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ORIGINAL PAPER

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Ectomycorrhizas associated with a relict population of *Dryas octopetala* in the Burren, western Ireland. I. Distribution of ectomycorrhizas in relation to vegetation and soil characteristics

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Abstract The distribution of ectomycorrhizas on *Dryas octopetala* L in grass heaths of the 450 km^2 karst region known as the Burren in Western Ireland was examined in relation to soil factors and vegetation type. Ectomycorrhizas were identified or characterised from 56 soil cores from 30 sites, and the occurrence of each ectomycorrhizal (EM) type was quantified by estimating the total length of mycorrhizal tips of each type. Soil organic matter, total nitrogen, extractable phosphorus, pH and depth were the soil factors determined. In total, 24 EM types were recorded. The EM community of *Dryas* roots was significantly more species-rich in one vegetation type—Hyperico-Dryadetum—than in others (Arctostaphylo-Dryadetum or Asperulo-Seslerietum). Multiple linear regression analyses indicated that soil organic matter and soil depth explained a significant portion of the variation in EM abundance, while soil organic matter and extractable phosphorus explained a significant portion of the variation in EM diversity. Canonical correspondence analysis showed that some individual EM types (e.g. *Craterellus lutescens*, *Cenococcum geophilum*, *Tomentella* sp., *Boletus* sp.) exhibited distinct soil preferences, most markedly in relation to soil organic matter, which, in this analysis, was the main significant soil variable distinguishing the three vegetation types.

Keywords Ectomycorrhizas · Burren vegetation · Soil organic matter content · Soil available phosphorus

Introduction

Mountain avens (*Dryas octopetala* L.) is widely distributed in arctic-alpine habitats in the northern hemisphere and is frequently an important component of the dwarf shrub vegetation in these habitats. *D. octopetala* also occurs in lowland areas of western Europe as relict populations that have survived postglacial climate warming. The 450 km^2 karst region in western Ireland known as the Burren contains the largest of these populations. Much of the Burren is covered by treeless grass heaths on shallow soils over limestone.

In its usual arctic-alpine habitats, roots of *D. octopetala* are colonised by a wide range of ectomycorrhizal (EM) macrofungi (Bledsoe et al. 1990; Kernaghan and Currah 1998; Kernaghan and Harper 2001; Kernaghan 2001), particularly by members of the genera *Cortinarius*, *Inocybe*, *Lactarius* and *Russula*, which are adapted to arctic-alpine conditions. In the Burren, *D. octopetala* is colonised by at least 34 ectomycorrhizal (EM) morphotypes (Harrington 2001) and 21 of these have been described (Harrington and Mitchell 2002a). In a 3-year basidiome survey of the Burren grass heaths, 39 species of putative EM fungi were recorded (Harrington 1996, 2003). All of these are EM associates of forest trees, and even though forested by Scot's pine and oak up to 2,000 years ago (Watts 1984), the grass-heaths of the Burren are now treeless and lack any potential tree hosts for these fungi.

In the absence of trees, there are three potential hosts in the grass heaths: *D. octopetala*, *Helianthemum canum* and *Arctostaphylos uva-ursi*. *Helianthemum* and *Arctostaphylos* are much more restricted in their distribution than *Dryas* in the Burren grass heaths, and do not appear to support ectomycorrhizas of any of the common EM fungi found in the Burren (Harrington 2001). In the Burren, EM-like structures have been observed on root systems of *Carex flacca* and *Carex pilulifera* due to colonization by *Cortinarius* (*Dermocybe*) *cinnamomomeus* but no other EM fungi have been found associated with root systems of these sedges (Harrington and Mitchell 2002b). Thus, over

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most of the grass heaths, *Dryas* is the only potential host for EM fungi.

The vegetation is phytogeographically unusual as it includes arctic-alpine, temperate and Mediterranean elements, growing together in a mild oceanic climate. *D. octopetala* is the most conspicuous of the arctic-alpines, and occurs in three main vegetation types in the Burren. The Hyperico-Dryadetum association (Ivimey-Cook and Proctor 1966) is the most extensive, and here *Dryas* is usually abundant and frequently dominant. Heather (*Calluna vulgaris*), blue grass (*Sesleria albicans*) and pleurocarpous mosses are important components of this vegetation type, conferring the appearance of a grass heath. The Arctostaphylo-Dryadetum (Ivimey-Cook and Proctor 1966) is a more healthy derivative, usually on higher ground where *A. uva-ursi* largely replaces *C. vulgaris*, and in which *D. octopetala*, *Empetrum nigrum*, and *Juniperus communis* are common. The Asperulo-Seslerietum (Shimwell 1971) is a species-rich grassland community rather than a heath, with varying amounts of *Dryas* but usually less than in the other two communities. This is found on the lower slopes of the hills on soils with increasing proportions of limestone drift. *S. albicans*, *H. canum* and *Antennaria dioica* are frequently abundant in this community.

The soils of the *Dryas* communities vary considerably. They range from mineral soils derived from limestone drift to highly organic soils formed from the accumulation on limestone surfaces of plant detritus derived especially from pleurocarpous mosses. They are very shallow (generally less than 20 cm depth) and have no horizon development. While there is little vertical variation in the soil profile, there is considerable lateral variation even over scales of a metre or less. The soils are free-draining and subjected to leaching because of the oceanic influence of the climate. Periodic summer drought is thought to be the main factor that limits grass growth and maintains the presence of the alpine plant species in these communities, particularly on the shallow organic soils (Jeffrey 2003).

This study was undertaken to test the hypotheses that (1) there are differences in composition between the EM communities on *Dryas* in the three vegetation types in which *Dryas* occurs in the Burren, and (2) there is a relationship between soil characteristics and the composition of the EM community on *Dryas* roots.

Materials and methods

Sampling

Soil cores were collected in late October 1999 from 30 sites located in the main areas of *Dryas* distribution in the Burren: Slieve Elva (M102032); Poulacopple (M180045); Gleninagh Mt. (M178103); Slievecarran South (M295023); Bouleevin (M343030) and Mullagh More (R329955) (Fig. 1). The sites were located at altitudes of between 20 and 300 m a.s.l. Apart from *Dryas*, no other EM species were present at any of the sites. The vegetation of each site was classified by visual inspection as belonging to either the Hyperico-Dryadetum, the Arctostaphylo-Dryadetum or the Asperulo-Seslerietum, and the percentage cover of *Dryas* was estimated visually.

Cores were taken using a 53-mm internal diameter cylindrical stainless steel corer, which was inserted as far as

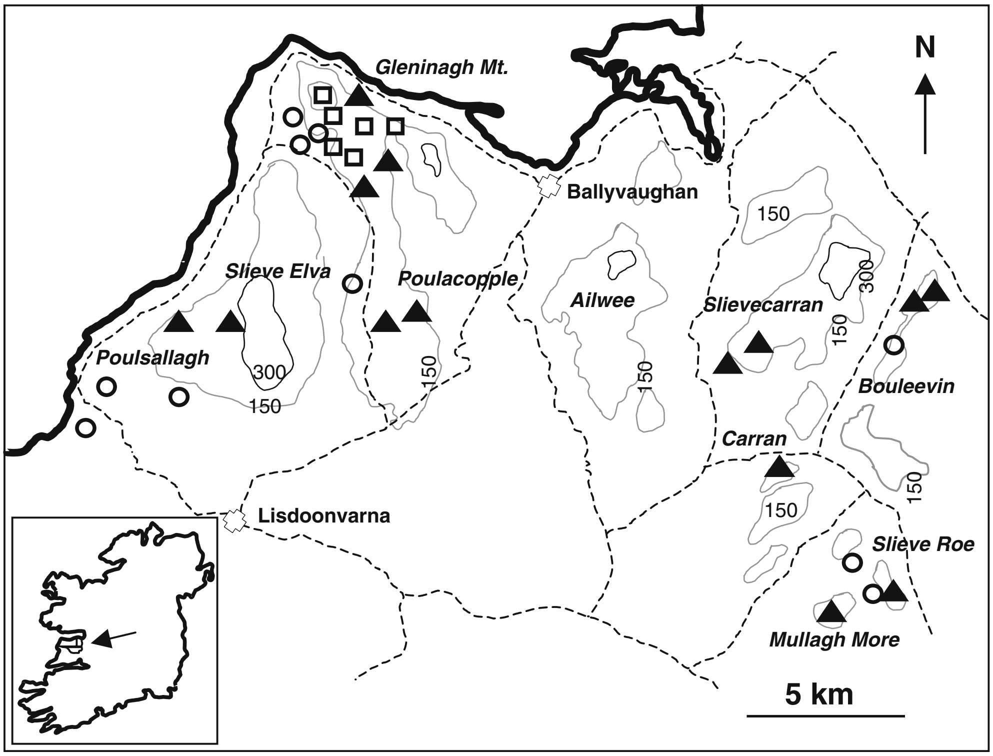

Fig. 1 Locations in the Burren, western Ireland, of 30 sites from which soil samples were collected and assessed for the occurrence of ectomycorrhizas on *Dryas* roots. Vegetation types: ▲ Hyperico-Dryadetum, □ Arctostaphylo-Dryadetum, ○ Asperulo-Seslerietum

the bedrock. Soil depth was measured as the depth of soil to the underlying bedrock. Cores were collected from the edge of *Dryas* mounds where adventitious roots from the creeping stems could be easily distinguished. At each site, one to two *Dryas* plants (1–3 m apart) were sampled. Care was taken to ensure that each core encompassed an adventitious root. A second core of the same size was collected alongside the first core as a sample for soil analysis. Cores were stored in plastic bags at 4°C for no longer than 3 weeks before examination of ectomycorrhizas.

EM enumeration

After soaking overnight in tap water, each core was then washed free of soil material over a 400-µm sieve in running tap water. *Dryas* roots and attached and detached mycorrhizas were picked manually from the washed sample. Moribund and dead EM tips were distinguished from live tips by lack of turgidity or shrunken appearance, and dark discolouration of the mantle and cortex. Live tips were then sorted into morphotypes based on general appearance. Representative examples were selected for a more detailed examination, which followed the protocols described by Agerer (1986). Identification of some of the main EM types was made by PCR-RFLP and sequence analysis of the ITS region of the rDNA gene (see Harrington and Mitchell 2002a for primers and protocols). The abundance of individual EM types was determined by three different measures: tip density (number of EM tips per 100 cm^3 soil), EM length (centimetres per 100 cm^3 soil), frequency (percentage of soil cores in which the EM type occurred). The numbers of live mycorrhizal tips of each morphotype were counted. The total lengths of live mycorrhizal tips of each morphotype and the length of non-ectomycorrhizal *Dryas* roots were then determined by the grid-line-intersect method (Tennant 1975) using a 10- or 5-mm grid (depending on the number of tips in the sample) in 8.5-cm diameter plastic Petri dishes. Samples were counted three times and were redistributed between counts. Lengths were calculated from the average of three counts. Large samples were subdivided and the lengths determined for the subdivisions were pooled to give the total length. The accuracy of the method was checked several times before sampling began, using different grid sizes and roots of predetermined total length.

Soil analyses

Percentage soil organic matter was determined as loss-on-ignition at 400°C. Extractable phosphate was determined using Morgan's extractant (0.74 M sodium acetate-acetic acid solution), which gave more reliable extraction of phosphorus from highly organic soils samples (Byrne 1979), followed by colorimetric assay using the ammonium molybdate method (Murphy and Riley 1962). Extractable phosphate estimates were checked against a reference loam. Soil pH was determined by glass electrode (1:1 soil/deionised water paste) using a Jenway 3310 pH meter. Total Kjeldahl soil nitrogen was determined by digestion in H_2SO_4 followed by analysis of NH_4^+-N by titration with 1.0 M HCl (Bremner and Mulvaney 1982). Total Kjeldahl-nitrogen estimates were checked against the reference loam.

Data analyses

Correlations between mycorrhizal variables and soil variables were calculated using Pearson's correlation coefficient (r) (Zar 1999). Variation in soil and EM variables between the three vegetation types was tested using one-way analysis of variance, and multiple comparisons of means were made using Bonferroni's post hoc test. The contribution of the soil variables to explain variation in EM abundance and number of EM types (log_{10}-transformed) on *Dryas* roots was assessed by multiple regression analysis (SPSS, Chicago, Ill.).

Comparisons of EM species richness in the three vegetation types was made by rarefaction (Heck et al. 1975) in order to take account of the unequal sampling effort in each vegetation type. Species richness estimates and their standard errors were calculated using 12 samples for each vegetation type.

The relationships between EM distribution and soil factors or vegetation types were assessed by canonical correspondence analysis (CCA) using the CANOCO 4 program of ter Braak and Šmilauer (1998). Multiple response permutation procedure (MRPP; Biondini et al. 1988; with Relative Sorensen as the distance measure) was used to test the hypothesis that there was a significant difference between the three vegetation types with respect to EM composition and environmental variables. The significance (P) of the chance-corrected within-group agreement A [$=1-$(observed δ/expected δ)] was tested using a Monte Carlo permutation procedure.

Results

EM types

The survey distinguished 24 distinct mycorrhizal morphotypes on *Dryas* roots (Table 1). The four most common EM types, *Craterellus lutescens*, *Tomentella* sp., *Cenococcum geophilum* and *Dryadirhiza fulgens,* collectively comprised 81% of the EM length from the 56 cores, and were also the most frequent. Three EM types were assigned to '*Cortinarius* types' on the basis of their plectenchymatous mantle and shape and ramification. Six types had orange-coloured mantles and were not characterised further. Three of these (orange types 2, 3 and 4) occurred only once in soil cores and were similar to *D. fulgens* (Harrington and Mitchell 2002a) in general appearance but differed in details of the mantle and extramatrical hyphae. Orange types 1 and 5 had plectenchymatous mantles and were more common, occurring in four and three soil cores, respectively. 'Brown type' was very similar in mantle structure and mycorrhizal morphology to *Dryadirhiza nigra* (Harrington and Mitchell 2002a), but differed in having an apparently thinner and less pigmented mantle.

Table 1 Occurrence of ectomycorrhizal (EM) types in the three main vegetation types in *Dryas* heaths of the Burren, western Ireland. HD Hyperico-Dryadetum association, AD Arctostaphylo-Dryadetum, AS Asperulo-Seslerietum

	Frequency (%)[a]				Total EM length (%)[b]			
	HD	AD	AS	T	HD	AD	AS	T
Craterellus lutescens	51.9	66.7	29.4	48.2	35.6	55.9	38.8	40.70
Tomentella sp.	77.8	91.7	94.1	85.7	13.0	29.4	33.6	22.40
Cenococcum geophilum	59.3	8.3	11.8	33.9	18.9	2.2	7.8	12.30
Dryadirhiza fulgens	40.7	8.3	29.4	30.4	11.3	0.3	1.0	6.04
Brown	7.4	–[c]	11.8	7.1	1.4	–	14.8	5.04
Cortinarius infractus	3.7	–	–	1.8	7.2	–	–	3.63
Hebeloma sp.?	18.5	16.7	–	12.5	5.1	2.4	–	3.05
Cortinarius mussivus	18.5	8.3	–	10.7	1.1	4.4	–	1.44
Cortinarius odorifer	14.8	16.7	–	10.7	0.8	2.9	–	1.00
Boletus sp.	18.5	25.0	11.8	17.9	1.4	1.3	0.1	0.98
Dryadirhiza cerina	18.5	–	–	8.9	1.9	–	–	0.97
Orange 5	–	–	17.6	5.4	–	–	1.7	0.49
Cortinarius 6	14.8	8.3	–	8.9	0.8	0.1	–	0.41
Orange 1	–	8.3	17.6	7.1	–	0.1	1.2	0.37
Tricholoma myomyces	7.4	8.3	–	5.4	0.4	0.2	–	0.24
Orange 2	3.7	–	–	1.8	0.3	–	–	0.17
Orange 3	–	8.3	–	3.6	–	0.8	–	0.17
Cortinarius 1	7.4	–	5.9	5.4	0.2	–	0.3	0.15
Dryadirhiza rugosa	7.4	–	–	3.6	0.3	–	–	0.14
Cortinarius 7	3.7	–	11.8	5.4	0.1	–	0.3	0.12
Cortinarius calochrous	3.7	–	–	1.8	0.2	–	–	0.11
Orange 4	–	–	5.9	1.8	–	–	0.4	0.11
Cortinarius atrovirens	3.7	–	–	1.8	0.3	–	–	0.02
Dryadirhiza truncata	–	–	5.9	1.8	–	–	0.1	0.02

[a] Percentage of soil cores containing the EM morphotype, in each vegetation type and in the total of 56 cores (T)

[b] Percentage proportion of total EM length in soil cores from each of the vegetation types and in the total of 56 cores (T)

[c] Not present

Correlation between EM, vegetation and soil variables

The 56 sites were classified according to the three common vegetation types of the Burren *Dryas* heaths, the Hyperico-Dryadetum association, the Asperulo-Seslerietum association and the Arctostaphylo-Dryadetum, which were represented by 27, 17 and 12 soil cores, respectively (Table 2). Extractable soil phosphorus and total soil nitrogen were significantly higher in the Hyperico-Dryadetum than in the other vegetation types. *Dryas* cover and soil organic matter were significantly less in the Asperulo-Seslerietum than in the Hyperico-Dryadetum or Arctostaphylo-Dryadetum, which were not significantly different from each other (Table 2). Nineteen EM types were recorded from the Hyperico-Dryadetum sites and 12 each from the Arctostaphylo-Dryadetum and Asperulo-Seslerietum sites. The mean number of EM types recorded per soil core was significantly greater ($P<0.01$) in the Hyperico-Dryadetum sites (3.8) than the Asperulo-Seslerietum and Arctostaphylo-Dryadetum sites, but there was no significant difference between the Asperulo-Seslerietum and Arctostaphylo-Dryadetum sites. Rarefaction estimates of species richness showed that Hyperico-Dryadetum sites were significantly richer ($P<0.0001$) in EM species than either Arctostaphylo-Dryadetum or Asperulo-Seslerietum sites, which did not differ significantly from each other (Table 2). There was no significant difference in the total length of *Dryas* roots per core or the length of EM root tips per core between the vegetation types.

In the 56 cores, soils ranged from calcareous clay soils to very shallow, highly organic soils, formed on limestone surfaces. Extractable phosphorus, total nitrogen and altitude showed significant positive relationships with organic matter, but the relationships between soil pH or depth and organic matter were significantly negative (Table 3). All of

Table 2 Soil and EM community characteristics of the three vegetation types in *Dryas* heaths of the Burren, western Ireland. Rarefaction estimates of species richness (estimated number of species) were made using a common sample size of 12 cores. Values given represent means (standard error in parentheses). For each variable, means followed by the same letter are not significantly different at $P \leq 0.05$

	HD	AD	AS
Number of soil cores	27	12	17
Altitude (m a.s.l.)	193 (9.6)a	237 (21.1)b	106 (15.5)c
Dryas cover (%)	63 (2.69)a	46 (5.20)a	32 (3.15)b
Soil depth (cm)	4.9 (0.4)a	6.6 (0.9)a	5.4 (0.5)a
Soil organic matter (% dry mass)	79.7 (2.4)a	66.8 (5.7)a	43.7 (6.2)b
Soil pH	6.5 (0.1)a	6.6 (0.1)ab	7.0 (0.1)b
Extractable phosphorus (μg g^{-1} dry mass)	42.7 (3.6)a	24.0 (4.9)b	17.7 (4.1)b
Total nitrogen (% dry mass)	1.31 (0.1)a	1.23 (0.1)b	0.61 (0.1)c
Total number of EM types	19	12	12
Species richness	17.8 (0.8)a	11.1 (0.8)b	11.2 (0.7)b
Number of EM types per soil core	3.8 (0.3)a	3.0 (0.4)b	2.5 (0.3)b
EM length per core (cm)	48.4 (7.9)a	43.9 (8.3)a	44.9 (13.9)a
Dryas root length per soil core (cm)	175.6 (22.1)a	147.1 (18.8)a	136.1 (22.0)a

Table 3 Pearson's correlation coefficients (r) between soil variables in 56 soil cores from the Burren, western Ireland

	Organic matter	Total N	Soil extractable P	Soil pH	Soil depth	Altitude	EM length	Root length
Total N	0.65**							
Soil extractable P	0.83**	0.42**						
Soil pH	−0.69**	−0.44**	−0.63**					
Soil depth	−0.45**	−0.22	−0.36*	0.01				
Altitude	0.49**	0.47**	0.23	−0.46**	0.15			
EM length	0.29*	0.07	0.31*	−0.06	−0.11	0.17		
Root length	0.33*	0.12	0.38**	−0.13	−0.19	0.16	0.64**	
Number of EM types	0.46**	0.21	0.45**	−0.46**	−0.02	0.24	0.34**	0.41**

*Significant correlation at $P \leq 0.05$
**Significant correlation at $P \leq 0.01$

the other correlations between soil variables were significant, except the relationships between soil depth and total nitrogen, between soil depth and soil pH, and between altitude and extractable phosphorus or depth (Table 3). Number of EM types was positively correlated with soil organic matter, extractable phosphorus and *Dryas* root length, and negatively correlated with soil pH. EM length was positively correlated with soil organic matter and extractable phosphorus (Table 3). Multiple linear regression analyses of EM length and numbers of EM types (log-transformed) against the four soil variables, altitude and *Dryas* root length per core, were carried out using backward selection of independent variables. Soil organic matter and soil depth together explained 25% of the variation in EM length ($F_{2,51}$=4.2, P<0.05, adjusted r^2= 0.252) and both variables were significant (t_{55}=2.72, P<0.05 and t_{55}=2.55, P<0.05, respectively). Soil organic matter, extractable phosphorus, total soil nitrogen and altitude together explained 39% of the variation in the number of EM types ($F_{4,\ 51}$=4.08, P<0.05, adjusted r^2=0.393) but only the first two variables were significant (t_{55}=3.30, P<0.01 and t_{55}=3.07, P<0.01, respectively).

EM distribution patterns

The distribution of individual EM types, and the relationships between them and the soil variables and vegetation, were analysed using CCA (Figs. 2, 3). A Monte Carlo permutation test (199 permutations) showed that the relationship between the ectomycorrhizas and the first four canonical axes representing the environment variation was

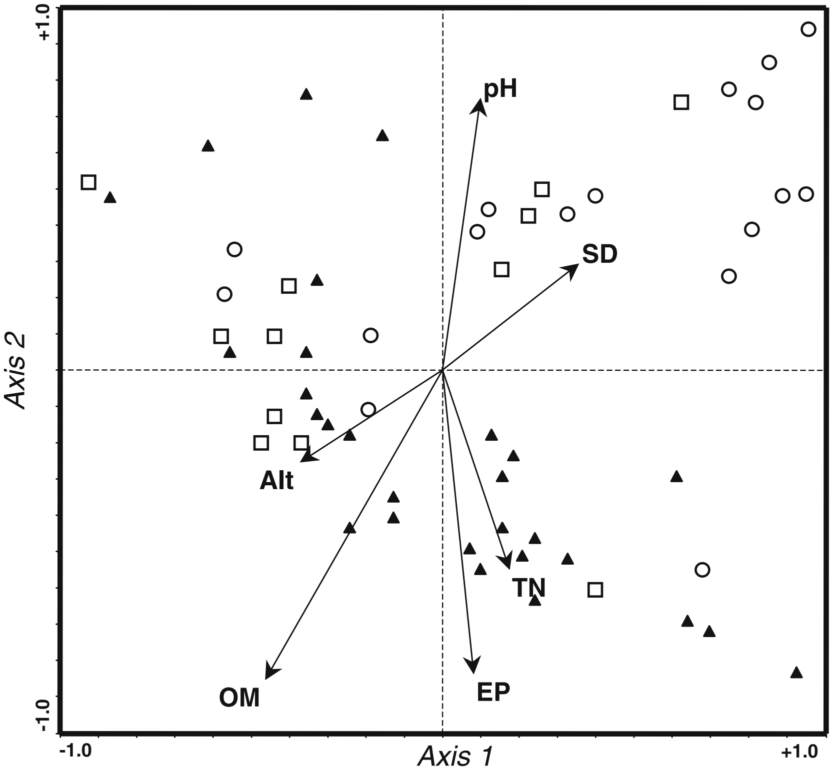

Fig. 2 Canonical correspondence analysis (CCA) site ordination of 56 soil cores from the Burren grass heaths, western Ireland, based on relative abundance (percentage of total length, log-transformed) of ectomycorrhizas on *Dryas* roots. Environmental variables: Alt altitude (m a.s.l.), EP extractable phosphorus (μg g^{-1}), OM soil organic matter (%), pH soil pH, SD soil depth (cm), TN total soil nitrogen (%). Vegetation types: ▲ Hyperico-Dryadetum, □ Arctostaphylo-Dryadetum, ○ Asperulo-Seslerietum

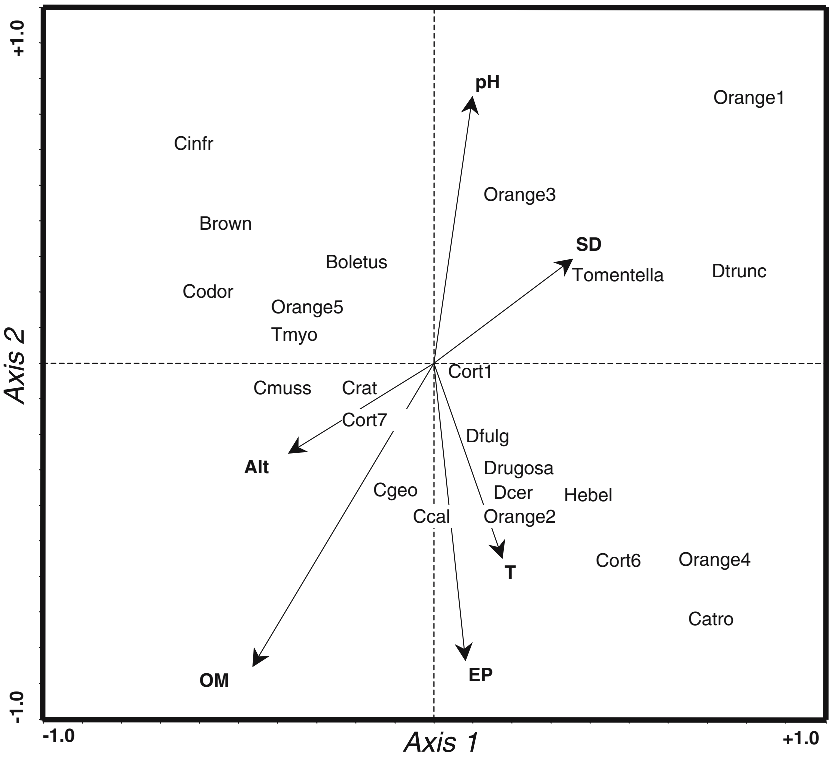

Fig. 3 CCA species ordination of EM morphotypes in 56 soil cores from the Burren, western Ireland. Environmental variables: Alt Altitude (m), EP extractable phosphorus (µg g^{-1}), OM soil organic matter (%), pH soil pH, SD soil depth (cm), TN total soil nitrogen (%). Ectomycorrhizas: Brown Brown type, Cgeo *Cenococcum geophilum*, Catro *Cortinarius atrovirens*, Cort1 *Cortinarius* 1, Ccal *Cortinarius calochrous*, Cinfr *Cortinarius infractus*, Cmus *Cortinarius mussivus*, Codor *Cortinariusodorifer*, Cort6 *Cortinarius* 6, Cort7 *Cortinarius* 7, Crat *Craterellus lutescens*, Boletus *Boletus* sp., Dcer *Dryadirhiza cerina*, Dfulg *Dryadirhiza fulgens*, Hebel *Hebeloma* sp., Tomentella *Tomentella* sp., Drugosa *Dryadirhiza rugosa*, Dtrunc *Dryadirhiza truncata*, Orange1–5 Orange types 1–5, Tmyo *Tricholoma myomyces*

statistically significant ($P<0.05$), indicating that the variation in the mycorrhiza data set is not random in relation to variation in the environmental data set. Eigenvalues for the first two axes were 0.42 and 0.27, and both axes explained 10.4% of the variance in the mycorrhiza data. The species-environment correlations of the first and second axes were 0.80 and 0.60, respectively. Forward selection of environmental variables showed that only organic matter and extractable phosphorus contributed significantly ($P<0.01$) to the variance found in the EM data. These two soil variables explained 58% of the explained variance. Removing the unidentified and uncharacterised ectomycorrhizas from the dataset did not alter the site ordination, Monte Carlo significance values, or the significance of the soil variables in forward selection.

In the site ordination (Fig. 2), most of the Hyperico-Dryadetum sites are located in the lower half of the ordination diagram corresponding to increasing soil organic matter, total nitrogen, extractable phosphorus and altitude, and decreasing pH and soil depth. The Asperulo-Seslerietum sites corresponded to increasing soil pH and depth (Fig. 2) and are well differentiated from the other vegetation types on the basis of the composition of their EM communities (Table 1). The majority of the Arctostaphylo-Dryadetum sites corresponded to higher altitude, although they are not well differentiated from the Hyperico-Dryadetum sites by their EM communities (Table 1). Nonetheless, MRPP revealed highly significant levels of concordance between the classification of the sites based on vegetation, and the EM composition (A=0.071; P=0.0009) and environmental composition (A=0.141; P=0.00002) of the sites, with relatively high values for within-group agreement.

The species ordination (Fig. 3) shows that most of the EM types were found in sites containing soils with increasing soil organic matter, total nitrogen and extractable phosphorus. The occurrences of ectomycorrhizas of *Craterellus lutescens*, *Cenococcum geophilum*, *T. myomyces*, *D. fulgens*, *Cortinarius calochrous* and *D. rugosa* were correlated with these variables, and consequently these EM types were more abundant and/or more frequent in samples from the Hyperico-Dryadetum sites than from the other sites. *Cortinarius mussivus* and *Cortinarius odorifer* were most common in the Arctostaphylo-Dryadetum sites. Asperulo-Seslerietum sites are characterised by the highest level of abundance of *Tomentella* sp. and *D. truncata*.

There were marked discontinuities in the distribution of certain EM types in relation to the soil variables. Ectomycorrhizas of *Craterellus lutescens* and *Cenococcum geophilum* were confined to soils in which organic matter content exceeded 30% (Fig. 4a, b). Ectomycorrhizas of *D. cerina*, *D. fulgens*, *D. rugosa*, *Cortinarius calochrous* and *Cortinarius atrovirens* were also most abundant and frequent in highly organic soils (data not shown). In contrast, ectomycorrhizas of *Boletus* sp. (Fig. 4a) and *D. truncata* were more abundant in the less organic soils. Ectomycorrhizas of *Tomentella* sp., the most frequent type (Table 1), were widely distributed, but were more abundant in the less organic soils (Fig. 4b), which were also generally deeper.

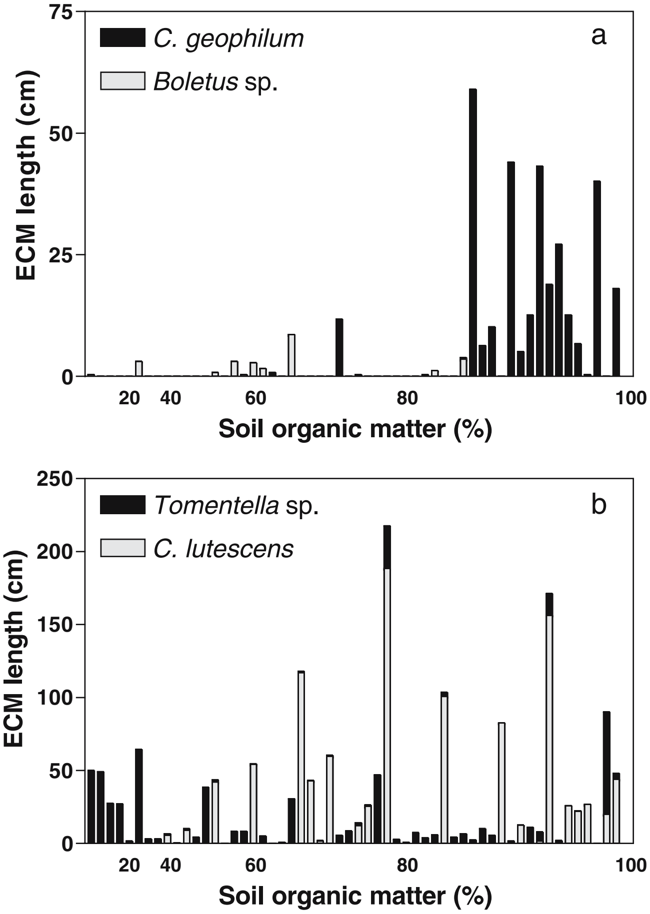

Fig. 4 **a**–**b** Distribution of ectomycorrhizas of *Dryas octopetala* in relation to soil organic matter in 56 soil cores from the Burren, western Ireland. **a** *Cenococcum geophilum* and *Boletus* sp. **b** *Craterellus lutescens* and *Tomentella* sp. *x*-axis not drawn to scale

Discussion

In this study, soil organic matter was found to be the most significant positive factor associated with EM abundance and EM diversity on *Dryas*. Extractable phosphorus was strongly correlated with soil organic matter, probably reflecting the greater availability of soil phosphorus in organic soils compared to the more alkaline mineral soils. In many studies of EM distribution, soil organic matter has been identified as the most important positive influence on diversity of the EM community and the occurrence of certain EM types. Harvey et al. (1976, 1979) found that most of the EM tips occurred in the humus layer of a Douglas fir/larch forest. Significant differences have been observed in EM occurrence and EM community diversity between the organic humus layers and mineral horizons of forests (Jonsson et al. 1999; Fransson et al. 2000) and EM diversity showed a strong significant correlation with accumulation of organic matter in developing woodland stands (Gardner and Malajczuk 1984;Yang et al. 1998; Conn and Dighton 2000). Tyler (1985) has shown that soil organic matter is the most important soil factor influencing the distribution of basidiomes of EM genera in Swedish beech forests.

The vegetation types in the Burren, in which *Dryas octopetala* occurs, exhibited variations in the EM community found on *Dryas* roots. This was most marked for the Hyperico-Dryadetum community, which is found on the most organic soils and which had significantly greater EM diversity compared to either the Asperulo-Seslerietum or the Arctostaphylo-Dryadetum. This is most likely related to differences in soils between the vegetation types. Variation in *Dryas* root development between the vegetation types may also have influenced EM diversity. The mean length of roots per core was greatest in the Hyperico-Dryadetum and although the differences between the vegetation types were not significant because of large variation, EM diversity and *Dryas* root length were significantly correlated.

Some of the common EM associates of *Dryas* were restricted to part of the edaphic range occupied by *Dryas*. *Craterellus lutescens* and *Cenococcum geophilum*, for example, were confined to soils of more than 30% organic matter and were therefore largely absent from the Asperulo-Seslerietum community. In Swedish beech woodlands, Tyler (1985) found that the distribution of basidiomes of *Craterellus* (*Cantharellus*) *tubaeformis*, which is closely related to *C. lutescens*, was confined to soils with high organic-matter accumulation. Other widely distributed types, such as *Tomentella* sp., were more abundant on *Dryas* roots in mineral soils than in organic soils. Such discontinuities in EM distribution have been observed before over the edaphic range of host species, both for EM root tips and basidiomes. Van der Heijden et al. (1999) observed compositional differences between the EM assemblages of contrasting *Salix repens* stands in Holland: *Inocybe* ectomycorrhizas were confined to calcareous sites whereas *Russula*, *Lactarius* and *Xerocomus* ectomycorrhizas were more abundant in older acidic sites. Goodman and Trofymow (1998) found that distributions of Douglas-fir ectomycorrhizas were related strongly to within-stand heterogeneity in soil composition. The study of Gehring et al. (1998) on *Pinus edulis* growing on two sites with contrasting soil types found that the dominant EM fungi on *P. edulis* were different in each site, and four of the five dominant types were exclusive to one site. Danielson and Visser (1989) found that ectomycorrhizas of *Tomentella* and *Suillus* species were more abundant on the roots of *Pinus contorta* seedlings grown in mineral soil compared to organic soil.

In forest studies, it is difficult to disentangle the direct effects of soil factors in the organic horizons on EM abundance and diversity from the unequal distribution of host roots between the organic and mineral horizons. Most root tips, for example, are likely to be found in the organic horizons and therefore most EM diversity is likely to occur here as well. In the soils of *Dryas* heaths, which lack horizons, it appears that the marked lateral variation in soil organic matter is the main influence on EM distribution patterns. The abundance of *Craterellus lutescens* and *Cenococcum geophilum* in organic soils may reflect an ability on the part of these EM fungi to preferentially exploit organic substrates. Abuzinadah and Read (1986) have suggested that the relative ability of EM fungi to utilise organic nutrient sources determines where they occur.

Kernaghan and Harper (2001) have suggested that the influence of soil factors may be more pronounced for EM fungi that lack host specificity, which may be the case for most of the EM fungi that associate with *Dryas* in the Burren.

Other factors, not yet investigated in the *Dryas* heaths, could also contribute to the EM distribution patterns. Differences in production by *Dryas* between different soil types, influenced by variation in soil aeration, drainage and grazing, could affect EM diversity and development, although Gehring et al. (1998) found no relationship between host production and diversity of ectomycorrhizas on pinyon pine, and Villeneuve et al. (1988) found that diversity of EM fungi based on basidiomes in Canadian forest stands remained unchanged along a gradient of decreasing host production, even though basidiome numbers declined. Rooting patterns could also be different in organic and mineral soils and could affect colonisation by EM fungi.

In conclusion, this study has shown that the EM community on roots of *D. octopetala* in the Burren, western Ireland, is dominated by four EM types (*Craterellus lutescens*, *Tomentella* sp., *Cenococcum geophilum* and *Dryadirhiza fulgens*). Of the three vegetation types where *D. octopetala* occurs in the Burren, the Hyperico-Dryadetum association was the most widespread and contained the most diverse group of EM types. Differences in overall EM diversity and abundance of individual EM types were correlated with soil factors, of which soil organic matter was found to be the most significant. A more intensive study on the composition and temporal variation in this EM community has also been carried out [Harrington and Mitchell 2005 (this volume)].

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