

Concepción Sigüenza · Ileana Espejel · Edith B. Allen

Seasonality of mycorrhizae in coastal sand dunes of Baja California

Accepted: 16 August 1995

Abstract Populations of arbuscular mycorrhizal fungi were estimated from spores associated with seven plant species in coastal dunes at El Socorro, near Ensenada, Baja California, during six months in 1992. The seasonal patterns of percent root colonization were also described in the same species during the wet season (January–March) and the dry season (April–July). Comparisons were made between the pioneer species (*Abronia maritima*) in the mobile dunes and six species (*Abronia umbellata*, *Atriplex julacea*, *Camissonia californica*, *Haplopappus venetus*, *Helianthus niveus* and *Lotus* spp.) in the fixed dunes. Mycorrhizal colonization in *Abronia maritima* was slight (<1%) and we observed few spores (<1/g soil). All of the species in the fixed dune formed mycorrhizae with up to 80% colonization in early summer, and no more than 4 spores/g soil by late summer. The highest percentages of total colonization and abundance of spores did not coincide temporally for any of the seven species, but the percentages were higher in summer than in spring. Arbuscules were more abundant when the soil was moist, and vesicles more abundant when it was dry.

Key words Coastal dunes · Arbuscular mycorrhizae · Seasonality · Baja California

Introduction

Nicolson (1959, 1960) hypothesized that mycorrhizae are important in coastal sand dunes, which are typically low in available phosphorus (Ranwell 1972). Arbuscular mycorrhizae (AM) occur consistently in temperate

climate dune systems where the dominant species are grasses (Koske 1975; Koske and Halvorson 1981; Koske and Gemma 1990). The symbiosis can be of great importance for plant establishment and growth (Koske and Polson 1984; Sylvania 1989; Allen and Allen 1990). In addition, the mycorrhizal hyphae bind sand grains, which facilitates dune stabilization (Koske 1975; Sutton and Sheppard 1976). Mycorrhizae were hypothesized to play an important role in plant growth in several dune restoration studies (Sylvania and Burks 1988; Sylvania 1989; Will and Sylvania 1990).

Coastal sand dunes typically consist of a number of successional stages, providing an opportunity to study plant and mycorrhizal succession. The highest percentages of mycorrhizal root colonization typically occurred in older fixed dunes, even where some of the same plant species were dominant across the mobile and fixed dunes (Nicolson 1960; Allen and Allen 1992). Mycotrophic plant species occur in all successional stages in sand dunes, although nonmycotrophic plants have been observed in fertile patches at the high tide line where nutrient accumulation occurs (Allen and Allen 1992). Fungal species as well as plant diversity increased with successional stage in British coastal dunes (Nicolson and Johnston 1979). In addition to successional changes, seasonal variations have also been observed in spore populations (Sylvania 1986; Gemma and Koske 1988; Gemma et al. 1989), as well as in root colonization of dune plants (Nicolson and Johnston 1979; Giovannetti 1985; Puppi et al. 1986).

Most of the investigations of mycorrhizae of sand dunes have been done in temperate climates, and only a few are from dunes in Mediterranean climates (Giovannetti and Avio 1983; Giovannetti and Nicolson 1983; Giovannetti 1985). No mycorrhizal studies have been done in the coastal dunes of Baja California, although Rose (1981) mentioned one mycorrhizal desert species on inland sand dunes (*Astragalus dispermus*). A first step in trying to ascertain the status of this symbiosis in an ecosystem is to determine its existence in the abundant plants. Thus the objectives of this present

C. Sigüenza (✉) · E. B. Allen
Department of Botany and Plant Sciences,
University of California, Riverside, CA 92521-0124, USA

I. Espejel
Facultad de Ciencias, Universidad Autónoma de Baja
California. Apdo. Postal 1880, Ensenada, 22800 BC, Mexico
Tel./Fax: (617) 44560

study were to describe the occurrence of mycorrhizae in seven abundant sand dune plants, and to study the seasonality of the symbiosis and possible differences in mobile and fixed dunes.

Materials and methods

Study site

The study was conducted in 1992 on a coastal dune system at El Socorro, situated south of San Quintín, Baja California, Mexico. The climate is Mediterranean, with dry summers and winter precipitation (from October to April). The 30-year mean annual precipitation is 136 (± 14) mm, and the mean temperature is 17.5°C. In 1992, when the study was carried out, the total annual precipitation was 135 mm. Little is known about the ecology of the dune system or the biology of the plant species. Johnson (1977) described the site as part of a large-range research project, and we are currently studying the dune vegetation but the results are not yet published. The foredune is 6 km in length, 1 km wide and 3–30 m in height, and was selected because it includes both fixed and mobile dunes. The northern part of the dune fringe is mobile and occupied by only one plant species, *Abronia maritima*, which grows in patches. The southern part is fixed (Fig. 1) by coastal dune scrub vegetation with several herbaceous plants including *Abronia umbellata*, *Camissonia californica*, *Lotus bryantii*, *Lotus distichus*, *Nemacaulis denudata*, several shrubs such as *Helianthus niveus*, *Haplopappus venetus*, *Atriplex julacea*, *Croton* spp., and *Asclepias* spp., and succulent species including the genera *Dudleya*, *Opuntia* and *Mammillaria*.

Seven common plant species were selected for mycorrhizal observation. *Abronia maritima* Nutt. ex Wats. (Nyctaginaceae) is a perennial prostrate herb which occurs in the mobile dunes. It is different from pioneer dune species in other areas because it does not reproduce vegetatively. It is distributed along the Pacific coast from Morro Bay, Calif. (35°N) to Playa de Oro in Colima, Mexico (19°N) (Johnson 1985). Its taproot is deep and it produces abundant adventitious roots; it flowers from February to August. Of the six species from the fixed dune, *Abronia umbellata* Lam. (Nyctaginaceae) is the only annual prostrate herb. *Atriplex julacea* S. Wats. (Chenopodiaceae), *Haplopappus venetus* (HBK) Blake and *Helianthus niveus* (Benth.) Brandege (both Compositae) are perennial, somewhat woody shrubs. *Camissonia californica* (Nutt. ex T. & G.) Raven. (Onagraceae) and *Lotus* spp. (Fabaceae) are perennial herbs. The roots are taprooted in *Abronia umbellata* and fibrous in *Atriplex julacea*. The main root is highly branched in *Haplopappus venetus*, with thick branches originating from the base of the stem in *C. californica* and *Helianthus niveus*, but with sparser secondary roots in the latter. None of these species reproduces vegetatively. In *Lotus* spp. two very similar species (*L. bryantii* and *L. distichus*) could not be differentiated vegetatively and were mixed.

Sampling

Rhizosphere soil and roots of 10 similar-sized plants of each of the seven dune species were sampled at five sample times at intervals of 6 weeks. At each sample time, one area of approximately 90 m² was selected in the fixed dune by a systematic sampling method. In the mobile dune, due to the sparse and patchy distribution of *Abronia maritima*, the area was larger in order to get the necessary number of plants. For each plant species, one root sample and about 200 g of soil were taken. On the first sample date (February), the most abundant roots occurred to a depth of approximately 10 cm, and were collected there. At the third sample date (May), the surface roots were dry and so the samples were taken from 10–20 cm. On the last sample date (August), roots from the fixed dune were collected at a depth of 30–40 cm,

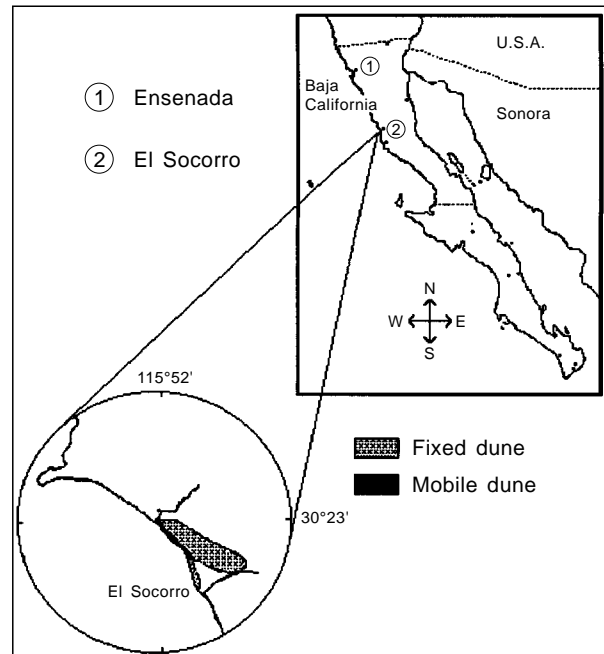


Fig. 1 San Quintín, Baja California, Mexico. The southern part of the bay has a large, coastal dune system. The study site was in the foredune, of which the northern half is mobile and the rest is fixed

but from the mobile dune, samples were collected at a depth of 1 m. Our objective was to collect roots from the depth where we observed the highest number of growing root tips, which varied with the soil drying front during the season.

The samples were stored at 4°C until stained (74–15 days). Five additional soil samples were taken from under each plant species in the fixed dune in order to determine total N in a compound sample for each species. Five additional soil samples were taken from interspaces between plants in three different microhabitats from both the mobile and fixed dunes (foredune, top of dune and backdune, 15 samples total), and total N (Kjeldahl) and P (Olsen) were determined. The detection limit was 10 mg/kg for both N and P.

The roots were processed according to Phillips and Hayman (1970). The percent colonization was evaluated using a compound microscope at $\times 100$. The presence of hyphae, vesicles and arbuscules was recorded in 20 fields of approximately 1 mm for each sample. Spores were extracted by a modification of the Ianson and Allen (1986) adhesion and flotation method, and were counted under the stereoscopic microscope at $\times 40$. The sporocarps were counted as one spore.

Results

In *Abronia maritima* colonization occurred in only one of the 50 plants collected throughout of 7 months, giving a percent of colonization of less than 1%. The number of spores was also low (less than 1 spore/g soil on each sample date). By contrast, *Abronia umbellata* had up to 70% colonization but fewer than 2 spores/g soil (Fig. 2). The mean values for spores and arbuscular and vesicular colonization showed a parallel pattern during the sample period, with lower values in March than Fe-

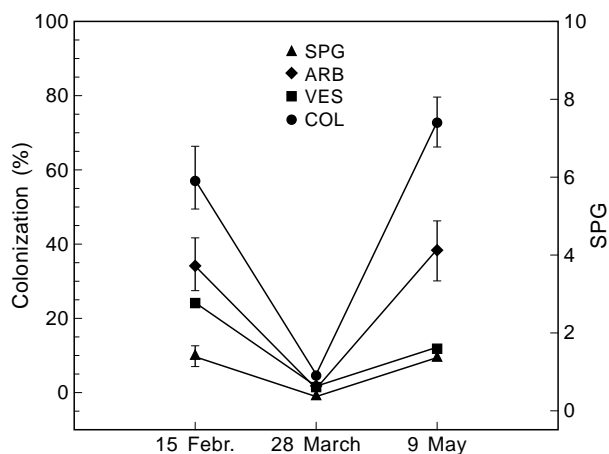


Fig. 2 *Abronia umbellata*. Percent colonization as total (COL), vesicles (VES) or arbuscules (ARB) and the spore number per gram soil (SPG). Bars show standard error of mean

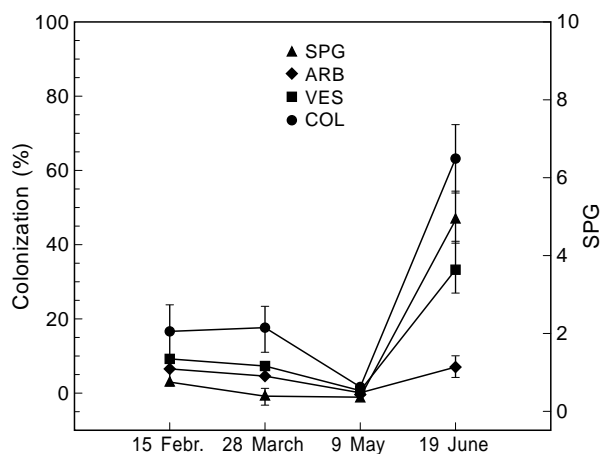


Fig. 4 *Camissonia californica*. Percent colonization and spore number per gram soil. Abbreviations as in Fig. 2

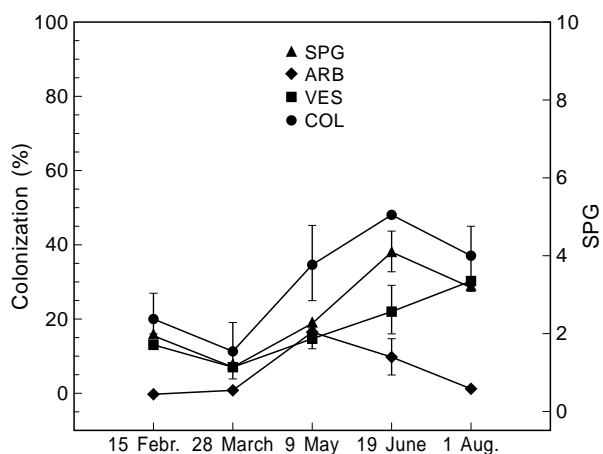


Fig. 3 *Atriplex julacea*. Percent colonization and spore number per gram soil. Abbreviations as in Fig. 2

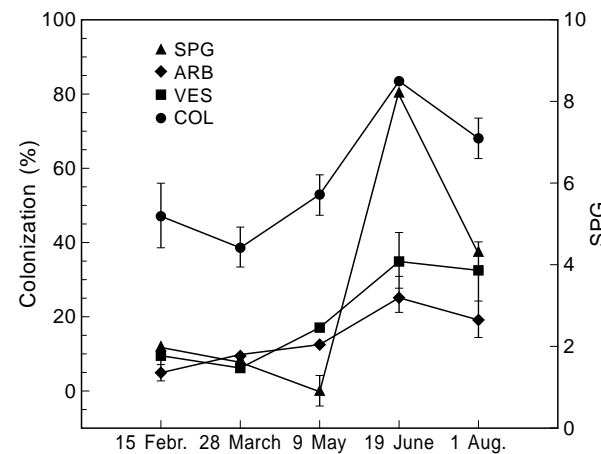


Fig. 5 *Haplopappus venetus*. Percent colonization and spore number per gram soil. Abbreviations as in Fig. 2

bruary and May. The decrease in colonization and number of spores observed in March could be related to two phenological events, fruit maturation and new root production, which appeared to be lower in March (Fig. 2). This species grow quickly, flower from February to May, and by the fourth sampling (June) were senescent.

Atriplex julacea was observed flowering in February. Total colonization as well as vesicular colonization and spore number showed similar trends. The lowest value of colonization was in March (Fig. 3). Only four of the 10 samples taken on that date had colonization and coincided with fruit maturation. Arbuscular colonization was higher in May. The samples with the highest number of spores (from February and May) contained a large amount (Fig. 3) of amber-colored sporocarps with 5–10 spores each, 150–250 μm in diameter.

In *C. californica*, samples were taken on only four sample dates since a beetle plague (*Chrysochus* sp.) se-

verely damaged the population (Fig. 4). Not all plants were colonized on each sampling date. Arbuscules, vesicles and spore numbers showed similar tendencies with a decrease in May, when fruits were observed and only one of the 10 sampled plants was colonized. An increase in colonization detected later reached an average of 63%, notwithstanding the herbivory (Fig. 4). This species flowered from February to March.

In *Haplopappus venetus*, arbuscular and vesicular colonization was low in February and March, and then increased. The development of flowers and fruits (beginning of June) coincided with the highest levels of colonization and production of spores (Fig. 5). *Helianthus niveus* had low arbuscular and vesicular colonization as well as spore numbers in February and March (Fig. 6). Total colonization was higher in June. This species flowered from February to August, although flowers, fruit and seeds were scarce late in the growing season.

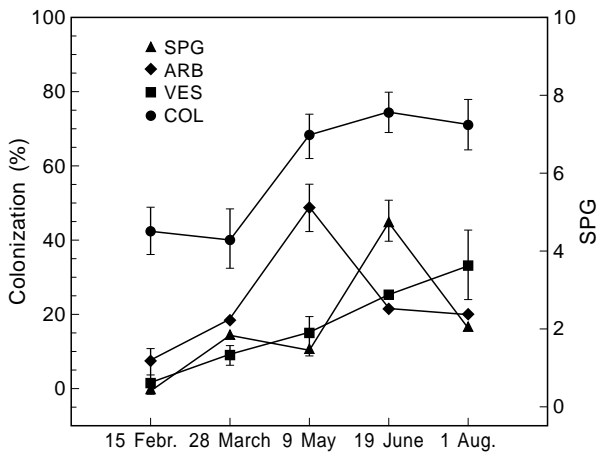


Fig. 6 *Helianthus niveus*. Percent colonization and spore number per gram soil. Abbreviations as in Fig. 2

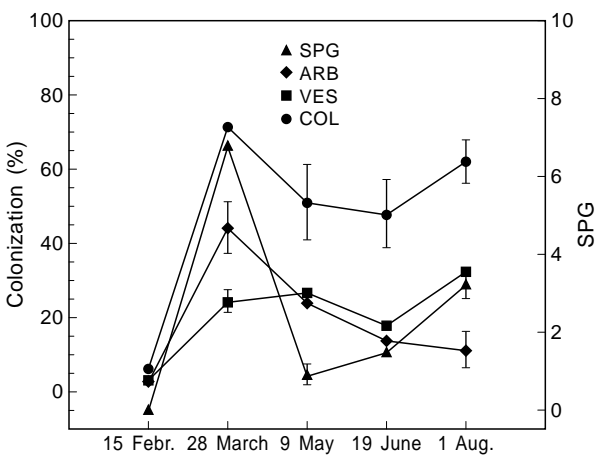


Fig. 7 *Lotus* spp. Percent colonization and spore number per gram soil. Abbreviations as in Fig. 2

In *Lotus* spp. total colonization and the number of spores were very low at the first sample date, with only one of the 10 samples taken showing colonization, and the highest values were in March (Fig. 7). This species flowered and produced fruit from February to August. With the drought (beginning in June) some flowers did not mature, and the pods did not fill. Although patterns of spore production and root colonization varied among the six species in the fixed dunes, values of both tended to be greater in summer than in spring (Figs. 2–7).

The concentration of soil N in the fixed dune interspaces from the foredune was 8.4 mg/kg, and in the top and backdunes it was 6.0 mg/kg. In the mobile dune, only one of the 15 samples of the interspace soil had a detectable concentration of N (34 mg/kg). The soil N under the different plant species was 140 mg/kg for *Abronia maritima* in the mobile dune, and varied from 210 to 670 mg/kg for the six species tested in the fixed dune. All samples had a P concentration lower than the detection limits of our method (10 mg/kg).

Some of the fungal species found were *Glomus geosporum*, *G. mosseae*, *G. aggregatum*, *G. albidum*, *G. deserticola* and *Acaulospora lacunosa*, but additional taxonomic work is necessary to determine the real number of species in the study site. Identification of the species was made with the Schenk and Perez (1988) manual.

Discussion

The species observed in the fixed dune showed distinct patterns of seasonality of the AM fungi that appeared to be related to the phenology of the plant. In *Abronia umbellata*, *Atriplex julacea*, and *C. californica*, maximum colonization and spore production were observed after the flowering stage, but in *Lotus* spp. and *Haplopappus venetus* the highest colonization levels coincided with flowering and fruit maturation. However, the pioneer species *Abronia maritima* on the mobile dunes had low or no colonization throughout the growing season.

Patterns of AM colonization

The highest percent AM colonization occurred during June for most species, an unexpected result that can be explained by the root sampling design. The roots were collected from progressively deeper depths, following the soil drying front during the course of the growing season. At each sample time, the soil was first excavated to determine the depth to moist soil where the most young roots tips occurred. Above this depth, only dried, senescent, fine roots and coarse, primary roots were found, and below it extensive fine root proliferation had not begun. Thus the results must be interpreted from the standpoint of this root sampling design. The occurrence of abundant colonization in June, several months after the last rainfall of the season, can be explained by residual moisture deeper in the sand dunes.

The low colonization of *Abronia maritima* was also unexpected, since its congener *Abronia umbellata* was mycorrhizal. However, due to constant wind action, *Abronia maritima* is subject to burial, to which it responds by almost doubling its growth rate (Johnson 1985). The consequent rapid growth rate of roots may result in a low colonization rate (Black and Tinker 1979), which also explains low spore reproduction as for *Ammophila arenaria* in British sand dunes (Nicolson and Johnston (1979). In addition, *Abronia maritima* does not reproduce vegetatively (Johnson 1985) like other pioneer dune species (rhizomatous grasses, graminoid plants or prostrate herbs such as *Ammophila* spp., *Carex* spp., *Spinifex* spp. and *Ipomoea pes-caprae*). This could also explain the low colonization, since each new plant must be initiated from seed in barren sandy interspaces on the foredunes. Other dune pioneers such as *Ammophila breviligulata*, *Solidago sempervirens* and

Uniola paniculata have greater AM colonization (Koske 1987). In this regard, Koske and Gemma (1990) mentioned that the close association between AM fungal propagules and vegetative fragments of the dune plants *Sporobolus virginicus* and *Jacquemontia sandwicensis* provides a mechanism of codispersion that appears to assure the maintenance of the symbiosis.

Janos (1980) observed that species of the Nyctaginaceae generally do not have mycorrhizae. Koske and Halvorson (1989b) reported the presence of the AM fungi *Scutellospora arenicola* and *Glomus trimurales* in soil adjacent to the roots of *Abronia maritima*, although they did not mention whether colonization was observed. Within the same family of plants, the perennials typically form mycorrhizae more frequently than the annuals (Williams and Aldon 1976; Trappe 1987). By contrast, the perennial *Abronia maritima* had slight colonization while the annual *Abronia umbellata* had abundant colonization in our study. However, *Abronia maritima* is a pioneer and the abundance of mycorrhizae can vary with the successional stage in which a plant is found (Nicolson 1960; Nicolson and Johnston 1979).

There is some controversy concerning the dependence of pioneer species on mycorrhizae. *Ammophila breviligulata* had varying percent mycorrhizal colonization depending upon its location in disturbed, early or late seral dunes (Allen and Allen 1992), but Koske and Polson (1984) felt that this species is highly dependent on mycorrhizae because they always found it associated with high levels of colonization. In other pioneer species of other ecosystems (Reeves et al. 1979; Janos 1980), the low colonization supports the near absence of mycorrhizae in *Abronia maritima*.

The results obtained from *Abronia umbellata*, *Atriplex julacea* and *C. californica* are similar to those observed by Hayman (1970) in wheat, in which high levels of colonization only occurred after flowering and growth of the roots. By contrast, the patterns of colonization observed for *Haplopappus venetus* are different but coincide with other dune species (Giovannetti 1985), in which the highest levels of colonization occurred at the same time as flowering. Various authors have observed the correspondence between plant and fungal phenology (Saif and Khan 1975; Bethlenfalvay et al. 1982; Allen 1983; Ebberts et al. 1987), but this apparently varies according to plant species.

The patterns of colonization in *C. californica* were likely due to beetle grazing. In spite of the almost total defoliation that occurred by May, when the lowest colonization level was recorded, the highest colonization was found in June after partial resprouting. The highest colonization in red clover was also observed in plants subjected to the partial removal of shoots (Vilariño et al. 1992). Bethlenfalvay et al. (1985) found that moderate grazing has no effect on colonization but with intense grazing it declines. Furthermore Wallace (1981) and Wallace et al. (1982) also found a positive and significant correlation between the intensity of grazing

and the frequency of mycorrhizal colonization in *Panicum coloratum*. The *C. californica* population almost disappeared because of the beetle grazing in August. Although some resprouting was detected, the population started its recovery in 1994 primarily from seed.

A common characteristic of the observed species was a decrease in colonization on one of the sample dates, followed by an increase on the next date. In the case of *Haplopappus venetus* and *Helianthus niveus*, the lowest colonization was about 40% in March while the highest was 80% in the summer in both species. In *Abronia umbellata*, *Atriplex julacea* and *C. californica*, this depression coincided with fruit set or with the maturation of the fruit. However, it is not clear that this is the direct cause of the decrease since physiological changes in the host are simultaneously influenced by seasonal variation (Giovannetti 1985). Moreover, the flowering and fruit set of *Haplopappus venetus* and *Lotus* spp. coincided with the highest colonization and spore density.

The absence of AM in some samples of the different species may confirm the proposal of Allen and Allen (1990) that sand dune plants are facultatively mycotrophic. *Lotus* spp. and *C. californica* had no colonization in 90% of the samples in February and May, and *Abronia umbellata* and *Atriplex julacea* in 60% of the samples in March. A congener of *C. californica*, *C. cheiranthifolia*, was also considered facultatively mycotrophic because of the absence of mycorrhizae at some sample times (Koske and Halvorson 1989a). On the other hand, the species that always had mycorrhiza in this study, *Haplopappus venetus* and *Helianthus niveus*, may have a greater dependence on mycorrhizae.

Variation in vesicles and arbuscules

There were often more arbuscules in the wet season and vesicles in the dry season, a trend that was clearer in *Abronia umbellata*, *Helianthus niveus* and *Lotus* spp. These results coincide with observations by Allen (1983) for *Atriplex gardneri* which showed more arbuscules during periods of active nutrient uptake and growth. In *C. californica*, vesicles were always more abundant than the arbuscules while in *Atriplex julacea* and *Haplopappus venetus*, arbuscules were slightly more abundant than vesicles on only one date (May and March respectively), but arbuscules still decreased late in the season.

Variation in spore density

Spore density tended to be higher late in the growing season, specially in *Abronia umbellata*, *Atriplex julacea*, *C. californica*, *Haplopappus venetus* and *Helianthus niveus*. This tendency toward sporulation later in the season has been reported by various authors (Hayman 1970; Sutton and Barron 1972; Ebberts et al. 1987).

Since fruit development may cause a decline in the availability of carbon to the fungus, the production of spores or colonization may also decrease. This was observed in *Abronia umbellata*, *Atriplex julacea* and *C. californica*, as in many other species (Saif and Khan 1975; Bethlenfalvai et al. 1982; Puppi et al. 1986). The highest percent colonization often coincided with higher spore numbers. This has been explained by Saif and Khan (1975) in wheat as a higher fungal biomass in the root generating a higher number of propagules.

When spore numbers of different species were compared, the peaks did not coincide in time. The association of different plant species with different species of VAM fungi would partially explain this. Sylvia (1986) and Gemma et al. (1989) found that different fungal species had different responses to phenology, and early variation has also been demonstrated in mycorrhizal activity (Gay et al. 1982; Brundrett and Kendrick 1988; Cooke et al. 1992). During the year of this work, the precipitation did not differ from the 30-year annual mean; therefore the observed patterns may be valid for years with similar conditions.

In summary, root colonization and arbuscule development start with the rainy season. As the soil dries, the number of arbuscules declines and vesicle numbers begin to increase. At this point, the levels of colonization are also high, and the fungus produces spores, many of which will remain in the soil until adequate moisture initiates their germination in the next growing season. In these sandy soils, colonization and sporulation occur at ever greater depths as surface moisture declines. The phenology of plant and fungus varied among plants, with maximum colonization at flowering for some species and after flowering for others.

Acknowledgements We appreciate the kind help provided by Raúl Tovar, especially during the field work, and we thank Rafael Solana for his valuable comments during the development of this work. This investigation was financed by the SEP Project C89-0184 Registro 891157, CONACyT-0218 CCOC 881145, César Valenzuela and by the UABC/Management of Arid Land Ecosystems Master's Program.

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