

# 11 Arbuscular Mycorrhizas in Coastal Dunes

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## 11.1 Introduction

Sand dune systems are among the best studied of primary successional sites and have attracted the attention of plant ecologists for over a century (Cowles 1899). Surprisingly, the traditional explanation of dune succession overlooks the critical contribution of mutualistic fungi that facilitate the invasion of barren areas. In fact, many of the dominant, dune-building plants appear to be incapable of growing in the dune environment if their roots are not associated with arbuscular mycorrhizal (AM) fungi, the topic of this chapter.

The roots of dune species, like the vast majority of vascular plants, form symbiotic associations with fungi in the order Glomales (arbuscular mycorrhizas). The fungal mycelia provide mineral nutrients in exchange for carbon compounds of the host plant (Smith and Read 1997).

Arbuscular mycorrhizas were first reported in sand dunes in *Pancreticum maritima*, *Convolvulus soldanella* and *Cineraria maritima* in Italy (Stahl 1900). Since then, all the surveys of dunes throughout the world have shown that most of the plants distributed in embryo dunes and foredunes, mobile, semi-fixed and fixed dunes are heavily colonized by AM fungi, e.g., in US mainland (Koske and Halvorson 1981, 1989), Canada (Dalpé 1989), Hawaii (Koske and Gemma 1996), Australia (Peterson et al. 1985; Logan et al. 1989), Brazil (Trufem 1995), Chile (Godoy and González 1994), India (Kulkarni et al. 1997), Italy (Giovannetti and Nicolson 1983), Mexico (Corkidi and Rincón 1997a), and Poland (Blaszkowski 1993, 1994; Tadych and Blaszkowski 2000a).

AM fungi are obligate symbionts, unable to complete their life cycle without a host plant (Smith and Read 1997). Less recognized is the fact that most plants grown under natural conditions (as opposed to greenhouse conditions with added fertilizer, water, and pesticides) cannot thrive without AM fungi (Trappe 1987). The AM association may be of considerable ecological significance for the establishment and growth of sand dune pioneer plants, because the fungi enhance plant nutrient uptake, particularly phosphorus (P), increase plant tolerance to drought and salt stress, and protect against soil

pathogens (Newsham et al. 1995; Little and Maun 1996, 1997; Perumal and Maun 1999; Tsang and Maun 1999; Augé 2001; Gemma et al. 2002).

While most studies of AM fungi in dunes have focused on maritime sites, arbuscular mycorrhizas are also well represented in lacustrine (Koske et al. 1975) and inland dunes (Al-Agely and Reeves 1995). Other kinds of mycorrhizas are formed by some dune species. Ericoid mycorrhizas are formed by Ericaceae, and Ectomycorrhizas by Pinaceae, Fagaceae, and some Salicaceae (see Read 1989).

The objectives of this chapter are to review a variety of studies on AM fungi and plants associated with AM fungi in coastal dunes and to point out some topics that are especially poorly known. Constraints on space prevented us from writing a more complete review.

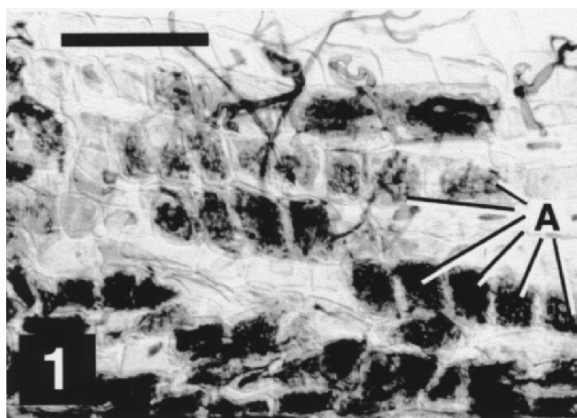
## 11.2 Life History of AM Fungi in Coastal Dunes

As the roots of plants grow through the soil they are contacted by hyphae of AM fungi. The hyphae can originate from large spores (some up to 1 mm diameter), roots and rhizomes of plants already mycorrhizal, or from dead fragments of AM roots and rhizomes. The fungal hyphae invade the root cortex, producing intercellular hyphae and intracellular hyphal coils, vesicles, and arbuscules (the site of exchange between plant and fungus) (Smith and Read 1997; Figs. 11.1, 11.2). Hyphae grow out into the soil for several centimeters, greatly enlarging the absorbing capacity of the root system, and acquire phosphate and other nutrients that often are too distant to be available to the relatively coarse root system. A prodigious amount of hyphae grows from the roots into the soil. In Florida dunes, Sylvia (1986) found ca. 9 m of hyphae/g of sand and ca. 462 m of hyphae/cm of root length associated with *Uniola paniculata*. New spores are formed on the hyphae, in the soil or in roots, completing the life cycle of the fungus (Smith and Read 1997).

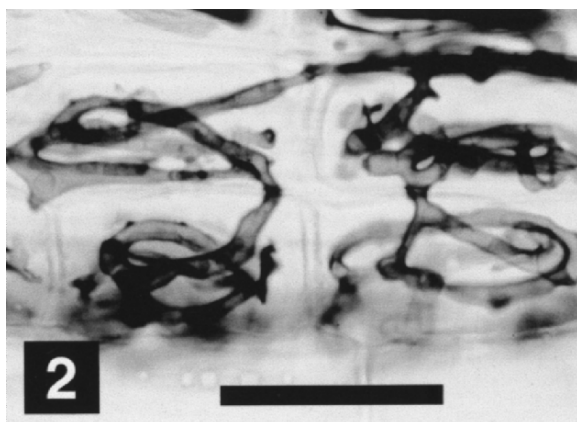
Unlike spores of AM fungi, the network of AM fungal hyphae in soil is easily and rapidly disrupted by a variety of abiotic and biotic factors. Destruction of this network typically leads to a significant reduction in the rate at which roots are colonized by the fungi (e.g., Read and Birch 1988; Koske and Gemma 1997), depriving transplants or seedlings the benefits of the association (Fig. 11.3). Hyphal networks in soil can be destroyed by shrinkage and expansion of soils (resulting from cycles of drought and hydration or freezing and thawing), by mechanical damage such as that caused by cultivation or compaction, by burrowing animals, by destruction of the hyphae by grazing microfauna or parasitic microorganisms, and by loss of vegetative cover (e.g., Read and Birch 1988; Jasper et al. 1989; Koske and Gemma 1997).

With the exception of *Gigaspora gigantea*, very little is known of the biology of individual species of AM fungi that can be isolated from dunes. *G.*

**Fig. 11.1.** Dark-staining hyphae and arbuscules of AM fungi in roots of American beachgrass (*Ammophila breviligulata*). Note high percentage of cortical cells with arbuscules (A). Bar 270  $\mu$ m

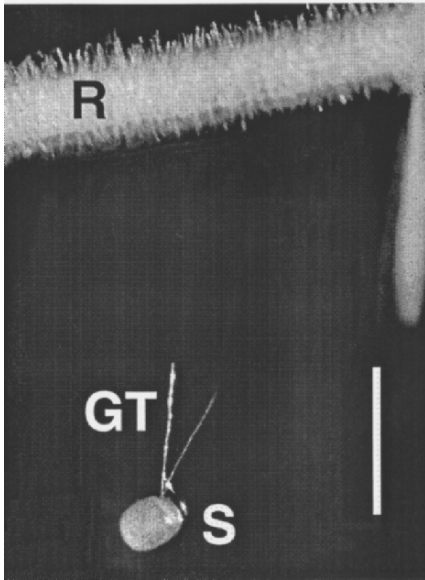


**Fig. 11.2.** Hyphal coils of AM fungi in roots of *A. breviligulata*



**Fig. 11.3.** Effect of disruption of the hyphal network of AM fungi in dune soil. Two cores were taken from the dune. Core on *left* was removed, shaken, and replaced into corning tube. Core on *right* was undisturbed. Corn plants (*Zea mays*) were grown for 8 weeks. Note reduced growth in plant growing in disturbed soil





**Fig. 11.4.** Germinating spore (*S*) of *Gigaspora gigantea*. Germ tube (*GT*) grows towards the plant root (*R*). Bar 1 cm

*gigantea* is a common species in dunes of the Atlantic coast of the US (Koske and Halvorson 1981; Koske 1987), but it has also been found in other ecosystems (e.g., Gerdemann 1955). Newly formed spores (produced from August through December) are dormant, requiring exposure to cold temperatures to break dormancy (Gemma and Koske 1988a). Spores germinate in spring when soil temperatures reach ca. 20 °C, producing long germ tubes that grow up to 10 cm or more (Koske 1981b). The germ tubes are attracted to plant roots by volatile root exudates (Fig. 11.4; Koske 1982; Gemma and Koske 1988b). Germination occurs equally well in the presence or absence of host roots (Koske 1982). Spores are capable of producing up to ten consecutive germ tubes, so a single spore has numerous chances of contacting a plant root (Koske 1981a). Spores of *G. gigantea* retain high viability even after immersion in seawater for more than three weeks (Koske et al. 1996), suggesting that transport in longshore currents is possible.

### 11.3 AM Fungi in Coastal Dunes

Almost half of the ca. 150 described species of AM fungi have been found in dune ecosystems. However, many species remain undescribed, and accurate identification of species is difficult. Within the root zone of a single dune plant, 1–14 species of AM fungi have been found (Koske 1987), and the range typically is 3–7 (Rose 1988; Tadych and Blaszkowski 2000a).

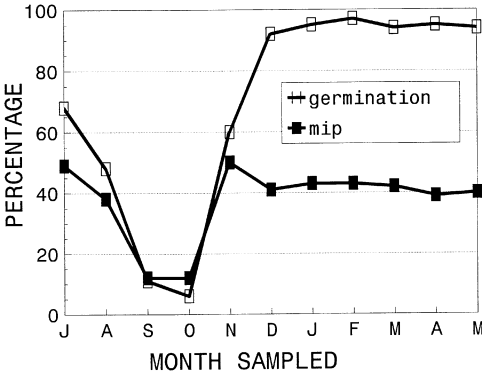
Some studies report higher spore richness in stabilized dunes than in early successional or disturbed sites (Giovannetti and Nicolson 1983; Koske and Gemma 1997), but edaphic factors, temperature, and plant species may also influence the spore distribution (Koske 1987, 1988; Trufem 1995). As with plant species, temperature affects the distribution of AM fungi in dunes. In a 355-km-long transect in the Atlantic coast dunes of the US, some species of AM fungi (*Scutellospora weresubiae* and *S. fulgida*) were limited in their northern distribution by cooler temperatures, while others (e.g., *S. calospora*), were less common in the warmer, southern end of the transect (Koske 1987). However, some isolates of *S. calospora* are tolerant to warm conditions, occurring in Australian dunes (Koske 1975). Reports of the same species of AM fungi from diverse dune sites suggest that ecotypes may also be common (e.g., Koske 1975; Tadych and Blaszkowski 2000a).

## 11.4 Seasonality of AM Fungi in Coastal Dunes

The population of spores of AM fungi and the rate at which plant roots are colonized by AM fungi vary seasonally (Nicolson and Johnston 1979; Giovannetti 1985; Gemma and Koske 1988a; Corkidi and Rincón 1997a; Sigüenza et al. 1996). The mycorrhizal inoculum potential (MIP) of a soil is a measure of how rapidly roots growing in soil will be colonized by AM fungi. In soils with a high MIP, plant roots will be contacted by hyphae sooner and become colonized more rapidly than will roots in soil with a low MIP (Moorman and Reeves 1979). Early colonization of roots leads to early benefits to the plant (Fig. 11.3; Read and Birch 1988).

Seasonality of spore abundance is influenced by biotic and abiotic factors (e.g., the species and phenology of the host plant, temperature, and the abundance of other AM fungi present) (Koske 1981c, 1987; Gemma et al. 1989; Sigüenza et al. 1996; Tadych and Blaszkowski 2000a,b). Spore populations increase as a result of sporulation and decline because spores germinate, emptying their contents into the resulting hyphae, and from losses due to predation, parasitism, and age (Lee and Koske 1994a,b). Fluctuations in spore abundance in 1 year can be dramatic, some species changing by 400–2000 % in a period of 3–4 months (Stürmer and Bellei 1994; Lee and Koske 1994a). No consistent relationship between sporulation and plant phenology has been found. Some studies showed higher spore abundance at the end of the growing season (Giovannetti 1985), while others report that individual species sporulate at different times (Sylvia 1986; Gemma et al. 1989; Stürmer and Bellei 1994; Sigüenza et al. 1996).

Less is known of the causes of declining spore abundance. A detailed study of parasitism of spores of *Gigaspora gigantea* in a Rhode Island sand dune showed that numerous species of Fungi Imperfecti and actinomycetes iso-



**Fig. 11.5.** Seasonal variation in mycorrhizal inoculum potential of dune soil from Rhode Island compared to germination rate of spores of *Gigaspora gigantea*, a dominant AM fungus in the dune. Spores are dormant in September and October when inoculum potential is lowest

lated from the dune soil were capable of penetrating and killing large numbers of healthy spores (Lee and Koske 1994a,b). Some pathogens attacked AM fungal hyphae as well as spores. Parasitism of AM fungi in non-dune systems has also been shown to reduce their ability to colonize roots (Ross and Rutenctter 1977).

Seasonal differences of MIP in dunes reflect not only the population of spores, but their physiological state as well as the abundance of other types of inocula (hyphae, roots, and rhizome fragments) (Gemma and Koske 1988a; Koske and Gemma 1997). In dunes of the North Atlantic coast of the US, MIP was relatively consistent throughout the year except in the months of September and October when it declined by ca. 75%. This reduction generally coincided with the very low germination rate of newly produced (but dormant) spores of *G. gigantea* (Fig. 11.5; Gemma and Koske 1988a).

## 11.5 Effects of Arbuscular Mycorrhizas on the Establishment and Growth of Coastal Dune Plants

Plant growth response to arbuscular mycorrhizas has been assessed in relatively few sand dune species. AM inoculation of European and American beachgrass (*Ammophila arenaria* and *A. breviligulata*), two premier dune-builders, increased survival (Koske and Polson 1984) and growth (Nicolson and Johnston 1979; Tadych and Blaszkowski 1999) in greenhouse studies. In field studies, addition of AM fungi improved establishment and tillering of *A. breviligulata*, greatly stimulated root formation (Fig. 11.6), and increased panicle production (Gemma and Koske 1989, 1997).

Similarly, mycorrhizal inoculation of the warm-season grass *Uniola paniculata* significantly increased the height, dry mass, and tissue phosphorus concentration (Sylvia 1989), and mycorrhizal plants of this species grew 219%

**Fig. 11.6.** Effect of AM fungi on growth of *Ammophila breviligulata* in a field study. Plant on *right* was inoculated 6 weeks before photo. Two plants on *left* were planted 40 cm away from first plant but were not inoculated. All plants were started as rootless tillers. Note profuse rooting and leaf elongation

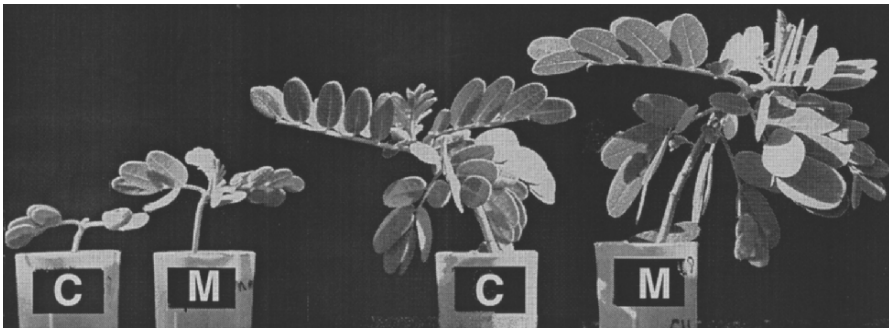


larger (shoots) and had 53 % more tillers than nonmycorrhizal plants when they were transplanted from a nursery to a barren replenishment beach in Florida (Sylvia 1989). Addition of AM fungi increased growth of the temperate tree *Prunus maritima* (280 % increase in shoot weight after 20 weeks; Gemma and Koske 1997) and of the four tropical species *Chamaecrista chamaecristoides* (280 % increase in shoot weight, 500 % increase in root weight), *Palafoxia lindenii* (shoots 200 %, roots 50 %) and *Trachypogon plumosus* (shoots 350 %, roots 904 %) from Mexico (Corkidi and Rincón 1997b), and *Sesbania tomentosa*, an endangered Hawaiian species (shoots 116 %) (Gemma et al. 2002). AM fungi also improved the growth of five of six dune colonizers in Poland, some in excess of 5300 % (Tadych and Blaszkowski 1999). In the Polish study, the grass *Festuca rubra* ssp. *rubra* was unable to grow without AM fungi, a striking demonstration of its dependency on the symbiosis.

Species of AM fungi vary in their effectiveness in stimulating growth, and plant species vary in their response to inoculation (e.g., Sylvia and Burks 1988; Corkidi and Rincón 1997b). *Leymus arenarius* plants inoculated with indigenous AM fungi from a sand dune in Iceland had higher dry mass than plants inoculated with commercial inoculum (of non-dune origin) (Greipsson and El-Mayas 2000).

The presence of mycorrhizas does not necessarily indicate a beneficial association to plant growth. *Ipomoea pes-caprae* and *Sporobolus virginicus* are species reported as highly mycorrhizal in the sand dune natural conditions, but did not improve their growth response in presence of mycorrhizal inoculation (Corkidi and Rincón 1997b; Koske and Gemma 1990).

The degree to which plants are dependent on AM fungi is typically assessed by comparing the growth of inoculated and non-inoculated plants in pots (vs. field conditions) (e.g., Corkidi and Rincón 1997b). It should be noted that “dependency” in this sense refers only to growth, not to non-growth benefits. Because AM fungi are important to plants under stress conditions (for most plants in the wild, this is most of the time), it is necessary to measure dependency when plants are subjected to stress. In the artificial conditions that pot-grown plants experience (especially in maintaining levels of P and moisture comparable to those in the field), it is extremely difficult to determine dependency accurately, and too little or too much P can lead to large underestimations of dependency (Fig. 11.7; Miyasaka et al. 1993; Gemma et al. 2002). The concept of ecological mycorrhizal dependency has been suggested to emphasize the need for assessing mycorrhizal dependency under appropriate conditions (Gemma et al. 2002). This focus on growth in assessing dependency ignores the non-nutritional benefits of AM that may be more important, such as drought tolerance. For example, in greenhouse trails, AM fungi often have little effect on growth of *A. breviligulata* (Koske and Gemma, unpub. obser.), but when plants experienced moderate drought conditions, only 20 % of the controls survived in contrast to 78 % of the AM plants (Koske and Polson 1984). In addition, other studies on sand dune species have also shown that the mycorrhizal association can contribute to plant tolerance against salinity (Tsang and Maun 1999), burial (Perumal and Maun 1999), and infection with nematodes (Little and Maun 1996, 1997).



**Fig. 11.7.** Interaction of soil P and inoculation with AM fungi in *Sesbania tomentosa*. At low P (equivalent to field levels), plant inoculated with AM fungi (M) is 2.2 times larger than uninoculated plant (C). When soil P is similar to that of a productive agricultural field (plants on right), little difference between M and C plants is detected



### 11.6 Arbuscular Mycorrhizas and Coastal Dune Succession

Succession and AM fungi in sand dunes has been studied from two viewpoints: (1) plant succession as related to the activity of AM fungi in soil, and (2) fungal succession as related to the plant community and edaphic conditions. Several studies have demonstrated a strong positive correlation between the population of AM fungi (spore abundance, species richness, extent of root colonization, and inoculum potential) in dunes and the percent cover/successional stage of the vegetation (Nicolson 1959, 1960; Nicolson and Johnston 1979; Koske and Halvorson 1981; González et al. 1995; Trufem 1995; Corkidi and Rincón 1997a; Sigüenza et al. 1996; Koske and Gemma 1997; Tadych and Blaszkowski 2000b). In most cases, after increasing during early and mid-succession, AM fungal populations decline in the latest stage (Fig. 11.8), often as sites include ectomycorrhiza-forming species (Read 1989). As with plants, species of AM fungi have been identified as early-, mid-, and late colonizers in the dunes (Koske and Gemma 1997; Rose 1988; Tadych and Blaszkowski 2000b). Many of the species show a wide tolerance of conditions, occurring throughout much of the dune succession.

The means by which pioneer plant species that require AM fungi are able to become established in barren, primary successional dune sites is incompletely known. It was assumed that primary successional species could not be dependent upon AM (Read 1989). While this notion had intuitive appeal (pioneer sites lack plants [and therefore AM fungi], so only plants that do not require AM fungi can be pioneers), there has been little evidence to support this hypothesis. Nearly all of the major dune-building species have arbuscular mycorrhizas even in the earliest stages of dune formation (e.g., Nicolson 1960;

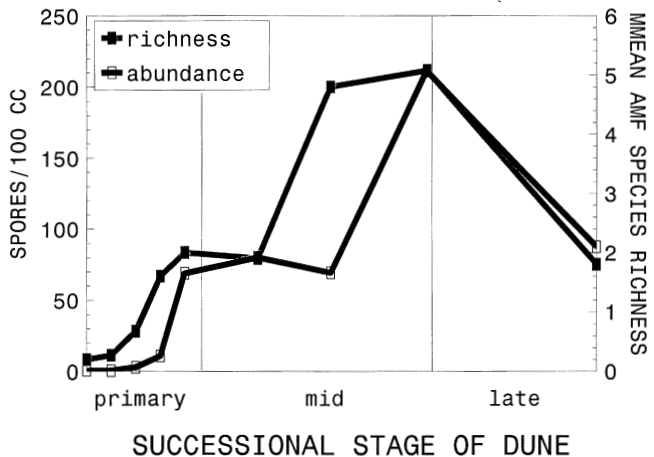


Fig. 11.8. Relationship between successional stage in a dune and abundance of spores of AM fungi and mean species richness of AM fungi. (Adapted from Koske and Gemma 1997)

Koske et al. 1975; Peterson et al. 1985; Koske and Gemma 1990; Gemma and Koske 1992; Corkidi and Rincón 1997a).

There are two ways by which plants and AM fungi become associated in the dunes. The first, which is the less efficient, depends upon the fungi being present in a site of potential plant establishment (by seed or vegetative fragment) before the plant arrives. Spores and fragments of roots and rhizomes could arrive at these sites in drift material (deposited by waves or blown in from vegetated areas of the dune) (Nicolson 1960; Sylvia 1986; Koske and Gemma 1990). However, in contrast to the prolific spore production of most wind-dispersed fungi, AM fungi form very few spores, limiting their capacity for dispersal. Spores and fragments in the dunes do not migrate downward into the sand with rainfall, so many of the propagules are too distant from the root zone to be able to form arbuscular mycorrhizas with seedlings (Friese 1984). While significant populations of AM fungi can occur in drift lines on the beach and berm (Nicolson 1960; Koske and Gemma 1990), in barren dune areas, soil collected from a few centimeters below the surface may have few or no AM fungi (Sylvia 1989; Koske and Gemma 1997).

A much more efficient mechanism for ensuring that AM fungi and plant arrive simultaneously at the same site (co-dispersal) has evolved in a number of primary colonizers (Gemma and Koske 1992). While the benefits of reproduction by vegetative fragmentation for primary colonizers of unstable habitats such as sand dunes is recognized (e.g., Grubb 1987), the co-dispersal of vegetative fragments with AM fungi may be more important (Koske and Gemma 1990). AM fungal spores and hyphae occur in the rhizomes (in addition to the roots) of several dune-building species including the grasses *A. breviligulata*, *Distichlis spicata*, *Ischaemum byrone*, *S. virginicus*, and *U. paniculata*, and in the tropical *Jacquemontia sandwicensis* (Convolvulaceae) (Koske and Gemma 1990; Koske and Gemma, unpubl. observ.). When rhizome fragments arrive in barren dune sites and sprout new roots and shoots, the resident AM fungi spread into the new roots, benefiting the recruit as well as establishing a hyphal network in the soil that facilitates the establishment of other plants that do not co-disperse (Gemma and Koske 1989, 1992, 1997). AM fungi in root fragments (like spores) retain their viability after immersion in seawater (Koske and Gemma 1990).

The extent of the hyphal network increases in the early stages of succession, as does the abundance of AM fungi spores and AM fungi species richness, increasing the MIP of the site (Corkidi and Rincón 1997a; Koske and Gemma 1997). Establishment of mid- and late-successional species in the dunes appears to be prevented until a hyphal network has developed in the dunes (Koske and Gemma 1997).

In addition to this important role, the hyphal network builds soil structure, binding sand grains into larger aggregates that resist wind erosion (e.g., Koske et al. 1975; Sutton and Sheppard 1976; Clough and Sutton 1978; Forster and Nicolson 1981; Jehne and Thompson 1981; Rose 1988). In sand

dunes of Lake Huron in the US, up to 9% of the sand in the mobile dunes is held in aggregates greater than 2 mm diameter by AM fungal hyphae (Koske et al. 1975). The network also links plants in the dune, and nutrients may be shunted from larger to smaller plants, even of different species (Smith and Read 1997).

Driftline vegetation is inconsistently associated with AM fungi (Nicolson 1960; Giovannetti and Nicolson 1983; Peterson et al. 1985; Koske and Halvorson 1989; Koske and Gemma 1990; Sigüenza, pers. observ.). The instability of this habitat prevents long-term colonization by plants, and the contribution of mycorrhizas to plant survival is of unknown significance there.

As a final note, the absence of arbuscular mycorrhizas from root samples does not always indicate that the plants lack mycorrhizas; unsampled roots may have had AM fungi. In some species, only the smaller roots had AM (Koske and Halvorson 1981). Also, rhizomatous species can be misleading because roots of young ramets may lack AM fungi, while older ramets (connected to the AM-free ramets) are highly mycorrhizal (Koske and Gemma, unpubl. observ.).

## 11.7 Arbuscular Mycorrhizas and Sand Dune Stabilization and Restoration

With the realization of the importance of AM fungi to the growth of dune species, field trials using AM inoculum in dune stabilization and restoration were initiated (Sylvia and Will 1988; Sylvia et al. 1993; Gemma and Koske 1989, 1997). These trials showed that inoculation resulted in more rapid establishment of transplants, stimulating the formation of AM hyphal networks that allow recruitment by mid- and late-successional species. Thus, addition of AM fungi has the potential to accelerate succession and stabilization of dunes (Gemma and Koske 1997).

One reason that arbuscular mycorrhizas were overlooked as important components of dune succession and restoration is that field plantings of dune-building species made without the intentional addition of AM fungi were successful. This apparent paradox was resolved when AM fungi spores and hyphae were found in the roots and rhizomes of planting stock used for dunes (*A. breviligulata*, *Prunus maritima*, *Rosa rugosa*, and *Spartina patens*) (Gemma and Koske 1997). When tillers of *A. breviligulata* were planted in barren sites in Cape Cod, MA (without addition of AM fungi), 78% of the root samples from these plants were mycorrhizal 47 weeks after planting (Gemma and Koske 1997). Nevertheless, even though both “non-inoculated” and inoculated plants developed mycorrhizas, the inoculated ones grew and tillered faster, and the significant differences were noted for 81 weeks when the experiment was ended (Gemma and Koske 1997).

For species that establish from seed (e.g., *Uniola paniculata*), co-dispersal is not possible. Addition of mycorrhizal inoculum at the time of planting may be necessary if such species are planted in barren or sparsely vegetated areas (Sylvia 1989). Addition of particularly effective species or isolates of AM fungi at the time of sowing or outplanting can result in greater benefits to plants than are provided by the native species (Sylvia and Burks 1988; Sylvia 1989; Sylvia et al. 1993).

Future research will address methods to produce inoculum for use in dune restoration. In addition, it is necessary to identify the species and isolates of AM fungi that are most effective for particular conditions, possibly fitting particular isolates to specific seral stages. Much still is to be learned about the ecology of AM fungi in sand dunes ecosystems.

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