Ecology of Sonoran Desert Plants and Plant Communities

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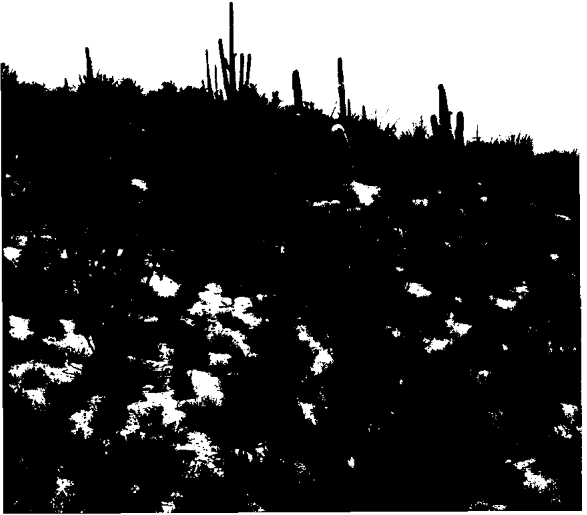

2 Vegetation and Habitat Diversity at the Southern Edge of the Sonoran Desert

Alberto Búrquez, Angelina Martínez-Yrízar, Richard S. Felger, and David Yetman

More than one third of Forrest Shreve's (1951) Sonoran Desert lies within the boundaries of Sonora, the second largest state in Mexico. Five of the seven major vegetational subdivisions of the Sonoran Desert are found within Sonora as well, more than in any other state. It is safe to say that the specific biological diversity found in the Sonoran portion of the Sonoran Desert is greater than in any other desert in the world.

This abundance and diversity of species are due in large part to the extensive variation in topography and the degree of continentality that occur within the desert's boundaries; these combine to create a complex mosaic of plant associations influenced by different climatic and edaphic conditions. At its northeastern and eastern limits, the Sonoran Desert is variously replaced by Chihuahuan desertscrub, grasslands, and oak woodlands. To the northwest lies the drier and less varied Mojave Desert. Along the northern boundary extends a broad band of chaparral. To the east lies the Sierra Madre, to the west the Sea of Cortez and the Pacific Ocean. In the south the desert merges with thornscrub and tropical deciduous forest, which make the southern region of the Sonoran Desert rich in tropical elements.

The major features of the southern portion of the Sonoran Desert are (1) the islands of the Gulf of California, where maritime influence and isolation have fostered biological endemism; (2) the extensive xeric plains along the coast of the Gulf of California; (3) the once-forested river deltas and river basins, both now nearly devoid of vegetation due to reductions in stream flow; (4) the more mesic hills, canyons, and small sierras within the desert; and (5) the low-elevation escarpments and foothills of the western slope of the Sierra Madre.

In this chapter we review the relationships between physical environment, habitat diversity, vegetation structure, and ecosystem dynamics in the central and southern desert regions of Sonora, which produce a remarkable richness of biological diversity.

Physical Environment

Climate

The Sonoran Desert has the highest temperatures and the lowest precipitation in North America (Schmidt 1989; Turner et al. 1995). The climate is characterized by very hot summers, mild winters, large day/night temperature variations, high levels of sunshine, and highly variable annual rainfall of bimodal distribution with peaks in summer and winter. Temperature and precipitation also vary markedly depending on elevation and the relative importance of continental or coastal influence.

Because of this climatic variability, rainfall is better described by fitting the data to gamma distributions than by calculating the arithmetic means (unfortunately, most of the available data are averaged; Mosiño and García 1981; Ezcurra and Rodríguez 1986). Extended rainless periods occur on the plains along the Gulf Coast northward from the Río Sonora delta. May (1973) recorded 34 consecutive months with no precipitation in the Gran Desierto. The reported mean of 9.6 rainless months/year for Bahía Magdalena in Baja California Sur (Schmidt 1989) does not show the large interannual variability.

Much of the rain in the Sonoran Desert is produced by thunderstorms during the "monsoon" season of July to early September. Generally localized, these storms are often accompanied by strong winds and flash flooding. Most of the remaining precipitation occurs during the winter and early spring in the form of gentle and more widespread rains. Rainfall totals generally increase from west to east. Summer rains contribute more than half the annual precipitation in the eastern portion of the desert, decreasing in percentage as one moves west (fig. 2.1). Mean annual rainfall in the Sonoran Desert ranges from less than 30 mm near the Colorado River delta to more than 350 mm at the eastern desert margin (Hastings and Turner 1965; Hastings and Humphrey 1969; García 1973; Schmidt 1989). Rainfall normally begins in the southeastern portion of the desert in late

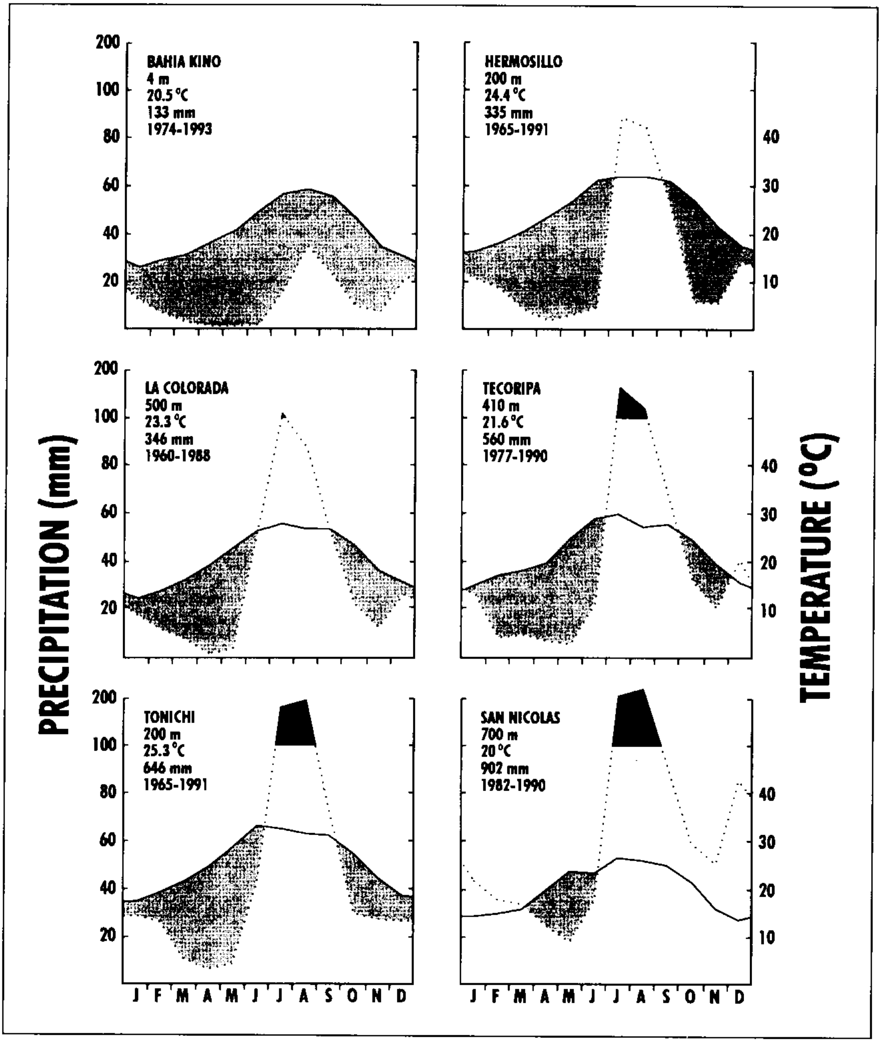

Figure 2.1 Ombrothermal climograms for selected localities along Highway 16, Sonora, Mexico. Solid line = mean monthly temperature, dotted line = monthly precipitation. Values were recalculated from Comisión Nacional del Agua data, accounting for missing values of precipitation and temperature. The values on the upper left corner on each diagram indicate locality, elevation, mean annual temperature, mean annual precipation, and period of observation. The gray areas indicate periods of water deficit and the black areas, water surplus. Localities are arranged from west to east.

June (traditionally on June 24, "el día de San Juan"), while in the western portion, rains seldom begin until well into July. Rainfall is more reliable in the southeastern Sonoran Desert than in the northwestern part. In general, then, rainfall totals and seasonality form a southeast-to-northwest gradient in the region.

Temperatures exhibit a similar trend, with the greatest extremes occurring in northwestern Sonora, where summer highs frequently exceed 49°C and winter lows occasionally fall below freezing. The southern limit of periodic, damaging freezes establishes the northern limits of many Sonoran Desert plant species (Shreve 1914, 1951; Hastings and Turner 1965; Steenbergh and Lowe 1977; Bowers 1980; Felger and Moser 1985; Turner et al. 1995). Perhaps once a decade, cold air masses blast down through the Great Basin into the Sonoran Desert, with catastrophic results for tropical outliers and with important consequences for vegetation structure as well as plant and animal population dynamics. Subfreezing temperatures have been recorded as far south as the Guaymas region, damaging mainly species with distributions that extend well south of the Sonoran Desert (Gentry 1942; Krizman 1972). For example, mangroves at Estero Sargento, north of Bahía Kino, were severely damaged in 1971 and again in 1978. Catastrophic freezes have been reviewed by Bowers (1980) and Felger and Moser (1985).

The climatic extremes along the region's northern border gradually give way to a more moderate climate along the southern coastal plains and foothills in Sonora. For example, the 20°C isotherm roughly follows a northwest-southeast line abruptly veering when approaching the 22°C and 24°C isotherms northeast of Hermosillo (INEGI 1988).

South of the plains of the Río Sonora, frosts seldom occur, temperatures are milder, humidity increases, and summer rainfall provides the bulk of annual precipitation. Similarly, maritime influences ameliorate the aridity on the Baja California peninsula, the Gulf islands, and a narrow band along the coast of Sonora. In these areas, temperatures are moderated by the ocean and maritime fog condenses as dew, which is an important source of moisture.

Geomorphology and Hydrology

The most prominent features of the southern portion of the Sonoran Desert are the tectonics that produced the Basin and Range Province (geomorphologically the Buried Ranges, *sensu* Raisz 1964): a marked northwest-

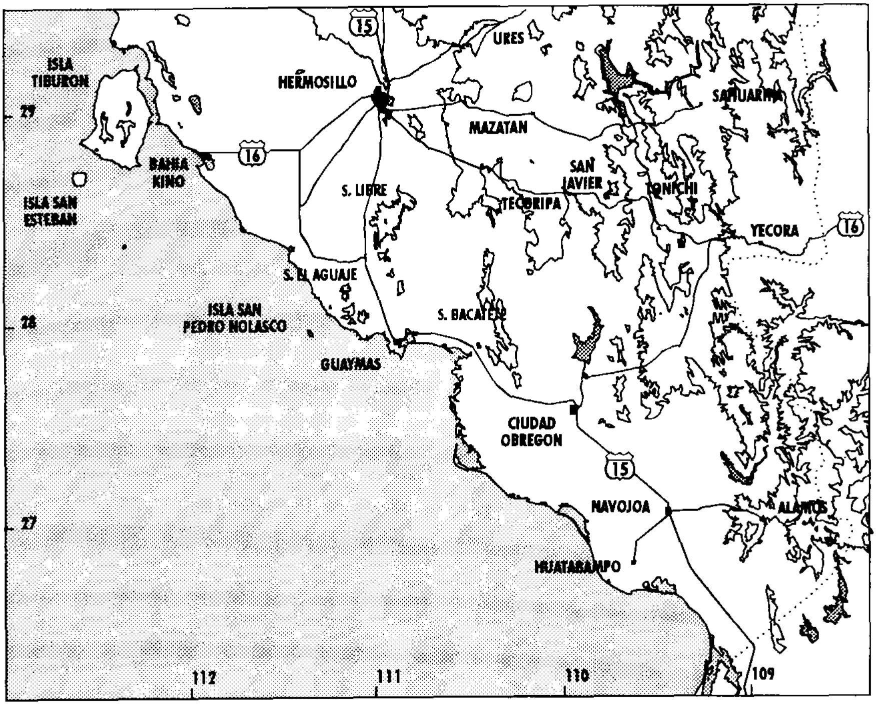

Figure 2.2 Map of southern Sonora, Mexico, showing main roads, localities, and topography at 0, 400, and 1000 m altitudes. Based on INEGI (1988).

southeast alignment of mountain ranges with broad valleys in between. Toward the west are broad plains broken by isolated granitic sierras of the Sonoran batholith and, on top of it, volcanic ranges. Toward the east, ash flows and basalts mark the start of the extensive volcanism of the Sierra Madre Occidental (fig. 2.2).

The region is geologically complex, including an extensive stratigraphic column (Crosswhite and Crosswhite 1982; INEGI 1988); Quaternary regolith and alluvial sediments predominate in the plains. The plains are also dotted by inselbergs and small mountains of Paleozoic shales, Cretaceous granites, Tertiary conglomerates, and Tertiary-Quaternary extrusive rocks (basalts and ignimbrites). Conglomerates of the Baucarit Formation (Miocene) show striking erosive patterns along the Río Yaqui and elsewhere in the sierra foothills. The coastal plain narrows near Guaymas because of three moderately high (about 1000 m elevation) Tertiary volcanic ranges: the Sierras El Aguaje, Libre, and El Bacatete.

Three major river systems run through the Sonoran Desert in Sonora: the Río Magdalena (comprising the Ríos Magdalena, Asunción, and Concepción), the Río Sonora, and the Río Yaqui. The three river systems have extensive deltas with fine sediments and high water tables. However, on the Magdalena and Sonora river deltas, water table levels have been drastically lowered by agricultural pumping. The Río Yaqui, with headwaters in the Sierra Madre in Chihuahua, has a flow at times rivalling that of the Colorado. In recent times, only the Yaqui reached the sea with a continuous flow. All three rivers owe their flow to montane watersheds to the east, and all have been dammed to such an extent that flows are greatly reduced and intermittent. Their upper basins run along Sierra Madre valleys with a gross north-south orientation, while on the coastal plains they flow east to west.

Four small rivers of purely Sonoran Desert origin are worth noting: the Río Sonoyta, which flows along the east flank of the Sierra El Pinacate and disappears into the dunes of the Gran Desierto a few kilometers east of Puerto Peñasco; the San Ignacio/Arivaipa and the Bacoachi, whose small basins are located north of Bahía Kino; and the Río Mátape, which originates in the isolated granitic dome of the Sierra Mazatán and drains into the Estero El Rancho near Guaymas.

The prevailing soils in the plains and undulating hills of the coast are Xerosols and Yermosols (INEGI 1988). Regosols are the most widespread soil unit in the Sonoran Desert. These soils are without developed horizons and resemble their parent rock. Substantial areas of Lithosols occur in the Sierra Madre foothills and isolated coastal sierras. More restricted are the Feozem and Vertisols, which occur as long, narrow strips along the major waterways and large arroyos.

Soils determine the vegetation character by changes in their nutrient content, in the particle sizes, and in the degree of infiltration of rainfall. Soils with a high proportion of sand and rock are more favorable to plant development than soils with clay, caliche layers, or pavement. The former allow for rapid water infiltration, while the latter—with a hard, impermeable crust—impede water penetration and favor what Shreve (1951) called sheet flood erosion. Extreme examples of this relationship are the Lithosols found in rocky slopes that act as rain catchment areas. Water larger statures and greater canopy cover in the southern and eastern boundaries and desert gives way to thornscrub and tropical deciduous forest, light competition heralds a major community change.

Major trends along these ecoclines are (1) the proportional decrease of ephemerals toward the east and south with an attendant increase in perennials and overall diversity, (2) the loss of cold-hardiness in southern populations of species that are frost-resistant in the north, and (3) the change in morphology and function associated with heat loss (Felger and Lowe 1967; Gibson and Nobel 1986). The differences in cold-hardiness between southern and northern populations of many Sonoran Desert species are well known among horticulturists but remain poorly documented and offer intriguing areas for research.

Intermediate-Scale Habitat Variation

On a local scale, species of mesic affinities occur as patches within desert environments. Topography, soils, or slope orientation are major factors affecting local vegetation. Species growing in a particular environment in one phytogeographic desert subdivision are often present in a different habitat in another subdivision.

The most striking feature of desert vegetation when viewed from the air is its patchiness. Flat areas exhibit an almost regular pattern of distribution of trees and shrubs with large gaps between them. Small arroyos have a linear canopy, while large arroyos are wide corridors with a closed canopy of trees along the margins. These distributional patterns have important consequences for the population biology of single species. For example, near Hermosillo, *Ipomoea arborescens* (tree morning-glory) is present in dense stands on steep north-facing slopes within localized thornscrub, but it is confined to linear populations in the small arroyos flowing from the mountains into more desertlike vegetation. This distribution suggests that the main source of *Ipomoea* propagules are the mountain populations and that individuals in the desert are stragglers (A. Búrquez and F. Molina, unpublished data).

Such linear patterns of distribution along ephemeral watercourses seem to be the rule for many desert species. On the Plains of Sonora, the vine *Merremia palmeri* is restricted to small desert arroyos, a pattern that imposes a very special genetic structure on its population—pollen flow and seed dispersal occur primarily along a linear vector (Willmott and Búrquez 1996). True desert dwellers, such as *Olneya tesota* (ironwood), *Larrea tridentata* (creosote bush), *Cercidium microphyllum* (foothill paloverde), different species of *Fouquieria* (ocotillo), columnar cacti, and many other species, are usually not restricted to arroyos. Yet even these can be confined to dry watercourses in the driest habitats, such as in Reserva de la Biosfera El Pinacate y El Gran Desierto de Altar (El Pinacate and Gran Desierto de Altar Biosphere Reserve) in northwestern Sonora (Felger 1980; Turner 1990).

The degree of rockiness, the geological origin of the substrate, and slope aspect and steepness also restrict the distribution of many species. For example, in El Pinacate and Gran Desierto de Altar Biosphere Reserve, *Fouquieria splendens* (ocotillo) largely determines the structure of vegetation on rocky soils (Ezcurra et al. 1987). Similarly, throughout its range, *Acacia willardiana* (palo blanco) is the most prominent species on rocky soils, usually on steep slopes.

Even on modest hills, slopes with coarse rocky soil, particularly those oriented north and east, harbor a very different species assemblage from the fine-textured soils on the plains (and from those slopes facing south and west). For example, in transects of less than 1000 m near Hermosillo, the typical Plains of Sonora dominants—*Encelia farinosa* (brittlebush), *Jatropha cardiophylla* (sangrengado), and *Olneya tesota*—give way on gentle slopes to *Cercidium microphyllum*. On steeper, rocky slopes, this association is replaced by thornscrub of *Acacia willardiana, Agave angustifolia, Ambrosia cordifolia* (chicurilla), *Bursera fagaroides* (torote blanco), *Croton sonorae, Hechtia montana, Ipomoea arborescens,* and *J. cordata* (torote papelillo). *Olneya* is rarely found on slopes on the Plains of Sonora, yet to the west, on small extrusive volcanic hills, it grows with *J. cuneata* (matacora) and *Carnegiea gigantea* (saguaro) in vegetation more closely resembling the Central Gulf Coast subdivision of the Sonoran Desert.

Certain mesic habitats within the desert, such as mountain canyons, ravines, and north-facing slopes, support a wealth of species with more tropical affinities. The Sierras Libre, El Aguaje, and El Bacatete share many species with tropical deciduous forests to the south. Within the desert, tropical "islands" develop where areas are protected from extreme temperature oscillations, furnished with shade and humidity, and provided with more available water. These mountain oases are like closed microcosms that maintain relict and disjunct populations of organisms. Their volcanic origin allows greater biological diversity than if they were granitic or metamorphic: the welded tuffs and ignimbrites are porous, full of contact zones where seeps develop, and sufficiently cracked and eroded to produce deep canyons with numerous *aguajes* (waterholes). An excellent example of a special mountain/canyon habitat is Cañón del Nacapule in the Sierra El Aguaje, which hosts numerous species with restricted distributions (Felger, in press). Wetland plants, mostly of tropical origin, grow along the permanent streams. Tropical vines climb through the shrubs and small trees, lacing into gallery groves of tall palms. Several plant species, including *Vallesia baileyana* and *Verbesina felgeri*, are known only from here and certain other nearby canyons. The rich flora includes three species of fig (*Ficus insipida, F. palmeri,* and *F. pertusa*) and three native palms (*Brahea elegans, Sabal uresana,* and *Washingtonia robusta*). One fig, *F. insipida,* forms short buttresses from a massive trunk. Despite its small population size and extreme isolation, this fig maintains healthy populations of its pollinators by flowering throughout the year (Smith 1994). Nacapule and nearby canyons are the only places this species occurs within the Sonoran Desert, as is the case with the large shrubs *Coccoloba goldmanii* and *Zanthoxylum mazatlanum*. Likewise, other riparian canyons in the region support disjunct populations of plants from more tropical regions in southern Sonora or Baja California Sur (Felger 1966; Yetman and Búrquez 1995).

Microhabitat Variation

Long-lived plants, the desert old growth, create islands of much greater biological diversity than the surrounding desert (Búrquez and Quintana 1994; Tewksbury and Petrovich 1994). The role of paloverde canopies as a major element in the recruitment of *Carnegiea gigantea*, the "nurse-plant syndrome," was recognized by Turner et al. (1966) and Steenbergh and Lowe (1977). Although the causes of increased survival of cacti seedlings is still debated, the role of shrubs and trees in the regeneration niche (*sensu* Grubb 1977) of columnar cacti is well-established (Valiente-Banuet and Ezcurra 1991; Nabhan and Suzán 1994). *Olneya tesota* is associated not only with cacti but also with dozens of other desert species (Felger 1966; Búrquez and Quintana 1994; Tewksbury and Petrovich 1994). Larger trees have more species per unit area under them than smaller trees. Graphical data representing species diversity as a function of area clearly demonstrate that habitat beneath O. *tesota* has a richer flora than areas outside the canopy shadow (fig. 2.3, table 2.1).

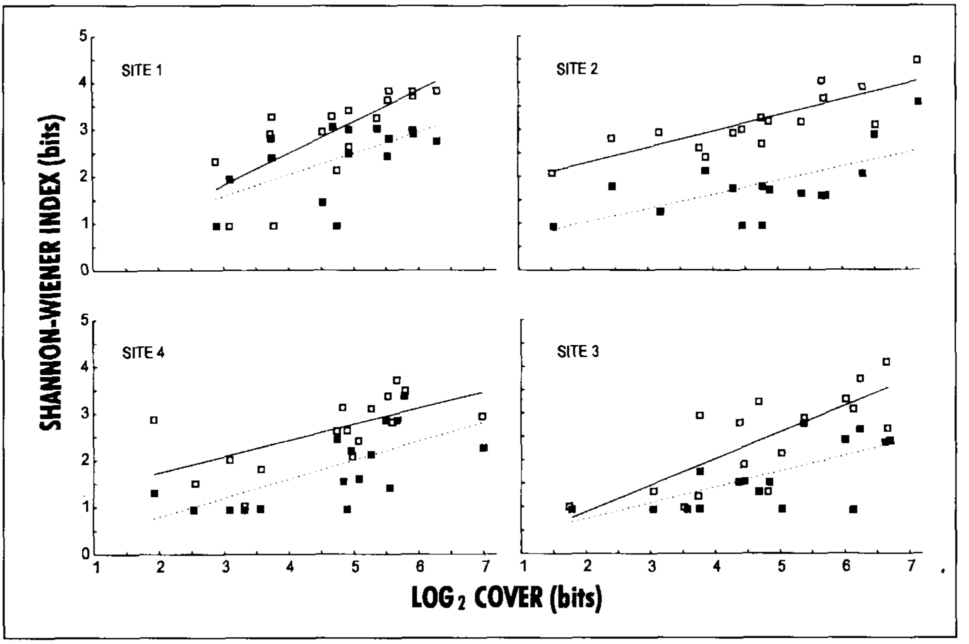

Figure 2.3 Shannon-Wiener index of heterogeneity used as a measure of species diversity for plots of different size located under (solid line) and outside (dotted line) ironwood trees at four sites near Hermosillo, Sonora. Sites 1 and 3 are on dry level terrain; sites 2 and 4 are along temporary desert arroyos. Curves are significantly different either in slope or intercept (see statistics in table 3 in Búrquez and Quintana 1994). Axes units in bits as indicated by Krebs (1985, pp 523).

Greater diversity associated with nurse plants is related to several factors. The environment under the canopy of desert trees has a lowered irradiance (Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991) and an increased water infiltration and nutrient availability (Paulsen 1953; García-Moya and McKell 1970). Plants that have animal-dispersed seeds are better represented under the canopy of desert trees, probably because trees provide shelter, nesting, or roosting sites for various organisms (Búrquez and Quintana 1994). Plants growing under trees are also protected from herbivory (McAuliffe 1984). The most important nurse trees in the southern Sonoran Desert include spreading desert legumes such as *Cercidium*, *Olneya*, and *Prosopis*. These trees promote a further partitioning of habitat at a smaller scale.

Table 2.1 Similarity matrix comprising all the species found in four sites where ironwood grows.

		Under			Outside		
		3	2	1	3	2	1
	3	*52*	.77	.72	.63	.56	.42
Under	2	35	*39*	.71	.63	.55	.52
	1	30	25	*31*	.62	.67	.57
	3	27	23	20	*34*	.74	.61
Outside	2	21	17	18	21	*23*	.68
	1	14	14	13	15	13	*15*

Source: Búrquez and Quintana (1994).

Note: Values in italics along the main diagonal indicate the number of species in each plot size (1 = small; 2 = medium; 3 = large), either under or outside canopies of ironwood. Values below the main diagonal are the numbers of species in common between samples, whereas those above it are the similarity ratios using Sorensens index. $N = 20$ for each plot size, except for plot size 3, where $N = 24$.

Ecosystem Dynamics

The vegetation, flora, fauna, and physical environment establish complex functional relationships. Energy flow and nutrient cycling are important features of the community metabolism. These include the processes of above- and belowground accumulation of organic matter, and the production and decomposition of litter.

Variation in standing crop biomass and primary productivity of terrestrial ecosystems is correlated to rainfall (see Lieth and Whittaker 1975; Noy-Meir 1985). In the Sonoran Desert, primary productivity increases from west to east with increasing rainfall. Productivity in the Lower Colorado Valley and Central Gulf Coast is much lower than that of the other Sonoran Desert subdivisions. However, much temporal and spatial heterogeneity occurs because site-specific water catchment and between-year rainfall are not uniform. Furthermore, nutrients and their variable distribution in the soil are critical to primary productivity, standing crop biomass, and floristic composition (Ehleringer and Mooney 1983; Webb et al. 1983; Ludwig 1987; Polis 1991).

Few studies have documented the dynamics of the Sonoran Desert at the ecosystem level, and most of them have focused on the northern region, emphasizing single species measurements. Annual aboveground net primary productivity varies from a low of 55 g m^{-2} in a desertscrub community in the Tucson Basin, Arizona (Szarek 1979), to a high of nearly 130 g m^{-2} in Arizona Upland desertscrub in the Santa Catalina Mountains in Tucson (Whittaker and Niering 1975). Dramatic changes in primary productivity also occur at local scales. Plant communities in the plains near Hermosillo have a litter production of about 90 g m^{-2} y^{-1}. In contrast, adjacent sites in the densely vegetated xeroriparian habitats produce around four times more litter (370 g m^{-2} y^{-1}). Thornscrub on adjacent hillsides produces an intermediate value of 178 g m^{-2} y^{-1} (Martínez-Yrízar et al. 1993). This extreme variability in productivity between sites has also been observed in other desert ecosystems (Ludwig 1986; Polis 1991; Martínez-Carretero and Dalmasso 1992).

The shedding of plant parts and the fate of the litter are important elements of ecosystem nutrient cycling and energy flow. Surface litter on desert substrates is usually sparse and patchy in distribution due to its accumulation around the base of shrubs or in wind-protected areas (West 1979). On the Plains of Sonora near Hermosillo, standing crop litter varies spatially from 21 g m^{-2} in open areas to 210 g m^{-2} beneath trees and shrubs (A. Martínez-Yrízar, A. Búrquez, and S. Núñez, unpublished data).

Ephemerals, despite their brief presence in the desert, can make an appreciable contribution to productivity (Inouye 1991). Near Cave Creek, Arizona, Halvorson and Patten (1975) found that annuals produced a mean biomass of 45 g m^{-2}. Annuals growing under shrubs contributed more than twice as much biomass as those growing outside plant canopies (Halvorson and Patten 1975; Patten 1978). The magnitude of temporal variation in productivity is illustrated by the study of Patten (1978), who found a tenfold increase in aboveground net primary productivity of winter annuals during a wet versus a dry year.

Studies of standing crop biomass for the Sonoran Desert are very limited. *Simmondsia chinensis* (jojoba) at Punta Chueca, Sonora, has an aboveground biomass of 1.57 Mg ha^{-1} (Braun and Espericueta 1979). A lower value, 1.16 Mg ha^{-1}, was reported for an *Ambrosia deltoidea* (triangle-leaf bursage)–*Larrea tridentata–Olneya tesota* desertscrub community at Silverbell, Arizona (Thames 1973). In contrast to these low biomass values, communities in the southern Sonoran Desert yield considerably larger amounts (5 to 20 Mg ha^{-1}; Búrquez et al. 1992b). These higher values are related to the less harsh climate that supports a more complex structure of vegetation.

Mesquite forests have a much higher standing crop biomass and productivity than those of desertscrub. In southeastern California, close to the Salton Sea, a stand of *Prosopis glandulosa* var. *torreyana* (mesquite) had 13 Mg ha^{-1} of aboveground biomass (Rundel et al. 1982). Similar or higher values are likely to be found in southern localities. Large mesquites have restricted distributions along major drainage channels and fine silty plains on river deltas where the water table is shallow and most nutrients are not a limiting factor. Other exceptions to the relationship between precipitation and productivity are coastal swamps and lagoons, and wetlands with underground water sources or remote sources. These oases have been studied mainly in northwestern Sonora, including the Ciénaga de Santa Clara and El Doctor wetlands (Glenn et al. 1992) and the *pozos* ("springs") at Bahía Adair (Ezcurra et al. 1988), Quitovac (Nabhan et al. 1982), and Quitobaquito (Felger et al. 1992). These wetland habitats exhibit high productivity and standing crop biomass. However, there are no formal studies on their productivity. Desert oases also occur as seeps in the foothills of most large ranges (e.g., Felger and Moser 1985) but have not been studied for localities in the southern Sonoran Desert. Despite their relevance in ecosystems in which water is the main limiting factor, no studies of ecosystem dynamics have been carried out in these communities.

Geographic Limits

The delimitation of the Sonoran Desert has posed problems since its formalization by Shreve (1951). As Schmidt (1989) has shown, the Mexican portion of the Sonoran Desert has been broadly interpreted to include northern Sinaloa, most of Sonora, and the peninsula of Baja California, or narrowly interpreted to include only a coastal strip from west-central Sonora to the Colorado River delta (fig. 2.4).

There is general agreement about the northern boundaries of the Sonoran Desert, which are largely determined by winter freezing (e.g. White 1948; Shreve 1951; Steenbergh and Lowe 1977; Crosswhite and Crosswhite 1982; Turner and Brown 1982). However, the limits in the south and east have been much debated. The lack of agreement illustrates well the Gleasonian paradigm that in the absence of major environmental discontinuities, populations distribute independently of each other, and communities merge seamlessly. The ecosystem dynamics at the southern desert edge are remarkably similar to those of tropical deciduous forest (Martínez-Yrízar et al., in press). In fact, the southern reaches of the Sonoran

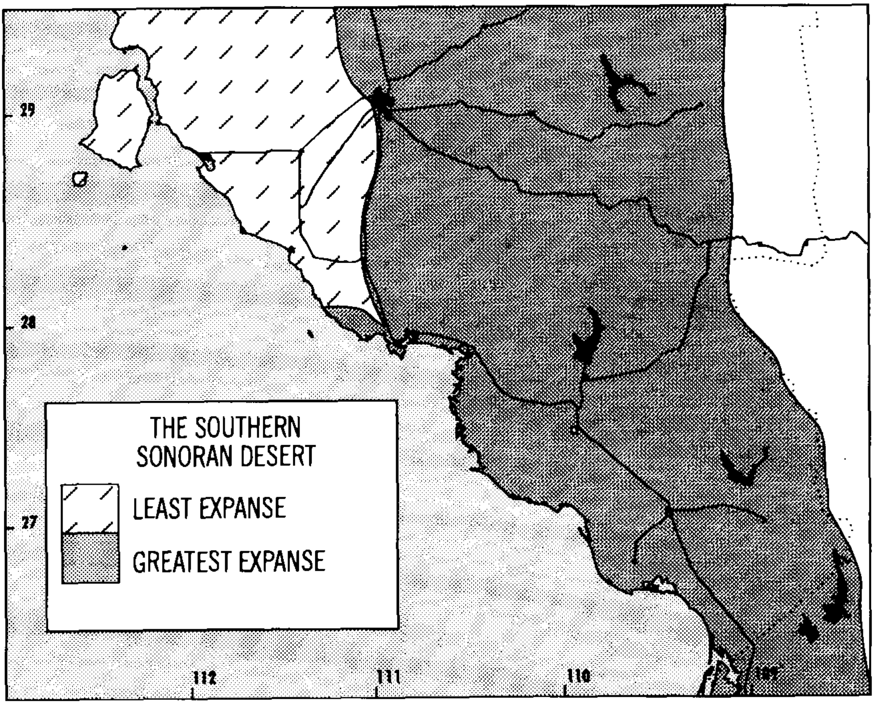

Figure 2.4 Least and greatest expanse of the Sonoran Desert in southern Sonora, Mexico, according to Schmidt (1989).

Desert resemble dwarfed tropical deciduous forest. Many species are common to both these vegetation types, but individual species of trees and shrubs are often much smaller and different in growth form in the desert. The proportion of climbers is comparable in both habitats (Rundel and Franklin 1991), as are the complex structural and diversity patterns.

Several authors have defined the southern and eastern boundaries of the Sonoran Desert using mainly temperature and rainfall data (see Arbingast et al. 1975; Schmidt 1989). This scheme includes most of the Baja California peninsula and a narrow coastal strip continuing well into Sinaloa, and excludes the relatively narrow valleys in the foothills of the Sierra Madre in Sonora. However, a purely climatic delimitation of the desert suffers from oversimplification. Climatic boundaries do not take into consideration differences in soil permeability, water table height, local maritime influence, or slope aspect and steepness. The use of mean annual values

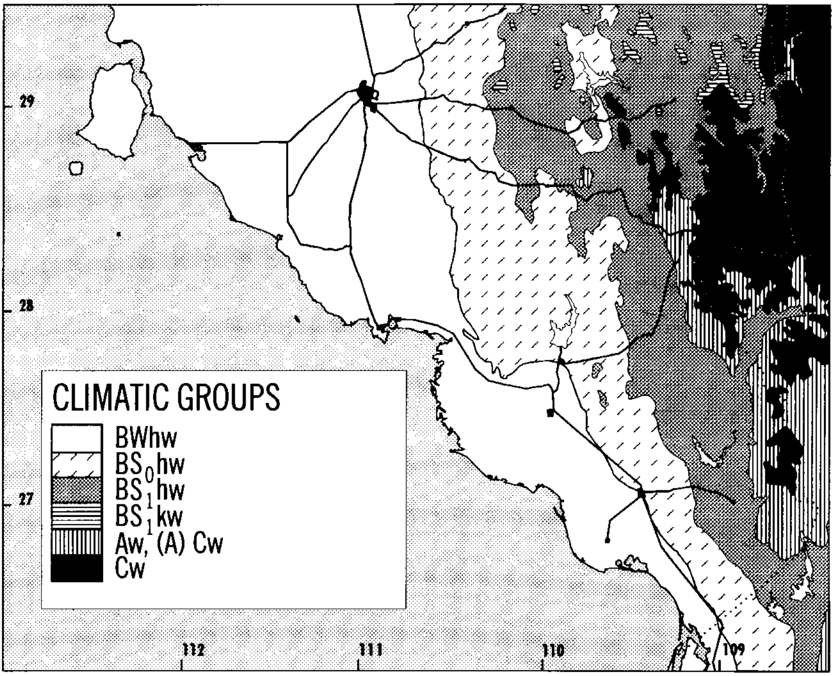

Figure 2.5 Climates of southern Sonora, Mexico, based upon INEGI (1988).

ignores the temporal distribution of temperature and rainfall. These factors are of paramount importance in understanding vegetation structure and ecosystem dynamics. For example, the large deltas of the Sonoran rivers (about 40 km wide for the Río Sonora and more than 150 km wide for the Yaqui-Mayo Rivers) have formed expansive plains of fine-textured, level soils with a historically shallow water table. These deltas harbor a vegetation unlike that which would be predicted by considering major climatic parameters alone, namely desertscrub, grasslands, or open shrubland (Whittaker 1975). The presence of dense mesquite forests and impenetrable thornscrub at the coastal southern boundary of the Sonoran Desert seems similar to the occurrence of some Australian *Eucalyptus* associations outside forest climatic zones.

The modification to the climate scheme of Köppen by García (1973) gives more resolution to the correlation between climate and vegetation (see fig. 2.5). The very dry–very warm climates (BWhw group) represent the more xeric Sonoran Desert communities, while the dry-warm climates (BShw group) indicate different stages in the transition to tropical communities. The presence of tropical climates (Aw group) indicates unequivocally tropical forests, while desert-steppe and temperate climates (BS_1 and Cw groups) are well correlated with dry woodlands and pine-oak forests.

Other authors have relied on the use of vegetation and plant and animal distributions to define the boundaries of the Sonoran Desert (Shreve 1951; Leopold 1950; Felger and Lowe 1976; MacMahon 1979; Brown 1982). By these criteria, of multivariate nature, the southern limits of the desert in Sonora are set around the latitude of Guaymas and exclude the long coastal strip southward. To the east, the limits are determined by the effects of elevation. Mountain ranges, having small areas of nondesert vegetation, appear as isolated islands within the desert. Examples of these nondesert islands are Sierras La Giganta and La Laguna in Baja California Sur, Sierra Kunkaak on Isla Tiburón, and Sierras Mazatán, San Javier, Libre, El Bacatete, and El Aguaje in Sonora.

The west-to-east increase in summer precipitation and the north-to-south decrease in frost damage induce changes in the stature and structure of vegetation—to the south and east vegetation is generally denser and taller. At the southern and eastern limits of the Sonoran Desert, unlike the northern and western portions, the vegetation lacks the winter-spring flurry of biological activity brought about by winter-spring Pacific frontal storms. At the southern and eastern boundaries, the desert merges with a type of vegetation that has been called thorn forest (Gentry 1942), thornscrub (Felger and Lowe 1976), and Sinaloan thornscrub (Gentry 1949; Brown 1982). Thornscrub varies greatly in complexity, from relative simplicity at the desert margin to complex communities that intergrade into tropical deciduous forest. Rzedowski (1978) relates thornscrub to his "Bosque Espinoso" type, but indicates considerable overlap with both desert and tropical deciduous forest.

Two major types of thornscrub can be recognized for Sonora (*sensu* Felger and Lowe 1976): Foothills and Coastal Thornscrub. The former is broadly equivalent to the Foothills of Sonora, as originally proposed by Shreve (1951) as a subdivision of the Sonoran Desert. This, however, has been excluded as part of the desert in most modern accounts. On the basis of structural criteria, some areas of the Arizona Upland subdivision could be considered thornscrub (Felger and Lowe 1976; Turner and Brown

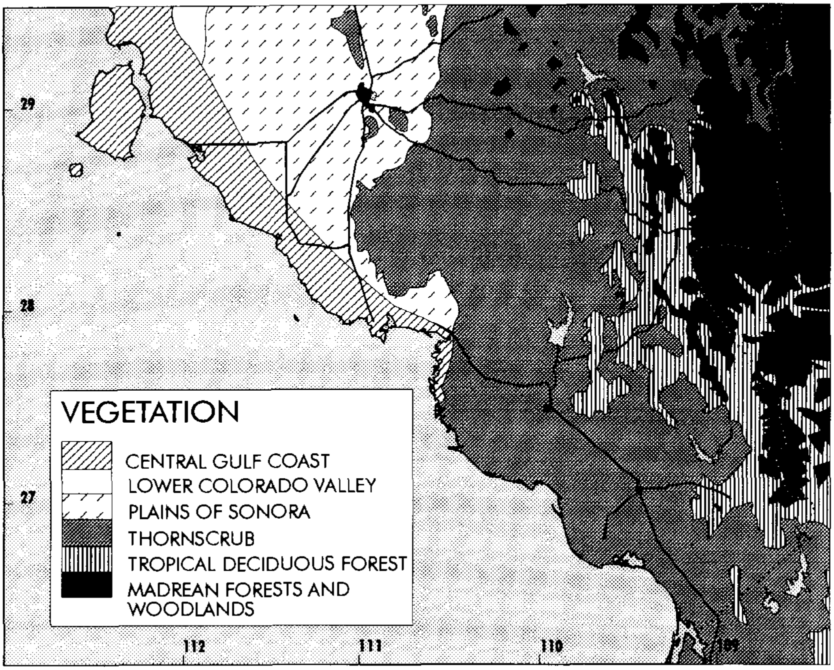

Figure 2.6 Delineation of the vegetation of southern Sonora, Mexico, based upon Shreve (1951), Brown and Lowe (1980), Wiseman (1980), INEGI (1988), Búrquez et al. (1992a), and personal observations.

1982). Also, thornscrub communities are found in coastal southern Sonora and northern Sinaloa. Other vegetation types related to thornscrub include the riparian woodlands and thornscrub that occur near large desert arroyos, canyons, and springs.

Coastal thornscrub shows a gradient of structural change from the coast to the interior. Near the coast it is low and poorly structured, while farther inland a more intricate vertical structure develops with the addition of more arborescent species. Probably the most striking features of these communities are the remarkably dense growth of columnar cacti, mainly *Stenocereus alamosensis, S. thurberi* (organ pipe cactus) and *Pachycereus pecten-aboriginum* (etcho), and the occurrence of several species of epiphytic *Tillandsia.* Gross ecosystem changes occurring along the Pacific coast of Mexico from Jalisco and Nayarit northward are mirrored in short transects (less than 100 km) from the desert to the Sierra Madre at latitudes 27° to 30° N (fig. 2.6 and fig. 2.7).

Foothills thornscrub represents the transitional vegetation between the Sonoran Desert proper in western Sonora and the most northern tropical deciduous forests on the western flank of the Sierra Madre. It is also prevalent on desert mountain slopes (mainly northern slopes). This vegetation can be broken into several units or associations. Examples of this are the *Acacia willardiana–Jatropha cordata–Mimosa laxiflora–Croton sonorae* mixed scrub on hillsides (mostly north-facing) within the Sonoran Desert proper, and the *Pachycereus pecten-aboriginum–Ipomoea arborescens–Fouquieria macdougalii–Ceiba acuminata* associations on the plains near Tecoripa.

Structural criteria such as vegetation cover have been used to distinguish desert from thornscrub (Gentry 1949; Felger and Lowe 1976; Brown 1982: wide open spaces = desert; dense cover with few open spaces = thornscrub). Gentry (1942) used vegetation structure (such as the height of the columnar cactus *Pachycereus pecten-aboriginum* taller than the canopy = thornscrub) as well as floristics (e.g., *Acacia cochliacantha* (boat-thorn acacia) = thornscrub; *Lysiloma divaricatum* = tropical deciduous forest) to separate thornscrub from tropical deciduous forest. The difficulties of defining thornscrub have been elegantly summarized by Rzedowski (1978) as translated here "thornscrub communities . . . often are not well delimited because they imperceptibly change into other vegetation types such as tropical deciduous forest, desertscrub, and grasslands."

Delimiting the southern and eastern Sonoran Desert boundaries, as happens with ecotones, seems to depend on researchers' biases. Researchers with a northern hemisphere bias, accustomed to the more discrete nature of temperate communities, seem to include thornscrub as allied to the Sonoran Desert. Researchers with a southern bias, who place greater emphasis on the tropics, include thornscrub as a subset of the more developed tropical deciduous forests.

A Transect along Highway 16

Mexico Highway 16 running between Bahía Kino and Maycoba in Sonora (28°30′–29°15′N, 109°30′–113°W) provides a transect of plant communities from marine to montane forests and reveals their extensive intergradation with desert associations (Búrquez et al. 1992a; fig. 2.7).

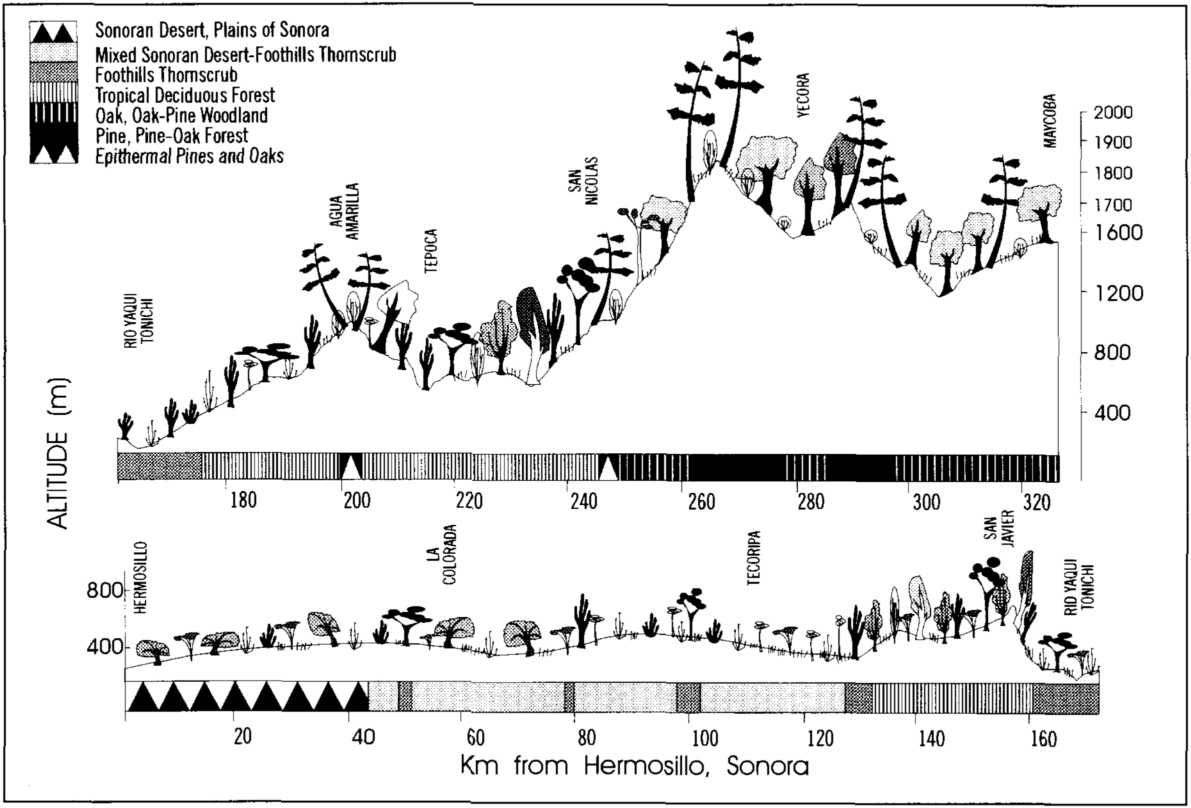

Figure 2.7 Diagramatic view of changes in vegetation along the road from Hermosillo to Maycoba (Highway 16, Sonora, Mexico). Distances are as marked on the road signs. The section from Bahía Kino to Hermosillo, although not illustrated, is discussed in the text. Modified from Búrquez et al. (1992a).

Altitudinal changes along this route are typical of the transition from the southern Sonoran Desert to tropical deciduous forest to temperate forests. In this section we discuss these changes from sea level at the Gulf Coast eastward to the Sierra Madre foothills.

Marine macroalgae communities are well developed in shallow coastal waters (Norris 1978). In addition, there are extensive sea grass meadows. These consist of submerged pastures of *Zostera marina* and *Ruppia maritima* growing along protected, subtidal waters in sandy-muddy substrates (Felger et al. 1980). These are best developed in the Canal del Infiernillo and also occur at Estero de la Cruz at Bahía Kino and from the Guaymas region southward to central Sinaloa.

Littoral scrub, including mangroves and saltscrub, occurs at desert river deltas, lagoons, and esteros. Mangroves (*Avicennia germinans, Laguncularia racemosa,* and *Rhizophora mangle*) reach their distribution limits in North America at about 29°20′N along the shores of the Canal del Infiernillo, with a small outlier population of *Avicennia* at Puerto Lobos (30°15′N). Mangroves bordering the desert are relatively dwarfed and usually shrubs less than 5 m tall. Southward, mangroves gradually increase in extent and height.

Coastal vegetation is varied and has sharp boundaries imposed mainly by environmental factors such as exposure to prevailing winds, degree of rockiness, drainage, salinity, and dew deposition. These factors are usually represented at the extremes, resulting in a few dominant species. Coastal dunes are common at the mouths of large arroyos or major rivers, forming narrow bars along the coast. These are different from continental dunes like the ones in the Gran Desierto region that result from long-distance aeolian transport (Felger 1980) and do not have a strong coastal influence. However, these dune systems share a large proportion of their specialized flora, having a remarkable uniformity of species. Aside from Felger and Lowe (1976) and Felger (1980, 1992), few studies have been conducted on the distribution of the vegetation and flora of these dunes.

Along tidal channels, leeward sides of sand dunes, and depressions isolated from the sea, saltscrub appears next as a narrow band of salt grasses (*Jouvea pilosa, Monanthchloe littoralis,* and *Sporobolus virginicus*), halophytic shrubs (*Allenrolfea occidentalis, Atriplex barclayana, Maytenus phyllanthoides,* and *Suaeda moquinii*) and succulent forbs (*Batis maritima, Salicornia* spp., and *Sesuvium* cf. *verrucosum*) as the major elements (Felger and Lowe 1976).

Desertscrub is well represented in the vicinity of Bahía Kino. This vegetation is readily ascribed to the Central Gulf Coast subdivision of the Sonoran Desert. However, further inland (eastward) the vegetation is a complex patchwork without clear boundaries unless obvious environmental changes occur. Common Central Gulf Coast perennials include *Bursera microphylla* (elephant tree), *Fouquieria splendens, Jacquinia macrocarpa* subsp. *pungens* (san juanico), *Jatropha cuneata, Olneya tesota, Viscainoa geniculata* (guayacán), and many others. The columnar cacti *Carnegiea gigantea, Pachycereus pringlei*, and *Stenocereus thurberi* are dense and have high recruitments, while *F. splendens, Krameria grayi* (white ratany), *Lophocereus schottii* (senita), and *Prosopis glandulosa* occur in close proximity to halophyte associations but on higher, nonsaline ground. These species form veritable islands on sandy mounds within salt flats near the coast.

Mesquites and columnar cacti are dominant on slightly higher terrain. *Pachycereus pringlei* attains truly gigantic sizes, being by far the largest columnar cactus in the Sonoran Desert and one of the largest succulents in the world. The mainland *P. pringlei* forests occur along a narrow band less than 30 km wide, from Caborca southward near the coast to the Guaymas region, where it is replaced by its close relative *P. pecten-aboriginum* (Turner et al. 1995). To the east the mesquite forests on the ancient Río Sonora delta have been replaced by large-scale agriculture. Derelict farmland in this region attests to the failure of groundwater irrigation in the desert.

At Siete Cerros, a small linear succession of rocky hills surrounded by deltaic silt, the Central Gulf Coast vegetation gives way to the Plains of Sonora (about 55 km east of Bahía Kino). The vegetation becomes denser, with *Bursera laxiflora* (torote prieto), *B. microphylla, Carnegiea gigantea*, and *Olneya tesota* on the slopes. These hills also show a dense cover of the invasive newcomer *Pennisetum ciliare* (buffelgrass). Prominent species in the plains include *Cercidium microphyllum, C. praecox* (palo brea), *Encelia farinosa, Larrea tridentata, O. tesota, Stenocereus alamosensis* (sina), and *S. thurberi. Prosopis velutina* (velvet mesquite) occurs in the more mesic areas next to the main road and along irrigation canals. At Siete Cerros, *S. alamosensis* reaches its westernmost limit (Felger and Moser 1985). This vegetation continues eastward with little variation until reaching Hermosillo.

In the vicinity of Hermosillo, increased precipitation and changes in topography and geological substrate produce discontinuities in the vegetation. Granitic and calcareous ranges (Espinazo Prieto, La Cementera, Agualurca, and Santa Teresa) support thornscrub primarily on the north- and east-facing slopes, and desertscrub on the plains and more arid slopes. Prominent species of these sierras include *Acacia willardiana, Agave angustifolia, Bursera fagaroides, B. microphylla, Cercidium floridum* (blue paloverde), *C. microphyllum, C. praecox, Croton sonorae, Fouquieria macdougallii, Hechtia montana, Ipomoea arborescens, Jatropha cordata,* and *Stenocereus thurberi.* On the desert plains *B. laxiflora, B. microphylla, Encelia farinosa, Guaiacum coulteri* (guayacán), *Mimosa laxiflora, Olneya tesota,* and *S. alamosensis* are common. Large areas of the Plains of Sonora have been cleared of natural vegetation to create *Pennisetum ciliare* pasture. This grass is widely naturalized, forming dense, almost monospecific stands in many areas. Colonization by *P. ciliare* introduces fire as a major factor in the dynamics of desert vegetation. Desert and thornscrub communities are not fire-adapted, and the establishment of *P. ciliare* is leading to irreparable destruction of the Sonoran Desert (Búrquez and Quintana 1994; Yetman and Búrquez 1994; Búrquez et al. 1998; M. Miller and A. Búrquez, unpublished data).

The Plains of Sonora desertscrub and thornscrub alternate with elevational changes along the transect eastward from Hermosillo. Initially, desertscrub vegetation is dominant with thornscrub as isolated islands, especially on north-facing slopes. Moving eastward, there is an increased diversity, density, and size of individual plants, particularly of tropical species including *Ceiba acuminata, Erythrina flabelliformis* (coral bean), *Ipomoea arborescens, Pachycereus pecten-aboriginum,* and *Piscidia mollis* (palo blanco). Farther east, near Tecoripa, thornscrub almost completely replaces the desertscrub. Before reaching the Río Yaqui crossing at Tonichi, the first tropical deciduous forest is seen on Sierra San Javier. The more xerophytic thornscrub and desertscrub lose their identity a few kilometers after the river crossing. Here many species typical of tropical deciduous forests are present, including *Bursera lancifolia, Ficus petiolaris* and scattered *F. insipida, Helicteres baruensis, Heliocarpus attenuatus, Lysiloma divaricatum, L. watsoni* (tepeguaje), *Montanoa leucantha, Randia echinocarpa* (papache), *Senna atomaria* (palo zorrillo), *Solanum erianthum, Tabebuia chrysantha* (amapa amarilla), *T. impetiginosa, Lonchocarpus hermannii,* and many others. At the Río Yaqui crossing, Sonoran

Desert species reappear only to quickly disappear as the elevation increases toward the Sierra Madre. From here the ascent is rapid as one traverses tropical deciduous forest, oak woodlands, and pine-oak forests.

The vegetation of the Gulf islands represents a special case. Due to differences in isolation, size, and topography, each island harbors distinct assemblages of animal and plant species. The vegetation and flora of Isla Tiburón, Mexico's largest island, is remarkably similar to that of the mainland—no doubt due to its close proximity and relatively recent connection to Sonora as well as its large area. Its vegetation includes sea grass meadows, mangroves, saltscrub, and dune vegetation along its coast, desertscrub on the plains, and thornscrub on the north-facing slopes of the highest mountain range (Felger and Lowe 1976). In contrast, Isla Angel de la Guarda has not been recently connected to the mainland and, despite its large size and relief, has a rich but relatively arid vegetation lacking thornscrub. Evidence of elevational zonation is exemplified by the presence of a population of *Fouquieria columnaris* (boojum tree) near the summit of the island (Moran 1983). The other smaller islands have special physical features (such as differences in topography, elevation, and geology), an absence of larger herbivores, and probably haphazard colonization, which make them singular in terms of biodiversity. Angel de la Guarda and smaller islands all support endemic plant and animal species (see Case and Cody 1983).

Conclusions

Vegetation in northwestern Mexico forms a continuum from the dry shores of the Gulf of California to the foothills of the Sierra Madre Occidental. The climate changes from extremely xeric to tropical and temperate in the short distance of 200 km. The multitude of plant communities and ecotones are an indication of the exceeding richness of habitats. The gradual change in floristics, structure, and ecosystem dynamics makes vegetation difficult to classify and complicates the delimitation of the boundaries of the Sonoran Desert. Present land-use policies in Sonora, particularly the clearing of large tracts of land for introduced exotic grasslands, are forcing the Sonoran Desert toward a new, less complex, and less diverse ecological status. Given the paucity of data for this region, there is an urgent need to document the pace of change and to set aside significant areas for conservation.

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Note

Added in proof: Several important papers concerning the region have recently appeared. Among these are contributions in a special issue of the *Journal of the Southwest* 39 (3–4), 1997, devoted to northwestern Sonora, Baja California, and southwestern Arizona.

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