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## Presence of arbuscular mycorrhizas in typically ectomycorrhizal host species from Cameroon and New Zealand

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**Abstract** Ectomycorrhizas (EcM) and arbuscular mycorrhizas (AM) were screened for in saplings of 14 EcM tree species from the N'Dupé and Korup National Park rainforests, SW Cameroon, belonging to Caesalpiniaceae and Uapacaceae. The pattern of EcM and AM colonisation of a dual mycorrhizal species from this rainforest (*Uapaca staudtii*, Uapacaceae) was compared with dual EcM/AM colonisation of *Leptospermum scoparium* (Myrtaceae) from New Zealand. Both species were collected in a range of habitats. EcM and AM colonisation differed among species in the Korup National Park rainforest: 12 species belonging to the Caesalpiniaceae (Amherstieae) were consistently EcM, and AM structures occurred occasionally in six of them; two other species belonging to Caesalpiniaceae (*Afzelia bipindensis*) and Uapacaceae (*U. staudtii*) were dual mycorrhizal with variable levels of colonisation by both EcM and AM fungi. EcM and AM dual colonisation varied with both habitat and identity of the partners. The presence of EcM fungi in most of the root samples of *U. staudtii* and a negative relationship between AM and EcM colonisation within the same root system suggested a greater EcM affinity of this species. In contrast, most root samples of *L. scoparium* were colonised by AM, but only a few by EcM. Genuine dual EcM/AM associations in root samples of *U. staudtii* where the two mycorrhizal types co-occurred could be attributed to an AM-EcM succession. However, differences between predicted and observed frequencies of genuine dual EcM/AM associations in several samples of both *U. staudtii* and *L. scoparium* indicated that other factors influenced dual EcM/AM associations. The re-

sults of this study showed the importance of the identity of the host species in determining the pattern of dual EcM and AM colonisation.

**Key words** Ectomycorrhiza · Arbuscular mycorrhiza · Saplings · Tropical · Temperate

### Introduction

Field surveys of the mycorrhizal habit of plants generally show most mycorrhizal species to be associated with only one type of mycorrhiza, most commonly either arbuscular mycorrhizas (AM) or ectomycorrhizas (EcM). However, Molina et al. (1992) listed 42 genera reported to form both AM and EcM, and the capacity of species to associate with both EcM and AM is well documented in *Populus* (Lodge 1989; Lodge and Wentworth 1990), *Salix* (Lodge 1989; Dhillion 1994), *Eucalyptus* (Lapeyrie and Chilvers 1985), *Alnus* (Molina 1994) and in Pinaceae (Vardavakis 1992; Cázares and Trappe 1993). The pattern of EcM and AM natural colonisation in these dual EcM/AM taxa may vary in relation to soil or other habitat conditions (Lodge 1989; Cázares and Trappe 1993). The colonisation process of EcM and AM within the same root system may be influenced by interactions between fungi involved in the two types of mycorrhiza (Chilvers 1987; Lodge and Wentworth 1990), and a succession from AM to EcM during the growth of dual EcM/AM plants has been attributed to a competitive displacement of AM by EcM (Lapeyrie and Chilvers 1985).

The nature of the mycorrhiza formed by a plant species may be an important factor in determining its ecological specialisation (Read 1991). Pirozynski and Malloch (1975) hypothesised that the AM habit was a prerequisite for the early development of a land flora, and the association of most extant plant species with AM, in addition to fossil and molecular evidence (Simon et al. 1993; Taylor et al. 1995), suggest that AM have played an important role in plant ecology ever since. Relative-

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ly few species are non-mycorrhizal, and although the mechanisms responsible for the non-mycorrhizal state are not well understood, it is associated with habitat specialisation (Peat and Fitter 1993). The EcM association arose after AM evolved (Malloch et al. 1980) and apparently several times independently (Fitter and Moyersoen 1996). It also seems to have led to ecological specialisation, as it confers advantages in soils where both P and N are particularly limiting (Janos 1985; Read 1991). The co-occurrence of AM with EcM in the same root system show that the ability to form AM has been maintained to some degree in plant taxa that are typically EcM (Vardavakis 1992; Cázares and Trappe 1993). Evidence is accumulating which suggests that mycorrhizal habit is an important factor determining the success of plants in different habitats (Read 1991; Trappe and Luoma 1992), and differences in the ability of EcM and dual EcM/AM plant species to colonise a range of habitats might be expected.

In the present study, we screened for EcM and AM colonisation in a number of EcM tropical species across a range of habitats in order to evaluate the extent to which AM colonisation varies between EcM host taxa under field conditions. To evaluate whether the pattern of EcM and AM colonisation, and the interaction between these two mycorrhizal types within the same root system, is similar in different dual EcM/AM species, EcM, AM and dual EcM/AM colonisation within the

same root system of plants from contrasting habitats was compared. The two species examined belong to Uapacaceae (*Uapaca staudtii*) and Myrtaceae (*Leptospermum scoparium*) and were previously described as dual EcM/AM (Baylis 1962; Newbery et al. 1988). The habitat effect on mycorrhizal colonisation was also evaluated.

## Materials and methods

### Screening of AM in EcM species

In a first experiment, 2–13 saplings (between 20–200 cm in height) of 14 tropical EcM species belonging to the Caesalpiniaceae (tribes Amherstieae and Detarieae) and Uapacaceae and from three different habitats were harvested for EcM and AM screening (Table 1). Young plants were preferred to older ones as greater AM colonisation in seedlings has been observed in other EcM genera (Read et al. 1977; Lapeyrie and Chilvers 1985). These saplings were sampled in May 1995 (beginning of rainy season) in two different Atlantic rainforests (Letouzey 1968) situated in the N'Dupé and Korup National Park rainforests, SW Cameroon. Previous characterisation of Korup National Park vegetation (Newbery et al. 1988) allowed us to sample several species in areas of low and high EcM abundance. Plant species were recognised with the help of local botanists and their identification confirmed in Yaoundé National Herbarium. The roots were carefully traced from identified stems and a sample of fine roots (less than 2 mm, not lignified) taken. Fine roots of the same species and from the same habitat were pooled, cut into approximately 1-cm root pieces and a subsample (of approximately 1 m length) was

**Table 1** EcM, AM and genuine dual EcM/AM colonisation (i.e. where AM and EcM structures co-occurred in 1-cm root pieces) in EcM tree species harvested in three different habitats in Atlantic rainforests. (1) Korup National Park rainforest, high EcM abundance areas; (2) Korup National Park rainforest, low EcM

abundance areas; (3) N'Dupé rainforest (*H* high colonisation: >60% of root pieces colonised, *M* medium colonisation: 5–60% of root pieces colonised, *L* low colonisation: <5% of root pieces colonised, – mycorrhizas not observed, + genuine dual colonisation observed)

Tree species	1			2			3		
	EcM	AM	Dual	EcM	AM	Dual	EcM	AM	Dual
<sup>a</sup> Caesalpiniaceae Amherstieae									
<i>Anthonotha fragans</i> (Bak. f.) Exell & Hillcoat				H	L	–			
<i>A. macrophylla</i> P. Beauv.							H	–	–
<i>Aphanocalyx</i> <i>cynometroides</i> Oliver							H	–	–
<i>Berlinia</i> sp.				H	L	–			
<i>Didelotia africana</i> Baill.	H	L	–	H	–	–			
<i>D. letouzeyi</i> Pellegr.							H	–	–
<i>Gilbertiodendron</i> sp. 1				H	–	–			
<i>Gilbertiodendron</i> sp. 2	H	L	–						
<i>Microberlinia bisulcata</i> Chev.	H	–	–						
<i>Monopetalanthus</i> sp.	H	L	+						
<i>Tetraberlinia bifoliolata</i> (Harms) Hauman	H	–	–	H	L	+			
<i>T. moreliana</i> Aubr.	H	–	–						
<sup>b</sup> Caesalpiniaceae Detarieae									
<i>Afzelia bipidensis</i> Harms	M, H	M, H	+						
<sup>c</sup> Uapacaceae									
<i>Uapaca staudtii</i> Pax				–, H	–, H	+	M, H	M	–

<sup>a</sup> Mycorrhizal colonisation in pooled samples of 2–13 plants per species

<sup>b</sup> Mycorrhizal colonisation of 3 plants

<sup>c</sup> Mycorrhizal colonisation of 11 plants

selected randomly for later mycorrhizal observation. Roots were cleared and mycorrhizas were stained using a phenol-free modification of Phillips and Hayman's (1970) method. EcM and AM were screened using a microscope (magnification  $\times 200$ ) and their colonisation was ranked in the following four categories: no colonisation, low ( $< 5\%$  of root pieces colonised), medium (5–60% of root pieces colonised) and high ( $> 60\%$  of root pieces colonised). Genuine dual EcM/AM colonisation was recorded where AM and EcM co-occurred in a single 1-cm root piece; the frequency of dual colonisation and of EcM and AM structures was estimated.

#### Comparison of EcM and AM pattern of colonisation in dual EcM/AM species

In a second experiment, EcM, AM and genuine dual EcM/AM colonisation were quantified in one EcM/AM tree species from Korup National Park rainforest (*Uapaca staudtii*) and one from New Zealand (*Leptospermum scoparium*). Plants of *U. staudtii* and *L. scoparium* were sampled in contrasting habitats to get a range of colonisation by EcM and AM. Saplings (150–200 cm in height) of *U. staudtii* were sampled in May 1995 in dry soil conditions in the forest (six plants) and on a riverside in a waterlogged area (five plants). The dry and waterlogged habitats were adjacent and located in an area of low EcM host abundance described previously by Newbery et al. (1988) along a transect (referred to as P) in the forest. *L. scoparium* roots were sampled in August 1995 from young trees ( $< 2$  m) in areas of vegetation characterised by the dominance of an AM tree species (*Podocarpus* sp.) (two plants) and an EcM tree species (*Nothofagus* sp.). Roots of nine plants were sampled along a 100-km transect along the coast of South Island from near Jacksons Bay in the southwest (samples 1 and 2) in EcM *Nothofagus* forest to Bruce Bay in the northeast (sample 9), where no EcM species were found. Samples 1 and 2 were collected on ultramafic soils with very impoverished vegetation. The tenth sample was collected 60 km inland near Lake Hawea, again near *Nothofagus* sp. trees. EcM, AM and genuine dual EcM/AM fractional colonisation (i.e. proportion of root system colonised by mycorrhizas) were scored in a subsample of fine roots (selected randomly) from each plant. The roots were cleared and stained for the mycorrhizas as above. Fractional colonisation was scored with a microscope (magnification  $\times 200$ ) in 1-cm root pieces aligned on microscope slides using the intersection method described by McGonigle et al. (1990). Two to four slides and 9–70 root pieces per slide were scored per sample (depending on the total amount of roots). EcM and AM structures were recorded. Colonisation data was arcsin transformed before further statistical analysis in order to meet the assumption of normal distribution.

The relationship between EcM and AM colonisation within the same root system was evaluated in a correlation (Pearson) analysis. The relationship between predicted and observed genuine dual colonisation in *U. staudtii* was analysed in a Kendall's rank correlation test (Snedecor and Cochran 1971). This test was not applied with the data from *L. scoparium* because genuine dual association was only observed in one sample. Habitat influence on EcM and AM fractional colonisation of *U. staudtii* and *L. scoparium* plants was evaluated using an ANOVA (GLM) test.

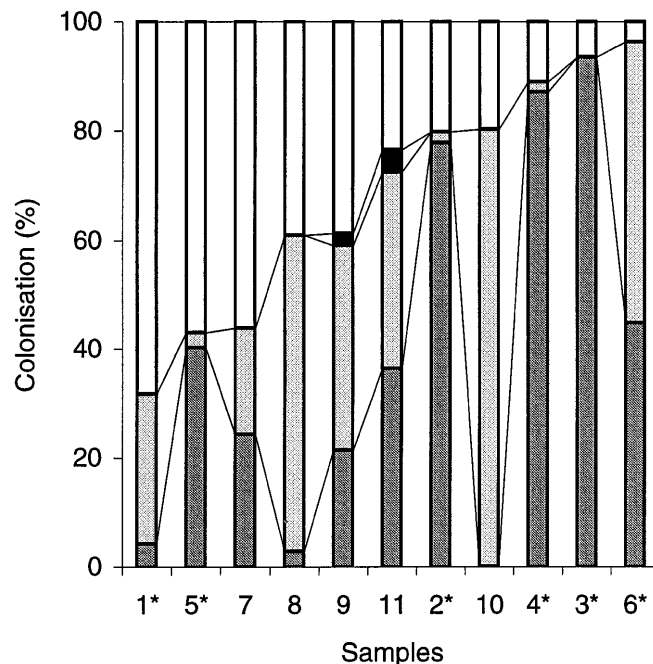
## Results

In Korup National Park, most plant species in the Amherstieae (Caesalpiniaceae) were consistently predominantly EcM, even when collected in environments where EcM tree basal area in the forest varied (Table 1). AM structures (arbuscules, hyphal coils, hyphae, vesicles, spores) were observed in the same root samples of half of the 12 predominantly EcM species, and

hyphae, vesicles and spores were observed in root pieces partially covered by EcM mantle in two of these (*Tetraberlinia bifoliolata*, *Monopetalanthus* sp.). Two plant species, one belonging to the subfamily Detarieae of Caesalpiniaceae (*Azelia bipindensis*) and one to the Uapacaceae (*U. staudtii*), showed variable colonisation by EcM and AM between plants, as well as genuine dual EcM/AM associations. AM structures observed in *A. bipindensis* included vesicles, spores and hyphae, whereas arbuscules, hyphal coils, vesicles and hyphae were observed in roots of *U. staudtii* whether or not colonised by EcM.

Variation in EcM, AM and genuine dual EcM/AM fractional colonisation in root samples of *U. staudtii* is shown in Fig. 1. Most of the root samples were colonised by both types of mycorrhiza. Out of the six samples with higher total mycorrhizal colonisation, three were colonised predominantly by EcM, whereas only one was colonised mostly by AM fungi. A significant negative correlation ( $r_7 = -0.713$ ,  $P = 0.031$ ) was found between AM and EcM fractional colonisation in root samples colonised by both types of mycorrhizas. In contrast, root samples of *L. scoparium* were mostly colonised by AM fungi and EcM were present in six out of 10 samples (Fig. 2). AM structures included arbuscules, hyphal coils, vesicles and hyphae and were observed in root pieces whether or not colonised by EcM.

If the presence of genuine dual EcM/AM associations depends solely on the probability that the two mycorrhizal types colonise the same root piece and not on any interaction between them, the number of observa-



**Fig. 1** Ectomycorrhizal (EcM) (□), arbuscular mycorrhizal (AM) (■) and genuine dual EcM/AM (■) fractional colonisation, and proportion of roots not colonised (□) in *Uapaca staudtii* root samples (sorted by ascending mycorrhizal colonisation) from dry (\*) and waterlogged habitats

tions (counts) of genuine dual EcM/AM associations in a root sample could be predicted from the product of both EcM and AM fractional colonisation (i.e. the probabilities that each mycorrhizal type occurs in the sample) times the total number of observations (total count) in this sample. Observed and predicted values of true genuine dual EcM/AM fractional colonisation in *U. staudtii* and *L. scoparium* are presented in Tables 2 and 3. Figure 1 and Table 2 show genuine dual EcM/AM associations were observed in most of root samples of *U. staudtii* where EcM and AM co-occurred, except for sample 6. In contrast, the absence of genuine dual EcM/AM associations in samples of *U. staudtii* (sample 6, Table 2) and *L. scoparium* (sample 7, Table 3) where the predicted probability of finding this dual association was high, and the occurrence of genuine dual EcM/AM associations in a sample of *L. scoparium* (sample 10, Table 3) where the predicted probability was low, both suggest that the presence of genuine dual associations is also influenced by factors other than EcM and AM colonisation in the same root system.

*Uapaca staudtii* showed a tendency towards greater EcM and lower AM fractional colonisation in samples from dry areas than waterlogged habitats (Table 4). Differences in both EcM and AM fractional colonisation

**Table 2** EcM and AM fractional colonisation and predicted and observed counts of genuine dual EcM/AM associations in root samples of *Uapaca staudtii* where EcM and AM co-occurred

Sample number	EcM (%)	AM (%)	Total counts	EcM/AM counts	
				Pre-dicted	Observ-ed <sup>a</sup>
1	4.2	27.5	58	0.7	0
2	77.8	2	28.5	0.4	0
4	87.1	1.8	52.7	0.8	0
5	40.3	2.8	54.5	0.6	0
6	44.8	51.5	50	11.5	0
7	24.3	19.6	29	1.4	0
8	2.8	58.0	40.3	0.7	0
9	21.4	37.6	42.5	3.4	2.2
11	36.5	36	58.7	7.7	4

<sup>a</sup> No significant relationship ( $P > 0.05$ ) between predicted and observed genuine dual EcM/AM association counts in a Kendall's rank correlation test

**Table 3** EcM and AM fractional colonisation and predicted and observed counts of genuine dual EcM/AM associations in root samples of *Leptospermum scoparium* where EcM and AM co-occurred

Sample number	EcM (%)	AM (%)	Total counts	EcM/AM counts	
				Pre-dicted	Observ-ed
4	79.3	5.8	24.8	1.1	0
6	38.2	13.9	19.5	1.0	0
7	36.0	46.1	30.5	5.1	0
9	1.6	59.7	31	0.3	0
10	42.5	5	14.5	0.3	12.5

**Table 4** Mean EcM and AM fractional colonisation in root samples of *U. staudtii* from dry and waterlogged habitats

Habitat	EcM		AM	
	Mean	SEM	Mean	SEM
Dry (n=6)	54.1 <sup>a</sup>	6.8	18.0 <sup>b</sup>	7.6
Waterlogged (n=5)	15.7 <sup>a</sup>	5.6	41.8 <sup>b</sup>	6.7

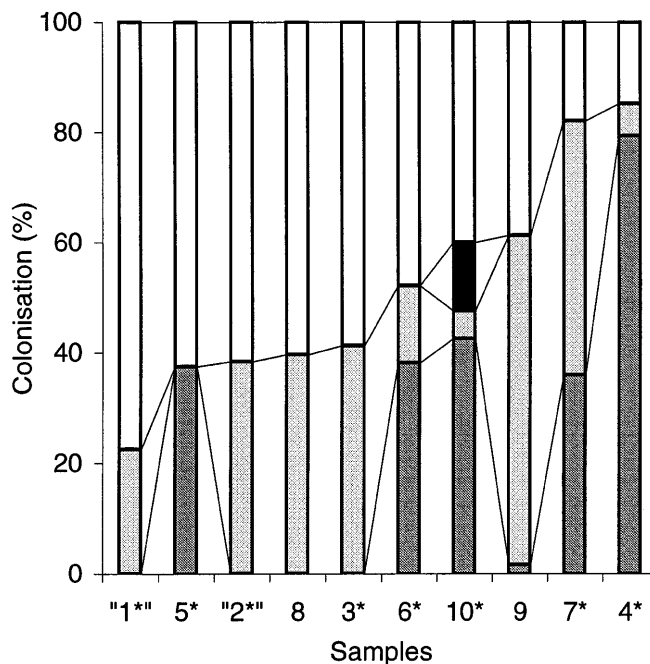
<sup>a</sup> ANOVA (GLM):  $F_{(1,9)} = 18.02$ ,  $P = 0.002$

<sup>b</sup> ANOVA (GLM):  $F_{(1,9)} = 5.27$ ,  $P = 0.047$

tion of *U. staudtii* between habitats were statistically significant. In the same way, the results in Figure 2 show that EcM colonisation occurred in *L. scoparium* plants principally in areas colonised by an EcM tree species (*Nothofagus* sp.) and was scarce in areas dominated by an AM tree species (*Podocarpus* sp.) and altogether absent on ultramafic soil. The effect of sampling site (under *Nothofagus* sp. or *Podocarpus* sp.) on EcM fractional colonisation of *L. scoparium* was weakly significant in an ANOVA (GLM) test ( $P < 0.10$ ), but no statistically significant differences were found between these habitat types in AM fractional colonisation (Table 5).

## Discussion

The occurrence of AM structures in root samples of eight of the 14 EcM tree species from Korup National



**Fig. 2** EcM (■), AM (□) and genuine dual EcM/AM (■) fractional colonisation, and proportion of roots not colonised (□) in *Leptospermum scoparium* root samples (sorted by ascending mycorrhizal colonisation) collected near *Nothofagus* sp. (\*) and *Podocarpus* sp. Samples 1 and 2 were on ultramafic soil

**Table 5** Mean EcM and AM fractional colonisation in root samples of *L. scoparium* from habitats under *Nothofagus* sp. and *Podocarpus* sp.

Habitat	EcM		AM	
	Mean	SEM	Mean	SEM
<i>Nothofagus</i> (n=6)	36.1 <sup>a</sup>	8.3	21.9	6.8
<i>Podocarpus</i> (n=2)	3.7 <sup>a</sup>	2.1	44.8	3.3

<sup>a</sup> ANOVA (GLM):  $F_{(1,6)}=4.55$ ,  $P=0.077$

Park rainforest suggests that many EcM tree species can be colonised to some degree by AM. This occurrence of AM in EcM species is consistent with the observation of AM fungi within the root system of plants in most lowland tropical rainforest EcM tree families and in several plant families from other areas (Fassi 1957; Grand 1969; Read et al. 1977; Malajczuk et al. 1981; Malloch and Malloch 1981; Reddell et al. 1996; Newberry et al. 1988; Lodge 1989; Vardavakis 1992; Moyersoen 1993; Cázares and Smith 1996).

The results also confirm that the pattern of AM fungal colonisation varies between EcM species. Most EcM species were consistently colonised by EcM fungi, some of them with low levels of AM colonisation. In contrast, EcM and AM co-occurred with variable colonisation in *A. bipindensis*, *U. staudtii* and *L. scoparium*. The comparison of the latter two species in their natural habitat suggests that the predominance of EcM or AM in dual mycorrhizal plants varies between taxa. Frequent EcM colonisation of *Uapaca* sp. has been reported previously (Högberg 1982; Högberg and Pearce 1986; Newbery et al. 1988) and root samples of *Uapaca bojeri* from Madagascar were only colonised by EcM (Moyersoen, unpublished data). However, roots of seedlings (1 to 3-month-old) and saplings (more than 1 year old) of *U. guineensis* growing in the same forest area in Ghana (Moyersoen, unpublished data) were colonised only by AM. In *Leptospermum*, Warcup (1980) reported the presence of AM only. Due to the limited number of EcM species within the same genera and in families other than Caesalpinioideae (Amherstieae) in our study area, we could not compare the pattern of dual EcM/AM association between genera or families. However, the observation by Thoen and Ba (1989) of only EcM in *Afzelia africana* in Senegal and the dual EcM/AM association of *A. bipindensis* in Korup National Park rainforest suggest that the pattern of AM colonisation can vary between species within the same genus. Differences in AM and EcM colonisation between species from different areas have also been reported in *Salix* (Dhillon 1994).

The absence or consistently low frequency of AM colonisation in a wide range of EcM species observed in this study raises the question as to whether the host can control AM colonisation. To our knowledge, no comparative studies have been published on root reactions to AM colonisation in predominantly EcM and

dual EcM/AM plant species. Differences in the degree of colonisation by EcM between dual EcM/AM species across a range of habitats described in this study suggest that the receptivity for EcM fungi in dual EcM/AM species can vary. For example, the predominantly AM Casuarinaceae (Diem et al. 1981; Peterson et al. 1985; Reddell et al. 1986) include species from the genus *Allocasuarina*, which more often form typical EcM than do species from the genus *Casuarina* when inoculated with broad range EcM fungus species (Theodorou and Reddell 1991). EcM soil inoculum potential probably depends on the receptivity of the host, so the colonisation of plant taxa (like *Alnus*) receptive to a narrow range of fungus species (Molina 1981) could be limited by the availability of compatible inoculum.

The effect of habitat on the relative proportion of EcM and AM observed on both *U. staudtii* and *L. scoparium* further demonstrates that the co-occurrence of the two mycorrhizal types is also influenced by external factors including moisture (*U. staudtii*), inoculum potential (*L. scoparium*) and soil chemistry (as suggested by the absence of EcM on *L. scoparium* on ultramafic soil). The effect of soil moisture on the relative proportion of EcM and AM has been described by Lodge (1989) on *Populus* and *Salix*, in which AM occupied extremes of a moisture gradient as a consequence of their displacement in moisture conditions (intermediate) favourable for EcM. Ocampo et al. (1980) demonstrated that typically non-mycorrhizal plants such as Brassicaceae can become colonised by AM fungi when grown in association with strongly AM hosts, and Smith et al. (1998) showed that AM colonisation of a typically EcM host (*Pseudotsuga menziesii*) is promoted when grown in dual culture with the AM grass *Calamagrostis rubescens*. The occurrence either of AM or of both EcM and AM in *L. scoparium* depending on the mycorrhizal habit of the dominant vegetation and consequently the availability of EcM inoculum has been reported previously by Cooper (1976) in a pot experiment. Apparently, *L. scoparium* is unable to maintain EcM colonisation in the absence of alternative EcM hosts (here *Nothofagus*). It thus appears to be facultatively ectomycorrhizal.

The data on *U. staudtii* EcM and AM colonisation suggests that EcM and AM can interact within the same root system. The capacity of EcM to out-compete AM has been demonstrated previously on *Populus* (Lodge 1989; Lodge and Wentworth 1990) and *Eucalyptus* (Chilvers et al. 1987) and has been attributed to the possibility of the EcM mantle acting as a mechanical barrier preventing subsequent AM colonisation (Chilvers et al. 1987). If the EcM mantle does prevent AM colonisation, genuine dual EcM/AM colonisation would only be possible in roots already colonised by AM as proposed by Chilvers et al. (1987), and its occurrence would increase in root samples where both EcM and AM co-occur, as observed in two samples of *U. staudtii*. However, the apparent absence of genuine dual EcM/AM associations in one sample of *U. staudtii*

where both EcM and AM co-occurred, and the observation of genuine dual EcM/AM associations only in one sample of *L. scoparium* where AM was relatively low, suggest that other factors influence the presence of these genuine dual associations. Although the mechanisms involved are unclear, the reports by Lodge (1989) and Dhillion (1994) of an influence of ectomycorrhizal type on the co-occurrence of AM suggest that small-scale interactions between EcM and AM within the same root system could be specific.

Differences in the pattern of EcM and AM colonisation and their interaction depending on the partners involved should therefore be taken into account when evaluating the ecological significance of dual EcM/AM association. The pattern of colonisation by EcM and AM fungi within the same root system might vary across a range of habitats, depending on the plant species and the mycorrhizal fungal species involved, with obvious implications for the ecology of the host plant.

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