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Mycorrhiza

Seasonal variation of vesicular-arbuscular mycorrhizae in eroded soils from southern Spain

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Abstract. A survey was carried out of the seasonal variations in the number of spores in the soil and of the percentage of root infection. The stage of development of the host plants, environmental variations and physicochemical characteristics of the soil were taken into account. Fifteen plants valid as forage and adaptable to semi-arid conditions and poor soils were selected. In general, the maximum spore density was reached in the fruit-bearing period of the plants. It remained high during autumn, fell to a minimum in winter and tended to increase in spring. Root infection was at a maximum when the plants flowered, after which it decreased to a minimum in summer.

Key words: Vesicular-arbuscular mycorrhizae – Seasonal variation – Eroded soils – Spain

Introduction

The advance in desertification of great areas of the region of Murcia (south-east Spain) is reaching alarming proportions. Improverished soils, extreme temperatures, irregular rainfall, misuse of the soil and overgrazing for cattle-raising are several of the factors which contribute to the eroded landscapes. In these areas, where conditions are unfavourable for plant growth, mycorrhizae play an essential role (Trappe 1981), above all the vesicular-arbuscular mycorrhizae (VAM) associated with herbaceous plants and shrubs.

To understand the behaviour and the importance of endomycorrhizae in one particular area, it is necessary to ascertain the quantity and the type of propagules in the soil and also the increase of root infection in the plants and the variation of both parameters with time. The seasonal variation of the mycorrhizal inoculum potential is an important factor to be taken into account in the practical application of inocula (Gemma and Koske 1988). The aim of this work is to find a suitable approach for studying the presence of VAM in natural areas of Spanish semi-arid zones and their seasonal variations.

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Materials and methods

Site description

All the sampled sites are located in the north-west region of Murcia, except site 1 on the Murcia University Campus at Espinardo (Fig. 1). The north-west region of Murcia province is a cereal and cattle-raising area which covers some 2500 km^2. Rainfall is highly seasonal and irregular, varying between 350 and 600 mm. The edaphic conditions are fairly homogeneous. Limestone soil is predominant and to a lesser extent gypsum-marl and alluvial (Correal et al. 1986). Due to continual overgrazing, which has exhausted the vegetation, and adverse climatic conditions (long, hot summers; cold winters; insufficient rain), this area has a very high erosion rate. The study sites are described in Tables 1 and 2.

Selected plants

The plants chosen for this study are shown in Table 1. Five belong to the Poaceae family, five to the Fabaceae, two to the Asteraceae and three to the Chenopodiaceae family. There were two basic criteria for selection: (1) Good adaptability to arid conditions and poor soils. They are plants which would be taken into account in reforestation programmes for highly eroded soils, where more expansive or more dependent plants are basically not viable. (2) High nutritional value and sufficient growth in aerial biomass. This makes them good alternatives as wild forage.

Apart from natural areas, a barley crop area (site 15), a fallow area (site 8) and crop-growing areas unexploited for several years (sites 6 and 7) were also studied.

Sampling

Roots and rhizosphere soils from the selected plants were collected between spring 1987 and spring 1988. They were stored in polyethylene bags at 4° C until being processed. The roots were separated, washed and preserved in formol acetic alcohol (FAA). Great difficulty was encountered and it was at times impossible to

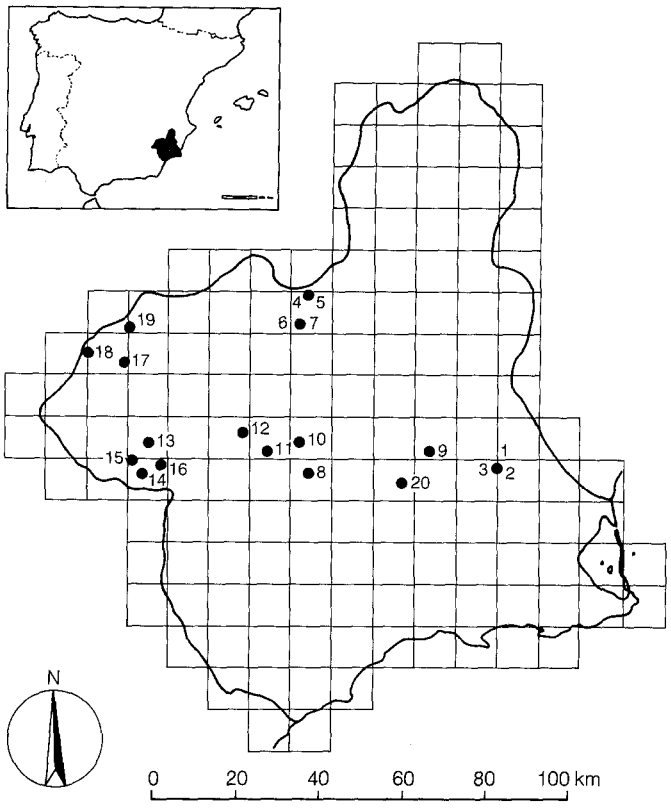

Fig. 1. Distribution of sampled sites

distinguish the roots of one plant from those of the accompanying samples, as in the case of site 18 (*Poa bulbosa* and *Festuca hystrix*).

Parameters studied

Spore density. Aliquots of soil (25 g) were taken from each sample in order to extract the spores. The wet-sieving and decanting method described by Gerdemann and Nicolson (1963) was used. The spores were counted under a stereomicroscope in an eelworm dish.

Mycorrhizal infection percentage. In order to discolour and stain the roots, a modified version of the Phillips and Hayman (1970) technique was used. The degree of root infection was measured according to the method of Giovannetti and Mosse (1980). Both parameters were studied in relation to stage of development of host plants. Three periods were considered: vegetative, flowering and fruit-bearing. The variation in spore density was also studied in relation to the different seasons: summer, autumn, winter, early and late spring. In Murcia, the onset of spring is very early, at the beginning of March, and many plants flower early. Therefore, we have distinguished between early and late spring. The quantity of external mycelium in the soil is indicated following a subjective scale from 0 to 5.

Germination of spores. Spores were wet-sieved from soils of the sites 4, 10, 14, 18 and 20, sterilized with chloramine T (5%) + antibiotic + tergiton and placed in agar-water Petri dishes (20 spores/dish; 3 Petri dishes/locality). They were kept at 20° C in the dark and observed every 3 days during 1 month.

Results

The data obtained are shown in Tables 3 and 4. The parameter "mycorrhizal infection percentage" turned out to be more homogeneous than the "spore density" (number of spores in the soil). Therefore, the latter parameter was studied according to the phenology of the plants and the time of year.

Number of spores in the soil, percentage of root infection and phenological state of host plants

The percentage of infection varied from 3% (*Atriplex glauca*) to 92% (*Genista mugronensis*). The average was 56%. Examining the information in Figs. 2 and 3, the following observations can be made. Mycorrhizal infection tends to be at a maximum in the flowering period (62% of the processed samples), coinciding with a minimum in the number of spores (50% of the processed samples). When the plants have formed fruit (fruit-bearing period), the degree of infection tends to be at its lowest, whereas the spores at this point reach a maximum density. During the vegetative period (when the plant awakes from winter lethargy), both parameters tend to indicate average values.

Number of spores in the soil and the time of year

The average number of spores in 100 g soil is 391, and varies from 5 to 1290. In general, the spore density varies greatly from one soil to another. Soils rich in organic material tend to have more spores, while those high in P or total calcium carbonate and sandy soils give lower levels of spores (Fig. 4).

Spore density tends to reach a minimum in winter, a trend observed in 65% of processed samples. In spring, spore density tends to increase, reaching a maximum in summer. During autumn spore density tends to remain high (Fig. 5).

VAM fungi detected

The predominant genus of VAM fungi in all sampled sites was *Glomus*, in which *G. mossae* (Nicolson & Gerdemann) Gerdemann & Trappe, *G. constrictum* Trappe, *G. fasciculatum* Thaxter ss. Gerdemann, *G. aff. pansihalos* Berch & Koske were the recognized species.

Scutellospora dipurpurascens Morton & Koske were observed regularly in site 14; *Acaulospora* sp. in site 20; *Sclerocystis rubiformis* Gerdemann & Trappe and *S. sinuosa* Gerdemann & Bakshi in site 18 and *Entrophosphora infrequens* (Hall) Ames & Schneider in site 10.

Germination of spores

Only 5% of spores from sites 4, 14 and 20 germinated (germ tubes longer than 100 μm), and no spores from sites 10 and 18.

Table 1. Localities and selected plants. M, Mycorrhizal plant; NM, no mycorrhizal plant

Locality	UTM	Selected plants	Family	Status	Vegetation
1	30S XH 6009	*Lygeum spartum*	Poaceae	M	Nitrophilous marly watercourse plants
2	30S XH 6009	*Brachypodium retusum*	Poaceae	M	Nitrophilous marly watercourse plants
3	30S XH 6009	*Anthyllis cytisoides*	Fabaceae	M	Nitrophilous marly watercourse plants
4	30S XH 2779	*Dorycnium pentaphyllum*	Fabaceae	M	Esparto field
5	30S XH 2779	*Stipa tenacissima*	Poaceae	M	Esparto field
6	30S XH 2233	*Artemisia herba-alba*	Compositae	M	Marly land uncultivated
7	30S XH 2233	*Salsola genistoides*	Chenopodiaceae	M	Marly land uncultivated
8	30S XH 1506	Annuals	—	M	Fallow land plants
9	30S XH 4311	*Atriplex glauca*	Chenopodiaceae	M	Nitrophilous plants
10	30S XH 1114	*Brachypodium retusum*	Poaceae	M	Pinewood undergrowth
11	30S XH 0417	*Salsola genistoides*	Chenopodiaceae	M/NM	Nitrophilous bank plants
12	30S WH 9915	*Genista scorpius*	Fabaceae	M	Marly road bank
13	30S WH 8904	*Salsola vermiculata*	Chenopodiaceae	NM	Crop border plants
14	30S WG 7995	*Ononis tridentata*	Fabaceae	M	Supralimely plants
15	30S WG 8398	*Hordeum murinum*	Poaceae	M	Crop
16	30S WH 8999	*Genista mugronensis*	Fabaceae	M	Thorny scrub
17	30S WH 7923	*Artemisia glutinosa*	Compositae	M	Nitrophilous plants
18	30S WH 7027	*Poa bulbosa, Festuca hystrix*	Poaceae	M	Supralimely pasture
19	30S WH 8031	*Genista scorpius*	Fabaceae	M	Marly scrub
20	30S XH 0635	*Anthyllis cytisoides*	Fabaceae	M	Pinewood

Table 2. Characteristics of the soils at the sampled sites

Locality	Gravel (%)	Sand (%)	Slime (%)	Clay (%)	pH	Electrical conductivity ds/m	Organic matter (%)	$CaCO_3$ eq. (%)	P mmol/kg	K mmol/kg	Na cmol/kg	Cl cmol/kg	SO_4 cmol/kg
1, 2, 3	0	12.9	48.4	28.7	7.40	1.08	1.50	10.00	0.06				
4, 5	0	13.2	43.1	33.7	7.60	0.17	1.98	56.00	0.10	0.47	0.14	0.18	0.17
6, 7	0	15.5	52.9	31.6	7.23	0.20	1.02	54.00	0.16	0.50	0.16	0.18	0.17
8	0	21.8	43.5	34.7	7.48	0.22	0.84	63.00	0.55	0.72	0.14	0.13	0.23
9	0	40.9	31.5	27.6	7.13	2.77	0.71	49.00	0.26	0.82	2.93	2.18	6.57
10	0	41.11	37.9	20	7.76	0.18	1.98	45.00	0.03	0.44	0.15	0.15	0.17
11	32.9	60.1	20.9	19	8.15	0.24	1.98	76.00	2.45	0.82	0.11	0.13	0.29
12	0	2.2	44.4	43.8	7.78	0.16	0.74	69.00	0.26	0.44	0.12	0.15	0.23
13	0	3.4	55.5	41.1	8.16	0.29	2.55	55.00	0.52	2.56	0.30	0.13	0.35
14	0	17.7	44.2	38.1	8.50	0.23	2.90	51.00	0.26	0.92	0.12	0.13	0.29
15	0	31.2	33.9	34.9	7.39	0.27	1.31	74.00	0.61	0.37	0.17	0.15	0.23
16	0	32.1	30.4	37.5	7.18	0.27	2.76	64.00	0.19	0.72	0.12	0.13	0.17
17	0	59.4	25.4	15.2	7.59	0.20	1.31	79.00	0.65	0.25	0.12	0.13	0.35
18	0	17.7	49.2	27.1	6.88	0.30	8.79	5.00	0.32	0.92	0.16	0.15	0.23
19	0	53.8	19.2	27	7.58	0.25	1.69	68.00	0.32	0.16	0.14	0.13	0.23
20	0	46.9	26.6	26.5	7.45	0.19	2.33	51.00	0.23	0.46	0.11	0.13	0.23

External soil mycelium and time of year

A seasonal variability in extramatrical mycelium was not established. However, a decrease in summer, coinciding with a minimum in root infection and an increase in spore density was noted.

Discussion

Of the 15 plants selected, 13 were found to be mycorrhizal, and of the other 2, 1 is mycorrhizal facultative and the other mycorrhizal independent. Trappe (1977) showed that 95% of vascular plants belong to mycorrhizal families. The highest levels of mycorrhizae formation were found in species of the Fabaceae family, followed by those of the Asteraceae and Poaceae and lastly the Chenopodiaceae. In general, the Fabaceae are highly dependent on mycorrhizae. Their root system is quite poor, for example, in comparison with, that of the Poaceae. They have high requirements for P, since they need it not only for growth but also for nodulation and N_2 fixing (Barea and Azcón-Aguilar 1983).

The Poaceae are highly VA mycorrhizal (Nicolson 1959, 1960; Boullard 1963; Hayman 1970; Crush 1973; Khan 1975; Saif and Khan 1975). The mycorrhizal association seems to be particularly important for their growth in nutritionally poor soils (Molina et al. 1978).

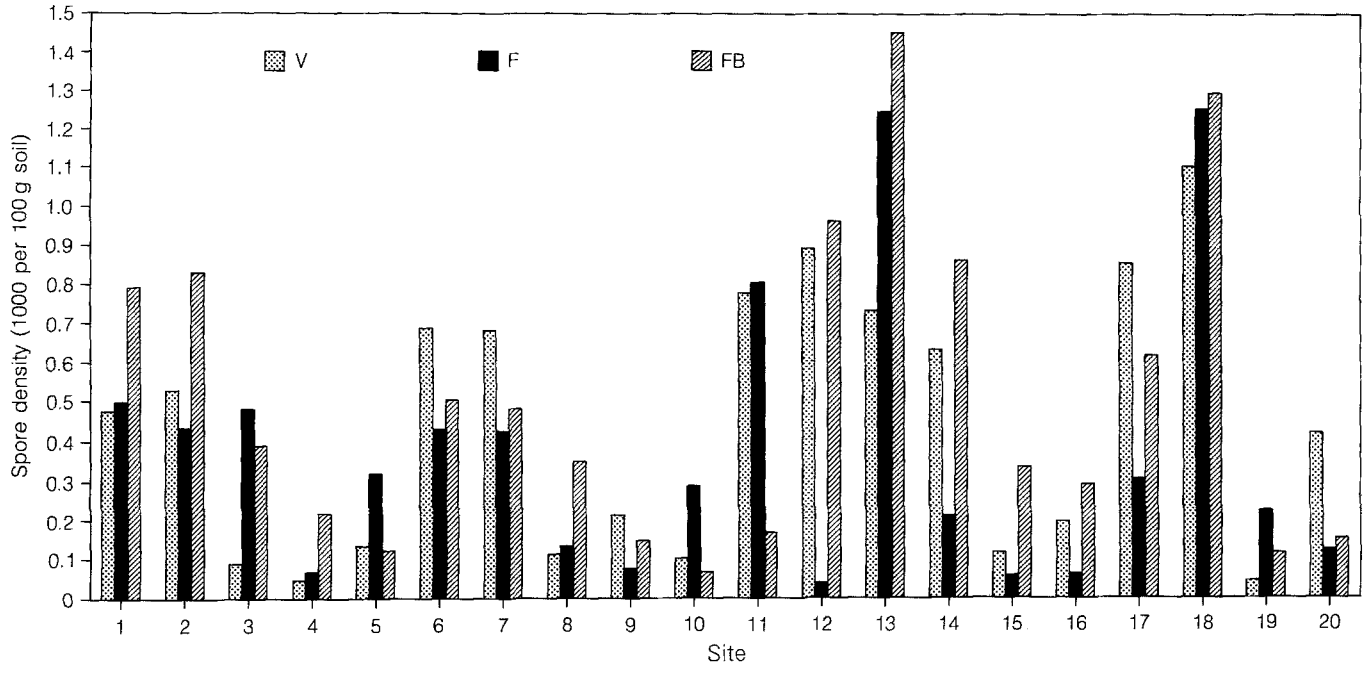

Fig. 2. Variation of spore density in relation to the stage of development of the host plant. *V*, Vegetative stage; *F*, flowering stage; *FB*, fruit-bearing stage

Table 3. Variation of studied parameters according to stage of development of the host plant. S, Spore number/100 g soil; I, mycorrhizal infection (%)

Locality	Vegetative stage		Flowering stage		Fruit-bearing state	
	S	I	S	I	S	I
1	476	42.4	500	69	792	40
2	532	63.4	436	72.8	832	59
3	92	60.2	483	71.6	392	64
4	52	50.4	73	62	222	65
5	139	46	321	42.5	127	59.8
6	687	66.6	433	78	503	74
7	681	59	425	23.7	483	3
8	116	19	136	60	352	52.2
9	215	6	76	17	149	9.6
10	101	58	288	62.5	67	66.9
11	774	0	803	0	170	0
12	890	70.3	37	60	960	50
13	728	0	1240	0	1449	0
14	627	72	210	60.4	858	43
15	116	28	53	30	330	8.5
16	197	82	60	92	292	75
17	850	79	302	79	614	60
18	1100	74	1245	67.2	1290	30
19	44	82	221	91	115	75.8
20	419	75	118	76.8	149	65

Table 4. Seasonal variation of spore density and amount of extramatrical mycelium. S, Spore number/100 g soil; M, extramatrical mycelium amount according to a subjective scale of 0–5

Locality	Summer		Autumn		Winter		Early spring		Late spring	
	S	M	S	M	S	M	S	M	S	M
1	775	2	476	5	342	3	500	1	792	4
2	820	4	532	5	326	4	436	3	882	4
3	175	4	32	1	92	2	483	4	392	4
4	235	2	251	4	52	5	73	2	222	3
5	5	0	356	1	139	1	321	1	529	1
6	715	2	687	4	433	3	503	3	456	3
7	681	1	424	2	483	1	319	3	270	1
8	335	1	263	2	136	1	352	2	112	2
9	302	1	149	3	115	2	215	1	76	4
10	375	3	208	3	101	2	288	4	275	2
11	774	0	803	1	170	3	40	2	436	2
12	261	4	890	5	37	4	122	2	130	2
13	1240	1	1449	3	449	1	728	0	693	3
14	858	2	356	3	612	3	627	4	209	4
15	429	0	368	1	44	1	116	1	65	2
16	138	4	167	4	197	3	56	2	374	0
17	417	2	367	3	302	2	614	3	355	3
18	1290	0	723	0	470	1	1100	1	1245	1
19	215	5	84	2	44	2	221	1	115	1
20	149	1	517	3	18	1	419	3	118	4

Of the Poaceae studied *F. hystrix* and *Poa ligulata* (site 18) show the highest root infection (74–67.2%) except in the fruit-bearing period (30%), followed by *Brachypodium retusum* (59–72.8%). The barley crop (*Hordeum murinum*) shows reasonably low infection rates (8.5–30%) in spite of the fact that the spore density of the site soil (site 15) is similar to that of sites located nearby in natural areas (site 16). This could be because barley is unreceptive to mycorrhization or because it is limited by P levels higher than those in the adjacent uncultivated soils.

Species of the Chenopodiaceae family were not at first considered to be mycorrhizal, but are now recognized as mycorrhizal facultative. In this study, *Salsola*

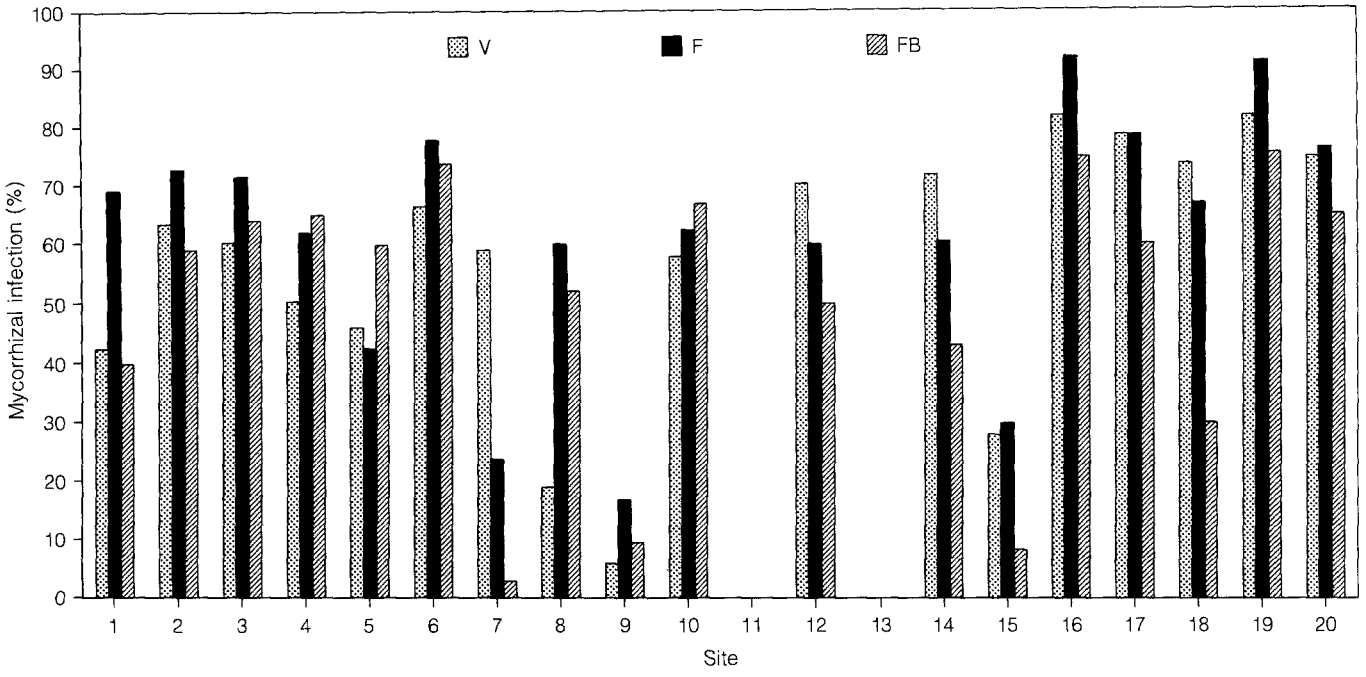

Fig. 3. Variation of mycorrhizal infection percentage in relation to the stage of development of the host plant. *V*, Vegetative stage; *F*, flowering stage; *FB*, fruit-bearing stage

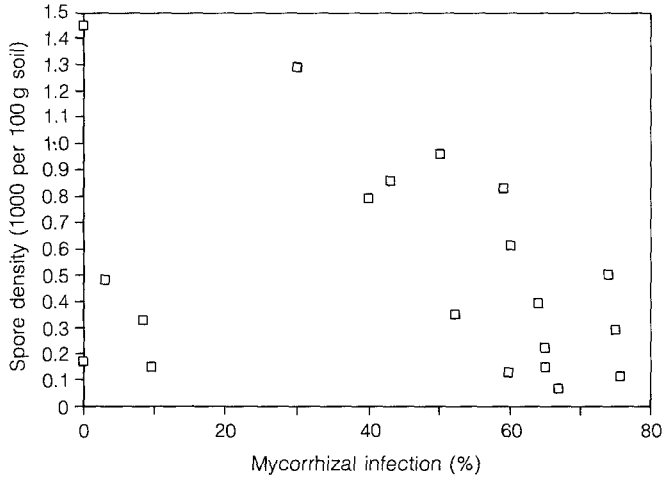

Fig. 4. Relationship of spore density to mycorrhizal infection in sampled sites of Murcia

vermiculata proved to be mycorrhizal independent, *S. genistoides* mycorrhizal facultative and *Atriplex glauca* gave fairly low infection rates (3–16%). Root fungi parasites of the *Olpidium* and *Pythium* type are quite common in these species. Miller et al. (1983) also recorded the presence of numerous parasites in the roots of *Atriplex confertifolia*. These authors suggest that in this family the mycorrhizae perhaps represent a parasitic relation, basing their argument, among other things, on the shortage of arbuscules observed in *A. confertifolia*. However, we have found numerous arbuscules in the roots of *S. genistoides*. This species reached average to high mycorrhizal levels (59%) but does not always present this symbiosis. In sampling site 7, with poor soil deficient in P, it is mycorrhized, while in site 11 with a higher P, it only presents traces of infection. So the type of plant with which it is associated in each site must be taken into consideration. Miller et al. (1983) found *A. confertifolia* infected when growing alongside *Artemisia spinescens* (M+) and not infected when with *Atriplex gardnerii* (M−). In our case *S. genistoides* is found together with *Artemisia herba-alba* (M+) in site 7 and growing alone in site 11.

With regard to the presence of spores, the variation in density from site to site is consistent with the observations of Miller (1978), Reeves et al. (1979) and Allen et al. (1984). The relation between the number of spores in the soil and the size of the sand grains has already been noted by Koske and Halvorson (1981), among others. Overall, spores are unlikely to be important for the initiation of VAM in plants. In this study, the majority show delayed germination. The cause of the delay in the germination of spores from the surface soil is unknown. It could perhaps be related to the different VAM-fungi strategies for survival under the stress of a semi-arid habitat (McGee 1989). Particular microbiological and environmental conditions, innate dormancy, etc. could also be involved (Tommerup 1983). From the results obtained in this study on the behaviour of mycorrhizal fungi, it is difficult to determine a conclusive pattern but it is possible to note some general tendencies.

The seasonal variation in the activity of VAM is still fairly unknown and based on relatively few data (Gemma and Koske 1988). Most of the studies on this subject have been carried out on agricultural soils (Hayman 1970; Sutton and Barron 1972; Saif and Khan 1975; Smith 1980). Yet the seasonal changes are the environ-

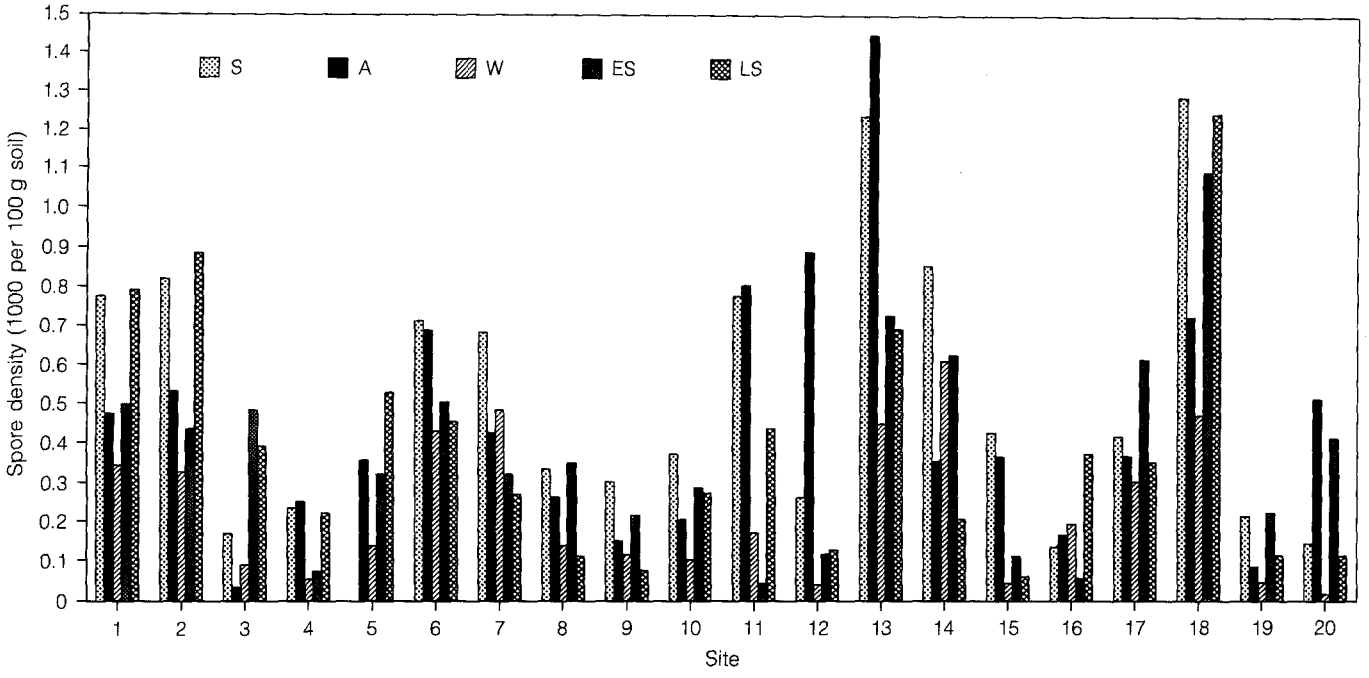

Fig. 5. Seasonal variation of spore density. *S*, Summer; *A*, autumn; *W*, winter; *ES*, early spring; *LS*, late spring

mental conditions that most greatly influence the physiology of the host plants and, therefore, those which most directly affect mycorrhizal symbiosis (Giovannetti 1985).

The most successful model for seasonal variation in spore density is the one proposed by Smith (1980). There is an extensive germination of spores at the beginning of the growth stage and a massive formation of spores during ripening. Khan (1975) also came to the conclusion that the number of spores increases after the period of maximum root growth. The increase in spores in summer noted in our study coincides with that obtained by Mason (1964), Hayman (1970), Sutton and Barron (1972) and Saif and Khan (1975). The spore minimum recorded in winter fits in with the seasonal decrease noted by Giovannetti (1985) in maritime dunes. With regard to the seasonal changes in mycorrhizal infection in general it reaches a maximum in the months of plant growth, and after flowering it begins to decrease, reaching very low rates in summer (Rabatin 1979; Giovannetti 1985). This decrease in mycorrhizal infection in the roots is probably due to hot, dry environmental conditions, which cause vegetative stasis of the host plant (Giovannetti 1985).

Vesicles are always predominant in colonization of roots by VAM fungi, but an increase in the presence of arbuscules and mycelium during spring was observed. In winter, most authors find that the percentage of infection is maintained (Read et al. 1976; Sparling and Tinker 1978; Nicolson and Johnston 1979). In this study, a slight increase was noted in autumn, which decreases again in winter, but without reaching the low rates of summer. The increase in root infection in this period could be due to the fact that many plants sprout again and even flower (*A. cytisoides*, *S. genistoides*) in autumn, since temperature and humidity conditions tend to be suitable.

There is no positive correlation (Fig. 4) between the number of spores in the soil and root infection, which coincides with the findings of Hayman and Stovold (1979) in different soils in New South Wales, and Giovannetti and Nicolson (1983) in maritime sand dunes. However, the results obtained by Hayman (1970) for wheat crops and Giovannetti (1985) for *Ammophila arenaria*, *Helichrysum stoechas* and *Eryngium maritimum* in maritime sand dunes differ.

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