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Post-fire, seasonal and annual dynamics of the ectomycorrhizal community in a *Quercus ilex* L. forest over a 3-year period

Abstract Two study plots, burned and control, were established in autumn 1998 in a *Quercus ilex* forest located in northern Spain, part of which had been affected by a low intensity fire in 1994. Soil samples for ectomycorrhizae (ECM) were taken over a 3-year period in each study plot in spring, summer, autumn and winter. ECM morphotypes were identified and the relative abundance of each morphotype in each soil sample calculated, along with species richness, Shannon diversity index and percentage of mycorrhization in each soil sample. The relative abundance of certain ECM morphotypes differed between burned and control plots, and the percentage of mycorrhizal tips was significantly lower in the burned than in the control plot. Nevertheless, there were no significant differences in the diversity, species richness or species composition of the ECM community in the burned and control plots. The dominant ECM morphotypes in both stands were *Cenococcum geophilum* and several thelephoroid fungi. *Sphaerosporella brunnea* and *Pisolithus tinctorius* thrived especially in the burned plot, whereas three ectomycorrhizal morphotypes assigned to the genus *Hebeloma* were especially abundant in the control plot. There was no significant variation in the relative abundance of the ECM morphotypes between seasons, but ECM community species richness was highest in autumn and lowest in summer. The percentage of mycorrhizal tips reached a maximum in winter, with its minimum in autumn. Collection of samples over the 3-year period also enabled us to detect a significant increase in percentage of ECM colonisation in the burned stand over time.

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Introduction

Mycorrhizal symbiosis has evolved as a mechanism of survival both for plants and fungi, enabling both to thrive in areas with poor soils, periodic droughts, extreme temperatures and other natural stresses (Gupta et al. 2000). For this reason, it is well known that mycorrhizae play an important role in the colonisation of new areas of land or in the regeneration of disturbed zones (Allen 1991; Baar et al. 1999).

As fire is one of the most common disturbances in natural communities, there is an increasing interest in analysing the effects of burning on the ectomycorrhizal (ECM) communities of different ecosystems worldwide and determining the extent to which ECM are involved in the regeneration of the area. However, most of the studies on the post-fire dynamics of the ECM community have been performed in conifer forests (Baar and Kuyper 1998; Baar et al. 1999; Dahlberg et al. 2001; Danielson 1984b; Grogan et al. 2000; Horton et al. 1998; Jonsson et al. 1999; Mah et al. 2001; Purdy et al. 2002; Stendell et al. 1999; Visser 1995), with one exception, a study carried out in a *Eucalyptus regnans* forest (Launonen et al. 1999).

All these studies were carried out in temperate and boreal areas, and little is known about the effect of fire on the ECM community of Mediterranean ecosystems, where fire is a common hazard. In these ecosystems, the only data available also come from gymnosperm-dominated forests (Horton et al. 1998; Martínez de Aragón et al. 2001; Torres and Honrubia 1997); studies dealing with host species such as *Quercus ilex* or *Quercus suber* have focused on the description of the ECM morphotypes encountered and have not investigated the effect of fire on these communities (Azul and Freitas 1999; García 2001; Sarrionandía et al., unpublished data).

Moreover, there is a lack of information on the seasonal and annual dynamics of the ECM community (Dahlberg

et al. 1997), as most of the studies undertaken so far are based on single collections of ECM; very few reports present data gathered over 1 year or more (Azul and Freitas 1999; García 2001; Mineo and Majumdar 1996).

The aim of this work was therefore to determine the effects of a low-intensity wildfire on the ECM of a Mediterranean *Q. ilex* forest over a period of 3 years. Gathering data over this extended period also enabled the seasonal and annual variations in the ECM community of the *Q. ilex*-dominated ecosystem to be investigated.

Materials and methods

Field sampling

In September 1994, a low-intensity wildfire burned 38 ha of a *Q. ilex* forest at Nazar, Navarra, in northern Spain (latitude 42°38′29″N and longitude 2°16′37″W), while 30 ha of the forest remained undisturbed. We can describe the wildfire as being of low intensity because the loss of organic matter was minor, trees and shrubs were able to resprout easily, and the seed bank was not particularly affected. This study began 4 years later, when the trees from the burned stand had the appearance of 1.5- to 2-m-tall shrubs lacking a defined main trunk. Other shrubs and plants from the understorey had already attained heights of up to 1.5 m, making the stand difficult to enter due to the continuous vegetation cover. The burned and control plots were separated by a road and were 50 m apart.

The study site is located at an altitude of 746 m and has a south-facing aspect. The mean annual precipitation is 699 mm with peaks in April and November and a dry period in July and August, and the mean annual temperature is 11.7°C, varying between 4.7°C in the coldest month (January) and 20.8°C in the warmest month (August) (Departamento de Agricultura, Ganadería y Alimentación del Gobierno de Navarra, personal communication).

Both stands, burned and control, were visited in autumn, winter, spring and summer from autumn 1998 until summer 2001. After litter removal, five soil samples of ca. 450 g to a depth of 10 cm were randomly collected from each stand in each sampling date, placed in plastic bags, stored at 4°C and processed in the laboratory within 2 weeks. The soil was stony and usually dry, resulting in difficulties with the collection of a fixed volume using a soil corer as initially planned. A fixed soil weight was collected, therefore, using a spade instead. The type of soil in both stands was a lithic–calcixerollic Xerochrept according to the USA Soil Taxonomy, i.e., a calcareous and stony soil typical of areas with high slopes.

Extraction and identification of ECM and calculation of abundance and diversity parameters

Approximately 300 g of each soil sample was randomly taken with a gardening spade to extract and identify the ECM morphotypes occurring in them. The samples were soaked in a 1% sodium metaphosphate solution for 24 h to clean the soil and debris from the roots before passing through a combination of 1.7- and 0.7-mm sieves. The roots extracted were kept in water in labelled tubes, stored at 4°C and analysed within 2 weeks.

Roots were observed under a stereomicroscope at a magnification of 15× in order to extract the mycorrhizal tips. Each mycorrhizal tip was analysed and assigned to an ECM morphotype according to morphological and anatomical features (Agerer 1986, 1987–2002, 1994, 1999). The descriptions of ECM morphotypes were then compared with other published descriptions of ECM to establish the identity of the fungal symbiont. In some cases, the identification was carried out through personal communications or by tracing the sporocarp to the ECM. ECM morphotypes which could not be identified were given a reference number. Voucher specimens of all ECM morphotypes were deposited in the Herbarium of the University of Navarra (PAMP).

After counting the number of mycorrhizal tips in each ECM morphotype, the relative abundance of each ECM morphotype in each soil sample was calculated (number of tips of a certain ECM morphotype/total number of mycorrhizal tips extracted in the sample), the species richness (number of different ECM morphotypes encountered in a given sample) and the Shannon diversity index ($H=-\sum p_i \ln p_i$, where p_i is the relative abundance of ECM morphotype i in a sample; Barbour et al. 1999). The cumulative species richness over the 3 years of study was also calculated.

Percentage of total mycorrhization in each soil sample

The degree of ECM colonisation in the soil samples collected was calculated in order to compare quantities in the burned stand and the control plot. One hundred and fifty grams of each soil sample was taken randomly, cleaned and sieved as explained above to extract the roots. The percentage of total mycorrhization of a given sample (%M) was calculated using the gridline intersect method (Brundrett et al. 1996). The extracted roots were placed randomly in a grid divided into 1×1 cm squares, and the number of roots intersecting with the gridline counted under a stereomicroscope at 15× magnification. Whether the root at an intersection point was mycorrhizal or not (%M=100*n_i/N, where n_i is the number of intersections of mycorrhized roots and N the total number of root intersections) was also determined. All live secondary roots intersecting the grid were counted, not only root tips. (The *Q. ilex* roots were very fragile, and were mostly broken after processing the soil samples, so it was impossible to distinguish whether a piece was part of a root tip or not.)

Statistical analysis

The relative abundance of ECM morphotypes was analysed with the multivariate ordination technique Detrended Correspondence Analysis (DCA; Hill and Gauch 1980)

due to the large number of soil samples and ECM morphotypes studied. The purpose was to analyse if there was any difference amongst soil samples regarding the relative abundance of the ECM morphotypes occurring in them. Variables included in the secondary matrix were: sampling stand (burned or control), sampling season (autumn, winter, spring or summer) and sampling year (first, second or third). Analyses were performed using the statistical programme PC-ORD version 4.25 (McCune and Mefford 1999). The Pearson correlation coefficient (r) was then calculated for each pair ECM morphotype-axis to determine if the relative abundance of each ECM morphotype was correlated with any group of soil samples (burned, control, autumn, winter, etc.). Rohlf and Sokal's (1995) critical values were used to confirm that the correlations were not due to chance ($P<0.01$) according to the number of degrees of freedom.

The data on species richness and Shannon diversity index were tested for normal distribution by Kolmogorov–Smirnov test (Zar 1998). No normal distribution was found, and therefore differences between sampling plots, seasons and years were tested with Kruskal–Wallis and Mann–Whitney U tests by using the statistical programme SPSS for Windows version 11.0. Since the percentage of total mycorrhization was not a continuous variable, the same non-parametric tests were also applied to analyse these data.

Results

Dynamics of the relative abundance of ECM morphotypes

A total of 96 soil samples were collected over 11 seasonal samplings, 51 in the burned stand and 45 in the control plot; on some occasions only two or three, instead of the five soil samples initially planned, could be collected in each stand due to field sampling constraints. A total of 8,539 mycorrhizal tips, assigned to 32 different ECM morphotypes, were observed over the 3 years of study (see Table 1 for the most important characteristics; detailed descriptions can be obtained from the corresponding author). The mean number of mycorrhized tips analysed per 300 g soil sample was 89.5, ranging from 29 to 201. Although the identification of ECM morphotypes was exclusively based on morphology, and no molecular tools were used, the detailed analysis of morphological and anatomical characteristics was accurate enough to identify those ECM morphotypes showing significant distinguishing features. Eight ECM morphotypes were identified to species level, four to genus, one to family, three were unidentified ECM morphotypes whose description had been published, and the remaining 16 were unidentified ECM morphotypes. Sixteen of the 32 ECM morphotypes described were thelephoroid, i.e., attributed to the family Thelephoraceae (*Tomentella galzinii*, *Tomentella pilosa*, *Pinirhiza dimorpha*, *Quercirhiza cumulosa*, *Quercirhiza stellata*, and the ECM morphotypes 3, 4, 7, 15, 17, 31, 37, 39, 40, 41 and AD). Features shared by the thelephoroid

ECM morphotypes included the dark colour (ranging between dark brown and black) of the ECM system, the pseudoparenchymatous structure of the outer mantle, and the presence of hyphae mostly coloured and with clamp connections, which in some cases formed slightly differentiated rhizomorphs (type C according to Agerer 1987–2002).

The mean relative abundance of each ECM morphotype in the burned and control stands over the 3 years is shown in Table 2. Only four ECM morphotypes had a relative abundance greater than 0.05 in each sampling stand over the 3 years of study, accounting for more than 5% of the mycorrhizal tips: *Cenococcum geophilum*, *Q. cumulosa*, morphotype 4 and type *Hebeloma–Cortinarius* in the control stand, and the same, except for morphotype 7 instead of *Hebeloma–Cortinarius*, in the burned stand.

DCA results showed that the data on relative abundance of the ECM morphotypes in the 96 soil samples were sufficiently dispersed at least along axis 1 (eigenvalue >0.5). The variable causing such dispersion appeared to be the sampling stand, because soil samples collected in the burned stand were grouped together to the right of axis 1 and on the upper part of axis 2 (positive correlation with both axes; Fig. 1), whereas those collected in the control stand appeared to the left of axis 1 and on the lower part of axis 2 (negative correlation with both axes). The other two variables studied, the sampling season and sampling year, did not cause any dispersion of data, and therefore were not considered further. Table 3 shows the ECM morphotypes correlated with axes 1 and 2 with Pearson correlation coefficient values greater than |0.267|, which is Rohlf and Sokal's (1995) critical value for 94 degrees of freedom ($n-2$) to confirm that the correlation is not due to chance ($P<0.01$). Those ECM morphotypes correlated positively with any of the two axes were more abundant in the burned stand, while the negatively correlated ECM morphotypes were more abundant in the control stand.

Dynamics of the species richness and Shannon diversity index of the ECM community

The number of ECM morphotypes encountered increased steadily with the number of samplings performed (Fig. 2). There were no significant differences in either species richness or the Shannon diversity index between the burned and control stands ($P=0.18$ and $P=0.4$, respectively, Mann–Whitney U). There was, however, a significant change in both parameters depending on the sampling season (Table 4). The species richness was significantly lower in summer than in any other season; the maximum values occurred in autumn, and were significantly greater than those in winter and summer. There was no significant difference, however, between species richness in the autumn and spring samples ($P=0.08$, Mann–Whitney U). The Shannon diversity index was only significantly greater in autumn than in summer, without showing any significant ($P>0.05$, Mann–Whitney U) difference in any other comparison between sampling seasons. Whereas the Shannon

Table 1 Description of the most important morphological and anatomical characteristics (Agerer 1986, 1987–2002, 1994, 1999) of the 32 ECM morphotypes encountered in the *Q. ilex* forest at Nazar

ECM morphotype	Macroscopic description	Outer mantle	Inner mantle	Cystidiae	Rhizomorphs	Emanating hyphae
Cenococcum geophilum Agerer and Gronbach (1988)	Black; mostly unbranched; grainy and shiny	Plectenchymatous; hyphae arranged star-like	Plectenchymatous	Lacking	Lacking	Dark brown; without clamps
Genea verrucosa Jakucs and Bratek (1998), Jakucs et al. (1998a)	Reddish brown; woolly	Pseudoparenchymatous with angular cells bearing mounds of roundish cells	Transitional type between plectenchymatous and pseudoparenchymatous	Lacking	Lacking	Brown to yellowish; without clamps; warty
Hebeloma cf. *sinapizans*, Linked with sporocarp	Whitish brown; cottony	Plectenchymatous; surface with crystals	Plectenchymatous	Lacking	Undifferentiated, hyphae loosely woven; surface with crystals	Hyaline; with clamps; swollen septa; anastomoses with crystals
Pinirhiza dimorpha Golldack et al. (1999)	Reddish brown to black; short-spiny	Pseudoparenchymatous with angular cells bearing mounds of cells	Plectenchymatous with ring-like arrangement of hyphal bundles	Bottle-shaped; 20–60 μm long; brown	Lacking	Scarce; brown; rarely with clamps
Pisolithus tinctorius, Linked with sporocarp, Weiss (1991, 1992)	Golden brown; loosely cottony	Plectenchymatous	Plectenchymatous	Lacking	Hyphae compactly arranged; with inflated cells	Hyaline to yellowish; with clamps; sometimes with a brown content
Quercirhiza cumulosa De Román et al. (2002)	Dark brown to black; loosely woolly	Pseudoparenchymatous with angular cells bearing mounds of cells	Transitional type between plectenchymatous and pseudoparenchymatous	Lacking	Slightly differentiated	Brown; with clamps and secondary septa; warty
Sphaerosporella brunnea Danielson (1984a), Meotto and Carraturo (1988)	Yellowish brown to reddish brown; woolly	Pseudoparenchymatous with angular cells bearing a hyphal net	Transitional type between plectenchymatous and pseudoparenchymatous	Lacking	Lacking	Brown; without clamps; constricted at septa
Tomentella galzinii Jakucs et al. (1997, 1998b), Kõljalg et al. (2001)	Greenish brown; short-spiny	Pseudoparenchymatous with angular cells	Transitional type between plectenchymatous and pseudoparenchymatous	Awl-shaped with a clamp; 40–55 μm long; basal cell yellow	Undifferentiated, hyphae loosely woven	Hyaline to yellowish; with clamps and secondary septa
Tomentella pilosa Jakucs and Agerer (1999)	Light to dark brown; loosely short-spiny	Pseudoparenchymatous with angular cells bearing a hyphal net of angular cells	Transitional type between plectenchymatous and pseudoparenchymatous	Awl-shaped with a clamp; 40–60 μm long; hyaline	Slightly differentiated, with nodia	Hyaline to yellowish; with clamps and secondary septa
Tuber brumale Granetti (1995), Zambonelli et al. (1995)	Light to dark brown; short-spiny	Pseudoparenchymatous with epidermoid cells bearing a hyphal net	Pseudoparenchymatous	Awl-shaped with a basal septum; 50–90 μm long	Lacking	Lacking

Table 1 (continued)

ECM morphotype	Macroscopic description	Outer mantle	Inner mantle	Cystidiae	Rhizomorphs	Emanating hyphae
Type *Boletaceae* R. Agerer (personal communication)	Greyish white; loosely cottony	Plectenchymatous; surface with crystals	Plectenchymatous	Similar to ends of normal hyphae; 15–30 µm long	Highly differentiated; surface with crystals	Hyaline; sometimes with a brown content; without clamps; with crystals
Type *Chroogomphus* Agerer (1990a, b)	Whitish brown to greyish brown; short-spiny	Pseudoparenchymatous with angular cells bearing a hyphal net of inflated cells	Transitional type between plectenchymatous and pseudoparenchymatous	Sickle-shaped with a basal clamp; up to 160 µm long	Lacking	Lacking
Type *Hebeloma–Cortinarius* R. Agerer (personal communication)	Whitish brown; cottony	Plectenchymatous	Plectenchymatous	Lacking	Undifferentiated, hyphae compactly arranged	Hyaline; with clamps; swollen at septa; with anastomoses
Type *Sebacina* Urban et al. (2003)	Greyish brown; shiny and cottony	Transitional type between plectenchymatous and pseudoparenchymatous bearing a hyphal net; with gelatinous matrix	Plectenchymatous with ring-like arrangement of hyphal bundles	Lacking	Undifferentiated, hyphae loosely woven; scarce	Hyaline to yellowish; Y-shaped or trifurcate ramification; without clamps
Type *Tuber* R. Agerer (personal communication)	Light to dark brown; smooth	Pseudoparenchymatous with epidermoid cells bearing a hyphal net	Pseudoparenchymatous	Lacking	Lacking	Scarce; yellowish; without clamps
ECM 2	Light brown to greyish brown; loosely cottony	Pseudoparenchymatous with angular cells bearing a hyphal net	Pseudoparenchymatous	Capitate with septa; 40–70 µm long	Lacking	Lacking
ECM 3	Reddish brown to black; reticulate and shiny	Pseudoparenchymatous with angular cells arranged star-like bearing mounds of cells	Transitional type between plectenchymatous and pseudoparenchymatous	Brown; awl-shaped with inflated base (65–140 µm) and similar to ends of normal hyphae (15–25 µm)	Lacking	Scarce; brown; with clamps and secondary septa; warty
ECM 4	Dark brown to black; woolly	Pseudoparenchymatous with angular cells bearing mounds of cells	Plectenchymatous with ring-like arrangement of hyphal bundles	Awl-shaped with inflated base; 150–460 µm, brown; without septa or only a basal one	Lacking	Scarce; yellowish; without clamps
ECM 7	Dark brown to black; loosely cottony and grainy	Pseudoparenchymatous with angular cells bearing mounds of cells	Transitional type between plectenchymatous and pseudoparenchymatous	Lacking	Slightly differentiated, with nodia	Brown to yellowish; without clamps; warty
ECM 15	Dark brown; cottony	Transitional type between plectenchymatous and pseudoparenchymatous; hyphae arranged star-like	Plectenchymatous with ring-like arrangement of hyphal bundles	Lacking	Lacking	Hyaline; sometimes with a brown content; with clamps and many secondary septa

Table 1 (continued)

ECM morphotype	Macroscopic description	Outer mantle	Inner mantle	Cystidiae	Rhizomorphs	Emanating hyphae
ECM 17	Light to dark brown; grainy	Pseudoparenchymatous with angular cells bearing mounds of cells and a hyphal net with angular cells	Plectenchymatous with ring-like arrangement of hyphal bundles	Bottle-shaped; 25–30 μm long; brown	Lacking	Scarce; hyaline to yellowish; with clamps and secondary septa; small warts
ECM 30	Grey with orange spots; cottony	Plectenchymatous; some areas coloured brown; surface with crystals	Plectenchymatous	Lacking	Undifferentiated; surface with crystals	Hyaline; with clamps; swollen at septa; anastomoses with crystals
ECM 31	Greenish brown; loosely reticulate	Pseudoparenchymatous with angular cells bearing a hyphal net	Middle mantle pseudoparenchymatous with angular cells arranged star-like. Inner mantle plectenchymatous with ring-like arrangement of hyphal bundles	Similar to ends of normal hyphae; 14–25 μm long; hyaline to yellowish	Undifferentiated, hyphae loosely woven	Scarce; hyaline to yellowish; with clamps and many secondary septa
ECM 32	White to greyish; stringy	Plectenchymatous	Plectenchymatous with hyphae arranged in parallel	Lacking	Undifferentiated, hyphae compactly arranged	Hyaline; with clamps and secondary septa
ECM 36	Light to dark grey; smooth	Pseudoparenchymatous with angular cells bearing a hyphal net	Transitional type between plectenchymatous and pseudoparenchymatous	Lacking	Lacking	Hyaline; without clamps
ECM 37	Dark brown to black; loosely cottony and grainy	Pseudoparenchymatous with angular cells bearing mounds of cells	Plectenchymatous with ring-like arrangement of hyphal bundles	Lacking	Slightly differentiated, with nodia	Brown to yellowish; with clamps and secondary septa; warty
ECM 39	Light to dark brown; loosely cottony	Pseudoparenchymatous with angular cells bearing a hyphal net	Transitional type between plectenchymatous and pseudoparenchymatous	Lacking	Slightly differentiated, with nodia	Yellowish; with clamps and many secondary septa
ECM 40	Dark reddish brown to black; long-spiny	Pseudoparenchymatous with angular cells	Transitional type between plectenchymatous and pseudoparenchymatous	Awl-shaped with inflated base; 30–75 μm; brown; without septa or only a basal one	Lacking	Scarce; brown; with clamps and secondary septa
ECM 41	Dark reddish brown to black; densely grainy	Transitional type between plectenchymatous and pseudoparenchymatous	Plectenchymatous with ring-like arrangement of hyphal bundles	Globular; 20–30 μm long; brown	No true rhizomorphs, but hyphae start to form bundles	Brown to yellowish; with clamps and secondary septa; warty
ECM 43	Pinkish grey to greenish grey; smooth to loosely cottony	Pseudoparenchymatous with epidermoid cells bearing a hyphal net	Plectenchymatous with ring-like arrangement of hyphal bundles	Lacking	Lacking	Scarce; hyaline; without clamps

Table 1 (continued)

ECM morphotype	Macroscopic description	Outer mantle	Inner mantle	Cystidiae	Rhizomorphs	Emanating hyphae
ECM 47	Whitish brown; cottony	Pseudoparenchymatous with angular cells bearing a hyphal net	Transitional type between plectenchymatous and pseudoparenchymatous	Lacking	Lacking	Hyaline; without clamps; inflated at middle parts
ECM AD Giraud (1988)	Orange brown to dark brown; loosely wooly	Pseudoparenchymatous with angular cells	Pseudoparenchymatous	Branched at a right angle; 300–530 μm; with septa	Lacking	Lacking

The identified ECM morphotypes appear in alphabetical order and are followed by the unidentified ones according to their reference number. When the identification of a given ECM morphotype is based on a published description, the source is cited after the name of the morphotype. Identifications based on physical links with the sporocarp or personal communications are also noted

diversity index did not change significantly over the 3 years (P=0.07, Kruskal–Wallis), the species richness was significantly lower in the first year than in the second and third years. To test whether this variation over time was related to the differences between the burned and control stands, data on species richness from each stand were analysed separately (Table 5). The only significant change detected was in the burned stand, where the species richness was significantly lower the first year compared to the second year, while there was no significant difference (P>0.05, Mann–Whitney U) in any other comparison between years.

Dynamics of the degree of ECM colonisation

The percentage of total mycorrhization was significantly lower in the burned stand compared to the control plot (Table 4). There was also a significant change in the percentage of total mycorrhization in the samples collected in different sampling seasons, with the lowest and greatest values recorded in autumn and winter, respectively; no further differences were found between seasons in paired comparisons. The percentage of total mycorrhization observed in first year samples was significantly lower than in the third year, although the values from the second year were not significantly different (P>0.05, Mann–Whitney U) from any other. As described above for species richness, data from the burned and control stands were analysed separately (Table 5). There was a significant difference over the 3 years in the burned stand, with significantly lower values during the first year compared to the second year.

Discussion

Analysis of the ECM community of the *Q. ilex* forest at Nazar between 1998 and 2001 demonstrated that there was a change in the relative abundance of certain ECM morphotypes when comparing the stand affected by fire and the undisturbed plot. Although the number of mycorrhizal tips was significantly lower in the burned stand, there were no significant differences in diversity or species composition between plots. Caution is required in interpreting these results, but it is likely that fire played a significant role in the differences found between both plots.

Similar results to those found in our study site have been reported in the ECM community of a *Pinus sylvestris* forest in Sweden (Jonsson et al. 1999) and a *Picea* forest in Canada (Mah et al. 2001), where it was concluded that fire induced a shift in the relative abundance of each species rather than a change in the species composition. Several studies have also reported a decrease in the number of mycorrhizal tips after fire (Dahlberg et al. 2001; Stendell et al. 1999; Torres and Honrubia 1997).

In contrast, several published studies report results that differ in several aspects from those reported here. For example, Baar et al. (1999) found a shift in the species composition of the ECM community of a *Pinus muricata* forest in California after fire, and in Scandinavia, Dahlberg et al. (2001) cited not only a change in the species composition but also a decrease in the ECM diversity of several conifer forests affected by fire.

Many factors would influence the impact of fire on the ECM community, of which the intensity of fire could be important (Dahlberg et al. 2001; Dahlberg 2002; Grogan et al. 2000). After a low-intensity fire, many trees survive, and the organic matter remains intact; in this situation, the effects of the fire on the ECM community are mostly small. The fire affecting the *Q. ilex* forest in Nazar was of low intensity, resembling those studied by Jonsson et al. (1999) and Mah et al. (2001). In contrast, the work of Baar et al. (1999) focused on forests severely affected by high-intensity fires.

Two other factors that may influence the effect of fire on the ECM community of the *Q. ilex* forest under study are: (1) *Q. ilex* is a host species which resprouts easily (Castell and Terradas 1993; Pausas 1997; Torres and Honrubia 1997), and is, therefore, probably able either to keep the ECM symbiosis while suffering the disturbance or reestablish it

Table 2 Mean relative abundance of the 32 ECM morphotypes over the 3-year period in the burned and control stands in the Nazar site

ECM morphotype	Control stand	Burned stand
Cenococcum geophilum	0.404	0.466
Quercirhiza cumulosa	0.167	0.081
ECM 4	0.120	0.058
Type *Hebeloma–Cortinarius*	0.079	0.016
Pinirhiza dimorpha	0.039	0.001
Genea verrucosa	0.029	0.008
ECM 30	0.022	0.005
ECM 32	0.019	–
Hebeloma cf. *sinapizans*	0.018	0.008
ECM 15	0.011	0.008
Sphaerosporella brunnea	0.010	0.030
ECM 17	0.010	0.013
ECM 3	0.009	0.003
Tuber brumale	0.008	0.046
Type *Chroogomphus*	0.007	0.002
ECM 7	0.007	0.096
Type *Sebacina*	0.005	0.034
Tomentella galzinii	0.005	0.044
ECM 36	0.005	0.008
ECM 31	0.004	–
Type *Boletaceae*	0.003	–
ECM 2	0.003	0.013
Tomentella pilosa	0.002	–
ECM 37	0.001	0.001
ECM 39	0.001	–
ECM 47	0.001	0.004
Pisolithus tinctorius	–	0.022
ECM 43	–	0.013
Type *Tuber*	–	0.008
ECM AD	–	0.008
ECM 41	–	0.003
ECM 40	–	0.001

The ECM morphotypes are ordered according to their mean relative abundance in the control stand

in a short time; (2) half of the area of the *Q. ilex* forest at Nazar remained undisturbed, which could act as a source of ECM inoculum readily dispersed into the burned stand by wind or small animals, leading to a rapid recovery of the ECM community (Goodman and Trofymow 1998).

C. geophilum was by far the most abundant ECM found in the 32 morphotypes encountered both in the burned and control stands. This species has very low host specificity, is highly competitive, and is considered to have the broadest host range of all ECM fungi (Molina et al. 1992). Most ECM studies published report the presence of *C. geophilum* (Horton and Bruns 1998); in many reports this species is the most abundant within the ECM communities analysed, with relative abundance ranging from 11 to 29% (Abourouh and Najim 1995; Al Sayegh Petkovsek and Kraigher 2000; Arveby and Granhall 1998; Baxter et al. 1999; Dahlberg et al. 1997; Durall et al. 1999; Kranabetter et al. 1999; Massicotte et al. 1999; Meotto et al. 1994; Trost et al.
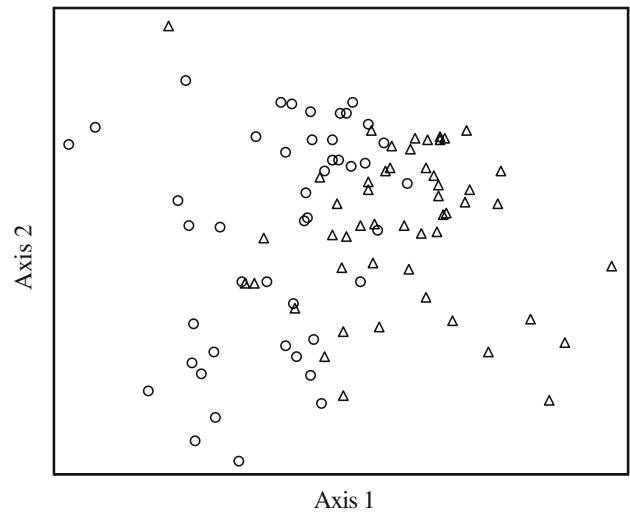

Fig. 1 Ordination graph of the 96 soil samples collected over the 3-year period in the Nazar site after applying the multivariate ordination technique DCA to the relative abundance of the ectomycorrhizae morphotypes recorded in each soil sample. Soil samples collected in the burned stand are represented by a *triangle*, and those collected in the control stand are represented by a *circle*. Eigenvalue of axis 1=0.53

1999). The mean relative abundance of *C. geophilum* recorded in both plots in the Nazar site was 40%. One possible explanation for such a high abundance could be the resistance of this species to drought (LoBuglio 1999; Pigott 1982) and its good adaptation to Mediterranean ecosystems. Possibly, the relative abundance recorded was never so high because previously reported work was conducted in boreal or temperate forests; however, more research is needed to confirm this hypothesis.

Table 3 ECM morphotypes correlated with axes 1 and 2 with Pearson correlation coefficient values (r) greater than $|0.267|$, critical value for 94 degrees of freedom ($n-2$) to confirm that the correlation is not due to chance ($P<0.01$; Rohlf and Sokal 1995)

ECM morphotype	Pearson's r, axis 1	Pearson's r, axis 2
Hebeloma cf. *sinapizans*	−0.294	–
Pinirhiza dimorpha	–	−0.464
Pisolithus tinctorius	0.454	–
Quercirhiza cumulosa	−0.580	–
Sphaerosporella brunnea	–	0.327
Tomentella galzinii	–	0.318
Type *Hebeloma–Cortinarius*	−0.274	−0.502
ECM 4	−0.455	–
ECM 7	–	0.652
ECM 30	–	−0.271
ECM 32	–	−0.282
ECM 43	0.435	–
ECM AD	0.309	–

The ECM morphotypes correlated positively with axis 1 and/or axis 2 were more abundant in the burned stand, while the ECM morphotypes correlated negatively with them were more abundant in the control stand

Fig. 2 Cumulative species richness in the burned stand, the control stand, and in total plotted against the seasonal samplings performed over the 3-year period in the Nazar site. *Au* Autumn, *Wi* winter, *Su* summer, *Sp* spring, *1* first year, *2* second year, *3* third year
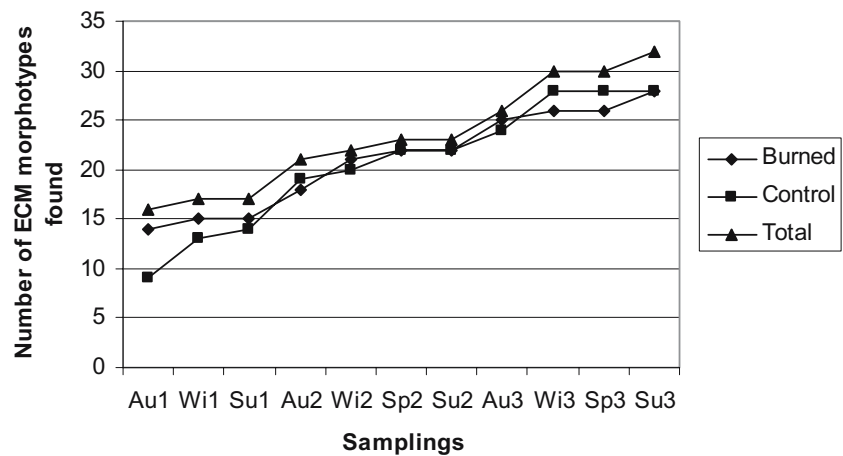
Some of the ECM morphotypes encountered were more abundant in the burned stand than in the unburned plot. Although it is not possible to draw any substantial conclusions, the higher abundance of these morphotypes in the burned stand might result from a greater tolerance of the disturbance or a more competitive re-colonization strategy than other ECM morphotypes under such unfavourable conditions. *Sphaerosporella brunnea*, an ascomycete fungus regarded as a pioneer in the colonisation of burned areas has this life strategy (Meotto and Carraturo 1988); it is also a severe contaminant in nurseries where plants have been deliberately inoculated with other ECM fungi (Bencivenga et al. 1995). *S. brunnea* forms ectendomycorrhizae (Molina et al. 1992), thereby increasing the range of host species with which it can establish mycorrhizal symbioses.

The presence of *Pisolithus tinctorius* also appeared to be linked to the burned stand, as it was totally absent from the undisturbed stand. This fungus is well adapted to disturbed sites and enhances the reestablishment of plants, but only in areas where other fungi are absent (McAfee and Fortin 1988). *P. tinctorius* has been used for inoculation of seedlings in reforestation projects, but these experiments were not always successful (Castellano 1996).

The abundance of the group of thelephoroid ECM morphotypes differed between the burned or control stands. *T. galzinii* and the ECM morphotypes 7 and AD were particularly abundant in the burned stand, whereas *P. dimorpha*, *Q. cumulosa* and ECM morphotype 4 thrived in the control stand. There is little published information on the behaviour of thelephoroid fungi after disturbance. On the one hand, Visser (1995) affirmed that fruitbodies of these fungi are more abundant in mature undisturbed forests, because of a dependence on the presence of woody debris and organic matter for fruiting. In contrast, Agerer (1999) supported the idea that thelephoroid ECM are well adapted to cope with environmental stresses because many species form rhizomorphs, enabling exploitation of a greater volume of soil to obtain water and nutrients (Harley and Smith 1983). In the Nazar site, the three thelephoroid ECM morphotypes which were especially abundant in the burned stand had rhizomorphs or very long emanating elements, whereas two of the three morphtypes linked with the control stand lacked such structures.

Hitherto, the ECM morphotype AD ("Angle Droit"; Giraud 1988) was only reported in truffle plantations or nurseries (Bencivenga et al. 1995; De Miguel et al. 2001; Giraud 1988; Granetti and Baciarelli Fallini 1997; Sáez and De Miguel 1995). In the current work, morphological and anatomical investigation suggested the morphotype could be attributed to the Thelephoraceae (R. Agerer, personal communication). This report marks the first time the mor-

Table 4 Mean values of species richness, Shannon diversity index and percentage of mycorrhization (%*M*) in the Nazar site according to sampling stand, sampling season and sampling year

Sampling variable	Sample origin	Species richness	Shannon diversity index	%*M*
Sampling stand	Burned	6.5 a	1.242 a	22.7 a
	Control	7.1 a	1.324 a	27.6 b
Sampling season	Autumn	7.9 a	1.409 a	22 a
	Winter	6.8 b	1.302 ab	28.1 b
	Spring	6.7 ab	1.319 ab	24.8 ab
	Summer	5.8 c	1.134 b	27.6 b
Sampling year	First	5.5 a	1.157 a	21.1 a
	Second	7.3 b	1.362 a	24.8 ab
	Third	6.9 b	1.262 a	27.6 b

For each sampling variable, means in the same column followed by a common letter are not significantly different (*P*<0.05)

Table 5 Mean values of species richness and percentage of mycorrhization (%*M*) in the burned and control stands in the Nazar site over the 3-year period

Parameter	Sampling year	Burned stand	Control stand
Richness	First	5.2 a	6 a
	Second	7.3 b	7.4 a
	Third	6.5 ab	7.2 a
%*M*	First	18 a	26.2 a
	Second	23.9 b	25.7 a
	Third	24.8 b	30.6 a

For each parameter, means in the same column followed by a common letter are not significantly different (*P*<0.05)

photype has been partially identified. ECM morphotype AD appears to be a pioneer species as in the current work it was more abundant in the burned stand, and it is able to colonise roots of seedlings introduced into truffle plantations or grown in nurseries, as stated above (Bencivenga et al. 1995; De Miguel et al. 2001; Giraud 1988; Granetti and Baciarelli Fallini 1997; Sáez and De Miguel 1995).

Some ECM morphotypes were especially abundant in the undisturbed control stand. Amongst the most common were those in or closely related to the genus *Hebeloma*: *Hebeloma* cf. *sinapizans*, the type *Hebeloma–Cortinarius*, and ECM morphotype 30. It is possible that these ECM fungi are sensitive to fire, although further work is required for proof.

Only a few of the ECM morphotypes found were abundant and well distributed; most were rare species which occurred sporadically, a common pattern reported at any taxonomic level (Baar et al. 1999; Dahlberg et al. 2001; Durall et al. 1999; Gardes and Bruns 1996; Gehring et al. 1998; Grogan et al. 2000; Hagerman et al. 1999; Jonsson et al. 1999; Peter et al. 2001; Stendell et al. 1999; Taylor 2002). Most studies on ECM community structures suggest that *C. geophilum* and ECM in the Russulaceae, Thelephoraceae and other resupinate fungi dominate within all ECM communities (Dahlberg 2001; Horton and Bruns 2001; Peter et al. 2001). With the exception of the ECM of Russulaceae, which were not recorded in this study, the *Q. ilex* forest at Nazar was also dominated by the same ECM fungi.

The present results also follow a well-known trend for ECM communities: a steady increase in the number of ECM morphotypes encountered as more samplings are undertaken (Erland et al. 1999). Although the dominant ECM morphotypes are detected with less sampling effort, increasing number of samples help to gain a deeper insight into the true species diversity in the ECM community.

There was a significant change in the species richness of the ECM community and in the percentage of mycorrhizal tips depending on the season. The other parameters analysed, i.e. the relative abundance of ECM morphotypes and the Shannon diversity index, did not demonstrate any significant difference amongst seasons. The species richness was maximum in autumn and minimum in summer, whereas the degree of ECM colonisation was lowest in autumn and highest in winter. Azul and Freitas (1999) also recorded seasonal variations in the numbers of mycorrhizal tips in a *Q. suber* forest, with the lowest numbers also recorded in autumn. In contrast, Mineo and Majumdar (1996) found that the maximum amount of mycorrhizae in two *Quercus alba* and *Quercus rubra* forests occurred in autumn. García (2001) found no significant difference amongst seasons in the number of mycorrhizal tips occurring in a *Q. ilex* stand, with maximum diversity in winter and summer and the minimum in spring and autumn.

Due to the limitations of the present study and the contrasting reports in the literature, it is not possible to draw definitive conclusions on the seasonal dynamics of the ECM community in forests. Climatic conditions in differ-

ent areas must play an important role, and only ecosystems sharing the same climatic, edaphic and tree species compositions should be compared in order to define the impact of stresses on ECM communities.

The collection of samples over 3 years enabled the increase in percentage of ECM colonisation in the burned stand from the first to the second and third sampling years to be detected. Species richness also appeared to increase over time, although the results are not clear. There seemed to be a progressive recovery of the ECM community in the burned stand, but more detailed investigations are required. In the undisturbed stand, no change was detected in the ECM community over the 3-year period.

Further studies on the potential effects of fire on the ECM communities of Mediterranean ecosystems are required, because these areas are particularly threatened by fire. Moreover, little information is available overall on seasonal variations in ECM and their succession, so far exclusively analysed through the study of the fruit bodies of ECM fungi.

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