OCCURRENCE AND ECOLOGICAL SIGNIFICANCE OF VESICULAR ARBUSCULAR MYCORRHIZA IN THE SALT MARSH ENVIRONMENT

J. ROZEMA, W. ARP, J. VAN DIGGELEN, M. VAN ESBROEK, R. BROEKMAN and H. PUNTE

Vakgroep Oecologie en Oecotoxicologie, Biologisch Laboratorium, Vrije Universiteit, De Boelelaan 1087, 1081 HV Amsterdam

SUMMARY

The infection by vesicular arbuscular mycorrhizal fungi (VAM) of various salt marsh plant species has been estimated and compared. This kind of infection appeared to be high or intermediate and frequent in *Aster tripolium, Plantago maritima, Glaux maritima* and *Festuca rubra* ssp. *litoralis,* rare or absent in *Spartina anglica, Triglochin maritima, Juncus gerardii, J. maritimus, Atriplex hastata* and *Suaeda maritima* and variable or intermediate in *Salicornia dolichostachya* and *S. brachystachya.*

The sodium content of shoots of mycorrhizal *Aster tripolium* plants was lower than of nonmycorrhizal plants when grown at 300 mM NaCl. The potassium and phosphorus content of the shoot was not significantly affected by the presence of mycorrhiza. Improved growth of mycorrhizal plants of *Aster tripolium* under salinity stress could be related to increased leaf elongation and to smaller diurnal changes in the leaf thickness. Both parameters indicate increased water uptake by mycorrhizal roots. The causes of increased water uptake in mycorrhizal plants are discussed in terms of reduced root resistance to water transport and its consequences for prolonged stomatal opening and increased photosynthesis.

1. INTRODUCTION

The occurrence of vesicular-arbuscular mycorrhiza (VAM) is widespread in many plant species from different habitats, including agricultural plant species (MOSSE 1975, SANDERS et al. 1975). The association between the particular soil fungi involved and plant roots is symbiotic with limited inter and intracellular fungal spread within the root system, usually leading to improved growth of the host plant (SANDERS et al. 1975, ROVIRA et al. 1983). In habitats with a poor nutrient status mycorrhizal plants show enhanced nutrient (e.g. N, P.) concentrations due to extra absorbtion by fungal hyphae (SANDERS & TINKER 1971). In salt marshes, more or less frequently flooded with seawater, nutrient deficiency is not the primary factor limiting plant growth (ROZEMA et al. 1985a).

Variation of salinity and flooding governs interspecific and intraspecific plant relationships in salt marsh ecosystems (ROZEMA et al. 1985a, SCHOLTEN & ROZEMA 1986). Salinity stress consists of ion toxicity and reduced water availability. Salt-resistant plants can usually regulate uptake of sodium and chloride (salt-exclusion versus salt-accumulation, GREENWAY & MUNNS 1980) but may also

have an efficient water economy. The possible role of VAM in the reduction or alleviation of stress due to excess salt, anaerobiosis and reduced water availability is only partly understood (ALLEN et al. 1981, BACH, ALLEN & CUNNINGHAM 1983). The purpose of the present study was to describe the occurrence of VAM in salt-marsh species, relate it to salinity and flooding conditions, and to assess the ecophysiological significance of this symbiosis.

2. MATERIALS AND METHODS

2.1. Field observations

In May 1983 salt-marshes near Bergen op Zoom (51°39′N, 4°19′E) and Kwade Hoek (51°49′N, 3°59′E), see ROZEMA et al. 1978 for a description, were sampled for mycorrhiza of salt marsh species. Plant roots and adhering soil (15 cm deep) were collected in plastic bags and transported to the laboratory. Here the roots were rinsed with tap water to remove soil particles, and fixed for at least 24 h in a 10% KOH solution. They were then stained in 0.05% trypan blue in a lacto-phenol solution (48 h), rinsed with distilled water and then examined for mycorrhiza (PHILLIPS & HAYMAN 1970). The degree of mycorrhization was measured by assessing the percentage of root length segments (0.5 mm) with internal mycelium (hyphae, vesicles and arbuscules) along the first 30 mm from the root tip (GIOVANNETTI & MOSSE 1980, cf. ERNST et al., 1984). Per plant species ten pieces of roots were analysed for mycorrhization. Also the presence of external hyphae and spores was assessed.

2.2. Greenhouse and climate room experiments

Seed of *Aster tripolium* was collected in 1982 in the Bergen op Zoom salt marsh, and germinated on filter paper in plastic trays (30 × 30 × 10 cm³) on rubber foam floating on distilled water. Sandy soil (containing roots of different salt marsh species) from the salt marshes near Bergen op Zoom (middle marsh) was dried in the air and thoroughly mixed. The salt marsh sand thus obtained was steam-sterilized.

Before steaming the roots, present in the salt marsh soil, were removed and chopped up and used as a mycorrhizal inoculum. Seedlings were precultured for three weeks in nutrient solution. Fresh inoculum (5 gram) was added to half of the pots containing 100 g steam-sterilized salt marsh sand. The salinity of this sand was 100 mM NaCl and stepwise addition of sodium chloride resulted in a concentration of 300 mM NaCl. The precultured seedlings were transferred to these pots and grown in the greenhouse with a 16 h light, 20°C (300 $\mu E.m^{-2}.s^{-1}$)/8 h dark (20°C) regime. Transplanted seedlings of *Aster tripolium* transferred to pot culture recovered more rapidly from wilting when growing on sterilized soil with VAM inoculum added. Only when plants in both the mycorrhizal and non-mycorrhizal treatment had become fully turgescent (cf. LEVY & KRIKUN 1980), NaCl in the soil moisture was increased to 300 mM NaCl. The experiments were done with five replications (plants) per treatment.

2.3. Leaf elongation rate and leaf thickness measurement

Leaf elongation and leaf thickness measurements were done in a climate room (20 °C day and night, 300 μE m^{-2}s^{-1} (Philips HPIT lamps), 75% RH and a 12 h light, 12 h dark regime). Comparisons were always made between leaves in the same developmental phase. Four pairs of mycorrhizal and non-mycorrhizal plants were monitored for leaf elongation and leaf thickness. Data given in *fig. 3* are representative for these analyses.

Leaf elongation rate was measured clipping a thin copper wire to the youngest emerging leaf from the rosette of *Aster tripolium*, and stretched over a wheel connected to a 10 g counter weight. Leaf elongation results in the rotation of a potentiometer (Duncan 2201 servopotmeter) axle with a voltage output connected to a Kipp BD 41 mV recorder linearly related to the leaf length growth. Continuous recording was realized using a Kipp double channel multivoltrecorder. The method used is essentially the same as described by KLEINENDORST & BROUWER (1970). Leaf thickness was measured using a related set up, but with much greater sensitivity, using a Blue Pot CP-24 rotation potentiometer, with a low rotation resistance as described elsewhere (ROZEMA et al. 1986).

2.4. Chemical analysis

Plants were weighed at harvest (after four weeks of growth), thoroughly rinsed with distilled water, dried overnight (80 °C) and digested with a HClO$_4$/HNO$_3$ mixture. Cations were measured using a Perkin Elmer 4000 Atomic Absorption spectrophotometer. Phosphate was determined colorimetrically according to CHEN et al. (1951).

The results were statistically analysed and values of the Least Significant Difference (L.S.D.) were calculated at $\alpha = 0.05$, according to SOKAL & ROHLF (1969).

3. RESULTS

3.1. Field observations

There is a substantial degree of variation in VAM percentages among some twenty salt marsh halophytes sampled in spring 1983 (*table 1*). Some of the species show a high or intermediate degree of infection by VAM fungi (*Aster tripolium, Limonium vulgare, Festuca rubra* ssp. *litoralis, Salicornia brachystachya, S. dolichstachya, Plantago maritima*), other species have a very low percentage or absence of infection by VAM-fungi their hyphae in the root segments (*Atriplex hastata, Juncus gerardii, J. maritimus, Spartina anglica, Cochlearia anglica, Spergularia maritima* and *Triglochin maritima*), while other species have an intermediate degree of infection by mycorrhizal fungi (*Glaux maritima, Puccinellia maritima*).

3.2. Greenhouse experiment

Because VAM structures were found to be usually present and easy to detect in *Aster tripolium*, this species was chosen to investigate the effect of experimentally increased soil salinity and anaerobiosis on infection by VAM fungi and
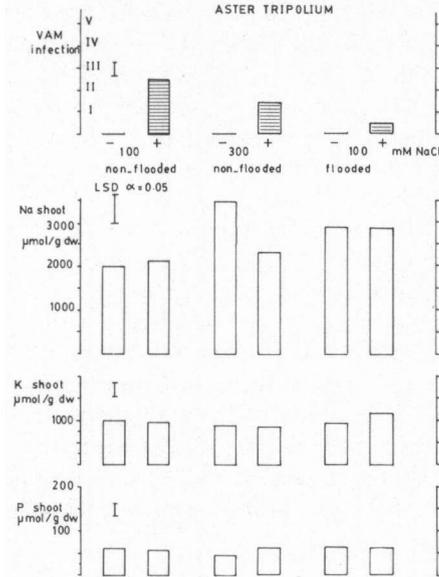
Fig. 1. A. Degree of mycorrhization of the root system of *Aster tripolium* plants after three weeks of growth in sterilized salt marsh soil without (−) or with (+) VAM inoculum added and with variation of soil salinity (mM NaCl) and flooding conditions. B. Mineral content (mmol Na, K/g dw of the shoot. Average values of four replications with L.S.D. calculated at $\alpha = 0.05$.

on the growth response of this halophyte. Although increased soil salinity (300 mM NaCl) slightly reduces such infection of *Aster tripolium* roots (*fig. 1*), growth of mycorrhizal *Aster tripolium* is less depressed compared to the growth of nonmycorrhizal seedlings (*fig. 2*).

In an experiment with seedlings of *Aster tripolium* either growing in steam-sterilized salt marsh soil without (-VAM) or with inoculum added (+VAM), both soil salinity and flooding conditions were varied (*fig. 1*). After three weeks of growth, infection by VAM fungi of *Aster tripolium* seedlings in salt marsh (100 mM NaCl) sand was between 1 and 5% in the inoculated group, while no VAM could be detected in *Aster* seedlings on steam-sterilized soil.
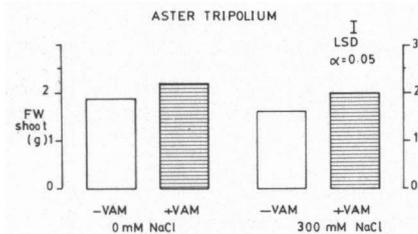

Fig. 2. The influence of VAM on the growth response to increased soil salinity of seedlings of *Aster tripolium* grown on sandy salt marsh soil. Average values of four replications.
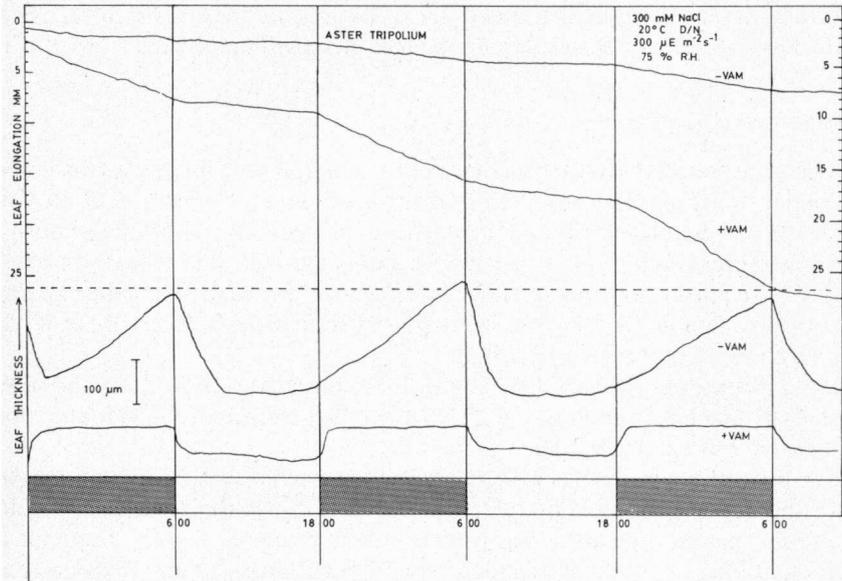
Fig. 3. Diurnal variation of leaf elongation (mm) and leaf thickness (mm) of VA mycorrhizal (+) and non-mycorrhizal (–) seedlings of *Aster tripolium*, growing in sandy salt marsh soil (300 mM NaCl) in a climate room.

With soil salinity increased from 100 mM to 300 mM NaCl, infection by VAM fungi was reduced, but less than due to flooding conditions (*fig. 1*). There was no significant change of the phosphorus and potassium content of the shoot tissue of non-mycorrhizal and mycorrhizal plants under the salinity or inundation treatment (*fig. 1*). The sodium content of mycorrhizal plants grown at 300 mM NaCl under non-flooded conditions was lower than in non-mycorrhizal plants. Lower sodium concentrations were observed in the low salinity treatment (100 mM NaCl). There was an increase of the sodium content in the flooded plants at 100 mM NaCl, but no difference between mycorrhizal and non-mycorrhizal plants.

3.3. Leaf elongation and leaf thickness measurements
In another experiment with mycorrhizal and non-mycorrhizal plants cultured in a climate room, leaf elongation and leaf thickness was continuously recorded (*fig. 3*). Leaf elongation of plants grown at 300 mM NaCl during the light period exceeds daytime values, a phenomenon frequently observed for Dicotyledon plant species (ROZEMA et al. 1986). Leaf elongation is higher in mycorrhizal plants than in non-mycorrhizal plants.
Variation of the leaf thickness also follows a diurnal rhythm (*fig. 3*), with swelling in de dark when the stomata are closed. Water loss through open stomata during the day results in shrinking of the leaves. In mycorrhizal plants the leaves shrink less during the light period and swell more rapidly in the dark period, compared to non-mycorrhizal plants grown at 300 mM NaCl (*fig. 3*). Both the

variation of leaf elongation and leaf thickness indicate that mycorrhizal plants suffer less from the water stress component of increased salinity (300 mM NaCl).

4. DISCUSSION AND CONCLUSIONS

Vesicular-arbuscular mycorrhiza represent a common root-fungus symbiosis occurring in many plants groups in a wide range of habitats (MOSSE 1975, ROVIRA et al. 1983). Vesicular-arbuscular mycorrhiza are generally reported to improve the mineral nutrition of plant species, including agricultural crops (SANDERS et al. 1975). In particular, uptake of phosphorus is enhanced in mycorrhizal plants (SANDERS & TINKER 1971). More recently, improved drought tolerance by VAM has been reported (ALLEN et al. 1981).

Early inventories (MASON 1928, FRIES 1944, BOULLARD 1958, 1964 and more recently KHAN 1974 and PUGH 1979) revealed the presence of VAM in the roots of different salt marsh species.

The present paper reports differences in the presence of VAM in halophytes from the upper and lower marsh parts (*table 1*). Since the zonated character of the salt marsh vegetation can primarily be considered to be a response to a gradient of the environmental factors salinity and inundation (ROZEMA et al. 1985a), soil salinity and anaerobiosis can be reasonably considered as possible factors determining the presence of VA mycorrhiza in salt marshes.

As a rule, both soil salinity and anaerobiosis decrease along a transect from the lower to the upper parts of a salt marsh. Therefore one could expect more mycorrhizal plant species with a higher degree of infection in the upper marsh zone, but this is not readily confirmed by the data presented in this paper. There is a difference in mycorrhization between plant species in general, and this can be expected among salt marsh halophytes too.

Although VAM fungi are neither generally host nor habitat specific (MOSSE 1975), differential sensitivity to saline and flooding conditions of species of VAM fungi cannot be ruled out beforehand. VAM fungi seem to be more habitat specific than host specific. In salty primary coastal dunes NICOLSON & JOHNSTON (1979) found the common species *Glomus fasciculatus* as the endophyte in *Agropyron junceiforme*. The same *G. fasciculatus* was found in the C-4 grass species *Bouteloua gracilis* of arid rangeland (ALLEN & BOOSALIS 1983), as well as in the salt-tolerant desert grass *Distichlis spicata* (BACH ALLEN & CUNNINGHAM 1983). These data suggest that the same VAM could occur in the lower and upper parts of salt marshes. The zonation of salt marsh halophytes is not clearly followed by a gradation in the appearance of VA mycorrhiza (*table 1*), since both the group of lower and upper marsh species differ markedly with respect to the presence of VAM. Perhaps a quantitative analysis of mycorrhiza comparing VAM in plants of the same plant species in the lower and upper marsh could illustrate the influence of soil salinity and anaerobiosis on VAM infection.

KIM & WEBER (1985) report the presence of VAM in West-American desert halophytes *Salicornia pacifica* and *S. rubra,* where the degree of mycorrhization decreased with a high soil salinity.

Table 1. The degree of infection by vesicular arbuscular mycorrhizal fungi (percentage in three root samples), the occurrence of external hyphae, vesicles and spores in salt marsh plants from Bergen op Zoom, I (51°29′N, 4°19′E) and Kwade Hoek, II (51°49′N, 3°59′E), collected in May 1983.

Species	% infection	external hyphae	vesicles	spores	
I. Bergen op Zoom salt marsh					
Ameria maritimia	0	0	0	0	U
Aster tripolium	II-III	–	–	0	M
Atrix hastata	0	0	0	0	U
Cochlearia anglica	0	0	0	0	U
Festuca rubra ssp. *litoralis*	I	–	–	0	U
Glaux maritima	I	–	0	0	M
Halimione portulacoides	0-I	0	0	0	M
Juncus gerardi	0	0	0	0	U
Juncus maritimus	0	0	0	0	U
Limonium vulgare	I-II	–/+	0	0	M
Plantago maritima	III	–	0	0	M
Salicornia brachystachya	I-II	–	0	0	M
Salicornia dolichostachya	II-VI	+ +	0	–	L
Spartina anglica	0	0	0	0	L
Spergularia maritima	0	0	0	0	M
Suaeda maritima	I	–	0	–	L
Triglochin maritima	0	0	0	0	M
II. Kwade Hoek salt marsh					
Atriplex hastata	0	0	0	0	U
Cochlearia anglica	0	0	0	0	U
Festuca rubra ssp. *litoralis*	III-VI	+	–/+	0	M
Glaux maritima	I-II	–/-	0	0	M
Plantago maritima	III-V	+ +/+ + +	–/+	0	M
Puccinellia maritima	II	–/-	0	0	L
Salicornia brachystachya	0-I	0/–	0	0	M
Suaeda maritima	0-I	–	0	0	L

% infection	external hyphae	vesicles	spores
0 = 0%	0 = 0	0 = 0	0 = 0
I = <0.1%	– = 1–10	– = 1–10	– = 1–5
II = 0.1 t/m 1%	- = 11–15	- = 11–30	- = 6–10
III = 1 t/m 5%	+ = 16–20	+ = 31–50	+ = 11–15
IV = 5 t/m 10%	+ + = 21–25	+ + = 51–90	+ + = 16–20
V = 10 t/m 20%	+ + + = >25	+ + + = >90	+ + + = >20
VI = 20 t/m 30%			

In the present study, using an inoculum consisting of plant roots from the middle marsh, experimentally raised soil salinity did not significantly decrease the infection by VAM fungi in *Aster tripolium* (*fig. 1A*), which agrees with results established for *Glaux maritima* and *Festuca rubra* ssp. *litoralis* (Rozema et al.

1985b). Waterlogging conditions on the other hand, even at relatively low salinity, depressed infection by VAM fungi in *Aster tripolium,* but not in *Glaux* and *Festuca* (ROZEMA et al. 1985b). In this respect, the presence of a well-developed system of air chambers in the root system may well reduce primary (low oxygen tension) and secondary anaerobiosis stress (accumulation of reduced and toxic substances like Fe (II) and Mn (II), not only to the plant itself, but also to its VA mycorrhizal endophyte. A comparison can be made between the presence and degree of mycorrhization and the amount of aerenchyma in root tissue of salt marsh halophytes (ROZEMA et al. 1985b). A high degree of mycorrhization in *Aster tripolium* is related to a well developed aerenchyma in this species. However, high values of the root porosity in *Spartina anglica, Juncus gerardii* and *J. maritimus* are not accompanied by any presence of VAM. Their mycorrhizal status is unexplained, but is in accordance with other observations on Juncaceae (MASON 1928, FRIES 1944). The lack of mycorrhiza in *Triglochin maritima* (with an aerenchyma system developed) can possibly be ascribed to resistance of fungal infection, based on the presence of the toxic cyanogenic glucosides and sulphurous substances (cf. BOULLARD 1964). The absence of mycorrhiza on the Cruciferae species *Cochlearia anglica* is in accordance with the more general non-mycorrhizal status of this family (HIRREL et al. 1978). In addition to this, *Cochlearia anglica* is a winter annual developing from the late autumn to spring in low temperatures with hampered VAM-fungal spore germination and hyphal growth.

The absence of VAM in Chenopodiaceae species, discussed by HIRREL et al (1978) seems to be less absolute, considering the data in this paper for *Salicornia* species, although the degree of mycorrhization was low, (cf. KIM & WEBER 1985). More generally ERNST et al. (1984) explained the absence or low degree of mycorrhizal infection in dune (winter) annuals to unfavourable temperatures of the winter period.

Although nutrient deficiency (N-deficiency in particular) may locally occur in salt marshes, nutrients other than the excessive levels of Na and Cl are not likely to limit primarily the growth of salt marsh halophytes (ROZEMA et al. 1985a). In mycorrhizal *Aster tripolium* plants, there was no significantly enhanced phosphorus and potassium concentration in the shoot under the salinity and inundation treatment applied.

Seawater salinity (about 500 mM NaCl) may not only cause NaCl toxicity; its osmotic stress to the plant is considered to be significantly related to growth reduction at increased salinity in halophytes (GREENWAY & MUNNS 1980, ROZEMA et al. 1985a, 1986). In salt marshes and other habitats with reduced availability of water, like deserts, the importance of VAM could lie in the improvement of the water relations of the plant (ALLEN et al. 1981).

Depression of leaf elongation during the day is a consequence of stomatal opening, necessary for CO_2 uptake, but unavoidably leading to water loss through evaporation, eventually causing a fall of turgor pressure potential. The turgor pressure potential is restored during the dark period when stomata close and water loss through transpiration is strongly reduced (ROZEMA et al. 1986).

Leaf elongation, a sensitive indicator of response to water stress (CUTLER et al. 1980, TYREE & JARVIS 1982), was increased by VAM on *Aster tripolium*. The recovery from leaf shrinking during the day in the dark period, took place more rapidly in infected than in non-mycorrhizal plants. Both observations indicate an improved water uptake in mycorrhizal roots. Measuring photosynthesis and establishing a diminished stomatal resistance to water vapour diffusion in mycorrhizal soy beans lead SAFIR et al. (1971, 1972) to a similar conclusion. Of course, improved water uptake by the roots may delay or prevent the day time turgor drop in the shoot tissue, allowing prolonged stomatal opening which in turn leads to increased CO_2 fixation and growth as a whole. Particularly in the dark, increased water uptake will promote cell extension and thus leaf elongation (*figs. 2* and *3*).

There are some possible explanations for the improved water relations of mycorrhizal plants observed in *Aster tripolium*.

i. External fungal hyphae may increase the total absorptive surface of the root system, comparable to the effect of an increased number of root hairs. This could imply increased uptake of water and also of ions including potentially toxic Na and Cl. Improved growth of mycorrhizal plants may be caused by enhanced water uptake but less likely by increased absorbtion of NaCl. It remains unclear how plant roots manage to absorb more water and, at the same time exclude the sodium and chloride ions. DUECK et al. (1986) report enhanced zinc tolerance of mycorrhizal dune grass species explained by retention of zinc in or on the internal hyphae, as found for some ericoid mycorrhiza (BRADLEY et al. 1981). To our opinion, the increased growth of infected plants grown compared to non-infected plants as reported in DUECK et al. (1986) also suggests improved water uptake (no VAM effect on nutrients uptake was observed).

ii. The penetration of fungal hyphae between and into the cells of the cortex may cause a lowered resistance to water transport across the root (cf. SAFIR et al. 1971, ALLEN 1982).

iii. The presence of mycorrhiza infection may stimulate root growth and thus increase the capacity of water uptake. Increased branching of mycorrhizal roots can also lead to an increaed root surface, without a higher root biomass (ALLEN et al. 1981).

iiii. The presence of VAM is reported to change the hormonal balance in the rangeland species *Bouteloua gracilis* (ALLEN et al. 1981) causing increased root permeability to water transport (ALLEN 1982).

Further research is being carried out to test these hypotheses. Through improved water uptake, mycorrhizal infection will enhance photosynthesis and growth of salt marsh halophytes. The presence or absence of VA mycorrhizal fungi in various salt marsh species will surely interact with zonation of salt marsh vegetation. It has also been suggested that infection by mycorrhizal fungi is a prerequisite for successful establishment of pioneering salt marsh species (BACH ALLEN & ALLEN 1980, ROZEMA et al. 1985a). In those parts of salt marshes with intensive interspecific competion, efficient uptake and use of nutrients becomes important and CHRISTIE et al. (1978), and FITTER (1985) have emphasized the

importance of VAM in this respect. In future research both the mechanism of VAM-improved water uptake and the occurrence of VAM in salt marsh halophytes in relation to environmental factors will be studied in more detail.

ACKNOWLEDGEMENTS

REFERENCES

ALLEN, M. F., W. K. SMITH, T. S. MOORE & M. CHRISTENSEN (1981): Comparative water relations and photosynthesis of mycorrhizal and non-mycorrhizal Bouteloua gracilis. *New Phytol.* **88**: 683–693.
—, & M. G. BOOSALIS (1983): Effects of two species of vesicular-arbuscular mycorrhizal fungi on drought tolerance of winter wheat. *New Phytol.* **93**: 67–76.
BACH ALLEN, E. & M. F. ALLEN (1980): Natural re-estabilishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. *J. appl. Ecol.* **17**: 139–147.
—, & G. L. CUNNINGHAM (1983): Effect of vesicular-arbuscular mycorhizae on Distichlis spicata under three salinity levels. *New Phytol.* **93**: 227–236.
BOULLARD, B. (1958): Les mycorrhizes des espèces de contact marin et de contact salin. *Rev. de Mycol.* **23**: 282–317.
—, (1964): Halophytes et mycorrhizes. *Bull. Soc. Franç. phys. véget.* **10**: 292–299.
BRADLEY, R., A. J. BURT & D. J. READ (1982): The biology of mycorrhiza in the Ericaceae VIII. The role of mycorrhizal infection in heavy metal resistance. *New Phytol.* **91**: 197–209.
CHEN, P. S., T. Y. TORIBARA & H. WARNER (1951): Microdetermination of phosphorus. *Anal. chem.* **28**: 1737–1756.
CHRISTIE, P., E. I. NEWMAN & CAMBELL, (1978): The influence of neighbouring grassland plants on each others' endomycorrhizas and root-surface micro-organisms. *Soil Biology and Biochemistry* **10**: 521–527.
CUTLER, J. M., P. L. STEPONKUS, M. J. WACH & K. V. SHAHAN (1980): Dynamics aspects and enhancement of leaf elongation in rice. *Plant Physiol.* **66**: 147–152.
DUECK, TH. A., P. VISSER, W. H. O. ERNST & H. SCHAT (1986): VA-mycorrhiza decreases zinctoxicity in grasses growing in zinc-polluted soil. *Soil Biology and Biochemistry*, in press.
ERNST, W. H. O., W. E. VAN DUIN & G. T. OOLBEKKING (1984): Vesicular-arbuscular mycorrhiza in dune vegetation. *Acta Bot. Neerl.* **33**: 151–160.
FITTER, A. H. (1985): Functioning of vesicular-arbuscular mycorrhiza under field conditions. *New Phytol.* **99**: 257–265.
FRIES, N. (1944): Beobachtungen über die thamniscophage Mykorrhiza einiger Halophyten. *Bot. Not.* **2**: 255–264.
GIOVANETTI, M. & B. MOSSE (1980): An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. *New Phytol.* **84**: 489–500.
GREENWAY, H. & R. MUNNIS (1980): Mechanisms of salt tolerance in non halophytes. *Ann. Rev. Plant Physiol.* **31**: 149–190.
HEUKELS, H. & R. VAN DER MEIJDEN (1983): *Flora van Nederland.* Wolters-Noordhoff, Groningen.
HIRREL, M. C., H. MEHRAVAN & J. W. GERDEMAN (1978): Vesicular-arbuscular mycorrhiza in the Chenopodiaceae and Cruciferae: do they occur? *Can. J. Bot.* **56**: 2813–2817.
KHAN, A. G. (1974): The occurrence of mycorrhizas in halophytes, hydrophytes and endophytes, and of Endogone spores in adjacent soils. *J. Gen. Microbiol.* **81**: 7–14.

KIM, C. K. & D. J. WEBER (1985): Distribution of VA mycorrhiza on halophytes on inland salt playas. *Plant Soil* 83: 207–214.

KLEINENDORST, A. & R. BROUWER (1970): The effect of temperature of the root medium and of the growing point of the shoot on growth, water content and sugar content of maize leaves. *Neth. J. Agric. Sci.* 18: 140–148.

LEVY, I. & J. KRIKUN (1980): Effect of vesicular-arbuscular mycorrhiza in Citrus jambhiri water relations. *New Phytol.* 85: 25–32.

MASON, E. (1928): Note on the presence of mycorrhizae in the roots of salt-marsh plants. *New Phytol.* 27: 193–195.

MOSSE, B. (1975): Specificity of vesicular-arbuscular mycorrhizas. In: F. E. SANDERS, B. MOSSE & P. B. TINKER, (eds.): *Endomycorrhizas*, pp. 469–484. Academic Press, London.

NICOLSON, T. H. & C. JOHNSTON (1979): Mycorrhiza in the Gramineae. III. Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. *Trans. Br. Mycol. Soc.* 72: 261–268.

PHILLIPS, J. M. & D. S. HAYMAN (1970): Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Br. Mycol. Soc.* 55: 158–161.

PUGH, G. J. F. (1979): The distribution of fungi in coastal regions. In: R. J. JEFFERIES & A. J. DAVY (eds.): *Ecological processes in coastal environments* pp. 415–427. Blackwell, Oxford.

ROVIRA, A. D., G. D. BROWEN & R. C. FOSTER (1983): The significance of rhizosphere microflora and mycorrhizas in plant nutrition. In: A. LÄUCHLI, & R. L. BIELESKI (eds.): *Encycl. Plant Physiology N.S. vol. 15, Inorganic plant nutrition Part A* pp. 61–93. Springer, Berlin.

ROZEMA, J., E. ROZEMA-DIJST, A. H. J. FREIJSEN & J. J. L. HUBER (1978): Population differentiation within Festuca rubra L. with regard to soil salinity and soil water. *Oecologia (Berl.)* 34: 329–341.

—, T. DUECK, H. WESSELMAN & F. BIJL (1983): Nitrogen dependent growth stimulation by salt in strand-line species. *Acta Oecologia Oecologia Plantarum* 4: 41–52.

—, P. BIJWAARD, G. PRAST & R. BROEKMAN (1985a): Ecophysiological strategies of coastal halophytes from fore dunes and salt marshes. In: W. G. BEEFTINK, J. ROZEMA & A. H. L. HUISKES (eds.): *Ecology of coastal vegetation* pp. 499–521. Junk, The Hague.

—, E. LUPPES & R. BROEKMAN (1985b): Differential response of salt marsh species to variation of iron and manganese. In: W. G. BEEFTINK, J. ROZEMA & A. H. L. HUISKES (eds.): *Ecology of coastal vegetation* pp. 293–301. Junk, The Hague.

—, W. ARP, J. VAN DIGGELEN & E. KOK (1986): Comparative ecophysiology of the water, carbon and mineral relations of salt resistant Monocotyledonae and Dicotyledonae. In: A. SAN PIETRO & R. AHMAD. (eds.): *Proc. Biosaline Workshop Karachi 1985* University of Karachi (in press).

SAFIR, G. R., J. S. BOYER, & J. W. GERDEMAN (1971): Mycorrhizal enhancement of water transport in Soybean. *Science* 152: 581.

—, J. S. BOYER & J. W. GERDEMANN (1982): Nutrient status and mycorrhizal enhancement of water transport in soy beans. *Plant Physiol.* 49: 700–703.

SANDERS, F. E. & P. B. TINKER (1971): Mechanism of absorption of phosphate from soil by Endogone mycorrhizas. *Nature* 233: 278–279.

—, MOSSE, B. & P. B. TINKER (eds.) (1975): *Endomycorrhizas.* Academic Press, London.

SCHOLTEN, M. C. TH. & J. ROZEMA (1986): The competitive ability of Spartina anglica on Dutch salt marshes. In: A. J. GRAY (ed.): *Proc. Spartina Workshop* In press, ITE Furzebrook.

SOKAL, R. R. & F. J. ROHLF (1969): *Biometry.* Freeman, San Francisco.

TYREE, M. T. & P. G. JARVIOS (1982): Water in tissues and cells. In: O. L. LANGE, P. S. NOBEL, C. B. OSMOND & H. ZIEGLER (eds.): *Physiological Plant Ecology II. Water and Carbon Assimilation. Encycl. Plant Physiol. N.S. 12B* pp. 36–77. Springer Verlag, Berlin.

WHITTINGHAM, I. & READ, D. J. (1982): Vesicular-arbuscular mycorrhiza in natural vegetation systems. III. Nutrient transfer between plants with mycorrhizal interconnections. *New Phytol.* 90, 277–284.