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Vegetation dynamics and arbuscular mycorrhiza in old-field successions of the western Italian Alps

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Abstract The relationships between vegetational and arbuscular mycorrhizal (AM) dynamics were investigated in an old-field succession in the western Italian Alps. Vegetation and AM colonization were determined in eight sites corresponding to different stages of successional dynamics: (a) a field under cultivation; (b) fields abandoned for 1, 2 and 3 years supporting ruderal vegetation; (c) grasslands; (d) shrublands; (e) early wood communities; (f) mature woods. AM colonization was evaluated on the roots of representative plants from each community. The data thus obtained, together with those from the literature, were then used to calculate the plant community mycorrhizal index. This index provides qualitative and quantitative information concerning the relative percentage of non-mycorrhizal, AM and ectomycorrhizal plant cover in an entire plant community. The AM inoculum potential of each site was also determined using a bait approach. Farming disturbance temporarily reduced soil infectivity. Non-mycorrhizal ruderal annuals dominated after 1 year abandonment and covered 90–100% of the surface. After 2 or 3 years, a rapid change to AM-colonized competitive and competitive-ruderal perennials was observed. The increase in AM inoculum was associated with an increase in floristic richness and equitability in the community. AM were also dominant in the shrublands and early wood communities, but gave way to ectomycorrhizal species in the mature woods. The observed AM inoculum potentials are in accordance with these findings. The results of this study further emphasize the need to take into account AM infection in plans for the renaturalization of degraded areas.

Key words Alps · Arbuscular-mycorrhiza · Inoculum potential · Old-field succession · Vegetational dynamics

Introduction

Investigations of the functioning of arbuscular mycorrhiza (AM) in the field, in particular at the ecosystem level, are attracting increasing attention (Allen 1991; Brundrett 1991). One reason for this is the recognition that the symbiosis may play an important role in sustainable agriculture (Miller and Jastrow 1992a; Gianinazzi and Schüepp 1994; Schreiner and Bethlenfalvay 1995) and in the revegetation of disturbed areas (Miller and Jastrow 1992b; Jasper 1994).

Plant species dependency on mycorrhiza establishment varies along a continuum from obligate, through facultative to non-mycorrhizal. Consequently, mycorrhizal symbiosis is beneficial for the plant in many but not all cases (Francis and Read 1995; Smith and Smith 1996). Furthermore, characteristics of the symbionts influence the functioning of the mycorrhiza at the individual level. Benefits of AM fungal colonization seem to be confined to particular times (Hartnett et al. 1994; Johnson et al. 1997), namely the seedling stage (Birch 1986; Gange et al. 1990, 1993) and during reproduction (Fitter 1989, 1991; Koide et al. 1994; Wilson and Hartnett 1998).

The effects of differential responses to mycorrhizal colonization are shifts in the balance of competition between coexisting plants influenced by the level and type of mycorrhizal inoculum present in the soil (Fitter 1977; Hall 1978; Allen and Allen 1984; Hetrick et al. 1989; Hartnett et al. 1993). Mycorrhizal symbiosis, by influencing interspecific plant competition and plant demographic responses, can play a crucial role in determining species composition, community diversity (Grime et al. 1987; Bergelson and Crawley 1988; Hetrick et al. 1994; Wilson and Hartnett 1997; van der

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Heijden et al. 1998) and the successional dynamics of some plant communities.

The degree of mycotrophy of dominant plants changes among different seral stages. This trait was first recognized by Nicolson (1960), who noted that an early colonizing species on sand dunes was non-mycotrophic, whereas the later seral grasses were AM. Similar behaviour has been observed in subsequent work carried out in highly disturbed areas, where secondary successions take place in natural or in restored conditions. Most studies on mycorrhizal associations in highly disturbed habitats, such as mine sites, have found reduced number, diversity and functioning of AM propagules (Miller 1979; Moorman and Reeves 1979; Allen and Allen 1980; Powell 1980; Doerr et al. 1984; Johnson and Mc Graw 1988; Jasper et al. 1992). Less severe forms of soil disturbance, including agricultural practices such as ploughing and harrowing, can also have a detrimental effect on mycorrhizal associations (O'Halloran et al. 1986; Evans and Miller 1988; Read and Birch 1988; Douds 1994). Janos (1980) suggested that mycorrhizal activity following disturbance increases during succession associated with vegetational shifts from non-mycorrhizal, through facultative to obligate mycorrhizal plant species. The view that early successional habitats after disturbance are colonized by non-mycotrophic species or species little colonized by AM has been supported by many studies (Miller 1979, 1987; Reeves et al. 1979; Allen and Allen 1980), while other investigations conclude that some disturbed habitats can also be colonized by mycorrhizal species (Pendleton and Smith 1983; Allen et al. 1984; Koske and Polson 1984; Medve 1984; Allen 1987, 1988; Cuenca and Lovera 1992; Corkidi and Rincón 1997). This variability depends on the type of disturbance (Pendleton and Smith 1983), nutrient availability (Allen and Knight 1984; Allen and Allen 1990) and climate. Late seral stages consist of obligate mycorrhizal species that take advantage of the symbiosis and are capable of exclusive competition with other species typical of the early stages. The AM fungi which are ubiquitous in mature habitats may also exclude the early-stage species by direct antagonism (Grubb 1986; Allen and Allen 1988; Allen et al. 1989; Francis and Read 1995). In climatically stressed ecosystems, recovery from disturbance is slow (Reeves et al. 1979; Allen and Allen 1980; Janos 1980; Waaland and Allen 1985; Allen et al. 1987; Roldan et al. 1997), whilst in temperate situations it is much more rapid (Medve 1984 ; Johnson and Mc Graw 1988).

The research described in this paper was based on a multiple experimental approach with particular emphasis on field work. It examined the vegetational dynamics particularly common throughout the Alps as a result of recent progressive abandonment of farming and pasturage in areas 1000–2000 m above sea level. The aims of the work were to provide:(1) an interpretation of temporal factors in the dynamics of an old-field succession through study of the relations between plant communities and mycorrhization, and (2) a quantitative and qualitative assessment of the state of mycorrhization of plant communities at different stages in the succession.

Materials and methods

The study area

The study was conducted in the Susa Valley running westwards from the mouth of the Turin flatlands (about 300 m a.s.l.) to Colle di Monginevro (1854 m) astride the Cottian and Graian Alps (western Italian Alps). The area examined (45° 07′ 30 N, 06° 58′ 08 E) lies between 1000 and 1400 m on the orographic left side of the valley facing S and SW. Its dominant lithotypes are arenaceous gneisses and micaschists. The low weatherability of the bedrock has resulted in the formation of a coarse-textured superficial soil.

The climate of the Susa Valley is generally dry. The mean annual precipitation in the study area is 925 mm, with rainfall peaks in the spring and autumn. The mean annual temperature is 7.8 °C with mean monthly temperatures above 0 °C except in January (–1.1 °C).

The sites are terraced and were planted with vines and cereals from the earliest times but more recently with potatoes. Crop rotation included a fallow period, during which the herbaceous cover was used as pasture and cattle provided manure. Cultivation was progressively abandoned in the 1960s and 1970s and replaced by mowing and grazing. These practices have also been mainly abandoned. Thorny shrubs that have not been cut for 7–30 years cover large areas. Woods occupy the sites that have not been mown for 30–40 years. *Larix decidua*, *Quercus petraea*, *Acer pseudoplatanus* and *Corylus avellana* are the dominant species in the most mature community.

Vegetation analysis

The results of a preliminary examination of the communities were used to select eight study sites representing individual dynamic stages. The main features of selected sites are illustrated in Table 1.

A plot bearing homogeneous vegetation and large enough to be fully representative of each vegetation stage was used to determine the herbaceous, shrub and tree total cover percentages as well as the relative cover of each plant species as a per-

Table 1 Study sites and sequences of vegetation development following abandonment

Site	Years of abandonment	Vegetation type
1	0	Potato field, cultivated
2	1–3	Ruderal and then early-successional community
3	1–3	Ruderal and then early-successional community (abandoned 3 months before site 2)
4	20	Meadow, still mown
5	10	Mid-successional community: meadow with shrubs
6	20	Mid-successional community: shrubland
7	40–45	Early wood community with *Fraxinus excelsior*
8	>60	Mature wood

centage. Species represented by one or few individuals covering less than 1 % are indicated with + in the results tables.

The second and third sites were sampled for 3 years consecutively, while the other sites were sampled once. Authorities for species follow Tutin et al. (1964–80).

Soil analysis

Soil samples were collected from each site for determination of: pH, organic C, organic matter (S.I.S.S. 1985), C/N ratio, total P (expressed as P_2O_5 – ICP atomic emission spectroscopy), available P (expressed as P_2O_5 – modified Olsen's method), total N and texture.

Mycorrhizal colonization of field plants

Five samples of the dominant species and of other species for which type and degree of colonization/non-colonization were not available in the literature were taken from each site. A distinction was drawn between plants reported to be non-mycorrhizal, arbuscular mycorrhizal, or ectomycorrhizal.

The mycorrhizal status of each species was evaluated critically. Where no arbuscules were present, mycelial morphology and presence of vesicles was considered.

Sampling was carried out once for each species at flowering time. The roots were stained according to Phillips and Hayman (1970) and examined by the gridline intersect method (Giovannetti and Mosse 1980), appropriately modified for the observation of roots collected in the field under a light microscope. Four readings each corresponding to 100 intersects were taken for a set of roots from five plants of each species. The degree of root colonization was expressed as percentage of mycorrhizal root length.

On the basis of the cover percentages of each plant species in the plot and of its mycorrhizal status (the field findings were combined with data from the literature; Harley and Harley 1987), we propose a new index: the plant community mycorrhizal index (CMI). This is intended to provide qualitative and quantitative information concerning the relative percentages of non-mycorrhizal, arbuscular mycorrhizal and ectomycorrhizal plant cover in the entire plant community.

The plant community mycorrhizal index is calculated according to the following formula:

$$\mathrm{CMI}=\sum_{i_{\mathrm{NM}}=0}^{i_{\mathrm{NM}}=n}(\%\mathrm{cover}\ i_{\mathrm{NM}});\ \sum_{i_{\mathrm{AM}}=0}^{i_{\mathrm{AM}}=n}(\%\mathrm{cover}\ i_{\mathrm{AM}});\ \sum_{i_{\mathrm{E}}=0}^{i_{\mathrm{E}}=n}(\%\mathrm{cover}\ \ i_{\mathrm{E}}) \qquad (1)$$

i_{NM} are non-mycorrhizal plant species, i_{AM} are the arbuscular mycorrhizal plant species and i_E are the ectomycorrhizal plant species.

AM inoculum potential

Four soil cores were collected using cylinders (250 ml, 9 cm deep) from a transect across each site on two occasions in the first and in the third year after abandonment for sites 2 and 3 and on one occasion for sites 1, 4, 5, 6, 7 and 8. The AM soil inoculum potential was evaluated on half of each of the four samples from each site using *Trifolium repens* cv. Huia as a bait plant. The other half was used as a control after autoclaving at 120 °C for 40 min. The assay was conducted in pots held at 20 °C for 60 days in a thermostatically regulated greenhouse. The roots of the bait plants were prepared and examined in the same way as those of the field plants. Three subsamples corresponding to 100 roots per grid intersect were examined for each sample.

The results were subjected to analysis of variance using the Student-Newmann Keuls multiple comparison test.

Results

Ruderal and early-successional communities (sites 1–3)

Soil analysis of sites 1–3 established the highest available P values (Table 2).

As a result of ongoing disturbance, the potato field (site 1) contained no other plant species. The communities of the field abandoned in the previous November and September (sites 2 and 3; Table 3) were dominated in the first year after abandonment by annuals with a ruderal strategy, as defined by Grime (1979). These communities are characterized by a low floristic richness (a mean of 22 species per relevé) and low equitability (Shannon index mean 1.6). The field abandoned in September (site 3) already carried some perennials (*Silene alba*, *Centaurea scabiosa*) with appreciable cover percentages, along with *Trifolium pratense* and *Poa trivialis.* The cover percentages of the annuals were 100 % in site 2 and 90 % in site 3.

Examination of these sites 1 year later (i.e. 2 years after abandonment) showed that the early-spring germinating annuals had disappeared. A few annuals with a competitive-ruderal (CR) strategy found together with perennials typical of grasslands still survived. The rate of replacement of the annuals by these perennials was rapid at site 3 (annuals: 40 % cover in site 2 and

Table 2 Analyses of pH, carbon (% C), organic matter (% OM), C:N ratio (C/N), nutrient availability, and texture of soils at the study sites

Site	pH	% C	% OM	C/N	Total P (P_2O_5 g/kg)	Available P (P_2O_5 mg/kg)	Total N %	Sand %	Silt %	Clay %
1	7.2	2.6	4.4	11.8	1.9	24.3	0.2	89.0	10.1	0.9
2	7.0	3.3	5.7	11.8	1.7	22.7	0.3	86.8	12.5	0.7
3	7.1	4.5	7.8	12.9	1.7	26.0	0.4	90.9	8.1	1.0
4	6.7	2.3	4.0	8.7	1.6	<5	0.3	88.1	10.8	1.1
5	6.7	2.4	4.1	10.8	1.5	<5	0.2	93.3	6.4	0.3
6	6.9	2.3	3.9	10.3	1.5	<5	0.2	89.4	8.6	2.0
7	6.6	2.5	4.3	10.0	1.0	<5	0.3	92.3	7.1	0.6
8	6.7	1.8	3.1	11.8	1.2	7.0	0.2	86.4	10.6	3.0

Table 3 Simplified relevés for sites 2 and 3 with literature data. The considered mycorrhizal status using the notation of Harley and Harley (1987) is shown in bold (*Abs* absence of infection, *AM* % AM infections in field plants, *Ecto* ectomycorrhizal plant, *Lit* literature data, *VA* arbuscular mycorrhizal plant)

	Site 2	2	2	Site 3	3	3	Lit	AM %
Year	1	2	3	1	2	3		
Altitude (m)	1090	1090	1090	1090	1090	1090		
Exposure	SW	SW	SW	SW	SW	SW		
Slope (°)	5	5	5	5	5	5		
Investigated area (m^2)	8	8	8	8	8	8		
Herbaceous cover (%)	60	100	100	95	100	100		
Buglossoides arvensis	60	·	·	+	·	·	**Abs**	0
Veronica hederifolia	20	·	·	+	·	·	-	20
Consolida regalis	10	·	·	+	·	·	-	53
Senecio vulgaris	·	·	·	5	·	·	**VA**/Abs	-
Stellaria media	+	+	·	45	+	·	VA/**Abs**	0
Papaver rhoeas	+	10	·	5	+	+	VA/**Abs**	-
Viola arvensis	10	+	+	5	+	+	**VA**/Abs	65
Convolvulus arvensis	+	25	45	+	15	40	**VA**	15
Erodium ciconium	+	20	+	·	+	·	-	0
Galium aparine	·	+	5	+	+	+	VA/**Abs**	5
Bromus sterilis	·	+	35	·	·	+	**Abs**	20
Bromus tectorum	·	10	+	·	·	+	-	10
Vicia hirsuta	·	5	·	10	+	·	**VA**	-
Silene alba	·	·	·	5	30	10	**Abs**	0
Centaurea scabiosa	·	·	·	10	·	·	**VA**	-
Poa pratensis	+	+	5	+	+	10	**VA**/Abs	30
Trifolium pratense	·	10	+	+	15	·	**VA**	70
Arrhenatherum elatius	·	+	5	·	+	+	**VA**/Abs	70
Poa trivialis	·	+	5	+	15	25	**VA**/Abs	-
Vicia sativa	+	10	+	15	10	+	**VA**	75
Agrostis capillaris	·	·	·	·	15	15	**VA**/Abs	33
Arenaria serpyllifolia	·	10	·	+	·	·	**Abs**	-

10 % in site 3). The dynamics of succession in the first 3 years were very quick in relation to regeneration from the seed-bank and the vegetative regeneration of some species. It was associated with a rapid increase in AM colonization, as shown by both the CMI (Fig. 1) and the AM inoculum potential (Table 4). The CMI values indicate that the first dynamic stage was dominated by non-mycorrhizal plants and was followed by stages in which AM plant cover increased. This was particularly evident at site 3, where there were more perennial plants.

The mean AM inoculum potential values were: 0.3 % in the potato field (site 1), 7.4 % and 11.6 % after 1 year abandonment, and 9.4 % and 12.1 % after 3 years abandonment at sites 2 and 3, respectively (Table 4). Differences among samples from each site were high relative to the more mature stages, probably due to a patchy distribution of plants and inoculum in the soil.

Grasslands (site 4)

Since the 1960s and 1970s, nearly all ruderal herbaceous formations had converted to grasslands that were mown twice in the summer, followed by a late-summer grazing. Reduction of livestock numbers and their droppings had resulted in impoverishment of soil nutrients and organic matter (Table 2). The herbaceous community was dominated by *Bromus erectus*

Table 4 Mycorrhizal inoculum potential (MIP) expressed as mycorrhizal root length percentage in four samples of *Trifolium repens* cv. Huia bait plants. Means denoted with different letters are significantly different ($P<0.05$)

Site	Years of abandonment	MIP of four samples				Mean MIP
1	0	0	1.0	0	0	0.3^{g}
2	1	7.0	7.0	8.2	7.5	7.4^{bf}
2	3	11.8	17.2	3.9	4.6	9.4^{cf}
3	1	11.2	12.3	11.3	11.5	11.6^{bf}
3	3	10.1	22.7	13.4	2.3	12.1^{ae}
4	20	10.0	13.6	13.4	13.5	12.6^{bf}
5	10	18.0	16.5	22.3	19.0	18.9^{a}
6	20	9.0	7.6	8.8	8.5	8.5^{df}
7	40	15.0	16.2	19.5	9.7	15.1^{ac}
8	>60	4.0	5.8	4.2	2.5	4.1^{f}

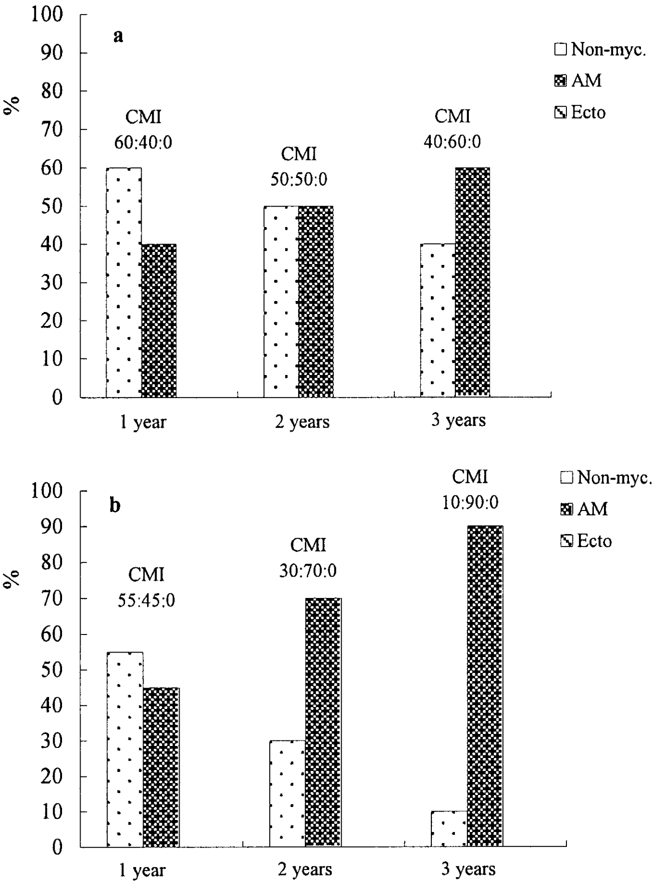

Fig. 1 Community mycorrhizal index (CMI) values for ruderal and early-successional communities at sites 2 (**a**) and 3 (**b**) in the first 3 years after abandonment. CMI was calculated from the mycorrhization data according to the cover percentages of each species. Plant species indicated with + in the tables were not considered

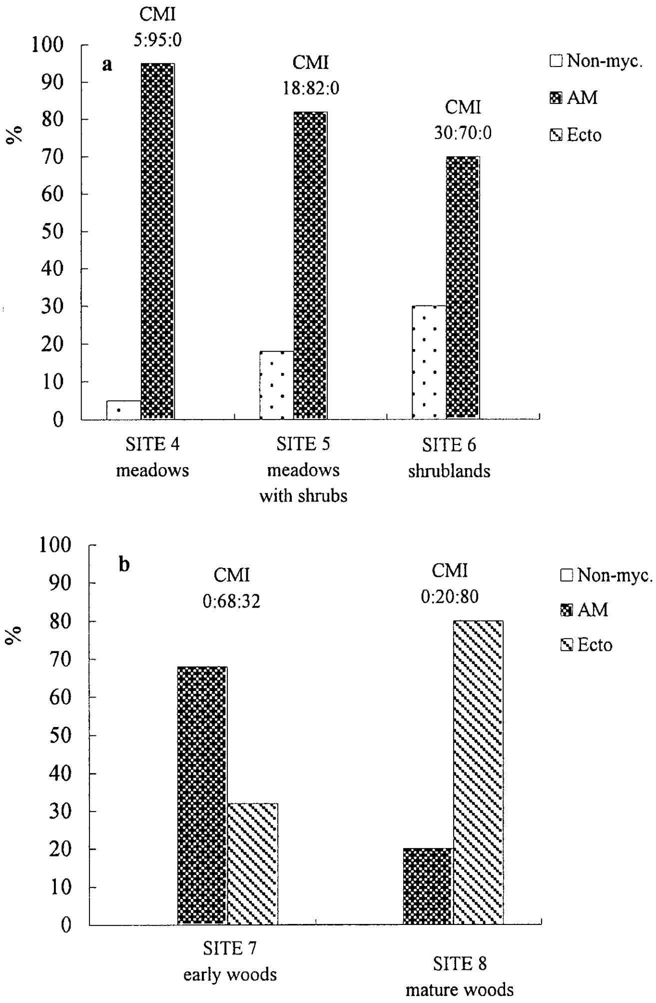

Fig. 2 CMI values for sites 4–8 calculated from the mycorrhization data according to the cover percentages of each species. Plant species indicated with + in the tables were not considered

and was typically xerophilous (Table 5) with high floristic richness (mean 38 species per relevé) and equitability (Shannon index mean 2.2). AM species covered 95 % of the surface and non-mycorrhizal plants 5 % (Fig. 2a). The presence of an active, evenly distributed inoculum in all the species of this community was clear from its 12.6 % mean AM inoculum potential. This can be compared to the 18.9 % observed for the herbaceous formations in the shrub site (see next section).

Mid-successional communities (sites 5 and 6)

The abandonment of mowing led to the formation of what are now very extensive shrublands (Table 6). The dominant species (*Rosa canina*) established after 4–5 years and its cover percentage rose to 50–70 % after 15–20 years abandonment. The herbaceous cover, however, was still very similar to that on the grassland site. Species such as *Trisetum flavescens* and *Trifolium pratense*, which require high nutrient availability, had disappeared. Some ruderals, such as *Bromus sterilis*, that were dominant in the initial stages of the succession had reappeared in areas disturbed by wild boars. The CMI values show an increase in non-mycorrhizal plant cover (18:82:0, site 5 and 30:70:0, site 6) in accordance with the vegetational data.

The AM inoculum potential was the highest for the series in areas with 10–20 % shrub cover and prairie grasses. In shrublands with 50–60 % cover, the formation most frequented by wild boars, the inoculum potential fell to 8.5 % owing to the return of non-mycorrhizal species.

Late-successional communities (sites 7 and 8)

Fraxinus excelsior was the initially dominant species in the early wood community (Table 7, site 7). The CMI was 0:68:32 (Fig. 2b) and the inoculum potential values were still very high (Table 4). At this stage, the

Table 5 Simplified relevés for site 4 with literature data. The considered mycorrhizal status using the notation of Harley and Harley (1987) is shown in bold (*Abs* absence of infection, *AM %* AM infections in field plants, *Ecto* ectomycorrhizal plant, *Lit* literature data, *VA* arbuscular mycorrhizal plant)

	Site 4	4	4	4	Lit	AM %
	a	b	c	d		
Altitude (m)	1038	1120	1080	1230		
Exposure	S-SW	S-SE	E-SE	E-SE		
Slope (°)	4	10	7	35		
Investigated area (m^2)	10	10	10	10		
Herbaceous cover (%)	100	100	100	85		
Bromus erectus	30	25	30	.	**VA**	40
Arrhenatherum elatius	5	10	30	25	**VA**/Abs	-
Trifolium campestre	30	10	+	.	-	54
Anthyllis vulneraria	5	15	5	.	**VA**	
Salvia pratensis	5	+	5	+	**VA**	-
Festuca cinerea	+	10	+	10	-	10
Brachypodium pinnatum ssp. *rupestre*	10	.	+	20	**VA**	90
Anthoxanthum odoratum	+	5	+	20	**VA**/Abs	-
Trisetum flavescens	+	10	20	.	**VA**	-
Dactylis glomerata	5	.	+	15	**VA**	-
Trifolium pratense	+	5	+	+	**VA**	78
Pimpinella saxifraga	.	.	10	.	**VA**/Abs	-
Achillea millefolium	.	5	.	+	**VA**	48
Prunella grandiflora	.	.	.	10	-	25
Plantago lanceolata	5	+	.	.	**VA**	35
Calamintha nepeta	5	.	.	.	-	23
Campanula patula	.	5	.	.	**VA**	-

Table 6 Simplified relevés for sites 5 and 6 with literature data. The considered mycorrhizal status using the notation of Harley and Harley (1987) is shown in bold (*Abs* absence of infection, *AM %* AM infections in field plants, *Ecto* ectomycorrhizal plant, *Lit* literature data, *VA* arbuscular mycorrhizal plant)

	Site 5	5	5	Site 6	6	6	Lit	AM %
	a	b	c	a	b	c		
Altitude (m)	1080	1080	1090	1120	1050	1080		
Exposure	S-SW	S	S-SE	S	S-SW	S		
Slope (°)	5	10	10	15	5	7		
Investigated area (m^2)	12	12	12	12	12	12		
Shrub cover (%)	5	10	20	50	60	65		
Herbaceous cover (%)	100	100	100	95	100	100		
Rosa canina	100	100	100	100	100	100	**VA**	-
Calamintha nepeta	20	+	30	10	+	5	-	20
Poa nemoralis	.	.	.	.	5	.	**VA**/Abs	-
Viola reichenbachiana	.	.	.	.	5	.	**VA**	-
Bromus erectus	+	10	.	5	+	10	**VA**	48
Artemisia absinthium	+	10	5	.	+	+	**Abs**	0
Festuca cinerea	5	35	.	5	+	10	-	10
Centaurea scabiosa	.	.	+	+	+	5	**VA**	-
Salvia pratensis	.	.	5	.	+	+	**VA**	53
Brachypodium pinnatum ssp. *rupestre*	.	25	.	.	.	.	**VA**	75
Trifolium campestre	.	.	.	.	5	+	-	51
Arrhenatherum elatius	30	+	40	55	30	+	**VA**/Abs	-
Anthoxanthum odoratum	10	+	+	+	.	.	**VA**/Abs	-
Trisetum flavescens	20	+	.	.	+	+	**VA**	-
Silene vulgaris	5	.	+	.	.	.	**Abs**	-
Holcus lanatus	.	.	.	10	.	.	**VA**	35
Trifolium pratense	.	15	.	.	.	.	**VA**	80
Galium aparine	+	.	+	5	15	10	VA/**Abs**	-
Bromus sterilis	10	.	20	10	40	50	**Abs**	0
Viola arvensis	.	.	.	.	+	5	**VA**/Abs	65
Rumex acetosella	.	5	.	.	.	.	**Abs**	-
Carex muricata	.	+	+	.	.	5	**Abs**	-

Table 7 Simplified relevés for sites 7 and 8 with literature data. The considered mycorrhizal status using the notation of Harley and Harley (1987) is shown in bold (*Abs* absence of infection, *AM* % AM infections in field plants, *Ecto* ectomycorrhizal plant, *Lit* literature data, *VA* arbuscular mycorrhizal plant)

	Site 7	7	7	Site 8	8	Lit	AM %
	a	b	c	a	b		
Altitude (m)	1330	1140	1250	1250	1310		
Exposure	S	S	E-SE	E	SE		
Slope (°)	10	15	15	20	25		
Investigated area (m^2)	50	50	50	50	50		
Tree cover (%)	70	90	50	40	60		
Shrub cover (%)	30	50	55	80	70		
Herbaceous cover (%)	40	40	35	30	30		
Quercus petraea	.	.	+	15	60	**Ecto**	-
Fraxinus excelsior	80	40	55	30	+	**VA**/Ecto	-
Larix decidua	20	.	45	50	20	**Ecto**	-
Castanea sativa	.	.	+	5	15	**Ecto**	-
Prunus avium	+	60	.	.	.	VA/**Ecto**	-
Acer pseudoplatanus	.	.	.	.	5	**VA**/Ecto/Abs	-
Corylus avellana	.	.	100	100	100	**Ecto**	-
Rosa canina	100	35	+	.	+	**VA**	-
Rubus caesius	.	40	.	.	.	**VA**	-
Prunus spinosa	.	25	.	.	.	**VA**/Abs	-
Melittis melissophyllum	.	.	+	+	10	**VA**/Abs	-
Poa nemoralis	45	90	5	25	35	**VA**/Abs	17
Luzula nivea	+	.	+	+	40	-	0
Euphorbia dulcis	+	.	+	5	+	**VA**	-
Geranium robertianum	+	+	5	+	.	**VA**/Abs	-
Hepatica nobilis	.	.	30	50	.	-	22
Hieracium sylvaticum	+	.	5	+	+	**VA**	-
Polystichum filix-mas	.	.	10	.	.	**VA**/Ecto/Abs	-
Holcus lanatus	10	.	.	.	.	**VA**	-
Astrantia major	.	.	10	+	.	**VA**/Abs	30
Fragaria vesca	+	+	+	5	15	**VA**	47
Viola arvensis	.	5	.	.	.	**VA**/Abs	-
Primula veris	+	.	10	10	+	**VA**/Abs	21
Festuca heterophylla	.	.	10	.	.	**VA**	-
Holcus mollis	10	.	.	.	.	**VA**	-
Rubus idaeus	35	.	15	5	+	**VA**/Abs	-
Galium aparine	+	5	.	.	.	VA/**Abs**	-

dominant tree species was AM. Ectomycorrhizal species (such as *Larix decidua*) were subordinate at this stage.

The formation of increasingly mature wood communities was accompanied by a gradual reduction in AM fungal populations. The mature wood at site 8 (Table 7) included *Quercus petraea*, *Castanea sativa* and *Larix decidua* as dominants. Ectomycorrhizal species covered 80% of the surface, compared with 20% for the AM species (Fig. 2); this was associated with a reduction in the AM inoculum potential to 4%.

Discussion

A reduction in soil infectivity associated with agricultural disturbance appears to be followed by an increase in inoculum potential in the first season after abandonment. The high resilience of the AM inoculum may be linked to the type of disturbance associated with mountain farming, where the soil is superficially ploughed and harrowed with light machines. The soil in the area studied was often the subject of crop rotation (potatoes, mown meadow) and often left fallow for 2–3 years. It appears that such practices allowed the survival of a vital population of AM fungi, though its species diversity may be lower than that of communities not disturbed for a long time. Repeated disturbance during potato growing destroys the network of hyphae in the soil which is the source of more immediate infection for new seedlings (Read and Birch 1988; Jasper et al. 1989). It is, therefore, likely that the inoculum in cultivated fields is primarily maintained in the form of unevenly distributed spores which are tolerant of disturbance and are subsequently stimulated in germination by exudates from the establishing host plants (Gianinazzi-Pearson et al. 1989). The high resilience observed of both the infectivity of the AM inoculum and the plant community is evidence of their very close interaction. Plant and fungal communities reciprocally influence one another with hypothesized feed-back mechanisms (Johnson et al. 1992).

Interactions between plant communities and mycorrhiza establishment were detected in all stages of the dynamic series and, in particular, provided a possible explanation for the speed of the initial dynamism. The absence of immediately infective inoculum, when nutrient availability was high, was associated with the establishment of typically non-mycorrhizal ruderals. Their initial dominance is also favoured by their high seeding abilities. This biological characteristic of ruderal species, along with other features, confines them to disturbed habitats and also results in their exclusion by CR or competitive stress-tolerant ruderal (CSR) perennials as soon as a reduction in disturbance permits the spread of AM fungi in the soil and host plant roots. These perennials became dominant 2 and 3 years after abandonment, possibly because of their competition mechanisms or direct antagonism between the AM mycelium and non-host species, as suggested by Francis and Read (1994, 1995). Competitive exclusion of ruderals can subsequently help maintain the stable grassland community. Localized disturbance in these stable communities, as happened at sites 5 and 6 where wild boars rutted the sites, opens gaps in the herbaceous cover to which ruderals can spread temporarily from seeds in the seed-bank.

Progressive reduction in available nutrient capital associated with establishment of a perennial vegetation cover and mowing may encourage floristic richness. This process will be assisted by the formation under reduced disturbance of a complete hyphal network. Even species for which the intrinsic below- and above-ground morphology and physiology should result in their being subordinate or even excluded, become a co-occurring part of the plant community (Grime et al. 1987; Theodose and Bowman 1997; Grime 1998). The close integration of species rendered possible by mycorrhization in the grassland enables it to be regarded as a community rather than a simple collection of individuals. AM values in CMI and AM inoculum potential were still high in the prairie, shrub and early wood formations. Establishment of ectomycorrhizal tree species and regression of AM colonization as observed in the mature wood community was observed in other secondary successions in mesic conditions (Johnson et al. 1991; Francis and Read 1994). The gradual build-up of litter in which the nutrients are further immobilized favours ectomycorrhizal fungi, since their complement of proteolytic enzymes would enable them to take a direct part in the mobilization of the nutrients (Read 1991).

The CMI index summarizes the state of a plant community in relation to mycorrhization. Its calculation acquires particular significance if conducted on the basis of experimental data and controls on the mycorrhizal status of plant species. Parallel analysis of plant communities and their state of mycorrhiza development in the field, with checks and measurements in a controlled environment, has allowed more complete interpretation of the vegetational dynamics. Despite the well-known difficulties of field research, adoption of a multiple experimental approach has provided further knowledge of the mechanisms and times of development of the various vegetational stages.

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