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# Arbuscular Mycorrhizal Fungi in Hawaiian Sand Dunes: Island of Kaua'i[1]

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ABSTRACT: Fourteen species of arbuscular mycorrhizal (AM) fungi were isolated from the roots of plants growing on sand dunes of Kaua'i. The dominant AM fungal species included *Scutellospora hawaiiensis* Koske & Gemma, *Glomus* 807 (an undescribed species), *G. intraradices* Schenck & Smith, and *G. spurcum* Walker ined. Species richness per sample was low and ranged from 0 to 6 (avg. 2.0). Mean abundance of live spores was 8.9 spores per 100 $cm^3$, and many more dead or parasitized spores were present. The AM fungal community of the dunes of Kaua'i was very similar to that of the dunes of the island of Hawai'i. The long-distance dispersal mechanisms and similarity of habitats that have resulted in a relatively uniform angiosperm flora on dunes of the tropical Pacific may have produced a corresponding AM fungal community in these sites.

SPECIES OF ARBUSCULAR mycorrhizal (AM) fungi form mutualistic associations with a wide variety of plant species (Harley and Smith 1983, Harley and Harley 1987) and appear to be intimately involved in primary succession in sand dunes (e.g., Koske and Gemma 1990). Sandy shores of the Hawaiian Islands are colonized by a limited number of plant species, many of them indigenous to the tropical Pacific (Fosberg 1963, Carlquist 1974, 1980, Whistler 1980), and nearly 75% of these species are mycorrhizal (Koske and Gemma 1990). AM fungi apparently are early arrivals in primary succession on sandy beaches and dunes in Hawai'i (Koske and Gemma 1990), where their presence can influence the outcome of plant competition and influence community structure (Janos 1980). Despite their importance, the identity of the species of AM fungi in Hawaiian dunes is poorly known (Koske 1988), and there has been no survey of species from the island of Kaua'i.

The purpose of this study was to identify species of AM fungi that occur in dunes of Kaua'i, determine which species are most common, and compare the AM fungal community of Kaua'i with that of the island of Hawai'i (Koske 1988).

## MATERIALS AND METHODS

Populations of AM fungi were estimated from two surveys of the dunes of Kaua'i. The first was a preliminary study, and the second was planned to sample the dunes more comprehensively. In the first survey, soil samples were taken from the root zones of 10 dune plants (eight species) between July and November 1987 from five areas (Fig. 1, Table 1). In the second survey, a total of 30 root zone samples was collected from five dune systems (Fig. 1) on 23–27 May 1989. At each site, six 1-liter samples were collected from beneath plants growing on the dunes. Sampling sites were selected haphazardly to include a variety of plant species along a 100-m-long belt transect that paralleled the shoreline. A total of 10 species of plants was sampled in 1989, but not all 10 species were sampled at each site (Table 1). In the laboratory, a subsample of 150 $cm^3$ was taken from each sample, and spores were recovered using wet-sieving/su-

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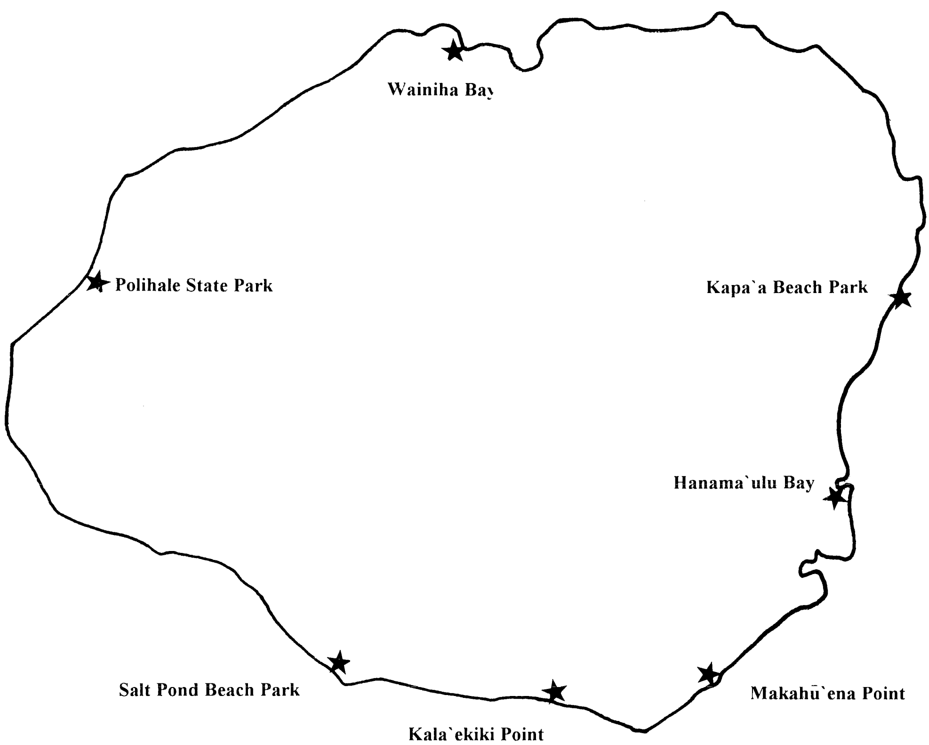



FIGURE 1. Collecting sites on the island of Kaua'i.

crose centrifugation (Walker et al. 1982). All spores in each subsample were mounted in a polyvinyl alcohol solution (Omar et al. 1979) and examined at 400–1000× using differential interference contrast microscopy. Only spores that appeared to be healthy were recorded and counted. Species were identified by comparison with type or authenticated specimens. Voucher specimens are preserved in the authors' collection. Spore terminology follows that of Walker (1983, 1986) and Morton (1986). Angiosperm nomenclature is that of Wagner et al. (1990).

Differences in average species richness between sites were analyzed using the adjusted chi-square test. The same test was used to compare the frequency of occurrence of individual species at the different sites. Similarity between the AM mycofloras of dunes of the islands of Kaua'i and Hawai'i was compared using Sorenson's index of similarity (Southwood 1978). Average richness per collection on each island was compared using a *t* test.

## RESULTS AND DISCUSSION

Spores of 14 species of AM fungi were recovered from the dune samples (Table 2). Many of the species have been illustrated previously from collections on the island of Hawai'i (Koske 1988), and complete descriptions and illustrations of them are not included in this report.

### 1. *Acaulospora scrobiculata* Trappe

Spores were found only in a single collection from Wainiha Bay. The species also occurs on the island of Hawai'i (Koske 1988) and seems to have a cosmopolitan distribution (Koske 1975, 1987, Trappe 1977, Chris-

TABLE 1

COLLECTION SITES AND PLANTS

| SPECIES | STATUS[a] | COLLECTION SITES, DATES, AND NO. OF SAMPLES COLLECTED[b] | TOTAL NO. OF SAMPLES COLLECTED |
|---|---|---|---|
| *Batis maritima* L. | I | Salt Pond (1987)[c]-1 | 1 |
| *Boerhavia repens* L. | I | Makahū'ena (1987)[c]-1 | 1 |
| *Coccoloba uvifera* (L.) L. | A | Kalaekīki (1987)[e]-1 | 1 |
| *Cocos nucifera* L. | A | Wainiha (1987)[c]-1 | 1 |
| *Dodonaea viscosa* Jacq. | I | Polihale (1989)-2 | 2 |
| *Ipomoea pes-caprae* (L.) R. Br. subsp. *brasiliensis* (L.) Ooststr. | I | Wainiha (1989)-3, (1987)[c]-1; Kapa'a (1989)-4; Salt Pond (1989)-1; Hanamā'ulu (1989)-1 | 10 |
| *Leucaena leucocephela* (Lam.) de Wit | A | Polihale (1989)-1, Salt Pond (1989)-2 | 3 |
| *Scaevola sericea* Vahl | I | Polihale (1989)-2, (1987)[d]-1; Wainiha (1989)-3, (1987)[e]-1; Kapa'a (1989)-3; Hanamā'ulu (1989)-3 | 13 |
| *Sida fallax* Walp. | I | Polihale (1989)-1, Salt Pond (1989)-1 | 2 |
| *Sporobolus virginicus* (L.) Kunth | I | Polihale (1989)-3, Wainiha (1989)-2, Kapa'a (1989)-2, Salt Pond (1989)-4, Hanamā'ulu (1989)-2, Kalaekīki (1987)[c]-1 | 14 |
| *Thespesia populnea* (L.) Sol. ex Correa | A | Kalaekīki (1987)[e]-1 | 1 |
| *Verbesina encelioides* (Cav.) Benth. & Hook | A | Salt Pond (1989)-1 | 1 |
| *Vigna marina* (J. Burm.) Merr. | I | Kapa'a (1989)-1 | 1 |
| *Vitex rotundifolia* L. fil. | I | Polihale (1989)-1, Salt Pond (1989)-1 | 2 |
| *Waltheria indica* L. | I | Salt Pond (1987)[c]-1 | 1 |
| *Wedelia trilobata* (L.) Hitch. | A | Salt Pond (1989)-1, Kapa'a (1989)-1 | 2 |

[a] I, indigenous to tropical Pacific and Hawaiian Islands; A, alien, introduced to Hawaiian Islands.
[b] Six samples were collected from each of the following sites in May 1989: Polihale State Park, Wainiha Bay, Kapa'a Beach Park, Salt Pond Beach Park, and Hanamā'ulu Bay. Ten samples were collected in 1987: one from Polihale, three from Wainiha Bay, two from Salt Pond, three from Kalaekīki Point, and one from Makahū'ena Bay. Because the roots of more than one plant sometimes occurred in the location where a sample was collected, the total number of root systems sampled (47) exceeds the number of soil samples collected (40) for the 1987 and 1989 collections.
[c] Collected 12 July 1987.
[d] Collected 20 August 1987.
[e] Collected 9 November 1987.

tie and Nicolson 1983, Koske and Tews 1987).

2. *Acaulospora* 869
   Figures 2–4

Spores globose, pale yellow, 100–125 $\mu$m diam. Spore wall structure of five walls (Figs. 2, 3). Wall 1 membranous, hyaline, <0.5 $\mu$m thick, wrinkling in crushed spores (Figs. 3, 4). Wall 2 laminated, yellow, 1.6–3.5 $\mu$m thick. Wall 3 a flexible wall, hyaline, 0.6–1.0 $\mu$m thick. Wall 4 a beaded membranous wall, hyaline, 0.5–0.8 $\mu$m thick, adherent to wall 5. Wall 5 an amorphous wall, hyaline, 1.4–1.8 $\mu$m thick, up to 12 $\mu$m thick when crushed.

Spores of *Acaulospora* 869 are very similar to those of *A. rugosa* Morton (Morton 1986), differing mainly in having only a single wall between the laminated and beaded membranous walls. Spores of *A. rugosa* have two thin walls in that position. Further, the outer membranous wall of *A. rugosa* is very prominent, forming coarse wrinkles on the surface of the spore in contrast to the thinner wall and finer wrinkling in *Acaulospora* 869 (Fig. 4). Examination of more Hawaiian specimens is necessary to fully characterize the species.

Spores of *Acaulospora* 869 occurred in just two collections from Kaua'i, one at Kapa'a Beach Park and one from Makahū'ena Bay.

TABLE 2

FREQUENCY OF OCCURRENCE OF AM FUNGI IN DUNE SITES ON KAUA'I

| AM FUNGAL SPECIES | POLIHALE ($n = 6$)[a] | WAINIHA ($n = 6$) | KAPA'A ($n = 6$) | SALT POND ($n = 6$) | HANAMĀ'ULU ($n = 6$) | ALL SAMPLES ($n = 40$)[b] |
|---|---|---|---|---|---|---|
| *Acaulospora scrobiculata* | 0[c] | 0 | 0 | 0 | 0 | 2.5D[d] |
| *Acaulospora* 869 | 0 | 0 | 17 | 0 | 0 | 5.0CD |
| *Gigaspora* 807 | 0 | 0 | 0 | 0 | 17 | 5.0D |
| *Glomus constrictum* | 0 | 17 | 0 | 0 | 0 | 2.5D |
| *Glomus intraradices* | 0 | 17 | 17 | 50 | 33 | 22.3BC |
| *Glomus microaggregatum* | 17 | 0 | 0 | 17 | 0 | 10.0C |
| *Glomus nanolumen* | 0 | 0 | 0 | 0 | 0 | 2.5D |
| *Glomus spurcum* | 0 | 0 | 17 | 67 | 33 | 20.0BC |
| *Glomus* 807 | 0 | 67 | 33 | 33 | 50 | 35.0AB |
| *Glomus* 901 | 0 | 0 | 0 | 17 | 0 | 5.0CD |
| *Sclerocystis sinuosa* | 33 | 0 | 0 | 0 | 0 | 12.5C |
| *Scutellospora gregaria* | 0 | 0 | 0 | 0 | 17 | 2.5D |
| *Scutellospora hawaiiensis* | 83 | 0 | 33 | 67 | 67 | 47.5A |
| *Scutellospora* 836 | 67 | 0 | 17 | 0 | 17 | 15BC |
| Total Richness | 4 | 3 | 6 | 6 | 7 | 14[e] |

[a]Number of soil samples analyzed at this site.
[b]Total number of samples collected includes 30 from 1989 and 10 from 1987 (see Table 1).
[c]Percentage of samples from this site that contained spores of this species of AM fungus.
[d]Values in this column followed by the same capital letters did not differ significantly.
[e]Total number of species of AM fungi collected.

3. *Gigaspora* 807

A single collection from the root zone of *Sporobolus virginicus* (L.) growing near Hanamā'ulu Bay contained spores of this species. *Gigaspora* 807 also occurs on the island of Hawai'i (Koske 1988).

4. *Glomus constrictum* Trappe

Spores occurred in a single sample from Wainiha Bay. The species is known from the island of Hawai'i (Koske 1988) and from Samoa (unpubl. obs.) and has a wide distribution (e.g., Trappe 1977, Hetrick and Bloom 1983, Koske 1987).

5. *Glomus intraradices* Schenck & Smith

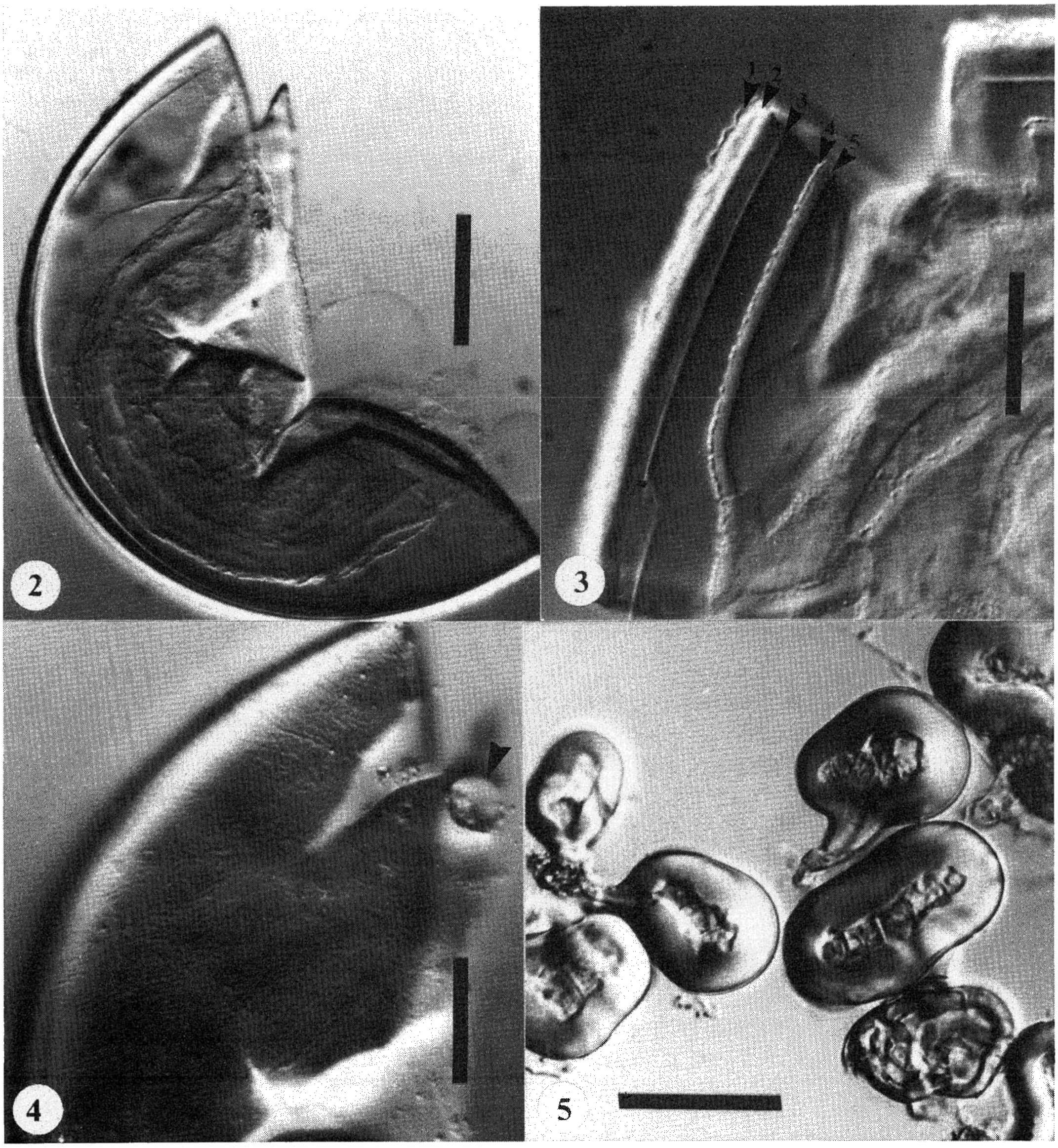
Spores of this species were isolated frequently. In addition to occurring in the root zones of a variety of plant species, spores were found between the leaf sheaths and the rhizomes of *Sporobolus virginicus*. This arrangement of AM fungal spores and vegetative fragments seems to function in codispersal (Koske and Gemma 1990). Spores of *G. intraradices* have previously been found on the islands of O'ahu (R.E.K., pers. obs.) and Hawai'i (Koske 1988) as well as the continental United States (e.g., Schenck and Smith 1982, Koske and Halvorson 1989).

6. *Glomus microaggregatum* Koske, Gemma & Olexia

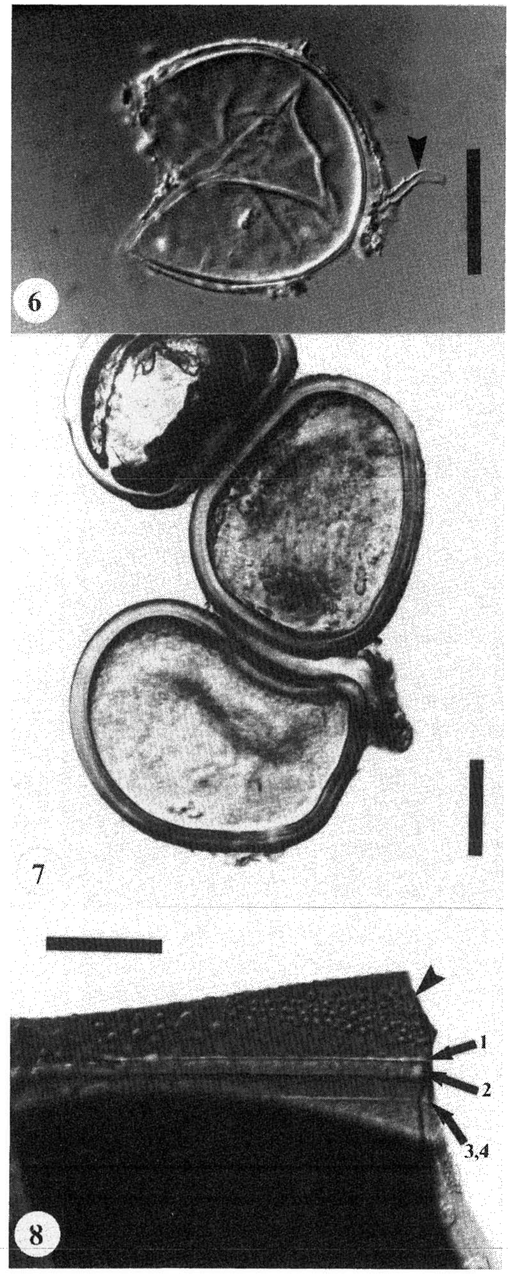
Spores of *G. microaggregatum* occurred inside the spores of other AM fungi, especially *Scutellospora hawaiiensis* Koske & Gemma. The spores would be overlooked in most collections unless larger, dead spores of *Scutellospora* and *Glomus* are crushed and examined. The species is common in sand dunes of the island of Hawai'i; San Miguel Island, California; the Great Lakes; and the Atlantic coast of the United States (Koske et al. 1986, Koske 1987, 1988, Koske and Tews 1987, Koske and Halvorson 1989) and in agricultural soils in Ohio (Rabatin and Stinner 1988).

7. *Glomus nanolumen* Koske & Gemma
Figure 5

Spores were found in abundance in a single sample from Polihale State Park. The species is characterized by the relatively thick walls



FIGURES 2–5. Spores of AM fungi from Kauaian sand dunes. 2–4. *Acaulospora* 869. 2, Crushed spore showing general view of walls. Bar = 40 $\mu$m. 3, Portion of crushed spore showing walls 1–5. Note wrinkling of wall 1 and beaded appearance of wall 4. Walls 4 and 5 are adherent. Bar = 20 $\mu$m. 4, Surface view of spore showing fine wrinkling of the outermost wall and cicatrix (arrow). Bar = 20 $\mu$m. 5, Spores of *Glomus nanolumen*. Note very thick wall and small lumen. Bar = 40 $\mu$m.




FIGURES 6–8. Spores of AM fungi from Kauaian sand dunes. 6, Spore of *Glomus spurcum*. Walls have separated in this crushed specimen. Note narrow attachment hypha (arrow). Bar = 40 μm. 7, Spores of *Glomus* 901. Note thick, laminated wall. Bar = 40 μm. 8, Crushed spore of *Scutellospora gregaria*. Walls 1–4 are indicated. Wall 1 is thin and ornamented with warts, which are seen in the surface view of this wall (arrow). Walls 3 and 4 are too closely appressed to each other to be visible as separate walls in this figure. Bar = 40 μm.

and small lumen of its silvery yellow spores. To date it has been isolated only from Kaua'i (Koske and Gemma 1989).

8. *Glomus spurcum* Walker ined.
Figure 6

The hyaline, globose to subglobose spores of *G. spurcum* are often encrusted with soil debris. Spores are small (64–120 μm diam.), and the spore wall structure consists of two walls: a thin, outer, membranous wall and a thicker, inner, laminated wall. The narrow hyphal attachment is easily broken from the base of the spore. This species was reported from the island of Hawai'i as *Glomus* 840 (Koske 1988). The wrinkling of the outer wall in crushed spores can give the appearance of an innermost membranous wall, leading to the error in the 1988 report. The composition of the spore wall structure was evident when pot cultures of this species were established during the study reported here.

9. *Glomus* 807

This is one of the most common species of AM fungi in dunes of Kaua'i and the island of Hawai'i (Koske 1988) and also occurs in Samoa (unpubl. obs.). The globose to subglobose spores are dark reddish brown and have a bimodal size distribution. The larger spores of this species average ca. 170 μm diam. and typically are very dark, whereas the smaller spores (avg. 110 μm diam.) are lighter in color. Because stages intermediate between the two are notably rare, as in *G. mosseae* (Nicol. & Gerd.) Gerd. & Trappe (pers. obs.), the smaller spores appear not merely to be an immature stage. Attempts to establish this species in pot culture have not been successful.

10. *Glomus* 901
Figure 7

The yellow-orange to orange-brown, subglobose spores of this species are characterized by the relatively thick laminated wall (8–10 $\mu$m thick) in relation to the spore size (108–160 by 60–140 $\mu$m). The spores that we observed were smooth, but possessed some debris on the laminated wall that suggested the earlier presence of an evanescent wall (as found in *Glomus* 807). Spores of *Glomus* 901 have a stout, yellow attachment hypha 8–10 $\mu$m wide with hyphal walls ca. 3 $\mu$m thick. Typically the subtending hypha is short, broken off ca. 8 $\mu$m below the base of the spore, but some extend for up to 44 $\mu$m from the spore.

11. *Sclerocystis sinuosa* Gerd. & Bakshi

Sporocarps of *S. sinuosa* were less frequently isolated on Kaua'i (frequency of 12.5%) than on the island of Hawai'i where they occurred in 33% of the samples (Koske 1988). The species has a worldwide distribution (Gerdemann and Bakshi 1976, Nemec et al. 1981, Wu 1993) and was previously found in dunes of Kaua'i (near the Polihale site reported here) in association with roots of the endemic fern *Ophioglossum concinnum* Brack. (Gemma et al. 1992).

12. *Scutellospora gregaria* (Schenck & Nicolson) Walker & Sanders
Figure 8

Spores of *S. gregaria* were recovered from a single sample on Kaua'i in the root zone of *Ipomoea pes-caprae* (L.) R. Br. subsp. *brasiliensis* (L.) Ooststr. growing near Hanamā'ulu Bay. The dark, nearly black spores are large (up to 448 $\mu$m diam.) and covered with warty ornamentation. The species is known to occur in Florida (Nicolson and Schenck 1979) and dunes of Maryland (Koske 1987), but has not been reported previously in Hawai'i.

13. *Scutellospora hawaiiensis* Koske & Gemma

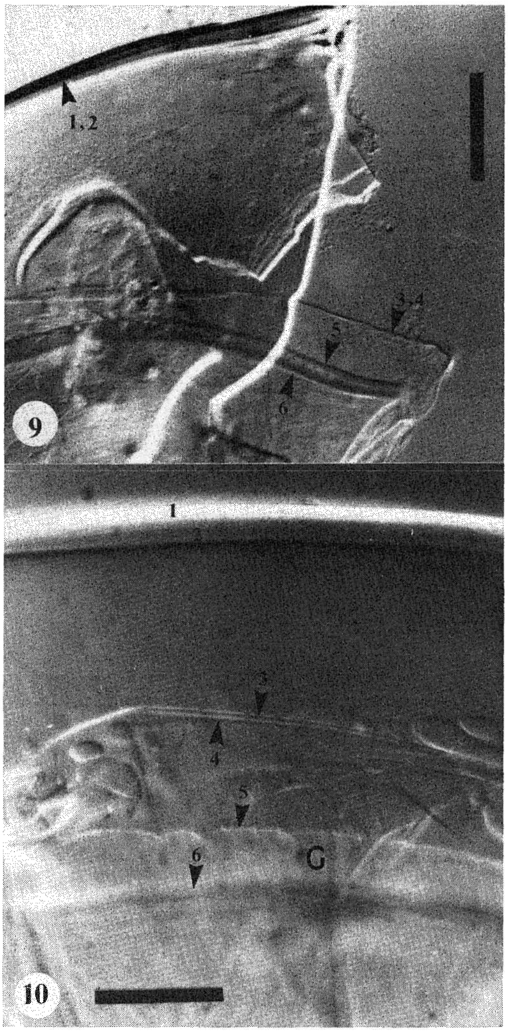
This is one of the dominant species of Hawaiian dunes. Spores occurred in 47.5% of the samples from Kaua'i and from 38% of those from the island of Hawai'i, where it was identified as *Scutellospora* 816 (Koske 1988). The dark orange-brown mycelium and auxiliary cells of *S. hawaiiensis* were prominent in many collections, even in samples where no spores were recovered. *Scutellospora hawaiiensis* is known to occur only in the Hawaiian Islands (Koske and Gemma 1995).

14. *Scutellospora* 836
Figures 9–10

Spores of this undescribed species are smooth, hyaline, globose to subglobose, (160–)220–270(–320) $\mu$m diam., with a wall structure consisting of six walls. Wall 1 a unit wall 0.5 $\mu$m thick, adherent to wall 2. Wall 2 laminated, 3–6(–9) $\mu$m thick. Walls 3 and 4 membranous, tightly paired, each $<0.5$ $\mu$m thick. These two thin walls are so closely adherent that they often appear to be a single wall. Walls 5 and 6 are coriaceous, paired, but separating under pressure. Wall 5, 1.2–2.5 $\mu$m thick, with a slightly wrinkling outer surface. Wall 6, 0.5–1.6 $\mu$m thick, staining pink in Melzer's reagent. Suspensorlike cell concolorous with spore or slightly darker, 44–56 $\mu$m broad, with walls up to 1.5 $\mu$m thick. Auxiliary cells not seen. This species is most similar to *S. pellucida* (Nicolson & Schenck) Walker & Sanders, but differs in having an innermost wall that is coriaceous rather than amorphous.

*Scutellospora* 836 was the fifth most commonly isolated AM fungus in Kauaian dunes. It has been found on the island of Hawai'i and in Samoa (unpubl. obs.), but is not known to occur elsewhere.

Spores of AM fungi were present in 85% of all samples. Species richness per sample was low and ranged from 0 to 6 (avg. 2.0) in Kaua'i dunes, with no significant differences between collection sites ($F = 2.59$, df $= 4$, $P = 0.06$). A similar low average richness (2.4) was recorded from the island of Hawai'i (Koske 1988). Spore abundance in the Kaua'i dunes also was low (avg. 8.9 spores per 100 $cm^3$), and many spores were parasitized. Dead spores typically outnumbered live spores at most sites, although no counts were made. Possible causes of low richness and abundance in Hawaiian dune soils include parasitism and predation, fluctuations in seasonal abundance, and selection for nonsporulating species (Koske 1988).




Figures 9–10. Spores of *Scutellospora* 836. 9, Crushed spore showing general view of walls. Appressed walls (1, 2 and 3, 4) cannot be distinguished as separate in this figure. Bar = 40 $\mu$m. 10, Walls 1–6. Note paired membranous walls (3 and 4) and the wrinkling of the surface of wall 5. Wall 6 is separated from wall 5 in this specimen by a gap (G). Bar = 20 $\mu$m.

In the Kauaian data there were almost no significant differences in frequency of occurrence of species of AM fungi in the five main sampling areas (Table 2). The lack of significance resulted mostly from the small sample size ($n = 6$ for most sites). Only *S. hawaiiensis* occurred with significantly greater frequency in the Polihale samples than in the Wainiha Bay samples ($\chi^2 = 5.49$, df = 1, $P = 0.05$).

The AM fungal community of Kauaian dunes is similar ($S = 0.74$) to that of Hawai'i Island's dunes (Koske 1988), and 10 of the 14 species found in Kaua'i also occurred on Hawai'i. On Kaua'i the dominant species were ranked as *S. hawaiiensis*, *Glomus* 807, *G. intraradices*, and *G. spurcum*. On Hawai'i the ranking was *S. hawaiiensis*, *Glomus* 807, *Sclerocystis sinuosa*, *G. microaggregatum*, and *G. intraradices*.

The similarity in the AM fungal community on the two islands results from several factors. Although the islands differ greatly in age (Kaua'i is 3.9–5.8 myr old and Hawai'i is less than 1 myr old [Clague and Dalrymple 1987]) and are separated by ca. 500 km, the dune habitat and coastal vegetation on both islands are alike. Hawaiian sand dunes are areas of continuing primary succession, and the plants that colonize these sites are well adapted to long-distance dispersal (Carlquist 1974, 1980). Indeed, most of the plants of the coastal strand of the Hawaiian Islands are indigenous, occurring on many of the island shores of the tropical Pacific (Carlquist 1974, 1980, Whistler 1980). The lack of endemism in dune plants in Hawai'i is in striking contrast to the high rate of endemism in the rest of the Hawaiian flora (more than 89% of the inland species are endemic to the Hawaiian Islands [Wagner et al. 1990]). The uniformity of the dune habit and the high incidence of recolonization of dune sites by indigenous species account for the existence of a common coastal strand flora that is found on many islands of the Pacific, despite their geographical isolation (Fosberg 1963, Carlquist 1974, 1980).

The same plant strategies (e.g., good mechanisms for long-distance dispersal, tolerance of propagules to seawater, and other adaptations to the dune habitat) and circumstances that produced this relatively uniform strand flora similarly may have resulted in a characteristic AM fungal mycoflora in these sites. That is, the AM fungal community of the dune habitat in the Hawaiian Islands may be similar to that of other Pacific islands that have similar angiosperm floras. There is some evidence to support such a view. First, AM fungi from Hawaiian dunes are capable of codispersal with their host plants and can survive immersion in seawater (Koske and Gemma 1990), suggesting a capacity for long-distance oceanic dispersal to sandy shores. Second, preliminary examinations of the AM fungal communities in dunes on Maui (Hawaiian Islands) and Samoa have revealed great similarities with the AM fungal mycoflora of Kaua'i and the island of Hawai'i (unpubl. obs.). Finally, although there has been no published study of the AM fungi of the interior regions of the Hawaiian Islands, a small survey suggests that the AM mycoflora of inland sites differs greatly from that of the coastal dune habitat (unpubl. obs.). Although the parallels between the angiosperm flora and AM fungal mycoflora of the strand are notable, further collecting is necessary to confirm the existence of a stable, indigenous AM fungal community in dune habitats of the tropical Pacific.

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