Plant Geography of Southwestern Sand Dunes

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Abstract

Patterns of plant distribution among eight dune fields in the southwestern USA and northwestern Mexico are analyzed and discussed. Each dune flora is characterized by three to five geographic components; the regional flora in which each dune field occurs is the dominant component. Endemic species, that is, species restricted to sand dunes, comprise ten percent or more of five of the eight floras. All possible combinations of the eight dune floras taken two at a time (28 pairs) were analyzed using Sorensen's similarity index. Only seven have a similarity value of 0.200 or greater. The lack of similarity among dune floras is due in part to their distribution among four floristically distinct biogeographic provinces and in part to localized recruitment of species from adjacent, non-dune plant communities. Geographic, edaphic and temporal barriers to dispersal and establishment also promote high dissimilarity among the eight floras. Eighty-three of the 533 species composing the eight dune floras are either endemic to sand dunes or occur at three or more of the dune fields studied. These 83 species fall into two subgroups: a group of 36 species characteristic of southwestern sand dunes east of 113° Longitude, and a group of 57 species characteristic of sand dunes west of 113° Longitude. Ten species are common to both groups. In the Southwest, dune fields are habitat islands, but dune floras do not behave in all respects as predicted by the MacArthur and Wilson theory of island biogeography. Southwestern sand dunes are not now floristic islands, but additional insular characteristics may develop over time.

Introduction

Although sand dunes are characteristic of many deserts, such as the Sahara Desert in northern Africa and the Gobi Desert in central Asia, dunes cover only a small fraction — about 0.5% — of the North American deserts (Fig. 1). Dunes in the Southwest (southern Utah, southern Nevada, southeastern California, Arizona, New Mexico, western Texas and northern Mexico) are widely scattered, lie between 90 and 1800 m in elevation and receive less than 300 mm precipitation annually. Most were formed during the Pleistocene as sand deposited in lakes in interior drainage basins was exposed and blown into dunes.

Dune plant communities throughout the Southwest are physiognomically similar. Active dunes, that is, dunes where sand is loose and blows about freely, are barren or support only widely spaced shrubs and grasses. Stabilized dunes, where sand is anchored by vegetation, are dominated by denser grass and shrub associations. Trees are uncommon on desert dunes, but do occur in favorable situations such as interdune depressions or on some stabilized dunes. Plant communities on dunes are derived from three sources: plants adapted and restricted to active sand; more widely distributed plants which occur on stabilized dunes and in sandy soils; and plants from adjacent, non-dune habitats.

Loose sand is an unfavorable substrate for plants in two major ways. Plants growing on active dunes are in constant danger of burial or excavation. In addition, dune sand is low in nutrients necessary for normal plant growth. On the other hand, active dunes act like sponges, absorbing precipitation and storing it with no runoff and little evaporation. Although the moisture-holding capacity of sand is low compared to silt or clay, sand particles hold water at much less negative matrix potentials than fine-textured particles, so that even small amounts of water in sand are readily available to plants. Since dune sand is constantly moist below the surface, active dunes are among the most mesic of desert habitats.

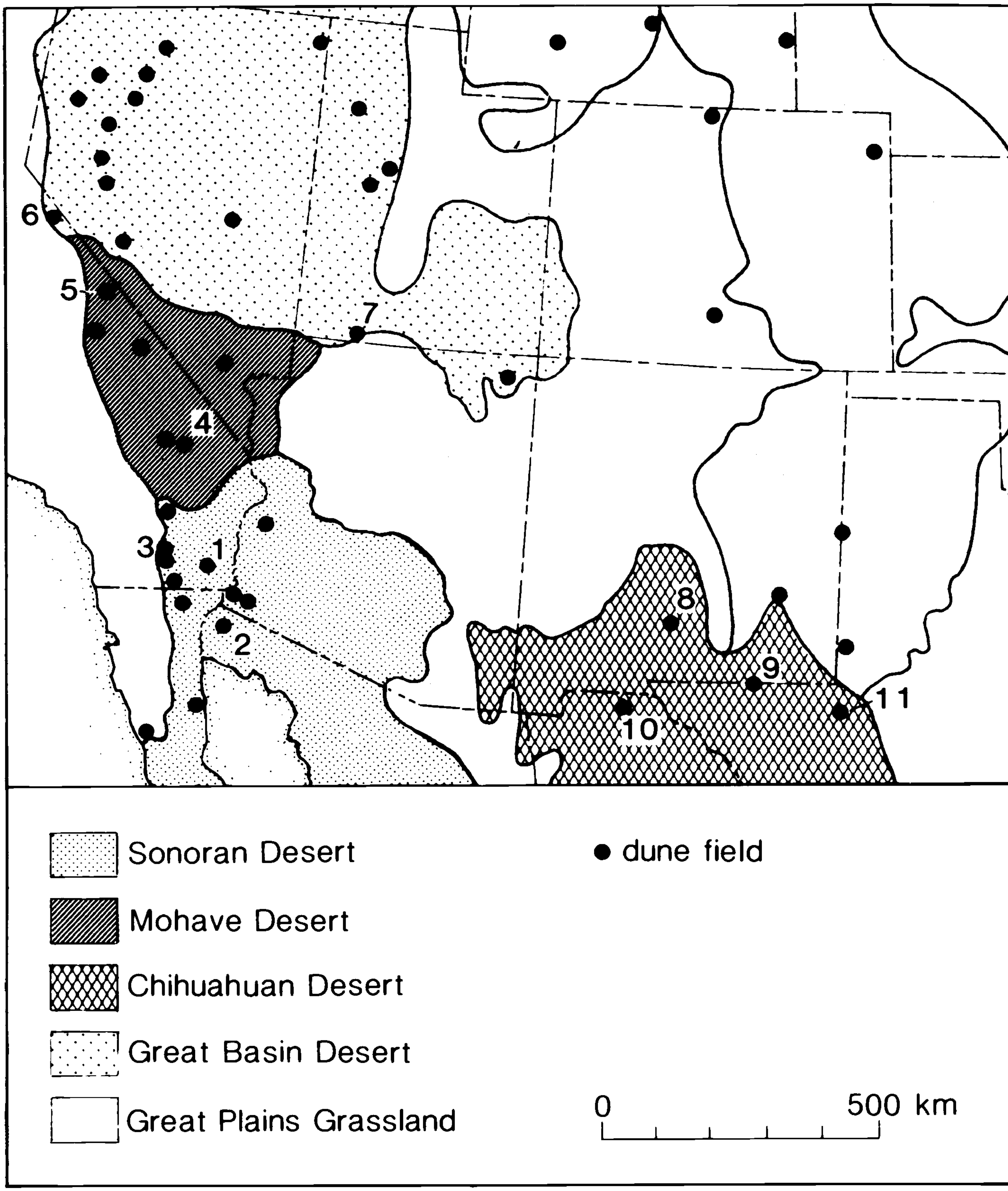

Figure 1. *Major dune fields in the Southwest with localities mentioned in the text (vegetation types after Shreve, 1942; Benson, 1959). 1. Algodones Dunes; 2. Gran Desierto Dunes; 3. Salton Sea Dunes; 4. Kelso Dunes; 5. Death Valley Dunes; 6. Eureka Dunes; 7. Coral Pink Dunes; 8. White Sands; 9. Guadalupe Mountains Dunes; 10. Samalayuca Dunes; 11. Sand Hills State Park. A complete map of dune fields in North American deserts was prepared by Smith (1982).*

Table 1. Some physical and environmental characteristics of eight southwestern dune fields.

	Kelso	Gran Desierto	Algodones	Coral Pink	White Sands	Eureka	Guadalupe Quartz	Guadalupe Gypsum
Basal elevation (m)	780	130	90	1800	1190	90	1100	1100
Area (km²)	117	4500	709	18	712	8	31	10
Annual precipitation (mm)	140	50	76	297	203	115	230	230
Distance to closest dune field (km)*	260	110	110	390	140	300	140	140
Sand type	quartz	quartz	quartz	quartz	gypsum	quartz	quartz	gypsum

*of the eight dune fields studied

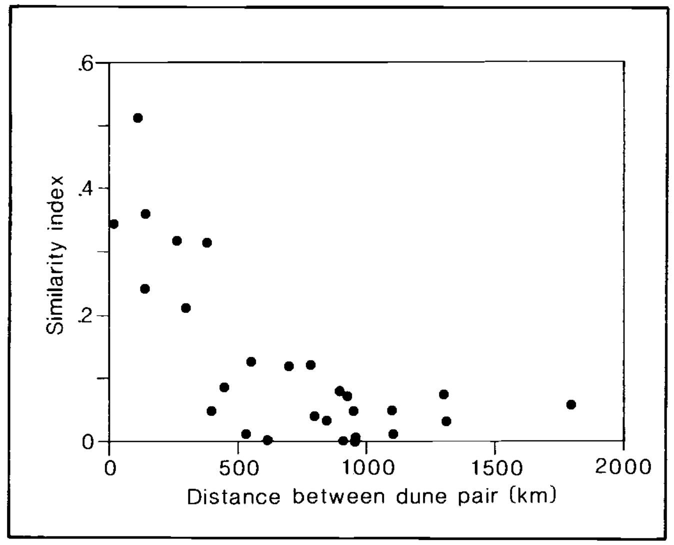

Figure 2. *Similarity index versus distance apart for 28 pairs of southwestern dune floras.*

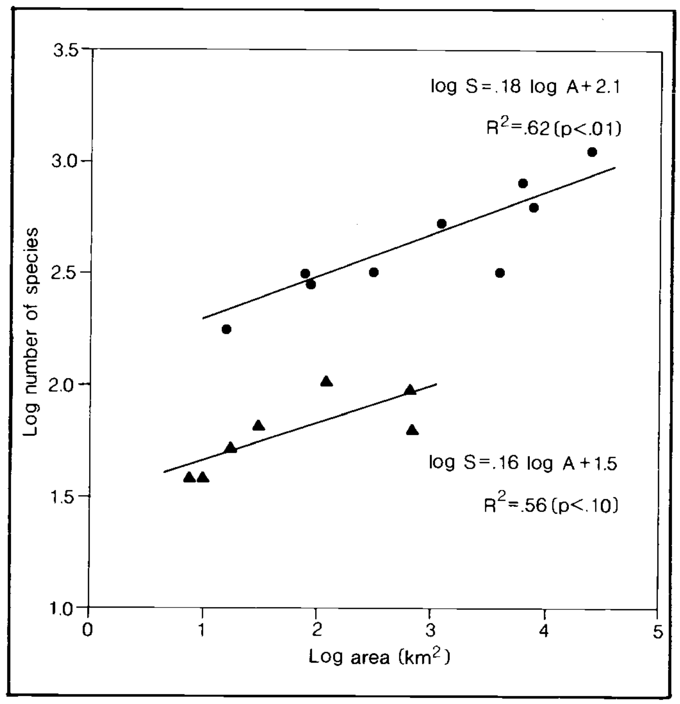

Figure 3. *Log-log relationship bewteen number of species and area for seven dune floras (triangles) and ten non-dune floras (circles).*

Those few species which thrive on active dunes have evolved specific adaptations to moving sand and are seldom, if ever, found in other habitats. Such adaptations include rapid growth of stem tips, keeping flowers and leaves above the level of accumulating sand; rapid elongation of radicles to prevent excavation of seedlings; development of a few vine-like lateral roots for anchorage rather than of numerous fibrous roots for water uptake; and symbiotic association with mycorrhizal fungi or with nitrogen-fixing bacteria which supply nutrients, particularly nitrogen and phosphorus.

Some dune endemics are characteristic of active sand — *Eriogonum deserticola* Wats., *Palafoxia arida* Turner & Morris var. *gigantea* (Jones) Turner & Morris, *Swallenia alexandrae* (Swallen) Soderstrom & Decker — while others are more typical of stabilized dunes — *Hilaria rigida* (Thurb.) Benth., *Psorothamnus emoryi* (Gray) Rydb., *Tiquilia palmeri* (Gray) Richards. Some are narrow endemics; that is, they are known from only one dune field. The majority are more widely distributed, occurring on several southwestern dune fields or even on dunes outside the Southwest. Dune endemics are obligate psammophiles, since the very adaptations which enable them to thrive on active sand make them unfit for or unable to compete in non-dune habitats. Pioneers on active sand are often dune endemics. They begin the process of stabilization and are eventually joined by plants from adjacent, non-dune plant communities. These and other topics relating to the plant ecology of sand dunes are discussed in greater detail by Bowers (1982).

The relative scarcity of dune fields in the Southwest has created interesting patterns in plant distribution. The objective of this paper is to analyze these patterns, first characterizing the geographic composition of eight southwestern dune floras; then determining how similar these floras are to one another and whether or not there is a southwestern dune flora, that is, a group of plants characteristic of dune fields throughout the Southwest, and finally, examining southwestern dune floras in the light of current concepts of island biogeography.

Methods

Floristic Analysis. - I selected eight southwestern dune fields for which floras had been compiled: the Coral Pink Dunes (Castle, 1954); Eureka Dunes (DeDecker, 1976), Kelso Dunes (Thorne et al., 1981), Algodones Dunes (WESTEC Services, 1977), Gran Desierto Dunes (Felger, 1980), White Sands (Shields, 1956), the Guadalupe Mountains quartz dunes (Burgess & Northington, 1977, 1984) and the Guadalupe Mountains gypsum dunes (Burgess & Northington, 1977, 1984) (Fig. 1). Some physical and environmental characteristics of each dune field are listed in Table 1. Using regional floristic manuals (Harrington, 1954; Kearney et al., 1960; Shreve & Wiggins, 1964; Munz & Keck, 1968; Correll & Johnston, 1970; Cronquist et al., 1977; Martin & Hutchins, 1980; and Hastings et al. 1972), I assigned each species in the eight dune floras to one of 15 geographic categories based on distribution. These categories are defined in Appendix 1. I then calculated the percent contribution of each category to every dune flora (Table 2).

Figure 4. *Algodones Dunes, showing barren active crests. Photo by Steven P. McLaughlin.*

Similarity Analysis. - I calculated an index of similarity for each of the 28 possible pairs of floras using Sorensen's index (Mueller-Dombois & Ellenberg, 1974):

$$IS = \frac{2C}{A + B}$$

Where A = the number of species in one flora, B = the number of species in a second flora, and C = the number of species common to both (Table 3). I also plotted the airline distance between each pair of floras against the similarity index for the pair (Fig. 2). Finally, I divided the list of all species occurring in the eight floras into two groups: 1) those endemic to sand dunes or occurring in three or more dune floras, a category which I believe defines the plants characteristic of dune fields, and 2) all other species.

Results and Discussion

Geographic Composition. - Each dune flora is characterized by three to five geographic components: the Kelso Dunes by species with Mohavean, Sonoran-Mohavean, Southwestern and Endemic affinities; the Gran Desierto Dunes by Sonoran, Sonoran-Mohavean, Southwestern and Endemic species; the Guadalupe quartz dunes by Chihuahuan, Southwestern and Plains species; etc. (Table 2). The regional flora in which each dune field occurs is the dominant component. On the Gran Desierto Dunes, for example, species with Sonoran and Sonoran-Mohavean distribution account for 48% of the flora; similarly, Chihuahuan species comprise 24%, 26% and 31% of the Guadalupe gypsum, White Sands and Guadalupe quartz dune floras, respectively. Species which occur throughout the Southwest are an important component of seven of the eight dune floras.

Further examination of Table 2 shows that most of the geographic components are important only in one or two floras. For example, the Intermountain component comprises 15% and 11% of the species at the Coral Pink and Eureka dunes, respectively, but is negligible in the other dune floras. Species endemic to gypsum are important only on the Guadalupe gypsum dunes, Mohavean species only in the Kelso and Eureka dune floras and Sonoran species only in the Algodones and Gran Desierto floras.

In general, the eight dune floras are highly individualistic in their geographic composition. Only the Algodones and Gran Desierto dune floras are much alike. Other dune fields in the same desert, such as the Kelso and Eureka dunes in the Mohave Desert or the Guadalupe quartz and Guadalupe gypsum dunes in the Chihuahuan Desert, differ in several important respects.

The most striking aspect of the floristic analysis is the high proportion of endemics at five of the eight dune fields: Kelso, Gran Desierto, Algodones, Coral Pink and Eureka dunes. Endemic species comprise a much higher proportion of these dune floras than of non-dune desert areas of similar extent.

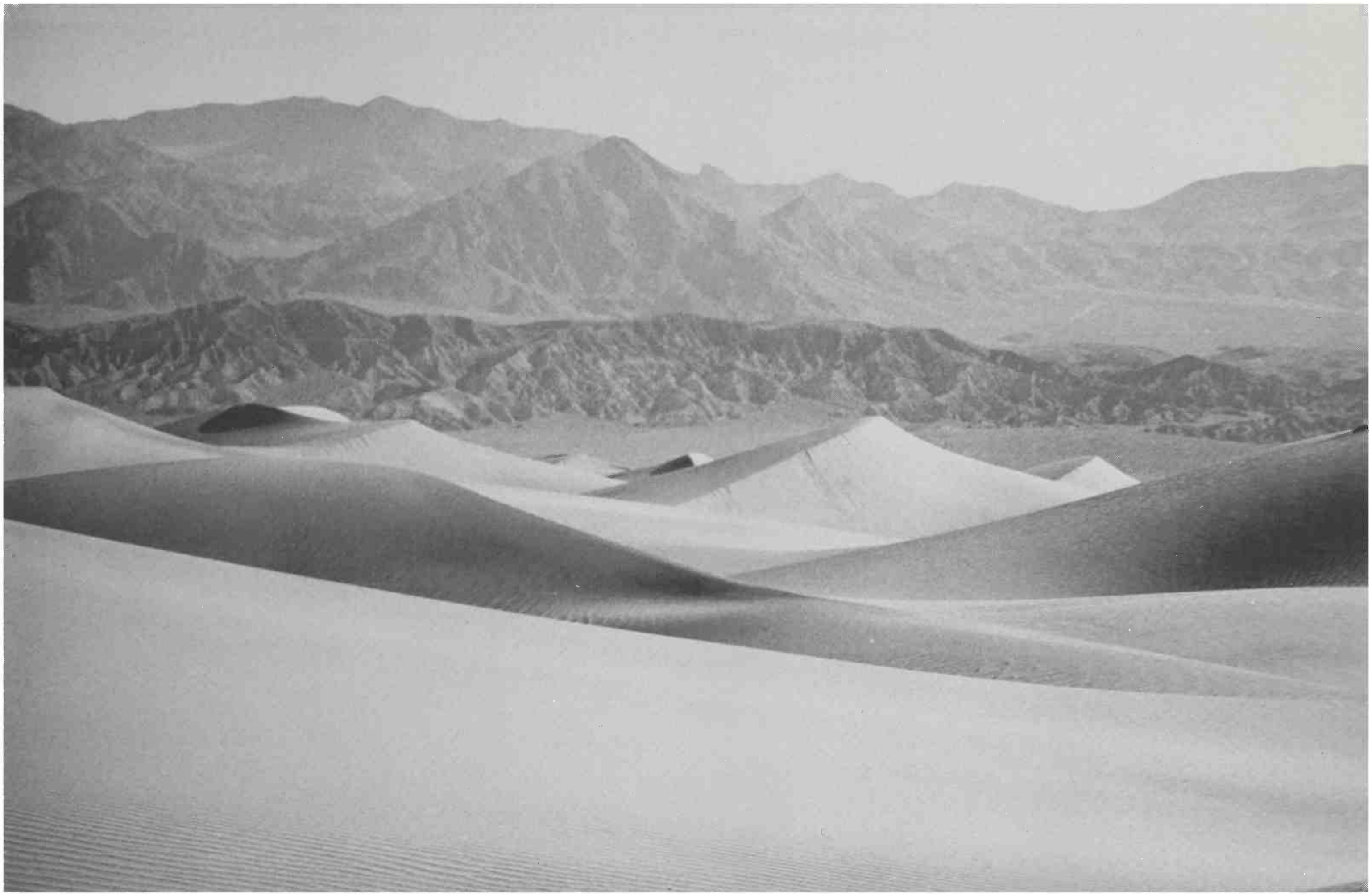

Figure 5. *Much of the Death Valley dune field is too active for plants to gain a foothold. Photo by Janice E. Bowers.*

High rates of endemism may be due both to adaptation of plants to moving sand and to various dispersal factors, which will be discussed later.

At the Coral Pink Dunes, White Sands and the two Guadalupe dune fields, geographic components distributed mostly in colder and wetter regions — Plains, Rocky Mountain and Western Montane — are important (Table 2; see also Burgess & Northington, 1977; Sherwood & Risser, 1980). This is most likely due to the favorable moisture relations of dune sand. Since active sand is moist and cool just 10-15 cm below the surface even in the hottest and driest months, non-desert plants such as *Arctostaphylos patula* Greene, *Quercus gambelii* Nutt., *Populus angustifolia* James, *Tradescantia occidentalis* (Britt.) Smyth, *Rhus trilobata* Nutt. and *Cyperus schweinitzii* Torr. can become established and thrive, at least on stabilized dunes.

Similarity of Southwestern Dune Floras. - The distinctive geographic composition of eight dune floras that was revealed by the floristic analysis is also demonstrated by the similarity analysis. Of the 28 pairs of dune floras studied, only seven have a similarity value above 0.200 (Table 3). This indicates that most of the 28 pairs are very dissimilar, since the lower the similarity values, the less similar are the floras. This lack of similarity is due in part to the distribution of the eight dune fields among four floristically distinct biogeographic provinces: the Mohavean, Sonoran, Chihuahuan and Great Basin deserts (Fig. 1). The three pairs with the greatest similarity — Algodones/Gran Desierto, White Sands/Guadalupe gypsum and Guadalupe gypsum/Guadalupe quartz — each lie within a single biogeographic province.

Similarity and distance are poorly correlated. Dune fields farther than 400 km apart are more or less equally dissimilar regardless of distance, and dune fields less than 400 km apart range in similarity values from 0.050 to 0.512. Clearly there is not a simple, linear relationship between similarity and distance (Fig. 2).

One possible reason for the lack of similarity between southwestern dune floras may be that recruitment of plants from non-dune plant communities is highly localized. Examination of plant lists for various dune fields confirms this hypothesis. Of the 55 species at the Kelso Dunes with Mohavean or Sonoran-Mohavean affinities, 24 occur in one or more of the other dune floras studied. The remaining 31 species occur at the Kelso Dunes alone. For example, *Chrysothamnus paniculatus* (Gray) Hall is one of the latter group. It occurs locally across the Mohave Desert (Munz & Keck, 1968), and neither its presence on the Kelso Dunes nor its absence from the other seven dune fields is surprising. This type of localized recruitment, when repeated on dune fields throughout the Southwest, is in large part responsible for the dissimilarity of southwestern dune floras. Localized recruitment masks the similarities between dune floras, making them appear to have less in common than they in fact have, as will be discussed later.

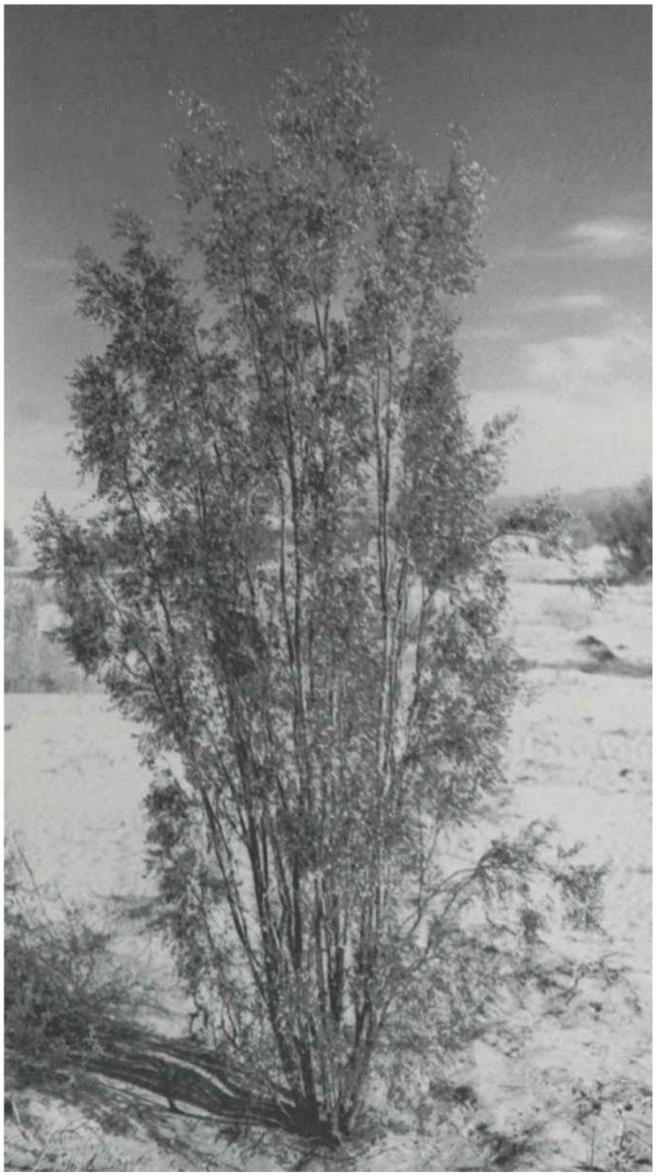

Figure 6. *Larrea tridentata var. arenaria on the Algodones Dunes differs from the typical variety in its upright habit, long branches, and drooping clusters of twigs and leaves. Photo by Steven P. McLaughlin.*

Barriers to dispersal and establishment also promote high dissimilarity among southwestern sand dune floras. The gypsum sand of the Guadalupe gypsum and White Sands dune fields is a formidable edaphic barrier to plant establishment. The intolerance of many plants to gypsum is well-documented (Waterfall, 1946; Powell & Turner, 1977) and may in part account for the low similarities of dune pairs such as Coral Pink Dunes/White Sands, White Sands/Eureka Dunes and Coral Pink Dunes/Guadalupe gypsum dunes. Salinity may also promote dissimilarity. The dunes in Death Valley support halophytes such as *Allenrolfea occidentalis* (Wats.) Kuntze, *Suaeda torreyana* Wats. and *Distichlis spicata* (L.) Greene (Hunt & Durrell, 1966), none of which occur on the eight dune fields studied.

The relatively brief period of time involved in speciation and species migration may also explain in part the dissimilarity of southwestern dune floras. Some narrowly endemic dune plants, that is, species which are known from only one dune field, may have evolved since dune formation in the Pleistocene. Such plants, including *Wyethia scabra* var. *attenuata* W. A. Weber, *Palafoxia arida* var. *gigantea, Oenothera avita* W. Klein ssp. *eurekensis* (Munz) Klein, *Asclepias welshii* Holmgren & Holmgren and *Astragalus lentiginosus* Dougl. var. *micans* Barneby, may not yet have had enough time to disperse to other dune fields.

Table 2. Geographic composition (%) of eight southwestern dune floras.

	Kelso	Gran Desierto	Algodones	Coral Pink	White Sands	Eureka	Guadalupe Quartz	Guadalupe Gypsum
Mohavean	15	1	3	-	-	16	-	-
Sonoran	3	17	14	-	-	-	-	-
Sonoran-Mohavean	36	31	37	4	-	26	-	-
Intermountain	3	-	-	15	2	11	-	-
Chihuahuan	-	1	1	1	26	-	31	24
Southwestern	23	20	15	1	13	16	20	16
Plains	3	-	2	11	15	-	30	16
Rocky Mountain	-	-	-	15	8	-	2	8
Western Montane	-	-	-	13	-	-	-	-
Western North America	3	4	1	8	13	8	5	3
Temperate	2	-	1	8	3	-	-	3
Introduced-Cosmopolitan	2	4	5	8	2	3	2	-
Latin American	-	1	2	-	7	3	3	-
Endemic-Sand	10	20	18	15	5	18	8	8
Endemic-Gypsum	-	-	-	-	7	-	-	24
Total number of species	107	75	97	53	61	38	64	38

Table 3. Similarity indices for eight southwestern dune floras.

	Kelso	Gran Desierto	Algodones	Coral Pink	White Sands	Eureka	Guadalupe Quartz
Gran Desierto	0.308						
Algodones	0.324	0.512					
Coral Pink	0.050	0	0.013				
White Sands	0.012	0.044	0.025	0.123			
Eureka	0.207	0.124	0.133	0.088	0.061		
Guadalupe Quartz	0.047	0.086	0.050	0.068	0.240	0.078	
Guadalupe Gypsum	0.014	0	0	0.066	0.364	0.026	0.353

Geographic isolation has also played a role in maintaining dissimilarity between southwestern dune floras. The Eureka Dunes are very dissimilar to every other dune flora, with similarity values ranging from 0.026 to 0.207 (Table 3). The Eureka Dunes are located at the south end of a narrow valley that is surrounded by high mountain ranges. Evidently the three taxa endemic to the Eureka Dunes have not been able to surmount this barrier, since they have not spread to dune fields in nearby valleys.

Characteristic Dune Species. - To discover whether or not there is a group of plants characteristic of sand dunes in the Southwest, I examined the list of all 533 species comprising the eight dune floras. First, I decided that any plant occurring in three or more of the floras could be considered characteristic of dunes, and that dune endemics are by definition also characteristic of sand dunes. I found that 83 species (Group 1) are either endemic to sand dunes or occur in three or more of the eight floras. The remaining 450 species (Group 2) occur in only one or two of the eight dune floras and cannot be con-

Figure 7. *Swallenia alexandrae is endemic to the Eureka Dunes, where it flourishes on active sand. Photo by Steven P. McLaughlin.*

sidered characteristic of southwestern sand dunes. Of the 83 species in Group 1, 43 are dune endemics; they are obligate psammophiles and are restricted to active sand. The remaining 50 species are facultative psammophiles which have been recruited from the surrounding flora, for the most part.

The species in Group 1 fall naturally into two subgroups —36 species in an eastern group comprising the Guadalupe gypsum, Guadalupe quartz, White Sands and Coral Pink dune fields, and 57 species in a western group comprising the Kelso, Eureka, Gran Desierto and Algodones dune fields (Tables 4a & 4b). The eastern dune flora shares many species in common with the floras of sand hills of the Great Plains (Table 4a), including *Andropogon hallii* Hack., *Artemisia filifolia* Torr., *Erigeron bellidiastrum* Nutt. and *Heliotropium convolvulaceum* (Nutt.) Gray. With the exception of narrow endemics, these are plants which could be expected on any southwestern dune field east of about 113° Longitude. The western dune flora is characterized by a greater development of narrow endemics than is the eastern dune flora (Table 4b), but the majority of species in the western group could be found on any southwestern dune field west of about 113° Longitude.

Only 10 species are shared by the eastern and western dune floras, giving a similarity value of 0.108 for the two groups. One reason for the sharp separation of the southwestern dune flora into two distinct groups may be climate. Dunes in the eastern group occur in summer rainfall areas, while those in the western group lie in predominantly winter rainfall areas.

The 440 species in Group 2 are all facultative psammophiles. They are the reservoir from which the preponderance of each dune flora (75-95%) is recruited. Most are distributed in only one of the four North American deserts.

Sand Dunes as Island Habitats. - Although southwestern dune fields are habitat islands in a sea of desert, dune floras do not behave in all respects as predicted for insular biotas by MacArthur and Wilson (1967). The analogy between true islands and dunes as islands is not perfect. True islands are separated from mainland sources of colonizing propagules by expanses of uninhabitable ocean, but dunes are immersed in the mainland from which their biota is derived. However, the parallel between dunes and oceanic islands is no weaker than that between vacant urban lots and islands (Crowe, 1979) or insects on thistle patches and islands (Brown & Kodric-Brown, 1977). It is impossible to define a sandy mainland which is the source of colonizing propagules for dune islands in the same sense that continental mainlands are the sources of propagules for oceanic islands. Since the actual source of colonizing propagules on dunes is the surrounding, non-dune desert, this desert has been assigned the role of mainland for purposes of the following discussion.

According to the theory of island biogeography as it has been applied to island habitats on continents (Harper et al., 1978; Crowe, 1979; Carter-Lovejoy, 1982), insular floras should have:

1) Steeper species-area curves than mainland floras,

Figure 8. *Wyethia scabra var. attenuata growing normally on the Coral Pink Dunes. Photo by Janice E. Bowers.*

Figure 9. *Wyethia scabra var. attenuata continuing to grow through an advancing dune. Photo by Janice E. Bowers.*

Figure 10. *Roots of Croton wigginsii on the Algodones Dunes function as underground vines, providing anchorage in a mobile substrate. Photo by Janice E. Bowers.*

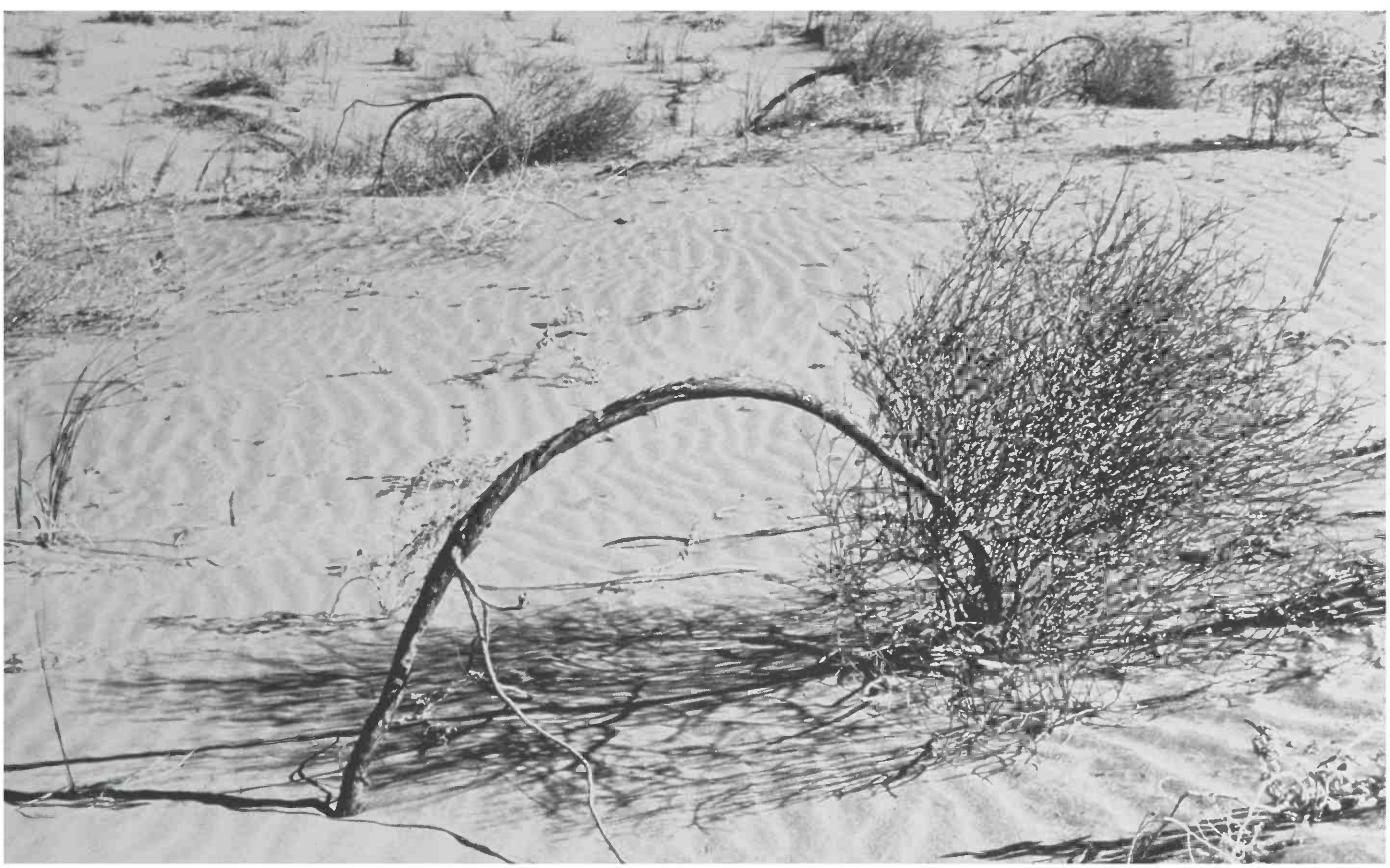

Figure 11. *Stems of Eriogonum deserticola at the Algodones Dunes take on bizarre shapes when buried by moving sand. Photo by Janice E. Bowers.*

Figure 12. *Hilaria rigida is common on stable dunes in the Mojave and Sonoran deserts. Photo by Steven P. McLaughlin.*

2) Fewer species per unit area than mainland floras,
3) An inverse relationship between species richness and distance from the mainland,
4) Higher rates of endemism than mainland floras.

Of these four hypotheses, two seem to fit dune islands in the Southwest. Levels of endemism on dunes are appreciably higher than on non-dune desert habitats (i.e., the mainland) of comparable size, as discussed earlier, and dune floras appear to have fewer species per unit area than non-dune floras. I will discuss each of these hypotheses in turn.

The log-log relationship between the number of species on southwestern dune fields and their areas (Fig. 3) is only weakly statistically significant ($r^2 = 0.56$, $p < 0.10$), in part because of the small sample size. However, it is still worthwhile to discuss the curve in the light of the MacArthur and Wilson model. The slope of the curve, 0.16, is within the range predicted for mainland floras (0.12-0.17), and below that observed on islands (0.20-0.35) (Harper et al., 1978). Gilbert (1980) observed that slopes of regressions obtained for species-area curves from continental islands are frequently lower than those from oceanic islands. Non-dune desert floras in the Southwest also have a slope close to the range predicted for mainland floras (0.18) (Fig. 3). This relationship is highly statistically significant ($r^2 = 0.62$, $p < 0.01$). In Arizona, deserts are poor in plant species relative to community types such as Madrean evergreen woodland and desert grassland, since low beta diversity across large expanses of desert masks the input from localized communities with high diversity (Bowers & McLaughlin, 1982). Similarly, on dune fields wide expanses of barren or nearly barren sand reduce the significance of the input from localized areas where plants are more abundant.

Dune floras have a lower number of species per unit area than non-dune floras (Fig. 3). The range for number of species/km^2 among ten desert floras is 0.045-11.667 and among seven dune floras, 0.086-4.750. (The Gran Desierto was omitted from this analysis due to its disproportionate size.) As expected, the number of species per unit area is high for small areas and declines as area increases, both for dune and non-dune areas. One explanation for the lower values on dunes is lack of habitat diversity. Non-dune habitats support more species per unit area because the greater variety of habitats provides suitable conditions for more species. In addition, only a handful of species can occupy the large areas of active sand that comprise a substantial proportion of many southwestern dune fields.

The hypothesis that number of species should decrease with increasing distance from the mainland is difficult to test on southwestern dunes, where no clearly defined mainland exists. Crowe (1979), facing a similar problem when dealing with weeds on vacant lots in Chicago, explored the relationship between species number and distance from the nearest source of propagules. However, among the eight dune floras studied, there is no significant relationship between number of species on a dune field and distance to the nearest of the

Figure 13. *Asclepias welshii is endemic to the Coral Pink Dunes. Photo by Janice E. Bowers.*

Figure 14. *Helianthus niveus (typically of coastal dunes) is represented on inland dunes by subspecies tephrodes, pictured here on the Algodones Dunes. Photo by Janice E. Bowers.*

Figure 15. *Panicum urvilleanum survives on active sand at the Algodones Dunes by means of rapid growth from deep-seated rhizomes.*

eight. This is not surprising, since 75-95% of the species on dune fields are desert mainland species; that is, they are not restricted to dunes and should not be distributed in accordance with dune distribution. Nor is the number of sand dune endemics on a given dune field significantly related to the distance to the nearest dune field. Turner and Powell (1979), studying endemism on gypsum outcrops from Mexico to Montana, found that number of endemic species was related not to distance from a hypothetical source area but rather to time. Gypsum outcrops in Mexico had been exposed longer than those in Montana, and therefore more time had been available for the evolution of gypsum endemics on the southern outcrops than on the northern. A similar phenomenon may be operating on dunes: the number of narrow endemics on a dune field may well be related to its age. This is a problem which has received little study and deserves further attention.

In sum, dune floras fit some of the characteristics of insular floras predicted by the MacArthur and Wilson model. Although dune floras do exhibit higher rates of endemism than non-dune floras of comparable extent and have fewer species per unit area than mainland floras, the species-area curves of dune floras do not show steeper slopes than those for non-dune mainland floras, and dune floras do not show an inverse relationship between species richness and distance from the nearest source of propagules. Dunes are habitat islands, but since 75-95% of the flora of a given dune field is drawn from the desert mainland species pool, dunes are not floristic islands.

What other attributes of island biotas do dune floras possess? Carlquist (1974) discusses 24 principles of dispersal and evolution for island biotas. Some of those which seem to describe dune floras, particularly the endemic dune flora, are:

1) The size and species composition of insular biotas are determined by a variety of factors which differ in relative importance from one island to another.
2) Immigrants to island biotas evolve rapidly after arrival.
3) Plants on oceanic islands evolve new growth forms, with a particular tendency toward increased stature.
4) Competitive ability among insular endemics is often reduced.

I will discuss each of these principles and its applicability to dune floras in turn.

The size and species composition of dune floras is determined by a variety of factors. These include location of the dune field with respect to regional biogeographic provinces, climate, age of the dune field, proportions of stabilized and active sand and, perhaps, area.

Rapid evolution at the subspecific level has occurred in many dune taxa, presumably since dune formation in the Pleistocene. Barneby (1964) suggested that eustatic sea level changes during the Pleistocene separated the progenitor of *Astragalus magdalenae* Greene var. *peirsonii* (Munz & Barneby) Barneby into coastal and inland dune populations. The populations evolved *in situ*, producing a coastal dune endemic —*Astragalus magdalenae* var. *niveus (Rydb.)* Barneby—and an

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(continued from page 42)

inland dune endemic — *Astragalus magdalenae* var. *peirsonii.* A similar mechanism may account for the existence of other coastal/inland dune species pairs, notably *Croton californicus* Muell. Arg./*Croton wigginsii* Wheeler, *Helianthus niveus* (Benth.) Brandegee ssp. *niveus/Helianthus niveus* ssp. *tephrodes* (Gray) Heiser and *Palafoxia linearis* (Cav.) Lag./*Palafoxia arida* var. *gigantea.* It is worth noting in passing that many dune endemics belong to aggressive, genetically plastic families such as the Compositae, Gramineae and Leguminosae (Bowers, 1982).

This is not meant to suggest that all sand dune endemics evolved during and since the Pleistocene. It seems likely that some evolved earlier on riverine dunes or on dunes adjacent to large inland lakes. *Swallenia alexandrae*, a grass genus endemic to the Eureka Dunes, is most closely related to halophytic genera such as *Distichlis, Jouvea* and *Monanthochloe* (Soderstrom & Decker, 1963), a fact which argues for an origin along the margin of an inland lake.

Increased stature of dune plants takes two forms. The first is gigantism, noted on dunes for *Larrea tridentata* (Moc. & Sesse) Cov. ssp. *arenaria* L. Benson (Felger, 1980; Benson & Darrow, 1981), *Petalonyx thurberi* Gray (Felger, 1980), *Atriplex canescens* (Pursh) Nutt. (Stutz et al., 1975) and others. Gigantism in dune plants may be an adaptation permitting the plants to grow quickly enough to outstrip sand accumulation and may also reflect the favorable moisture conditions of active sand (Bowers, 1982). The second form of increased stature seen in dune plants is woodiness in usually herbaceous taxa. Carlquist (1974) suggested that insular woodiness is due to several factors, including release from seasonality, absence of large vertebrate herbivores and shifts in ecological preference due to presence of unoccupied niches. On southwestern dunes, insular woodiness is seen in *Helianthus niveus* ssp. *tephrodes, Astragalus magdalenae* var. *peirsonii, Wyethia scabra* var. *attenuata* and *Palafoxia arida* var. *gigantea.*

Competitive ability in dune plants has not been studied. However, the absence of dune-adapted plants from non-dune habitats implies that such plants are unable to compete in non-dune environments. Root systems of some dune endemics have evolved to maximize anchorage rather than water uptake. The roots of such plants are vine-like and probably lack sufficient surface area to compete for water with fibrous-rooted non-dune plants in fine-textured desert soils.

Although Carlquist (1974) found that dispersal patterns in insular floras were different from those in mainland floras —including loss of dispersibility in taxa which are adapted for long-distance dispersal on the mainland — I have not been able to find similar patterns in dune floras. Seeds of most perennial dune endemics disperse only a short distance away from the parent plant, but this does not constitute evidence for loss of dispersibility. These species are more likely to be perpetuated by seeds which remain in the habitat to which they are best adapted (Bowers, 1982). Seeds of some dune endemics are adapted for long-distance dispersal by wings — *Dicoria canescens* T. & G., *Abronia crux-maltae* Kell., *Abronia villosa* Wats. — or by parachute-like pappuses — *Chaetadelpha wheeleri* Gray, *Senecio riddellii* T. & G., *Erigeron bellidiastrum.* As one would expect, such species occur on several dune fields.

Whether dunes are islands in the sense of MacArthur and Wilson (1967) or Carlquist (1974) remains unresolved since dune floras display characteristics of both insular and mainland floras. Dune floras could develop additional insular characteristics with increasing age. As they stand now, full expression of insular qualities has been impeded by close ties with the desert mainland.

Conclusions

The floristic composition of southwestern sand dune floras is strongly influenced by the regional flora in which each dune field occurs. Species characteristic of the Mohave Desert are important in Mohave Desert dune fields, those of the Chihuahuan Desert in Chihuahuan Desert dune fields, etc. Each dune flora is highly individualistic in its geographic composition, and can be characterized by three to five geographic components.

Endemic species comprise a much higher proportion of dune than of non-dune floras in southwestern deserts; this is due to adaptation of plants to the dune environment and to other factors such as isolation.

With few exceptions, southwestern dune floras are dissimilar in species composition. Possible reasons for this dissimilarity are the distribution of dune fields among the four North American deserts; localized recruitment of species from adjacent, non-dune habitats; the recent formation of southwestern dune fields; and edaphic barriers to establishment.

Over 500 species of vascular plants occur on the eight dune fields studied. Eighty-three species were found to occur on three or more of the eight dune fields or to be endemic to sand dunes. These plants fell naturally into an eastern dune flora of 36 species which is characteristic of southwestern sand dunes east of 113° Longitude and a western dune flora of 57 species which is characteristic of southwestern sand dunes west of 113° Longitude.

The evidence for dunes as island-like enclaves is contradictory. In some ways — higher rates of endemism, fewer species per unit area, rapid evolution of dune-adapted taxa and development of insular woodiness — sand dune floras resemble those of oceanic islands. In other ways, dune floras are practically indistinguishable from the surrounding mainland floras from which they are evolving.

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Appendix 1. Geographic components of eight Southwestern dune floras.

Mohavean — Mainly within the Mohave Desert in southern California, southern Nevada, northwestern Arizona and southwestern Utah; includes species such as *Psorothamnus polyadenius* (Torr. ex Wats.) Rydb., *Chrysothamnus paniculatus* and *Brickellia incana* Gray.

Table 4a. Plants characteristic of southwestern sand dunes east of 113° Longitude.

	Guadalupe Quartz	Guadalupe Gypsum	White Sands	Coral Pink	Samalayuca (Jaeger, 1957)	Little Sahara (Sherwood & Risser, 1980)	Northeastern Colorado (Ramaley, 1939)	Sand Hills State Park (Warnock, 1974)
**Andropogon hallii* Hack.		x				x	x	
**Artemisia filifolia* Torr.	x			x	x	x		x
***Asclepias welshii* Holmgren & Holmgren				x				
**Astragalus striatiflorus* M. E. Jones				x				
Atriplex canescens (Pursh) Nutt.	x		x		x		x	
Bouteloua barbata Lag.	x		x					
**Calamovilfa gigantea* (Nutt.) Scribn & Merr.				x		x		x
Dalea lanata Spreng. var. *terminalis* (Jones) Barneby	x	x				x	x	x
Dithyrea wislizenii Engelm.	x	x	x			x		x
Ephedra torreyana Wats	x	x	x		x			
Ephedra trifurca Torr.	x							
**Erigeron bellidiastrum* Nutt.	x					x	x	
Eriogonum inflatum Torr & Frem.				x				
**Heliotropium convolvulaceum* (Nutt.) Gray						x	x	x
Lycium berlandieri Dunal	x	x	x					
**Muhlenbergia pungens* Thurb.			x	x			x	
Oenothera pallida Lindl. ssp. *runcinata* (Engelm.) Munz & Klein	x	x	x	x		x		
Oryzopsis hymenoides (Roem & Schult.) Rick.	x	x	x	x			x	
Pectis papposa Harv. & Gray	x							
**Petalostemum compactum* (Spreng.) Swezey	x						x	
**Poliomintha incana* (Torr.) Gray	x	x	x		x			x
Prosopis glandulosa Torr. var. *torreyana* (Benson) M. C. Johnst.	x			x				x
**Psorothamnus scoparius* (Gray) Rydb.	x	x		x				x
**Redfieldia flexuosa* (Thurb.) Vasey				x		x	x	
**Reverchonia arenaria* Gray			x		x			
Rhus trilobata Nutt.			x	x	x	x	x	
Salsola kali L.				x		x	x	
**Senecio riddellii* Torr. & Gray			x			x	x	
Sphaeralcea ambigua Gray				x				
Sporobolus cryptandrus (Torr.) Gray	x	x	x		x			
Sporobolus flexuosus (Thurb.) Rydb.	x	x	x					x
Sporobolus giganteus Nash.	x	x	x			x		x
Thelesperma megapotamicum (Spreng.) Kuntze		x	x		x			
Tidestromia lanuginosa (Nutt.) Standl.	x		x					
***Wyethia scabra* Hook. var. *attenuata* W. A. Weber				x				
Yucca elata Engelm.	x	x	x		x			

*Dune endemic

**Narrow dune endemic

Sonoran — Mainly within the Sonoran Desert and including the Colorado Desert along the Lower Colorado River Valley; in southern Arizona, southeastern California, northern Sonora and Baja California; includes species such as *Olneya tesota* Gray, *Cercidium floridum* Benth. and *Brandegea bigelovii* (Wats.) Cogn.

Sonoran-Mohavean — Occurring locally in or throughout both deserts; includes species such as *Encelia farinosa* Gray, *Atriplex polycarpa* (Torr.) Wats. and *Asclepias subulata* Decne.

Intermountain — Mainly in the Great Basin Desert between the Sierra Nevada to the west and the Rocky Mountains to the east; in Nevada, Utah, northern Arizona and southeastern Idaho; includes species such as *Juniperus osteosperma* (Torr.) Little, *Artemisia tridentata* Nutt. and *Abronia turbinata* Torr.

Chihuahuan — Mainly within the Chihuahuan Desert from western Texas to Arizona and in northeastern and north-central Mexico; includes species such as *Croton dioicus* Cav., *Maurandya wislizenii* Engelm. and *Bahia absinthifolia* Benth.

Southwestern — At lower elevations locally or throughout the greater Southwest; in Utah, Nevada, Colorado, New Mexico, west Texas, Arizona, southern California and northern Mexico; includes most species which occur in two or more of the first five categories, such as *Opuntia leptocaulis* DC., *Ephedra viridis* Cov. and *Acacia greggii* Gray.

Plains — Mainly within but not restricted to the Plains states east of the Rocky Mountains: eastern Idaho, eastern Colorado, Nebraska, Kansas, North and South Dakota, Oklahoma, Texas panhandle and eastern New Mexico; includes species such as *Bouteloua gracilis* (H.B.K.) Lag.,

Table 4b. Plants characteristic of southwestern sand dunes west of 113° Longitude.

	Gran Desierto	Algodones	Kelso	Eureka	Salton Sea (Rempel, 1936)
*Abronia villosa Wats. var. villosa	x	x	x		
Ambrosia dumosa (Gray) Payne	x	x	x		x
*Ammobroma sonorae Torr.	x	x			
*Astragalus insularis Kell. var. harwoodii Munz & McBurney	x				
*Astragalus lentiginosus Dougl. var. borreganus Jones		x	x		
**Astragalus lentiginosus Dougl. var. micans Barneby				x	
*Astragalus magdalenae Greene var. peirsonii (Munz & Barn.) Barneby		x			
Atriplex canescens (Pursh) Nutt.	x				x
Baileya pleniradiata Harv. & Gray	x	x	x	x	
Bouteloua barbata Lag.	x	x		x	x
Camissonia boothii (Dougl.) Raven ssp. condensata (Munz) Raven	x	x	x		
*Camissonia claviformis (Torr. & Frem.) Raven ssp. yumae (Raven) Raven	x	x			
*Chaetadelpha wheeleri				x	
*Chamaesyce ocellata (Dur. & Hilg.) ssp. arenicola (Parish) Thorne			x	x	
*Chamaesyce platysperma (Engelm.) Shinners	x				
Chorizanthe brevicornu Torr. ssp. brevicornu	x	x	x		
Chorizanthe rigida (Torr.) Torr. & Gray		x	x	x	
*Croton californicus Muell. Arg. var. mohavensis Ferg.			x		
*Croton wigginsii Wheeler	x	x			
Cryptantha angustifolia (Torr.) Greene	x	x	x		
Cucurbita palmata Wats.	x	x	x		
Dalea mollis Benth.	x	x	x		x
*Dicoria canescens Torr. & Gray ssp. canescens	x	x	x		
*Dicoria canescens Torr. & Gray ssp. clarkae (Kenn.) Keck		x		x	
*Dimorphocarpa pinnatifida Rollins	x				
Ephedra trifurca Torr.	x	x			
*Eriogonum deserticola Wats.	x	x			x
Eriogonum inflatum Torr. & Frem.		x	x	x	
Geraea canescens Torr. & Gray	x	x	x		x
*Helianthus niveus (Benth.) Brandegee ssp. tephrodes (Gray) Heiser	x	x			
*Heliotropium convolvulaceum (Nutt.) Gray			x		
Hesperocallis undulata Gray	x	x	x		x
*Hilaria rigida (Thurb.) Benth.	x	x	x		
*Larrea tridentata (Moc. & Sesse) Cov. ssp. arenaria L. Benson		x			
Larrea tridentata (Moc. & Sesse) Cov. ssp. tridentata	x		x	x	x
*Lupinus shockleyi (Wats.)			x	x	
*Machaeranthera leucanthemifolia (Greene) Greene			x		
Mentzelia multiflora Gray ssp. longiloba (Darl.) Thompson & Zavortink	x	x	x		
**Oenothera avita W. Klein ssp. eurekensis (Munz) Klein				x	
Oenothera deltoides Torr. & Frem. ssp. deltoides	x	x	x		x
Oryzopsis hymenoides (Roem. & Schult.) Rick.				x	x
Palafoxia arida Turner & Morris var. arida	x	x	x	x	x
**Palafoxia arida Turner & Morris var. gigantea (Jones) Turner & Morris		x			
*Panicum urvilleanum Kunth.		x	x		
Pectis papposa Harv. & Gray	x	x	x	x	
Petalonyx thurberi Gray ssp. thurberi	x	x	x		
Plantago insularis Eastw. var. fastigiata (Morris) Jeps.	x	x	x		
Prosopis glandulosa Torr. var. torreyana (Benson) M.C. Johnst.	x	x			
*Psorothamnus emoryi (Gray) Rydb.	x	x			x
Salsola kali L.			x	x	
Sphaeralcea ambigua Gray			x	x	
*Stillingia spinulosa Torr.	x	x	x		
**Swallenia alexandrae (Swallen) Soderstrom & Decker				x	
Tidestromia lanuginosa (Nutt.) Standl.	x				
*Tiquilia palmeri (Gray) Richards.	x	x			x
Tiquilia plicata (Torr.) Richards.	x	x	x	x	
*Triteliopsis palmeri (Wats.) Hoover	x				

*Dune endemic
**Narrow dune endemic

Penstemon ambiguus Torr. and *Munroa squarrosa* (Nutt.) Torr.

Rocky Mountain — At higher elevations in the Rocky Mountains and outlying ranges east of the Sierra Nevada-Cascade chain; includes species such as *Eriogonum alatum* Torr., *Populus angustifolia* and *Quercus gambelii.*

Western Montane — At higher elevations in the Sierra Nevada, Rocky Mountains and outlying ranges throughout the western states and provinces; includes species such as *Arctostaphylos patula, Cryptantha fendleri* (Gray) Greene and *Castilleja linearifolia* Benth.

Western North America — Throughout the western states and provinces, mainly from the 100th meridian west; includes species such as *Atriplex canescens, Helianthus annuus* L. and *Pinus ponderosa* Lawson.

Temperate - Mainly throughout the cooler, moister states and provinces in North America; includes species such as *Andropogon scoparius* Michx., *Salix bebbiana* Sarg. and *Cyperus schweinitzii.*

Introduced-Cosmopolitan — Not native to North America, or widespread throughout the northern or western hemispheres; includes species such as *Salsola kali* L., *Tamarix aphylla* (L.) Karst. and *Bromus tectorum* L.

Latin American — In the southern tier of states and continuously or disjunctly into Central or South America; includes species such as *Aristida adscensionis* L., *Solanum elaeagnifolium* Cav. and *Panicum hirticaule* Presl.

Sand Dune Endemics — Restricted to active or stabilized dunes, occasionally occurring on sandy soil; includes species found on several dune fields, e.g., *Psorothamnus emoryi* and *Eriogonum deserticola*, as well as those known from only one, e.g., *Wyethia scabra* var. *attenuata* and *Asclepias welshii.*

Gypsum Endemics — Restricted to gypsum outcrops or gypsum sand; also occurring on gypsiferous soils; includes species such as *Bouteloua breviseta* Vasey, *Nama carnosum* (Woot.) C.L. Hitchc. and *Nerisyrenia linearifolia* (Wats.) Greene.

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