Mycorrhizal Associations of Selected Plant Species from San Miguel Island, Channel Islands National Park, California

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ABSTRACT: Vesicular–arbuscular mycorrhizae (VAM) were detected in six native plant species: Camissonia cheiranthifolia ssp. cheiranthifolia, Coreopsis gigantea, Distichlis spicata, Dudleya greenei, Eriogonum grande ssp. rubescens, and Lavatera assurgentiflora. Levels of root colonization were greater in November than in July. No mycorrhizae were apparent in plants of Cakile maritima, Mesembryanthemum crystallinum, or M. nodiflorum. A total of ten species of VAM fungi, three of them undescribed, were recovered from root zones of Dudleya, Coreopsis, and Lavatera. Genera of fungi included Entrophospora, Glomus, and Scutellospora. The reinvansion of barren areas of the island from which some native plant species were extirpated by overgrazing and erosion may depend on the reestablishment of a population of VAM fungi.

SAN MIGUEL ISLAND (Figure 1) has had a long history of disturbance from ranching and military activities (Roberts 1978). Loss of vegetation from more than a century of grazing by sheep, whose damage was accentuated by periodic droughts and the nearly constant wind-scouring of the island, has led to the formation of large denuded areas [c. 37 km², 15% of the habitable island surface; Johnson (1980)]. This has resulted in the reduction of the distribution of many native plant species, which are now scattered on steep slopes and in inaccessible canyons. Also, alien species are now dominant over much of the land that was not denuded. A long-term research project is underway to determine the characteristics and dynamics of the plant assemblages on the island as they recover from this disturbance. Recovery has been in progress since the National Park Service (NPS) began carrying out a program of conservation management in 1974. At present, the floral list includes 233 species, of which 75.1% are native (5.6% Channel Islands endemics) and 24.9% are alien (Halvorson, 1989).

Other studies have suggested that vesicular–arbuscular mycorrhizae (VAM) may be of critical importance in the reinvansion of disturbed sites by extirpated plant species (Janos 1980; Miller 1979, 1987; Reeves et al. 1979). Approximately 50% of angiosperm species appear to have an absolute requirement for forming the VAM type of association (Trappe 1987). Since all the VAM fungi apparently are obligate symbionts they are absent from soils that have been unvegetated for long periods of time (Harley and Smith 1983); such is the case in the denuded areas of San Miguel Island. The recovery of a disturbed community to its earlier, undisturbed state can be slowed or prevented by the absence of VAM fungi from that site, resulting in a taxonomically different community composed of species that do not require the association (Janos 1980; Miller 1979, 1987; Reeves et al. 1979). In addition, the presence of VAM fungi in a soil may affect the outcome of competition between plant species that require VAM and those that do not (Janos 1980). Therefore, the ability of extirpated species to reinvade areas vegetated by other species may depend on the mycorrhizal requirements of each of the plant species and...
on the presence of VAM fungi (Miller 1979, 1987; Reeves et al. 1979).

On San Miguel Island, removal of sheep in the 1950s has permitted the reinvasion of some disturbed sites by species formerly restricted to a small refugia. An understanding of the mycorrhizal requirements of these species is needed, however, in order to understand the potential rate at which these small populations may grow and expand into barren sites and areas presently colonized by alien species.

The purpose of this study was to assess the mycorrhizal status of these reinvading species.
and species that are widespread on the island. Such information is important to the understanding of population dynamics and to the success of attempts at habitat restoration. We selected four native species whose distributions are expanding, _Coreopsis gigantea_ (Kell.) Hall., _Dudleya greenei_ Rose, _Eriogonum grande_ Greene ssp. _rubescens_ (Greene) Munz, and _Lavatera assurgentiflora_ Kell., to determine the extent of mycorrhizal development. The mycorrhizal status of these plants was compared to two native species widely distributed on the island, _Camissonia cheiranthifolia_ (Hornem ex Spreng.) Raimann in Engl. & Prantl. ssp. _cheiranthifolia_ Raven and _Distichlis spicata_ L., and to three widely distributed alien species that frequently colonize barren areas, _Cakile maritima_ Scop., _Mesembryanthemum crystallinum_ L., and _M. nodiflorum_ L.

**STUDY AREA**

San Miguel is a 4000-ha island off the coast of southern California. It is the westernmost of the northern Channel Islands, lying about 45 km south of Point Conception and 100 km west—northwest of Ventura. Bedrock on the island is composed primarily of Cretaceous and early-to-mid-Tertiary conglomerates, sandstones, siltstones, shales, and volcanics. Structurally, the island represents the north flank of a folded and faulted anticline whose axis trends northwest—southeast (Johnson 1979, Weaver et al. 1969). Much of the island is covered with sand, both stabilized and un-stabilized. Soils of the upland areas are of thevertisol group with high amounts of expandable clays and shrink—swell characteristics (Johnson 1979). The island has a Mediterranean type of climate with distinct wet winter and dry summer periods. The summer, while having little rain, is characterized by heavy and long-lasting fogs, providing a minimum amount of moisture. Rainfall is in the range of 330—355 mm per year, and the mean annual temperature is 13.7°C, with an annual range of 3°C. The island is also very windy, with an annual average of 25 km/hr. The island vegetation is low-growing, with trees (willows) confined to deep drainages. The major communities are grassland, _Haplopappus_ scrub, coastal sage scrub, coastal bluff, and coastal dune.

**MATERIALS AND METHODS**

Root and soil samples were collected in July and November 1985 (Table 1). Care was taken to exclude roots of neighboring species. Roots were fixed in the field in a solution of formalin, acetic acid, ethanol, and water (in a ratio of 2 : 1 : 5 : 7). In the laboratory, roots were cleared and stained using a modification of the methods of Bevege (1968) and Phillips and Hayman (1970). The fixed roots were cleared by autoclaving for 3 min in 10% KOH. If still dark, they were bleached in 60% Chlorox (c. 3% NaOCl) until straw yellow. Cleared roots were rinsed in a dilute HCl solution, and mycorrhizal roots were stained by autoclaving the roots for 3 min in 0.05% trypan blue in a solution of lactic acid, glycerol, and water (in a ratio of 1 : 2 : 1). Roots were destained by autoclaving for 3 min in the lactic acid, glycerol and water solution lacking trypan blue.

The extent of colonization of roots by VAM fungi was determined by estimating the percentage (to the nearest 10%) of the length of the absorbing root system that contained arbuscules, vesicles, hyphal coils, or internal hyphae of VAM fungi.

To determine the species of VAM fungi associated with roots of _Lavatera, Dudleya_, and _Eriogonum_, soil samples (c. 500 cm³) mixed with root fragments were collected at a depth of 5—15 cm beneath the soil surface when root samples were collected (Table 1). A 75-cm³ subsample, composed of 20—30 smaller subsamples withdrawn from each 500-cm³ sample, was processed to recover spores. Spores were extracted from the soil by a water—sucrose centrifugation technique (Walker et al. 1982). Following centrifugation, spores were collected on a 5.5-cm filter paper (Whatman no. 1) in a Buchner funnel. The filter paper was examined at 30× with a dissecting microscope, and spores were removed, mounted in a polyvinyl alcohol mountant (Koske and Tessier 1983), and identified with the aid of a compound microscope at 400—1000×. Identifications were confirmed by comparison with type or authenticated specimens and by con-
sultation with other VAM fungal taxonomists. Voucher specimens have been deposited in the mycological herbarium at the University of Rhode Island.

Soil pH was determined with a Fisher Accumet pH meter by placing the electrode in the liquid phase of a slurry of soil mixed with 0.01 M CaCl₂ after a 1-hr equilibration (Schofield and Taylor 1955).

RESULTS AND DISCUSSION

Ten species of VAM fungi were recovered from the soil samples (Table 2, Figures 2–8).
FIGURES 2–8. Crushed spores of VAM fungi from San Miguel Island. 2, *Glomus intraradices*, note pale outermost wall (arrow) and two darker laminations of innermost wall (bar = 50 μm); 3, *Entrophospora infrequens*, ornamentations of outermost spore wall (bar = 50 μm); 4, *Glomus pansihalos*, note thick, pale outer wall and darker, laminated wall (bar = 50 μm); 5, *Glomus etunicatum* (bar = 50 μm); 6, *Scutellospora 581*, note wrinkling innermost wall grouping (arrow) (bar = 200 μm); 7, *Glomus pansihalos*, warty surface of laminated wall (bar = 20 μm); 8, *Scutellospora 581*, walls 1–4 are indicated, note heavy wrinkling of wall 4 (arrow) (bar = 10 μm).
The root zones of *Dudleya*, *Lavatera*, and *Eriogonum* contained 9, 6, and 4 species of VAM fungi, respectively. Five of the species, *Scutellospora calospora*, *Glomus etunicatum* (Figure 5), *G. intraradices* (Figure 2), *G. monosporum*, and *Entrophospora infrequens* (Figure 3), have been previously isolated from the southwestern United States (Ams and Schneider 1979, Bethlenfalvay et al. 1984, Bloom and Walker 1987, Nemec et al. 1981). Both *E. infrequens* and *G. monosporum* occurred in agricultural areas in Ventura County, adjacent to Santa Barbara County in which San Miguel Island is located (Ams and Schneider 1979, Nemec et al. 1981). Of the other VAM fungal species recovered, *G. pansihalos* (Figures 4, 8), *G. aggregatum*, and *G. microaggregatum* are known from sand dunes in Michigan and along the Atlantic Coast of the United States (Berch and Koske 1986, Koske 1985, Koske et al. 1986). The latter two species also occur in Hawaiian sand dunes (Koske 1988).

Two of the VAM species, *Scutellospora* 581 (Figures 6, 7) and *Glomus* 601, could not be identified. Descriptions of the first are in preparation. Spores of *Glomus* 601 resemble those of *G. diaphanum* Morton & Walker (1984) in size, features of the attachment hypha, and wall structure, but differ in having a pale-yellow to brownish-yellow color and in possessing an ephemeral outermost wall 1–2 μm thick.

The six genera of native plants were mycorrhizal, although not every specimen possessed VAM at the time of sampling (Table 1). None of the alien species was mycorrhizal, supporting the observation that members of the Aizoaceae and Brassicaceae routinely lack VAM (Gerdemann 1968). Vesicular–arbuscular mycorrhizal colonization levels were greatest in *Lavatera* and *Distichlis*, and many root segments of the former were densely colonized, with most cortical cells containing arbuscules (Figure 9). The *Coreopsis* root systems were also mycorrhizal (Figure 10). Collections of *Dudleya* and *Eriogonum* included some root systems that lacked VAM. The level of colonization was very low in *Dudleya* (max. colonization = 10%), and two of the plants were nonmycorrhizal. The three *Eriogonum* specimens collected in July had 80–90% colonization (Figures 11, 12), while the November collections of this species showed only 0–10% colonization. The July samples contained abundant arbuscules, and nearly every cortical cell was occupied in some root segments.

The low levels of colonization present in both November collections (all the *Dudleya* plants and four of the *Eriogonum* plants) may be indicative of seasonal fluctuations in VAM intensity. These collections were made at the beginning of the growing season on San Miguel Island when root extension rates were high. Colonization of roots by VAM fungi typically is very low or absent during the first few weeks of rapid root growth following emergence, and levels of colonization reach a maximum when growth of root systems slows at the end of the growing season (Gemma 1987, Sutton 1973).

Members of the Polygonaceae frequently are nonmycotrophic (Gerdemann 1968), but exceptions are not uncommon, and both *Eriogonum fasciculatum* Benth. and *E. nodosum* Small formed VAM in Anza Borrego State Park, a desert site in southern California (Bethlenfalvay et al. 1984).

Results from the assessment of the mycorrhizal status of the extirpated and widespread native species and of the alien species suggest that the reinvasion of barren areas and restoration of plant communities on San Miguel Island may be dependent upon the reestablishment of a population of VAM fungi. Plant species in which all individuals sampled possessed mycorrhizae (*Coreopsis*, *Distichlis*, and *Lavatera*) are putative obligate mycotrophs, having an absolute requirement for VAM to complete their life cycles (Janos 1980, Trappe 1987), although additional sampling and experimentation are needed to confirm this assumption. Such species would compete poorly against facultative mycotrophs (*Dudleya*, *Camissonia*, and *Eriogonum*) and nonmycotrophs (*Cakile* and *Mesembryanthemum* spp.) in barren sites lacking VAM fungi (Janos 1980). The addition of VAM fungi to soil in certain sites may be necessary to restore the plant communities to their natural condition.
FIGURES 9-12. Vesicular-arbuscular mycorrhizae of three native plant species. 9. *Lavatera assurgentiflora*, darkly stained arbuscules in nearly every cortical cell (bar = 100 μm); 10. *Coreopsis gigantea*, two areas of root densely colonized by VAM fungi (arrows) (bar = 500 μm); 11,12. *Eriogonum grande*, darkly staining vesicles and runner hyphae (bars = 100 μm in Figure 11 and 50 μm in Figure 12).
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