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Responses of mycorrhizal and non-mycorrhizal *Erica cinerea* and *Vaccinium macrocarpon* to *Glomus mosseae*

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Abstract An investigation was carried out on the mycorrhizal colonisation, growth and nutrition of two members of the Ericaceae in close proximity to an arbuscular mycorrhizal (AM) association. This was undertaken by separating mycorrhizal (EM) and non-mycorrhizal (NEM) *Erica cinerea* and *Vaccinium macrocarpon* from AM (inoculated by *Glomus mosseae*) and non-mycorrhizal (NAM) *Plantago lanceolata* using a 30 μm nylon mesh in a sand culture/pot system. Ericoid mycorrhizal colonisation by *Hymenoscyphus ericae* on root systems of *E. cinerea* and *V. macrocarpon* was in the range 14–22% and 58–69%, respectively. The presence of AM *P. lanceolata* had no effect on the ericoid mycorrhizal colonisation of *E. cinerea* and *V. macrocarpon*. NEM *E. cinerea* showed reductions in shoot biomass and shoot nitrogen concentrations after exposure to AM *P. lanceolata* after incubations of 6 and 9 weeks but there were no differences in dry mass, length, and nitrogen and phosphorus concentrations of the root systems between the treatment combinations. Reductions were also found, after incubations of 6 and 9 weeks, in shoot dry mass, leaf area and shoot nitrogen concentrations of NEM *V. macrocarpon* in the presence of AM *P. lanceolata* but no changes occurred in the length and dry mass of the root systems. There were no differences in maximum photosynthesis in *V. macrocarpon* between treatment combinations but NEM *V. macrocarpon* in the presence of AM *P. lanceolata* had the lowest transpiration rates and stomatal conductance and the highest nitrogen- and phosphorus-use efficiencies compared with the other treatment combinations. These results are discussed in relation to the type of interaction found in these compatible and incompatible mycorrhizal associations.

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Introduction

The effects of arbuscular mycorrhizal (AM) fungi on the growth, nutrition and survival of 'incompatible' plants has been the subject of a number of studies (Allen and Allen 1984, 1988; Grime et al. 1987; Allen et al. 1989; Francis and Read 1994, 1995). Although 'compatible' is not normally used for mycorrhizal associations, this term may be defined as a modification of that between host and pathogen, in which a disease develops (Halliday 1998). Thus, 'incompatibility' in a mycorrhizal association can be described by the absence or malfunction of various recognition events essential for normal mycorrhizal colonisation (Anderson 1988). The response is more likely to be somewhere on a continuum, in which both host and fungus contribute to the level of 'compatibility'.

In pot and field experiments, inoculation of *Salsola kali* with AM fungi, in the presence of mycorrhizal grasses, resulted in reduced stomatal conductance and survival compared with uninoculated plants (Allen and Allen 1984, 1986, 1988). These results were later attributed to root death in seedlings as a consequence of colonisation by AM fungi (Allen et al. 1989). In microcosms containing AM-compatible plants, incompatible species grew less vigorously and had poor survivorship (Grime et al. 1987), but these experiments failed to show if inhibition was caused by competition with compatible mycorrhizal roots or by the direct action of the AM fungi. Francis and Read (1994) used a compartment system allowing fungal hyphae, but not roots, to invade the compartment containing seedlings of incompatible plant species. It was found that not only do AM fungi inhibit growth and reduce survivorship of incompatible species such as *Echium vulgare*, they can also cause browning of roots and swelling of meristem regions (Francis and Read 1995).

Glomus mosseae was shown not to infect the ericoid mycorrhizal plant *Vaccinium myrtillus* but AM hyphae were found on the root surface (Giovanetti et al. 1994). As the ericaceous hosts *Erica* and *Vaccinium* lack any AM colonisation in the wild, it is hypothesised that heavy inoculation by the use of a colonized companion would adversely affect the growth, nutrition and photosynthesis of plants belonging to the Ericaceae, which form compatible ericoid endomycorrhizal association. The aim of this study was to investigate the influence of extraradical hyphae of AM *Plantago lanceolata* L. inoculated with *G. mosseae* (Nicolson & Gerdemann) Gerdemann & Trappe on the growth of two test plants, *Erica cinerea* L. and *Vaccinium macrocarpon* Aiton. A further objective was to examine photosynthesis and related parameters in *V. macrocarpon* in order to determine the physiological responses of this host to the presence of AM *P. lanceolata*.

Materials and methods

Plants and mycorrhizal fungi used and experimental design

Seedlings of *P. lanceolata* (plantain) and *V. macrocarpon* (cranberry) and rooted cuttings of *E. cinerea* were used in these studies. Plantain seeds, collected from flowerheads of plants growing on the University College Dublin campus, were germinated at room temperature on moist, sterile Whatman No. 1 filter paper in 9 cm diameter Petri dishes. Cranberry seeds, extracted from fruits (Ocean Spray Cranberries, Middleboro, Mass.), were surface-sterilised by soaking in 5% sodium hypochlorite for 20 min and were then washed three times in sterile deionised water. They were germinated on 1.5% Technical No. 3 agar medium in 9 cm diameter Petri dishes in a 25°C constant temperature room under continuous fluorescent lights at an irradiance of 80 μmol photon m^{-2} s^{-1}. Rooted cuttings of *E. cinerea* var. Pink Ice, obtained from Kilternan Nursery (Co. Dublin, Ireland), were taken as slips from shrubs and allowed to root for 3 weeks in a steam-sterilised nursery soil:peat (1:2) mix under glasshouse conditions. The plants were then incubated for 1 week in washed and then autoclaved (125°C under steam pressure for 20 min) horticultural silica sand (Pioneer Supamix, Nuneaton, UK) containing no nutrients before being used in experiments.

A single ascospore isolate of *Hymenoscyphus ericae* (Read) Korf was grown on 1.5% malt extract agar medium (Oxoid) in the dark at 25°C. After 6 weeks, the growing margins of colonies were removed and homogenised (one colony per 3 ml), using a Sorvall omni-mixer (Newtown, Conn.), in sterile deionised water for 30 s over ice. The homogenate was applied to the soil at 300 ml homogenate per square metre of soil surface area. Chlamydospores and hyphae of *G. mosseae* strain YV in clay carrier form (MicroBio, Cambridge, UK) were applied at 100 g/m^{-2} soil surface area.

A nylon mesh similar to the system of Francis and Read (1995) was used to prevent direct competition between the root systems of donor plants and test plants. The AM donor plants were two, 2-week-old, *P. lanceolata* seedlings that were placed in the outer compartment, using a 30 μm nylon mesh sock (approx 6 cm in depth and 5.5 cm diameter; Stewart Filtration, Dublin, Ireland), in 18 cm diameter plastic pots filled with autoclaved sand. The AM donor plants were pre-inoculated with *G. mosseae* 10 days before two test plants (4 weeks old) of either seedlings of *V. macrocarpon* or rooted cuttings of *E. cinerea* were transferred to the inner compartment. The nylon mesh then allowed hyphae of *G. mosseae* but not roots of plantain to pass into the inner compartment. Treatments were set up as follows: (1) control: 3 g autoclaved *G. mosseae* in outer compartment and 3 ml autoclaved *H. ericae* inoculum in inner compartment, (2) *G. mosseae*: 3 g *G. mosseae* in outer compartment and 3 ml autoclaved *H. ericae* in inner compartment, (3) *H. ericae*: 3 g autoclaved *G. mosseae* in outer compartment and 3 ml *H. ericae* in inner compartment, (4) *H. ericae* and *G. mosseae*: 3 g *G. mosseae* in outer compartment and 3 ml *H. ericae* in inner compartment. The pot units were placed in a plant growth cabinet (Vindon Scientific, Oldham, UK) and the plants were grown at an irradiance of 183±17 μmol photon m^{-2} s^{-1} (λ=400–700 nm) at the canopy level with a 16:8 h day:night cycle, 22:18°C at 65% relative humidity. Modified one-fifth strength Rorison's medium (10 ml; Hewitt 1966) was applied to each pot at time zero and at weekly intervals, and deionised water was added as a supplement in between to keep the sand moist.

Biomass and nutrient determination

Plants (eight replicates) were harvested after 3, 6 and 9 weeks incubation. The roots were washed in deionised water, blotted dry and separated from the shoot. Root length was determined using a gridline intersect method (Tennant 1975). Sub-samples of roots were removed prior to drying and stored in 50% ethanol. The shoots and root sub-samples were oven-dried at 80°C for 48 h. Total nitrogen and phosphorus determinations were carried out on oven-dried component plant parts. Total nitrogen was determined using a micro-Kjeldahl method (Hendershot 1985) and phosphorus analyses were undertaken on the digests using the method of Murphy and Riley (1962). Tests have shown that this digestion procedure does not reduce nitrate but only determines organic nitrogen and ammonium.

Determination of colonisation by *G. mosseae* and *H. ericae*

The method used for clearing and staining of roots and determination of fungal colonisation is based on that described by Brundrett et al. (1994). Roots were washed under running tap water, cleared in 10% (w/v) KOH at 90°C for 90 min, washed under running tap water for 3 min, acidified in 1% HCl for 30 s and stained in 0.03% chlorozol black E at 90°C for 90 min. The root portions were then destained for 12 h in 50% glycerol. Samples were examined for percentage root length infection containing ericoid hyphal coils or AM-like surface hyphae along approximately 100 intersects per replicate with an eyepiece graticule attached to a compound microscope. Prior to inoculation of rooted cuttings of *E. cinerea*, the roots of six replicates were examined for any fungal colonisation. Root squashes were examined under a Leica DMLB compound microscope, and images were captured by means of a JVC KY-F55BE video camera and saved using Acquis image software (Syncroscopy, Cambridge, UK).

Photosynthesis and associated measurements

One week prior to *V. macrocarpon* seedlings being harvested after 6 and 9 weeks incubation, photosynthetic measurements were carried out on the three youngest fully expanded leaves on a shoot positioned in a Parkinson leaf chamber attached to a CIRAS-1 infrared gas analyser (PP Systems, Hitchin, Herts, UK). Measurements were carried out about 3 h into the light phase (between 9:00 and 18:00), with leaf temperature held constant at 20°C. Because of the diurnal variation in photosynthesis, replicates from each treatment were grouped into three time periods, namely 9:00–12:00, 12:00–15:00 and 15:00–18:00. Leaves were illuminated with an artificial light source (fan-cooled quartz halogen light bulb). Light response curves were determined by varying the incident light on the chamber using a series of wire meshes. Measurements began at 40 μmol photon m^{-2} s^{-1} and were increased in a series of non-linear steps up to 470 μmol photon m^{-2} s^{-1} (light saturation occurred at 250 μmol photon m^{-2} s^{-1}). The gas exchange parameters, such as stomatal conductance, transpiration and rate

of photosynthesis, were recorded at a constant vapour pressure deficit of 1.0 kPa. Maximum rate of photosynthesis was determined at light saturation. All photosynthetic parameters were calculated using standard equations (von Caemmerer and Farquhar 1981). Photosynthetic nitrogen- and phosphorus-use efficiencies were determined by calculating maximum rate of photosynthesis as a function of either leaf N or P concentrations.

Statistical analyses

Although initial experiments were undertaken on the mycorrhizal fungi/plant combinations, the results of this study are based on single experiments. The data were first examined for homogeneity using the Bartlett's test (Zar 1974) and any heterogeneity of variance was corrected for by transformation, which reduces the variances and thus normalises the data. Prior to transformation, data below the value of 1 were incremented by the value of 1 to prevent transformation to negative values (e.g. when data were log transformed). Transformations used on the data were log transformations [$\log_{10}$ (x+1)], where the treatment effects were multiplicative, the arcsin transformation (arcsin $\sqrt{x}$), where the data were percentages, and the square root transformation ($\sqrt{x+1}$), where treatment variances were proportional to means. After these transformations, all the data were shown to be homogeneous by the Bartlett's test. One-way and two-way ANOVA were carried out using the Datadesk statistics package for Apple Macintosh (Data Description, Ithaca, N.Y.). The treatments were distinguished at the 5% level using a Fisher's post hoc least significant difference test.

Results

Colonisation of roots by *G. mosseae* and *H. ericae*

Root systems of *P. lanceolata* colonised by *G. mosseae* formed intercellular hyphae and arbuscules but no vesicles were observed. Between 20 and 28% of the total root length of *P. lanceolata* was colonised but infection differed little between 3 and 9 weeks after inoculation. There was no infection of roots of *P. lanceolata* by *H. ericae*. Colonisation of root systems of *E. cinerea* and *V. macrocarpon* by *H. ericae* was characteristic of ericoid mycorrhizal infection. The extent of ericoid mycorrhizal colonisation was unaffected by the presence of *G. mosseae*/*P. lanceolata* association, although there was a lower mycorrhizal colonisation on the root systems of *E. cinerea* in the presence of non-mycorrhizal (NAM) *P. lanceolata* compared with AM *P. lanceolata* after 3 weeks incubation (Table 1).

In roots of *E. cinerea* and *V. macrocarpon* inoculated with *H. ericae* and in the presence of AM *P. lanceolata*, each type of surface colonisation could be distinguished. AM-like surface hyphae were thicker than hyphae of *H. ericae* and ran parallel to the root axis, while external hyphae of *H. ericae* were found at an angle to the root axis. Hyphae of *H. ericae* were septate, whereas hyphae of *G. mosseae* were mainly aseptate. Both types of surface hyphae never occurred together and were usually several millimetres apart. AM-like hyphae were observed to be in contact with the root surface of *E. cinerea* and *V. macrocarpon* over distances up to 0.5 mm covering 12–18% (*E. cinerea*) and 7–10% (*V. macrocarpon*) of root length. There was no observed penetration by these AM-like hyphae into the root tissues of these ericaceous hosts. In some surface hyphae, segregation of cytoplasm occurred (Fig. 1), as well as cross wall formation in hyphae devoid of cytoplasm. The morphology and colour of non-mycorrhizal root systems in the presence of either AM or NAM *P. lanceolata* were similar. There was neither browning of roots nor swelling of root tips.

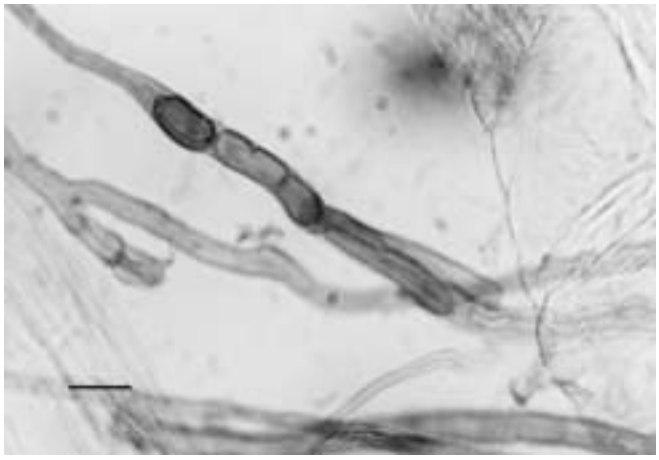

Fig. 1 Hypha undergoing segregation of cytoplasm on the root surface of *Vaccinium macrocarpon*. *Bar* 10 µm

Table 1 Percentage root length colonisation of mycorrhizal (EM) *Erica cinerea* and *Vaccinium macrocarpon* exposed to mycorrhizal (AM) and non-mycorrhizal (NAM) *Plantago lanceolata* 3, 6 and 9 weeks after inoculation. Values represent means of six replicates ±SE; values with the same letter within each column are not significantly different

Time (weeks)	Treatment	*E. cinerea*	*V. macrocarpon*
3	EM + NAM	14.3±0.9 b	60.4±2.2 a
	EM + AM	19.4±0.9 a	64.3±2.0 a
6	EM + NAM	21.1±1.4 a	63.1±1.6 a
	EM + AM	22.4±2.3 a	58.1±0.8 a
9	EM + NAM	19.5±0.8 a	69.3±1.9a
	EM + AM	22.2±1.7 a	62.4±1.7 a

Influence of *P. lanceolata*/*G. mosseae* association on the growth and nutrition of *E. cinerea*

Non mycorrhizal (NEM) rooted cuttings of *E. cinerea* exposed to AM *P. lanceolata* had reduced shoot dry mass 6 and 9 weeks after inoculation compared to all other treatments, but there were no differences between treatments in shoot dry mass after 3 weeks incubation (Table 2). There were no differences between treatments in root dry mass and root length throughout the incubation period (Table 2). EM *E. cinerea* exposed to AM or NAM *P. lanceolata* had a significantly higher shoot nitrogen concentration compared with all other treatments after 3, 6 and 9 weeks incubation (Table 2). However, NEM *E. cinerea* exposed to NAM *P. lanceolata* had a significantly higher shoot nitrogen concentration compared with NEM

Table 2 Dry mass, length and nitrogen and phosphorus concentrations of shoot and root systems of mycorrhizal (EM) and non-mycorrhizal (NEM) *E. cinerea* exposed to mycorrhizal (AM) and non-mycorrhizal (NAM) *P. lanceolata*. Treatments at each time interval with different letters are significantly different at the 5% level using one-way ANOVA

Incubation time (weeks)	NEM + NAM	NEM + AM	EM + NAM	EM + AM
Shoot dry mass (mg ± SE, *n*=8)				
3	51.0±12.3 a	53.1±12.6 a	57.5±11.2 a	55.0±10.1 a
6	121.4± 9.0 a	61.3±6.6b	119.4±7.4 a	124.6± 9.6 a
9	148.0±13.5 a	66.0±7.7b	154.2±13.0 a	154.4±21.0 a
Root dry mass (mg ± SE, *n*=8)				
3	14.2±3.5 a	13.3±2.3 a	16.7±6.8 a	15.3±5.1 a
6	32.9±4.8 a	28.9±4.3 a	35.3±7.9 a	34.2±10.0 a
9	49.1±11.5 a	43.2±12.4 a	46.1±12.9 a	45.6±12.3 a
Root length cm ± SE, *n*=8)				
3	92.2±20.2 a	88.3±17.7 a	97.3±18.1 a	91.2±19.2 a
6	175.3±44.8 a	176.2±41.4 a	192.3±38.3 a	199.3±30.1 a
9	215.7±22.7 a	220.7±26.1 a	224.7±21.9 a	230.7±27.5 a
Shoot nitrogen concentration [µmol N (g dry mass)$^{-1}$ ± SE, *n*=4]				
3	111.2±2.4 b	108.2±25.9 b	309.7±6.5 a	306.4±9.8 a
6	200.2±11.0 b	105.1±1.9 c	332.0±6.0 a	315.2±12.5 a
9	205.1±5.6 b	107.2±6.4 c	334.9± 5.7 a	337.5±7.4 a
Root nitrogen concentration [µmol N (g dry mass)$^{-1}$ ± SE, *n*=4]				
3	46.8±11.9 a	60.5± 5.6 a	50.8± 7.4 a	49.4± 4.8 a
6	43.8± 7.6 a	45.6±13.7 a	59.9±13.3 a	48.8± 6.5 a
9	54.7±16.8 a	59.6±13.4 a	55.9±18.6 a	55.7±14.9 a
Shoot phosphorus concentration [µmol P (g dry mass)$^{-1}$ ± SE, *n*=4]				
3	38.6±7.3 b	43.0±2.3 b	83.4±6.3 a	83.4±7.2 a
6	38.9±7.1 b	36.3±4.3 b	85.8±5.7 a	79.9±1.0 a
9	43.1± 8.0 b	46.5±9.9 b	82.9±4.9 a	78.6±6.1 a
Root phosphorus concentration [µmol P (g dry mass)$^{-1}$ ± SE, *n*=4]				
3	10.7±2.8 a	9.6±2.4 a	9.6±1.7 a	10.4±1.3 a
6	12.3±0.8 a	12.0±2.0 a	9.2±1.1 a	11.8±2.6 a
9	9.6±2.7 a	8.9±0.5 a	10.8±0.2 a	10.8±1.3 a

Table 3 Dry mass and nitrogen and phosphorus concentration of the shoot, leaf area and dry mass and length of root systems of mycorrhizal (EM) and non-mycorrhizal (NEM) *Vaccinium macrocarpon* exposed to mycorrhizal (AM) and non-mycorrhizal (NAM) *P. lanceolata*. Treatments at each time interval with different letters are significantly different at the 5% level using one-way ANOVA

Incubation time (weeks)	NEM +NAM	NEM + AM	EM + NAM	EM + AM
Shoot dry mass (mg ± SE, *n*=8)				
3	6.4±0.5 a	5.5±0.9 a	6.5±1.0 a	6.7±1.0 a
6	17.9±2.2 a	7.4±1.1 b	18.1±2.5 a	21.4±3.7 a
9	31.1±1.6 a	15.9±1.5 b	29.1±2.7 a	28.4±3.0 a
Shoot nitrogen concentration [μmol N (g dry mass)$^{-1}$ ± SE, *n*=4]				
6	210.1±11.1 b	78.1±0.9 c	481.2±5.0 a	476.1±2.0 a
9	177.6± 2.9 b	72.3±7.2 c	445.6±37.0 a	443.8±30.7 a
Shoot phosphorus concentration [μmol P (g dry mass)$^{-1}$ ± SE, *n*=4]				
6	20.9±3.2 b	20.0±3.5 b	45.3±1.0 a	44.0±1.6 a
9	22.6±1.5 b	23.4±2.6 b	43.1±0.1 a	44.4±1.1 a
Leaf area (cm^2±SE, *n*=8)				
3	0.6±0.1 a	0.5±0.1 a	0.7±0.1 a	0.7±0.1 a
6	1.3±0.1 a	0.8±0.1 b	1.2±0.1 a	1.4±0.2 a
9	2.6±0.2 a	1.7±0.2 b	2.7±0.2 a	2.6±0.3 a
Root dry mass (mg ± SE, *n*=8)				
3	2.2±0.5 a	1.3±0.3 a	1.6±0.4 a	1.8±0.4 a
6	3.1±0.5 a	2.6±0.3 a	3.5±1.0 a	3.3±0.5 a
9	4.0±0.8 a	4.4±0.9 a	3.7±1.0 a	3.9±1.0 a
Root length (cm ± SE, *n*=8)				
3	17.7±3.5 a	10.2±3.1 a	11.1±1.8 a	11.3±1.7 a
6	31.0±4.2 a	21.7±3.9 a	23.7±4.7 a	24.1±4.8 a
9	25.2±5.5 a	24.6±2.8 a	26.3±6.1 a	27.8±6.0 a

Table 4 Maximum photosynthesis, transpiration rate, stomatal conductance and nitrogen- and phosphorus-use efficiencies of the three youngest expanded leaves of mycorrhizal (EM) and non-mycorrhizal (NEM) *V. macrocarpon* exposed to mycorrhizal (AM) and non-mycorrhizal (NAM) *P. lanceolata* 6 and 9 weeks after inoculation. Values represent means of three replicates ± SE and those along each row showing the same letter are not significantly different at the 5% level

Incubation time (weeks)	NEM +NAM	NEM + AM	EM + NAM	EM + AM
Maximum photosynthesis (μmol CO_2 m^{-2} s^{-1})				
6	12.6±1.6 a	10.8±0.9 a	11.0±0.6 a	11.4±1.1 a
9	11.7±1.4 a	10.4±0.7 a	11.2±0.8 a	12.4±1.9 a
Transpiration rate (mmol H_2O m^{-2} s^{-1})				
6	6.1±0.4 a	2.0±0.3 b	5.8±0.2 a	6.1±0.2 a
9	5.5±0.3 a	1.8±0.2 b	5.7±0.3 a	5.4±0.6 a
Stomatal conductance (mmol H_2O m^{-2} s^{-1})				
6	195±26 a	52±13 b	177±27 a	194±30 a
9	207±11 a	39± 9 b	243±27 a	261±31 a
Nitrogen-use efficiency (μmol CO_2 g^{-1} N s^{-1})				
6	140±16 b	245±42 a	68±6 c	65±17 c
9	139±27 b	222±18 a	88±4 c	84±8 c
Phosphorus-use efficiency (μmol CO_2 g^{-1} P s^{-1})				
6	471±11 a	455±14 a	209±26 b	211±15 b
9	448±17 a	427±42 a	207±7 b	205±39 b

E. cinerea exposed to AM *P. lanceolata* 6 and 9 weeks after inoculation (Table 2). EM *E. cinerea* exposed to AM or NAM *P. lanceolata* had a significantly higher shoot phosphorus concentration compared with the other treatments 3, 6 and 9 weeks after inoculation (Table 2). No differences were found between treatments for root nitrogen and phosphorus concentrations throughout the course of the experiment (Table 2).

Influence of *P. lanceolata*/*G. mosseae* association on the growth, nutrition and photosynthesis of *V. macrocarpon*

NEM seedlings of *V. macrocarpon* exposed to AM *P. lanceolata* had reduced leaf area and shoot dry mass 6 and 9 weeks after inoculation compared to all other treatments, but there were no differences between treatments in leaf area and shoot dry mass after 3 weeks incubation (Table 3). There were no differences between treatments in the length and dry mass of root systems throughout the incubation period (Table 3). NEM *V. macrocarpon* exposed to NAM *P. lanceolata* had a significantly higher shoot nitrogen concentration compared with NEM *V. macrocarpon* exposed to AM *P. lanceolata* 6 and 9 weeks after inoculation (Table 3). During exposure to AM or NAM *P. lanceolata*, EM *V. macrocarpon* had a significantly higher shoot nitrogen and phosphorus concentrations compared with all other treatments after an incubation of 6 and 9 weeks (Table 3).

Maximum rates of photosynthesis did not differ between treatments 6 and 9 weeks after inoculation (Table 4). The minimum light level required for maximum photosynthesis was 250 μmol photon m^{-2} s^{-1}, which is just above the irradiance of 183±17 μmol photon m^{-2} used for plant growth. NEM *V. macrocarpon* exposed to AM *P. lanceolata* had reduced transpiration rates and stomatal conductance (Table 4). EM *V. macrocarpon* had significantly lower photosynthetic nitrogen- and phosphorus-use efficiencies compared with NEM *V. macrocarpon* (Table 4). NEM *V. macrocarpon* exposed to AM *P. lanceolata* had a higher photosynthetic nitrogen-use efficiency compared with all other treatments (Table 4).

Discussion

The results presented in this study are the first to show the detrimental effects of a compatible AM/plant association on the growth and nutrition of plants that normally form compatible ericoid mycorrhizal associations. Other studies involving incompatible mycorrhizal associations have concentrated on the morphology of infection (Glenn et al. 1985, 1988; Giovanetti and Lioi 1990; Giovanetti et al. 1993), or on the effect of the association on the growth of the incompatible host plant (Allen and Allen 1984 1988; Allen et al. 1989; Francis and Read 1994, 1995). The present study, however, is in contrast to those on non-mycotrophic plants, where the reduction in the growth was attributed to inhibition of root growth either by the direct action of the AM fungus or inhibitory compounds released by the AM fungus (Allen and Allen 1984, 1988; Francis and Read 1994, 1995). The presence of the *G. mosseae*/*P. lanceolata* association did not elicit any incompatible response, such as browning or reduced growth, from the roots of *E. cinerea* or *V. macrocarpon*.

Surface hyphae of *G. mosseae* have also been observed previously on *V. myrtillus* (Giovanetti et al. 1994). *G. mosseae* has a positive effect on the growth of its compatible host, *P. lanceolata* (data not shown) but the same AM fungus had an adverse effect on the growth of NEM *V. macrocarpon* and NEM *E. cinerea*. The reduced shoot biomass of NEM *V. macrocarpon* and NEM *E. cinerea* in the presence of AM *P. lanceolata* association was correlated with a decrease in shoot nitrogen and phosphorus concentration in both species, and lower leaf area in *V. macrocarpon*. However, biomass and nitrogen and phosphorus concentration of the root were unaffected. Why is the shoot and not the root affected by the presence of *G. mosseae*? There are several possible reasons, which will require further study. The change may be due to a

signal in the root, or it may be due to some host mechanism resulting in the redirection of organic resources from the shoot. Although the AM fungus is attached to another host and thus has access to organic carbon, the same fungus could be extracting organic resources from the ericaceous host. Maximum photosynthesis did not differ between treatments. Thus, any drain by the AM fungus for carbon is bound to have a negative impact on shoot biomass of the ericaceous host.

Various photosynthetic-related parameters between EM and NEM *V. macrocarpon* in close proximity to a compatible AM/plant association have been compared for the first time. NEM *V. macrocarpon* grown in the presence of AM *P. lanceolata* had lower transpiration rates and stomatal conductance but higher photosynthetic nitrogen-use and phosphorus-use efficiencies compared with the other treatment combinations. Changes in these parameters, along with lower shoot nitrogen concentrations, suggest that NEM *V. macrocarpon* seedlings were suffering from nitrogen deficiency. Nitrogen- and phosphorus-deficient plants, particularly cotton, have been shown to have lower stomatal conductance and transpiration rates as a result of increased abscisic acid concentrations (Radin and Ackerson 1981; Radin 1984, 1989).

This study has revealed that the presence of *H. ericae* alleviates the effects of *G. mosseae* on two members of the Ericaceae. This suggests that in environments where ericoid mycorrhizal fungi are present, such as natural bogland, the introduction or presence of AM fungi would have no impact on the growth, nutrition or fitness of ericaceous plants. Artificial environments, in which ericaceous plants are grown, such as commercial horticultural nurseries, may contain ericoid mycorrhizal fungi. It is proposed that ericoid mycorrhizal associations in this environment would, if present, reduce the influence of AM fungi on the fitness of ericoid plants in commercial nurseries.

While the present study has provided evidence of a competitive relationship in ericaceous plant/AM fungus incompatible associations, other studies (Francis and Read 1994, 1995) have shown that antagonistic relationships occur between incompatible plants and AM fungi. Different types of incompatible associations, therefore, should be studied further to provide useful information on the colonisation and infection processes involved in the formation of compatible mycorrhizal associations.

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