on the germination of spores of VA mycorrhizal fungi. However, the available data indicate inhibition of spore germination by increasing concentrations of NaCl (Hirrel 1981; Estaun 1989, 1991; Juniper and Abbott 1991).

It has not been firmly established whether the effects of NaCl on germination of spores of VA mycorrhizal fungi are primarily due to an osmotic effect or to toxicity of a specific ion. An attempt has been made to identify a specific-ion effect of NaCl on the germination of *Gigaspora margarita* spores in solution culture, using an ion substitution technique (Hirrel 1981). However, the results were unclear. After 12 days in distilled water, spores had germinated and formed numerous hyphae, on which clusters of auxiliary cells were developing. Germination and production of auxiliary cells were not affected by concentrations of sodium or chloride below 0.086 mol l^{-1}. At this concentration of NaCl, the osmotic potential was −0.36 megapascals (MPa). As solution concentrations increased, maximum percent germination and germination rate

Table 1. Maximum percentage germination (%) and regression coefficients (RC) for germination rates of spores of *Gigaspora margarita* after 12 days incubation in agar containing different concentrations of sodium or chloride at a variety of osmotic potentials (−MPa) (from Hirrel 1981)

Compound with Na^+ or Cl^-	Concentrations of Na^+ or Cl^- (mol l^{-1})														
	0.043			0.086			0.128			0.171			0.214		
	−MPa	%	RC	−MPa	%	RC	−MPa	%	RC	−MPa	%	RC	−MPa	%	RC
NaCl	0.18	100	8.47	0.36	100	7.49	0.54	58	4.37	0.72	11	0.65	−0.90	20	0
KCl	0.17	100	7.36	0.35	100	8.07	0.53	7	0.32	0.71	0	0	0.88	0	0
$CaCl_2$	0.17	100	7.46	0.34	100	7.99	0.51	95	6.58	0.68	13	1.34	0.84	13	1.44
$NaNO_3$	0.17	100	8.52	0.34	100	8.09	0.48	100	7.88	0.68	52	3.03	0.84	25	1.73
Na_2SO_4	0.16	100	7.52	0.20	100	8.52	0.32	100	8.24	0.43	73	4.15	0.54	47	2.73

declined, particularly in solutions containing chloride (Table 1) and auxiliary cells were not produced.

It was suggested that differential effects of $NaNO_3$ and Na_2SO_4 in solutions of similar osmotic potential (−0.48 and −0.43 MPa, respectively) may be attributable to a higher concentration of Na^+ in the latter. However, rate of germination and maximum germination were lower in KCl than in NaCl solutions of similar concentration and osmotic potential. As suggested by Hirrel, faster germination in the $CaCl_2$ solution may have been due to the fact that calcium is divalent and was, therefore, present at half the concentration of the monovalent cations.

Observed differences between the effects of KCl and NaCl and those of the other three salt solutions could have been due in part to differences in osmotic potential. If germination was inhibited due to a reduction in the ability of the spores to take up water in solutions of low osmotic potential, then it might be expected that spores would be prevented from germinating in solution concentrations above a critical level. In a range of marginal concentrations below the critical level, spores would hydrate slowly and germination would occur eventually. In concentrations below the marginal range, spores would hydrate and germinate normally.

It was observed that after 12 days in 0.17 mol l^{-1} solutions, previously ungerminated spores began to germinate (Hirrel 1981). This seems an unlikely occurrence if the primary limitation on germination was ion toxicity but is in keeping with the interpretation that the primary limitation at that concentration was osmotic.

Data obtained from experiments using spores incubated in artificial media do not necessarily represent the responses that occur in soil (Bowen 1987). Two studies have investigated the effect of NaCl on the germination of spores of VA mycorrhizal fungi in soil. Juniper and Abbott (1991) incubated spores of *Acaulospora laevis, A. trappei, Scutellospora calospora* and *Gigaspora decipiens* between filter papers buried in soil watered to field capacity with a range of saline solutions from 0 to 0.3 mol l^{-1} NaCl. Estaun (1991) conducted a similar experiment with spores of two isolates of *Glomus mosseae* in soils watered with saline solutions up to 0.14 mol l^{-1} NaCl. A range of tolerance to NaCl was observed between species (Juniper and Abbott 1991) and between isolates of the same species (Estaun 1991) of VA mycorrhizal fungi. In general, increasing the concentration of NaCl delayed germination and reduced the rate of hyphal extension of the fungi in both studies.

If the primary effect of NaCl on spore germination were due to changes in the osmotic and, therefore, the water potential of the growth substrate, then it may be expected that increasing concentrations of NaCl would be similar in effect to decreasing water potential by other means. This relies on the perhaps over simplistic (Brownell and Schneider 1985) assumption that responses of the fungus to matric and osmotic forces are similar. In the absence of evidence that VA mycorrhizal fungi respond differently to matric and osmotic potentials, it may be useful to compare growth data obtained in matrically and osmotically adjusted media.

An attempt has been made to differentiate between the specific-ion and osmotic effects of NaCl on germination and growth of hyphae of *Glomus mosseae* spores (Estaun 1989). Spores were incubated in water agar adjusted to a range of osmotic potentials with either mannitol or NaCl. In NaCl, germination was unaffected by low concentrations but was reduced by decreasing osmotic potential below −0.35 MPa (0.07 mol NaCl l^{-1}), becoming almost zero at −0.65 MPa (0.14 mol NaCl l^{-1}). In mannitol-adjusted solutions, germination began to decline at −0.21 MPa. Germination was apparently more reduced or delayed in the mannitol than in the NaCl treatments (no statistical analyses were provided). This was obviously not expected, since the mannitol treatments were included in the design to act as a control for the osmotic effects of NaCl. Estaun did not state how the concentrations of mannitol corresponding to the NaCl treatments were calculated or empirically derived, nor whether or how the osmotic potentials of the solutions were measured. Unfortunately, the relative influences of osmotic potential and sodium and chloride ions on spores can not be determined from these data. Assuming that the osmotic potentials of the NaCl and mannitol solutions were equivalent as intended, the data could indicate: (1) a toxic effect of mannitol on *Glomus mosseae*

spores and a similar but less severe toxic effect of NaCl; (2) an effect of osmotic potential in addition to toxic effects of both mannitol and NaCl; or (3) an effect of osmotic potential which was ameliorated in some way by NaCl, for instance by some mechanism of osmoregulation requiring uptake of ions from the growth medium. Osmoregulation mechanisms in VA mycorrhizal fungi have not been described. However, the data obtained by Estaun (1989) are at variance with observations on numerous other fungi that appear to have a greater tolerance for low water activity adjusted with sugars or polyols than in solutions adjusted with salts (Javor 1989).

Several other workers have investigated the effect of water potential on spore germination and growth of hyphae of VA mycorrhizal fungi. Lowering water potential of washed sand from 0 to −1 MPa with additions of polyethylene glycol (PEG) produced a linear reduction in germination of *Gigaspora gigantea* spores (Koske 1981). A similar effect of water potentials between −0.017 and −3.1 MPa has been observed on germination of *Glomus epigaeus* spores incubated in soil with a range of water contents (Daniels and Trappe 1980). Sylvia and Schenck (1983) investigated the effect of matric potential on the germination of *Glomus clarum, G. etunicatum* and *G. macrocarpum* spores incubated in soil. Maximum spore germination for all three species occurred at −0.01 MPa in nonpasteurized soil. Germination in pasteurized soil was also maximised at −0.01 MPa, except for *G. clarum,* which reached maximal germination at −0.1 MPa in pasteurized soil. In both pasteurized and nonpasteurized soil, germination at −1 MPa was reduced 95%, 92% and 67% from the maximum for *G. macrocarpum, G. clarum* and *G. etunicatum* respectively.

The studies cited above all indicate an important inhibitory effect of low water potentials on spore germination. The range of potentials over which responses were observed was similar in all cases, regardless of substrate and whether water potential was controlled by NaCl, mannitol, PEG or water content.

The results reported by Daniels and Trappe (1980), Koske (1981), Sylvia and Schenck (1983) and Estaun (1989) were obtained at single harvests and, therefore, did not differentiate between delayed germination and prevention of germination. Data on growth of hyphae were not presented by Daniels and Trappe (1980) or Sylvia and Schenck (1983). Germ tube length was measured by Koske (1981), who reported this to be reduced by decreased water potential. Estaun (1989) reported that hyphal growth was reduced by osmotically adjusted solutions relative to the control solution; thus it could have been more affected by osmotic potential than was spore germination. These data and those presented by Koske (1981) could also be interpreted as indicating that low water potentials delayed rather than reduced germination, since in this case it would be expected that hyphae would be younger and, therefore, less extensive in the more concentrated solutions. This interpretation is supported by the observations of Hirrel (1981) and Koske (1981), who reported "germination recovery" after extended incubation of stressed spores.

The availability of soil water has been observed to change the duration of each phase of germination of spores of *Acaulospora laevis* and *Glomus caledonium* and, therefore, the amount of germination after any given time (Tommerup 1984). The amount of time between the commencement of incubation and the onset of germination increased with decreasing matric potential of the substrate and was also related to the hydration status of the spores at the commencement of incubation. Spores which were prehydrated commenced germination earlier than spores which were initially dry. Germination did not commence until spores were fully hydrated. However, once germination had commenced, germination rate was not affected by soil matric potential between −0.001 and −1.5 MPa. At matric potentials below −1.5 MPa, rates of germination and hyphal extension were reduced. No germination was observed with spores incubated for 4 weeks at −5.0 MPa (Tommerup 1984).

Most of the of the studies cited so far in this section did not include in their methodology a means of testing the effect of NaCl or water potential on water uptake and hydration, which is the initial phase of spore germination. Spores were isolated for experimentation by wet-sieving (Daniels and Trappe 1980; Hirrel 1981; Sylvia and Schenck 1983; Estaun 1989) or flotation-adhesion (Koske 1981). These techniques involve wetting and, therefore, at least partial hydration of the spores prior to the imposition of treatments. Koske (1981) compared germinability of spores picked out of dry sand ("dry extracted") with those collected by flotation-adhesion ("wet extracted") and found germination of the "dry extracted" spores to be marginally reduced in sand and substantially reduced on agar, relative to the "wet extracted" spores. Unfortunately, neither data nor statistical analyses were given.

The inhibitory effects of NaCl (Hirrel 1981; Estaun 1989), mannitol (Estaun 1989) and matric potential (Tommerup 1984) on spore germination are reversible. Spores removed from low water potential treatments and placed in water germinated "normally".

The data discussed above indicate that germination of spores of some species of VA mycorrhizal fungi is delayed where the water potential of the substrate is low and is prevented at very low water potentials, e.g. in dry soil. The effect appears to be similar under conditions of matric or osmotic control of water potential and is probably related to the ability of spores to take up and retain sufficient water from the substrate to become and remain hydrated. It is considered likely that the primary effect of NaCl on spore germination is due to osmotic forces rather than the toxicity of sodium or chloride ions.

More work is needed to investigate the effects of salinity on different stages of germination and to compare the sensitivities of different species and isolates of fungi to salt stress.

The effect of soil salinity on the growth of hyphae

In some VA mycorrhizal fungi, growth of the germ tube from a germinating spore may be stimulated by proximity to a plant root (Mosse and Hepper 1975) and by root exudates (Graham 1972). If root exudates stimulate growth and alter the morphology of germ tubes, then this stimulation could be altered in saline conditions since exudation is greatly influenced by soil chemistry and soil moisture availability (Rovira 1969).

Growth of hyphae of *Glomus mosseae* was reported to be inhibited by NaCl in agar culture (Estaun 1989). However, as has been discussed earlier, the reported data were collected at a single harvest, and thus apparent growth reductions in saline treatments could have been a reflection of delayed onset of germination rather than due to an effect on growth of hyphae. Rates of hyphal growth of *Acaulospora trappei, Scutellospora calospora* and *Gigaspora decipiens* were differentially reduced by increasing concentrations of NaCl in the growth medium (Juniper and Abbott 1991). Hyphal growth of *Acaulospora laevis* and *Glomus caledonium* may have a high requirement for soil water and is reduced in conditions of low water availability (Tommerup 1984).

Salts in the growth medium may induce changes not only in the length but also in other morphological properties of hyphae. High concentrations of $CaCl_2$, KCl or NaCl in the growth medium apparently shortened primary germ tubes and stimulated lateral branching of hyphae of *Gigaspora margarita,* while in high concentrations of $NaNO_3$ and Na_2SO_4, germ tube growth was "normal" (Hirrel 1981). Increasing the concentration of NaCl in the soil solution reduced the growth and increased the diameter of hyphae produced by spores of *Gigaspora decipiens* but did not affect the diameter of hyphae of *Scutellospora calospora* (Juniper and Abbott 1992).

Effects of water potential and salinity on the growth of hyphae of ecto and nonmycorrhizal fungi have been measured. However, it is not known if similar physiological processes occur in VA mycorrhizal fungi. The effect of PEG-moderated water potential on the growth of the ectomycorrhizal fungi *Cenococcum graniforme, Suillus luteus* and *Thelephora terrestris* have been investigated (Mexal and Reid 1973). It was observed that *C. graniforme* was tolerant of water potentials as low as -1.5 MPa, in which growth of the other two fungi was severely limited. Water potentials of the hyphae of all three fungi were measured with a thermocouple psychrometer and were in close agreement with the measured water potentials of the media in which they were grown.

Decreasing osmotic potential reduced rates of growth and respiration, increased oxygen requirements for growth and increased the lag phase before commencement of growth of colonies of *Geastrum* sp., *Fusarium moniliforme, Penicillium canescens* and *Phytophthora cinnamomi* (Wilson and Griffin 1975). Adebayo et al. (1971) showed that reduced growth of *Mucor hemialis* and *Aspergillis wentii* in low water potentials was not related to a reduction in the turgor pressure of the hyphae as they had expected, but was likely to have been due to an inhibitory influence of low internal osmotic potential. Decreased internal water potential may inhibit intracellular biochemical reactions and enzyme activities. It was suggested (Adebayo et al. 1971) that energy normally used for growth is diverted for osmoregulation, in media with low osmotic potentials. This is supported by the observation that oxygen consumption per unit of growth increased with decreasing water potential (Wilson and Griffin 1975). However, the observed phenomenon could also be due to disruption of oxidative processes in ATP synthesis and thus reduced efficiency of oxygen use at low water potentials. It has been argued that substrate cycles which dissipate energy are necessary processes when fungi are subjected to osmotic or water stress (see review by Jennings and Burke 1990).

The mechanisms of osmoregulation of VA mycorrhizal fungi are unknown. Adjustment of osmotic potential by uptake of sodium and chloride ions has been well documented in halophytic plants (Flowers et al. 1977). However, most osmophilic fungi have been shown to maintain low internal osmotic potentials by the synthesis of simple polyhedric alcohols such as glycerol, erythritol and mannitol rather than by ion uptake (Javor 1989). Polyols had not been found in VA mycorrhizal fungi until recently, when trace amounts of glycerol were detected in spores of *Glomus etunicatum, G. intraradix* and *Gigaspora margarita* isolates (Becard et al. 1991). The same study also established the presence of trehalose in spores of the three fungi.

Osmophilic fungi grown in media with high concentrations of solutes generally maintain low internal osmotic potentials by the synthesis of polyhedric alcohols, (Javor 1989; Jennings and Burke 1990), sugars (Luard 1982a,b) and possibly also of negatively charged amino acids (Javor 1989). In at least some osmophilic fungi, accumulation of glycerol and mannitol in response to osmotic stress is compatible with enzyme activity. In addition to their role in osmoregulation, these and other putative compatible solutes may be important contributors to the "energy spilling" substrate cycles mentioned above (Jennings and Burke 1990). The ability to actively take up potassium ions and to extrude sodium ions may also be an indicator of the halotolerance of some fungi (Javor 1989).

The relationship between osmotic and matric water potential in their effects on the growth of fungi is complex and varies according to the relative susceptibility of each organism to water stress and the toxic effect of specific ions. Optimum water potentials for the growth of both *Phytophthora cinnamomi* and *Alternaria tenuis* in agar and in soil were similar in matric and osmotically controlled systems (Adebayo and Harris 1971). However, at low water potentials both fungi were more tolerant of matric stress, probably indicating a toxic effect of high concentrations of solutes. This observation would depend on the susceptibility of a fungus to water stress, because if hyphal growth was highly sensitive to low water potentials, growth would be limited before

solute concentrations reached the critical level for ion toxicity. Growth of *P. cinnamomi* was inhibited less by PEG than by NaCl, KCl and $MgSO_4$ and more by PEG than by $CaCl_2$ and $MgCl_2$, in solutions of equivalent osmotic potential (Sterne et al. 1976). Growth of hyphae of *Fusarium oxysporum* has been observed to be inhibited by reduction of matric potentials from 0, stimulated by reduction of osmotic potentials from 0 to about −1.5 MPa and inhibited by osmotic potentials below −1.5 MPa (Brownell and Schneider 1985). In addition, temperature interacted differently with the effects of matric and osmotic potentials on the growth of hyphae of *F. oxysporum* (Brownell and Schneider 1985).

Effects of water potential and high concentrations of solutes on the growth of non-mycorrhizal fungi indicate that their ability to grow in saline conditions may depend on their ability to maintain low internal osmotic potentials either by uptake of ions or by synthesis of polyols. The relative importance of matric and osmotic stresses appear to differ between fungi and to be dependent on the composition and the concentration of the osmoticum.

Investigation into the physiological mechanisms of growth inhibition of VA mycorrhizal fungi in saline media as well as descriptive study, may provide some ability to predict those VA mycorrhizal fungi which are likely to be tolerant of high concentrations of particular solutes and of low water potentials.

The effect of salinity on the formation of mycorrhizas

When discussing the formation of mycorrhizas, it is often useful to distinguish between the initial or "primary" infection, which is the first entry into the root by the fungus, and "secondary" infection, which occurs after fungal hyphae have ramified from sites of initial colonization (Wilson 1984). Initial infection is dependent on (1) germination of spores or other fungal propagules; (2) growth of hyphae through the soil; and (3) entry into the plant root. Each of these stages can be a limiting step in the formation of mycorrhizas (Bowen 1987).

Secondary infection is influenced by the physiology of the host plant, because most of the energy for the spread of hyphae is obtained from photosynthates translocated from the plant to the fungus, either at the arbuscules or via the internal hyphae. Consideration of the effects of salinity on the formation of VA mycorrhizas must, therefore, include the effects of salinity on the growth of the host plant.

Plants growing in saline soil are subject to two distinct physiological stresses. Firstly, the toxic effects of specific ions such as sodium and chloride, prevalent in saline soils, which disrupt the structure of enzymes and other macromolecules, damage cell organelles, disrupt photosynthesis and respiration, inhibit protein synthesis and induce ion deficiencies (Epstein 1972).

Secondly, plants exposed to the low osmotic potentials of saline soil solutions are at risk of "physiological drought" because they must maintain still lower internal osmotic potentials in order to prevent water moving by osmosis from the roots into the soil. Plants may take up electrolytes in order to maintain low internal osmotic potentials, but this may result in "ion excess" which reduces growth of some plants (Greenway and Munns 1980). In addition, high concentrations of salt may cause a decrease in the permeability of the roots to water and hence lower the rate of water entry into the plant (Epstein 1972). Soil salinity may also interfere with uptake of cations such as calcium and magnesium (Bernstein 1975).

The effects of salinity on photosynthesis differ between plant species and also between plants at different stages of development. In general, however, photosynthesis of glycophytes is reduced by salinity, probably due to changes in the osmotic concentration of the leaf sap and thus water potential and stomatal aperture (Gale et al. 1967). In many nonhalophytes, the early stages of salt stress are associated with elevated concentrations of sucrose and/or starch in the shoots and roots, due to NaCl-induced disturbance of sucrose metabolism (Greenway and Munns 1980). In later stages of stress, carbohydrate concentrations tend to be lower (Greenway and Munns 1980), possibly as a result of interference with photosynthetic processes by the mechanisms described by Gale et al. (1967).

Since the fungus in a mycorrhizal symbiosis is dependent for its carbohydrate nutrition on photosynthesis by the host plant, modification of the availability of photosynthetic products would affect mycorrhizal development and function. This has been demonstrated by tests of the effect of light availability on VA mycorrhizal (Furlan and Fortin 1977) and ecto mycorrhizal (Piche and Fortin 1982) plants. The photosynthetic activity of the plant would be expected to affect the carbohydrate status of the root and, therefore, the amount of VA mycorrhizal colonization (Jasper et al. 1979; Thomason et al. 1990).

Plant-mediated reductions in levels of VA mycorrhizal colonization with increasing soil salinity may be due to physiological changes in the plants such as those described above which may directly affect their symbionts, or to an indirect effect on VA mycorrhizal fungi via influence on other soil parameters.

Most studies which have considered the effect of soil salinity on the plant-VA mycorrhizal fungus association have been concerned with identifying interactive effects of VA mycorrhizas and soil salinity on plant growth rather than with the effects of salinity on mycorrhiza formation. Experimental designs have, therefore, often not allowed plant-mediated effects on colonization and fungus activity to be distinguished from direct edaphic effects.

Despite the limitations on interpretation, several sets of data suggest that the formation of mycorrhizas may be reduced by increasing soil salinity (Table 2). However, other workers have observed no effect of salinity on the formation of mycorrhizas (Table 2).

Where increasing salinity produced no change in the percentage of roots which were mycorrhizal but de-

Table 2. The effect of soil salinity on colonization of plant roots by VA mycorrhizal fungi

Range of salinity	Host plant	Fungus species	Effect of salinity on plant growth	References
Studies in which colonization was reduced by salinity				
1–9 dS m^{-1}	*Allium*	*Glomus deserticola*	Roots, shoots reduced	Poss et al. (1985)
1–12 dS m^{-1}	*Allium*	*G. fasciculatus* *Gigaspora margarita*	Roots, shoots reduced	Hirrel and Gerdemann (1980)
1–12 dS m^{-1}	*Capsicum*	*G. fasciculatus* *G. margarita*	Roots, shoots reduced	Hirrel and Gerdemann (1980)
0.06–0.41 MPa (soil solution)	*Allium*	*G. fasciculatus* *G. monosporus*	Shoots reduced, roots unknown	Ojala et al. (1983)
0.025–0.1 mol l^{-1} NaCl (soil solution)	Citrange	*G. intraradices*	Roots, shoots reduced	Duke et al. (1986)
0–0.3 mol l^{-1} NaCl (soil solution)	*Aster*	Unknown	Unknown	Rozema et al. (1986)
Studies in which colonization was not reduced by salinity				
0–2.7 dS m^{-1} (water)	Citrus	Unknown	Unknown	Levy et al. (1983)
0–0.15 mol l^{-1} NaCl (soil solution)	Citrus Citrange	*G. intraradices*	Shoots reduced, roots unaffected	Hartmond et al. (1987)

creased total root growth (Poss et al. 1985), the total length of mycorrhizal root decreased with increasing salinity.

Where increasing salinity was associated with a decrease in shoot growth and thus a reduction in the photosynthetic area of the plant (Hirrel and Gerdemann 1980; Ojala et al. 1983; Poss et al. 1985), growth of both plant and fungus could be limited by a reduction in availability of photosynthates, brought about by the effects of water stress or toxic ions on plant growth. Plant and VA mycorrhizal fungus may effectively be in competition for photosynthates (Buwalda and Goh 1982). As concentrations of toxic ions in the soil increase and become a more important limitation on plant growth, the availability of nutrients such as phosphorus would be expected to become a progressively less important limitation. Under these conditions, expenditure of photosynthates by the plant for maintenance of the fungus produces a diminishing return unless, as has been suggested by some workers (Allen et al. 1981), there are non-nutritional benefits of VA mycorrhizas to the plant.

The electrical conductivity of soil water had little or no effect on the number of VA mycorrhizas in the roots of citrus trees (Levy et al. 1983). However, salt treatments were applied as saline water to 4-year-old trees in orchard soil with a native population of VA mycorrhizal fungi and, therefore, the trees were presumably colonized prior to the imposition of the salt stress. Similarly, in other studies the salinity treatments were imposed after mycorrhizas had formed (Poss et al. 1985; Duke et al. 1986; Rozema et al. 1986). In another study (Pfeiffer and Bloss 1988), mycorrhizal seedlings were transplanted into saline soil. In all these cases, sufficient time elapsed between inoculation and imposition of the salinity stress to allow colonization to occur; therefore, the effect of salinity on initial formation of mycorrhizas could not be assessed.

No effect of salinity up to 0.15 mol l^{-1} was observed on either root growth or mycorrhizal colonization of citrus and citrange seedlings inoculated with a mixture of chopped root and spore inocula of *Glomus intraradices* and grown in a soil-less medium (Hartmond et al. 1987). In this experiment, the salt treatments were added incrementally to reduce osmotic shock. The inconsistency between the results of Hartmond et al. (1987) and Duke et al. (1986) (Fig. 2) is particularly interesting because these studies used similar ranges of salinity and both used citrange plants and isolates of *Glomus intraradices*. Duke et al. imposed the salinity treatments for 8 weeks, commencing when the mycorrhizal seedlings were 10 weeks old. Hartmond et al. maintained the salinity treatments for 24 days, commencing when the mycorrhizal seedlings were 6 months old. In the latter study, therefore, there was much more opportunity for mycorrhizas to develop in the absence of salinity stress. Even if imposition of the salt treatments

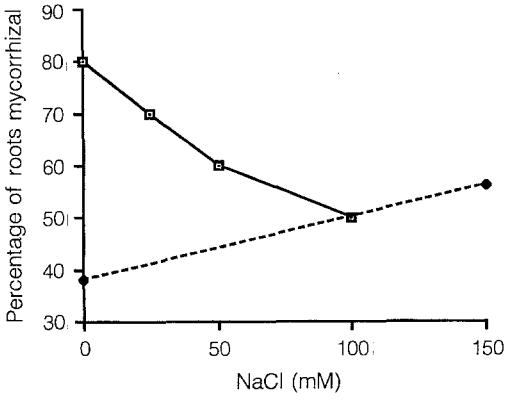

Fig. 2. The effect of NaCl on the percentage of citrange roots colonized by *Glomus intraradices* in two separate studies, Duke et al. 1986 (——) and Hartmond et al. 1987 (– – –)

Table 3. The effect of NaCl on percentage root length of guayule roots colonized by *Glomus intraradices* (from Pfeiffer and Bloss 1988). NaCl treatments are: +NaCl (750 mg NaCl per kg soil) and −NaCl (no salt added). Values for intensity of colonization are relative scores based on 80 visual observations per plant

Treatment	Fungal structures present			
	Hyphae	Arbuscules	Vesicles	None
−NaCl	8.1	54.4	32	5.6
+NaCl	14.8	37.7	10.6	36.9
	Intensity of colonization			
	Light	Moderate	Heavy	
−NaCl	18.1	24.7	51.7	
+NaCl	17.2	12.5	33.4	

had retarded the growth of soil hyphae and thus formation of new entry points, colonization density could have continued to increase via growth of hyphae in the intercellular spaces of the root cortex. In addition, the isolates of *Glomus intraradices* used in the two studies may have differed in their ability to grow in the presence of NaCl (Estaun 1991).

The effect of salinity on the intensity of colonization and occurrence of vesicles and arbuscules has been quantified in one study (Pfeiffer and Bloss 1988) (Table 3). Plant growth was not affected by addition of NaCl. NaCl reduced the incidence of fungal arbuscules and vesicles but did not reduce the growth of hyphae in the roots. The intensity of colonization also decreased with increasing NaCl. Unfortunately, data for percentage and total length of mycorrhizal root were not presented.

Where salinity treatments have been introduced in one application (Poss et al. 1985; Duke et al. 1986; Pfeiffer and Bloss 1988), the fungus was subjected to osmotic shock when the salt treatments were imposed, which may have caused turgor loss and desiccation of fine hyphae.

The staining techniques commonly used to quantify VA mycorrhizal colonization in root segments do not allow living or active fungal structures to be distinguished from dead or inactive fungal material (Harris and Paul 1987). These techniques may thus give inadequate estimates of fungal activity, especially where soil treatments could have resulted in damage to or death of hyphae. Assessment of colonization at a single harvest compounds this problem, particularly where treatments have been imposed after the symbiosis is established.

A reduction in root growth with increasing salinity (Hirrel and Gerdemann 1980; Ojala et al. 1983; Poss et al. 1985) may lower the probability of contact between roots and fungal hyphae and thus decrease colonization levels. Early in the growth cycle, the percentage colonization of roots should be independent of root density. However, after initial mycorrhizas have formed, the probability of secondary hyphae encountering and infecting roots may be dependent on root density (Abbott and Robson 1984). Application of salt to the soil surface decreased the occurrence of VA mycorrhizas on established *Acer* trees (Guttay 1976). Salt in the soil may have had a direct effect on the fungi or it may have reduced colonization indirectly via its deleterious effect on root growth in surface soil.

Despite the extensive investigations of interactive effects of soil salinity and mycorrhizas on the growth of plants, there are clearly large deficiencies in our knowledge of the effects of salinity on the formation of mycorrhizas. Work is needed which emphasises the growth and physiology of the fungal symbiont in saline conditions.

Effects of salinity on sporulation

There are no published reports of investigations into the effect of soil salinity on spore production by VA mycorrhizal fungi. If soil salinity reduces spore germination, hyphal growth and formation of mycorrhizas, then total spore production is likely to be reduced in saline relative to non-saline soils unless salt stress stimulates sporulation, as occurs in some Mucorales and *Aspergillus* species (Tressner and Hayes 1971). There has been some experimentation on the effect of water availability on sporulation by VA mycorrhizal fungi, but beyond indicating differences in the requirements of different fungi, the results are inconclusive.

Spore production by some VA mycorrhizal fungi may be increased by drought. *Glomus mosseae* and *Gigaspora margarita* produced 40% more spores after 18 weeks in pots from which water had been withheld for 9 days during incubation (Sylvia and Schenck 1982). However, spore production by *Glomus clarum* was not affected by this treatment.

In contrast, sporulation by some VA mycorrhizal fungi may be reduced by water deficit. Sieverding and Toro (1988) examined the effect of soil water regime on the growth of *Cassava* plants inoculated with seven different VA mycorrhizal fungi and counted spore numbers in the pots at the conclusion of the experiment (Table 4). There were two water treatments: "wet", in which soil was maintained at field capacity (33% water content), and "dry", in which pots were initially watered to field capacity, allowed to decline to 15% water content and re-watered to field capacity. Total numbers of *Acaulospora longula* and *Entrophospora colombiana* spores were significantly reduced in the dry relative to the the wet treatments. Since the dry treatment reduced dry matter production and the length of root colonized by each fungus, it would be reasonable to expect spore production to be reduced in these pots. When spore production is expressed as a ratio of spore number and length of mycorrhizal root, the differences between values obtained by the two treatments are eliminated or substantially reduced.

Interpretation of these data also requires knowledge of the relationship between sporulation and levels of root colonization for each fungus (Gazey et al.

Table 4. The effect of watering regime on numbers of spores recovered from soil inoculated with seven VA mycorrhizal fungi. Watering regimes were: "wet" (soil maintained at field capacity) and "dry" (soil initially at field capacity, allowed to dry to field capacity then re-watered). (From Sieverding and Toro 1988)

Fungus	Length infected roots per plant (m)		Spores per 100 g dry soil		Spores per m infection	
	Wet	Dry	Wet	Dry	Wet	Dry
Acaulospora longula	100	10.2	2120	292	21.2	29.2
A. myriocarpa	15.7	7.2	3900	94	24.8	13.1
Entrophospora colombiana	126.8	51.1	31265	5600	246.6	109.6
Glomus fasciculatum	35.7	16.3	150	83	4.2	5.1
G. manihotis	157.8	80.3	2714	350	17.2	4.4
G. occultum	117.2	30.6	790	325	6.7	10.6
Scutellospora heterogama	2.1	2.1	12	48	5.7	22.8

1992). No attempt was made to distinguish between spores placed in the pots as inoculum and spores produced during the experiment.

Interactions between soil salinity and other edaphic factors on VA mycorrhizal fungi

So far in this review, soil salinity has been discussed as an isolated stress on plants and fungi. In the field, several environmental stresses on organisms commonly occur simultaneously and are often interactive in their effects.

Waterlogging

Soil salinity and waterlogging frequently co-occur in low-lying areas. Plant roots and soil organisms are likely to be subjected to periods of anoxia in waterlogged soil, preventing aerobic respiration and, therefore, limiting growth of aerobes. There have been no studies of the possible interactive effects of waterlogging and soil salinity on the growth of VA mycorrhizal fungi.

Spores of VA mycorrhizal fungi germinate readily at or near zero water potential, i.e. in waterlogged conditions. However, a distinction should be drawn between waterlogging and the often associated conditions of anoxia and increased concentrations of ethylene and carbon dioxide (Bowen 1987). The observed effects of oxygen deficit and excessive carbon dioxide may be similar but the physiological consequences of the stresses may differ. Spores of *Glomus mosseae* did not germinate at oxygen concentrations below 0.4% unless they had been pre-incubated in air, but were not affected by 5% carbon dioxide (Le Tacon et al. 1983). The growth of hyphae from pregerminated spores was suppressed by a reduction in oxygen supply and also by increased concentrations of carbon dioxide. The suppressive effects of low oxygen concentration were reversed after spores were returned to air (21% oxygen) but the suppressive effect of carbon dioxide on growth of hyphae persisted after post-incubation in air (Le Tacon et al. 1983).

Activity of VA mycorrhizal fungi has been observed to increase in response to increased availability of oxygen (Saif 1981, 1983). Increased aeration of soil to a concentration of 16% oxygen resulted in increased production of vesicles by *Glomus macrocarpus* (Saif 1983). *G. macrocarpus, G. mosseae* and an unidentified VA mycorrhizal fungus produced more vesicles in 2% oxygen than in unaerated control soil (Saif 1983). However, oxygen increased the growth of the host plants, possibly increasing the availability of carbon substrates to the fungus and contributing to the observed effect.

If fungal osmoregulation is an energy-expensive process, as suggested by Adebayo et al. (1971), then reduced availability of oxygen would be expected to diminish the capacity of VA mycorrhizal fungi to grow in saline environments. Propagules of VA mycorrhizal fungi and mycorrhizal plant roots have been observed in inundated saline marshes (Rozema et al. 1986; Cooke and Lefor 1990; Sengupta and Chaudhuri 1990). None of these workers reported anoxic conditions in the marshes they sampled but it is likely that marsh soils become anaerobic at least during part of the year, since oxygen diffuses through water at approximately one-tenth the rate at which it diffuses through the air in a soil. In constantly inundated sediments, the oxygenated layer may be no more than a few millimeters deep (Jorgensen and Revsbach 1985). In addition, as the concentration of salts in a solution increases, the diffusivity and solubility of gases decrease; thus saline marsh soils are likely to become anoxic more quickly when inundated than are soils under non-saline marshes. A survey of halophytes in a Dutch salt marsh found that plant species in which VA mycorrhizas were not observed tended to be those growing in the lower part of the marsh, which was frequently inundated with seawater (Van Duin et al. 1989). The percentage of roots colonized by VA mycorrhizal fungi has been observed to be reduced by increased frequency of irrigation (Levy et al. 1983). Reduced availability of oxygen may have been the limiting factor in both the above studies but this parameter was not measured. VA mycorrhizas may form on some wetland plants only in seasons when the soil is not waterlogged (Cooke and Lefor 1990). Some species or isolates of VA mycorrhi-

zal fungus may be adapted to grow in conditions of low oxygen availability, but this has not been demonstrated.

Soil texture and structure

Two other factors that may interact with soil salinity in its effect on VA mycorrhizal fungi are soil texture and structure, due to their influences on soil hydrology. In an unsaturated soil, water retention and conductance are directly dependent on pore space and size. The suction at which water is held in the soil and against which organisms must take up water is inversely proportional to pore size.

Matric potentials of field soil fluctuate daily due to inflow and outflow of water and to temperature variations. As water is removed from a soil by plants or by evaporation, the matric potential becomes more negative in a relationship dependent on the pore size of the soil. The osmotic potential also decreases in proportion to the increase in concentration of the soil solution as water is removed. The ability of spores to take up water from soil at a given matric potential is, therefore, reduced if the water is salty.

At a given (unsaturated) water content, organisms can more easily take up water from a sandy soil than from a soil with a high clay content; therefore, at a given water content and salt concentration, the effects of marginal salinity on water uptake might be expected to be most severe where the soil has a high clay content. However, water availability to a spore will also be influenced by the zone of contact between the spore and the soil, which in turn depends on the pore size distribution of the soil. The spores of VA mycorrhizal fungi are much larger than water-filled pores under most field conditions. As a soil dries, impedance to the movement of water at the spore-soil interface increases and the surface area of the spore wall which is wetted decreases (Tommerup 1984). At a given matric potential, contact impedance increases with increasing coarseness of structure or texture (Tommerup 1984). Spore germination has been observed to decrease as the proportion of large soil crumbs increased in soils of equivalent matric potential (Tommerup 1984).

Other micro organisms

VA mycorrhizal fungi are one group of a suite of organisms that inhabit the rhizosphere and surrounding soil. The activity of other soil organisms may influence the survival and reproduction of VA mycorrhizal fungi either directly or indirectly via effects on the growth of host plants (see review by Bagyaraj 1984). Direct influences include those of the "companion fungi" described by Williams (1985), bacterial epiphytes (Mosse 1962), parasitic microflora (Ross and Ruttencutter 1977) and predatory microfauna (Warnock et al. 1982). High concentrations of salts in the soil solution tend to alter the composition of the microflora and microfauna in the bulk soil. In addition, water stress produces changes in root exudation (Rovira 1969) which may alter the composition of the microflora (Hale et al. 1971) and microfauna in the rhizosphere.

Changes in the availability of water may produce physiological changes in VA mycorrhizal fungi which influence associated microorganisms. The occurrence of *Fusarium, Penicillium, Trichoderma* and *Chaetomium* species associated with spores of *Glomus* spp. was greater at low water potentials than in moist soil. The abundance of contaminating fungi was negatively correlated with germination of spores under some conditions (Sylvia and Schenck 1983).

There are no published data on the influence of the activity of other soil microorganisms on the growth of VA mycorrhizal fungi in saline soils.

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